



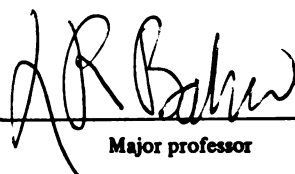
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TO NORTHERN ROOT-KNOT NEMATODE (MELOIDOGYNE HAPLA CHITWOOD)
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Lawrence Wm. Yarger

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A STUDY OF TOLERANCE IN CARROTS
(DAUCUS CAROTA L.)
TO NORTHERN ROOT-KNOT NEMATODE
(MELOIDOGYNE HAPLA CHITWOOD)

By
Lawrence Wm. Yarger

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
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ABSTRACT

A STUDY OF TOLERANCE IN CARROT (DAUCUS CAROTA L.) TO NORTHERN ROOT-KNOT NEMATODE (MELOIDOGYNE HAPLA CHITWOOD)

- I. Selection in Carrot for Tolerance to Northern Root-knot Nematode
- II. Influence of Carrot Cultivar on Marketability as Affected by Northern Root-knot Nematode

By

Lawrence Wm. Yarger

Section I

A technique for screening carrot (Daucus carota L.) seedlings under described greenhouse conditions was used to classify carrot cultivars and breeding lines for their response to northern root-knot nematode (Meloidogyne hapla Chitwood). Breeding lines, 'MSU 872' and 'MSU 5988' exhibited tolerance; whereas 'MSU 9555', 'MSU 1394' and 'Gold Pak 28' exhibited susceptibility to M. hapla.

These same accessions were also screened for their galling response in muck soil under naturally infested field conditions. 'Spartan Classic' and 'MSU 872' were tolerant; whereas 'MSU 1394' and 'MSU 9555' were susceptible to M. hapla.

Section II

Differences in responses of carrot (Daucus carota L.) cultivars to northern root-knot nematode (Meloidogyne hapla Chitwood) were

demonstrated when grown in muck soil, under naturally infested field conditions. Significant differences among carrot cultivars for galling, forking and fasciculation were noted, but no significant difference was noted for stubbing. A tolerance index (T_i) was calculated to compare the overall response of the carrot cultivars to M. hapla. 'Spartan Classic' was the most; whereas 'Danvers 126' was the least tolerant to M. hapla.

LITERATURE REVIEW

Carrot breeding is a time-consuming process because of the bien-nial habit of carrot, and breeding for nematode tolerance has been unusually difficult and unsuccessful. The technique of screening seedlings in the greenhouse affords a rapid method of assaying carrots for nematode tolerance. Carrot lines and cultivars have been screened and tested under infested field conditions (3, 7), but nematode infestation depends upon several factors including its reproductive potential, host plant species and soil environment favorable for reproduction (1). These factors cannot be readily controlled in the field by the researcher. Moreover, nematodes are seldom, if ever distributed uniformly over a field due to differences in soil, moisture, host plant species, nematode migration and other biological aspects of the nematode (6). Screening for nematode tolerance under these conditions can lead to the selection of carrot roots appearing to be tolerant due to absence of the nematodes. Unfortunately, this is commonly the case (6), and most such selections are actually "escapes" which limit the progress of a selection program. The need for controlled inoculation and incubation conditions is evident.

Due to the probable heterogeneity of carrot to nematode infestation and the lack of a truly "resistant" species, it is difficult to determine a classification system for nematode tolerance. Susceptibility to M. hapla is based upon the ability of the nematode to grow and

reproduce in the host plant (6, 8). Most crops classified as "resistant" to nematode infestation are not truly resistant; i.e., they tolerate the nematode attack, but symptoms such as gall formation are still present (7, 10). These "tolerant" plants may function normally, but such "tolerant" carrots would be commercially culled from the fresh market. As a root crop for human consumption, carrots must be practically blemish-free to be marketable. Therefore, a tolerant cultivar must utilize a resistance mechanism which precludes visual damage to the carrot root crop. Although there are reports of degrees of tolerance and resistance in carrots (3, 4, 7), there are no cultivars exhibiting "tolerance" or true "resistance" available to growers.

Crop species have been classified as being immune, resistant, tolerant or susceptible to the root-knot nematode disease (2). These are relative categories describing the host response in the D. carota/M. hapla disease complex. Plants may display a number of resistance responses. Generally, nematode larvae enter the roots of tolerant or resistant plants as readily as they do susceptible plants (9). The resistance reaction is triggered when the host/nematode relationship is upset in some way. These responses may be expressed as larvae failing to mature, larvae repelled or killed, extension of the development cycle or an alteration of the sex ratio towards maleness (2).

The most common resistance response is hypersensitivity. This describes the rapid death of the immediate host tissue cells soon after nematode penetration, which results in either the rapid exit of the nematode larvae or death of the larvae within the dead tissues (5). There is no documented mechanism for resistance in carrots tolerant to M. hapla, though there has been speculation that heterosis may play a

role in the tolerant response of hybrid carrot cultivars by "out-growing" nematode attack and conditioning tolerance (7). The criterion for rating nematode tolerance in the greenhouse seedling test was the count of galls per plant. Fassuliotis reports (2) that galling alone was not indicative of the degree of tolerance and could be misleading. The purpose of assaying carrots for nematode tolerance, however, was to obtain cultivars and breeding lines that would not develop hyperplastic and hypertrophic reactions, such as galling, that result in unmarketable carrots.

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DEDICATION

To my family and friends who have
given so much of themselves so I could pursue
this opportunity in my life;
And to the carrot growers of Michigan, for whom
I pray it benefits and without whom I
would not have been able to conduct this research

ACKNOWLEDGEMENTS

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Readers:

The journal format which was utilized in this thesis meets the requirements stipulated by the Horticulture Department and the University. The thesis body was separated into two sections. Section I was prepared for publication in Plant Disease, and Section II for the Journal of the American Society of Horticultural Science. Each section follows the manuscript style adopted by the respective journal.

SECTION I
SELECTION IN CARROT
FOR TOLERANCE TO
NORTHERN ROOT-KNOT NEMATODE

Selection in Carrot for Tolerance to
Northern Root-knot Nematode

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ABSTRACT

A technique for assaying carrot (Daucus carota L.) seedlings under described greenhouse conditions was used to classify 21 carrot cultivars and breeding lines for their response to northern root-knot nematode (Meloidogyne hapla Chitwood). Breeding lines, 'MSU 872' and 'MSU 5988' were tolerant; whereas 'MSU 9555', 'MSU 1394' and 'Gold Pak 28' exhibited susceptibility to M. hapla. The number of galls per root for the two tolerant lines was 3-4; whereas the susceptible roots exhibited 20-41 galls.

The same 21 lines and cultivars were also assayed for their galling response in muck soil under naturally infested field conditions. 'Spartan Classic' and 'MSU 872' were tolerant; whereas 'MSU 1394' and 'MSU 9555' were susceptible to M. hapla. The two tolerant accessions averaged 21.6 and 23.2% galled roots; whereas the two susceptible averaged 44.8 and 48.8%.

Northern root-knot nematode (Meloidogyne hapla Chitwood) is a serious pathogen of carrots (Daucus carota L.) in Michigan (2) where 6600 acres of carrots were harvested in 1979 (1). M. hapla and D. carota form a complex host-parasite relationship characterized by a number of symptoms including galling, forking, stubbing and fasciculation of the roots; and yield reduction (6, 9, 10).

Carrot roots attain full length during the first 2-3 weeks of growth (9, 14). Carrots are most susceptible to M. hapla during this period. Obstacles to root elongation such as rocks, nondecomposed organic material, compacted soil and soil insects can cause tap root malformations (13, 14). Diseases caused by other pathogens can also

cause root malformations such as stubbing, forking and fasciculation (6). Yield losses and plant mortality due to nematode damage are extensive (6, 9). Moreover, nematode control by soil fumigation is costly and may approximate \$250-\$500/acre on Michigan mucklands.

Such symptoms, caused by the D. carota-M. hapla disease complex or by the environment are definitely yield-limiting. To study this complex system, controlled conditions are necessary to eliminate undesirable environmental interactions. This is especially important to the carrot breeder selecting for nematode tolerance based upon a straight and marketable root shape. The object of this research was to develop a seedling assay to evaluate carrots for their response to northern root-knot nematode under controlled greenhouse conditions. By such a technique an array of carrot lines and cultivars could be classified for their response to M. hapla infestation.

MATERIALS AND METHODS

Carrot breeding lines and cultivars with different root types (Table 1) were assayed for nematode tolerance. The hybrid cultivars and their parents were recently described (5); whereas the standard cvs. were described previously (2). Six soil media were tested and compared to determine an acceptable medium for nematode infestation (Table 2). A stream-sterilized mixture of muck and sand (1:1) resulted in the induction of the most galls per plant, though not significantly different from the sand medium. This medium supplied nutrients to the emerging carrots and could be easily removed from the seedlings to count the number of galls with minimal damage to the roots.

Table 1. Carrot lines and cultivars assayed for their response to M. hapla in a greenhouse seedling test at 25°C in a sand: muck medium

Accession	Source/Lot no.	Root type ^a	Top length ^b
Cultivars			
Spartan Delux F ₁	Crookham	I	L
Spartan Delite F ₁	Crookham	I	M
Spartan Fancy F ₁	Crookham	I	M
Spartan Premium F ₁	Crookham	LN	M
Spartan Classic F ₁	Crookham	ND	M
Spartan Bonus 80 F ₁	Crookham	D	L
Danvers 126	Northrup King	D	L
Scarlet Nantes	Northrup King	N	M
Gold Pak 28	Ferry Morse	I	M
Red Core Chantenay	C6051	C	L
Breeding lines			
MSU 1394	75W338	I	L
MSU 5986	71W33	I	M
MSU 1302	75W92	I	M
MSU 871	C5009	I	S
MSU 6000	421013	I	S
MSU 8549	75H2	IN	S
MSU 5988	72W161	LN	M
MSU 872	C534	LC	M
MSU 1475	C5019	LC	M
MSU 9555	78W190	CD	L
MSU 9541	72W91	D	L

^aC = Chantenay, L = long, D = Danvers, I = Imperator and N = Nantes root types (see Babb, et al. for description of root types).

^bS = short, M = medium and L = long top lengths.

Table 2. Comparison of steam-sterilized media for the induction of nematode galls on carrot cultivar, Gold Pak 28

Soil medium	Galls per plant ^a
Sand: Muck (1:1)	19.1 a
Sand	12.6 ab
Muck	10.3 bc
Loam: Peat: Sand (1:1:1)	5.3 bc
Metro Mix 200 ^b	3.0 c
Vermiculite	0.3 c

^aMeans in a column followed by the same letter are not significantly different using Tukey's HSD test, $P = 0.05$.

^bGrace Horticultural and Agricultural Products, W.R. Grace and Co., Cambridge, MA 02140.

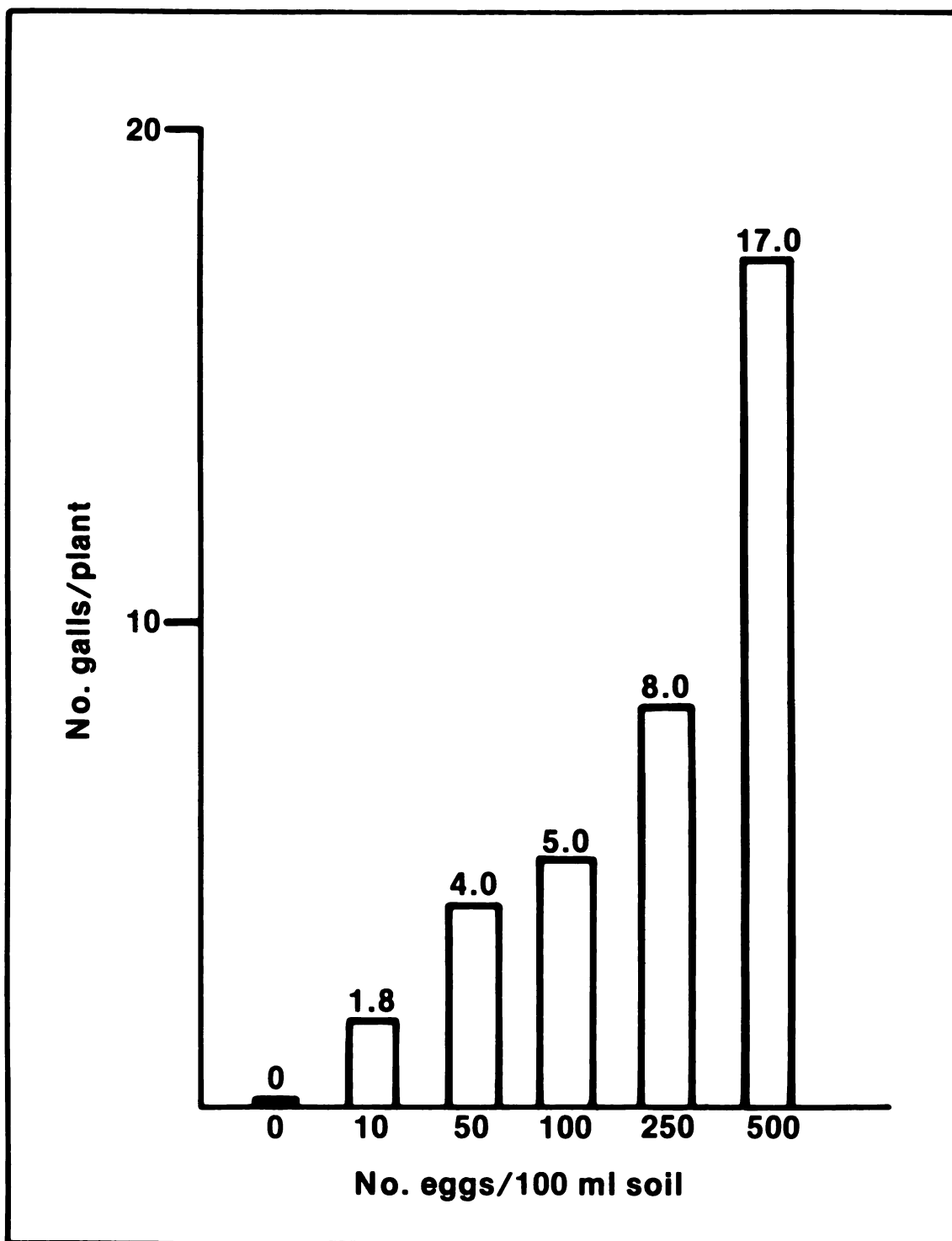
Greenhouse evaluation. Nematodes were reared in the greenhouse on tomato (Lycopersicon esculentum Mill.) and the eggs used for inoculum were extracted with a 1.0% NaOCl solution (7). They were calibrated and refrigerated (5°C) in a water suspension for up to six months and used as needed for experimentation.

A concentration of 500 eggs/100 ml medium was used as inoculum to produce galls on carrot seedlings for evaluation (Figure 1). The number of galls produced was directly proportional to the number of eggs added to the medium. Other screening techniques have utilized different inoculum levels (11, 15). However, with 500 eggs/100 ml medium, the number of galls per plant was such that the carrot roots could be evaluated and classified from susceptible to tolerant to nematode attack.

Seeds of each line or cultivar were individually sown into 2.5 x 2.5 x 12.5 cm cells of styrofoam 'Speedling Trays' (Speedling, Inc., Sun City, FL 33586). Each cell (seed) was inoculated with a suspension of nematode eggs to approximate 370 eggs per seed. In the greenhouse the trays were randomly arranged in a mist chamber with periodic overhead misting every 30 min. The chamber was temperature controlled to provide a constant soil temperature of 25°C.

The life cycle of M. hapla is approximately 45 days, but galls can be detected as early as three weeks after infestation (10). Accordingly, carrot roots were examined for galls four weeks after inoculation. Each accession was classified for its response to nematode attack by counting the number of galls per plant and arbitrarily dividing them into classes from susceptible to resistant (Table 3).

The experimental design was completely randomized. Data were subjected to statistical analysis to determine significant differences



**Fig. 1. The incidence of nematode galls on carrot seedling roots as affected by the inoculum level.
(Correlation coefficient = 0.99; P = 0.001.)**

Table 3. Classes used to characterize carrot lines and cultivars for M. hapla attack under controlled greenhouse conditions in the seedling stage and in the field at maturity

<u>Greenhouse</u>	
No. of galls/root	Class
0	Resistant
1-5	Tolerant
6-15	Tolerant-susceptible
16-25	Susceptible-tolerant
> 25	Susceptible
<u>Field</u>	
% galled roots	
0-10	Resistant
11-20	Resistant-tolerant
21-30	Tolerant
31-40	Tolerant-susceptible
41-50	Susceptible-tolerant
> 50	Susceptible

in nematode response among carrot lines and cultivars.

Field evaluation. The same 21 carrot lines and cultivars were also grown and evaluated under naturally infested field conditions in a Houghton muck soil with a four year history of root-knot infestation (Table 1). The carrots were seeded in May in rows 3 m long and 0.5 m apart. After three weeks the seedlings were thinned to 36 plants/m. Standard cultural practices were used for muck-grown carrots (3).

The carrot roots were harvested in September and examined to determine the percent of roots with nematode galls. A sample of 25 roots was harvested from the center of each plot. Nematode infestation was verified by soil assay and the presence of galls on the roots. The experimental design was a Youden Square (16) with five replications, utilized to minimize possible variation in the nematode population throughout the testplot (8). The data were statistically analyzed and the carrot lines and cultivars described in relation to their galling response to M. hapla.

RESULTS AND DISCUSSION

In the greenhouse evaluation, the more tolerant lines were 'MSU 872', 'MSU 5988', and 'MSU 1475 (Table 4). The response among inbred breeding lines was great as evidenced by a range of 3 to 41 galls per plant. A wide response among cultivars was also observed. The number of galls per plant ranged from 6 to 28. The more tolerant cultivar was 'Spartan Classic' although the significance among cultivars was not great. Noteably, the more susceptible cultivars were the standard cultivars commonly used in carrot production.

The same array of carrot lines and cultivars was tested under M. hapla infested field conditions (Table 4). The percentage of plants

Table 4. Classification of carrot breeding lines and cultivars tested in the greenhouse and field for tolerance to M. hapla

Accession	Greenhouse test ^a		Field test ^a	
	No. galls per plant	Rank Class	% plants galled	Rank Class
Cultivars				
Spartan Classic	6.2 a	1 T-S	21.6 a	1 T
Spartan Delux	6.6 a	2 T-S	28.0 a	5 T
Spartan Bonus 80	7.1 a	3 T-S	24.8 a	3 T
Spartan Delite	7.2 a	4 T-S	28.0 a	5 T
Scarlet Nantes	8.5 a	5 T-S	27.2 a	4 T
Spartan Fancy	8.7 a	6 T-S	24.8 a	3 T
Danvers 126	9.3 a	7 T-S	38.4 a	7 T-S
Red Core Chantenay	13.1 ab	8 T-S	37.6 a	6 T-S
Spartan Premium	20.6 bc	9 S-T	23.2 a	2 T
Gold Pak 28	27.9 c	10 S	28.0 a	5 T
Breeding lines				
MSU 872	3.3 a	1 T	23.2 a	1 T
MSU 5988	4.3 a	2 T	28.8 abc	3 T
MSU 1475	5.0 a	3 T	28.8 abc	3 T
MSU 8549	6.2 a	4 T-S	31.2 abcd	4 T-S
MSU 1302	6.6 a	5 T-S	26.4 ab	2 T
MSU 5986	6.7 a	6 T-S	36.0 abcd	5 T-S
MSU 871	7.5 a	7 T-S	51.2 d	10 S
MSU 6000	9.3 a	8 T-S	44.0 abcd	7 S-T
MSU 9541	19.4 a	9 S-T	41.6 abcd	6 S-T
MSU 1394	20.3 a	10 S-T	44.8 bcd	8 S-T
MSU 9555	41.3 b	11 S	48.8 cd	9 S-T

^aMeans in a column followed by the same letter are not significantly different using Duncan's multiple range test, $P = 0.05$.

with galled roots within cultivars varied from 21.6 to 38.4%. Within lines, the range was from 23.2 to 51.2%.

The carrot lines and cultivars were ranked for nematode tolerance (Table 4). There was a significant correlation of field with greenhouse test results among breeding lines ($r = 0.63$; $P = 0.05$). In each case, MSU lines '872', '5988' and '1475' exhibited tolerance to root-knot infestation; whereas '9555' and '1394' exhibited susceptibility. There was no significant correlation between the results of the field and greenhouse tests for the cultivars. This absence of significance might be due to the major change in rank of 'Spartan Premium' and 'Gold Pak 28' (Table 4).

There appears to be an association of root type with nematode gall formation and tolerance (Tables 1, 4). In the field experiment, carrots with Nantes and Long Chantenay root types ('Spartan Classic', 'Spartan Premium', 'Scarlet Nantes', 'MSU 8549', 'MSU 872' and 'MSU 1475') exhibited tolerance. These same seven accessions in greenhouse tests were tolerant of nematode galling, except for 'Spartan Premium'. In both experiments, carrots with Danvers root types, except for 'Spartan Bonus 80' exhibited susceptibility. 'Spartan Bonus 80', however, is a three-way hybrid cross of (Long Chantenay x Imperator) x Danvers root types (5). Thus, the Long Chantenay x Imperator maternal parent may exhibit dominance over the susceptible Danvers paternal root type for nematode tolerance.

Screening for nematode tolerance under naturally infested field conditions often leads to the selection of non-diseased roots appearing to be tolerant, but which are actually "escapes" from nematode infestation (8). Our greenhouse seedling test alleviates this and permits

rapid controlled screening and evaluation of carrots for root-knot tolerance based on gall formation. Possibly, a carrot cultivar with tolerance to M. hapla could be developed based on 'MSU 872', 'MSU 5988' and 'MSU 1475'. However, carrots must be blemish-free to be acceptable for fresh-market consumption. Accordingly, cultivars tolerant or resistant to M. hapla must utilize a resistance mechanism which precludes visual damage to the carrot root. Many more lines and cultivars should be screened to identify other accessions with tolerance that could be used in carrot breeding programs. In future studies we propose to study the relationship of other root-knot nematode disease symptoms with tolerance in carrots.

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LITERATURE CITED

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SECTION II

INFLUENCE OF CARROT CULTIVAR ON MARKETABILITY
AS AFFECTED BY NORTHERN ROOT-KNOT NEMATODE

Influence of Carrot Cultivar on Marketability
as Affected by Northern Root-knot Nematode

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East Lansing

Abstract. Differences in responses of carrot (Daucus carota L.) to northern root-knot nematode (Meloidogyne hapla Chitwood) were demonstrated when grown in muck soil, under naturally infested field conditions. Significant differences among cultivars for galling, forking and fasciculation were noted, but no significant difference was noted for stubbing. A tolerance index (T_i) was calculated by numerically combining the effects of each response to compare the total reaction of the carrot cultivars to M. hapla. 'Spartan Classic' was the most tolerant; whereas 'Danvers T26' was the least tolerant to M. hapla.

Carrots are a major vegetable crop produced in the United States and Michigan with a gross income of approximately \$2,000/a for fresh market carrots (4, 10). The marketability of fresh market carrots depends heavily on the appearance of the root. Deep, loose soils with good water-holding capacity are necessary for the development of long, straight (marketable) roots (3).

Michigan ranks fifth in the production of carrots in the U.S. (4), but due to intensive cropping and mono-cropping methods employed by Michigan carrot growers, northern root-knot nematode has become a serious pest. Moreover, approximately \$100 million is spent annually on nematode control in the U.S. (8). Disease symptoms typical of M. hapla infection include reduced crop vigor and reduced marketable yields due to forked, stubbed and fasciculated roots (3, 6, 8, 10). However, these same symptoms can be induced by a number of other

pathogens (3, 10) and environmental factors (3, 7, 10, 11). The presence of nematode galls in conjunction with these symptoms is necessary to verify M. hapla infestation.

The purpose of this study was to evaluate the response of nine hybrid and open-pollinated carrot cultivars to M. hapla, and how their response relates to the breeding and production of marketable roots grown in naturally infested muck soil.

Materials and Methods

Carrot cultivars and breeding lines were grown with standard cultural practices (1) in test plots at the Muck Research Station of Michigan State University. The site was naturally infested with northern root-knot nematode (M. hapla) as determined by soil assay and the presence of nematode galls. The carrot roots were harvested and evaluated for forking, galling, stubbing and fasciculation.

Symptomatology. Twenty-one breeding lines and cultivars were sown in May, 1979 in rows 3 m long and 0.5 m apart (Table 1). After 3 weeks, the seedlings were thinned to 36 plants/m.

A sample of 25 roots was randomly harvested from the center of each plot in September (approximately 120 days from seeding). The percentage of roots damaged from forking and stubbing was recorded. Severity of galling and fasciculation was rated on a scale of 1 to 5 (1 = least damage; 5 = most damage) (Table 2). The experimental design was a Youden Square (14) with five replications to minimize possible variation in the nematode population throughout the test plot (5).

Tolerance evaluation. Nine cultivars of varied root types (Table 1) were grown and evaluated for their response to M. hapla under the same field conditions as those in the symptomatology experiment. At

Table 1. Carrot cultivars and breeding lines assayed for their response to M. hapla in muck soil under naturally infested field conditions

Accession	Source/Lot no.	Root type ^z
<u>Cultivars</u>		
^y Spartan Delite F ₁	Crookham	I
^y Spartan Delux F ₁	Crookham	I
^y Spartan Fancy F ₁	Crookham	I
^y Spartan Bonus 80 F ₁	Crookham	D
^y Spartan Classic F ₁	Crookham	ND
^y Spartan Premium F ₁	Crookham	LN
^y Danvers 126	Northrup King	D
^y Scarlet Nantes	Northrup King	N
^y Gold Pak 28	Ferry Morse	I
Red Core Chantenay	C6051	C
<u>Breeding line</u>		
MSU 1394	75W338	I
MSU 5986	71W33	I
MSU 1302	75W92	I
MSU 871	C5009	I
MSU 6000	421013	I
MSU 8549	75H2	IN
MSU 5988	72W161	LN
MSU 872	C534	LC
MSU 1475	C5019	LC
MSU 9555	78W190	CD
MSU 9541	72W91	D

^zC = Chantenay, L = long, D = Danvers, I = Imporator and N = Nantes root types (see Babb, et al. for description of root types).

^yCultivars evaluated in experiment 2.

Table 2. Response of carrot cultivars and breeding lines grown under muck field conditions, naturally infested with M. hapla.

Accession	Percent forked roots	Percent stubbed roots	Galling ^z severity	Fascicu- ^z lation severity
Cultivars				
Scarlet Nantes	12.8 a ^y	13.6 b ^y	1.2 a ^y	1.0 a ^y
Red Core Chantenay	20.8 b	40.0 e	3.2 d	2.2 b
Spartan Bonus 80	23.2 bc	19.2 c	1.4 ab	1.4 ab
Spartan Classic	24.8 bcd	20.8 cd	1.2 a	1.0 a
Danvers 126	25.6 cd	40.0 e	2.4 cd	1.4 ab
Gold Pak 28	28.8 d	12.0 b	2.2 bc	1.4 ab
Spartan Premium	36.0 e	24.0 d	1.4 ab	1.4 ab
Spartan Delite	36.0 e	8.0 a	2.0 abc	1.6 ab
Spartan Delux	39.2 ef	24.0 d	2.0 abc	1.6 ab
Spartan Fancy	41.6 f	20.0 c	1.6 abc	1.2 a
Breeding lines				
MSU 5988	23.2 a ^y	15.2 ab ^y	1.4 a ^y	1.2 ab ^y
MSU 872	24.8 a	23.2 c	1.6 ab	2.0 bcd
MSU 1475	27.2 ab	24.0 c	2.2 abcd	1.0 a
MSU 8549	30.4 bc	16.0 ab	2.0 abcd	2.0 bcd
MSU 1302	32.8 c	18.4 b	1.8 abc	1.4 abc
MSU 9555	33.6 c	46.4 e	2.2 abcd	2.4 de
MSU 6000	40.8 d	14.4 ab	3.0 d	3.2 e
MSU 871	40.8 d	32.8 d	2.6 bcd	1.2 ab
MSU 5986	46.4 e	13.6 a	1.8 abc	1.4 abc
MSU 9541	49.6 ef	36.0 d	2.4 abcd	2.4 de
MSU 1394	51.2 f	16.0 ab	2.8 cd	2.2 cd

^zRated subjectively on a scale of 1 (least damage) to 5 (most damage).

^yMean separation within columns by Duncan's multiple range test, 5% level.

harvest the percentage of roots galled, fasciculated, stubbed and forked was noted. The severity of galling and fasciculation was subjectively rated on a scale of 1 to 5 (1 = least damage; 5 = most damage).

A cumulative tolerance index, T_i , was calculated to measure the overall response to M. hapla as follows:

$$T_i = A_g + B_s + C_f + D_h + E_s + F_s$$

where A_g = percent galled roots, B_s = percent stubbed roots, C_f = percent forked roots, D_h = percent fasciculated (hairy) roots, E_s = galling severity and F_s = fasciculation severity. Low index values are indicative of a greater tolerance to M. hapla in contrast to high values indicating susceptibility.

Results

Symptomatology. The results of this experiment were used as a preliminary test to see if there were differences in severity of damage among carrot cultivars and breeding lines due to M. hapla. Among cultivars, 'Spartan Classic' and 'Scarlet Nantes' were the most tolerant to galling with a severity rating of 1.2, though they were not significantly different from the other 'Spartan' cultivars. Conversely, 'Red Core Chantenay', rated 3.2, was the most susceptible (Table 2). 'Scarlet Nantes' had the lowest percentage of forked roots with 12.8%, while 'Spartan Fancy' had the highest with 41.6%. 'Spartan Delite' responded with 8.0% stubbed roots; whereas 'Red Core Chantenay' responded with 40.0%. Fasciculation severity ranged from 1.0 with 'Spartan Classic' and 'Scarlet Nantes' to 2.2 with 'Red Core Chantenay' though accessions were not significantly different.

'MSU 5988' was most tolerant to galling with a severity rating of 1.4; whereas 'MSU 6000' was most susceptible with a rating of 3.0 (Table 2). 'MSU 5988' was also the most tolerant of forking with 23.2% forked roots; whereas 'MSU 1394' was most susceptible with 51.2%. 'MSU 5986' had the fewest stubbed roots with 15.2%; whereas 'MSU 9555' had the most with 46.5%. 'MSU 1475' was rated 1.0 for fasciculation severity with 'MSU 6000' rated 3.2.

Tolerance evaluation. The responses of the nine cultivars in this experiment to galling, forking, stubbing and fasciculation were evaluated individually; then overall, in the form of a tolerance index (T_i).

Forking. Under the conditions of the experiment, forking appeared to be prevalent in carrots with Emperor root types (Tables 1, 3). The cultivars were ranked in order of their response, ranging from 14.8 to 51.2% forked roots (Table 3). 'Scarlet Nantes' was the most and 'Spartan Delite' the least tolerant.

Stubbing. Percent stubbed roots ranged from 28.8 to 47.2%, but there were no significant differences among cultivars (Table 4).

Galling. Percent galled roots ranged from 61.2 to 85.2%, with 'Danvers 126' and 'Spartan Fancy' exhibiting the least tolerance, but with no significant differences among the other cultivars (Table 5).

Fasciculation. Percent fasciculated roots ranged from 14 to 50% with 'Spartan Classic', 'Spartan Bonus' and 'Scarlet Nantes' exhibiting the most tolerance (Table 6). The tolerant cultivars also demonstrated the lowest ratings for severity of fasciculation.

Tolerance index (T_i). The tolerance index demonstrated significant differences among carrot cultivars. The hybrid, 'Spartan Classic',

Table 3. Forking of carrot cultivars grown under muck field conditions, naturally infested with M. hapla

Cultivars	Percent forked roots
Scarlet Nantes	14.8 a ^z
Spartan Classic	22.0 ab
Spartan Delux	28.8 bc
Spartan Premium	30.0 bc
Spartan Bonus 80	31.2 bc
Spartan Fancy	34.8 bc
Gold Pak 28	42.0 cd
Danvers 126	42.0 cd
Spartan Delite	51.2 d

^zMean separation within column by Duncan's multiple range test, 5% level.

Table 4. Stubbing of carrot cultivars grown under much field conditions, naturally infested with M. hapla.

Cultivars	Percent stubbed roots
Spartan Bonus 80	28.0 a ^Z
Spartan Classic	30.0 a
Spartan Delux	37.2 a
Spartan Premium	38.0 a
Spartan Delite	39.2 a
Scarlet Nantes	40.8 a
Danvers 126	44.0 a
Gold Pak 28	47.2 a
Spartan Fancy	47.2 a

^ZMean separation within column, by Duncan's multiple range test, 5% level.

Table 5. Galling of carrot cultivars grown under much field conditions, naturally infested with M. hapla.

Cultivars	Percent galled roots	Gall ^z severity
Spartan Delux	61.2 a ^y	2.3
Spartan Premium	61.2 a	2.7
Spartan Bonus 80	64.0 a	2.7
Gold Pak 28	66.0 a	3.2
Spartan Classic	66.8 a	2.3
Scarlet Nantes	69.2 ab	2.8
Scarlet Delite	72.0 ab	2.8
Spartan Fancy	83.2 b	3.8
Danvers 126	85.2 b	4.0

^zRated subjectively on a scale of 1 (least damage) to 5 (most damage).

^yMean separation, within column, by Duncan's multiple range test, 5% level.

Table 6. Fasciculation of carrot cultivars grown under muck field conditions, naturally infested with M. hapla.

Cultivars	Percent fasciculated roots	Fasciculation ^z severity
Spartan Classic	14.0 a ^y	1.5
Spartan Bonus 80	18.8 a	2.2
Scarlet Nantes	20.8 a	2.2
Spartan Premium	25.2 ab	2.7
Spartan Delux	27.2 abc	2.7
Gold Pak 28	38.0 bcd	3.5
Spartan Delite	42.8 cd	3.8
Spartan Fancy	43.2 cd	3.3
Danvers 126	50.0 d	4.3

^zRated on a scale of 1 (least damage) to 5 (most damage).

^yMean separation, within column, by Duncan's multiple range test, 5% level.

exhibited the most tolerance (least amount of damage) to M. hapla, and 'Danvers 126' exhibited the least (Table 7).

Correlation. Correlations among cultivars demonstrated an association of fasciculation with forking, stubbing and galling (Table 8). There was, however, no correlation among forking, stubbing and galling.

Discussion

Data from the symptomatology experiment demonstrated differential responses among carrot cultivars and breeding lines to M. hapla. In previous field and greenhouse tests, these cultivars were uniform in the galling response from M. hapla infestation (13). In this experiment, there was variation within cultivars for forking and fasciculation as well as galling. Moreover, forking, stubbing and galling appeared to be independent. This may indicate independent genetic control for these responses, which contributes directly or indirectly to the overall tolerance to M. hapla. A tolerance index (T_i) was used to measure the overall response of each cultivar to M. hapla and then to compare differences among cultivars. Though differences were not great, improvements might conceivably be made through successive generations of selection for tolerance. From this information we can justify further efforts toward breeding carrots for tolerance to northern root-knot nematode.

Table 7. Overall response of carrot cultivars grown under muck field conditions, naturally infested with M. hapla.

Cultivars	Tolerance ^Z index (T _i)
Spartan Classic	136.6 a ^Y
Spartan Bonus 80	146.9 ab
Scarlet Nantes	150.6 ab
Spartan Delux	159.4 abc
Spartan Premium	159.8 abc
Gold Pak 28	186.3 bcd
Spartan Delite	211.8 de
Spartan Fancy	215.5 de
Danvers 126	229.5 e

^ZT_i = A_g + B_s + C_f + D_h + E_s + F_s, where A_g = percent galled roots, B_s = percent stubbed roots, C_f = percent forked roots, D_h = percent fasciculated (hairy) roots, E_s = galling severity and F_s = fasciculation severity.

^YMean separation within cultivars by Duncan's multiple range test, 5% level.

Table 8. Correlation of responses of 9 carrot cultivars to M. hapla, grown under naturally infested field conditions

Response	Forked (%)	Stubbed (%)	Galled (%)	Fasciculated (%)	Gall severity	Fasciculation severity
Forked (%)	1.0	0.39 ^{NS}	0.36 ^{NS}	0.80 ^{**}	0.46 ^{NS}	0.84 ^{**}
Stubbed (%)		1.0	0.56 ^{NS}	0.78 [*]	0.81 ^{**}	0.78 [*]
Galled (%)			1.0	0.74 [*]	0.88 ^{**}	0.62 ^{NS}
Fasciculated (%)				1.0	0.81 ^{**}	0.97 ^{**}
Gall severity					1.0	0.75 [*]
Fasciculation severity						1.0

NS, *, ** Nonsignificant at 5% (NS) or significant at 5% (*) or 1% (**) level.

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