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Inheritance of resistance to *Meloidogyne* spp. in common bean and the genetic basis of its sensitivity to temperature

C. O. Omwega and P. A. Roberts*

Department of Nematology, University of California, Riverside, CA 92521, USA

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Summary. Bean lines PI 165426, PI 165435, and Alabama no. 1, possessing resistance to *Meloidogyne incognita*, and bean lines A315 and A445, possessing gene *Me1*, were tested against several *Meloidogyne incognita* and *M. javanica* isolates. Resistance in bean line PI 165426, PI 165435, and Alabama no. 1 was found to be complementary to resistance conferred by gene *Me1*. Resistance in PI 165426 was found to be dominant and conditioned by one dominant and one recessive gene at 26 °C. We propose *Me2me3* as the genotype symbol for this resistance. Resistance in lines PI 165435 and Alabama no. 1 was found to be recessive. Since Alabama no. 1 and PI 165435 were resistant at 26 °C but susceptible at 29 °C, and segregation of F_2 progeny derived from crosses involving PI 165426 was 13:3 at 26 °C and 1:2:1 at 28 °C, we concluded that the temperature at which transition from resistance to susceptibility occurs was determined by whether the resistance gene is dominant or recessive. Furthermore, the 1:2:1 segregation of F_2 plants and an intermediate resistance reaction of F_1 plants of crosses involving PI 165426 indicated that allelic dosage of the dominant gene also influenced the transition temperature.

Key words: Allelic dosage – Dominance – Nematode resistance – *Phaseolus vulgaris* – Temperature sensitivity

Introduction

Resistance to the root-knot nematode *Meloidogyne incognita* (Kofoid and White) Chitwood in common bean *Phaseolus vulgaris* L. has been identified in bean lines PI 165426, PI 165435, and Alabama no. 1 (Fassuliotis et al. 1970; Omwega et al. 1989). The inheritance of resistance in the first two lines is not known. The resistance in Alabama no. 1 was reported to be under the control of two (Barrons 1939) or three (Hartmann 1970) recessive genes. Resistance in bean lines PI 165426, PI 165435, and Alabama no. 1 was found to be effective against the same *Meloidogyne* spp. isolates (Omwega et al. 1989). From this data it was speculated that resistance in these lines could be under the same genetic control. In contrast, resistance to bean lines A315 and A445 was found to be effective against those *Meloidogyne* isolates to which the former group of bean lines was susceptible (Omwega et al. 1989). This resistance was found to be under the control of a single dominant gene, *Me1* (Omwega et al. 1990a).

Although resistance in PI 165426, PI 165435, and Alabama no. 1 was effective against the same nematode isolates, resistance in PI 165426 was found to be stable at higher temperature than that in PI 165435 and Alabama no. 1 (Omwega et al. 1990b). Influence of temperature on host plant resistance genes has been reported for nematode resistance in several interactions, e.g., in tomato (Dropkin 1969; Ammati et al. 1986) and alfalfa (Griffin 1969). This phenomenon also has been reported for other disease or pest plant interactions, e.g., in rust diseases in wheat (Luig and Rajaram 1972) and flax (Islam et al. 1989), and for Hessian fly resistance in wheat (Tyler and Hatchett 1983). As far as we know, no attempt has been made to study the genetic basis of temperature effects on expression of resistance genes in plant-nematode interactions. A shift towards susceptibility at 24°–26 °C in *M. incognita* resistant bean line A211 has been reported in an independent study (Mullin et al. 1991). The three bean lines PI 165426, PI 165435, and Alabama no. 1 with resistance to *M. incognita* provided a good model system

* To whom correspondence should be addressed.

for studying the genetic basis of differential temperature sensitivity. The resistance in bean line PI 165426 is effective at temperatures of above 28 °C, while resistance in PI 165435 and Alabama no. 1 is effective up to 26 °C. Thus, by understanding the inheritance of resistance in these two groups of resistant lines we could draw conclusions about their genetic basis of temperature sensitivity. Previous work demonstrated that resistance conferred by gene *Mel* in bean line A445 is conditioned by one dominant gene (Omwega et al. 1990a), and that resistance in Alabama no. 1 is conditioned by recessive genes (Hartmann 1970). Because resistance in A445 is effective at 28 °C and resistance in Alabama no. 1 is only effective up to 26 °C, we suspected that resistance in PI 165426 and PI 165435 also is conditioned by dominant and recessive gene(s), respectively.

The objective of this study was to determine the mode of inheritance of resistance to *Meloidogyne* spp. in common bean, in relation to the influence of temperature on the expression of resistance genes.

Materials and methods

Plant material

Resistant common bean lines PI 165426, PI 165435, and Alabama no. 1 and F_2 of the cross A445 × susceptible Kentucky Wonder (KW) were used in this study. F_1 plants were generated by crossing the resistant lines PI 165435 and Alabama no. 1 with KW, and PI 165426 with KW and susceptible G4017. Hybridity of the F_1 plants from the crosses PI 165426 × KW, PI 165426 × G4017, and PI 165435 × KW was confirmed by screening the enzyme malate dehydrogenase (MDH) for electrophoretic mobility variation at the slowest locus (unpublished data) using horizontal starch gel electrophoresis. Hybridity of F_1 plants from crosses of Alabama no. 1 × KW was confirmed by examining electrophoretic mobility variation of the enzyme shikimic dehydrogenase (SKDH) (unpublished data). When Alabama no. 1 was used as a male parent stem color (purple), which is dominant over green stem color, was used to distinguish the F_1 hybrids.

Approximately 10-day-old plants were used for isoenzyme analysis. A crude homogenate for electrophoresis was obtained by macerating pre-chilled primary leaf tissue in an appropriate extraction buffer. The extraction buffer, as outlined by Weeden (1984), was made up of 0.08 *M* potassium phosphate (pH 7.0), containing 20% sucrose (w/v), 0.5% polyvinyl-pyrrolidone (PVP-40), 0.5% Triton X-100, and 14 m*M* 2-mercaptoethanol. The homogenate was absorbed on filter paper wicks and inserted into the gels. Electrophoresis was performed at 4 °C. The starch gel system used for MDH was morpholine citrate, pH 6.1 (Clayton and Tretiak 1972). Shikimic dehydrogenase was assayed on Tris-citrate lithium borate gel system, pH 8.1 (Selander et al. 1971). The extraction buffer consisted of 0.07 *M* Tris-maleate (pH 7.4), containing 20% glycerol (v/v), 10% PVP-40, 0.5% Triton X-100, and 14 m*M* 2-mercaptoethanol (Weeden 1984). The morpholine citrate and the Tris lithium borate system was run for 4 h according to the methods of Weeden (1984).

After electrophoresis, the gels were sliced and stained for MDH and SKDH using the recipes outlined by Marty et al. (1984).

Nematodes

Meloidogyne incognita race 1: Muller isolate was from Denair, Stanislaus County, California; Beltran isolate was from Crows Landing, Stanislaus County, California. Rodari isolate of *M. incognita* race 3 was from Pixley, Tulare County, California; *M. incognita* race 2 was from North Carolina State University; Bisnelli isolate of *M. javanica* was from Patterson, Stanislaus County, California, and *M. arenaria* was from Le Grau du Roi, France.

Isoenzyme phenotypes were used to confirm species identity of the root-knot nematode isolates. Host differential tests (Hartman and Sasser 1985) were used to designate root-knot races at the beginning of the study. Esterase isoenzyme phenotypes were used to distinguish between *M. arenaria* (Neal) Chitwood, *M. incognita*, and *M. javanica* (Treub) Chitwood using the procedures of Esbenshade and Triantaphyllou (1985). Briefly, female nematodes were teased from plant roots and placed in a watch glass containing an extraction buffer consisting of 20% (w/v) glycerol and 2% (w/v) Triton X-100. A single nematode was transferred with a fine pipette into an extraction tube and then macerated with a glass pestle. Just before electrophoresis, samples were centrifuged at 13,000 *g* for 14 min in a microhematochrit centrifuge maintained at 4 °C. After centrifugation, each tube was broken just below the lipid/aqueous phase interface, and the aqueous phase in the lower part of the tube was then used for electrophoresis.

Electrophoresis was carried out in 0.5 or 1.5-mm-thick polyacrylamide Mighty Small II vertical slab gels (Hoefer Scientific Instruments, San Francisco/CA). Samples were layered in wells and run at 80 mV for 30 min, and thereafter at 200 V until the front reached the bottom buffer (Esbenshade and Triantaphyllou 1985). Separating and stacking gels were 7% and 4% polyacrylamide, respectively, and the bridge buffer was Tris-glycine, pH 8.3 (Esbenshade and Triantaphyllou 1985).

In each experiment, at least 20 female nematodes were picked randomly from cultures from which the inoculum was derived and checked for their isoenzyme phenotypes. At the end of each experiment at least 20 female nematodes from the test plants were assayed for their isoenzyme phenotypes, to ensure that no interspecies contamination occurred at any stage during the experiments.

Inoculation

Nematodes were multiplied on tomato (*Lycopersicon esculentum* Mill.) cv Tropic in the greenhouse. Inoculum consisting of second-stage juveniles (J_2) was prepared by extracting eggs from tomato roots with NaOCl (Hussey and Barker 1973) and hatching them in tap water at room temperature.

In all experiments, surface-sterilized bean seeds were germinated in petri dishes and grown singly in seedling growth pouches (Omwega et al. 1988). Seedlings (7–10 days old) were inoculated with 1,000 J_2 (unless specified) of the appropriate nematode. The plants were grown in a growth chamber where temperature was maintained at 24°, 26°, or 28 °C and the photoperiod was 16 h. F_1 plants and resistant and susceptible parents were tested for resistance to the appropriate nematode using a previously described method (Omwega et al. 1988). Egg masses were stained with 50 mg/l erioglaucine dye and 28 days (unless specified) after inoculation the egg masses on plant roots were counted. Plants supporting less than 13 egg masses were designated as resistant and those supporting 13 or more egg masses were designated as susceptible. After evaluation, if desired, the plants were transferred into 15-cm fiber pots filled with UC-mix soil and grown to maturity in the greenhouse, to obtain seeds for the next generation or for use in backcrossing.

Screening for resistance to several isolates of M. incognita, M. javanica, and M. arenaria

In an earlier study (Omwega et al. 1989) it was found that bean lines PI 165426, PI 165435, and Alabama no. 1 were resistant to those isolates of *Meloidogyne* spp. to which bean lines with resistance gene *Me1* were susceptible. Additional isolates of the three *Meloidogyne* spp. were used in this study to determine whether or not this trend of complementarity was consistent. Bean lines carrying resistance to *M. incognita* and lines A315 and A445 possessing gene *Me1* were screened to Muller and Beltran isolates of *M. incognita* race 1, Rodari isolate of *M. incognita* race 3, Bisnelli isolate of *M. javanica* and to *M. arenaria*, using ten plants per isolate × line combination and 1,000 J_2 per plant. Each was evaluated for number of egg masses 28 days post-inoculation.

Effect of temperature and inoculum density on resistance

Bean lines PI 165426, PI 165435, and Alabama no. 1 and susceptible KW were used in this experiment. The experiment was conducted in three growth chambers set at 24°, 26°, and 28 °C constant temperature, respectively, and photoperiod was 16 h in all chambers. For each temperature, ten plants of each bean line were inoculated with 1,000 J_2 and another ten plants with 2,000 J_2 of *M. incognita* race 3, and evaluated for egg masses 28 days post-inoculation.

Inheritance of M. incognita resistance in PI 165426

Experiments to study the inheritance of *M. incognita* resistance in PI 165426 were performed at 26 °C constant temperature and a photoperiod of 16 h in a growth chamber. *Meloidogyne incognita* race 1, race 2, and race 3 were used. The parents, and F_1 and F_2 progeny from the crosses PI 165426 × KW and backcross populations were screened for resistance to the appropriate nematode. After evaluation for resistance, selected plants from each test were transferred to 15 cm pots filled with UC-mix soil and grown to maturity, to obtain seeds for the next generation or for backcrossing. F_3 plants of the cross PI 165426 × KW obtained from F_2 plants inoculated with *M. incognita* race 2 were tested with the same race 2 isolate.

Effect of temperature on expression of resistance

Bean line PI 165426 was used to study the effect of temperature on genetics of resistance to *M. incognita*. F_1 and F_2 plants of the cross PI 165426 × KW were inoculated with 1,000 J_2 *M. incognita* race 1. One-half of the plants from each family were incubated at 24 °C and the other half at 28 °C. Twenty-five days post-inoculation the plants were evaluated for numbers of egg masses. The plants were maintained and re-evaluated again at 28, 32, and 36 days post-inoculation. This was done because at the first evaluation the F_1 plants supported an intermediate number of egg masses, and also it was difficult to assign resistant and susceptible phenotypes to some of the intermediates among the segregating F_2 population. Because of variability in size of root system, the bean plants supporting intermediate egg mass numbers could not be assigned phenotypic classes unambiguously at 25 days post-inoculation. However, by allowing plants to grow beyond 25 days post-inoculation and enumerating egg masses several times, the intermediate class in the F_2 could be assigned based on the rate of nematode development profile, which was similar to that of the F_1 plants. Since we demonstrated loss of dominance of resistance in PI 165426 at 28 °C, we wanted to find out if this phenomenon also occurs with gene *Me1*, which confers dominant resistance to *M. javanica* in A445 at 26 °C. Therefore, F_1 and F_2 plants of the cross A445 × KW were tested for resistance to *M. javanica* at 28 °C.

F_3 families of the cross PI 165426 × KW were screened for resistance at 24° and 28 °C to confirm the F_2 data, which indicated a shift from a two-loci segregation of resistance at low temperature to single-locus and semidominant segregation at higher temperature (28 °C). F_3 families from the cross PI 165426 × KW were inoculated with 1,000 J_2 of *M. javanica*, and half of the plants from each family were incubated at 24 °C and the other half at 28 °C. Twenty-eight days post-inoculation the plants were evaluated for resistance based on number of egg masses. The families were assigned genotypes based on whether the plants in each family segregated, were all resistant, or were all susceptible at a given temperature.

Results

Evaluation of resistance

Compared to susceptible Kentucky Wonder, bean accessions PI 165426, PI 165435, and Alabama no. 1 supported lower ($P=0.01$) numbers of egg masses of isolates Muller and Beltran of *M. incognita* race 1 and isolate Rodari of *M. incognita* race 3 (Table 1). However, they supported higher ($P=0.01$) numbers of egg masses of *M. javanica* and *M. arenaria*. Bean lines A315 and A445 supported higher ($P=0.01$) numbers of egg masses of isolates Muller and Beltran of *M. incognita* race 1 and Rodari isolate of *M. incognita* race 3. But these lines supported very low ($P=0.01$) egg mass numbers of *M. arenaria* and Bisnelli isolate of *M. javanica*.

Effect of inoculum density and temperature on resistance

Accession PI 165426 supported no egg masses of *M. incognita* race 3 at 24°, 26°, or 28 °C. Accession PI 165435 and Alabama no. 1 supported low (≤2) egg masses at 24 °C at both inoculum levels (Table 2). PI 165435 supported 15 and 50 egg masses at 28 °C following 1,000 and 2,000 J_2 inoculum densities, respectively. Alabama no. 1 sup-

Table 1. Egg mass production of several isolates of *Meloidogyne* species on common bean lines at 26 °C

	M. incognita R1		*M. incognita* R3	*M. javanica*	*M. arenaria*
	Muller[a]	Beltran	Rodari[a]	Bisnelli	
KW	40 a[b]	110 a	47 b	188 a	130 a
PI 165426	5 b	0 b	0 c	141 a	29 c
PI 165435	2 b	4 b	2 c	141 a	73 b
Alabama no. 1	6 b	13 b	1 c	134 a	63 b
A315	38 a	129 a	94 a	3 b	0.3 c
A445	28 a	160 a	24 c	0.4 b	1 c

[a] Plants were inoculated with 2,000 eggs of Muller isolate of *M. incognita* race 1 and Rodari isolate of *M. incognita* race 3; inoculum of 1,000 juveniles was used for other nematode isolates

[b] Values within a column followed by the same letter are not significantly different ($P = 0.01$) according to Duncan's multiple range test

Table 2. Egg mass production of *Meloidogyne incognita* on common bean lines at two inoculum levels and at 24°, 26°, and 28°C

	Temperature					
	24°C		26°C		28°C	
	1,000 J2	2,000 J2	1,000 J2	2,000 J2	1,000 J2	2,000 J2
KW	105.9	112.0	164.3	193.8	157.5	180.8
PI 165426	0.0	0.0	0.0	0.1	0.0	0.0
PI 165435	0.0	0.6	0.3	0.6	15.2	49.9
Alabama no.1	0.5	2.1	6.8	10.4	59.1	189.0
LSD (0.05) = 30.3						

ported 59 and 189 egg masses at 28°C following 1,000 and 2,000 J_2 inoculum densities, respectively. When the means of egg masses supported by the same bean line were compared for the same temperature at two inoculum densities, PI 165426 showed no significant inoculum density effect. Line PI 165435 supported higher ($P=0.05$) egg mass numbers at 28°C when inoculated with 2,000 J_2 compared to 1,000 J_2 at the same temperature. Alabama no. 1 also supported higher ($P=0.01$) egg mass numbers when inoculated with 2,000 J_2 compared to 1,000 J_2 at 28°C. No significant inoculum density effects were observed at other temperatures. When temperature effects within same line and inoculum density were examined, PI 165435 supported higher ($P=0.01$) numbers of egg masses at 28°C compared to 26°C following inoculation with 2,000 J_2. No significant temperature effects were observed at inoculum of 1,000 J_2 on bean line PI 165435. Alabama no. 1 supported high ($P=0.01$) egg mass numbers at 28°C compared to 26°C at both inoculum densities. No temperature effect at the same inoculum density was observed for PI 165426.

Genetics of resistance to M. incognita in PI 165426 at 26°C

F_1 plants of crosses of PI 165426 with Kentucky Wonder (KW) and G4017 supported very low numbers of egg masses of *M. incognita*. The F_2 plants of the crosses PI 165426 × KW and PI 165426 × G4017 in individual crosses and when pooled showed good fit ($\chi^2=0.264$) to 13:3 (Resistant: Susceptible) ratio (Table 3). The backcross data of the cross (PI 165426 × KW) × PI 165426 and (PI 165426 × KW) × KW did not distinguish between 13:3 and 3:1 genetic models. When plants from four F_2 families of the cross PI 165426 × KW were challenged with a higher inoculum density of 2,000 J_2 of *M. incognita* race 3 and incubated at 26°C, individual and pooled data of three of the four families (124 resistant:43 susceptible) fit 3:1 ($\chi^2=0.049$), but not 13:3 ($\chi^2=5.26$); one family did not fit any of the ratios.

Table 3. Reaction of F_2 populations of the common bean crosses PI 165426 × Kentucky Wonder (KW) and PI 165426 × G4017, and to plants of F_1 cross of PI 165426 × KW backcrossed to the resistant and susceptible parents to two isolates of *Meloidogyne incognita* race 2 (Mi2) and *M. incognita* race 3 (Mi3)

Cross	Nematode isolate	Obs. freq. R	Obs. freq. S	Expected ratio	Chi-square	*P* value
PI 165426 × KW	Mi2	70	17	13:3	0.0369	50–90
PI 165426 × KW	Mi3	122	27	13:3	0.0387	50–90
F_1 × KW	Mi3	26	19	1:1	1.08	10–50
F_1 × PI 165426	Mi3	14	0	All R	–	–
PI 165426 × G4017	Mi3	163	34	13:3	0.264	10–50

R – resistant reaction: plants support less than 13 egg masses per root system
S – susceptible reaction: plants support 13 or more egg masses per root system

Table 4. Reaction of F_3 families of the cross PI 165426 × Kentucky Wonder to *Meloidogyne incognita* race 2 at 26°C

No. of families	Response
From susceptible F_2	
4	All Susceptible
3	Segregating
From resistant F_2	
2	All Resistant
12	Segregating

F_3 plants from the cross PI 165426 × KW were tested with 1,000 J_2 of *M. incognita* race 2 at 26°C. Seven of the F_3 families were derived from susceptible F_2 plants; three of these families segregated for resistance, and when pooled gave 1 Resistant: 3 Susceptible ratio ($\chi^2=0.06$). Of the 14 families (F_3) derived from resistant F_2, two were all resistant and the rest segregated for resistance. The 1 Resistant: 3 Susceptible segregation in the families derived from susceptible F_2 gave additional evidence of a recessive gene in addition to a dominant gene conditioning resistance to *M. incognita* in bean line PI 165426. The F_3 data is summarized in Table 4.

Genetics of resistance to M. incognita in PI 165426 at 28°C

In order to study the genetic basis of temperature sensitivity of resistance to root-knot nematodes in common bean, plants from four F_2 families of the cross PI 165426 × KW were divided into two equal groups; one group was inoculated and incubated at 24°C and the second group was inoculated and incubated at 28°C. Egg masses on roots were enumerated 25 days post-inoculation and three more times at 3- to 4-day intervals. At 24°C, there was no significant difference in egg masses

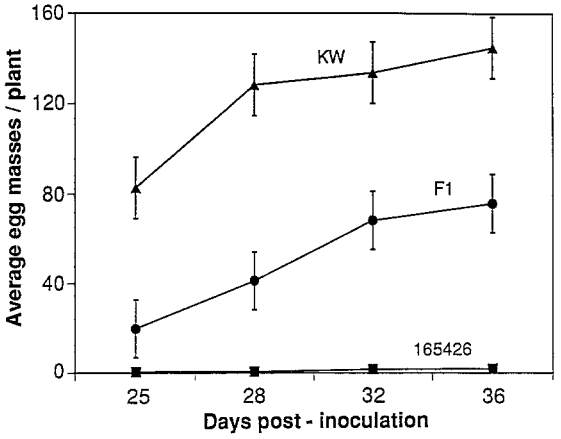

Fig. 1. Egg masses of *M. incognita* produced 25–36 days after inoculation on resistant PI 165426 and susceptible Kentucky Wonder (KW) parents and their F_1, maintained at 28 °C. *Bars* are standard errors

Table 5. Reaction of parental lines, F_1, and F_2 populations of the cross PI 165426 × Kentucky Wonder (KW) to *Meloidogyne incognita* race 3 at 24° and 28 °C

	24 °C					28 °C			
	Obs. freq.					Obs. freq.			
	R	I	S	χ^2 (3:1)	χ^2 (13:3)	R	I	S	χ^2 (1:2:1)
PI 165426	5	0	0	–	–	7	0	0	–
KW	0	0	7	–	–	0	0	5	–
165426 × KW-F_1	5	0	0	–	–	0	6	0	–
165426 × KW-F_2	84	0	25	0.25	1.25	35	74	44	0.63
P value				50–90	10–50				50–90

R – indicates resistant reaction (similar to PI 165426)
I – indicates intermediate reaction (similar to F_1)
S – indicates susceptible reaction (similar to KW)

supported between PI 165426 (resistant parent) and F_1 plants. However, at 28 °C egg mass numbers on F_1 plants were intermediate between susceptible KW and PI 165426 (Fig. 1). The genetic data showed a good fit to 3:1 (Resistant:Susceptible) ($\chi^2 = 0.25$) and satisfactory fit to 13:3 (Resistant:Susceptible) ($\chi^2 = 1.25$) at 24 °C and a good fit to 1:2:1 (Resistant:Intermediate:Susceptible) ($\chi^2 = 0.63$) at 28 °C (Table 5).

The experiment was also repeated for F_1 and F_2 plants involving KW and A445, which carries the gene *Me1* (Omwega et al. 1990a). F_1 plants of the cross A445 × KW showed intermediate reaction to *M. javanica* at 28 °C. Although F_2 plants did not give satisfactory 1:2:1 ratios, when susceptible and intermediate plants were grouped together, a satisfactory 1 Resistant:3 Susceptible ratio ($\chi^2 = 1.17$) was obtained, indicating that the dominance of gene *Me1* was diminished or lost at 28 °C. F_1 plants of the cross PI 165426 × Alabama no. 1 also supported intermediate numbers of egg masses of *M. incognita* race 3 at 28 °C.

F_3 families of the cross PI 165426 × KW were inoculated with 1,000 J_2 of *M. incognita* race 3 and divided into two groups; one group was incubated at 24 °C and the other group was incubated at 28 °C. Egg masses on the roots were enumerated at 28 days post-inoculation. Data from this experiment are given in Table 6. The data were interpreted and genotypes were assigned, based on the model of one dominant and one recessive gene and a dominant suppressor locus of the recessive gene. Two families were resistant at both temperatures and therefore their F_2 genotype was predicted as *--Me2Me2*. Six families were all resistant at 24 °C, but segregated at 28 °C and their genotype was designated as *llMe2me3*. One family was all resistant at 24 °C and all susceptible at 28 °C and its genotype was designated as *llme2me3*. Two families segregated at both temperatures and their genotype was designated as *L-Me2me3*; and four families segregated at 24 °C and were all susceptible at 28 °C and their genotypes were designated as *Llme2me3*. The *L* locus is proposed as the dominant suppressor of the recessive gene *me3*.

Table 6. Reaction of F_3 families of the cross PI 165426 × KW to *Meloidogyne incognita* race 2 at 24° and 28 °C

No. of F_3 families	Phenotype		Genotype
	24 °C	28 °C	
2	R	R	*--Me2Me2*
6	R	R/S	*llMe2me3*
1	R	S	*llme3me3*
2	R/S	R/S	*L-Me2me3*
4	R/S	S	*Llme3me3*

R – All plants in the family resistant
S – All plants susceptible
R/S – Plants segregating for resistance

Discussion

Sensitivity of host plant resistance genes to high temperature indicated by a shift towards susceptibility has been reported for several plant-nematode systems. In our study, we have used both the effects of temperature on the expression of resistance and the differential resistance to different root-knot nematode isolates in the genetic analysis of root-knot nematode resistance in common bean (see Omwega et al. 1989, 1990a, b). In this study we found that resistance to *Meloidogyne* spp. in PI 165426, PI 165435, and Alabama no. 1 was effective against the same isolates of *M. incognita*, but these lines were susceptible to the nematode isolates to which lines A315 and

Table 7. Reaction of resistant common bean lines to different species of root-knot nematodes showing complementary relationship between the resistance in "PI" and Alabama lines, on the one hand, and that of the "A" lines, on the other

	M. incognita	*M. javanica*	*M. arenaria*
PI 165426	R	S	S
PI 165435	R	S	S
Alabama no. 1	R	S	S
A315	S	R	R
A445	S	R	R

R – resistant reaction: plants of the bean line support an average of less than 13 egg masses per root system
S – susceptible reaction: plants of the bean line support an average of 13 or more egg masses per root system

A445 were resistant. Thus, resistance in these two groups of bean lines is complementary (Table 7). This finding of complementarity agrees with data from an earlier study (Omwega et al. 1989), even though nematode isolates used in this study were different from those used in the earlier study. In this study, PI 165426, PI 165435, and Alabama no. 1 were resistant to both isolates of *M. incognita* race 1, while A315 and A445 carrying gene *Me1* (Omwega et al. 1990 a) were susceptible to those two isolates of *M. incognita* race 1. These data are the reverse of what was reported earlier with a different *M. incognita* race 1 isolate (Omwega et al. 1989, 1990 a). This could be because bean lines PI 165426, PI 165435, and Alabama no. 1 are resistant to some isolates of *M. incognita* race 1 but susceptible to others. Similarly, in the pattern of complementarity, gene *Me1* carried in A315 and A445 is resistant to some isolates of *M. incognita* race 1 and susceptible to others. In the earlier study, identity of the cultures used was checked by perineal patterns of mature females at the beginning of the study, a less definitive criterion for species identity than isoenzyme phenotype, and possibility of contamination during that study cannot be ruled out completely.

The differential resistance reactions to diverse isolates of *Meloidogyne* spp. could be used to differentiate those bean lines possessing gene *Me1* from those with resistance to *M. incognita*. Temperature data provided some evidence that the three bean lines with resistance to *M. incognita* could be divided into two groups. Bean lines PI 165435 and Alabama no. 1 with recessive resistance were resistant at 24° and 26 °C, but susceptible at 28 °C, while PI 165426 with dominant resistance was resistant at 28 °C. With this information of the behavior of these resistance genes at different temperatures and assuming a dominant suppressor locus for gene *me3*, we were able to assign genotypes for the F_3 families of the cross PI 165426 × KW based on their reaction at 24° and 28 °C. However, this interpretation is based on limited data and should be subjected to further genetic analysis.

Initial inoculum density was not an important factor in host reaction of PI 165426. Inoculum-temperature interaction indicated that PI 165435 expresses a higher level of resistance than Alabama no. 1. It is not known whether this difference is genetic. Our preliminary data (not shown) indicate that resistance in PI 165435 and Alabama no. 1 is controlled by one or two recessive genes. Resistance in Alabama no. 1 is reported to be under the control of two (Barrons 1939) or three (Hartmann 1970) recessive genes.

The segregation of progeny data obtained from PI 165426 crossed with susceptible KW and G4017 tested at ≤ 26 °C indicated that resistance in PI 165426 is under the control of one dominant and one recessive gene. In some cases the data also fit a one dominant gene model. However, the segregation for resistance in some F_3 families that were derived from susceptible F_2 plants was consistent with a one dominant and one recessive gene model. We propose to assign *Me2me3* as the genotype for the resistance to *M. incognita* in PI 165426.

Since resistance which is controlled by recessive genes in Alabama no. 1 and PI 165435 was effective at 26 °C and not at 28 °C, the temperature at which the transition from resistance to susceptibility occurs was shown to be lower for resistance conferred by recessive genes than that conferred by dominant genes. The transition for recessive resistance occurs when temperature is increased from 26° to 28 °C, while transition for resistance conferred by dominant genes occurs when temperature is increased from 28° to 30 °C (Omwega et al. 1989). Bean line PI 165426 with resistance conferred by one dominant and one recessive gene provided an opportunity to further test this model of dominance determining the temperature at which transition from resistant to susceptible phenotype occurs. Segregation at 26 °C of F_2 populations of PI 165426 crossed with KW or G4017 showed segregation at two loci, one of which was recessive. Since transition to susceptibility of recessive resistance occurs when temperature is increased to 28 °C, it would be expected that F_2 populations screened at 28 °C will show segregation at a single locus. We found that F_1 plants were intermediate in resistance response at 28 °C, and the segregation ratios of F_2 plants fit a 1:2:1 ratio. From these data we inferred that the effect of the recessive gene was lost, and that the dominance of the dominant gene in PI 165426 was diminished or lost at 28 °C. Therefore, this finding was consistent with the conclusion that the effect of a recessive gene is lost when temperature is increased from 26° to 28 °C. The data further indicated that at 28 °C the dominant gene showed allelic dosage response, whereby a single copy of the resistance gene confers partial resistance while two copies confer complete resistance. Loss of dominance at 28 °C was also demonstrated with gene *Me1*, which is dominant at 26 °C. In Table 8 a summary is presented of root-knot

Table 8. Summary of nematode resistance genes and their reaction at low and high temperature

Bean	Resistance genes		Nature of resistance	
	Number	Symbol	Low temp. (26 °C)	High temp. (28 °C)
G1805, A445	1	*Me1*	Dominant	Semidominant
G2618, A315	1	*Me1*	Dominant	Semidominant
PI 165426	2	*Me2me3*	Dominant	Semidominant
PI 165435	1 or 2[a]	–	Recessive	Susceptible
Alabama no. 1	1 or 2[a]	–	Recessive	Susceptible

[a] Data not conclusive to confirm whether one or two recessive genes confer resistance

nematode resistance genes in common bean genotypes that indicates gene expression at low and high temperature, based on data presented here and on earlier reports.

Shift from dominance to recessiveness due to temperature has been reported for resistance genes in other systems. For example in wheat, gene *Sr6*, which confers resistance to stem rust, was found to be dominant at 18 °C, but recessive at 25 °C, and other wheat stem rust resistance genes *Sr5*, *Sr8*, and *Sr9* became susceptible or semisusceptible at or above 27 °C (Luig and Rajaram 1972). Resistance to Hessian fly in wheat showed allelic dosage response at 28 °C, whereby heterozygous plants were less resistant than homozygous plants (Tyler and Hatchett 1983). The present study for the first time demonstrates this phenomenon for plant-nematode interaction. Our data underscores the importance of taking into account temperature effects in the study of genetics of plant-nematode interactions. This information is also useful in breeding for resistance to root-knot nematodes in common bean in different regions, as it indicates the temperature range under which the resistance genes will be effective.

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