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CONTROL OF THE GOLDEN NEMATODE IN THE UNITED STATES*

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INTRODUCTION

The golden nematode is considered the most serious pest threatening the potato industry of the United States. Since its discovery on Long Island, New York, federal, state, and local governments have joined forces to eliminate the threat of the golden nematode to the potato industry of the United States. This effort has involved the close cooperation of research, regulatory, and extension personnel as well as potato growers. The resulting program is one of the largest pest-management efforts ever attempted. This article is an account of the golden nematode control program from its inception in the 1940s until the present.

The Nematode

Currently two species of cyst-forming nematodes are recognized that attack and reproduce on potatoes. Apart from differences in general morphology, these species are distinguished by the color of the immature females before they become brown cysts. Those with white or cream-colored females are *Globodera pallida* and those with golden females (golden nematode) are *G. rostochiensis* (1, 44).

Both species contain pathogenic variants designated pathotypes. However, repeated experiments indicate that only one pathotype, Ro1, of *G. rostochiensis* is present in the United States, a finding that has played a major role in decisions concerning its control. Because only *G. rostochiensis* with golden immature females occurs in the USA, the term "golden nematode" is commonly used in this country. In countries where both species occur, the common name potato cyst nematodes is used. In this paper the name golden nematode is used when referring to this nematode in the USA and the term potato cyst nematodes when we refer to both species that occur in other countries.

The Problem

The golden nematode is generally recognized as one of the most difficult of all crop pests to control. If left uncontrolled, it is capable of causing a 100% loss in potato yields. Because of strict quarantine and regulatory procedures, it has not caused economic losses of potato yields in the United States since the initiation of the control program in 1946 (42). The systematic soil survey (sponsored by the federal government) of potato lands in the infested areas of New York reveals its presence before densities reach damaging levels. These fields are dealt with by regulatory procedures that currently involve nematode management systems. Thus, only indirect losses such as costs of border inspections, soil surveys, and other regulatory procedures are realized from the golden nematode in the USA (12).

The golden nematode poses many problems in its control as it has a remarkable ability to survive unsuitable conditions. It is among the most highly specialized and successful plant-parasitic nematodes (13). About 3–4 weeks after infecting roots, female nematodes enlarge to spherical bodies that protrude from the roots. At maturity, they die and their body walls tan to become tough protective cysts containing several hundred eggs with infective juveniles in a quiescent state. These unhatched juveniles are protected by both the egg shell and the durable cyst wall that acts to protect against adverse environmental conditions, natural enemies, and pesticidal chemicals.

When potatoes are harvested, cysts are detached from the roots and become free in the soil where their contents can survive for many years until suitable conditions return (22). In addition to suitable temperature and moisture, the presence of host roots is necessary for the nematode to resume its activities. A chemical substance, whose true identity still eludes investigators, emanates from potato roots and stimulates juveniles to hatch and emerge from the cysts (38); these juveniles are then attracted to and invade host roots (13).

Once plants are infected, the lack of any one distinctive above-ground symptom to reveal the presence of the golden nematode is an asset to its survival. Low infestations may reproduce and increase in the soil undetected for many years (42). During this time, the nematodes spread to new areas because such low infestations are undetectable by the most sensitive of soil survey procedures. Thus, the nematode is most often one step ahead of the survey. Depending on cropping practices, six years or more are required after introduction of the pest into a field before populations increase sufficiently to be detected by soil surveys (32). This undramatic increase in nematode population densities and the inability to detect low populations has plagued the golden nematode control program since its beginning.

ORIGIN OF THE GOLDEN NEMATODE

The golden nematode was first believed to have originated in Europe (22, 42). Its preferred host, the potato, (*Solanum* spp.) was introduced into Europe around the end of the 16th Century but was not widely cultivated until some 200 years later (20). By the end of the 17th Century, the potato had become popular in small fields and gardens in Ireland. It slowly spread to Germany, western England, and Scotland by the end of the 18th Century. Areas planted to potatoes continued to increase and many peasant farmers came to depend on the crop. Then, suddenly, potato late blight appeared in the mid 19th Century bringing with it famine to Ireland. During the last half of the century many collections of potatoes were brought to Europe from South America to breed for resistance to late blight (20). Potato cyst nematodes were likely brought to Europe along with such potato collections. They were first reported from Germany in 1881, about 30 years after the introduction of breeding material began (22). During the first part of the 20th Century they were identified from several European countries. From Europe they spread to many parts of the world. At least 48 countries now report infestations of one or both species (13). Most likely they were spread in soil adhering to potato tubers, as encysted juveniles can resist desiccation and can spread by any means that transports soil. Europe became a secondary center for distribution of potato cyst nematodes and from there they spread throughout the world with seed potatoes of improved varieties developed in Europe (12).

In a routine inspection of a ship that arrived from Peru at the port of Seattle, Washington, in 1951, plant quarantine inspectors found the golden nematode in soil from potatoes in the ship's stores (42), and again later that year in a second ship from Peru anchored in New York harbor. The ship's log indicated that the contaminated potatoes had originated in Peru. A search conducted in Peru found the nematode in potato fields near the city of Tarma (42). Studies by Peruvian scientists indicated that the nematode was widespread and in fact was indigenous to Peru. The nematode was later discovered in the highlands of Bolivia and Argentina, where it is also considered indigenous (42). It is now generally accepted that the golden nematode originated in the South American Andes where it coevolved with its preferred host, the potato (12).

DISCOVERY IN THE USA

The first evidence that potato cyst nematodes occurred in the United States of America was when a potato grower near Hicksville, Long Island, New York, noticed a few isolated spots in his field where vines were stunted and off-color (6, 29, 42). Despite attempts to improve growth by practices such as fertilization and liming, the number of spots increased and there were significant yield losses in the field within 4 years. In 1941, O. S. Cannon, a graduate student of the Department of Plant Pathology, Cornell University, observed swollen nematode females on roots of poorly growing plants. These nematodes were identified as *Globodera (Heterodera) rostochiensis,* the golden nematode, by B. G. Chitwood, a nematologist with the U.S. Department of Agriculture, Agricultural Research Service (USDA/ARS) Bulb Laboratory in Babylon, Long Island. Subsequent examination of this field showed that it was entirely infested and that crop yield losses were as high as 70% (W. F. Mai, unpublished).

Where the inoculum originated and how and when it gained entry into the United States is not known. A possibility is that it was transported on military equipment returning from Europe after World War I (42). The original infested field was part of an air field of a temporary military camp. Available information on the distribution of the golden nematode on Long Island indicates that all infestations there might have originated from this field. More than 30 additional fields farmed by the operator of the original infested field were later found infested (W. F. Mai, unpublished).

EARLY PROGRAM DECISIONS

Soon after the golden nematode was discovered on Long Island in 1941, USDA/ARS and the Department of Plant Pathology, Cornell University, undertook a cooperative research program. At the same time, New York State Department of Agriculture and Markets and the USDA, Animal and Plant Health Inspection Service (USDA/APHIS) conducted surveys. With the involvement of the United States in World War II only limited effort could be devoted to this problem, but immediately after the war was over, an active cooperative golden nematode program was initiated. From its beginning and continuing until the present, this program has been a cooperative one. In addition to the federal and state research and regulatory agencies, New York State counties and townships were actively involved, along with potato growers and the New York potato industry. This cooperative nature of the program has contributed significantly to its success.

Preliminary pathogenicity tests and observations of growth and yield losses caused by the golden nematode in infested fields on Long Island indicated the serious nature of this pest. These conclusions were confirmed by observation of yield losses in infested potato fields in Europe by delegates from the USA and by discussions with scientists and growers in various potato-growing regions of the world.

The first and most important activity of specialists involved in this cooperative program was to determine its direction. At this time, the only adequate control measure available was rotations of from 3–7 years. Such long rotations were not practical for most commercial growers in infested potato-growing regions of New York. Thus, it became essential to conduct an extensive research program to develop more practical control measures.

By 1944, preliminary surveys revealed that this nematode was more widespread on Long Island than originally believed (42). However, large numbers of nematodes were found and yield losses occurred only in the first fields discovered to be infested. This information indicated that the golden nematode had been on Long Island for a relatively short period of time, possibly no more than 20 years, and that a regulatory program could effectively reduce its spread to noninfested parts of Long Island and to other potato-growing regions of the USA.

Another reason for deciding to proceed with a combined comprehensive regulatory and research program was that potato seed was not apparently involved in the spread of this nematode on and from Long Island. Although contaminated seed pieces are instrumental in the distribution of the potato cyst nematodes, this means of spread was not an important factor on Long Island because the high rate of virus spread kept seed production to a minimum. Contaminated soil associated with items such as reused containers, machinery, and plant materials were more important means of spread than were seed potatoes. Also, relatively high temperatures in Long Island potato soils were less favorable for golden nematode development and it was easier to prevent spread of the resulting lower nematode populations (16).

Thus, the overall approach to the golden nematode problem was to carry out an extensive regulatory program designed to minimize spread of this nematode and at the same time conduct a comprehensive research program to develop practical control measures. To carry on these two diverse programs simultaneously, close cooperation and communication were essential among personnel involved in research and regulatory activities. Research scientists had to limit their use of living nematodes to experiments that did not result in their spread. Concurrently, regulatory scientists had to modify their activities so that research scientists could use living nematodes to conduct efficient and effective research.

This approach has allowed many aspects of the golden nematode problem to be investigated including: (*a*) influence of crop rotation on nematode populations under Long Island conditions, (*b*) testing for nematode resistance, (*c*) testing for the presence of nematode races, (*d*) studies on the chemical nature of the host-produced nematode hatching agent, (*e*) breeding for nematode resistance, and (*f*) chemical control investigations.

Because they were considered more promising, breeding for resistance and chemical control investigations were emphasized. Breeding for resistance was a cooperative effort among nematologists and plant breeders from Cornell University and the USDA/ARS. The USDA/APHIS methods development program cooperated closely with nematologists in their research on chemical control. Here the objectives were to develop methods for applying fumigants to the soil and for space fumigation. Their other activities included developing treatments to free nursery stock, farm machinery, burlap bags, and other commodities of nematode infestation so that they could be safely moved (42).

THE GOLDEN NEMATODE QUARANTINE

Soon after its discovery on Long Island, the New York State Department of Agriculture and Markets, under the broad coverage of the State's Agriculture and Markets Law related to insect pests and plant diseases, took action designed to prevent spread of the golden nematode. In 1944, the State enacted a specific quarantine that has subsequently been modified and amended to reflect changing conditions, receipt of new information, and development of improved treatments (42). The state quarantine was drafted in conjunction with federal regulatory officials who have been a full partner with the State and have cooperated in its administration and enforcement (42). In 1948, the Federal Government, through the Golden Nematode Act formulated policy for the protection of the potato and tomato industries from the golden nematode, should further action become necessary.

The following is a condensation of the present New York State Quarantine as it relates to the growing of host crops in regulated areas.

No host crops or nonhost crops shall be grown, except on lands that:

1. have received a chemical treatment as prescribed by the Commissioner to control the golden nematode and have been declared safe for growing of host or nonhost crops; or
2. have not received a chemical treatment as prescribed by the Commissioner provided the owner or operator of such lands plant a variety of potato that is resistant to the golden nematode or a crop that is not a host to the golden nematode and is approved by the Commissioner; or
3. are regulated and have either previously received a chemical treatment to control the golden nematode or have been planted for two or more growing seasons with a variety of potato that is resistant to the golden nematode. The last planting of a resistant variety is followed by an analysis of

soil taken from these lands that show no viable golden nematodes. If no viable nematodes are present, the owner or operator may apply for a waiver of crop restrictions and enter these lands into a rotational system approved by the Commissioner.

Other sections of this document address the movement of soil in conjunction with various agricultural commodities and equipment, permits, quarantine areas, and the prohibition of seed potato production.

In 1969, after a reported discovery of the golden nematode in New Castle County, Delaware, a public hearing was held in Washington, D.C. and considered the imposition of a federal golden nematode quarantine. The participating state regulatory officials by unanimous vote requested that a federal golden nematode quarantine be established. This quarantine was invoked in 1969 and paralleled the existing state golden nematode quarantine. It empowered the federal government to regulate interstate movement of items that posed a potential risk of spreading the golden nematode (R. B. Gaines, personal communication).

RESEARCH TO ESTABLISH REGULATORY PROCEDURES

Survey Procedures

Extensive surveys to determine the distribution of the golden nematode were absolutely essential to establish a regulatory program, as large numbers of nematodes may be present in a potato field in which no symptoms are evident (42). Thus, this nematode must be found and identified in roots and/or soil to positively determine its presence. For this reason, surveys must be conducted continuously and systematically.

Several survey procedures were considered for detecting golden nematode infestations. The examination of live potato roots for cysts was found impractical for widespread use because many cysts fall off the roots, even when plants are carefully dug. Also, the stage of nematode development (white female) when this procedure can be effectively used lasts only 2 weeks. The examination of debris that accumulates under potato graders for cysts was also impractical for routine surveys. Apart from problems associated with processing the debris, a major, inherent disadvantage is determining where in a field the infestation occurred or, in some cases, which field was infested (W. F. Mai, unpublished data).

The most reliable detection method is the collection of soil samples at prescribed intervals from potato fields (42). The more soil samples collected per unit area the lower the density of golden nematode populations that can be detected, but the higher the cost of sampling. In surveys in the USA, about a tablespoon of soil is collected on the end of a pointed trowel every 8 paces on a grid pattern. This method results in one composite sample weighing 4–6 pounds every three-fourths to one acre of soil inspected. In more intensive surveys, soil is collected on a 4 × 4 or a 2 × 2 pace interval. The USDA/APHIS methods development program was responsible for a number of improved techniques, including a sampling wheel to increase the efficiency and cost effectiveness of soil sampling.

Soil Processing Procedure

The golden nematode extraction procedure used in the USA regulatory program is a modification of a flotation-sieving technique first developed by Fenwick (15), based on the fact that dry cysts float in water but soil particles sink to the bottom. USDA/APHIS developed a machine to effectively and efficiently float cysts and separate them from most extraneous material by screening (42). To prevent contamination, equipment must be washed thoroughly after processing each sample.

Disinfestation Procedures

In the absence of a host plant, the golden nematode survives for several years enclosed in egg shells inside protective cysts (43). Consequently, soil adhering to farm machinery provides an excellent way of spreading cysts from field to field. Portable steam generators have been widely used by regulatory workers to disinfest farm machinery (42). Although this method removes a high percentage of infested soil, it is difficult to thoroughly steam clean bulky machinery and virtually impossible to kill 100% of the nematodes. After testing many volatile chemicals, a methyl bromide treatment was made available to disinfest such equipment. (27).

RESEARCH TO ESTABLISH CONTROL PROCEDURES

Host Range

A knowledge of the host range of the golden nematode was required for the success of a regulatory program designed to minimize spread by keeping soil populations at low levels. The results of extensive host-range experiments showed that potatoes, tomatoes, and eggplant are the only commercial crops attacked by this nematode and that potato is the most important host (32). In addition, several solanaceous weeds including *Solanum rostratum* (Buffalo Burr), *S. triflorum* (cut-leaved nightshade), *S. blodgettii*, *S. dulcamara* (bitter nightshade), *S. xanthi* (purple nightshade), and *S. entegrifolium* (tomato eggplant) are lightly infected (32), but these weeds are rarely found in Long Island potato fields. In addition, four wild species of *Lycopersicon* were shown to be hosts of this nematode (28), but none is native to the United States.

Crop Rotation

In 1952, crop rotation was the chief control measure available to growers in countries where large areas of land were heavily infested with the potato cyst nematode (32). The length of rotation necessary for profitable potato yields increased with severity of infestation and when the number of nematodes in the soil reached a high incidence, 4, 5, or 6-year rotations were needed (31).

Before the Spanish conquest, the Incas controlled the potato cyst nematode in the potato-growing regions of the Peruvian Andes by an enforced 7-year rotation (8). Growing potatoes more frequently than once in seven years usually resulted in having ones's fingers cut off. After the Inca Empire was destroyed by the Spanish, this control program was abandoned.

To determine the influence of crop rotation on golden nematode populations under growing conditions on Long Island, New York, rotation experiments were conducted in heavily infested soil in microplots. Only 3-year rotations were considered in these experiments as longer rotations were impractical for local potato growers. In these experiments, vegetable, hay, and pasture crops adapted to Long Island conditions were rotated with potatoes. Although certain of these rotations, particularly those with grasses, significantly suppressed nematode development on succeeding potato crops, differences were not of sufficient magnitude to warrant their use in the golden nematode control program (7, 32).

Soil Fumigation

Because soil fumigation proved to be the best and most practical means of killing golden nematodes in soil, experiments to develop even more effective fumigation treatments received high priority in early research. Chitwood and coworkers from USDA/ARS and Cornell University found that of all soil fumigants tested, D-D Mixture (dichloropropene-dichloropropane) consistently gave the most promising results (7).

The first large-scale attempt at chemical control was in 1946 when D-D was applied to over 600 ha of infested land in Nassau County, New York. In some of the treated fields, golden nematode populations high enough to cause severe symptoms and economic yield losses had developed before infestations were discovered (7). The chemical was applied at 420 l/ha in a single application. Although this treatment reduced nematode populations to a very low density, complete control was not achieved. Further research and observations by federal and state research and regulatory personnel revealed that a high percent of the surviving nematodes were in the upper 5 or 10 cm of soil when a single treatment was used (7). This occurred because the movement of fumigant was more rapid in the upper soil levels and the nematodes were not exposed to the toxic vapors long enough to kill them. Consequently, a treatment was tried that gave a higher percent control. D-D was applied at the rate of 840 l/ha in two applications of 420 L each 10 days apart; the soil was turned between applications. This double treatment resulted in a very high level of control and served as a basis of the soil treatment in the golden nematode control program inaugurated in 1960 (42).

Nematode Resistance

In tests conducted by numerous workers, all European and American potato cultivars of *S. tuberosum* were susceptible to the golden nematode (35). In 1941, Ellenby started a major research project to search for resistance in tuber-forming and non tuber-forming *Solanum* spp. (9). More than 1200 lines belonging to more than 60 species from the Commonwealth Potato Collection (CPC) were tested. Most collections were susceptible, except one resistant line *Solanum ballsii* (now *S. vernei*) (10).

Mai & Lownsbery, working on Long Island, New York, and using CPC material, obtained similar results in preliminary tests conducted in 1946 (34). These tests showed that *S. vernei* is not immune but is highly resistant to the golden nematode. Because *S. vernei* is diploid and *S. tuberosum* is tetraploid, difficulties were encountered in crossing the two species. These problems were overcome and currently this species is of considerable importance because of its resistance to both *G. rostochiensis* and *G. pallida* (41).

Ellenby later discovered four lines, CPC 1673, 1685, 1692, and 1595, of *S. tuberosum* ssp. *andigenum* that were resistant to *G. rostochiensis* (11). This subspecies is cultivated in the Andean regions from Venezuela to northern Argentina and is closely related to *S. tuberosum*. Toxopeus & Huijsman later obtained evidence that the resistance in CPC 1673 is inherited and segregates as a single dominant gene, which was later designated H_1 (21, 45). Because *S. tuberosum* and *S. tuberosum* ssp. *andigenum* are closely related, it is relatively easy to transfer this single gene resistance to *S. tuberosum*. The major disadvantage is that this single gene does not confer resistance to *G. pallida*. However, resistance conditioned by the single dominant gene, H_1 derived from CPC 1673, has been used worldwide for developing cultivars with resistance to *G. rostochiensis* (Ro1) (golden nematode) (5, 14).

RESEARCH ON GOLDEN NEMATODE MANAGEMENT

Chemical Management

In the early 1960s, research was initiated at Cornell University on the use of nonvolatile nematicides to manage the golden nematode (19). This research approach became particularly important when the golden nematode was discovered in 1967 in western New York, where potatoes are grown on fine-textured and organic soils that are less suitable than sandy soils for fumigation. At this time, the major emphasis of the golden nematode control program began to change from its elimination from host-crop land to "living with" or managing it at desired population densities. Although soil fumigants had proven very effective in reducing population densities (17), high soil moisture and low temperature (7) often make them impossible to use on land in the northeastern USA the same year that a potato crop is produced. The nonvolatile organophosphates and oxime carbamates offered a viable alternative to soil fumigation.

Chemical control of the golden nematode in most countries is aimed at reducing population densities sufficiently to obtain profitable yields from infested fields (14, 22, 46). In the United States, the objective is to manage population densities at sufficiently low levels to minimize or eliminate the risk of golden nematode spread. Consequently, the goal of the research was to develop ways to manage golden nematode population densities at extremely low levels with the nonvolatile nematicides.

Initial studies concentrated on methods of applying the organophosphates and oxime carbamates. These studies involved seedpiece treatment, foliar applications, or soil applications of carbofuran, ethoprop, oxamyl, phenamiphos, and aldicarb (3, 25). Treatments of seedpieces with sufficient concentration of these chemicals were also phytotoxic and therefore ruled out the possibility of acceptable seed treatment for golden nematode control. Repeated foliar applications of 1.12 kg of active ingredients/ha of oxamyl or carbofuran at 10 day intervals for 50 days beginning when 90% of the plants had emerged significantly suppressed golden nematode population increase (3), but not to the extent required of an acceptable regulatory treatment. Aldicarb or oxamyl applied at 5.6 kg a.i./ha in the seed furrow at the time of planting potatoes suppressed golden nematode population development significantly enough to be considered as chemical management tools for the golden nematode (3).

Because of the quarantine, control measures to confine its spread in the United States had to reduce populations below detectable levels. Both aldicarb and oxamyl reduced golden nematode populations significantly but not to a level acceptable for a regulatory treatment when used alone. Less effective treatments are useful and promising when integrated with other management techniques, such as the use of resistant potato cultivars and nonhost crops (2).

Resistance as a Management Tool

When golden nematode-resistant potato cultivars became commercially available, their effectiveness in golden nematode control was recognized immediately (18). However, those available golden nematode resistant cultivars did not meet all the necessary market specifications, geographic adaptability, maturity dates, and disease resistance required for rapid grower adoption and widespread use. These needs and recognition of possible environmental hazards associated with continued chemical pesticide usage gave rise to a new program, initiated in 1979, to accelerate the development and release of golden nematode-resistant potato cultivars. This program, which is still active, is equally funded by USDA/ARS, USDA/APHIS, and New York State through its Department of Agriculture and Markets and the College of Agriculture and Life Sciences at Cornell University. It represents the largest potato-breeding program ever attempted and combines the expertise of plant breeding, plant pathology, nematology, and the development of disease-free nuclear seedstock. This program has the capacity to handle all aspects of cultivar development from generation of new germplasm, through the various selection processes for horticultural characters, and disease and nematode resistance, to development of disease-free nuclear seedstocks.

Apart from this Cornell University program, cooperative efforts in golden nematode resistance breeding were continued or expanded with several other potato-breeding programs, including USDA/ARS at Aberdeen, Idaho, USDA/ARS at Beltsville, MD, the University of Maine, North Dakota State University, University of Minnesota, Frito-Lay Inc., The Campbell Research Institute, and Agriculture Canada. Their combined efforts have resulted in the release of 21 golden nematode-resistant cultivars. Because of some weaknesses in performance under field conditions, several of these cultivars are no longer available in commercial quantities. However, certain others now play a key role in the golden nematode control program (24).

Several factors contribute to the effectiveness of this resistance in managing the golden nematode. Potato cultivars containing the H_1 gene, like susceptible cultivars, produce root exudates containing a substance that stimulates golden nematode eggs to hatch. The amount and potency of this factor is related to root biomass (38, 39). This factor can move up to 50 cm in the soil and persists for at least 3 weeks (23, 26, 40). After juveniles hatch, they find and invade roots. However, internal responses to nematode invasion of H_1-bearing resistant roots prevent normal development and reproduction of the nematode (22). This response approaches immunity as only 1–5 cysts may develop on resistant roots, while hundreds develop on susceptible roots (30, 31). This lack of development is attributed either to an early response that causes most of the invading juveniles to exit resistant roots or to a hypersensitive reaction causing death of cells surrounding those that remain and attempt to establish feeding sites (37). Such responses also markedly reduce development of males, thus affecting reproduction capabilities of the few females that develop on resistant plants. The progeny of such females are few and their ability to establish new populations is limited (36). These responses translate into a 90% or greater decline in golden nematode population density each time a resistant cultivar is grown (2, 4, 5, 12).

Integrated Management Systems

Although golden nematode resistance is extremely effective in reducing nematode populations, the diversity of available resistant cultivars in 1970 (2 cultivars, both round white tablestock) was insufficient to rely on host resistance as the only means of control. Consequently, research was initiated on an integrated system involving resistance, nonhost plants, and chemical pesticides. A 3-year system was developed involving a resistant cultivar the first year, followed by a nonhost crop the second, and a susceptible cultivar with chemical soil treatment (aldicarb or oxamyl) the third (2, 12). The key to this system's success is that the nematode was always at a disadvantage and was not allowed to increase in population density.

In the early 1980s, environmental concerns involving groundwater contamination had emerged. In response, the state and federal regulatory officials elected to discontinue the use of chemical pesticides in the golden nematode control program. At the same time, the federal regulatory agency (USDA/APHIS) had established a goal "to reduce the population of the golden nematode below detectable levels in host crop land in the United States by the end of calendar year 1985." The decision to withdraw all chemical pesticides and to support the goal established by USDA/APHIS placed heavy reliance on the use of host resistance to control the golden nematode. Consequently, studies were directed to developing an integrated system without chemical pesticides in the protocol. An acceptable management system emerged that involved two years of a resistant cultivar, followed by a nonhost crop the third year and a susceptible cultivar the fourth year (B. B. Brodie, unpublished data). This system manages the golden nematode at acceptable densities provided the initial nematode density is 4 eggs/cm^3 of soil or less. This system was implemented in the golden nematode control program in 1985 (Figure 1).

THE GOLDEN NEMATODE CONTROL PROGRAM

The golden nematode control program is administered by state and federal regulatory personnel with the objective of preventing spread and at the same time continuing profitable potato production in infested areas. The program depends upon research to provide improved control procedures, which regulatory officials have been quick to embrace as they have become available, frequently implementing them into the control program before experimental results are published. The program's success has been contingent upon how well control procedures have performed under practical conditions.

Prior to 1972, infested potato fields were fumigated with D-D or 1,3-D, and after a negative post-treatment survey were returned to the grower without any restrictions. The emerging availability of golden nematode resistant cultivars and their impact on population development redirected the program in 1972. In 1972 and 1973, infested fields were first fumigated and after a post-treatment negative survey were required to be planted totally to a resistant cultivar (W. T. Brown, personal communication). However, there was

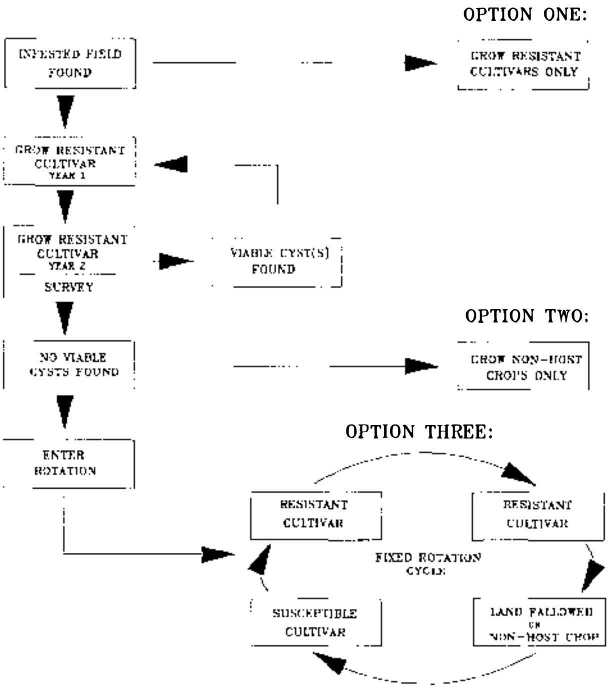

Figure 1 The current golden nematode control program implemented in 1985.

not sufficient seed available nor a sufficient diversity of resistant cultivars to accommodate such a stipulation.

Beginning in 1974, soil treatment with nonvolatile nematicides was incorporated into the control program. After the preliminary fumigation and the post-treatment negative survey only a portion of the affected fields was required to be planted to a resistant cultivar; the remainder could be planted to a susceptible cultivar provided an improved nematicidal soil treatment was used. The approved nematicide consisted first of carbofuran, then in 1976 replaced with aldicarb, which is more effective in controlling the golden nematode. When aldicarb was found in the groundwater, its use was discontinued and replaced with oxamyl. A progressive structure of annual area goals was established based on the availability of resistant cultivars, with 100% of regulated fields to be planted to resistant cultivars by 1988 (W. T. Brown, personal communication).

In 1980, state and federal regulatory officials entered into yet another redirected golden nematode control program. This program was structured around resistant cultivars as the key components of the management system. Beginning in 1980, after depopulation by soil fumigation, growers could elect to place regulated fields in an approved golden nematode management system provided all cultivated areas in the grower's operation were incorporated. This system consisted of a resistant cultivar the first year, followed by a nonhost the second, then a susceptible cultivar the third year provided soil treatment with an approved nematicide was used (12). The approved nematicide was aldicarb or oxamyl. The earlier option of planting a percentage of infested fields in resistant host and the remainder in a susceptible host with nematicide treatment also continued in effect.

In 1983, 1,3-D was found in the groundwater and its sale on Long Island was withdrawn. In an emergency meeting in March 1984, state and federal regulatory officials decided to discontinue the use of all chemical pesticides in the golden nematode control program and to adopt the current program (Figure 1). Now, golden nematode resistant potato cultivars are the primary control mechanism, supported by survey and regulatory activities; no chemical pesticides are required. On regulated fields a nematode management system is used in which a susceptible cultivar is allowed once in four years, provided two resistant crops have been grown on the field in the interim and a subsequent survey fails to detect viable nematodes. Essentially, resistant cultivars replaced soil fumigants as a depopulation measure and replaced nonvolatile nematicides in the management scheme.

The 1984 crop year was a transitional one. Infested fields or portions thereof that were planted to a resistant cultivar in 1983 could be planted to a susceptible cultivar in 1984, and vice versa. In 1984, new infestations on Long Island were required to be planted totally to a resistant cultivar while those upstate could still be fumigated. The current program has been in effect since 1985 and has been successful in managing the golden nematode.

THE FUTURE

Although golden nematode-resistance breeding has resulted in a sizeable number of resistant cultivars, those currently available are not now and probably will never be used widely enough to totally eliminate the threat of the golden nematode from the United States. These resistant cultivars can be grown with some success, but because of limited adaptability and constantly changing markets, they are by no means the final solution to the golden nematode problem. Consequently, there is an urgent need to provide growers with resistant cultivars acceptable for all niches of the potato industry. These should have geographical adaptability sufficient for growers outside the infested area and, hopefully, throughout the major potato growing areas of the United States.

New golden nematode resistant cultivars will most likely result from conventional breeding, but recent advances in gene-transfer capabilities in higher plants indicate the possibility of their resulting from gene transfer. Transferring the H_1 gene that confers resistance to the golden nematode into already accepted and widely grown potato cultivars is an exciting concept and would have far reaching implications. Apart from reducing established golden nematode populations, resistant cultivars also prevent the establishment of new infestations in case of accidental spread. Consequently, widespread growing of resistant varieties would make spread of the golden nematode of little or no consequence and would eventually lead to its elimination from potato lands in the USA.

Although procedures exist to manage the golden nematode at acceptable density, their use is currently confined to known infested fields. Consequently, once a field has been found to be infested, the golden nematode population can be successfully managed to prevent its spread to other fields. However, the golden nematode reaches population density at which spread occurs 3–6 years before it can be detected by a regulatory survey. Current regulations do little to prevent the spread of the golden nematode from fields where the nematode population density has not yet reached the detection level. Future research must address golden nematode population dynamics at currently subdetectable densities.

A population model has been developed to predict golden nematode population dynamics under various cropping systems involving resistant potato cultivars, nonhost crops, and susceptible cultivars (24). This model allows the design of management schemes to hold the golden nematode at desired population densities. It could be further fine-tuned to allow prediction of detection probabilities at different population densities. By incorporating the effects of all known biotic and abiotic factors on golden nematode survival and development, we could eventually predict the population dynamics of the golden nematode under any known conditions. Such information would add significantly to our ability to manage this pest at acceptable population densities without risk of spread to noninfested areas of the United States.

Research should be continued to identify biotic and abiotic signals that govern golden nematode behavior, particularly its ability to go into and come out of arrested development. Once the physical and/or chemical factors that govern such behavior as hatching, diapause, and dormancy are understood, this knowledge must be translated into practical ways to successfully manipulate the golden nematode.

CONCLUDING REMARKS

Through a highly cooperative program involving state and federal research, regulatory, and extension personnel as well as potato growers, the United States has maintained an enviable position in regard to the golden nematode.

Nematode populations have been kept extremely low and have incurred no economic losses to growers, essentially since their discovery in 1941. Infestations have been confined to two counties on Long island and four in upstate New York, spreading in the past 47 years no more than about 300 miles from its original point of discovery. With the increased use of resistant cultivars, fewer infestations are found each year, indicating a marked decline in its spread. Still only one pathotype of one species of potato cyst nematodes has been found in the USA and this pathotype is easily managed with H_1-mediated resistance.

The program has purposely been kept in low profile because of the nature of the golden nematode quarantine and the desire to prevent unnecessary national alarm. Yet the internal workings of the program have always been intense with the desire to protect the potato industry of the United States from this most damaging of all potato pests. Many factors have contributed to the program's success, but most significant are the people who were involved in the research, regulatory, and implementation aspects. From the highest decision maker to those on survey crews, over 100 people have worked in this program since its inception. Because of space limitation, it was not possible to list them all, but the authors hereby recognize their importance to the success of the program.

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