Inheritance of Root-knot Resistance in the Cowpea 
\textit{(Vigna unguiculata (L.) Walp.)}\(^1\)

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Abstract. The inheritance of resistance in cowpea to root knot incited by the root-knot nematodes \textit{Meloidogyne incognita} (Kofoid & White) Chitwood, \textit{M. javanica} (Treub.) Chitwood, and \textit{M. hapla} Chitwood was determined in 3 separate greenhouse experiments. Each seed was inoculated at planting with about 2,000 eggs of the appropriate \textit{Meloidogyne} species. In Experiment I, plants of parental, F\(_1\), F\(_2\), and F\(_1\) x F\(_1\) and F\(_1\) x F\(_2\) backcross generations of a cross between the resistant cultivar 'Mississippi Silver' and the susceptible breeding line CR 18-13-1 were tested for reaction to \textit{M. incognita}. In Experiment II, plants of parental, some F\(_1\), and all F\(_2\) generations of a series of crosses involving CR 18-13-1 and the resistant lines 'Colossus', 'Mississippi Silver', 'Iron', and PI 353383 were evaluated for resistance to \textit{M. incognita}. In Experiment III, plants of parental, F\(_1\), and 30 randomly chosen F\(_2\) lines of the 'Mississippi Silver' x CR 18-13-1 cross were evaluated in separate tests for reaction to \textit{M. incognita}, \textit{M. javanica}, and \textit{M. hapla}. A single dominant gene determined resistance to \textit{M. incognita}, \textit{M. javanica}, and \textit{M. hapla}; the same gene governed resistance in 'Colossus', 'Mississippi Silver', 'Iron', and PI 353383. The gene conditioned a high level of resistance, but it did not confer immunity. Roots of many resistant plants exhibited limited galling and supported some egg production by the parasites. We propose that this gene be designated \textit{Root-knot resistance} and symbolized \textit{Rk}.

Root knot, a disease incited by several species of the root-knot nematode genus \textit{Meloidogyne}, is one of the major root diseases of cowpeas, \textit{Vigna unguiculata}, in the United States. The southern root-knot nematode, \textit{M. incognita}, is the predominant species pathogenic on cowpeas, but the Javanese root-knot nematode, \textit{M. javanica}, is the most common species in some areas, e.g. southern California. The peanut root-knot nematode, \textit{M. arenaria} (Neal) Chitwood, and the northern root-knot nematode, \textit{M. hapla}, also attack the crop. Parasitism of susceptible cultivars often significantly reduces yield. Toler et al. (15) estimated that \textit{M. incognita} is responsible for annual yield losses of 5 to 10\% in Georgia. Dukes et al. (2) conducted field tests in South Carolina and they showed that nematocide treatment of \textit{M. incognita}-infested soil increased the seed yields of susceptible cultivars by 5 to 69\%. Webber and Orton's (16) 1902 report of resistance in the cowpea cultivar 'Iron' was one of the first reports of resistance in crop plants to root knot. Although breeding programs to incorporate resistance into cultivated cowpeas have been highly successful (6, 7, 10, 11), root-knot resistance has not been a high priority breeding objective. Several leading horticultural "southernpea" cultivars are root-knot susceptible.

The genetics of root-knot resistance in cowpea is not well documented. Orton (12), Mackie (11), Hawthorne (7), and Jones and Isbell (9) reported that resistance is dominant to susceptibility. Hare (5) studied the inheritance of resistance to \textit{M. incognita} in 80 F\(_2\) progenies of a cross between the resistant breeding line M455 and the susceptible 'Brown Sugar Crowder', and he suggested that resistance was governed by a single dominant gene. Amosu and Frankowiak (1) crossed each of the resistant cultivars 'Mississippi Silver' and 'Victor K798' with susceptible cultivars and inoculated the resulting F\(_2\) progeny populations with \textit{M. incognita}. Their data support Hare's (5) single dominant gene hypothesis. Although there are no published genetic data on resistance of cowpea to \textit{Meloidogyne} species other than \textit{M. incognita}, the reactions of a number of cowpea lines to 2 or more \textit{Meloidogyne} species have been reported. Hare (5) evaluated the reactions of 14 lines to \textit{M. incognita}, \textit{M. incognita acrita}, \textit{M. javanica}, and \textit{M. arenaria} and he found that 5 lines ("Iron", M255, M455, M755, and M855) were resistant and 9 lines were susceptible to all tested \textit{Meloidogyne} species. This data suggest that root-knot resistance is general for all \textit{Meloidogyne} species. Thomason and McKinney (14), however, tested 44 cowpea lines for the reactions to \textit{M. incognita acrita} and \textit{M. javanica} and found that all of the lines showed some resistance to \textit{M. incognita acrita}, but were moderately to highly susceptible to \textit{M. javanica}. They also reported that the asparagus bean, \textit{V. unguiculata} (L.) Walp. subsp. \textit{sesquipedalis} (L.) Verdc., was resistant to \textit{M. hapla} but susceptible to \textit{M. incognita}, \textit{M. incognita acrita} and \textit{M. javanica}. Because much of the available data are preliminary or limited, we initiated a series of experiments to obtain more definitive data on the inheritance of root-knot resistance in cowpea.

Materials and Methods

The data reported here are from a series of greenhouse experiments conducted at the U. S. Vegetable Laboratory, Charleston, South Carolina. Egg inocula for all tests were extracted from cowpea, sweet potato, or tomato roots infected with root-knot nematode using 0.525\%-sodium hypochlorite in a procedure described by Hussey and Barker (8). The tests were conducted in 4.1 x 1.7 x 0.2 m benches containing a steam-sterilized mixture of about 6 soil:3 sand:1 peat moss. The reaction of the medium was adjusted to pH 6.0. Randomized complete block experimental designs were used and the planting arrangement was a 10 x 12 cm rectangular pattern. To minimize the effects of moisture and temperature stress, the outermost 2 rows around each bench were utilized as buffers. Seeds of all parental, F\(_1\), F\(_2\), and backcross generations were produced in the greenhouse using standard crossing and sowing procedures. Seeds of the F\(_3\) generation were collected from single field-grown F\(_2\) plants.

At planting, single seeds were dropped into 2 cm deep holes and irrigated with an aliquant of water containing freshly extracted eggs (ca. 2,000) of the appropriate \textit{Meloidogyne} species. All \textit{M. incognita} populations were Race 3 (13). Greenhouse temperatures were maintained between 24\(\circ\) and

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32°C during the execution of each test and all plants were evaluated about 3 months after seeding. Each plant received 2 subjective scores, one for the prevalence of root galling and another for the prevalence of egg masses. The following scale was used to score the severity of galling: 1 = no galls; 2 = light galling, 1 to 25% of root system galled; 3 = moderate galling, 26 to 50% of root system galled; 4 = heavy galling, 51 to 75% of root system galled; and 5 = severe galling, 76 to 100% of root system galled. The number of egg masses per root system were scored as follows: 1 = no egg masses evident, 2 = scattered egg masses covering 1 to 25% of the root system, 3 = moderate number of egg masses covering 26 to 50% of root system, 4 = numerous egg masses covering 51 to 75% of root system, and 5 = extremely large numbers of egg masses covering 76 to 100% of root system. All plants with gall and egg mass indices of 1 to 3 were classified as root knot resistant: plants rated 4 or 5 for either galls or egg masses were classified as susceptible. Chi-square tests for goodness-of-fit were used in testing all genetic hypotheses.

**Experiment I.** Plants of the parental, F1, F2, and the F1 x P1 and F1 x P2 backcross generations of the cross ‘Mississippi Silver’ x CR 18-13-1 were tested for resistance to *M. incognita*. ‘Mississippi Silver’ is a leading southern pea cultivar and is highly resistant (6). The breeding line CR 18-13-1 is highly susceptible. Because previous experience with this cross indicated that it segregates hard seeded genotypes, all seeds were mechanically scarified. The test contained 64 replicates and each replicate contained 1 plant each of parental and F1 populations and 2 plants each of the F2 and backcross populations. The test was seeded on August 18 and the roots were evaluated on October 11 through November 10. The Hussey and Barker (8) procedure was used to extract eggs from each plant in 6 randomly chosen replicates.

**Experiment II.** Plants of the parental and F2 populations of the following crosses were tested for resistance to *M. incognita*: ‘Colossus’ x CR 18-13-1, ‘Mississippi Silver’, ‘Iron’ x CR 18-13-1, ‘Iron’ x ‘Mississippi Silver’, PI 353383 x CR 18-13-1, and PI 353383 x ‘Mississippi Silver’. The F1 generations of all crosses involving CR 18-13-1 were also tested. ‘Colossus’, ‘Mississippi Silver’, ‘Iron’, and PI 353383 are all highly resistant to *M. incognita* and CR 18-13-1 is highly susceptible (6, 16). The test contained 21 replicates and each replicate contained 1 plant each of the parental and F1 populations and 5 plants each of the F2 populations. The test was seeded on December 10 and the roots were evaluated on March 15.

**Experiment III.** Plants of the parents, F1 and 30 randomly chosen F3 lines of the ‘Mississippi Silver’ x CR 18-13-1 cross were evaluated in separate tests for reaction to *M. incognita*, *M. javanica*, and *M. hapla*. All tests had 4 replicates, each containing a single 5 plant plot of each of the 33 entries. The *M. incognita* test was seeded on January 10 and the roots were evaluated on April 1 and 2. The *M. javanica* and *M. hapla* tests were seeded on March 30 and the roots were evaluated on June 8 through 11 (*M. javanica*) and on June 18 and 19 (*M. hapla*).

**Results and Discussion**

The procedure used to infest the growing media with eggs at seeding was rapid and reliable. The only adverse consequence of placing a large number of eggs in close proximity to the seed at planting was the occurrence of some stem galling, but this phenomenon appeared to be independent of root galling (Fig. 1). Preliminary analyses revealed no significant differences between either reciprocal crosses or replicates. As a result, reciprocals and replicates were pooled for all genetic analyses. ‘Mississippi Silver’ and CR 18-13-1 reacted to *M. incognita* as expected (Fig. 2). CR 18-13-1 developed abundant galls and supported extensive egg production by the parasitic ‘Mississippi Silver’ exhibited a high level of resistance, but it was not immune; the roots exhibited limited galling and egg mass production. The frequency of phenotypes in the progeny generations indicated that the *M. incognita* resistance in ‘Mississippi Silver’ is conditioned by a single dominant gene (Table 1). All 60 F1 plants and all but 2 of 125 F1 x ‘Mississippi Silver’ backcross plants were of the expected resistant phenotype. The F2 segregated 3 resistant:1 susceptible and the F1 x CR 18-13-1 backcross segregated 1 resistant:1 susceptible.

**Fig. 1.** Stem and root galls on a CR 18-13-1 cowpea plant parasitized by *Meloidogyne incognita*.

**Fig. 2.** Examples of effects of the southern root-knot nematode (*Meloidogyne incognita*) on plants (Experiment I) of the susceptible breeding line CR 18-13-1 (right), the resistant ‘Mississippi Silver’ (left), and the resistant F1 of CR 18-13-1 x ‘Mississippi Silver’ (center plants). The root of the susceptible plant is severely galled and only minimal disease and some bacterial nodulation are evident on the roots of the resistant plants.
Table 1. Segregation for reaction to the southern root-knot nematode (Meloidogyne incognita) in parental, F1, F2, and backcross generations of the cross 'Mississippi Silver' x CR 18-13-1 (Experiment I).

<table>
<thead>
<tr>
<th>Generation</th>
<th>No. of plants</th>
<th>Expected ratios (R:S)²</th>
<th>χ²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mississippi</td>
<td>64</td>
<td>0</td>
<td>All R</td>
<td>–</td>
</tr>
<tr>
<td>CR 18-13-1</td>
<td>0</td>
<td>56</td>
<td>All S</td>
<td>–</td>
</tr>
<tr>
<td>F1</td>
<td>60</td>
<td>0</td>
<td>All R</td>
<td>–</td>
</tr>
<tr>
<td>F2</td>
<td>97</td>
<td>27</td>
<td>3:1</td>
<td>0.69</td>
</tr>
<tr>
<td>F1 x Miss. Silver</td>
<td>123</td>
<td>2</td>
<td>All R</td>
<td>–</td>
</tr>
<tr>
<td>F1 x CR 18-13-1</td>
<td>69</td>
<td>59</td>
<td>1:1</td>
<td>0.78</td>
</tr>
</tbody>
</table>

R = resistant, S = susceptible.
Pooled data from reciprocal crosses.

Table 2. Egg production by the southern root-knot nematode (Meloidogyne incognita) on roots of resistant and susceptible plants of the parental, F1, F2, and backcross generations of the cross 'Mississippi Silver' x CR 18-13-1 (Experiment I).

<table>
<thead>
<tr>
<th>Generation</th>
<th>No. of eggs per mg root tissue</th>
<th>Expected ratios (R:S)²</th>
<th>χ²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mississippi Silver</td>
<td>4.0 ± 0.9²</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>CR 18-13-1</td>
<td>4.7 ± 1.3</td>
<td>49.9 ± 8.5</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>F1</td>
<td>2.7 ± 1.0</td>
<td>30.9 ± 13.0</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>F1 x Miss. Silver</td>
<td>3.8 ± 0.8</td>
<td>33.3 ± 4.3</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>F1 x CR 18-13-1</td>
<td>3.6 ± 1.9</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

²SE.
Pooled data from reciprocal crosses.

M. incognita egg production on the roots of resistant 'Mississippi Silver' plants was only 8% of the number produced on the roots of the susceptible CR 18-13-1 (Table 2). Egg production on the roots of resistant and susceptible segregates in the progeny populations was of the same order of magnitude as egg production on resistant and susceptible parental plants, respectively.

Experiment II. Except for limited numbers of galls and egg masses on some roots, the parental lines 'Colossus', 'Iron', 'Mississippi Silver', and PI 353383 exhibited high levels of resistance to M. incognita. The roots of all CR 18-13-1 plants developed abundant galls and exhibited numerous egg masses. All F1 plants of the crosses involving CR 18-13-1 were resistant and all F2 populations of these crosses segregated 3 resistant:1 susceptible (Table 3). These results indicated that the resistances in 'Colossus', 'Iron', and PI 353383 are dependent upon the homozygous condition of single dominant genes. The lack of segregation in the F2 populations of the crosses involving 'Mississippi Silver' indicated that the dominant resistance genes in 'Colossus', 'Iron', and PI 353383 are all allelic to the dominant resistance gene in 'Mississippi Silver'. Thus, the gene that conditions resistance in 'Iron', the cultivar that Webber and Orton (16) reported resistant in 1902, is probably the same gene that conditions resistance in 'Colossus', 'Mississippi Silver', and PI 353383.

Experiment III. 'Mississippi Silver' and the F1 of the cross 'Mississippi Silver' x CR 18-13-1 exhibited high levels of resistances to M. incognita, M. javanica, and M. hapla. All 3 Meloidogyne species induced limited galling and egg mass production in some 'Mississippi Silver' plants. CR 18-13-1 was highly susceptible to all 3 species. The frequency distributions of the 30 random F1 families to M. incognita, M. javanica and M. hapla were quite similar (Fig. 3). These results indicated that the single dominant gene for resistance to M. incognita also conditions resistance to M. javanica and M. hapla. This single gene hypothesis for general resistance to several Meloidogyne species agreed with Hare's (5) findings, but it did not explain the differential response of the cowpea to M. incognita acrita and M. javanica reported by Thomason and McKinney (14). The choice of resistance criterion, the existence of races within Meloidogyne species, differential interactions with environment, or different optimum inocula densities for different Meloidogyne species, however, could reconcile a single gene hypothesis with the Thomason and McKinney (14) results.

Conclusions

This study indicated that a single dominant gene conditions
a high level of resistance in cowpea to *M. incognita*, *M. javanica*, and *M. hapla*. We propose that this gene be designated *Root-knot resistance* and symbolized *Rk* (3, 4). The availability of this gene in excellent cultivar backgrounds and the ease and reliability of the egg-inocula procedures for screening should make breeding for root-knot resistance in cowpeas quite feasible. Since the existence of races within 2 *Meloidogyne* species has been reported (13), the identification of the same single dominant resistance gene in the 4 resistance sources studied raises the question of genetic vulnerability of cowpeas to root-knot nematodes. Perhaps a search of cowpea germplasm should be initiated to identify other root-knot resistance genes.

**Literature Cited**