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ORIGINAL ARTICLE

Histological characterization of wild cucumber resistance to *Meloidogyne* species

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Abstract

Using nematode resistant varieties is one of effective and environmental sound strategies being adopted in the management of economically important *Meloidogyne* species. Wild cucumber (*Cucumis africanus*) has been reported to possess resistance to *Meloidogyne* species. Two mechanism of nematode resistance, pre- and post-penetration resistance, had been identified, with post-penetration mechanism being used in plant breeding programs and crop rotation systems. The objective of this study was to determine the mechanism of nematode resistance in *C. africanus* to *M. incognita* and *M. javanica*. 6 weeks old *C. africanus* seedlings were separately inoculated with 100 s-stage juveniles (J2) of *M. incognita* and *M. javanica.* For 30 days, five seedlings were harvested from both *M. incognita* and *M. javanica* experiments every other day. Seedlings' roots were examined for necrotic spots, rootlet interferences, giant cells and root gall numbers as indicators of successful or unsuccessful nematode penetration. Harvesting times were highly significant ($P \leq 0.01$) on necrotic spot, rootlet interference and root gall numbers in both *C. africanus—M. incognita* and—*M. javanica* relations, but were not significant for giant cell number in *C. africanus—M. incognita*. The results suggested that *C. africanus* have post-penetration nematode resistance to both *Meloidogyne* species.

Keywords *Cucumis africanus* · *Meloidogyne* · Nematode resistance · Post-penetration

Introduction

Global withdrawal of the highly effective synthetic chemical fumigant nematicides, which had been relied upon for over a century in the management of plant-parasitic nematodes (PPN), has had severe economic ramifications in crop production systems (Caboni et al. 2015). Parasitism by root-knot nematodes (RKN), *Meloidogyne* species is considered one of the main biotic factors responsible for reduced productivity in various agricultural crops (Mhatre et al. 2019). RKN results in up to 30% yield decline by direct infestation and indirect losses owing to predisposing or breakdown of resistance to other root diseases, such as bacterial wilt, attributing to quantity and quality losses (Muimba-Kankolongo 2018). *Meloidogyne* genus is a worldwide economically significant pest, comprising over 100 species, (Karuri et al. 2017) including approximately 22 described from Africa (Onkendi et al. 2014) widely distributed on leguminous and flowering plants.

Two *Meloidogyne* species, *M. incognita* and *M. javanica*, have been declared economically important to roughly 4000 host plants, including field crops, ornamentals, medicinal, aromatics plants, and even weeds (Jones et al. 2013; Onkendi et al. 2014). Second-stage juveniles (J2) penetrate roots to establish a feeding site, called giant cell, usually within the pericycle and vascular tissues and form root galls soon after their infection (Mashela et al. 2015). In nematode-susceptible hosts, infection by *Meloidogyne* species induces the formation of severe root galls, stunted growth, decreased water uptake, imbalances of essential nutrient elements, low evapotranspiration and increased root exudation of amino acids, which reduces soil pH (Saikia et al. 2013).

Up-to-date cultural management procedures are insufficient to fully manage RKN (Trudgill and Blok 2001), even more so with continued restrictions on synthetic chemical

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use (Desaeger et al. 2017). As a result, it has become critical to develop additional PPN management strategies that are environmentally friendly. Currently, there are numerous studies conducted on the subject all around the world (Baum et al. 2015; Brito et al. 2020; Damasceno et al. 2015; Gupta et al. 2017; Hussain et al. 2018; Laquale et al. 2015; Seo et al. 2019), including screening nematode-resistant genotypes (Chiamolera et al. 2018; Da Silva-Mattos et al. 2019; Hajihassani et al. 2019). These studies are proving to be beneficial, providing additional insights that can lead to increased profits for farmers.

Nematode-resistant hosts may exhibit pre- or post-penetration resistance (Thurau et al. 2010). Pre-penetration nematode resistance is the form of resistance that occurs prior to nematodes coming into contact with the root systems (Ferraz and Brown 2002). This form of resistance prevents penetration of nematode J2 and is characterized by pre-existing morphological factors or the production of root exudates that either attract or repel J2 (Trudgill 2003). Root penetration by RKN has also been attributed to the lack of metabolites required for host identification, repellent host exudates, or the existence of a physical barrier over which the nematode cannot pass (Lee et al. 2017).

In post-penetration nematode resistance J2 are allowed to penetrate the root systems (Desmedt et al. 2020), with passive chemicals previously called elicitors, activated to form the phytoalexins, that have nematicidal properties (Desmedt et al. 2020, 2022). Some of the phytoalexins induce hypersensitive response (HR), that appear as necrotic spots, where cells around the nematode wither (Huysmans et al. 2017), thereby preventing feeding, development of J2 and reproduction. According to Lopez-Gomez and Verdejo-Lucas (2017), post-penetration incompatibility in resistant crops is associated with failure of giant cells to develop further into root galls. Rootlet interference and small underdeveloped root galls are also characteristics of post-penetration nematode resistance (Benková and Bielach 2010). In sedentary RKN, this type of resistance is further subdivided into early and late resistance, wherein early resistance that occurs during migration or early site establishment, and late resistance that occurs after the establishment of a feeding site (Fuller et al. 2007).

Between the two mechanisms of resistance, only post-penetration nematode resistance can be introgressed (Thurau et al. 2010), dictating the need to establish the mechanism of nematode resistance in any nematode resistant plant species in order for it to serve as a candidate of introgression. Among the available alternative techniques to methyl bromide, plant resistance is one of the most investigated techniques in PPN management (Onkendi et al. 2014). Most crops lack resistant genotypes to *Meloidogyne* species as observed in four commercial genera of *Cucumis*, *Citrullus*, *Cucurbita* and *Lagenaria* within the Cucurbitaceae family (Liu et al. 2016; Thies et al. 2016; Verdejo-Lucas and Talavera 2019; Singh and Patel 2015). *Cucumis africanus* is highly resistant to *Meloidogyne* species (Pofu et al. 2012); however, the mechanism of nematode resistance in this crop has not been established.

Therefore, the objective of this study was to determine the mechanism of nematode resistance in *C. africanus* to *M. incognita* and *M. javanica*.

Materials and methods

Experimental procedures

Two separate experiments were conducted under greenhouse conditions at North-West University, South Africa. Greenhouse temperature were set at 25 ± 2 °C, with temperatures and humidity controlled using thermostatically activated fans and wet-wall at opposite ends. Seeds of *C. africanus* were sown in seedling trays filled with pasteurized (300 ℃ for 1 hour) fine sand and raised for 6 weeks. Uniform seedlings were transplanted into 250 ml polystyrene cups, filled with 200 ml pasteurized fine sand and placed at 10-cm inter- and intra-row spacing. In each experiment, the treatments comprised of 15 harvesting times, experimentally done in a randomized complete block design (RCBD), with five replications. Isolates of *M. incognita* and *M. javanica* were each raised on nematode-susceptible tomato (*Solanum lycopersicum*) cv. ‘Floradade’ seedlings and roots collected for egg masses when needed. Egg masses were hand-picked using a tooth pick and hatched in distilled water for 72 h (Powers et al. 1991). A day after transplanting, *Cucumis* seedlings were each inoculated by dispensing approximately 100 J2 of *M. incognita* or *M. javanica* using a 20 ml plastic syringe into 5-cm-deep furrow around the seedling stem and covered with growing medium. Harvesting was done every other day, for a period of 30 days starting from 2-days after inoculation. Seedlings were fertilized once with Super Phosphate (Efekto Care, Bryanston, South Africa) and NPK (2:3:2) and irrigated with 30 ml tap water every other day.

Data collection

At each harvest, seedling roots were severed and the shoots discarded. Roots were rinsed in tap water to remove soil particles, blotted dry using paper towel and stained (Bybd et al. 1983). The whole root system was soaked in 1.5% NaOCl solution for four minutes to remove any associated microbe, rinsed in tap water, followed by a 15 min immersion in tap water to remove excess NaOCl. Root samples were each stained by covering with 30 ml tap water mixed with 1 ml acid fuchsin and boiled for 30 s. The solution was cooled to room temperature and roots distained by putting in acidified glycerin with a few drops of 5 N HCl, which were heated to boiling, followed by cooling to room temperature. Root samples were each placed in a petri dish and closed with the top lid for assessment under the stereomicroscope at 45 × magnification for necrotic spots, rootlet interference, giant cells and root gall number.

Data analysis

Prior to analysis of variance (ANOVA), all data were transformed through log10(x + 1) to normalize the variances. Data were subjected to ANOVA through the 2008 SAS software. The mean sum of squares were partitioned to provide the contribution of sources of variation in the total treatment variation (TTV) of variables (Gomez and Gomez 1984). Treatment means were separated using Waller-Duncan Multiple Range test at 5% level of probability. Unless stated otherwise, all treatment effects were discussed at 5% level of probability.

Results

Harvesting times were highly significant ($P \leq 0.01$) on necrotic spot number, rootlet interference number and root gall number contributing 59, 64 and 50% in TTV of the respective variables, but were not significant on giant cell number (Table 1). In the first 18 days after inoculation, necrotic spots, rootlet interference and root galls were not noticeable. The first necrotic spots and root galls were observed after 20 days, whereas rootlets after 22 days (Table 2).

Harvesting time had highly significant effects on necrotic spot number, giant cell number, rootlet interference number and root gall number, contributing 55, 71, 63 and 59% in TTV of the respective variables (Table 1). HR was noticeable 26 days after inoculation, giant cells and root galls after 18 days, whereas, rootlets were observed after 16 days (Table 2).

Discussion

According to Chitambar and Raski (1984), *M. incognita* is more pathogenic and becomes aggressive with time in comparison with *M. javanica*, which could explain why necrotic spots for *C. africanus*—*M. javanica* relations were observed 6 days after *C. africanus*—*M. incognita* relations. HR is known to be a common response to RKN infection in resistant crops (Chitambar and Raski 1984; Das et al. 2008; Freire et al. 2010; Lee et al. 2021), resulting in cell death and prevention of nematode feeding site formation and nematode development, leading to subsequent nematode death (Postnikova et al. 2015). HR in nematode-infected cells representatives of hyperactive responses in nematode resistant plants (Mashela et al. 2016). According to Nicholson and Hammerschmidt (2003), HR indicates the presence of phenols that play a role in plant defense. When Abifarin et al. (2019) investigated phytochemical and antioxidant activities of *C. africanus*, they found that the plant has phenolic compounds in fruits, leaves and roots.

The presence of such phytochemicals could be responsible for pathogen-associated molecular patterns (PAMP) in *C. africanus*. PAMP result in incompatible nematode-host interactions that triggers the up-regulation of a network of host genes and corresponding proteins involved in an innate response known as pathogen-triggered immunity

Table 1 Total treatment variation (TTV) on necrotic spot, giant cell number, rootlet interference and root gall number in *Cucumis africanus* seedlings infected by *Meloidogyne incognita* and *Meloidogyne javanica* under greenhouse conditions at 30 days after inoculation ($n = 75$). Where DF is degrees of freedom and MS is mean sum of squares

		Necrotic spot		Giant cell number		Rootlet interference		Root gall number	
Source	DF	MS	TTV (%)	MS	TTV (%)	MS	TTV (%)	MS	TTV (%)
Meloidogyne incognita									
Rep	4	0.02927	21	0.05015	42	0.01023	11	0.02477	32
Treatment	14	0.08161	59^{***}	0.04106	34^{ns}	0.05811	64^{***}	0.03799	50^{***}
Error	56	0.02714	20	0.02963	24	0.02232	25	0.01355	18
Total	74	0.13802	100	0.12084	100	0.09066	100	0.07631	100
Meloidogyne javanica									
Rep	4	0.02154	28	0.02091	16	0.02704	21	0.02719	24
Treatment	14	0.04213	55^{***}	0.09017	71^{***}	0.08175	63^{***}	0.06584	59^{***}
Error	56	0.01294	17	0.01595	13	0.02028	16	0.01950	17
Total	74	0.07661	100	0.12703	100	0.12907	100	0.11253	100

^{ns}Not significant at $P \leq 0.05$,

**Significant at $P \leq 0.05$

***Significant at $P \leq 0.01$

Table 2 Mean separation for necrotic spot, giant cell number, rootlet interference and root gall number in *Cucumis africanus* infected by *Meloidogyne incognita* and *Meloidogyne javanica* under greenhouse conditions at 30 days after inoculation ($n = 75$)

	Meloidogyne incognita			*Meloidogyne javanica*			
Days	Necrotic spot^{z}	Rootlet interference^{z}	Root gall number^{z}	Necrotic spot^{z}	Giant cell number^{z}	Rootlet interference^{z}	Root gall number^{z}
2	0.0000^{c}	0.0000^{c}	0.0000^{c}	0.0000^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}
4	0.0000^{c}	0.0000^{c}	0.0000^{c}	0.0000^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}
6	0.0000^{c}	0.0000^{c}	0.0000^{c}	0.0000^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}
8	0.0000^{c}	0.0000^{c}	0.0000^{c}	0.0000^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}
10	0.0000^{c}	0.0000^{c}	0.0000^{c}	0.0000^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}
12	0.0000^{c}	0.0000^{c}	0.0000^{c}	0.0000^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}
14	0.0000^{c}	0.0000^{c}	0.0000^{c}	0.0000^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}
16	0.0000^{c}	0.0000^{c}	0.0000^{c}	0.0000^{b}	0.0000^{b}	0.0954^{b}	0.0000^{b}
18	0.0000^{c}	0.0000^{c}	0.0000^{c}	0.0000^{b}	0.1204^{b}	0.0954^{b}	0.1556^{b}
20	0.0954^{bc}	0.0000^{c}	0.0954^{bc}	0.0000^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}
22	0.3908^{a}	0.1806^{abc}	0.1556^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}
24	0.1398^{bc}	0.0602^{bc}	0.0602^{bc}	0.0000^{b}	0.0000^{b}	0.0000^{b}	0.0000^{b}
26	0.2760^{ab}	0.3362^{a}	0.3113^{a}	0.0954^{b}	0.0602^{b}	0.0000^{b}	0.0602^{b}
28	0.2408^{ab}	0.2408^{ab}	0.0602^{bc}	0.3496^{a}	0.5169^{a}	0.4919^{a}	0.4292^{a}
30	0.0000^{c}	0.0000^{c}	0.0000^{c}	0.0602^{b}	0.0954^{b}	0.0954^{b}	0.000^{b}
$P \leq$	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Standarad deviation	0.8116	1.0340	1.2731	0.8062	1.0271	1.2646	1.0468

^{z}Column means followed by the same letter were not different ($P \leq 0.005$) according to Waller–Duncan Multiple Range test

(PTI) (Melillo et al. 2006). Coffee (*Coffea canephora* cv. '*Apoata*'), resistant to *M. exigua* exhibited HR, which further inhibited formation of feeding site (Vieira et al. 2013). Moon et al. (2010) also observed necrotic spots in resistant *C. annuum* cultivars exposed to *M. incognita*. Two resistant alyce clover (*Alysicarpus ovalifolium* hybrids, FL-1 and FL-3), showed attributes of HR to *M. arenaria* (Powers et al. 1991). Marini et al. (2016) observed similar results for resistant oats (*Avena sativa* cv. 'IPR Afrodite') when exposed to *M. incognita* at 15 days after inoculation.

Delay in giant cells response had been previously reported in nematode resistant trials using molecular approaches (Escobar and Fenoll 2021). The giant cells appeared as deeper stained spots with multiple nuclei that failed to develop beyond the zygote-like size. In nematode-susceptible plant species, giant cells are formed as multinucleate structures formed when the feeding cell and those around it responds to RKN infection by undergoing repeated mitosis without cytokinesis (Huang et al. 2003). The successful establishment of giant cells is essential for nematode development. *Meloidogyne* species evolved strategies that enable them to induce giant cell formation on thousands of plant species by manipulating important factors of plant cell development (Caillaud et al. 2008). This group of notorious pathogens secrete chemical compounds called gene products through the sub-ventral and dorsal gland cells during migration and sedentary phases, respectively (Gheysen and Fenoll 2002; Tripathi et al. 2015). The release of gene products is important during RKN migration and feeding site establishment because it enables nematode growth to subsequent stages (Curtis 2008; Siddique et al. 2022). Anti-plant gene, on the other hand, is a strategy by host plants when plant genes that respond to nematode feeding and secretions to allow for successful partnerships between PPN and plants are silenced (Mashela et al. 2016). Thus, the phytotoxic chemical compounds that destroy the feeding structures, giant cells, are upregulated.

Marini et al. (2016) also noticed that *M. incognita* gradually initiated giant cells that failed to develop into root galls in resistant roots of *A. sativa* 18 days after inoculation. Similarly, Wehner et al. (1991) observed small, poorly formed giant cells in resistant cucumber (*C. sativus*) and African horned cucumber (*C. metuliferus*) exposed to *M. hapla*. Observation of the under-developed giant cells also agreed with observations in resistant soybean (*Glycine max* cvs. 'Jackson' and 'PI 200,538') exposed to *M. arenaria* (Pedrosa et al. 1996) and in resistant cayenne pepper (*Capsicum annuum* cvs. '02G132' and '03G53') (Moon et al. 2010). Pedrosa et al. (1996) indicated that resistance to *M. arenaria* was expressed in *G.*

max as small, poorly formed giant cells. In all the cited examples, the cultivars had post-penetration nematode resistance. The giant cell serves as a source of nutrients for the developing nematode (Bartlem et al. 2014). The post-penetration compatibility in susceptible crops is usually associated with optimal development of giant cells that form a large multinucleate structure which, however, fail to develop in nematode resistant crops (Ortiz 2011).

Compensatory rootlet growth was observed originating adjacent to the under-developed giant cells. Mechanisms behind compensatory rootlet development in RKN-infected resistant hosts have not been investigated. However, considering the tactics RKN implement throughout migratory phases, it is possible that resistant hosts develop lateral rootlets to supplement for roots that can no longer transport nutrients and water from soil to aboveground parts. After root penetration, RKN seek for a suitable feeding site and position themselves strategically in the vascular bundles. While host feeder roots absorb nutrients and water, which move in the plant's vascular system to aboveground plant parts, these nutrients are channeled into RKN throughout their development (Bartlem et al. 2014). Villordon and Clark (2018) noted an increase in lateral root growth on sweet potato resistant (cv. 'Bayou Belle') compared to susceptible variety (cv. 'Beauregard') hosts. The observations supported those in nematode-resistant *G. max* that was exposed to *M. javanica* (Doyle and Lambert 2003) and on nematode-resistant *Trifolium repens* that was exposed to *M. trifoliophila* (Mercer et al. 2004).

Generally, in nematode-susceptible plant species, when *Meloidogyne* J2 develop through J3, J4 and adult female stages, the adjacent root cells bulge to form a root gall. Of 39 cultivars of *C. annuum* screened for nematode resistance, six ('02G132', '03G62', '04G8', '99G198', '03G53' and 'CM334') were resistant to *M. incognita*, with few undeveloped root galls (Moon et al. 2010). Pedrosa et al. (1996) and Herman et al. (1991) noticed fewer J2 advancing to subsequent stages of *Meloidogyne* species.

In a host-parasitic interaction study, tomato host reactions to *Meloidogyne* species parasitism were initiated during the first 12 h after infection (Siddique et al. 2014). However, in the two *Cucumis* species against the *Meloidogyne* species in the current study, there was no evidence of rapid host reactions. Findings by Ramatsitsi and Dube (2020) explained and supported the findings in the current study wherein there were no detectable nematode juveniles in roots at 30 days after inoculation even though they were observed earlier after inoculation. At 30 days after inoculation, Marini et al. (2016) also found a decrease in nematode numbers inside the roots of a resistant *A. sativa* cv. 'IPR Afrodite' that was exposed to *M. incognita.* At the onset of feeding, the nematode becomes sedentary, going through three molts before becoming a mature adult female, with males migrating out of the plant without playing any role in reproduction (Caillaud et al. 2008).

The results showed similar mechanisms of resistance in the roots of nematode resistant *C. africanus* for both *M. incognita* and *M. javanica.* The discovery of post-penetration nematode resistance to *Meloidogyne* species would very certainly increase the use of *C. africanus* in plant breeding and crop rotation systems, hence extending the applications and economic relevance of *C. africanus*. For future research, efforts could be made to investigate whether *C. africanus* is predisposed to other soil-borne pathogens through puncture wounds from penetration of the nematodes.

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Data availability Data sets available at Harvard Data verse https://doi.org/10.7910/DVN/IVQAKM and https://doi.org/10.7910/DVN/D3CI4M

Declarations

Conflict of interest The authors report there are no competing interests to declare.

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