Ontogeny of Daucus carota Infected with Meloidogyne hapla[1]

L. A. SLINGER and G. W. BIRD[2]

Abstract: The ontogeny of carrots (*Daucus carota* cv. 'Spartan Premium') grown under greenhouse conditions in pots of organic soil infected with *Meloidogyne hapla* was influenced detrimentally as early as 4 days after seeding, as determined through analysis of plant surface area, dry weight, fresh weight, net assimilation rate, relative growth rate, and leaf-area ratio. Only 58% of the diseased carrots were suitable for fresh market, compared with 97% of those grown in nematode-free soil. Growth and development of the shoot system (height, surface area, dry weight, and fresh weight) were retarded by *M. hapla* as early as 12 days after seeding. During the first 12 days after seeding, root dry weight was greater for diseased plants than for controls. Root growth and development (surface area, dry weight, and fresh weight) associated with this nematode, however, were retarded as early as 16 days after seeding. *M. hapla* caused a delay in the occurrence of 2nd-, 4th-, and 5th-order roots, and an increase in the occurrence of 6th-order roots in infected plants. Parasitized plants had 44% fewer roots (primary through 6th-order) and 50% less total root length. *Key Words:* Carrots, northern root-knot nematode.

Meloidogyne hapla Chitwood is a serious limiting factor in carrot (*Daucus carota sativa* L.) production in Michigan (19), where about 6,000 acres of carrots are grown annually in organic soils (22). The problem is endemic in temperate carrot-growing regions. Symptoms of *M. hapla* infection of carrots include galling of both primary and secondary roots, tap-root malformation, root proliferation, yield losses, and plant mortality (1, 2, 3, 4, 7, 10, 25, 26). Aspects of the life history, host-parasite relationships, and pathogenicity of *M. hapla* have been studied in association with carrots (6, 9, 11, 16, 21, 26).

Carrots have two major phases of growth and development (12, 14, 17). Primary growth is completed with the development of centrifugal xylem, at about 11 days after germination (12). Secondary growth is derived primarily from periclinal vascular cambium division in the xylem, phloem, and parenchyma tissue, forming the hypocotyl and storage tap root. Carotene is visually detectable about 37 days after germination (12, 17). The morphogenesis and related biochemistry of the carrot plant has been studied in detail (5, 8, 12, 15, 24), including variations for crop production in organic soils (8, 16). Very little, however, is known about most aspects of the ontogeny of carrot plants infected with *M. hapla*. Such information is needed for developing predictive pest-crop ecosystem models. This study was done to analyze the ontogeny of carrot plants grown in *M. hapla*-infested organic soil in the presence of all normal components of the soil microflora and microfauna.

MATERIALS AND METHODS

Soil characterized as a coarse aggregate of organic material, with a pH of 6.8, insoluble salts of 66-73 mg/gm, nitrates of 54-67 mg/gm, and magnesium of 1.3-1.7 mg/gm, was obtained from a Grant (Michigan) carrot field. The population density of *M. hapla* was five second-stage larvae/100 cm^3 soil, as determined by centrifugation-flotation extraction (20). No attempt was made to estimate the number of *M. hapla* eggs present. The nematode infestation was the only property of the soil known to be deleterious to carrot growth. The percent total salts was 11.7-13.2 nitrates, 0.9-2.0 potassium, 17.2-17.3 calcium, and 4.5-4.9 magnesium. Half of the soil was steamed for 3.5 h at 60 C, and used to fill 125 plant containers. An additional 125 plant containers were filled with the unsteamed soil.

Four sizes of plant containers were selected to minimize greenhouse space use and maximize the volume of soil available for root development. Fifteen-cm-diameter clay pots were used for plants harvested within 28 days of seeding. Plants harvested from days 28 to 48 were grown in 20-cm-

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[2] Former Graduate Assistant, Dept. of Botany and Plant Pathology; and Professor, Depts. of Entomology, and Botany and Plant Pathology, Michigan State University, East Lansing, Michigan 48824.

diam pots, whereas plants for days 48 to 68 were grown in 25-cm-diam pots. Plants harvested during the last 32 days of the experiment were grown in clay drainage tiles (24.8 cm diam and 32.2 cm deep). All containers were steamed for 2 h at 60 C before use. Ten carrot seeds (cv. 'Spartan Premium') were planted in each of the 250 containers of organic soil. To assure nematode infection, a 5.0-ml water suspension containing 100 second-stage larvae of *M. hapla* was added at planting onto the seeds in each container of unsteamed soil. These nematodes were obtained from a greenhouse culture of *M. hapla* maintained on celery, and extracted from root tissue by a shaker technique (20).

The plants were maintained in a greenhouse under 18 h of natural and supplemental light, and were watered daily during the 100-day experiment. Relative humidity ranged from 0-40% ($\bar{X}$ = 30%). The mean daily minimum air temperature was 17.8 C (σ = 2.5, Y = 18.0 − 0.004X), and the mean daily maximum air temperature was 28.6 (σ = 3.5, Y = 27.5 + 0.042X). The mean daily degree accumulation at a base of 7.3 C ($DD_{7.3}$) was 15.9 C (σ = 2.4). Since the slopes of the maximum and minimum temperatures were close to zero, an estimated accumulated $DD_{7.3}$ can be calculated for any day during the experiment by multiplying the day by 15.9. No fertilizer or pesticides were applied before planting or during the experiment. Plants were thinned to three plants per pot on day 14 and to one plant per pot 21 days after seeding.

Four plants grown in steamed soil and four from the *M. hapla*-infested soil were randomly selected from the appropriate container size group every 96 h. The soil and root systems were removed from the pots intact, and soaked for several hours in cool water. Adhering soil was then carefully washed from roots, beginning with the lower portion. Organic matter was removed from the roots with forceps. The plants were blotted, wrapped in moist paper toweling, and stored at 5-7 C in closed plastic bags. Plant analysis was made within 96 h of washing (18). Plants harvested on days 80 and 84 were maintained with adequate moisture at 5-7 C for 8 and 4 days, respectively, before processing. Each shoot system was evaluated for number of leaves, height, fresh weight, dry weight, and area. Each root system was evaluated for root area, number, order, length, galling, fresh weight, dry weight, and economic value.

Leaf and root area were measured with a Li-Cor Model Li-3000 portable area meter equipped with a Li-3050A transparent belt-conveyor accessory. Secondary roots were spread as thin as possible on the belt, and each root system was analyzed three times. Each shoot system was divided into individual leaflets and stems and evaluated for area. Beginning with day 36, the surface area of the enlarged storage root was determined geometrically.

Root order, number, and length were obtained by two methods. The entire root systems of all plants were evaluated during the first 36 days. Only one carrot from each of the two soil environments was analyzed on each sampling date after day 36. These were selected to be average for each group of replicates. Each tap root was measured and divided into tenths. The 2nd-order root closest to each one-tenth division was removed and analyzed. These data and the number of 2nd-order roots present were used to estimate the number and lengths of 3rd-, 4th-, 5th-, and 6th-order roots. Root evaluations were made in a tray with an attached grid, where roots were floated in a thin film of water to prevent desiccation and facilitate root separation and analysis. Galls caused by *M. hapla* were counted by floating the roots on a dark surface in a thin film of water.

Fresh weights of the root and shoot systems were obtained by direct weight in a preweighed and dried crucible. Dry weights of the shoot and root systems were obtained by drying to a constant weight ($\pm$0.1 mg for the first 36 days and $\pm$1.0 mg for the remaining harvest days) at 105 C. Beginning 52 days after seeding, storage roots were graded for economic quality (percent of carrots deformed beyond fresh-market use). Before that date, economic analysis was based on the location and number of galls on the primary root.

Growth analyses of the whole plant in response to the environment and effects of *Meloidogyne hapla* infection were expressed in terms of the net assimilation rate (NAR), leaf-area ratio (LAR), and relative growth

rate (RGR). NAR (13) is the dry-weight increase of the plant in relation to the unit leaf area in relation to time [NAR = $(W_2 - W_1/T_2 - T_1)$ $(\ln L_2 - \ln L_1/L_2 - L_1)$], where L = leaf area ($cm^2$), T = time (days), W = plant dry weight (g), and ln = natural log = 2.7181. LAR (13) is the ratio of leaf area to dry weight of leaves [LAR = $L_1 + L_2/W_1 + W_2$]. RGR (13) is the increase in plant weight per unit of original weight over a given unit of time [RGR = $\ln W_2 - \ln W_1/T_2 - T_1$]. The experiment was not repeated. The curvilinear relations used to illustrate the various growth parameters were selected to best represent the nature of each biological phenomenon.

RESULTS

Shoot system: Shoot emergence in the presence or absence of *M. hapla* occurred by the eighth day after seeding. Infection (herein referring to *M. hapla)* retarded (P = 0.05) elongation of the shoot system between 12 and 52 days after planting. The maximum height of Spartan Premium uninfected carrots *M. hapla* was 47.1 cm (84 days after planting), whereas in the presence of *M. hapla* the maximum height was 44.8 cm (96 days after planting). Infection did not decrease (P = 0.05) the number of leaves. Uninfected mature carrots, however, had a mean of 10 leaves per plant, whereas infected carrots had a mean of 8.4 leaves.

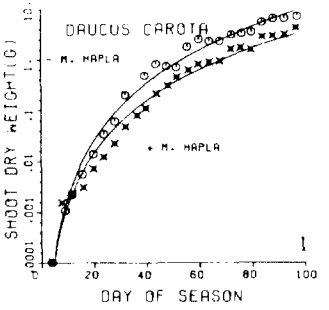
In the presence of *M. hapla* the shoot growth of Spartan Premium carrots was 48% less than that of the controls, and was inhibited (P = 0.05) from day 16 through day 88 (Fig. 1). The trend was the same for shoot fresh weight. The maximum average shoot fresh weights were 31 gm on day 84 for the nematode-free plants and 23 gm on day 96 for the infected carrots. Shoot surface area was 41% less for diseased mature plants than for plants grown in uninfested soil. This retardation (P = 0.05) was observed 12 days after seeding and continued through 88 days after seeding (Fig. 2).

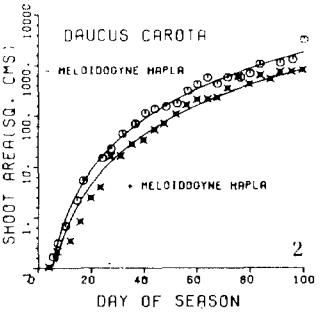
Root system: Healthy Spartan Premium carrots were marketable (about 70 gm) 76-80 days after seeding. Infected carrots did not reach that weight until 96 days after seeding. Carotene (orange appearance) was present by day 36 in uninfected carrots but not until day 44 in infected carrots. There was a steady increase in taproot fresh weight from day 36 to 88. It continued until day 96 for the infected carrots. The infected carrots were forked and occasionally had hairy root symptoms. Only 58% of the infected carrots analyzed during the first 52 days after seeding were potentially marketable. For days 52 through 100, 41% of the carrots analyzed were deformed beyond fresh-market use. Only 3% of all of the control carrots were unmarketable.

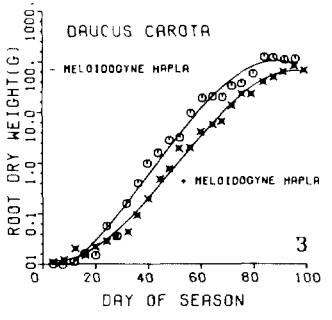
During the first 12 days after planting, infected seedlings grew more rapidly (P = 0.05) than the controls (Fig. 3). On day 16, the infected and uninfected carrots were about equal in root dry weight. From days 32 through 100, dry weight was less (P = 0.05) for infected carrots than for healthy carrots. The fresh weight of the root system followed a different trend. *M. hapla* retarded (P = 0.05) growth from days 24 through 96. The steady increase in fresh weight was observed through day 84 for the uninfected carrots and through day 96 for the infected carrots. The maximum weight of the uninfected carrots was 107 gm of roots, while the infected carrots reached a maximum of 72.2 gm of roots. Root area of healthy carrots increased for the first 88 days. *M. hapla* retarded (P = 0.05) root area from days 16 to 96 (Fig. 4).

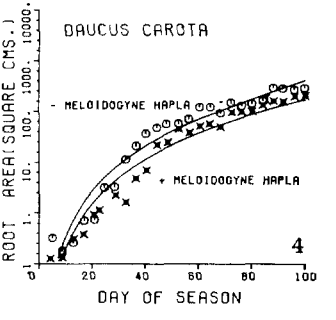
Germination occurred four days after seeding. Second-order roots were not present until after 8 days in infested soil but developed in 4 days in uninfested soil. Third-order roots were present on day 16 for both the infected and uninfected carrots. Fourth-order roots were first observed 28 days after seeding in uninfected carrots, and on day 32 in infected carrots. Fifth-order roots were first noted on days 40 and 44 in the uninfected and infected carrots, respectively. Sixth-order roots were present on uninfected plants by the 48th day, whereas infected carrots developed sixth-order roots, 64, 68, 76, and 80 days after seeding.

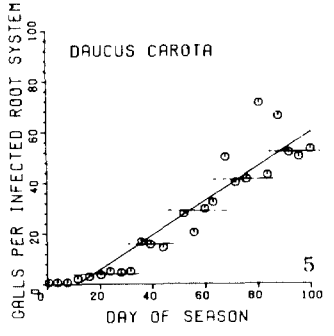
The number of roots per system increased rapidly for the first 40 days after seeding, and then more gradually. The maximum number of roots was estimated at 7,500 per plant on nematode-free carrots, and at ca 4,200 on infected carrots (Table 1). The estimated total lengths of healthy

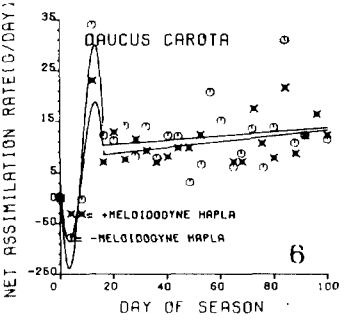

DAUCUS CAROTA
- M. HAPLA
+ M. HAPLA
SHOOT DRY WEIGHT(G)
DAY OF SEASON
1

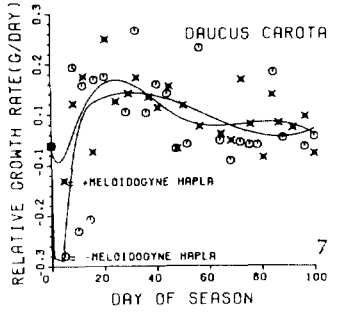

DAUCUS CAROTA
- MELOIDOGYNE HAPLA
+ MELOIDOGYNE HAPLA
SHOOT AREA(SQ. CMS)
DAY OF SEASON
2

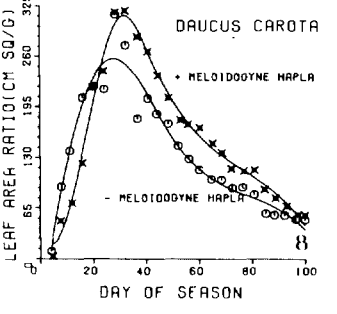

DAUCUS CAROTA
- MELOIDOGYNE HAPLA
+ MELOIDOGYNE HAPLA
ROOT DRY WEIGHT(G)
DAY OF SEASON
3


DAUCUS CAROTA
- MELOIDOGYNE HAPLA
+ MELOIDOGYNE HAPLA
ROOT AREA(SQUARE CMS.)
DAY OF SEASON
4


DAUCUS CAROTA
GALLS PER INFECTED ROOT SYSTEM
DAY OF SEASON
5


DAUCUS CAROTA
+MELOIDOGYNE HAPLA
-MELOIDOGYNE HAPLA
NET ASSIMILATION RATE(G/DAY)
DAY OF SEASON
6


DAUCUS CAROTA
+MELOIDOGYNE HAPLA
-MELOIDOGYNE HAPLA
RELATIVE GROWTH RATE(G/DAY)
DAY OF SEASON
7


DAUCUS CAROTA
+ MELOIDOGYNE HAPLA
- MELOIDOGYNE HAPLA
LEAF AREA RATIO(CM SQ/G)
DAY OF SEASON
8

and infected root systems were respectively 13,000 and 6,500 cm. The number of roots of each order increased rapidly during the first 36-40 days after seeding. After day 40, there was a slow increase in the number of 2nd-, 3rd-, and 4th-order roots and in the occurrence of 5th- and 6th-order roots. The number of roots on a mature 100-day-old plant was greatest for 4th-order roots and least for 6th-order roots, ranging from 4,200 to 10 per order for nematode-free plants and 2,200 (3rd-order) to 39 per order for infected plants (Table 1). The total length of roots for each order followed the same trend as the number of roots. Infected carrots had less total root length for each order except for the 5th- and 6th-order roots. The estimated lengths of roots for 100-day-old root systems of uninfected carrots ranged from 7,500 cm for 3rd-order roots to 3.1 cm for 6th-order roots. Infected carrots had shorter total root length, ranging from 3,800 cm for 3rd-order roots to 20.8 cm for 6th-order roots (Table 1).

The number of *M. hapla*-induced galls on the root systems increased throughout the 100 days of growth (Fig. 5). Five levels of gall densities were observed: $\bar{X}$ = 5 galls per plant from days 20 to 32, 17 galls per plant on days 36 to 48, 30 galls per plant on days 52 to 64, 45 galls per plant on days 72 to 84, and 52 galls per plant on days 92 to 100.

Carrot plant: Plant surface area was less ($P = 0.05$) from days 4 through 88 for infected carrots than for uninfected carrots. *M. hapla* retarded ($P = 0.05$) plant growth from days 32 through day 96. These data were used to estimate NAR, LAR, and RGR. The NAR of plants grown in the nematode-free environment decreased, followed by a rapid increase through the 12th day after seeding (Fig. 6). The NAR was close to equilibrium from days 16 to 100. Infected carrots followed the same trend with slightly lower rates. The RGR of infected carrots declined, increased through 36 days after planting, and then decreased gradually (Fig. 7). Uninfected carrots grown had a greater initial decrease in RGR, followed by an increase, and then a gradual decrease. The LAR of carrots increased rapidly initially through day 28 in steamed soil and through day 32 in infested soil, followed by a decrease as the carrot matured (Fig. 8).

DISCUSSION

Healthy 'Spartan Premium' carrots matured rapidly and were marketable 76-80 days after seeding, reaching senescence after 92 days. Carrots infected by *M. hapla* were delayed in maturity and had a slower growth, as well as deformed tap roots, root galling, and proliferation of 5th- and 6th-order roots. Delayed maturity was associated with an overall smaller plant surface area for nutrient, water, or light absorption. Fresh weight and dry weight indicated retarded growth. *M. hapla* gall formation on the root systems was an important factor in reducing the plant growth potential. Delayed maturity represented a potential economic loss in early-season market prices.

The LAR indicated that infected carrots

FIG. 1-8. Influence of *Meloidogyne hapla* (Mh) on the growth of *Daucus carota* cv. 'Spartan Premium.' Each point represents the mean of four plants.

1. Dry weight (gm) of shoot systems of Mh-infected plants ($\text{Log } Y = 1.386 \ln X - 5.88$, $R^2 = 0.93$) and controls ($\text{Log } Y = 1.487 \ln X - 5.93$, $R^2 = 0.97$).

2. Area (cm^2) of shoot systems of Mh-infected plants ($\text{Log } Y = 1.44 \ln X - 3.68$, $R^2 = 0.97$) and controls ($\text{Log } Y = 1.43 \ln X - 3.37$, $R^2 = 0.97$).

3. Dry weight (gm) of Mh-infected carrot roots ($\text{Log } Y = 1.47 \ln X - 5.47$, $R^2 = 0.80$) and controls ($\text{Log } Y = 1.70 \ln X - 5.95$, $R^2 = 0.86$).

4. Area (cm^2) of Mh-infected roots ($\text{Log } Y = 1.25 \ln X - 2.51$, $R^2 = 0.93$) and controls ($\text{Log } Y = 1.25 \ln X - 2.25$, $R^2 = 0.92$).

5. Root-knot galls per root system (R^2 for straight line = 0.87, $P = 0.05$).

6. Net assimilation rate (gm/day) of Mh-infected plants and controls, with cubic spline fitting routine used to construct the curves for days 0 to 16 (two third-degree equations and four coefficients for each curve). Regressions for Mh-infected plants for days 16 to 100 ($Y = 9.75 + 0.01X$, $R^2 = 0.01$) and controls ($Y = 8.06 + 0.04X$, $R^2 = 0.03$).

7. Relative growth rate (gm/day x 10^{-1}) of Mh-infected and control carrot plant, using cubic spline fitting routine to construct the curves (five third-degree equations and four coefficients per curve).

8. Leaf area ratio (cm^2/gm) of Mh-infected carrot plants (Days 0-36, $Y = 209.78 \ln X - 3.65{,}98$, $R^2 = 0.90$; days 36-100, $Y = 267.01 \ln X + 12.95$, $R^2 = 0.98$) and controls (days 0-28, $Y = 165.62 \ln X - 216.75$, $R^2 = 0.95$; Days 32-100, $Y = 209.88 \ln X + 1015.39$, $R^2 = 0.94$).

TABLE 1. Number, length, and root orders of Spartan Premium carrots after 100 days of growth in nematode-free and *Meloidogyne hapla*-infested organic field soil.

Root system	Roots per plant (root length, cm)					
	2nd order	3rd order	4th order	5th order	6th order	total
Uninfected	140(1,900)	3,100(7,500)	4,200(2,100)	220(130)	10(3.1)[a]	7,500(13,000)
Infected	110(1,300)	2,200(3,800)	1,600(1,100)	190(140)	39(20.8)[b]	4,200(6,500)

[a]Observed only 48 days after seeding.
[b]Observed only 64, 68, 76, and 80 days after seeding.

matured later and had less growth potential than healthy carrots. Infected carrots had a greater LAR, indicating a lower photosynthetic rate than uninfected carrots. The initial rapid increase in LAR of the uninfected carrots reflected a rapid change in plant weight.

The NAR indicated an initial utilization of seed reserves (days 0 to 4), followed by a rapid increase in NAR as the basic plant structures were formed. A rapidly increasing NAR continued through the time of radicle emergence, shoot emergence, secondary root initiation, and appearance of the cotyledon and first true leaf. As the carrot matured, an equilibrium was observed between the increase in plant weight and the shoot area. There was a decrease in NAR after maturity as the plant gradually began to senesce. Infected carrots followed the same trend, although NAR values were lower. The RGR reflected the same plant development trends as NAR. The gradual decline was more evident, however, in the RGR. This continuous decline with the development of the tap root was more gradual for infected plants with the delayed maturity and reduced growth rate.

The root system of Spartan Premium carrots was complex, with up to six orders of roots. There was an initial period of rapid increase of secondary root development, and then a steady, slower increase for the remaining days studied. Sixth-order roots were mainly the result of root proliferation near galls caused by *M. hapla*. The longer 5th-order roots on infected than on uninfected root systems was also probably indicative of root proliferation caused by *M. hapla*. The number of arrangement of the length of total roots of each order followed a pattern in the infected and uninfected carrots. There were more 3rd- and 4th-order roots than any other orders.

It appeared that the number of root galls present could be used as an indicator of the length of the life cycle of *M. hapla*. There was an increasing trend in the number of galls ($R^2 = 0.87$ for a straight line, $P = 0.05$), with five different levels of galling observed. Galls apparently induced by the initial population of *M. hapla* were formed during the first 32 days after seeding. By 36 days after planting there was a distinct increase in the number of galls present, indicating that hyperplastic symptoms had been induced by second-generation second-stage larvae. Increases in the number of galls per root system continued throughout the experiment at 16-to-20-day intervals.

The overall growth and development of Spartan Premium carrots was similar to that described by Phan and Hsu (17). Cultivar differences were that shoot height increased more slowly in Spartan Premium carrots, although to a greater total height (15-20 cm), than the cultivar studied by Phan and Hsu. Root development coincided with their observations. The phases of growth observed by Esau (12) and Havis (14) were also distinctly visible in the RGR and NAR growth analyses. It appeared, however, that a third growth phase could easily be added to indicate the time of initiation of taproot enlargement. The three phases of growth for Spartan Premium carrots would be days 0 to 4, 4 to 16, and 16 to maturity (ca 76-80 days after seeding).

The percent moisture in the Spartan Premium carrots was similar to Watt and Merill's (23) estimation of 88.2%, with respective moisture values of 88.6 and 89.7 for the uninfected and infected carrots. The overall development of infected and uninfected carrots grown in organic soil indicated a significant growth retardation 32 to 88 days after seeding, reflecting

symptoms typical of infection caused by *M. hapla*.

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