

The Development and Influence of *Meloidogyne incognita* and *M. javanica* on Wheat¹

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Abstract: The effects of soil temperature and initial inoculum density (P_i) of *Meloidogyne incognita* and *M. javanica* on growth of wheat (*Triticum aestivum* cv. Anza) and nematode reproduction were studied in controlled temperature baths in the glasshouse. Nematode reproduction was directly proportional to temperature between 14 and 30 C for *M. incognita* and between 18 and 26 C for *M. javanica*. Reproduction rates (P_f/P_i , where P_f = final number of eggs) for P_i 's of 3,000, 9,000, and 30,000 eggs/plant were greatest at each temperature when $P_i = 3,000$. Maximum *M. incognita* reproduction rate ($P_f/P_i = 51.12$) was at 30 C. At 26 C, *M. javanica* reproduction ($P_f/P_i = 14.82, 9.02, \text{ and } 4.23$ for $P_i = 3,000, 9,000, \text{ and } 30,000$, respectively) was about half that of *M. incognita* when $P_i = 3,000$ or 9,000 but similar when $P_i = 30,000$. Reproduction of both species was depressed between 14 and 18 C. Shoot and root growth and head numbers were inversely related to soil temperature between 14 and 30 C but were not affected by the P_i of *M. incognita* when 7 d old seedlings were inoculated. When newly germinated seedlings were inoculated with *M. incognita* or *M. javanica*, the P_i did not affect shoot and root fresh weights, shoot/root ratio, and tillering, but it did reduce root dry weight (*M. javanica* at 26 C) and increase shoot dry weight (*M. incognita* at 18-22 C). The optimum temperature range is lower for wheat growth than for nematode reproduction. Wheat cv. Anza is a good host for *M. incognita* and *M. javanica*, but it is tolerant to both species. **Key words:** temperature, root-knot nematodes, tolerance, population dynamics.

Recent studies have shown that *Meloidogyne incognita* (Kofoid and White) Chitwood can invade, develop, and reproduce on winter grown bread wheat (*Triticum*

aestivum (L.) Thell) under field conditions in southern California (11). Winter reproduction on wheat increased egg and juvenile populations in the soil in spring compared to winter fallowing, but it did not significantly affect grain yield (11). In southern California, *M. incognita* juveniles penetrated wheat roots in the autumn only when

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soil temperature was above 18 C (11). Nematode development and reproduction, however, can occur at temperatures as low as 10 C (11,17,18,21). In mild winter regions, 18–25 C soil temperatures occur only during the seedling and maturation stages of the crop (11,20). Glasshouse host range tests indicate that *M. incognita* and *M. javanica* (Treub) Chitwood can reproduce on many commercial cultivars of durum (*T. turgidum* L. var. *durum* Desf.) and bread wheat (3,7,12,17, and Roberts, unpublished data), although the reproduction rates (14) were not assessed. The influence of root penetration, development, and reproduction of these *Meloidogyne* spp. on the growth of wheat in the glasshouse or in the field has not been previously reported.

The purpose of these studies was to determine: (i) the ability of *M. incognita* and *M. javanica* to reproduce on wheat, (ii) the effect of nematode reproduction at different initial inoculum densities on wheat growth, and (iii) the influence of temperature on these host-parasite interactions in order to maximize the use of winter grown wheat as a management tactic for reducing *Meloidogyne* populations.

MATERIALS AND METHODS

Southern California populations of *M. incognita* and *M. javanica* were cultured from single egg masses on 'Tropic' tomato (*Lycopersicon esculentum* Mill.) plants grown in pots in the glasshouse. Plants received a weekly application of 20 cm³/plant of full strength Hoagland's complete nutrient solution (5). Eggs were extracted from mature tomato plants by macerating roots in NaOCl solution (6). Egg suspensions were prepared in tap water to enable the desired inoculum density to be added in 5 cm³ of water per plant.

T. aestivum cv. Anza seed was surface sterilized by soaking for 20 min in 1% NaOCl:95% ethanol, (79:21; v/v), rinsed three times in sterile water, and germinated at 26 C on moist filter papers in petri dishes. When the hypocotyls emerged, seedlings were planted singly 2 cm deep in 7.5-cm-d plastic cups containing 280 cm³ of steam-sterilized blow-sand (92.4% sand, 3.9% silt, and 3.7% clay). Plants were supplemented weekly with 10 cm³/plant of full

strength Hoagland's complete nutrient solution.

Experiment 1: Cups containing 7-d-old seedlings were inoculated with 5 cm³ of water containing 0, 3,000, 9,000, or 30,000 *M. incognita* eggs by injecting the suspension at mid soil depth. Plants were maintained in the glasshouse with ambient temperature between 21 and 30 C for 8 d and then buried to their cup rims in 21-cm-d plastic buckets containing steam-sterilized blow sand, four cups per bucket, one of each inoculum density. Eight buckets were transferred to 14, 18, 22, 26, or 30 C controlled-temperature baths in the glasshouse. Plants were harvested 78 d after inoculation. Wheat heads were counted, and plant tops were cut off at the soil surface, weighed, dried in a forced-air oven at 70 C for 24 h, and reweighed. Root systems were washed free of soil, damp dried in paper towels, and weighed. Roots of control plants were air dried as for tops and reweighed. Nematode inoculated root systems were stored in 10% formalin, and eggs were extracted by the NaOCl technique (6) and counted. Dry weights of inoculated root systems were estimated from fresh weights using the ratio of fresh weight/dry weight of control plants at the same temperature.

Experiment 2: Cups containing steam-sterilized blow sand were buried to their rims in buckets as described above and maintained at 18, 22, or 26 C in controlled-temperature baths. When the soil in the cups reached the required temperature, each cup was inoculated with 5 cm³ of tap water containing 0, 3,000, 9,000, or 30,000 *M. incognita* or *M. javanica* eggs. Three days later, newly germinated Anza seedlings were transplanted as described above into the nematode infested cups. Ambient temperature ranged from 21 to 32 C. Plants were harvested 64 d after inoculation, and tops and roots were processed for plant growth data and nematode egg counts as in experiment 1.

RESULTS

Experiment 1: *M. incognita* developed and reproduced at all initial inoculum levels (Pi) and temperatures (Table 1). Pi, temperature, and the interaction of Pi and temperature all significantly ($P = 0.01$) af-

Table 1. Reproduction, based on the ratio of final egg numbers (Pf)/inoculum density (Pi) of *M. incognita* on Anza wheat as affected by Pi on 7-d-old seedlings and temperature.

Pi	Egg Pf/Pi				
	14 C	18 C	22 C	26 C	30 C
0	0 a*	0 a	0 a	0 a	0 a
3,000	0.03 a	4.99 abc	18.33 e	33.16 f	51.12 g
9,000	0.02 a	2.23 a	10.82 cd	19.62 e	16.86 de
30,000	< 0.01 a	1.16 a	4.02 ab	9.22 bc	6.27 abc

Data are means of eight replicates.

*Means followed by same letter not significantly different ($P = 0.01$) according to Duncan's multiple-range test of Pi \times temperature interaction.

Effect of Pi significant at $P = 0.01$.

Effect of temperature significant at $P = 0.01$.

affected nematode reproduction. Reproduction rate (final egg numbers [Pf]/Pi) was greatest at each temperature when Pi was 3,000 eggs and was positively correlated with temperature at this Pi. The greatest Pf/Pi value was 51.12 at 30 C. At Pi's of 9,000 and 30,000, Pf/Pi was greatest at 26 C and slightly less at 30 C. Reproduction was depressed at 14 C at all Pi's with Pf/Pi < 1 (i.e., below the equilibrium density or maintenance density when Pf = Pi).

Soil temperature significantly ($P = 0.01$) affected shoot and root growth and production of wheat heads (Table 2). Shoot and root weights and head numbers were all inversely related to temperature, and the greater decrease in root than shoot growth at higher temperature is indicated by an increased shoot/root ratio.

M. incognita Pi had no effect on head production at each temperature, and the interaction of Pi and temperature was not significant. Similarly, shoot and root fresh and dry weights were unaffected by Pi, even at 30,000 eggs/pot at 26 and 30 C when *M. incognita* reproduction was optimal for the test. Therefore, shoot/root ratios were not significantly different due to Pi at each temperature (Table 2).

Experiment 2: M. incognita on newly germinated Anza seedlings reproduced at 18, 22, and 26 C at all Pi's (Table 3). However, reproduction was less than that observed in the first experiment at the corresponding Pi and temperature. *M. incognita* reproduction was significantly ($P = 0.01$) affected by Pi, temperature, and the interaction of Pi and temperature. At each temperature, reproduction rate was greatest

when Pi = 3,000. Reproduction rate was greatest at 26 C. At 22 C, Pf/Pi > 1 for Pi's of 3,000 and 9,000 but < 1 for Pi of 30,000. Pf/Pi < 1 at 18 C.

M. javanica reproduced at all Pi's at 18 and 26 C (Table 3), and reproduction was significantly ($P = 0.01$) affected by Pi, temperature, and the interaction of Pi and temperature. Maximum reproduction occurred at a Pi of 3,000 at 26 C. Pf/Pi < 1 at 18 C and > 1 at 26 C.

At 26 C, *M. incognita* reproduction was approximately twice that of *M. javanica* at Pi's of 3,000 and 9,000 but similar at a Pi of 30,000 (Table 3).

Shoot and root growth and tillering were significantly affected by temperature as indicated by control plants in *M. incognita* tests (Tables 4 and 5), although growth differences were generally smaller in this experiment than in the first experiment (terminated 2 wk later at 78 d). Shoot and root growth were greater at 22 C than at 18 or 26 C in *M. incognita* tests (Table 4), which may be due in part to less shading in the 22 C temperature bath that contained fewer plants/unit area. Analysis of variance showed no significant differences in tillering, root growth, and shoot/root ratio due to either *M. incognita* reproduction at different Pi's or to the interaction of Pi and temperature (Table 5), supporting the results of the first experiment. Shoot fresh weights were not significantly affected by Pi or the interaction of Pi and temperature. At 18 and 22 C shoot dry weight was significantly ($P = 0.05$) higher when Pi was 9,000 or 30,000 eggs/plant than 0 or 3,000 eggs/plant, but not at 26 C when nematode re-

Table 2. The influence of *M. incognita* inoculum density (Pi) and temperature (T) on seed head production, and shoot and root growth of Anza Wheat.

Pi (eggs)	14 C	18 C	22 C	26 C	30 C	Mean
Number of heads						
0	7.9	8.3	6.8	5.8	4.9	6.7
3,000	8.1	6.9	7.0	6.3	4.4	6.5
9,000	8.5	7.6	7.3	5.8	5.4	6.9
30,000	8.0	7.8	7.0	6.1	4.9	6.8
Mean*	8.2 a	7.6 ab	7.0 b	6.0 c	4.9 d	6.7
Root fresh wt. (g)						
0	7.8	6.6	4.6	2.9	2.4	4.8
3,000	6.7	6.3	4.0	2.4	1.6	4.2
9,000	8.2	6.8	4.1	2.7	2.1	4.8
30,000	8.4	6.0	4.1	3.1	2.0	4.7
Mean*	7.8 a	6.4 a	4.2 b	2.8 bc	2.0 c	4.6
Root dry wt. (g)						
0	2.1	1.6	1.2	0.8	0.5	1.2
3,000	1.8	1.7	1.1	0.6	0.3	1.1
9,000	2.2	1.8	1.1	0.7	0.4	1.2
30,000	2.3	1.6	1.1	0.8	0.4	1.2
Mean*	2.1 a	1.7 a	1.1 b	0.7 bc	0.4 c	1.2
Shoot dry wt. (g)						
0	3.9	4.9	3.3	2.0	1.5	3.2
3,000	3.6	3.6	3.3	2.0	1.3	2.8
9,000	3.7	4.1	3.8	1.9	1.4	3.0
30,000	3.5	3.5	3.9	1.9	1.2	2.8
Mean*	3.7 a	4.1 a	3.7 a	1.9 b	1.4 b	3.0
Shoot/root dry wt. ratio						
0	2.1	3.2	3.5	3.0	3.6	3.1
3,000	2.1	2.3	3.7	3.3	4.6	3.2
9,000	1.9	2.5	3.7	2.8	3.3	2.8
30,000	1.8	2.4	3.9	2.4	3.2	2.7
Mean*	1.9 a	2.6 ab	3.7 c	2.9 bc	3.7 c	3.0

Data are means of eight replicates.

*Temperature means for each growth character followed by same letter are not significantly different ($P = 0.01$) according to Duncan's multiple-range test.

Analysis of variance: Pi—significant ($P = 0.05$) for all growth characters. Interaction of Pi \times T—not significant ($P = 0.05$) for all growth characters. T—significant ($P = 0.01$) for all growth characters.

production was greatest.

M. javanica Pi did not significantly affect tiller production at 26 C when *M. javanica* reproduction rate was high (Tables 3 and 4), although significant increase ($P = 0.01$) in tillering was recorded due to increased Pi at 18 C (Tables 4 and 5). *M. javanica* Pi and reproduction did not significantly promote or restrict shoot growth at 18 and 26 C. Root dry weight was higher ($P = 0.01$) in noninoculated *M. javanica* controls at 26 C than in the other seven *M. javanica* Pi and temperature interactions, which were not significantly different (Tables 4 and 5). A

comparison of root fresh and dry weights of the *M. javanica* and *M. incognita* noninoculated control plants at 26 C indicates that the *M. javanica* control roots were not completely dried down. *M. javanica* Pi and the interaction of Pi and temperature did not significantly affect shoot/root ratios (Tables 4 and 5).

M. incognita and *M. javanica* development and reproduction at 26 C did not differentially affect tillering, shoot and root growth, and shoot/root ratio, although the interaction of nematode species and Pi was significant ($P = 0.01$) on root growth and

Table 3. Reproduction, based on the ratio of final egg numbers (Pf)/inoculum density (Pi), of *M. incognita* and *M. javanica* on Anza wheat as affected by inoculum density (Pi) on newly germinated seedlings (experiment 2) and temperature.

	Egg Pf/Pi		
	18 C	22 C	26 C
<i>M. incognita</i> Pi			
0	0 a*	0 a	0 a (a)†
3,000	0.04 a	2.96 a	31.72 c (c)
9,000	0.02 a	1.27 a	18.53 b (b)
30,000	0.01 a	0.78 a	4.68 a (a)
<i>M. javanica</i> Pi			
0	0 a‡		0 a (a)
3,000	0.07 a		14.82 d (b)
9,000	0.02 a		9.04 c (ab)
30,000	0.01 a		4.23 b (a)

Data are means of six replicates.

*Means for *M. incognita* followed by same letter not significantly different at $P = 0.01$ according to Duncan's multiple-range test.

†Means for *M. incognita* and *M. javanica* at 26 C followed by same letter in parentheses not significantly different at $P = 0.01$ according to Duncan's multiple-range test.

‡Means for *M. javanica* followed by same letter not significantly different at $P = 0.01$ according to Duncan's multiple-range test.

shoot/root ratio due to the higher root dry weights of *M. javanica* controls as described above.

DISCUSSION

Seinhorst (15) determined host status by the values of the equilibrium density (E, where $Pf = Pi$) and the maximum rate of reproduction (the maximum Pf/Pi ratio). Plants are good hosts if both values are high, poor hosts if both are low, and the values will be influenced by external or environmental conditions for any plant and nematode combination (15). High reproduction rates and predicted equilibrium density values for *M. incognita* and *M. javanica* at soil temperatures optimum for nematode reproduction (26–30 C) over the temperature range tested confirm that 'Anza' wheat is a good host for both species. The reproduction rates on wheat are comparable to *M. incognita* reproduction on susceptible soybean (9) and to observed reproduction rates for a range of endoparasitic and ectoparasitic nematodes reproducing on good hosts (15).

Meloidogyne reproduction was greatly affected by soil temperature and by initial inoculum density. Following a pretreatment of 21–30 C for 8 d to stimulate hatch and penetration into roots, *M. incognita* reproduced at all temperatures from 14 to 30 C, although reproduction rate was depressed at 14–18 C and greatest at 26–30 C. *M. javanica* reproduction rates were high at 26 C, although about half that of *M. incognita* at the lower Pi's, and were depressed at 18 C (Table 3), indicating that temperature requirements for good reproduction on wheat are similar to those for reproduction on other hosts; for example, *M. incognita* and *M. javanica* reproduce optimally on tomatoes at 25–35 C (2,4). Poor reproduction at 18 C in experiment 2 probably resulted from reduced egg hatch and motility of second-stage juveniles in soil that restricted the number of juveniles penetrating into roots. However, the 12,300 heat units (centigrade degree hours above a basal temp of 10 C) that had accumulated during the test period were enough, based on previous estimates (8,18,21), to allow development and egg production by nematodes that entered the roots. *M. incognita* migration through soil toward tomato roots (10) and penetration of field grown wheat roots in southern California is restricted below 18 C (11).

Meloidogyne reproduction rates were inversely related to initial inoculum density (Tables 1 and 3). Competition for adequate feeding sites is less at low Pi, allowing a greater proportion of juveniles to become adult females (4,14). As Pi increases, competition increases and a smaller proportion of the inoculum will develop successfully in roots; the equilibrium density is reached when $Pf = Pi$, after which further increases in Pi produce reproduction rates < 1 (14). The lack of significant plant growth reduction due to Pi (Tables 2, 4, and 5) indicates that Anza wheat is tolerant to *M. incognita* and *M. javanica* attack under controlled glasshouse conditions, even when seedlings are challenged from germination onward with high Pi's at soil temperature optimal for nematode penetration and reproduction. Shoot growth was not stimulated at the lowest Pi of 3,000 eggs/plant, although growth stimulation by low *M. javanica* inoculum

Table 4. The Influence of *M. incognita* and *M. javanica* inoculum density (Pi) and temperature (T) on tiller production, and shoot and root growth of Anza Wheat.*

Pi (eggs)	<i>M. incognita</i>				<i>M. javanica</i>		
	18 C	22 C	26 C	Mean	18 C	26 C	Mean
	Tiller (no.)						
0	4.5	5.5	3.7	4.6	3.3	3.8	3.6
3,000	5.8	5.2	3.7	4.9	4.7	3.0	3.8
9,000	4.2	4.3	3.7	4.1	6.0	2.7	4.3
30,000	4.3	4.5	3.8	4.2	5.8	3.5	4.7
Mean	4.7	4.9	3.7	4.5	5.0	3.3	4.1
	Root fresh wt. (g)						
0	5.6	9.0	6.5	7.0	5.4	6.4	5.9
3,000	6.4	7.6	5.8	6.6	5.8	4.8	5.3
9,000	6.7	8.6	6.3	7.2	6.3	4.7	5.5
30,000	5.9	8.1	6.2	6.7	6.1	4.6	5.4
Mean	6.1	8.3	6.2	6.9	5.9	5.1	5.4
	Root dry wt. (g)						
0	1.3	2.7	1.0	1.7	0.9	1.8	1.4
3,000	1.2	2.2	1.3	1.5	1.1	1.1	1.1
9,000	1.3	2.5	1.4	1.7	1.2	1.1	1.1
30,000	1.1	2.3	1.4	1.6	1.2	1.0	1.1
Mean	1.2	2.4	1.3	1.6	1.1	1.2	1.2
	Shoot dry wt. (g)						
0	2.3	3.4	3.0	2.9	3.1	2.9	3.0
3,000	2.3	3.2	2.9	2.8	2.4	2.7	2.6
9,000	3.5	4.8	2.9	3.7	3.1	2.5	2.8
30,000	3.5	4.2	2.7	3.4	2.7	2.7	2.7
Mean	2.9	3.9	2.9	3.2	2.8	2.7	2.8
	Shoot/root dry wt. ratio						
0	2.2	1.4	3.1	2.3	3.2	1.8	2.5
3,000	2.0	1.5	2.3	1.9	2.2	2.6	2.4
9,000	2.7	2.1	2.2	2.3	2.6	2.5	2.5
30,000	3.2	1.8	2.0	2.3	2.3	2.8	2.6
Mean	2.6	1.7	2.4	2.2	2.6	2.4	2.5

Data are means of six replicates.

*See Table 5 for results of analysis of variance on Anza wheat growth.

densities does occur in some, but not all, host plants (22). Also, increase in root weight with increased *Meloidogyne* Pi, which occurs on plants that develop extensive root galls (22), did not occur on wheat in response to either *M. incognita* or *M. javanica*, presumably because galls were small or absent on infected roots. Tolerance prevents or decreases the plant growth reduction and increased feeding site competition that is usually associated with nematode attack at densities above the tolerance or damage threshold on intolerant hosts (13,16). Therefore, reproduction rates and E values are likely to be higher on tolerant good hosts, such as wheat, than on intolerant hosts.

Wheat growth is inversely related to soil temperature resulting in submaximal plant growth at temperatures optimal for nematode reproduction, so competition for feeding sites will increase with temperature because root system growth is reduced. At low Pi, the temperature effect of reducing wheat growth does not influence *M. incognita* reproduction, and maximum rates are recorded at 30 C on the smallest plants (Table 1). However, at higher Pi's, reproduction rate is optimum at 26 C and decreases at 30 C, presumably due to the limitation of smaller root systems (Table 1). In temperate zone crops such as cereals, a warm climate shortens the period of development without sufficient compensation

Table 5. Summary of analysis of the influence of *M. incognita* and *M. javanica* inoculum density (Pi) and temperature (T) on several growth characters of Anza wheat (Table 4).

Variable	Growth character					
	Tillers	Root fresh wt.	Root dry wt.	Shoot fresh wt.	Shoot dry wt.	Shoot/root ratio
<i>M. incognita</i>						
T	5%* (0.97)	1%† (1.31)‡	1% (0.50)	5% (2.35)	5% (0.85)	5% (0.64)
Pi	NS§	NS	NS	NS	5% (0.70)	NS
Pi × T (interaction)	NS	NS	NS	NS	NS	NS
<i>M. javanica</i>						
T	5% (1.31)	NS	NS	NS	NS	NS
Pi	NS	NS	5% (0.22)	NS	NS	NS
Pi × T (interaction)	1% (1.80)	1% (1.34)	1% (0.43)	NS	NS	NS

*Significant difference at $P = 0.05$.†Significant difference at $P = 0.01$.‡Numbers in parentheses represent LSD at the respective level of P .

§No significant difference.

by faster growth, resulting in smaller plants than in a cool climate (19). The inverse relationship of wheat growth and temperature are shown by noninoculated controls (Tables 2 and 4). The increase in shoot/root ratio with temperature that is common for cereals (19) indicates a greater emphasis on shoot growth at higher temperature. In subtropical plants, such as corn and beans, the growth rate is stimulated by warm conditions so that plants grow larger despite a short growth period (19). Thus, tolerant subtropical host plants should facilitate the highest reproduction rates and E values for *M. incognita* and *M. javanica* at optimal temperature, although this nematode advantage may be lost in intolerant plants such as susceptible soybeans (9) because competition is increased by root damage.

Tolerance of Anza to *M. incognita* and *M. javanica* appears similar to that reported in corn to *M. incognita* (1), with high populations causing no apparent damage. All wheat cultivars so far tested appear to be good hosts for *M. incognita* and *M. javanica*, but whether cultivar differences in tolerance occur has not been determined.

Winter soil temperature promotes wheat growth and limits nematode reproduction, so the soil temperature balance favors host over parasite during the wheat season in warm wheat growing regions (11,20). Thus yield of intolerant cultivars would probably

also be unaffected by *Meloidogyne* reproduction during the winter. However, avoiding nematode reproduction even if the host crop is undamaged is important to a nematode pest management program (11).

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