Problems and Strategies Associated with Long-term Use of Nematode Resistant Cultivars[1]

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Abstract: Plant-parasitic nematodes are obligate parasites, and planting cultivars that are highly resistant to these organisms places extensive selection pressure on the target species and affects nontarget nematodes as well. Problems encountered with long-term planting of cultivars resistant to nematodes include shifts in nematode races or species and the occurrence of multiple species of nematodes within the same field. These problems can be alleviated to some extent when crop management is used to lessen the selection pressure for change on the nematode populations. Race shifts within populations and possibly shifts between nematode species can be delayed by rotating susceptible cultivars and nonhost crops with resistant cultivars. Nematicides in conjunction with resistant cultivars may be used to limit damage by multiple species of nematodes. Some cultivars have resistance to multiple species of nematodes, but greatly increased research effort is needed in this area. More intensive plant breeding effort will be required to make nematode resistant cultivars competitive in quality and yield with more productive, susceptible cultivars.

Key words: Globodera tabacum solanacearum, Heterodera glycines, management, *Meloidogyne arenaria, M. incognita,* nematode, resistance, rotation.

Planting cultivars resistant to nematodes has been an effective tool in managing plant-parasitic nematodes in several crops. For example, cultivars resistant to *Heterodera glycines* yield 10% to 50% more in infested soil than susceptible cultivars (2,4,22). Often resistant cultivars without nematicide treatment yield as much as high-yielding susceptible cultivars treated with nematicides (2). In Florida, yields from soybean (*Glycine max*) cultivars resistant to *Meloidogyne incognita* were five times greater than yields from highly susceptible cultivars (10). Over half of the hectarage planted to tobacco (*Nicotiana tabacum*) in the southeastern United States in 1986 was planted with cultivars resistant to *M. incognita* races 1 and 3 (6). When resistant cultivars are productive, growers are tempted to use these cultivars in a continuous monoculture because management is simpler and because there is no increased cost over normal production practices.

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PROBLEMS ENCOUNTERED WITH RESISTANT CULTIVARS

Nematodes that feed on plants are obligate parasites; planting highly resistant cultivars places selection pressure on the target nematode and may also affect nontarget nematodes. Problems encountered with long-term plantings of cultivars resistant to nematodes include shifts in nematode races or species and the occurrence of multiple species of nematodes within the same field. Resistant cultivars may have inferior quality or lower yield, especially when resistance is first introduced, compared to susceptible cultivars. Use of these resistant cultivars results in lower economic return, both in short-term and long-term situations.

A prominent example of shifts in races of a nematode in response to planting resistant cultivars occurs in the soybean–*H. glycines* interaction. Race 3 was the prevalent race in the southern United States when the first *H. glycines* resistant cultivar, Pickett, was released. Within a few years, race 4 (populations casually considered race 4 were later designated race 14 [13]) became the prevalent race in this region (4). 'Bedford' was released for planting where this race was a problem; later race 5 became a prevalent race in Tennessee (20).

Meloidogyne incognita races 1 and 3 predominate in flue-cured tobacco fields in North and South Carolina, but *M. arenaria* and *M. javanica* are increasingly problematic (1,6). This species shift is believed to result from continuous use of cultivars resistant to *M. incognita.*

Poor quality linked to nematode resistance may preclude the growing of resistant cultivars of some crops. Flue-cured tobacco cultivars resistant to *Globodera tabacum solanacearum* effectively reduce nematode population densities; but because these cultivars have lower leaf quality and yield, economic returns are lower than when susceptible cultivars are treated with nematicides (7,8).

Infestations of multiple nematode species often preclude the effective use of resistant cultivars. *Meloidogyne incognita, M. arenaria,* and *H. glycines* commonly occur together in soybean fields near the Alabama coast (14,17,18). Cultivars with effective resistance to *M. incognita* and *H. glycines* are available, but cultivars with resistance to *M. arenaria* and some races of *H. glycines* are not available. Therefore, production problems are encountered in fields infested with these two pests.

Strategies Involved with Use of Resistant Cultivars

Two strategies are commonly associated with use of resistant cultivars. The first is to preserve the effectiveness of resistance genes against the target nematode and thereby prevent or delay shifts in nematode races or species. The second is to optimize the frequency of planting resistant cultivars to obtain the best overall economic return from the cropping system. The latter strategy is used when resistant cultivars have lower productivity than susceptible cultivars or when there are multiple species of nematodes.

Reduction of selection pressure: The primary goal in the first strategy is to reduce the selection pressure on the nematode population. This strategy has been successful in short-term cycles but may be less successful in long-term cycles. Reduction of selection pressure on *H. glycines* populations has been attempted by alternating the resistant soybean cultivar with susceptible cultivars and nonhost crops. Young et al. (24) reported that an *H. glycines* population (originally race 9) reproduced less on resistant cultivar Bedford when susceptible cultivars were rotated with it than when the resistant cultivar was grown each year for 6 years. Rotating corn, a nonhost of *H. glycines,* with the resistant cultivar delayed the increase in ability of the nematode population to reproduce on Bedford for a few years. Blending Bedford with susceptible cultivars effectively maintained nematode reproduction at a low, acceptable level. In the last year of an 11-year study (continuation of 6-year-study above [24]), the relative ability of an *H. glycines*

TABLE 1. Relative reproduction of *Heterodera glycines* (originally race 9) on *Glycine max* cv. Bedford, a resistant cultivar, grown in soil from field plots exposed to different cropping sequences.

Cropping sequence†	Relative reproduction‡									
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
F F F F F F F F F F	8	7	12	4	3	4	11	8	23	20
B B B B B B B B B B	29	50	86	65	42	87	57	87	116	100
M M M M M M M M M M	10	6	16	8	11	24	32	34	38	77
F E B F E B F E B F	6	6	28	6	7	14	14	22	32	46
E B F E B F E B F E	12	11	8	6	7	15	8	37	22	31
B F E B F E B F E B	36	4	31	12	4	11	20	8	30	44
LSD (0.05)	22	ns	39	ns	13	40	34	30	28	54

† Each letter indicates the soybean cultivar grown for 1 year. F = Forrest, B = Bedford, E = Essex, and M = a blend of 70% Bedford and 30% Forrest. Bedford is resistant, and Forrest and Essex are susceptible.
‡ Number of cysts occurring on Bedford soybean expressed as a percentage of the number of cysts on Essex 35 days after planting in the greenhouse in the soil.
Data on relative production on Bedford soybean were not obtained in 1979, the first year of the experiment.

population to reproduce on Bedford increased dramatically when a blend of Bedford and susceptible cultivars was planted every year (Table 1, [23]). Neither rotating susceptible cultivar Tracy M with 2 years of the resistant cultivar Centennial for 10 years nor blending these cultivars for 10 years limited the ability of an *H. glycines* (originally race 3) population to reproduce on Centennial (21) at the conclusion of the test. Generally, in these tests yield of the susceptible cultivars was significantly less than yield of the resistant cultivars. Yield of soybeans in the rotations and blend of soybeans was about the same as yield of resistant Bedford in continuous monoculture. Number of cysts in Bedford field plots did not increase significantly over time, although the relative reproduction of the nematode on Bedford grown in greenhouse tests utilizing soil from continuous Bedford plots increased significantly.

A rotation of resistant cultivar, nonhost crop, and susceptible cultivar may merely slow the shift of races. After 6 years of such a rotation, the reproductive ability of *H. glycines* (originally race 14) on Bedford was significantly higher following both Bedford and a nonhost crop (*Zea mays*) than a continuous monoculture of a susceptible cultivar (Table 2). Additional data will determine if the trend for increasing reproductive ability of the population on the resistant cultivar in the rotation continues.

Rotation of resistance genes: Francl et al. (3) rotated 'Forrest' (resistant to *H. glycines* race 3) with Bedford (resistant to races 3 and 14) in an unsuccessful attempt to shift the ability of *H. glycines* populations to reproduce on resistant cultivars. They concluded that Bedford and Forrest did not have mutually incompatible reactions with their respective selected populations; this incompatibility was considered necessary for success in rotating cultivars with different sources of resistance. In contrast, greenhouse experiments have led others (12,19) to suggest rotating cultivars with different sources of resistance. In these studies, the ability of *H. glycines* to reproduce on PI 88788 had an inverse relation to ability to reproduce on PI 89772 or PI 90763. However, this relationship has not been confirmed in field studies. In our greenhouse, breeding line J82-21 (resistance from Peking and PI 90763) is mutually incompatible with Bedford (resistance from Peking and PI 88788) for *H. glycines* race 14 reproduction. Germplasm line J81-116 (resistance from Peking, PI 89772, and PI 90763 [5]) has resistance genes in common with both soybeans, although in greenhouse selection experiments, it behaves more like J82-21 than Bedford. In a field infested with race 14, rotations of Bedford with these breeding lines show a trend for increased reproductive ability of the nematode on Bedford (Table 3) when compared with continuous monoculture of J81-116, J82-21, or the susceptible cultivar Forrest. Additional data are needed to assess the effectiveness of rotating cultivars with different sources of resistance to *H. glycines*. Yields of Bedford, J81-116, and

TABLE 2. Relative reproduction of *Heterodera glycines* (originally race 14) on *Glycine max* cv. Bedford, a resistant cultivar, grown in the greenhouse in soil from field plots planted with cultivars in rotation.

Cropping sequence†	Relative reproduction‡					
	1985	1986	1987	1988	1989	1990
F F F F F F	8	35	18	15	32	24
B B B B B B	18	67	68	68	89	135
C E B C E B	11	20	46	17	33	77
E B C E B C	15	19	68	38	81	91
B C E B C E	13	13	14	31	33	51
LSD (0.05)	NS	NS	39	26	30	47

† Each letter designates the crop or soybean cultivar grown for 1 year: F = Forrest, B = Bedford, C = corn (*Zea mays*), and E = Essex. Forrest and Essex are susceptible; Bedford is resistant to race 14.

‡ Number of cysts on Bedford expressed as a percentage of number of cysts on Essex 35 days after planting in soil from field plots.

TABLE 3. Relative reproduction of *Heterodera glycines* (originally race 14) on *Glycine max* cv. Bedford, a resistant cultivar, grown in the greenhouse in soil from field plots planted with soybeans with different sources of resistance.

Cropping sequence†	Relative reproduction‡					
	1985	1986	1987	1988	1989	1990
F F F F F F	8	35	18	15	32	24
B B B B B B	18	67	68	68	89	135
J J J J J J	14	10	10	14	18	22
6 6 6 6 6 6	11	29	12	19	31	38
B B J J B B	16	78	18	27	36	62
J J B B B J	17	27	28	49	63	60
B B 6 6 B B	18	87	19	28	42	54
6 6 B B B 6	9	21	6	55	50	65
LSD (0.05)	NS	NS	39	26	30	47

† Each letter or number designates the soybean grown for 1 year: F = Forrest, B = Bedford, J = J82-21, and 6 = J81-116. Forrest is susceptible, Bedford and J81-116 are resistant, and J82-21 is moderately resistant to race 14.

‡ Number of cysts on Bedford expressed as a percentage of cysts on Essex 35 days after planting in soil from field plots.

J82-21 were approximately equal in both continuous monoculture and in the rotations. Nematode population densities were apparently not sufficient to cause yield reduction in these tests, even with susceptible cultivars.

Rotation of cultivars with different sources of resistance to nematodes is actually an effort to rotate different genes for resistance. Some sources of resistance have some or all resistance genes in common; therefore, rotation of these soybeans will not be more effective than continuously planting the same cultivar. The genetics of resistance must be understood before the concept of rotating genes can be implemented; the different genes for resistance must place differential selection pressure on nematode populations in order to achieve success.

Low yield and quality: Cultivars of tobacco resistant to *G. tabacum solanacearum* are economically inferior to susceptible cultivars because of lower yield and quality. The intolerance of resistant cultivars to nematode infection contributes to their lower yield. Johnson (7) proposed growing cultivars resistant to the nematode to reduce the initial inoculum and then planting susceptible cultivars in rotation with the resistant cultivars to maximize economic returns. Although planting resistant cultivars effectively reduced nematode population densities and resulted in significant yield increases of a subsequently planted susceptible cultivar, the inferior agronomic performance of the resistant cultivars prevented sufficient increase in economic return to justify their use. Treating a susceptible cultivar with the nematicide fenamiphos resulted in greater economic returns than planting the resistant cultivars for 2 years followed by the susceptible cultivar. Increased breeding effort will be required to improve agronomic characteristics if resistance to *G. tabacum solanacearum* is to be utilized by producers.

Multiple infestations: Multiple nematode species infestations can be managed with either multiple-species-resistant cultivars or other practices that are effective against a broad array of nematodes. Several soybean cultivars have resistance to *M. incognita* and to two races of *H. glycines.* A few cultivars have resistance to at least one race of *H. glycines* and to *M. arenaria.* These cultivars can be used where these species occur together (10,11). However, cultivars resistant to all the problem nematode species are not always available. In the coastal plain soils of the southern United States, *M. arenaria* and *H. glycines* may occur together in the same soybean fields. There are no cultivars with resistance to both *M. arenaria* and *H. glycines* race 14 (11). Usually, a cultivar with resistance either to *H.*

glycines race 14 or *M. arenaria* is planted in these fields, and other crop management practices, such as nematicide use or rotation of susceptible cultivars with nonhost crops, are used in combination with resistant cultivars to limit nematode damage (14,17,18).

Outlook

Although there are problems with long-term use of resistant cultivars, host plant resistance is expected to be a vital component in management of nematodes for several crops in the future. Some nematodes, such as *H. glycines* (15), can be managed with crop rotation, without resistant cultivars, and with other cultural practices. However, this limits flexibility in selection of crops. Integration of crop rotation and cultural practices with resistant cultivars can be effective in managing nematodes. Nonetheless, use of the integrated approach for 10–20 years may result in some of the same difficulties (e.g., shifts in nematode races or species) experienced with continuous planting of resistant cultivars in 5–10 years. It should be the goal of nematologists to develop and demonstrate the effectiveness of strategies to maximize the longevity of resistant cultivars. Sufficient research will be required to convince producers that it is in their long-term economic interest to manage the potential problems associated with resistant cultivars instead of merely taking only short-term financial gains provided by these cultivars. Also, strategies will have to be developed for each nematode species or mixture of species. For example, susceptible cultivars are recommended in rotations with resistant cultivars and nonhost crops for suppression of *H. glycines* (16). In contrast, susceptible cultivars cannot be rotated with cultivars resistant to *M. incognita* to prevent shifts in nematode species (9). Regardless of the present difficulties in specific situations, long-term use of resistant cultivars integrated with other control methods should grow in importance as a management tool in the next century.

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