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John Kennedy Saichuk

Louisiana State University and Agricultural & Mechanical College

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THE GENETIC BEHAVIOR OF RESISTANCE
IN SOYBEANS TO THE WARETTE RACE
OF ROOT-KNOT NEMATODE

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Agronomy

by

John Kennedy Saichuk
B.S., University of Southwestern Louisiana, 1972
M.S., Texas A and M University, 1974
December, 1977
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To my wife, Susette, and my son, John, I dedicate this dissertation.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIST OF TABLES.</td>
<td>iv</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>v</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>vi</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>LITERATURE REVIEW</td>
<td>2</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>19</td>
</tr>
<tr>
<td>RESULTS AND DISCUSSION</td>
<td>30</td>
</tr>
<tr>
<td>Performance of Parental Lines.</td>
<td>30</td>
</tr>
<tr>
<td>Performance of Cross Combinations.</td>
<td>33</td>
</tr>
<tr>
<td>Bragg X D69-6344.</td>
<td>33</td>
</tr>
<tr>
<td>Hill X D69-6344</td>
<td>35</td>
</tr>
<tr>
<td>Delmar X D69-6344</td>
<td>35</td>
</tr>
<tr>
<td>D69-6344 X Pickett 71</td>
<td>38</td>
</tr>
<tr>
<td>Delmar X Pickett 71</td>
<td>38</td>
</tr>
<tr>
<td>Bragg X Pickett 71</td>
<td>41</td>
</tr>
<tr>
<td>Hill X Pickett 71</td>
<td>43</td>
</tr>
<tr>
<td>Delmar X Bragg.</td>
<td>45</td>
</tr>
<tr>
<td>Genetic Model Development</td>
<td>45</td>
</tr>
<tr>
<td>SUMMARY</td>
<td>51</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>53</td>
</tr>
<tr>
<td>VITA</td>
<td>61</td>
</tr>
</tbody>
</table>
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Cross Combinations Evaluated</td>
</tr>
<tr>
<td>2</td>
<td>Backcrosses Used in the Study</td>
</tr>
<tr>
<td>3</td>
<td>Nematode Population and Date That Each Cross Combination Was Evaluated</td>
</tr>
<tr>
<td>4</td>
<td>The Number of Observations of Each Population in Each Experiment</td>
</tr>
<tr>
<td>5</td>
<td>Summarized Performance of Parental Lines</td>
</tr>
<tr>
<td>6</td>
<td>Reaction of Parents, F₁, and Segregating Generations From the Cross Bragg X D69-6344 to the Wartelle Race of Root-knot Nematode</td>
</tr>
<tr>
<td>7</td>
<td>Reaction of Parents, F₁, and Segregating Generations From the Cross Hill X D69-6344 to the Wartelle Race of Root-knot Nematode</td>
</tr>
<tr>
<td>8</td>
<td>Reaction of Parents, F₁, and Segregating Generations From the Cross Delmar X D69-6344 to the Wartelle Race of Root-knot Nematode</td>
</tr>
<tr>
<td>9</td>
<td>Reaction of Parents, F₁, and Segregating Generations From the Cross D69-6344 X Pickett 71 to the Wartelle Race of Root-knot Nematode</td>
</tr>
<tr>
<td>10</td>
<td>Reaction of Parents, F₁, and Segregating Generations From the Cross Delmar X Pickett 71 to the Wartelle Race of Root-knot Nematode</td>
</tr>
<tr>
<td>11</td>
<td>Reaction of Parents, F₁, and Segregating Generations From the Cross Bragg X Pickett 71 to the Wartelle Race of Root-knot Nematode</td>
</tr>
<tr>
<td>12</td>
<td>Reaction of Parents, F₁, and Segregating Generations From the Cross Hill X Pickett 71 to the Wartelle Race of Root-knot Nematode</td>
</tr>
<tr>
<td>13</td>
<td>Reaction of Parents, F₁, and Segregating Generations From the Cross Delmar X Bragg to the Wartelle Race of Root-knot Nematode</td>
</tr>
<tr>
<td>14</td>
<td>Proposed Parental Genotypes</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
</tr>
<tr>
<td>--------</td>
<td>-----------------------------------------------------------------</td>
</tr>
<tr>
<td>1</td>
<td>Parentage of D69-6344 and Hill</td>
</tr>
<tr>
<td>2</td>
<td>Parentage of Bragg</td>
</tr>
<tr>
<td>3</td>
<td>Parentage of Delmar</td>
</tr>
<tr>
<td>4</td>
<td>Response of Parent Lines to Nematode Population</td>
</tr>
</tbody>
</table>
ABSTRACT

The genetic behavior of resistance in soybeans (Glycine max (L.) Merrill) to the Wartelle race of root-knot nematode (Meloidogyne incognita (Kofoid and White) Chitwood was studied by screening F₁, F₂, and backcross populations of eight crosses between selected parental soybean lines. These lines, 'Bragg', 'Delmar', 'Hill', 'Pickett 71', and D69-6344, were chosen on the basis of their ancestry and their reaction to root-knot nematode. Root systems of individual seedlings, grown in naturally nematode infested soil in a greenhouse, were examined and given a subjective rating for degree of resistance to this organism. Segregation patterns were examined and tested for goodness of fit to expected ratios by X² analysis.

Results indicated that susceptibility was dominant to resistance and that inheritance of reaction was conditioned by genes at two loci which acted in a duplicate-dominant manner. Where reciprocal F₁'s were tested there was no indication of cytoplasmic or maternal effects. Variance estimates suggested that the environment or minor genes or both may influence disease reaction, but this should not prevent selection for resistance to the Wartelle race of root-knot nematode in conventional soybean breeding programs.

Delmar, Bragg, and Hill were reported to possess genes for resistance to other forms of root-knot nematode, but each was susceptible to the Wartelle race which suggested that they may have common genes for susceptibility. Delmar and Bragg segregated similarly when crossed with D69-6344 and did not segregate when crossed with
each other indicating identical genotypes. Resistance in D69-6344 is thought to have been derived from both Hill and 'Laredo', a soybean cultivar reported to be resistant to root-knot nematode.
INTRODUCTION

The root-knot nematode (Meloidogyne incognita (Kofoid and White) Chitwood) has been a recognized pest of soybeans (Glycine max (L.) Merrill) since 1882. The nematode has been the greatest threat in the lighter textured soils of the warmer regions of the United States, especially the Southeastern United States. Plants damaged by this organism have reduced growth, fewer and smaller leaves, excessive wilting in warm weather, and reduction in quantity and quality of fruit.

In the past, efforts to control this pest have been centered on the use of cultural practices, such as fallow plowing, rotation to non-host crops, and the application of nematicides. Recently, more emphasis has been placed on the development of resistant varieties. The results generally have been favorable, but in some instances, only temporary. The existence of new nematode races has shown the need for the development and release of new resistant varieties.

In 1973 a root-knot nematode was collected on the Wartelle farm in St. Landry Parish, Louisiana that was identified as Meloidogyne incognita and was later designated a new race, the Wartelle race, because of its inability to reproduce on 'Centennial' sweetpotatoes, (Ipomea batatis (L.) Lam.), a common host of M. incognita. This race was investigated because of its ability to parasitize certain soybean cultivars previously regarded as resistant to root-knot nematode. This study was designed to determine the number and behavior of genes involved in inheritance of resistance to the Wartelle race of root-knot nematode.
LITERATURE REVIEW

Plant damage from root-knot nematodes was first recorded in 1855 by Berkeley (13) who described "Vibrio" attacking the roots of cucumber (Cucumis sativus L.) plants growing in a greenhouse in London. The disease had acquired the names root-knot, beaded root-knot, root-gall, and big root by 1911. It had been found throughout the United States, particularly in the southern states, and it was common in greenhouses throughout the world (14). Neal (76) reported that the earliest knowledge of root-knot damage in Florida was around 1805, although the first records did not appear until 1857. Several authors (37, 66, 67, 68) have reported root-knot nematode in Louisiana, especially in the lighter textured soils of the state.

The root-knot nematode has a wide host range, encompassing some 2000 plant species. Although all the plant species are not highly susceptible, they do act as hosts for one or more nematode species. Often the host is susceptible to one nematode species but is resistant to other species (2, 23). According to Good (44), soybeans (Glycine max (L.) Merrill) was added to the list of host species by Frank, who discovered root-knot nematodes on roots of soybean plants grown in a greenhouse in Germany in 1882. Today, root-knot damage is a potential problem wherever soybeans are grown, and is of considerable economic importance in the southern United States.

Initial attempts to identify root-knot nematodes were often disorganized and inconsistent. New names were applied to previously described nematodes, genera names were changed, and species were shifted
from one genus to another as root-knot damage was observed on additional plant species. Atkinson (6) published a list of root-knot nematodes that had been identified by 1889 which included: *Heterodera schachtii*, described by Schacht in Europe in 1859; *H. radicicola*, first recorded in 1872 as *Anguillula radicicola* by Greeff but transferred to the genus *Heterodera* by Muller in 1884; *H. javanica*, found in Java in sugarcane (*Saccharum* spp.) roots by Treub; and *Meloidogyne* spp., found in 1878 in roots of coffee (*Coffea* spp.) by Goeldi.

In 1919, Kofoid and White (62) described a nematode found in human fecal samples and called it *Oxyuris incognita*. According to Wright (108) this organism was synonymized with *H. radicicola* by Sandground. Goodey (45) suggested that the new species *H. marioni* had priority due to its earlier application. Chitwood (21) revised the genus *Meloidogyne* in 1949 and included *M. incognita* (Kofoid and White, 1919), with the former name being preferred for the species. Other workers (7, 22), acknowledging the earlier work of Goodey as being correct, referred to *H. marioni* as the root-knot nematode. Wester (104), working with root-knot nematodes of lima beans (*Phaseolus lunatus* L.), concluded "... it (root-knot) was formerly attributed to a single species *H. marioni* (Cornu) Goodey, but it is now recognized to be caused by a group of species of a separate genus (*Meloidogyne* spp.)." Today the revision of the genus *Meloidogyne* by Chitwood (21) is still accepted and root-knot nematodes are considered members of the genus *Meloidogyne*.

The identity of the nematode itself was often the culprit when conflicting reports were published. This was demonstrated by the results of Winstead and Riggs (107) who reported that Bessey (1911)
found 'Striped Blue Ribbon' watermelon (Citrullus vulgaris Schrader ex. Ecklon and Zeyher) resistant to *Meloidogyne incognita acrita* (Chitwood), but in their studies, watermelon was susceptible to *Meloidogyne incognita acrita*. Winstead and Riggs concluded that Bessey had been working with *Meloidogyne hapla* (Chitwood) or a different population of *Meloidogyne incognita acrita*. The problem was recognized by Smith and Taylor (95) who suggested that data obtained in studies of a particular race of root-knot nematode be applied only to that nematode rather than to root-knot nematodes in general.

The identification of root-knot nematode species is based primarily on morphological characteristics of the adult female (100). Ibrahim et al. (55) were able to identify *Meloidogyne javanica* and *Meloidogyne incognita* by perineal patterns. In an earlier study Lordello (64) was unable to distinguish a nematode, whose female perineal patterns closely resembled *Meloidogyne incognita*, from *Meloidogyne incognita*. He used morphological characteristics of larvae and males to distinguish the group of nematodes from *Meloidogyne incognita* and concluded that the nematode was a new species. Dropkin (34) studied varietal response of soybeans to *Meloidogyne* spp. using galls and egg mass variation, differences in giant cell formation, and sex ratios of nematode populations. He found that variation in galls and egg masses and differences in giant cell formation were suitable criteria, but that sex ratios were not sufficiently reliable to distinguish nematode populations. Sasser (82) also used perineal patterns of adult females to identify nematodes, but indicated that this method was reliable only in the hands of a specialist. He then proposed a procedure for identifying unknown nematode populations by utilizing a series of four test species: peanuts (*Arachis hypogaea* L.),
watermelon or wheat (*Triticum aestivum* L.) or barley (*Hordeum vulgare* L.) or corn (*Zea mays* L.), pepper (*Capsicum* spp.), and the Peruvian tomato (*Lycopersicon peruvianum* (L.) Miller). Christie (23) also suggested that vague morphological characteristics were not always reliable in distinguishing nematode subspecies or races and suggested a technique like that developed by Sasser as the only sound means of nematode identification.

Evidence of physiological races of root-knot nematodes has been reported by several authors (4, 24, 63, 66, 67, 68, 82, 106). Christie and Albin (24) studied the reaction of 10 host species to 14 nematode populations that could not be distinguished morphologically. Hosts varied in reaction and in type of galling to different nematode populations. Martin (66) described differences in parasitism among isolates of *M. incognita* and *M. incognita acrita* on cotton (*Gossypium hirsutum* L.) which ranged from no parasitism to severe parasitism. Using morphological characteristics of anal plates, Allen (4) found that four nematode populations isolated in California were all *M. incognita acrita*. However, cotton cultivars reacted differently to the different nematode populations suggesting the existence of races. Allen hypothesized that the development of different races resulted from natural selection imposed on nematode populations by various crops. Martin and Birchfield (67) demonstrated that physiological races of *M. incognita* existed which were pathogenic on cotton, sweetpotatoes (*Ipomea batatia* (L.) Lam.), lima bean, okra (*Hibiscus esculentus* L.), tomato (*Lycopersicon esculentum* Miller), Crowder pea (*Pisum sativum* L.), *Amaranthus* spp., and gardenia (*Gardenia thunbergia* L.).
Cooperative research between Martin and Birchfield (68) and Williams et al. (106) resulted in isolation of a nematode that caused severe yield reduction in the soybean cultivar 'Bragg', which previously had been considered resistant to root-knot nematode. The new nematode was identified as *M. incognita*, but it failed to develop mature females on a susceptible sweetpotato cultivar, so it was designated the Wartelle race for the name of the landowner on whose farm it was first collected. Boquet et al. (18) studied four populations of nematodes from Louisiana, including the Wartelle race. Based on differential reactions of several soybean cultivars, they concluded that at least two physiological races existed. Of the two races, the Wartelle race was the most pathogenic.

Plants infected with root-knot nematodes exhibit symptoms which are visible in all plant parts. Symptoms include reduced plant growth, fewer and smaller leaves, excessive wilting in warm weather, and reduction in quantity and quality of fruit (2). These symptoms are consequences of destruction of root tissue which prevents normal uptake of water and minerals. Necrosis of root tissue and proliferation of lateral roots at the point of invasion are associated with nematode invasion. Internally, the invasion of roots by root-knot nematodes results in production of giant cells which appear as abnormal swellings of root tissue (i.e., knots or galls) thus producing the most characteristic symptom of the disease.

Formation of giant cells was confirmed by Peacock (77) to be a vital part of the host-parasite relationship involving root-knot nematodes. Giant cells develop as a result of a nematode secretion and provide a source of nutrients for feeding nematodes.
Crittenden (30) reported that susceptible host plants generally had the following characteristics: giant cells surrounding the head of the nematode, many giant cells present, large giant cell area, dense cytoplasm in giant cells, many enlarged nuclei in each giant cell, and enlargement of pericycle with giant cells in this region. Characteristics of resistant hosts were essentially the opposite of susceptible hosts.

Dropkin and Nelson (36) revealed that galls of soybeans are composed of parenchyma originating in the pericycle. They grouped giant cells into four classes and associated only one class with susceptibility. The host-parasite interaction was classed tolerant if both host and parasite growth was good. The interaction was considered intolerant if both parasite and host growth was poor. Plants were considered susceptible when parasite growth was good and host growth was poor, and resistant when the opposite occurred.

Tyler (104) defined resistance as the ability to obstruct the invasion of a parasite, and susceptibility as the condition of being a suitable host for a given parasite. Rohde (78) defined resistance as a set of characteristics of the host plant which act more or less to the detriment of the parasite.

Sasser (82) rated fifty plant species and cultivars for reaction to root-knot nematodes. He defined infection as invasion of the plant by larvae of root-knot nematodes and immunity as the ability to prevent infection with the effect of no disease development (i.e., total resistance). Resistance to infection was highly variable and was characterized by reduced nematode invasion of plant tissues.
In an early study, Sasser and Taylor (84) pointed out three forms of larval activity which could be equated with resistance. Larvae could fail to enter roots, enter in reduced numbers and fail to reach maturity, or enter in large numbers with varying degrees of development. Resistance was reported to vary from plant to plant because of these conditions.

Dean and Struble (33) studied plant reaction to root-knot nematodes in tomatoes and sweetpotatoes and found resistance in sweetpotatoes to be different from resistance in tomatoes. When root-knot larvae invaded either of the two crops, root necrosis was evident as a mechanism of resistance, but in tomatoes, there was also a reduction in numbers of invading larvae. There was no substantial difference in number of larvae entering resistant or susceptible sweetpotato tubers.

Dropkin (35) combined initiation of larval growth, induction of cell necrosis, and gall formation as criteria for resistance or susceptibility of tomatoes to *M. incognita*. He noticed that when cytokinins were supplied the response of resistant plants was shifted toward a susceptible reaction. Sawhney and Webster (86) studied effects of plant growth hormones on resistance of tomato plants to root-knot and showed that plant growth hormones played some role in resistance, but were not the only factor involved. Hutton et. al. (54) noted the possibility of chemotoxic effects of the roots of 'Siratro' (*Phaseolus atropurpureus* D. C.) when lines were screened for root-knot resistance.

Barrons (11) found no significant difference in rate of larval entry in resistant or susceptible hosts whether the hosts were in adult or seedling stage. He proposed that root-knot resistance is due to substance(s) synthesized by the plant that counteract the
giant cell inducing effect of salivary secretions of nematode larvae. Whether the phenomenon of host specialization was due to genetic differences in the chemical nature of the salivary secretions of the nematode rather than difference in ability of the nematode to enter the host was not determined.

Minton (72) investigated factors influencing cotton reaction to root-knot nematodes and reported that resistance was not due to morphological differences or root barriers which prevented penetration, but to root tip hypersensitivity to penetrating larvae and failure of root cells to respond to nematodes.

In a review of several papers concerning the nature of nematode resistance in plants, Rohde (78) concluded: "A resistant plant is resistant usually for several different reasons, and no one mechanism can be designated as most important. However, it appears that in most cases resistance results from upsets in the delicate balance of reactions that occur between a parasite and its host."

According to Rohde (78) resistance became more common as complexity of host parasite interaction increased. Therefore, resistance to root-knot and cyst nematodes, which require the formation of giant cells in order to feed, was much more common than resistance to ectoparasitic nematodes. Malloch (65) felt that plant breeders had two alternatives in breeding for resistance, find a source of resistance and make crosses or look for transgressive segregation. Although the work of Bailey (8) indicated good possibilities for resistant variety development, he felt a conservative attitude should be taken toward selection of highly root-knot tolerant plants due to the ability of nematodes to adapt to a new host species.
The interaction between root-knot nematode and wilt-inducing fungi has long been studied. Smith (94) found an association between resistance to both root-knot nematode and wilt in cotton. Shepherd (90) also reported that high root-knot nematode resistance appeared to provide high resistance to Fusarium wilt in cotton. The level of resistance to Fusarium wilt in soybeans grown in the Southeastern United States was not significantly reduced by root-knot nematodes, but cyst nematodes caused reduction in resistance according to research by Ross (80). *Rhizoctonia solani* Kuhn. has been reported to react with *M. hapla* and *M. javanica* by Taylor and Wyllie (97) and with *M. incognita* by Golden and Gundy (42). In all instances, the fungus-nematode complex had greater detrimental effects than either the fungus or nematode when inoculated separately. Wyllie and Taylor (109) inoculated 'Harosoy' soybeans with *Phytophthora megasperma* Drechs. var. *sojae* A. A. Hildeb. and *M. hapla* and obtained more severe damage than when either pathogen was used alone. When Agarwal and Goswami (1) investigated the interrelationships between a fungus (*Macrophomina phaseoli* (Maubl.) Ashby) and *M. incognita* in soybeans, significant synergistic effects were noted when nematode inoculation preceded fungus inoculation by three weeks. The nematode predisposed the fungus making the host much more susceptible than when plants were infected with the fungus alone. Goswami et. al. (46) also reported a synergistic virus-nematode (*M. incognita*) interaction with cowpea (*Vigna unguiculata* ssp. *unguiculata* (L.) Walp.).

Sayre (87) observed the larvae of an amoeba (*Theratromyxa weberi*) engulfing *M. incognita* and introduced another problem for scientists studying plant nematode reactions. In this study, during the winter
of 1975-76, a protozoan identified by Birchfield and Antonopoulos (16) as *Dubosquia penetrans*, parasitized some of the root-knot larvae. In this instance, the parasite did not provide a means of biological control, but it could have affected the outcome of the experiment by reducing the vigor of some nematodes.

Methods for effectively controlling the root-knot nematode have been sought for many years. As early as 1889, Neal (76) recommended drainage, frost, fire, sterile soils (in greenhouses), nonuse of land, nonuse of easily infected crops, insect pathogens, use of vermicide fertilizers, and use of non-infected stocks as methods of control. Christie (23), in 1959, listed trap crops, flooding, fallow and dry tillage, rotations and cover crops, chemicals, and nematode resistant plants as methods for controlling root-knot nematodes. Sasser (83), however, pointed out that changes in environment which are sufficiently severe to control nematodes often are detrimental for the host plant. He recommended using a multiple integrated approach which included good cultural practices, chemicals, and resistant varieties.

Chemicals are often recommended to control root-knot nematodes in both field and greenhouse conditions (2, 23, 100). However, the use of chemicals provide an added expense and the benefits derived from chemical application are usually transitory, requiring subsequent annual applications for effective control of the nematode population.

"The development of plants possessing genetically controlled resistance to nematodes has been recognized as one of the most effective and economical means of reducing the losses caused by these pests especially the root-knot nematodes" (58). Crittenden (29) suggested the use of a crop rotation system involving resistant crops for two
consecutive years as the best method for controlling *M. incognita acrita*. Resistant cultivars used either continuously or in a crop rotation system also has been suggested by others (14, 15). Good (43) stated that resistant varieties offered the least expensive and often only practical means of controlling some nematodes, but he acknowledged that pathogenic races may result from continued use of resistant varieties. Sasser (83) felt that a system which incorporated several means of nematode control would produce the most lasting beneficial effects since it should reduce the development of physiological races which often overcome resistant varieties. Kehr (58) suggested that race development might be reduced by the use of multiple-gene resistance coupled with rotations of susceptible, resistant, and non-host plants.

Resistance is valuable to plant breeders only if it can be transmitted from parent to progeny. Weimer and Harter (102) found varietal resistance in sweetpotatoes to *H. radicicola* in California in 1925. In 1931, Isbell (56) discovered two varieties of pole snap beans (*Phaseolus vulgaris* L.) which were highly resistant to nematodes.

Frazier and Dennett (38) studied resistance in *L. esculentum* lines using gall formation as an expression of resistance. Dominance of resistance in the *F*₁ was considered high, and resistance in seedlings was highly correlated with resistance in mature plants.

Lider (63) investigated inheritance of resistance in *Vitis* spp. to *M. incognita acrita*. He reported that resistance was dominant and, in at least one cross, monogenic in nature. Hare (47) examined *F*₁, *F*₂, *F*₃, and backcross populations of crosses between susceptible bell peppers and resistant hot peppers. He concluded resistance to
M. incognita in pepper was controlled by a single dominant gene and this same gene also controlled resistance to M. incognita acrita and possibly M. javanica and M. arenaria (Neal) Chitwood.

Collins and Hagan (25) used pineapple (Ananas sativus Schult.) root number and length as indicators of resistance to H. radicicola. No immune varieties were identified. Root number was not influenced by presence of nematodes, however, root length was reduced. Varying degrees of resistance were found, which suggested that resistance was conditioned by several genes and/or environmental influences.

Cordner et al. (26) classified F₁ offspring of sweetpotatoes for reaction to root-knot nematode. In crosses of resistant X susceptible plants approximately one third of the progeny were susceptible, one third intermediate, and one third were resistant. In resistant X resistant crosses, the ratio of resistant, intermediate, and susceptible plants was approximately 5:3:2. When susceptible X susceptible crosses were made, ten percent of the progeny were resistant, twenty-five percent were intermediate, and sixty-five percent were susceptible.

Weinberger et al. (103) examined roots of open pollinated peach (Prunus persica (L.) Batsch.) seedlings after one year of growth in nematode infested soil. They found that F₁ progeny of susceptible X resistant crosses were resistant, indicating that resistance was dominant. Resistance to M. incognita and M. javanica in peaches depends upon different genes according to Sharpe et al. (88) who reported resistance to M. incognita is monofactorial and dominant. They seemed uncertain concerning resistance to M. javanica, reporting only that two or more genes are involved.
Kochba and Speigel-Roy (60) reported a high degree of resistance to root-knot nematode in some bitter almond (Prunus amygdalus Batsch.) progenies. They suggested that either resistance was dominant to susceptibility or a cytoplasmic factor conditioned the character. Two susceptible almond X resistant peach F₁ progenies showed almost complete dominance of resistance to M. javanica. In a separate study they found all progenies from four of five reciprocal crosses of resistant bitter almond X susceptible sweet almond were completely resistant (61). Progenies of resistant peach X susceptible almond cultivars segregated, thus they suggested one mode of inheritance of resistance in peach and another in almond.

Inheritance of root-knot resistance in cotton was investigated by Wright (108). Using a visual estimate of the proportion of root tissue damaged by nematodes, he evaluated parents, F₂, and F₃ populations of a cross between 'Cleverwilt 6' (moderately resistant) and 'Deltapine 15' (susceptible) varieties. He concluded that resistance was partially dominant and quantitative in nature. Resistance to root-knot nematode also was reported to be dominant in cotton by Wiles (105). Shepherd (89) found that inheritance of root-knot resistance in progeny of G. barbadense X G. hirsutum appeared to be polygenic.

McFarlane et. al. (69), working with interspecific tomato hybrids, reported that resistance to the root-knot nematode was dominant and was controlled by a few factors. Watts (101) used L. peruvianum as a source of nematode resistance in tomatoes and reported resistance in early stages of plant growth was controlled by two dominant factors. Gilbert and McGuire (39) found variations in degree of galling, apparently because of wide differences in severity of root-knot infesta-
tion of commercial tomatoes in Hawaii. In other studies with tomatoes, resistance was reported to be dominant and conditioned by one major gene (9, 10, 40, 51, 98).

Sidhu and Webster (91) identified three genes for resistance to *M. incognita* in tomato. Resistance was attributed to a single dominant gene in two cultivars and to a single recessive gene in one cultivar. There was no evidence for allelism. In a later study of root-knot nematode - wilt-fungus complex in tomatoes (92), resistance to each disease was expressed as a single dominant gene which segregated independently. However, expression of fungus resistance was dependent on nematode resistance. Sikora et. al. (93) noted that one or more genes may directly or indirectly affect root-knot nematode resistance in tomatoes. They proposed screening cultivars in specific areas before making recommendations for the given area.

Amosu and Frankowiak (5) examined *F₂* populations of crosses involving four susceptible and two resistant cowpea cultivars. They concluded that resistance to root-knot nematode populations from Nigeria was governed by a single dominant factor and was augmented by modifying gene(s).

Based on *F₂* segregation ratios of an 'Alabama No. 1' (resistant) X 'Kentucky Wonder' (susceptible) pole bean cross Barrons (12) reported that three or more genes of equal action condition the reaction to root-knot nematode. He indicated that a certain minimum number of genes for susceptibility was necessary before all resistance was lost.

Allard (3), in greenhouse experiments with lima beans, observed gradation from high resistance to high susceptibility, which indicated that either several genes, environmental influences, or both, condi-
tioned resistance to root-knot nematode. In another study with lima beans, McGuire et al. (71) indicated that only a few genes were involved in root-knot nematode resistance. Because of the presence of susceptible $F_1$ progeny of resistant $\times$ resistant crosses, genes governing resistance were thought to differ from plant to plant.

Boquet et al. (18, 19) reported that inheritance of resistance to *M. incognita* in soybeans was due to one or two major genes or one major gene and at least one modifying gene, and that susceptibility was partially dominant to resistance. These conclusions were based on screening trials with $F_1$, $F_2$, and $F_3$ progeny of a cross between resistant D69-6344 and susceptible D69-8178 soybeans.

At least 26 soybean cultivars and 14 strains have been listed as resistant to *M. incognita* (18, 19, 27, 28, 29, 32, 41, 44, 49, 55, 59, 74, 75, 81, 96, 99, 106). These genotypes represent several maturity groups and are an excellent source of germplasm for breeding for root-knot nematode resistance in soybeans. According to Williams et al. (106), resistance in soybeans to the Wartelle race of root-knot nematode may be derived from several sources, including 'Hill', Bragg, and D69-6344. In addition, the cultivar 'Delmar' has been reported to be resistant to root-knot nematode (32) and may provide a distinct source of resistance to root-knot nematode.

Although several authors (31, 84) have found field studies for resistance in soybeans to various nematodes to be quiet effective, nematode populations in the field commonly are not uniform, resulting in questionable results. Romshe (79), for example, had difficulty in field tests of nematode resistance in tomatoes due to a low nematode population. Wester (104) compared greenhouse and field methods for
evaluating lima beans for resistance to root-knot nematode and con­
cluded that the greenhouse method was more rapid and severe than
the field test. He also obtained higher root-knot indices in the
greenhouse test than in the field test. Greenhouse screening was
reported by Shepherd (90) to be more effective than field screening
for transgressive segregation for root-knot nematode resistance in
cotton. McGuire and Allard (70) were even more emphatic when they
stated, "Infestation by root-knot nematodes (Meloidogyne spp.) is
rarely uniform throughout a field. Population densities also tend to
vary from season to season and from year to year in local areas
within the same field. Dependable tests of resistance to root-knot
nematodes are therefore difficult to obtain in field trials." They
attributed the success of their greenhouse tests to favorable climate,
freedom from other pathogens, and uniform infestation.

Several methods have been developed to classify plants for reac­
tion to root-knot nematode. Sasser (85) and Boquet (17) preferred
using egg mass indices as a means of classifying resistant and suscep­
tible plants. Brodie (20) combined gall development with root necrosis
and the ability of nematodes to reach full maturity to distinguish
between resistant and susceptible upland cotton seedlings. Tyler (99)
was aware of the possibility of escapes in this type of technique and
suggested that the lack of gall formation should not be used as the
sole criterium for resistance. Holston and Crittenden (53) felt that
gall ratings might indicate tolerance and not resistance because
heavily galled and lightly galled plants contained the same nematode
population in their roots. This was sustained by Minton and Parker
(73), but they also reported that root-knot indices were more accurate
than nematode population as an estimator of damage. Gall indices are often preferred because galls represent the formation of giant cells which are necessary for nematodes to parasitize the host (30, 72, 78).
MATERIALS AND METHODS

Four commercial soybean cultivars and one advanced breeding line were selected for this study on the basis of their different reaction to root-knot nematode. Delmar, Hill, Bragg, and D69-6344, an advanced breeding line selected at Stoneville, Mississippi, have been reported to be resistant to one or more species of root-knot nematode (18, 19, 32, 44, 50, 52, 57, 59, 74, 81, 96, 106), whereas, 'Pickett 71' has consistently been reported to be highly susceptible to the organism (44, 50, 59, 81, 106).

Source of resistance to the root-knot nematode also was a criterion for selection of the resistant strains. Bragg, D69-6344, Hill, and Delmar were selected because they represented different sources of resistance to some forms of root-knot nematode. Since 'Haberlandt', one of the grandparents of Hill, has been reported to be resistant (27, 28, 99), then Hill must have derived its resistance from Haberlandt (Figure 1). Both Hill and 'Laredo', grandparents of D69-6344, have been reported to be resistant to root-knot nematode (19, 27, 41, 44, 49, 57, 75, 96, 99, 106). Since D69-6344 was reported to be more resistant to the Wartelle race than either Hill or Laredo it was likely that both cultivars contributed to the resistant characteristic of D69-6344 as was postulated by Williams et. al. (106) (Figure 1).

Neither D49-2491 nor its parents, CNS and S-100, have been reported to be resistant to root-knot nematode. 'Tokyo' and PI 54,610, parents of 'Volstate', which was a parent of 'Jackson',
Figure 1. Parentage of D69-6344 and Hill
also are not reported to be resistant to root-knot nematode. However, 'Palmetto' and Jackson are reported to be resistant (49, 52, 106). Hence, Bragg must have obtained its resistance from Palmetto via Jackson (Figure 2).

Delmar was an F6 out of the cross FC 33243 X C 799 (32). Neither C 799 nor any of its progenitors have been reported to be resistant to root-knot nematode. However, FC 33243, a selection out of 'Anderson', has been reported to be resistant (49) and, therefore, is probably the source of the genes for resistance to root-knot nematode in Delmar (Figure 3).

The parental lines were crossed in all possible combinations with the exception of Hill X Bragg, which was not attempted due to the absence of a suitable genetic marker (Table 1). Plants selected at random from each F1 population were backcrossed to the line possessing a dominant genetic marker (Table 2). These and other F1 plants also provided F2 seed used in the study. F1 Delmar X Hill plants did not survive, therefore, backcross and F2 seed from this combination were not obtained. All crossing was accomplished in the field at the Perkins Road Agronomy Farm in Baton Rouge, Louisiana during the summers of 1974, 1975, and 1976. Reciprocal F1 seed of D69-6344 X Pickett 71, Hill X Pickett 71, and Hill X D69-6344 (Table 1) were obtained from Dr. D. J. Boquet of the Northeast Louisiana Experiment Station, St. Joseph, Louisiana.

In the fall of both 1975 and 1976, Gallion very fine sandy loam soil naturally infested with the Wartelle race of root-knot nematode was collected from a field in St. Landry Parish, Louisiana. The soil was stored in bins in the greenhouse both years. The root-knot
Figure 2. Parentage of Bragg
Figure 3. Parentage of Delmar

- FC 33243 Anderson
- Delmar
  - Patoka sib PI 70-218-2-19-3
  - C 799
    - Lincoln
      - Mandarin sib
      - Manchu
Table 1. Cross combinations evaluated.

<table>
<thead>
<tr>
<th>Female</th>
<th>Male</th>
<th>Genetic Marker</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bragg</td>
<td>X D69-6344</td>
<td>purple hypocotyl</td>
</tr>
<tr>
<td>D69-6344</td>
<td>X Pickett 71*</td>
<td>purple hypocotyl</td>
</tr>
<tr>
<td>Delmar</td>
<td>X D69-6344*</td>
<td>purple hypocotyl, brown pubescence</td>
</tr>
<tr>
<td>Hill</td>
<td>X D69-6344</td>
<td>purple hypocotyl, brown pubescence</td>
</tr>
<tr>
<td>Delmar</td>
<td>X Pickett 71</td>
<td>purple hypocotyl</td>
</tr>
<tr>
<td>Bragg</td>
<td>X Pickett 71</td>
<td>purple hypocotyl</td>
</tr>
<tr>
<td>Hill</td>
<td>X Pickett 71*</td>
<td>purple hypocotyl</td>
</tr>
<tr>
<td>Delmar</td>
<td>X Bragg</td>
<td>brown pubescence</td>
</tr>
</tbody>
</table>

*Reciprocal F$_1$'s also evaluated
<table>
<thead>
<tr>
<th>Female Parent</th>
<th>Male Parent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bragg</td>
<td>X</td>
</tr>
<tr>
<td>Hill</td>
<td>X</td>
</tr>
<tr>
<td>Delmar</td>
<td>X</td>
</tr>
<tr>
<td>D69-6344</td>
<td>X</td>
</tr>
<tr>
<td>Delmar</td>
<td>X</td>
</tr>
<tr>
<td>Bragg</td>
<td>X</td>
</tr>
<tr>
<td>Hill</td>
<td>X</td>
</tr>
<tr>
<td>Delmar</td>
<td>X</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>(F₁ Bragg X D69-6344)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(F₁ Hill X D69-6344)</td>
<td></td>
</tr>
<tr>
<td>(F₁ Delmar X D69-6344)</td>
<td></td>
</tr>
<tr>
<td>(F₁ D69-6344 X Pickett 71)</td>
<td></td>
</tr>
<tr>
<td>(F₁ Delmar X Pickett 71)</td>
<td></td>
</tr>
<tr>
<td>(F₁ Bragg X Pickett 71)</td>
<td></td>
</tr>
<tr>
<td>(F₁ Hill X Pickett 71)</td>
<td></td>
</tr>
<tr>
<td>(F₁ Delmar X Bragg)</td>
<td></td>
</tr>
</tbody>
</table>
susceptible soybean cultivar, Pickett 71, was grown in the soil during the fall and winter of each year to maintain an adequate nematode population.

Each cross combination was evaluated in the same manner. Nematode infested soil was mixed and placed in 7.6 cm X 7.6 cm X 6.2 cm plastic pots. A greenhouse bench was filled with sand, then the pots were placed in the sand to within 1.5 cm of the top of the pot to minimize soil temperature and moisture fluctuations. Seeds were planted at the rate of three per pot for parental lines and one per pot for the F₁, F₂, and backcross generations. Pots containing parental lines were thinned to one plant per pot after emergence. A minimum soil temperature of 21°C was maintained with electrical heating coils. A minimum air temperature of approximately 27°C was maintained. Supplemental lighting was provided by three 40 watt fluorescent lights to increase light quality and intensity.

Two 1000 ml soil samples from each test were evaluated for root-knot nematode population level by the USDA Nematology Research lab at Louisiana State University in Baton Rouge. Approximately 500 ml of soil were mixed with 1000 ml of water and stirred vigorously. The suspension was strained to remove organic matter, large soil particles, and other soil debris and allowed to stand briefly so larger sand particles could settle out. The supernatant was strained through four 300 mesh screens into a petri dish containing water. The remaining water which contained the nemaes was poured into a 50 ml beaker and standardized to 50 ml. A 10 ml aliquot was placed in a Syracuse watch glass. Nematodes on one-fourth of the surface area of the dish were counted using a dissecting microscope. The nematode
population was computed by multiplying the actual count by 20. The nematode densities for each test are shown in Table 3.

Plants were rated for reaction to the root-knot nematode 30 days after planting using a previously described technique (81). Briefly, the plants were removed from the pots, washed carefully to remove adhering soil and other debris from the root systems, and examined under a 7X dissecting microscope. Plants were rated subjectively using a scale of 1 to 6, where: 1 = 0-10%, 2 = 11-20%, 3 = 21-30%, 4 = 31-40%, 5 = 41-50%, and 6 = 51-100% of the roots galled. This classification scale is a modification of a system used to classify plant reactions to root-knot nematode by numerous researchers (3, 5, 48, 55, 59, 93, 95, 106). The number of plants examined for each cross combination are reported in Table 4.

Segregation ratios from each cross combination were evaluated for goodness of fit to various genetic models using $X^2$ analysis.
Table 3. Nematode population and date that each cross combination was evaluated.

<table>
<thead>
<tr>
<th>Cross Combination</th>
<th>Nemas/500 ml soil</th>
<th>Date Examined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bragg X D69-6344</td>
<td>1980</td>
<td>11/18/76</td>
</tr>
<tr>
<td>Hill X D69-6344</td>
<td>6800</td>
<td>10/18/76</td>
</tr>
<tr>
<td>Delmar X D69-6344</td>
<td>3240</td>
<td>10/27/76</td>
</tr>
<tr>
<td>D69-6344 X Pickett 71</td>
<td>440</td>
<td>02/29/76</td>
</tr>
<tr>
<td>Delmar X Pickett 71</td>
<td>1780</td>
<td>12/16/76</td>
</tr>
<tr>
<td>Bragg X Pickett 71</td>
<td>2200</td>
<td>12/08/76</td>
</tr>
<tr>
<td>Hill X Pickett 71</td>
<td>1410</td>
<td>04/05/76</td>
</tr>
<tr>
<td>Delmar X Bragg</td>
<td>5700</td>
<td>11/09/76</td>
</tr>
</tbody>
</table>
Table 4. The number of observations of each population in each experiment.

<table>
<thead>
<tr>
<th>Cross Combination</th>
<th>Female Parent</th>
<th>Male Parent</th>
<th>F₁</th>
<th>Recip. F₁</th>
<th>F₂</th>
<th>Backcross</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bragg X D69-6344</td>
<td>12</td>
<td>10</td>
<td>2</td>
<td>0</td>
<td>340</td>
<td>7</td>
</tr>
<tr>
<td>Hill X D69-6344</td>
<td>8</td>
<td>8</td>
<td>10</td>
<td>8</td>
<td>324</td>
<td>27</td>
</tr>
<tr>
<td>Delmar X D69-6344</td>
<td>10</td>
<td>8</td>
<td>14</td>
<td>0</td>
<td>321</td>
<td>36</td>
</tr>
<tr>
<td>D69-6344 X Pickett 71</td>
<td>10</td>
<td>10</td>
<td>11</td>
<td>10</td>
<td>292</td>
<td>31</td>
</tr>
<tr>
<td>Delmar X Pickett 71</td>
<td>12</td>
<td>10</td>
<td>2</td>
<td>0</td>
<td>340</td>
<td>7</td>
</tr>
<tr>
<td>Bragg X Pickett 71</td>
<td>9</td>
<td>10</td>
<td>13</td>
<td>0</td>
<td>334</td>
<td>31</td>
</tr>
<tr>
<td>Hill X Pickett 71</td>
<td>10</td>
<td>8</td>
<td>8</td>
<td>10</td>
<td>236</td>
<td>31</td>
</tr>
<tr>
<td>Delmar X Bragg</td>
<td>8</td>
<td>9</td>
<td>14</td>
<td>0</td>
<td>309</td>
<td>58</td>
</tr>
</tbody>
</table>
RESULTS AND DISCUSSION

Root-gall ratings of all genotypes tended to be larger at higher nematode densities than at lower densities (Figure 4), as was previously reported (17). D69-6344, for example, consistently rated 1.0 at the lower inoculum levels, but rated slightly above 1.0 at the higher inoculum levels. Because of the increase in plant infection at higher nematode population densities, a threshold of approximately 2000 larvae per 500 ml soil was established. At nematode densities below 2000 per 500 ml soil, only plants with a root-gall rating of 1.0 were classed as resistant; whereas, plants with a rating of both 1.0 and 2.0 were considered resistant at nematode populations above 2000 per 500 ml soil.

Performance of Parental Lines

As an average over all cross combinations, D69-6344 had the lowest mean root-gall index (1.1) and Pickett 71 had the highest (5.9) (Table 5). These results indicated that D69-6344 was resistant and Pickett 71 was highly susceptible to the Wartelle race of root-knot nematode, which agreed with previous reports (17, 18, 19, 81, 106). Mean root-gall ratings for both Bragg and Hill were 5.5, indicating that both cultivars were susceptible to the Wartelle race. Root-gall ratings for Delmar plants ranged from 1.0 to 6.0, however, 23 of the 27 plants evaluated were classed as susceptible (Table 5). The mean root-gall index for Delmar was 3.8 which indicated that Delmar could have some genes for resistance to the Wartelle race.
Figure 4. Response of Parent Lines to Nematode Population

Root-Gall Index

D69-6344 — Bragg —
Pickett 71 — Hill —
Delmar —
Table 5. Summarized performance of parental lines.

<table>
<thead>
<tr>
<th>Parental Line</th>
<th>Root-Gall Indices</th>
<th>Classification</th>
<th>Mean</th>
<th>Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bragg</td>
<td>1</td>
<td>1 7 19</td>
<td>27</td>
<td>1</td>
</tr>
<tr>
<td>Pickett 71</td>
<td>1</td>
<td>1 1 36</td>
<td>38</td>
<td></td>
</tr>
<tr>
<td>D69-6344</td>
<td>29</td>
<td>4</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td>Hill</td>
<td>1</td>
<td>1 1 14</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>Delmar</td>
<td>2</td>
<td>4 8 2 6 5</td>
<td>23</td>
<td>4</td>
</tr>
</tbody>
</table>
Possible sources of the variation associated with Delmar included seed contamination, although no off-type plants were observed in Delmar monocultures; susceptibility to a soil pathogen that the other parental lines were resistant to; and the possibility that Delmar was heterogeneous for genes conditioning reaction to this race of the nematode. Since variation among Delmar plants was considerably larger than that among plants of the other parental lines even though all plants were exposed to similar environmental conditions, another likely explanation for the variation was that Delmar simply was more sensitive to environmental influences than the other genotypes studied.

**Performance of Cross Combinations**

**Bragg X D69-6344.** The mean root-gall index for Bragg was 5.2 and for D69-6344 was 1.0 (Table 6). One Bragg plant had a rating of 1.0. This plant presumably was an escape, and was responsible for the large variance estimate for Bragg (Table 6).

The F₁ plants were all highly susceptible, with a mean root-gall rating of 5.93 (Table 6). The mean response of the F₁ population was not significantly different from that of the susceptible parent, indicating that susceptibility to the Wartelle race of root-knot nematode is dominant to resistance.

Root-gall ratings of the F₂ plants ranged from 1.0 to 6.0, but were skewed toward the high infection level. When plants rating 1.0 and 2.0 were considered resistant and all other plants were considered susceptible, the F₂ segregation closely fitted a digenic model (Table 6). Plants from a backcross to the susceptible parent were susceptible. The results indicated that reaction to the Wartelle race in this cross was conditioned by two genes that acted in a duplicate-dominant
Table 6. Reaction of parents, F₁, and segregating generations from the cross Bragg X D69-6344 to the Wartelle race of root-knot nematode.¹

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean</th>
<th>Variance</th>
<th>No. plants per root-gall index ²/</th>
<th>No. plants grouped ³/</th>
<th>Expected Ratio</th>
<th>$\chi^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bragg</td>
<td>5.20</td>
<td>2.40</td>
<td>1</td>
<td>3 6</td>
<td>9 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D69-6344</td>
<td>1.00</td>
<td>0.00</td>
<td>7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₁</td>
<td>5.93</td>
<td>0.07</td>
<td>1</td>
<td>13 14</td>
<td>14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₂</td>
<td>5.51</td>
<td>1.49</td>
<td>12 7 12 3 28 262</td>
<td>305 19</td>
<td>15:1</td>
<td>0.08</td>
<td>.77</td>
</tr>
<tr>
<td>Bragg X F₁</td>
<td>5.83</td>
<td>0.22</td>
<td>1 3 25</td>
<td>29</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹/ Nematode population = 1980 nemas/500 ml soil
²/ 1 = 1-10% roots galled, 6 = 51-100% roots galled
³/ Plants rated 1 & 2 resistant, 3-6 susceptible
manner. The classification of F\textsubscript{2} plants in intermediate infection classes not shared by parental or F\textsubscript{1} plants, which resulted in a continuous-type F\textsubscript{2} distribution, presumably resulted from either minor genes, environmental conditions, or both.

Hill X D69-6344. Hill had a mean root-gall index of 5.88; whereas, the mean index for D69-6344 was 1.13 (Table 7). The F\textsubscript{1} population had a mean root-gall index of 6.00, which was not significantly different from that of the susceptible parent. Mean reactions of the F\textsubscript{1} and reciprocal F\textsubscript{1} populations did not differ significantly, indicating no maternal or cytoplasmic effects.

Of the 324 F\textsubscript{2} plants evaluated, 49 were classed as resistant and 275 were classed as susceptible. This segregation pattern did not fit any of the conventional ratios. The nematode population at which this cross was evaluated was extremely high (6800 larvae per 500 ml soil), which undoubtedly resulted in an underestimation of resistant plants. Although no conventional segregation ratio was detectable, the variation apparent among the F\textsubscript{2} plants indicated that the parental lines differ in reaction to the Wartelle race of root-knot nematode by at least one gene. There was no segregation in the backcross to the susceptible parent.

Delmar X D69-6344. Root-gall ratings for Delmar ranged from 2.0 to 6.0 and averaged 4.40 (Table 8). D69-6344 had a mean root-gall index of 1.38. The mean root-gall index for the F\textsubscript{1} population was 5.93.

Root-gall ratings of the F\textsubscript{2} plants ranged from 1.0 to 6.0, but were skewed toward the high infection level (Table 8). When plants rating 1.0 and 2.0 were considered resistant and all other plants
Table 7. Reaction of parents, F₁, and segregating generations from the cross Hill X D69-6344 to the Wartelle race of root-knot nematode.¹/

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean</th>
<th>Variance</th>
<th>No. plants per root-gall index ²/</th>
<th>No. plants grouped ³/</th>
<th>Expected Ratio</th>
<th>X²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 2 3 4 5 6</td>
<td>S R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hill</td>
<td>5.88</td>
<td>0.13</td>
<td>1 7 8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D69-6344</td>
<td>1.13</td>
<td>0.13</td>
<td>7 1</td>
<td></td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₁</td>
<td>6.00</td>
<td>0.00</td>
<td></td>
<td>10</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Recip. F₁</td>
<td>5.75</td>
<td>0.21</td>
<td>2 6</td>
<td></td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₂</td>
<td>5.14</td>
<td>3.09</td>
<td>44 5 3 0 28 244</td>
<td>275 49</td>
<td>3:1</td>
<td>16.86</td>
<td>0</td>
</tr>
<tr>
<td>Hill X F₁</td>
<td>5.93</td>
<td>0.07</td>
<td>2 25</td>
<td>27</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹/ Nematode population = 6800 nemas/500 ml soil
²/ 1 = 1-10% roots galled, 6 = 51-100% roots galled
³/ Plants rated 1 & 2 resistant, 3-6 susceptible
Table 8. Reaction of parents, F1, and segregating populations from the cross Delmar X D69-6344 to Wartelle race of root-knot nematode.1/

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean</th>
<th>Variance</th>
<th>No. plants per root-gall index 2/</th>
<th>No. plants grouped 3/</th>
<th>Expected Ratio</th>
<th>X²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delmar</td>
<td>4.40</td>
<td>2.93</td>
<td>0 2 2 0 2 4</td>
<td>8 2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D69-6344</td>
<td>1.38</td>
<td>0.27</td>
<td>5 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F1</td>
<td>5.93</td>
<td>0.07</td>
<td>13 5 3 3 14 283</td>
<td>303 18</td>
<td>15:1</td>
<td>.23</td>
<td>.63</td>
</tr>
<tr>
<td>F2</td>
<td>5.64</td>
<td>1.30</td>
<td>13 5 3 3 14 283</td>
<td>303 18</td>
<td>15:1</td>
<td>.23</td>
<td>.63</td>
</tr>
<tr>
<td>Delmar X F1</td>
<td>5.64</td>
<td>1.15</td>
<td>1 0 2 0 2 31</td>
<td>35 1</td>
<td>15:1</td>
<td>.23</td>
<td>.63</td>
</tr>
</tbody>
</table>

1/ Nematode population 3240 nemas/500 ml soil
2/ 1 = 0-10% of roots galled, 6 = 51-100% roots galled
3/ Plants rated 1 & 2 resistant, 3-6 susceptible
were considered susceptible, the F₂ segregated in a 15:1 ratio for susceptibility and resistance (Table 8). There was no detectable segregation pattern in the population from the backcross to Delmar. The results indicated that Delmar and D69-6344 differed in reaction to the Wartelle race at two loci.

**D69-6344 X Pickett 71.** The mean root-gall rating for D69-6344 was 1.00 and for Pickett 71 was 5.60 (Table 9). One Pickett 71 plant had a root-gall index of 3.0, however, galls present on the plant had large egg-masses, which indicated the plant was susceptible, but that the low inoculum level (440 larvae per 500 ml soil) prevented a reliable disease classification.

Mean root-gall ratings of the F₁'s and their reciprocals were not significantly different and were not different from that of the susceptible parent. The results indicated that susceptibility was dominant to resistance and that there were no maternal or cytoplasmic effects.

Of the 292 F₂ plants rated, 226 were classed as susceptible and 66 were classed as resistant, which gave a reasonably good fit to a 3:1 ratio (Table 9). The backcross to the resistant parent segregated in a 1:1 ratio for susceptibility and resistance. Results indicated that reaction to the Wartelle race in this cross was conditioned by one major gene pair. Variation apparent in the F₂ generation indicated that minor genes, environmental conditions, or both, also were involved in the disease reaction.

**Delmar X Pickett 71.** The mean root-gall rating for Delmar was 3.42 and for Pickett 71 was 6.00 (Table 10). All ten of the Pickett 71 plants had root-gall ratings of 6.00. The Delmar plants,
Table 9. Reaction of parents, F₁, and segregating generations from the cross D69-6344 X Pickett 71 to the Wartelle race of root-knot nematode.¹

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean</th>
<th>Variance</th>
<th>No. plants per root-gall index²</th>
<th>No. plants grouped ³/</th>
<th>Expected Ratio</th>
<th>$\chi^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>D69-6344</td>
<td>1.00</td>
<td>0.00</td>
<td>10</td>
<td></td>
<td></td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Pickett 71</td>
<td>5.60</td>
<td>0.93</td>
<td>1</td>
<td>1 1 8</td>
<td></td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>F₁</td>
<td>6.00</td>
<td>0.00</td>
<td>11</td>
<td></td>
<td></td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Recip. F₁</td>
<td>6.00</td>
<td>0.00</td>
<td>10</td>
<td></td>
<td></td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>F₂</td>
<td>4.31</td>
<td>4.61</td>
<td>66 20 19 4 19 164</td>
<td>226 66</td>
<td>3:1</td>
<td>.89</td>
<td>.34</td>
</tr>
<tr>
<td>D69-6344 X F₁</td>
<td>3.45</td>
<td>5.39</td>
<td>13 0 4 0 2 12</td>
<td>18 13</td>
<td>1:1</td>
<td>.81</td>
<td>.37</td>
</tr>
</tbody>
</table>

¹/ Nematode population = 440 nemas/500 ml soil
²/ 1 = 1-10% roots galled, 6 = 51-100% roots galled
³/ Plants rated 1 resistant, 2-6 susceptible
Table 10. Reaction of parents, $F_1$, and segregating population from the cross Delmar X Pickett 71 to the Wartelle race of root-knot nematode.1/

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean</th>
<th>Variance</th>
<th>No. of plants per root gall index 2/</th>
<th>No. Plants grouped 3/</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delmar</td>
<td>3.42</td>
<td>1.36</td>
<td>1 2 6 2 1 1</td>
<td>12</td>
</tr>
<tr>
<td>Pickett 71</td>
<td>6.00</td>
<td>0.00</td>
<td></td>
<td>10 10</td>
</tr>
<tr>
<td>$F_1$</td>
<td>6.00</td>
<td>0.00</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>$F_2$</td>
<td>5.61</td>
<td>0.99</td>
<td>1 5 27 6 19 282</td>
<td>339 1</td>
</tr>
<tr>
<td>Delmar X $F_1$</td>
<td>5.86</td>
<td>0.14</td>
<td>1</td>
<td>6 7</td>
</tr>
</tbody>
</table>

1/ Nematode population = 1780 nemas/500 ml soil
2/ 1 = 1-10% roots galled, 6 = 51-100% roots galled
3/ Plants rated 1 resistant, 2-6 susceptible
however, ranged in reaction from 2.0 to 6.0, with a preponderance of plants having ratings at the intermediate infection level.

The mean root-gall rating for the F₁ population was 6.00, which was not significantly different from the mean rating of the susceptible parent. Even though both parents were considered susceptible, there were detectable differences in degree of susceptibility between the two cultivars. Galls on Pickett 71 roots were larger and more numerous than those on Delmar. The resemblance of reaction of F₁ seedlings to those of Pickett 71 seedlings suggested that genes for susceptibility which were contributed by Pickett 71 were dominant to gene(s) contributed by Delmar.

Root-gall ratings of the F₂ plants ranged from 1.0 to 6.0, but were skewed toward the high infection level. Only one of the 340 F₂ plants was rated as resistant and that plant presumably was an escape. There also was no segregation in the population which resulted from the backcross to Delmar.

**Bragg X Pickett 71.** Root-gall indices averaged 5.56 for Bragg and 6.00 for Pickett 71 (Table 11). Although all Bragg and Pickett 71 plants were susceptible, differences in type and severity of infection were apparent. Root-galls were much larger and more numerous on Pickett 71 plants than on Bragg plants, which denoted a genotypic difference between the two cultivars. This was not surprising since Bragg has been reported to be resistant to many forms of root-knot nematode (18, 44, 59, 74, 96), whereas Pickett 71 has consistently been reported to be susceptible (44, 50, 59, 81, 106).
Table 11. Reaction of parents, F$_1$, and segregating generations from the cross Bragg X Pickett 71 to the Wartelle race of root-knot nematode.\(^1\)

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean</th>
<th>Variance</th>
<th>No. plants per root</th>
<th>No. Plants grouped (^3)/</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Gall index (^2)/</td>
<td>S</td>
</tr>
<tr>
<td>Bragg</td>
<td>5.56</td>
<td>0.53</td>
<td>1 2 3 4 5 6</td>
<td></td>
</tr>
<tr>
<td>Pickett 71</td>
<td>6.00</td>
<td>0.00</td>
<td></td>
<td>10</td>
</tr>
<tr>
<td>F$_1$</td>
<td>6.00</td>
<td>0.00</td>
<td></td>
<td>13</td>
</tr>
<tr>
<td>F$_2$</td>
<td>5.99</td>
<td>0.00</td>
<td>1 333 334</td>
<td></td>
</tr>
<tr>
<td>Bragg X F$_1$</td>
<td>6.00</td>
<td>0.00</td>
<td></td>
<td>31</td>
</tr>
</tbody>
</table>

\(^1\) Nematode population = 2200 nemas/500 ml soil  
\(^2\) 1 = 1-10% roots galled, 6 = 51-100% roots galled  
\(^3\) Plants rated 1 & 2 resistant, 3-6 susceptible
The F_1 plants were all susceptible, with a mean root-gall rating of 6.00, and all plants resembled Pickett 71 in infection characteristics.

The F_2 and backcross generation seedlings were all susceptible, but differences in reaction were observed within each population. The F_2 plants segregated in a ratio of 3 Pickett 71 infection type to 1 Bragg infection type ($\chi^2 = .20, P = .66$). The population which resulted from the backcross to Bragg segregated in a ratio of 1 Pickett 71 type to 1 Bragg type ($\chi^2 = .29, P = .59$). The results indicated that Bragg and Pickett 71 differed in reaction to the Wartelle race by one gene pair.

**Hill X Pickett 71.** Both Hill and Pickett 71 were susceptible, with mean root-gall indices of 5.20 and 6.00, respectively (Table 12). Again, there was a difference between the two cultivars in degree of reaction, with Pickett 71 exhibiting a more susceptible reaction than Hill.

The F_1's and their reciprocals were all susceptible and more closely resembled Pickett 71 than Hill. This suggested that Pickett 71 possessed genes which played a greater role in expression of disease reaction than Hill. The similar reactions of the F_1 and reciprocal F_1 seedlings indicated no maternal or cytoplasmic effects.

The backcross generation was completely susceptible, however, there was variation in reaction among seedlings from the severity of Pickett 71 to the mildness of Hill. The F_2 population ranged in reaction from 1.0 to 6.0, but only one of the 236 plants evaluated had a rating of 1.0. That plant presumably was an escape. In all
Table 12. Reaction of parents, $F_1$, and segregating generations from the cross Hill X Pickett 71 to the Wartelle race of root-knot nematode.1/

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean</th>
<th>Variance</th>
<th>Gall index 2/</th>
<th>No. Plants grouped 3/</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 2 3 4 5 6</td>
<td>S R</td>
</tr>
<tr>
<td>Hill</td>
<td>5.20</td>
<td>1.32</td>
<td>2 1</td>
<td>7 10</td>
</tr>
<tr>
<td>Pickett 71</td>
<td>6.00</td>
<td>0.00</td>
<td></td>
<td>8 8</td>
</tr>
<tr>
<td>$F_1$</td>
<td>6.00</td>
<td>0.00</td>
<td></td>
<td>10 10</td>
</tr>
<tr>
<td>Reciprocal $F_1$</td>
<td>6.00</td>
<td>0.00</td>
<td></td>
<td>8 8</td>
</tr>
<tr>
<td>$F_2$</td>
<td>5.88</td>
<td>0.34</td>
<td>1 1 2 5 4</td>
<td>223 235 1</td>
</tr>
<tr>
<td>Hill X $F_1$</td>
<td>6.00</td>
<td>0.00</td>
<td></td>
<td>31 31</td>
</tr>
</tbody>
</table>

1/ Nematode population - 1410 nemas/500 ml soil
2/ 1 = 1-10% roots galled, 6 = 51-100% roots galled
3/ Plants rated 1 resistant, 2-6 susceptible
likelihood a segregation pattern similar to that of the F\textsubscript{2} population of Bragg X Pickett 71 existed but these data were not obtained.

**Delmar X Bragg.** The mean root-gall indices for Bragg and Delmar were 5.78 and 4.39, respectively (Table 13). Two Delmar seedlings were rated as resistant but these seedlings had damaged root systems, which might have prevented detection of the disease expression.

The F\textsubscript{1} plants were all highly susceptible, with a mean root-gall index of 6.0 (Table 13). Root-gall indices of the F\textsubscript{2} population ranged from 1.0 to 6.0, but only two of the 309 plants evaluated were rated as resistant. These two plants were thought to be escapes. The backcross population had a mean root-gall rating of 5.64. Three plants from the backcross population had a root-gall rating of 1.0. These plants also had damaged root systems and probably would have had susceptible reactions if their root systems had been normal.

**Genetic Model Development**

The highly susceptible reaction of F\textsubscript{1} plants in all cross combinations indicated that susceptibility to the Wartelle race of root-knot nematode is dominant to resistance. Boquet et al. (19) reported that susceptibility to the Wartelle race in the soybean cross D69-6344 X D69-8178 was partially dominant to resistance. They found that F\textsubscript{1} plants were moderately resistant at low nematode population densities, moderately susceptible at medium densities, and highly susceptible at higher densities. Nematode densities used in this study were, with the exception of the cross D69-6344 X Pickett 71, comparable to or larger than the highest nematode density used by Boquet et al. (19). Therefore, F\textsubscript{1} plant reactions which were determined at comparable
Table 13. Reaction of parents, $F_1$, and segregating populations from the cross Delmar X Bragg to the Wartelle race of root-knot nematode.  

<table>
<thead>
<tr>
<th>Population</th>
<th>Mean</th>
<th>Variance</th>
<th>No. plants per root Gall index 2/</th>
<th>No. Plants grouped 3/</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delmar</td>
<td>4.38</td>
<td>2.13</td>
<td>2 2 3</td>
<td>3 3 2</td>
</tr>
<tr>
<td>Bragg</td>
<td>5.78</td>
<td>0.19</td>
<td>2 7 9</td>
<td>9</td>
</tr>
<tr>
<td>$F_1$</td>
<td>6.00</td>
<td>0.00</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>$F_2$</td>
<td>5.95</td>
<td>0.20</td>
<td>2 0 1 0 3</td>
<td>303 307 2</td>
</tr>
<tr>
<td>Delmar $F_1$</td>
<td>5.64</td>
<td>1.39</td>
<td>3 0 1 0 3</td>
<td>51 55 3</td>
</tr>
</tbody>
</table>

1/ Nematode population = 5700 nemas/500 ml soil  
2/ 1 = 1-10% roots galled, 6 = 51-100% roots galled  
3/ Plants rated 1 & 2 resistant, 3-6 susceptible
nematode densities were very similar in the two studies. Susceptibility to the Wartelle race appeared to be dominant to resistance at nematode densities at which plants are often exposed to in the field.

Data from the cross D69-6344 X Pickett 71 indicated that reaction to the Wartelle race was conditioned by a single gene pair. The F₂ segregation pattern of the cross Hill X D69-6344 approximated that expected for a single gene model, however, there was a deficiency of plants in the resistant class, which was presumably a result of the extremely high nematode population (6800 larvae per 500 ml soil) at which the cross was evaluated. If the high nematode population caused the smaller than expected number of plants in the resistant class by causing some resistant plants to appear susceptible, as has been previously reported (19), then the results indicated that D69-6344 and Hill also differ in reaction to the Wartelle race by genes at a single locus. Although progeny of the cross Hill X Pickett 71 were susceptible, parental types were detected in both the F₂ and backcross populations. These results indicated that the genes for susceptibility possessed by Hill and Pickett 71 were allelic. Resistance possessed by D69-6344 was recessive to the susceptibility of both Hill and Pickett 71, and the susceptible reaction of Hill was recessive to the highly susceptible reaction of Pickett 71.

When both Bragg and Delmar were crossed with D69-6344, the F₂ populations segregated in a 15:1 ratio for susceptibility and resistance (Tables 6 and 8, pages 34 and 37). This indicated that reaction to the Wartelle race in these two crosses was conditioned by two gene pairs. Although Delmar varied in disease reaction more than Bragg,
the preponderance of Delmar seedlings were as susceptible as Bragg, which indicated that the two cultivars were identical in genotype for this character. Progeny from the cross Delmar X Bragg were susceptible and there was no evidence for parental type segregation in either the F$_2$ or backcross population, which gave additional evidence that Bragg and Delmar had identical genes for reaction to the organism. All progeny from the cross Bragg X Pickett 71 were susceptible, which indicated that Bragg and Pickett 71 had a common gene for susceptibility. Based on the performance of the parental lines and the segregation ratios obtained in the crosses, the following genotypes were apparent: D69-6344 - aabb, Bragg and Delmar - AABB, Hill - AAbb, and Pickett 71 - A'A'bb (Table 14).

Boquet et al. (19) reported that inheritance of reaction to the Wartelle race of root-knot nematode was conditioned by one major gene and at least one modifying gene. Results obtained in this study, however, indicated that inheritance of reaction to the Wartelle race was conditioned by major genes at two loci that act in a duplicate-dominant manner. Three alleles appeared to exist at one locus and two alleles at the other. Variation among progeny of several crosses exceeded that of the parental lines, which indicated that minor genes, environmental conditions, or both, also condition the disease reaction.

Bragg, Hill, Delmar, and D69-6344 were selected for the study, in part, to represent different sources of resistance to root-knot nematode. Resistance possessed by Delmar, Hill, and Bragg were thought to have been derived from FC 33243, Haberlandt, and Palmetto, respectively, whereas, resistance possessed by D69-6344 had been suggested to have been derived from both Hill and Laredo (106). The susceptible
Table 14. Proposed parental genotypes.

<table>
<thead>
<tr>
<th>Parental Line</th>
<th>Genotype</th>
<th>Classification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delmar</td>
<td>AABB</td>
<td>susceptible</td>
</tr>
<tr>
<td>Bragg</td>
<td>AABB</td>
<td>susceptible</td>
</tr>
<tr>
<td>Hill</td>
<td>AAbb</td>
<td>susceptible</td>
</tr>
<tr>
<td>Pickett 71</td>
<td>A' A'bb</td>
<td>highly susceptible</td>
</tr>
<tr>
<td>D69-6344</td>
<td>aabb</td>
<td>resistant</td>
</tr>
</tbody>
</table>
disease reaction of Delmar and Bragg in this study indicated that
genes possessed by FC 33243 and Palmetto did not condition resistance
to the Wartelle race of root-knot nematode. Although Hill was suscep­
tible to the Wartelle race, D69-6344, a second generation selection
from a cross involving Hill, was highly resistant. These results
indicated that the resistance derived from Haberlandt by Hill condi­tioned resistance to the Wartelle race when in some genetic back­
grounds. The hypothesis that resistance possessed by D69-6344 appear­ed to be derived from Hill and Laredo was supported by the fact that
the cross between Hill and D69-6344 segregated for only one gene.
Since the results indicated that reaction to the Wartelle race was
conditioned by major genes at two loci, D69-6344 and Hill appeared to
have one gene for resistance in common.
SUMMARY

The purpose of this investigation was to study the number and behavior of genes for resistance in soybeans to the Wartelle race of root-knot nematode.

Five parental lines were selected on the basis of their ancestry and their reaction to root-knot nematode. Eight cross combinations were made in the field and the resulting populations were grown in nematode infested soil in a greenhouse. Root systems of individual seedlings of these populations were examined and rated subjectively for degree of resistance to this organism. The segregation patterns were tested for goodness of fit to expected ratios by $\chi^2$ analysis.

Results indicated that susceptibility to the Wartelle race of root-knot nematode in soybeans was dominant to resistance. Inheritance of reaction to the Wartelle race was conditioned by genes at two loci, which acted in a duplicate-dominant manner. Similar reactions of reciprocal $F_1$'s suggested that no maternal or cytoplasmic effects were involved. Variance estimates suggested that minor genes or environmental conditions or both may have contributed to the disease reaction. However, the role of either the environment or minor genes should not prevent selection for resistance in soybeans to the Wartelle race of root-knot nematode in conventional breeding programs.

Delmar, Bragg, and Hill were all susceptible to the Wartelle race and were thought to possess common genes for susceptibility even though they were reported to derive genes for resistance to other root-knot nematodes from separate sources. Delmar and Bragg were
thought to have identical genotypes while the common ancestry of
D69-6344 and Hill suggested that D69-6344 obtained genes for resis­
tance from Hill, as well as, the root-knot resistant cultivar Laredo.
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VITA

John Saichuk, son of Mrs. Therese Saichuk, was born April 22, 1950, in New Orleans, Louisiana. In 1968 he completed his high school education at Hanson Memorial High School in Franklin, Louisiana.

In the fall of 1968 he entered the University of Southwestern Louisiana where he received a Bachelor of Science degree in Agriculture in May of 1972. The following September he entered Texas A & M University from which he received a Master of Science degree in Agronomy in May of 1974. In September of that year he entered Louisiana State University in pursuance of a Doctor of Philosophy degree in Agronomy with a minor in Plant Pathology.

Shortly before completion of degree requirements he accepted a teaching position at the University of Southwestern Louisiana in Lafayette, Louisiana.

The author is married to the former Susette Anne Patin of New Roads, Louisiana. They have one son, John.

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EXAMINATION AND THESIS REPORT

Candidate: John Kennedy Saichuk

Major Field: Agronomy


Approved:

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Date of Examination:

August 1, 1977