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Effects of temperature on the duration of the life cycle of a *Meloidogyne incognita* population

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Summary – The generation time and reproduction of *Meloidogyne incognita* was studied under five soil temperatures. The life cycle was completed on tomato between average soil temperatures of 16.2°C and 30.0°C but not at 35.4°C. On the marigold (*Tagetes* hybrid) variety Polynema the life cycle was completed only at 30.0°C. Estimates for the base temperature (T_b) and the required heat sum (S) were 10.1°C and 400°C.day respectively. The thermal time relationship for completion of the life cycle of *M. incognita* is discussed in relation to those of other *Meloidogyne* species.

Résumé – ***Influence de la température sur la durée du cycle biologique d'une population de* Meloidogyne incognita** – La durée du cycle et la reproduction de *Meloidogyne incognita* ont été étudiées à cinq températures. Sur tomate, le cycle peut s'accomplir à des températures moyennes du sol s'étageant de 16,2 à 30,0°C, mais non à 35,4°C. Sur oeillet d'Inde (hybride de *Tagetes* de la variété Polynema), le cycle ne s'accomplit qu'à 30,0°C. La température de base (T_b) et la demande thermique (S) sont estimées à, respectivement, 10,1°C et 400°C/jours. La relation température/temps relative à l'accomplissement du cycle biologique est discutée et comparée au cas des autres espèces du genre.

Keywords – base temperature, development, heat sum, nematode, thermal time, tomato.

Tyler (1933) studied the effects of temperature on the development of an unknown *Meloidogyne* species and was the first to provide a general basis for the thermal-time relationships of nematode development. Between the optimum and lower temperature limits, the rate of development is usually linearly related to the temperature, and the number of heat units (S) above the lower temperature limit (T_b) required for completion of the life cycle is a constant (Garcia-Huidobro *et al.*, 1982). Trudgill and Perry (1994) and Trudgill (1995) reviewed data on the thermal-time relationships for nematodes and noted that the product of T_b and S for completion of the life cycle of *M. hapla* and *M. javanica* was a constant (Trudgill & Perry, 1994).

Information on the thermal-time relationships of plant-parasitic nematodes is necessary to predict geographical distributions, nematode population dynamics and resulting crop yield losses. *M. incognita* is an important plant parasite in (sub)-tropical regions, and in this study data on its thermal-time requirements are presented and compared to data published for other *Meloidogyne* species.

Material and methods

The methods used in this study were similar to those described by Lahtinen *et al.* (1988). A race 3 population of *M. incognita* originally obtained from cotton in the San Joaquin Valley, CA, USA was reared in a greenhouse on tomato cv. Pixie. Species identification was confirmed in a differential host test and by isozyme analysis (Eisenback & Triantaphyllou, 1991). Inoculum was prepared by extraction of eggs from infected tomato roots using 0.5% NaOCl (Ogallo *et al.*, 1997). The resulting egg suspension was left to hatch at 23°C over moist filter paper for 5 days and second stage juveniles (J2) were collected daily and stored at 15°C until use. Plants tested were tomato (*Lycopersicon esculentum*) cv. Pixie and marigold (*Tagetes* hybrid) var. Polynema. For each test plant 25, two-week-old seedlings were transferred to 1 l plastic pots three quarters filled with steam-sterilized sandy soil (93% sand, 4% silt, 3% clay). The pots were placed in a water bath at 25°C, with the level of soil inside the pots lower than the water level outside. The tops of the pots were insulated with polystyrene disks with a hole for the plant

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Table 1. *Number of* Meloidogyne incognita *juveniles collected over time (days after inoculation) at four temperatures. Results are means ± standard error of five tomato plants inoculated with 2000 J2 each. Only results for the first few days of emergence of juveniles are presented here.*

Average temperature (°C)							
16.2		19.5		25.0		30.0	
Days	J2	Days	J2	Days	J2	Days	J2
63	3.3 ± 2.4	39	0 ± 0	25	0 ± 0	20	3.8 ± 2.0
64	5.0 ± 3.0	40	–	26	0 ± 0	21	109.6 ± 41.9
65	6.3 ± 3.5	41	0 ± 0	27	32.4 ± 8.9	22	609.1 ± 132.4
66	5.0 ± 2.5	42	–	28	322.5 ± 77.8	23	1395.0 ± 244.9
67	18.0 ± 9.2	43	0 ± 0	29	956.0 ± 106.1	24	3090.0 ± 745.4
68	22.3 ± 6.9	44	2.6 ± 1.1	30	1992.4 ± 213.8		
69	30.0 ± 16.3	45	7.6 ± 1.6				
		46	33.4 ± 8.4				

stem. Two weeks later the pots were transferred to waterbaths set at 17, 20, 25, 30, and 35°C (five pots per test plant per waterbath). A temperature reader (HOBO, Spectrum Technologies Inc., Plainfield, Ill, USA) set to record the temperature at one-hour intervals was inserted into one pot in each waterbath. Three days later 2 ml of the J2 suspension containing *ca* 2000 J2 were pipetted into four shallow holes close to the plant stem of each pot. Plants were grown and fertilized weekly with a full-strength liquid fertilizer until four days prior to the expected emergence of newly developed J2. Plants were then carefully removed from the pots, the roots were washed with a gentle stream of water and transferred to new similar pots with five 3 mm diam. holes drilled in the bottom of each pot. The pots were carefully three-quarters filled with washed small (*ca* 5 mm diam.) stones, placed inside pots without holes and returned to the waterbaths. To collect newly hatched J2, every day 300 ml of water was added to the inside pot, allowed to percolate through the pot and collected. The collected suspensions were poured over a moist filter paper supported by a small sieve partially submerged in tap water and J2 having moved through the paper over a 16 h period were counted at 40 × magnification. Collection of J2 continued until twice the period of the estimated life cycle or until nematode number decreased to (close to) zero. At the end of the experiments, the temperature readers were removed from the pots and average temperatures were calculated.

Results

Average temperatures in the pots were 16.2, 19.5, 25.0, 30.0 and 35.4°C. At the average temperatures of 16.2°C and 30.0°C, J2 were already found at the first day of collection (day 63 and day 20, respectively). However, numbers were very low and J2 were not recovered from all five replicates (two of five and four of five pots, respectively). During the next few days the numbers increased and J2 were recovered from all five replicates. Thus, it is likely that at these temperatures the first day of collection was at or very close to the time when the life cycle was completed. Therefore, it was concluded that at the average temperatures of 16.2 and 30.0°C it took *M. incognita* 63 and 20 days respectively to complete its life cycle. At temperatures of 19.5 and 25.0°C it took 44 and 27 days respectively to life cycle completion (Table 1). At the highest average temperature (35.4°C) only four J2 were found, which appeared transparent and dead. Collection was stopped 31 days after inoculation and it was concluded that at this temperature the life cycle could not be completed. Collection of juveniles was stopped at day 80 at 16.2°C, at day 86 at 19.5°C, at day 54 at 25.0°C, and at day 40 at 30°C. During these respective periods the average total reproduction was greatest at 25.0°C (56, 617 J2), followed by 30.0°C (48, 882 J2), 19.5°C (38, 406 J2) and 16.2°C (208 J2) although only at the latter temperature was the total number of J2 recovered significantly different from the other three (Duncan's test at $P \leqslant 0.05$). The rate of juvenile hatching from the roots was compared by plotting the logit of the collected J2 against the calcu-

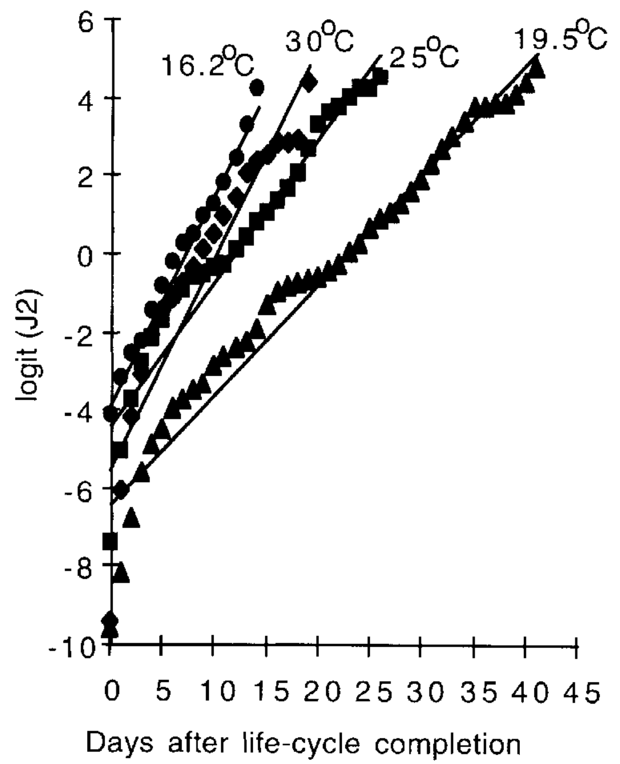

Fig. 1. *The average rate of juvenile emergence from tomato roots ($n = 5$) at four soil temperatures. Logit (J2) is* $\ln[(J2_d/J2_{total})/1-(J2_d/J2_{total})]$*, where* $J2_d$ *is the total number of J2 emerged between the day of life-cycle completion (day = 0) and day = d, and* $J2_{total}$ *is the total number of J2 that emerged during the experimental period.*

lated number of days after completion of the life cycle and fitting a line through the data points (Fig. 1). The rate of juvenile hatching from the tomato roots (indicated by the slope of the fitted lines) appeared highest at 30.0 and 16.2°C, intermediate at 25°C and lowest at 19.5°C.

When plotting the temperature against the rate of development (Fig. 2) and fitting a regression line according to:

$$R = 1/S * T_e - T_b/S$$

where R is the rate of development (day^{-1}), S is required heat sum (°C . day), T_e is the average environment temperature (°C) and T_b is the base temperature through the 30.0, 25.0, 19.5 and 16.2°C data, over 99% of the observed variation was accounted for by the model:

$$R = 0.0025 * T_e - 0.025$$

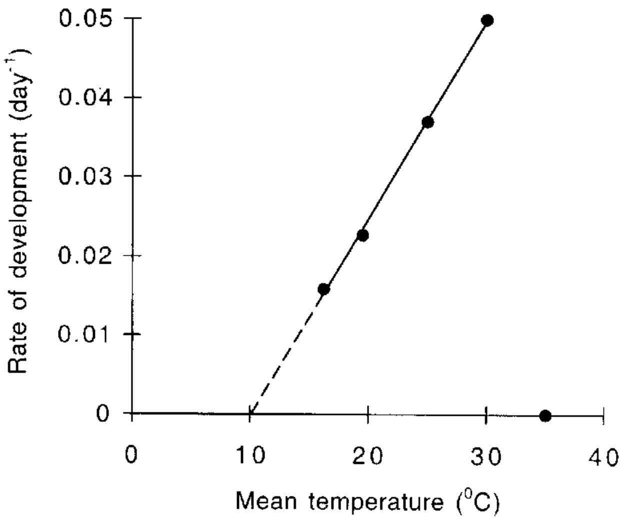

Fig. 2. *Effect of five temperatures on the reciprocal of the time in days (days^{-1}) taken for development from juvenile to juvenile on tomato for a* Meloidogyne incognita *population.*

Estimates for the base temperature T_b, at which $R = 0$ and for the required heat sum S were 10.1°C and 400 °C . day respectively.

Under *Tagetes* var. Polynema the *M. incognita* life cycle was completed only at 30°C, 25 days after inoculation which was slightly longer than under tomato (20 days). On days 51 and 52 no more J2 were recovered from any of the Polynema plants and the experiment was stopped. The average number of J2 recovered during the experiment from *Tagetes* Polynema was 573, which is significantly lower than the total recovery (4883 J2) from tomato at that temperature ($P \leqslant 0.05$).

Discussion

In spite of the agricultural importance of *M. incognita* few studies have focussed on the effects of temperature on the duration of its life cycle. Vrain *et al.* (1978) studied the effect of low temperatures on the development of *M. incognita* and reported that the life cycle was completed under clover at 20°C, but not at 16, 12, or 8°C. They assumed that after penetration the different *M. incognita* stages have similar temperature requirements and calculated a base temperature (T_b) of 10.08°C and from the 20°C data a heat requirement S of 410°C . days. Although in their study (Vrain *et al.*, 1978) S was calculated from one temperature only and although a different host was used (clover), their results are almost identical to ours: values for T_b and for S obtained by us

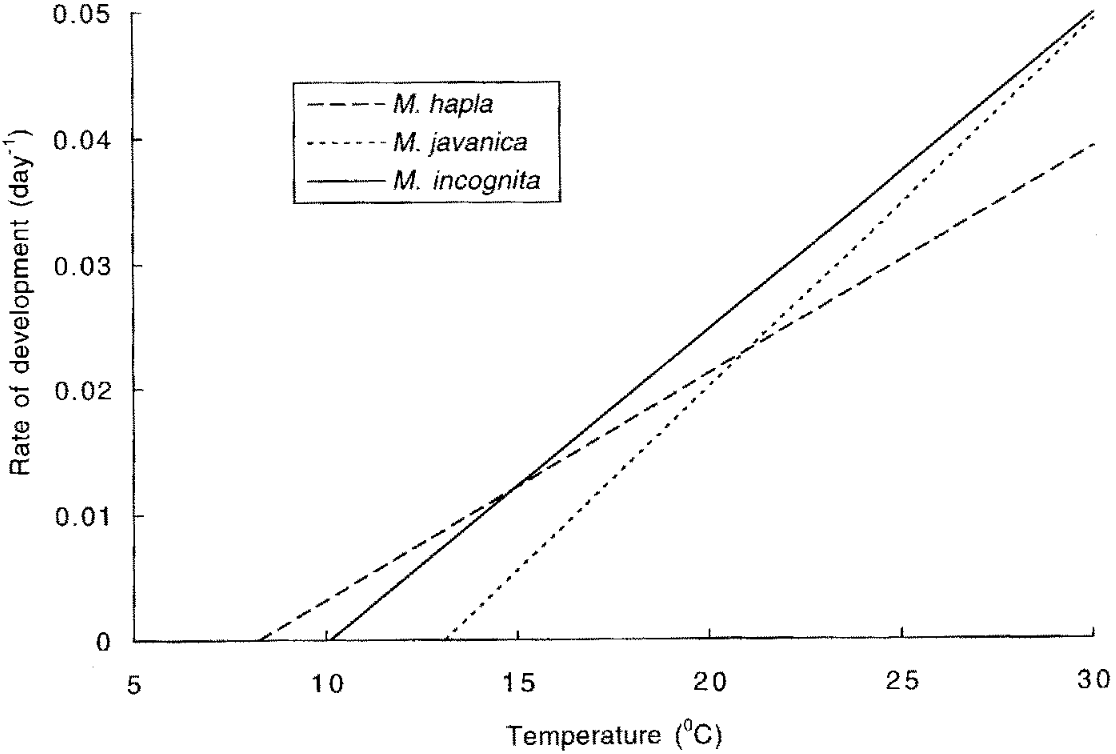

Fig. 3. *Relationships between average soil temperatures and rates of development (from juvenile to juvenile) on tomato for three* Meloidogyne *species. Regression lines for* M. hapla *and* M. javanica *calculated from Lahtinen* et al. *(1988) and Madulu and Trudgill (1994).*

were 10.1 and 400°C.days, respectively. When restricting our calculation for *S* to the 20°C setting (19.5°C actual temperature) the two values for *S* are even more similar (410 and 413°C). Vrain *et al.* (1978) did not observe reproduction of *M. incognita* at 16°C during the 51 day experimental period, which agrees with our results as reproduction at 16.2°C occurred only after 63 days.

In several studies (Prot & Van Gundy, 1981; Roberts *et al.*, 1981; Roberts, 1987; Jeffers & Roberts, 1993) it was shown that the motility of J2 and subsequent root penetration significantly decreased at soil temperatures below 18°C. This probably explains the significantly lower total reproduction of *M. incognita* at 16.2°C compared with 19.5, 25 and 30°C. No reproduction occurred at 35.4°C, indicating that the upper temperature limit for life cycle completion of *M. incognita* lies between 30 and 35.4°C. Other data for *M. incognita* are not available but the similar species *M. javanica*, completed its life cycle at 31 but not at 34.7°C (Trudgill, 1995).

Detailed experimental data on the effects of temperature on the duration of *Meloidogyne* spp. life cycles are available for *M. hapla* and *M. javanica* (Lahtinen *et al.*, 1988; Madulu & Trudgill, 1994; Trudgill & Perry, 1994; Trudgill, 1995). Comparing these data with those for *M. incognita* shows that estimates for T_b (10.1°C) and *S* (400°C.day) for *M. incognita* lie between values for *M. hapla* (T_b *ca* 8.25°C, *S* *ca* 554°C.day) and *M. javanica* (T_b *ca* 13.1°C, *S* *ca* 343°C.day). Plotting the thermal-time relationships for these three species in one graph (Fig. 3) shows that at temperatures below *ca* 15°C *M. hapla* would have a shorter life cycle than *M. incognita* and that *M. javanica* would have a shorter life cycle than *M. incognita* only at temperatures above 31°C. However, as Trudgill (1995) showed that the rate of development of *M. javanica* remained nearly constant between 27 and 31°C, it is unlikely that the life cycle of *M. javanica* is shorter than that of *M. incognita* at any temperature.

Trudgill and Perry (1994), analysing data for *M. hapla* and *M. javanica*, hypothesized that for biologically similar nematode species there exists an inverse relationship between T_b and *S*. Pinkerton *et al.* (1991) estimated from field studies T_b and *S* values for *M. chitwoodi* of 5 and

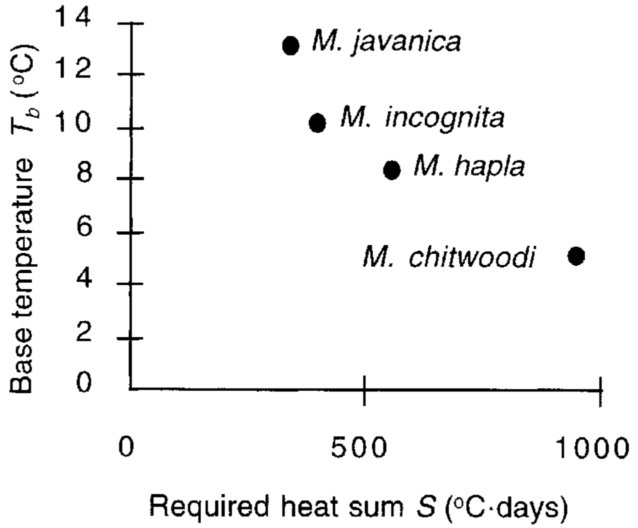

Fig. 4. *Relationship between the estimated base temperatures (T_b) and required heat sums (S) for life cycle completion of four* Meloidogyne *species. Data for* M. hapla, M. javanica *and* M. chitwoodi *from Lahtinen et al. (1988), Pinkerton et al. (1991), and Madulu and Trudgill (1994).*

950°C . day respectively. Regressing the estimated T_b values against corresponding S values for the four *Meloidogyne* species shows that there is a strong negative correlation ($R^2 = -0.93$) between S and T_b (Fig. 4). Thus, the hypothesis (Trudgill & Perry, 1994) that for biologically similar species T_b is inversely proportional to S appears true.

The observed differences in the rate of J2 emergence from the roots (see Fig. 1) probably reflect differences in activity and motility of the inoculated J2. At 16.2°C, below the activity threshold of 18°C (Prot & Van Gundy, 1981; Roberts *et al.*, 1981; Roberts, 1987; Jeffers & Roberts, 1993), few nematodes may have initially penetrated the roots and subsequently developed, while the majority became inactive soon after inoculation. With increasing temperatures, above the 18°C activity threshold, the activity of the inoculated J2 most likely increased (Prot & Van Gundy, 1981), resulting in more J2 penetrating the roots per unit of time with increasing soil temperatures.

It is not known whether the failure of *M. incognita* to reproduce on *Tagetes* Polynema at temperatures below 30°C resulted from the J2 not having penetrated the roots or from the J2 not having developed into reproducing females subsequent to penetration. It is possible that physiological changes in *Tagetes* Polynema occurred at 30°C allowing the reproduction of *M. incognita*. It can be concluded that this *Tagetes* variety should not be used for control of *M. incognita* when soil temperatures are expected to be close to 30°C.

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