Genetic Analysis of *Meloidogyne arenaria* Race 1 Resistance in Tobacco

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ABSTRACT

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Inheritance of resistance to the peanut root-knot nematode (*Meloidogyne arenaria* (Neal) Chitwood race 1) was investigated in the flue-cured tobacco cv. Speight G 28 and the breeding lines 81-RL-2K and SA 1214. The genetic relationship of this resistance in Speight G 28 to the resistance of the same cultivar to races 1 and 3 of *M. incognita* was also studied. Crosses were made between the root-knot nematode-susceptible flue-cured tobacco cv. NC 2326 and the three resistant genotypes. Parental, F₁, F₂ and backcross generations (BC₁P₁, BC₁P₂) were grown for each cross in randomized complete block designs with five replications in the greenhouse. Data indicated that resistance to *M. arenaria* race 1 in the three resistance sources is conditioned by a single dominant gene, but this resistance is partial compared to that for *M. incognita* races 1 and 3. Further, resistance to races 1 and 3 of *M. incognita* and resistance to *M. arenaria* race 1 in cv. Speight G 28 appear to be controlled by the same gene. These results, combined with the absence of segregation in the F₂ populations of the crosses between resistant parents 81-RL-2K × SA 1214, 81-RL-2K × Speight G 28, and SA 1214 × Speight G 28, suggest allelism of resistance among these genotypes.

Additional keywords: allelism, peanut root-knot nematode

The incidence of *Meloidogyne arenaria* (Neal) Chitwood in North Carolina and South Carolina on tobacco (*Nicotiana tabacum* L.) has been increasing in the past few decades, primarily due to the frequent use of cultivars having resistance to *M. incognita* (Kofoed and White) Chitwood races 1 and 3, and lack of effective nematocides such as ethylene dibromide (1,7,17).

Race 1 of *M. arenaria*, also commonly called the peanut root-knot nematode, is among the most important races of the four major root-knot nematodes causing root-knot disease in tobacco in certain regions (2-4,11). Resistance to this race in tobacco has been reported not only within the germ plasm pools of related *Nicotiana* spp., but also in a number of breeding lines (6,14) and in commercial flue-cured tobacco cultivars carrying the *Rk* gene for resistance against races 1 and 3 of *M. incognita* (2,3,14,18).

The genetics of resistance to race 1 of *M. arenaria* has not been reported. This information is vital in designing the most efficient breeding strategies to incorporate resistance into desired elite breeding lines or cultivars. The objectives of the study

were to (i) determine the inheritance of resistance to *M. arenaria* race 1 in tobacco breeding lines 81-RL-2K and SA 1214, and in the commercial flue-cured tobacco cv. Speight G 28; (ii) elucidate the genetic relationship of resistance among the three resistant genotypes; and (iii) determine whether or not the single dominant gene conferring resistance to races 1 and 3 of *M. incognita* is also responsible for the resistant reaction to *M. arenaria* race 1.

MATERIALS AND METHODS

Inheritance experiments. Crosses were made between the universal root-knot nematode-susceptible commercial flue-cured tobacco cv. NC 2326 and three genotypes resistant to *M. arenaria* race 1 and *M. incognita* races 1 and 3 (SA 1214, Speight G 28, and 81-RL-2K) to obtain F₁, F₂, BC₁P₁, and BC₁P₂ seed. Seed of each of parental genotype, F₁, F₂, and backcross generations to each of the parents was germinated in seedling trays containing Metro-Mix 220 (Grace-Sierra Horticultural Products Co., Milpitas, CA), covered with a clear polyethylene film, and placed in a growth chamber at 25°C with a 16-h photoperiod having a light intensity of 400 ± 50 µEm⁻²s⁻¹. A total of 15 4-week-old seedlings of each of the parental genotypes and the F₁ generation, and 100 seedlings of the F₂ and backcross generations to each of the parents, were singly transplanted into sterilized 10-cm-diameter clay pots containing a 1:1 (vol:vol) mixture of steam-sterilized sand and sandy loam soil (85%

sand, 10% silt, 5% clay) for each experiment. Seedlings were transferred to a greenhouse and allowed to recover from transplanting shock for a week prior to inoculation.

Seedlings of each cross were individually inoculated with 10,000 eggs of *M. arenaria* race 1 delivered in 30-ml aqueous suspensions. Eggs for inocula were collected using a sodium hypochlorite (NaOCl) technique (10) from galled roots of tomato (*Lycopersicon esculentum* cv. Rutgers) on which *M. arenaria* race 1 was maintained in greenhouse pot cultures. Extra plants of cv. NC 2326 also were inoculated with the same pathogen to determine root-knot nematode reproduction and disease development before terminating the experiment. Non-inoculated plants of cv. NC 2326, randomly located in each replicate of the experiment, served as checks for any contamination due to extraneous sources of inoculum. Each experiment utilized a randomized complete block design with five replications, each having 3 individual plants of parental genotypes and the F₁ generation and 20 individual plants of each of the F₂ and backcross generations to each of the parents. Basic nutrients were supplied by periodic watering, as needed, with either 20:20:20 (N:P₂O₄:KOH) Peter's (Grace-Sierra) at 741 µg/ml nitrogen, or Hoagland's solution (9).

The experiment was conducted twice for each cross. Experiments for the cross Speight G 28 × NC 2326 were conducted from 17 May to 26 July 1994 and 4 November 1994 to 24 January 1995 and the mean daily greenhouse temperatures were 29 ± 2°C and 25 ± 2°C, respectively. Experiments for the cross SA 1214 × NC2326 were conducted from 17 June to 16 August 1994 and 23 September to 21 November 1994 and the mean daily greenhouse temperatures were 30 ± 2°C and 29 ± 3°C, respectively. Experiments for the cross 81-RL-2K × NC 2326 were conducted from 31 December 1994 to 3 March 1995 and 1 March to 17 May 1995 and the mean daily temperatures were 28 ± 1°C and 25 ± 3°C, respectively.

At 8 to 11 weeks after inoculation, all plants were assessed for percent root area galled (4). Percent root area galled values were converted to a root-knot gall index as follows: 0 = no visible galls, 1 = 1 to 10%, 2 = 11 to 20%, 3 = 21 to 30%, 4 = 31 to 40%, 5 = 41 to 50%, 6 = 51 to 60%, 7 = 61 to 70%, 8 = 71 to 80%, 9 = 81 to 90%, 10 ≥ 91% root area galled. Other variables

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measured included percent root necrosis (4) and nematode reproduction (number of eggs/g root) extracted from individual 5-g root samples using a NaOCl extraction technique (10). Data were analyzed using the GLM and CORR procedures of SAS (Statistical Analysis System, SAS Institute, Cary, NC).

Relationship of resistance to *M. arenaria* race 1 and resistance to races 1 and 3 of *M. incognita*. Parental, F₁, and F₂ generations, and the control cv. NC 95 were also screened for their reaction to the NC 138 isolate of the M^{SNR} strain of potato virus Y (PVY). This virus produces necrotic lesions on *M. incognita*-resistant plants because of pleiotropic effects of the single dominant gene (*Rk*, 19) conferring *M. incognita* races 1 and 3 resistance (8,16). Two 8.5 ± 1.3-cm detached leaves of each plant were trimmed around the petiole and placed in plastic boxes (24 by 30 by 6 cm) with hinged lids containing 2-cm-deep water. Petioles were submerged in the water, and laminae were suspended over wire mesh above the water surface. Boxes were closed after inoculation and placed on a laboratory bench until symptoms developed. Inoculum was prepared by grinding systemically infected leaf tissue in a blender, using 1 g of tissue per 2 ml of 0.05 M Na₂ HPO₄-KH₂PO₄ buffer (pH 7.2). Carborundum (22-μm, 600-mesh) was added to the inoculum (10 mg of carborundum per 1 ml of inoculum) to serve as an abrasive. Leaves were rubbed with a cotton swab dipped in inoculum, then rinsed with water. Necrotic lesions appeared within 7 to 10 days in leaves from plants resistant to *M. incognita*.

Allelism tests. Crosses were made among the three resistant genotypes SA 1214, Speight G 28, and 81-RL-2K to obtain F₁ and F₂ seed. These crosses were used to determine whether resistance among these genotypes to *M. arenaria* race 1 was conditioned by the same or different gene loci. F₁ and F₂ generations of the three crosses were screened for resistance to *M. arenaria* race 1 under greenhouse conditions (daily mean temperature was 27 ± 3°C). Each cross was evaluated in a randomized complete block design with five replications. Each replicate consisted of two individual plants of parental and F₁ generations, 21 of the F₂ generation and one of the susceptible control NC 2326. All experiments were conducted in the same greenhouse from 16 July to 9 October 1995, measuring the same variables as above at termination of the experiments.

RESULTS

Inheritance studies. Except for highly susceptible control and progenies, root-knot egg population at termination of the tests generally paralleled root-knot galling. The highly susceptible plants typically exhibited severe root necrosis, resulting in lower egg numbers. Because of this, these data are not presented.

All resistant parents (SA 1214, Speight G-28, and 81-RL-2K) were assigned gall index ratings of 0, 1 and 2, whereas individual plants of the susceptible parent, NC 2326, were classified into four classes (6-9; Table 1). The reactions of plants of the resistant and susceptible parents were as expected, indicating that the criterion of

root-knot gall index of ≤3 for designating resistance, or >3 for designating susceptible classes, was valid. Individual plants of the F₁ generation were categorized into four classes (class 0, 1, 2, and 3) for the cross involving SA 1214, three classes (class 0, 1, and 2) for Speight G 28 × NC 2326 cross, and two classes (class 1 and 2) for the 81-RL-2K × NC 2326 cross. Individual plants of the backcross of F₁ to each of the resistant parents (BC₁P₁) were classified into four classes (class 0, 1, 2, and 3). Distinct bimodal distributions were evident in F₂ and BC₁P₂ generations of all crosses. Therefore, chi-square goodness of fit tests were used to fit a simple Mendelian gene model to root-knot gall index data from the crosses. However, BC₁P₂ data from the second run of the cross 81-RL-2K × NC 2326 did not fit a single gene model. Trends on the second run for the cross 81-RL-2K × NC 2326 were similar to those of the first run, with the F₂ data fitting a 3:1 ratio, but several plants were susceptible within the BC₁P₁ generation. Because of this, data from the second run of this cross were excluded from further analysis. Data from the other crosses were pooled over the two runs because analysis of variance using the GLM procedure of SAS (SAS Institute) indicated that run, replicate, and run × generation effects were not significant.

All parents responded as expected; that is, all 30 plants of cvs. SA 1214 or Speight G 28 and 15 plants of 81-RL-2K were resistant, and all of NC 2326 in each cross were susceptible (Table 2). F₁ plants of each cross were resistant, indicating that resistance was dominant over susceptibility

Table 1. Frequency (%) distribution of resistant and susceptible genotypes in parental and progeny generations as based on a root-knot gall index from three tobacco crosses after inoculation with *Meloidogyne arenaria* race 1 pooled over two runs^a

Cross and generation ^c	No. of plants	Root-knot gall index (0–10 scale) ^b										
		0	1	2	3	4	5	6	7	8	9	10
SA 1214 × NC 2326												
P ₁	30	13.3	80.0	6.7	...	...	...	...	...	...	...	...
F ₁	30	3.3	80.0	13.4	3.3	...	...	...	...	...	...	...
F ₂	200	11.0	55.5	10.5	1.0	4.0	4.0	8.0	1.5	1.5	3.0	...
BC ₁ P ₁	200	13.5	72.5	13.0	1.0	...	...	...	...	...	...	...
BC ₁ P ₂	200	9.0	32.5	9.0	5.0	5.0	5.5	6.0	12.0	7.0	9.0	...
P ₂	30	...	...	...	...	...	...	3.3	26.7	43.3	26.7	...
Speight G-28 × NC 2326												
P ₁	30	6.7	80.0	13.3	...	...	...	...	...	...	...	...
F ₁	30	3.3	93.4	3.3	...	...	...	...	...	...	...	...
F ₂	200	5.0	72.0	3.0	0.5	0.5	1.0	5.5	7.5	2.0	3.0	...
BC ₁ P ₁	200	7.5	86.0	6.0	0.5	...	...	...	...	...	...	...
BC ₁ P ₂	200	3.5	46.5	3.5	1.5	1.0	0.5	7.5	15.5	13.0	7.5	...
P ₂	30	...	...	...	...	...	...	20.0	23.3	40.0	16.7	...
81-RL-2K × NC 2326												
P ₁	15	...	100	...	...	...	...	...	...	...	...	...
F ₁	15	86.7	13.3	...	...	...	...	...	...	...	...	...
F ₂	99	1.0	55.6	17.2	2.0	4.0	4.0	8.1	8.1	...	...	...
BC ₁ P ₁	99	1.0	82.8	15.2	1.0	...	...	...	...	...	...	...
BC ₁ P ₂	100	0	35.0	13.0	2.0	7.0	9.0	13.0	17.0	2.0	2.0	...
P ₂	15	...	...	...	...	...	6.7	20.0	33.3	40.0	...	...

^a Data for the cross 81-RL-2K × NC 2326 are from the first run only.

^b Rating was from 0 (no visible galls) to 10 (severe galling) in 10% increments. Plants with root-knot indices of ≤3 were considered resistant and >3 were considered susceptible.

^c P₁ = resistant parent SA 1214, Speight G-28, or 81-RL-2K; P₂ = susceptible parent NC 2326; F₁ = P₁ × P₂; F₂ = F₁ × F₁; BC₁P₁ = F₁ × P₁; BC₁P₂ = F₁ × P₂.

Table 2. Response of parental and progeny generations of three tobacco crosses to inoculation with *Meloidogyne arenaria* race 1 based on a root-knot gall index pooled across two runs^a

Cross and generation ^c	Number of plants ^b		Expected ratio	Chi-square	P
	Resistant	Susceptible			
SA 1214 × NC 2326					
P ₁	30	0	all R	...	...
F ₁	30	0	all R	...	...
F ₂	156	44	3:1	0.96	0.41
BC ₁ P ₁	200	0	all R	...	...
BC ₁ P ₂	111	89	1:1	2.42	0.15
P ₂	0	30	all S	...	...
Speight G-28 × NC 2326					
P ₁	30	0	all R	...	...
F ₁	30	0	all R	...	...
F ₂	161	39	3:1	3.23	0.08
BC ₁ P ₁	200	0	all R	...	...
BC ₁ P ₂	111	89	1:1	2.42	0.15
P ₂	0	30	all S	...	...
81-RL-2K × NC 2326					
P ₁	15	0	all R	...	...
F ₁	15	0	all R	...	...
F ₂	76	24	3:1	0.05	0.84
BC ₁ P ₁	98	0	all R	...	...
BC ₁ P ₂	50	50	1:1	0.00	1.00
P ₂	0	15	all S	...	...

^a Data for the cross 81-RL-2K × NC 2326 are from the first run only.

^b Rating was from 0 (no visible galls) to 10 (severe galling) in 10% increment. Plants with root-knot indices of ≤3 were considered resistant and >3 were considered susceptible.

^c P₁ = resistant parent SA 1214, Speight G-28, or 81-RL-2K; P₂ = susceptible parent NC 2326; F₁ = P₁ × P₂; F₂ = F₁ × F₁; BC₁P₁ = F₁ × P₁; BC₁P₂ = F₁ × P₂.

Table 3. Reaction of parental, F₁, and F₂ generations of three crosses of tobacco and the control cv. NC 95 to inoculation with *Meloidogyne arenaria* race 1 and correlated response to the M^SN^R strain of potato virus Y (PVY) across two runs^a

Cross and generation ^c	No. of plants	Nematode/PVY-M ^S N ^R reaction ^b			
		R/N	R/S	S/N	S/S
SA 1214 × NC 2326					
P ₁	20	20	0	0	0
F ₁	19	19	0	0	0
F ₂	191	145	0	0	46
P ₂	20	0	0	0	20
NC 95 (control)	5	5	0	0	0
Speight G-28 × NC 2326					
P ₁	30	30	0	0	0
F ₁	30	30	0	0	0
F ₂	200	161	0	0	39
P ₂	30	0	0	0	30
NC 95 (control)	10	10	0	0	0
81-RL-2K × NC 2326					
P ₁	15	15	0	0	0
F ₁	14	14	0	0	0
F ₂	100	76	0	0	24
P ₂	15	0	0	0	15
NC 95 (control)	10	10	0	0	0

^a Data for the cross 81-RL-2K × NC 2326 are from the first run only.

^b R/N = resistant/necrotic, R/S = resistant/systemic or non-necrotic, S/N = susceptible/necrotic, S/S = susceptible/systemic or non-necrotic. Rating was based on a gall index system from 0 (no visible galls) to 10 (severe galling) in 10% increments. Plants with root-knot indices of ≤3 were considered resistant and >3 were considered susceptible.

^c P₁ = resistant parent SA 1214, Speight G-28, or 81-RL-2K; P₂ = susceptible parent NC 2326; F₁ = P₁ × P₂; F₂ = F₁ × F₁; BC₁P₁ = F₁ × P₁; BC₁P₂ = F₁ × P₂.

in all resistant genotypes. F₂ plants segregated three resistant to one susceptible with chi-square values of 0.96 ($P = 0.41$), 3.23 ($P = 0.08$), and 0.05 ($P = 0.84$) for the crosses SA 1214 × NC 2326, Speight G 28 × NC 2326, and 81-RL-2K × NC 2326, respectively. All plants of the backcross of F₁ to the resistant parents SA 1214, Speight G 28, and 81-RL-2K were resistant. Plants of the backcross of the F₁

to the susceptible parent, NC 2326, segregated one resistant to one susceptible with chi-square value of 2.42 ($P = 0.15$) in the SA 1214 × NC 2326 and Speight G 28 × NC 2326 crosses, and 0.00 ($P = 1.00$) for the 81-RL-2K × NC 2326 cross. These data further confirmed involvement of a single dominant gene for resistance to *M. arenaria* race 1 in SA 1214, Speight G 28 and 81-RL-2K.

Relationship of *M. arenaria* race 1 resistance and resistance to races 1 and 3 of *M. incognita*. All plants of the resistant parents were resistant to the nematode and necrotic in response to the M^SN^R strain of PVY (Table 3). Individual plants of cv. NC 2326 in all crosses were susceptible to the nematode and non-necrotic to the virus (the virus became systemic). Individual F₁ plants of each cross reacted similarly to their corresponding resistant parents. All plants of the F₂ generation that were resistant to the nematode were also necrotic to the virus. Also, all those which were classified as susceptible to the nematode were non-necrotic to the virus, segregating in a dominant fashion of three resistant to the nematode and necrotic to the virus, and one susceptible to the nematode and non-necrotic to the virus. A perfect, positive correlation ($R^2 = 1$) between reaction of plants to each of the nematode species and to the virus indicate that the same gene confers resistance to the nematode and the necrotic reaction to the virus. Both NC 95 and Speight G 28 have a single dominant gene conditioning resistance to races 1 and 3 of *M. incognita* (16), and necrotic reaction to M^SN^R strain of PVY. Examination of the pedigrees of both SA 1214 and 81-RL-2K indicated that *M. incognita*-resistant flue-cured commercial cultivars form part of the pedigree of these breeding lines (5,12).

Allelism tests. All individual parental plants of SA 1214, Speight G 28, and 81-RL-2K and the F₁ and F₂ generations from the crosses among the resistant genotypes were resistant (root gall index <3). Thus, no segregation was observed in F₂ generations among the three crosses (Table 4). Individual plants of the susceptible control NC 2326 had root-knot gall index values ranging from 6 to 9.

DISCUSSION

Our results show that resistance to *M. arenaria* race 1 in breeding lines SA 1214 and 81-RL-2K and the flue-cured tobacco cv. Speight G 28 is conditioned by a single dominant gene. We also propose that resistance from the three sources is allelic. Lack of segregation in the F₂ generations from resistant × resistant crosses indicated that resistance from the three sources is probably conditioned by the same dominant gene.

It has been further postulated that resistance to *M. arenaria* race 1 is governed by the same gene conferring resistance to races 1 and 3 of *M. incognita*. To test this hypothesis, F₁ and F₂ generations of the crosses between the resistant parents (SA 1214, Speight G 28, and 81-RL-2K) and the susceptible parent (NC 2326) were screened for their reaction to isolate NC 138 of the M^SN^R strain of PVY. The data obtained showed that resistance to *M. arenaria* race 1 and *M. incognita* races 1 and 3 was under the influence of the same genetic system. The positive, perfect cor-

Table 4. Allelism tests for *Meloidogyne arenaria* race 1 resistance among resistant tobacco genotypes Speight G-28, SA 1214, and 81-RL-2K

Cross and generation ^a	No. of plants	Resistant ^b	Susceptible ^b
Speight G-28 × SA 1214			
Speight G-28	10	10	0
SA 1214	10	10	0
F ₁	10	10	0
F ₂	104	104	0
NC 2326 (control)	5	0	5
Speight G-28 × 81-RL-2K			
Speight G-28	10	10	0
81-RL-2K	9	9	0
F ₁	10	10	0
F ₂	105	105	0
NC2326 (control)	5	0	5
SA 1214 × 81-RL-2K			
SA 1214	10	10	0
81-RL-2K	10	10	0
F ₁	10	10	0
F ₂	105	105	0
NC 2326 (control)	5	0	5

^a P₁ = resistant parent SA 1214, Speight G-28, or 81-RL-2K; P₂ = susceptible parent NC 2326; F₁ = P₁ × P₂; F₂ = F₁ × F₁; BC₁P₁ = F₁ × P₁; BC₁P₂ = F₁ × P₂.

^b Rating was based on a gall index system from 0 (no visible galls) to 10 (severe galling) in 10% increments. Plants with root-knot indices of ≤3 were considered resistant and >3 were considered susceptible.

relation between reactions to the virus and to the nematode in plants of both tobacco breeding lines SA 1214 and 81-RL-2K and the commercial flue-cured tobacco cv. Speight G 28 confirmed our expectations. It should be indicated, however, that resistance to *M. arenaria* race 1 is incomplete when compared to that for *M. incognita* races 1 and 3. This difference suggests that *M. arenaria* race 1 could have an additional gene for parasitism that is absent in *M. incognita* races 1 and 3.

The simple nature of inheritance of this resistance suggests that it can be incorporated relatively easily into suitable elite breeding lines or commercial flue-cured tobacco cultivars with desirable attributes. This gene is already present in many commercial flue-cured tobacco cultivars released since the release of the first root-knot nematode-resistant tobacco cv. NC 95 (2). Resistance to *M. arenaria* race 1, and races 1 and 3 of *M. incognita* from the three sources (SA 1214, Speight G 28, and 81-RL-2K), is controlled by the same gene, representing a narrow genetic base; therefore, the identification of additional sources of resistance will be important because repeated use of this resistance may select resistance-breaking biotypes. Also,

of long-term importance, the low level of nematode reproduction on these resistant genotypes could be sufficient to result in economic damage on susceptible crops such as peanut. This loss of resistance has occurred in other crops, such as tomato (15). Fortunately the *Rk* gene has remained effective against races 1 and 3 of *M. incognita* since its deployment in 1961 (11). With continuous usage in monoculture, however, its effectiveness may be lost (1,13).

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