Journal of Nematology 22(4):446–451. 1990.

Effect of Temperature on Expression of Resistance to *Meloidogyne* spp. in Common Bean (*Phaseolus vulgaris*)

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Abstract: The effect of soil temperature on the expression of resistance in several common bean lines carrying resistance to root-knot nematodes (*Meloidogyne* spp.) was studied under controlled temperatures in temperature tank and growth chamber conditions. Resistance to *M. javanica* and *M. incognita* race 1 in bean lines A315, A328, A445, G1805, and G2618 was stable at 24–30 C. However, there was a significant increase in reproduction of *M. javanica* on A315, A328, and A445 when temperature was increased from 26 to 30 C. This increase did not reflect a change from a resistant to a susceptible reaction or classification. Resistance in A315 is derived from G1805, whereas resistance in A328 and A445 is derived from G2618. Alabama No. 1, PI 165426, and PI 165435, with resistance to *M. incognita* race 2, were heat stressed at temperatures above 27 C. Resistance to *M. incognita* race 2 in Alabama No. 1 and PI 165435 was lost at 30 C, but PI 165426 supported low reproduction of *M. incognita* race 2 at all temperatures. Poor root development at 30 C may have been responsible, in part, for the poor development of *M. incognita* race 2 on PI 165426.

Key words: common bean, heat stability, *Meloidogyne* spp., *Phaseolus vulgaris,* resistance, root-knot nematode.

High soil temperature is an important factor affecting expression of resistance to root-knot nematodes in several crop plants. Plant resistance to nematodes generally is reduced as temperature increases beyond an upper threshold for heat stability. This threshold is determined by temperature effects on the nematode and (or) the crop plant. In common bean (*Phaseolus vulgaris* L.) the level of resistance to *Meloidogyne incognita* (Kofoid & White) Chitwood was reduced at 28 C, relative to 16 or 21 C (4). Penetration of *M. incognita* juveniles into the roots of resistant and susceptible sweet potato (*Ipomoea batatas* (L.) Lam.) cultivars increased with increasing temperature up to 30 C (7). Partial loss of resistance to *Meloidogyne hapla* Chitwood in alfalfa (*Medicago sativa* L.) occurs at 25 C (5). Similarly, resistance to *M. incognita* in cotton (*Gossypium hirsutum* L.) was reduced at 35 C (2), and resistance to *Meloidogyne* spp. in tomato (*Lycopersicon esculentum* Mill.) was reduced above 28 C (1,3). However, sources of resistance to root-knot nematodes that are stable at high soil temperature (32 C) have been identified in wild tomato (1).

New sources of resistance derived from two common bean landraces, G1805 and G2618, have been identified (10). This resistance is effective against *M. incognita* race 1, *Meloidogyne javanica* (Treub) Chitwood, and *Meloidogyne arenaria* (Neal) Chitwood. Furthermore, resistance genes in common bean line Alabama No. 1 and in accessions PI 165426 and PI 165435 confer resistance to *M. incognita* races 2, 3, and 4 (10); however, it is unknown if these sources of resistance are stable at high soil temperature. The objective of this study was to determine the effect of temperature on the expression of resistance conferred by genes from the various common bean lines.

Materials and Methods

Three nematode isolates were used in this study: *M. incognita* race 1 (NCSU #54), *M. incognita* race 2 (NCSU #1135), and *M. javanica* (NCSU-Mj). Nematodes were cultured on tomato cultivar Tropic in the greenhouse. The inoculum of eggs for temperature tank tests was extracted from roots in 0.5% NaOCl solution in a blender (6). For the growth chamber tests, second-stage juveniles (J2) were used as the inoculum. The J2 were obtained by incubating nematode eggs in tap water and collecting juveniles daily for 3 days. Collected J2 were

Received for publication 5 August 1989.

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The authors thank Lori Yates, Cooperative Extension, University of California Riverside, for statistical help.

stored in a cold room at 10 C under aeration before use.

Common bean line Alabama No. 1 and accessions PI 165426 and PI 165435 (all resistant to *M. incognita* races 2, 3, and 4) and lines A315, A445, G1805, and G2618 (all resistant to *M. incognita* race 1, *M. javanica,* and *M. arenaria*) were used in this study. Bean cultivar Black Valentine was included as a susceptible standard in all experiments.

Temperature tank tests

Temperature tests were conducted in temperature tanks in the greenhouse. Bean seeds, germinated in petri dishes, were planted singly into 10-cm² pots filled with steam-sterilized loamy sand (93% sand, 4% silt, 3% clay). The pots were buried to their rims in plastic pans filled with sand. The pans were placed in temperature tanks equilibrated to give soil temperatures of 24, 26, 28, or 30 C. Plants (7–10 days old) were arranged in a completely randomized design in each temperature tank and inoculated with 5,000 nematode eggs. Plants were harvested 33, 37, 41, or 47 days after inoculation at 30, 28, 26, and 24 C, respectively. These periods were chosen to allow an accumulation of ca. 666 degree-day heat units (base 10 C). The heat units chosen assured sufficient nematode reproduction prior to plant senescence. At the end of the experiment, root systems were washed free of soil, blot dried, and weighed. Roots were then macerated in a blender with NaOCl to release nematode eggs for counting (6). Four experiments were conducted as follows:

Experiments 1 and 2: A315, A328, A445, G1805, and G2618, resistant to *M. javanica* and *M. incognita* race 1, were evaluated for *M. javanica* reproduction at 26, 28, and 30 C and for *M. incognita* race 1 reproduction at 28 and 30 C. Five replicates were used for each test combination.

Experiment 3: Four resistant lines and accessions—A445, Alabama No. 1, PI 165426, and PI 165435—were evaluated for reproduction of *M. incognita* races 1 and 2 at 24 and 30 C. Five replicates of each line were used in each nematode–temperature combination.

Experiment 4: Alabama No. 1, PI 165426, and PI 165435 were evaluated for reproduction of *M. incognita* race 2 at 26, 28, and 30 C. Seven replicates were used for each test combination.

Growth chamber tests

In experiments 5 and 6, common bean lines and accessions were grown in growth pouches as previously described (9). One-week-old plants were inoculated with 1,000 J2 of the appropriate *Meloidogyne* spp. isolate and maintained in a growth chamber under controlled conditions. The root systems were stained with 50 mg/liter solution of erioglaucine dye, harvested 28 days after inoculation, and evaluated for egg mass numbers.

Experiment 5: A315, A328, A445, G1805, and G2618 were evaluated for nematode reproduction at three temperature regimes as follows: Thirty plants of each line were inoculated with 1,000 J2 of *M. incognita* race 1 or *M. javanica.* After inoculation, 10 plants from each bean line were incubated at 28-C day and 24-C night temperatures and 12-hour photoperiod for the duration of the experiment. The other 20 plants of each line were incubated in a growth chamber at 32-C day and 28-C night temperatures and a 12-hour photoperiod. After 7 days, 10 plants, chosen randomly from each nematode treatment, were moved into a growth chamber maintained at a constant temperature of 26 C and a 12-hour photoperiod for the remaining 21 days.

Experiment 6: Alabama No. 1, PI 165426, and PI 165435 were evaluated for *M. incognita* race 2 reproduction at three temperature regimes as in experiment 5.

Analysis of data

Data from experiments 1 and 2 were transformed to LN (eggs per root system + 1) and analyzed as a completely randomized design with a two-factor factorial. Untransformed data from the other experi-

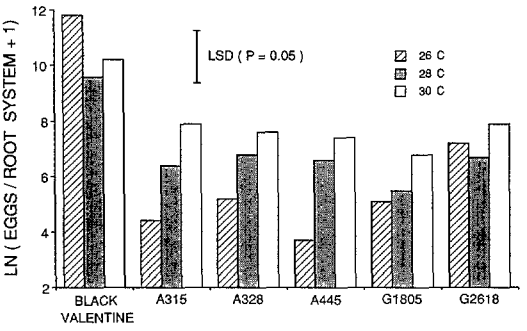

FIG. 1. Effect of three soil temperatures on reproduction of *Meloidogyne javanica* on six common bean lines. Nematode reproduction is based on eggs per root system. Statistical analysis was performed on LN (eggs per root system + 1).

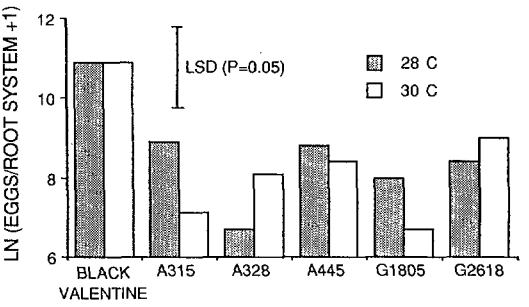

FIG. 2. Effect of two soil temperatures on reproduction of *Meloidogyne incognita* race 1 on six common bean lines. Nematode reproduction is based on eggs per root system. Statistical analysis was performed on LN (eggs per root system + 1).

ments were analyzed using a one-way analysis of variance.

RESULTS

Temperature tank tests

Experiment 1: Meloidogyne javanica reproduction on A315, A328, A445, G1805, and G2618 increased with increase in temperature (Fig. 1). At all temperatures *M. javanica* reproduction in resistant lines was lower ($P \leq 0.05$) than in the susceptible standard, Black Valentine. Resistant lines A315, A328, and A445 supported lower ($P \leq 0.05$) reproduction of *M. javanica* at 26 than at 30 C. Root weights declined ($P \leq 0.01$) when temperature was increased from 26 to 28 C (Table 1).

Experiment 2: Meloidogyne incognita race 1 reproduction at 28 and 30 C on A328 and G1805 was lower ($P \leq 0.05$) than on Black Valentine (Fig. 2). *Meloidogyne incognita* race 1 reproduction on G2618 was lower relative to Black Valentine at 28 C, but not at 30 C. A315 and A445 supported lower ($P \leq 0.05$) nematode reproduction than Black Valentine at 30 C, but not at 28 C. However, when LN (eggs per gram root + 1) was used as a measure of nematode reproduction, all the resistant lines showed lower ($P \leq 0.05$) nematode reproduction than susceptible Black Valentine at both temperatures.

Experiment 3: At 24 C, Alabama No. 1, PI 165426, and PI 165435 supported high ($P \leq 0.01$) reproduction of *M. incognita* race 1, but low reproduction of *M. incognita* race 2 (Table 2). A445 supported low reproduction of *M. incognita* race 1, but high reproduction of *M. incognita* race 2 (Table 2). Most of the plants did not survive at 30 C. Two surviving A445 plants supported an average of 16,400 eggs of *M. incognita* race 1 per root system. The few surviving

TABLE 1. Fresh root weights of six bean lines inoculated with *Meloidogyne javanica* and grown at three soil temperatures.

	26 C	28 C	30 C
Black Valentine	2.2	1.3	0.8
A315	2.8	1.6	1.4
A328	1.5	0.9	0.8
A445	2.8	1.7	1.7
G1805	2.5	1.3	1.2
G2618	1.6	1.1	1.0
LSD = 0.8 ($P = 0.01$)			

Means are based on five plants. The data were LN (fresh root weight in grams + 1) transformed and analyzed as a completely randomized block with two-factor factorial.

TABLE 2. Reproduction of *Meloidogyne incognita* races 1 and 2 on five bean lines at 24 C soil temperature. Reproduction is based on average eggs per root system.

	Race 1	Race 2
Black Valentine	99,000 a	92,000 a
PI 165435	87,000 b	1,200 b
PI 165426	61,000 b	1,000 b
Alabama No. 1	43,000 b	1,300 b
A445	100 c	73,500 a

Values within a column followed by the same letter are not different ($P \leq 0.01$) according to Duncan's multiple-range test.

Means are based on five plants.

TABLE 3. Reproduction of *Meloidogyne incognita* race 2 on four common bean lines at 26 C soil temperature.

	Eggs/root system
Black Valentine	57,814 a
Alabama No. 1	7,555 b
PI 165435	1,742 c
PI 165426	157 c

Values within a column followed by the same letter are not different ($P \leq 0.01$) according to Duncan's multiple-range test.

Means are based on seven plants.

plants of other lines tested supported high *M. incognita* race 1 reproduction. Three Alabama No. 1 plants survived at 30 C and averaged 82,700 eggs of *M. incognita* race 2 per root system. The only surviving plant of PI 165435 supported 81,900 eggs/root system. No PI 165426 plant survived at 30 C.

Experiment 4: Alabama No. 1, PI 165426, and PI 165435 did not survive well at 28 and 30 C. Therefore, only results of *M. incognita* race 2 reproduction at 26 C are given in Table 3. PI 165426 and PI 165435 showed low ($P \leq 0.01$) reproduction of *M. incognita* race 2. An average of 7,555 eggs/root system were recovered from Alabama No. 1; however, this exceeds the initial inoculum of 5,000 eggs.

Growth chamber tests

Experiment 5: A315, A328, A445, G1805, and G2618, which are resistant to *M. javanica* and *M. incognita* race 1, supported low ($P \leq 0.01$) egg mass numbers at all temperatures. However, G2618 supported more egg masses than the other resistant lines when kept at the 32–28-C day–night temperature regime for 28 days (Table 4).

TABLE 5. *Meloidogyne incognita* race 2 egg masses per root system on four common bean lines at three temperature regimes.

	30 C day 24 C night	32 C day 28 C night then 26 C†	32 C day 28 C night
Black Valentine	120 a	27.0 a	27 a
Alabama No. 1	30 b	23.0 a	37 a
PI 165435	4 b	12.0 b	38 a
PI 165426	2 b	0.2 b	4 b

Values are averages of 10 plants. Numbers in a column followed by same letter are not different ($P \leq 0.01$) according to Duncan's multiple-range test.

† Plants kept at 32 and 28 C day and night temperatures for 7 days then at 26 C constant temperature for 21 days.

Experiment 6: Nematode reproduction increased at high temperatures on lines and accessions resistant to *M. incognita* race 2 (Table 5). There was no difference ($P \leq 0.01$) in egg mass numbers between resistant Alabama No. 1 and susceptible Black Valentine when plants were maintained at a 32–28-C day–night temperature regime for 7 days or for the entire experiment. Egg mass numbers increased on PI 165435 only when the high temperatures were maintained for the entire experiment. PI 165426 supported very low egg mass numbers at all temperatures.

DISCUSSION

Resistance to *M. javanica* in A315, A328, A445, G1805, and G2618 was relatively

TABLE 4. *Meloidogyne javanica* (Mj) and *Meloidogyne incognita* race 1 (Mi) egg masses per root system on six common bean lines at three temperature regimes.

	30 C day 24 C night	32 C day 28 C night then 26 C†		32 C day 28 C night	
	Mj	Mj	Mi	Mj	Mi
Black Valentine	110.0 a	68.0 a	45.0 a	80.0 a	149.0 a
G2618	7.0 b	0.3 b	5.0 b	21.0 b	20.0 b
G1805	0.4 b	0.1 b	0.1 b	0.0 c	0.1 c
A328	0.1 b	0.0 b	0.2 b	0.2 c	1.0 c
A445	0.0 b	0.0 b	0.1 b	0.1 c	0.4 c
A315	0.0 b	0.3 b	0.0 b	0.0 c	0.0 c

Values are means of 10 plants. Values in a column followed by the same letter are not different ($P \leq 0.01$) according to Duncan's multiple-range test.

† Plants kept at 32 and 28 C day and night temperatures for 7 days then at 26 C constant temperature for 21 days.

stable at all temperatures tested. However, *M. javanica* reproduction increased ($P \leq 0.05$) in A315, A328, and A445 as temperature increased from 26 to 30 C. Root weights were reduced ($P \leq 0.01$) at 28 and 30 C. This was even more evident in plants grown in growth pouches. Poor root growth, reflected in low weights, may have reduced the potential for even higher nematode reproduction at elevated temperatures.

Bean lines and accessions resistant to *M. incognita* race 2 were more adversely affected by heat stress than the others. It was evident from the few surviving plants that resistance to *M. incognita* race 2 in Alabama No. 1 and PI 165435 is lost at 30 C. PI 165426 plants did not survive well at high temperatures; therefore, the low nematode reproduction at high temperature may be due, in part, to a small, unhealthy root system. Since PI 165426 supported significantly lower *M. incognita* race 2 reproduction than Alabama No. 1 and PI 165435, resistance may be more heat stable in PI 165426 than in PI 165435 and Alabama No. 1.

The effect of temperature on resistance to *M. incognita* was previously studied in the resistant accession PI 165426 (4). More female nematodes were recovered from PI 165426 at 28 C than at 21 C. However, the numbers were much lower in the resistant accession than in the susceptible standard. Our results are similar to those reported in other nematode–plant systems where there is a gradual reduction of resistance as temperature increases before resistance breaks down. Breakdown of resistance to root-knot nematodes at high temperatures has been documented in tomato (1,3), alfalfa (5), and sweet potato (7).

The temperature at which resistance breaks down depends on the crop–nematode combination, and this temperature may be determined by genes controlling the resistance. In tomato, for example, resistance conferred by the "Mi" gene is ineffective at temperatures above 28 C (1,3). However, certain plants in *Lycopersicon peruvianum* (L.) Mill. with resistance, apparently conferred by a different gene, are resistant at temperatures of 32 C (1).

The effect of temperature on resistance in bean lines with resistance from different sources was examined in this study. Based on reaction to different isolates of *Meloidogyne* spp., it has been postulated that resistance in bean line Alabama No. 1 and accessions PI 165426 and PI 165435 is under the same genetic control, but it differs genetically from the resistance in A315, A328, A445, G1805, and G2618 (10). Resistance in the latter group is conferred by a single dominant gene (11). Thus, differences in relative stability of resistance at high temperatures between the two groups of bean lines may be due to different resistance genes. Stability of resistance in PI 165426 relative to Alabama No. 1 and PI 165435 may also be explained in terms of differences in genetic background which modify the expression of the resistance gene(s) in these lines.

At 24 C, Alabama No. 1, PI 165426, and PI 165435 were susceptible to *M. incognita* race 1, but resistant to *M. incognita* race 2, whereas A445 was resistant to *M. incognita* race 1, but susceptible to *M. incognita* race 2. This is consistent with what has been reported (10).

Most common beans are produced in areas where temperatures during the growing season are between 17.5 and 25 C, with most production occurring in areas where average temperature is near 21 C (8). Thus, the effect of temperature on resistance to *Meloidogyne* may not seem as important in common bean as it is in other crops such as tomato. However, there are continuing efforts to breed for drought and heat tolerance in common bean. For bean cultivars adapted to hot climatic regions, stable resistance to root-knot nematodes at high soil temperatures will be important in the management of root-knot problems.

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