Ecosystems are comprised of many organisms, some of which may interact in such a way that their adverse effects are multiplied. The concept of multiple causes of combined and contributory causation seem to fit the facts best (Wallace, 1973). This point is well argued by Wallace (1973) in his discussion on the “nature of disease” and by Norton (1978) in his discussion on “biological interactions”. Much has been learned about disease etiology through experiments using a single pathogen, that is, testing Koch’s postulates. This single causation principle is probably the exception rather than the rule in the field. There are actually many factors operating under field conditions that involve numerous direct and indirect causes that form a web of interacting components with the plant at the center (Wallace, 1973).

Soybean cyst nematode is generally credited with causing more yield loss than any other soybean pathogen (Wrather et al., 2003). In reality, these losses are probably a consequence of numerous interacting biotic (Barker and McGawley, 1998) and abiotic fac-
tors (Norton, 1978). Multi-causal relationships are difficult to establish even though the crop encounters several pests and pathogens throughout the season. The ultimate yield is the response of the crop to the multitude of interacting factors. Considering only the interacting pathogens, some enhance disease while others reduce the effect of the primary pathogen (Francl and Wheeler, 1993). Still, others do not affect the amount of disease caused by the primary pathogen (Francl and Wheeler, 1993). A pathogen such as soybean cyst nematode can affect a change in growth, usually by stunting the plants that can make the canopy more attractive to insects and also weaken the crop so that it is not as competitive with weeds (Alston et al., 1991a).

Even though soybean cyst nematode has a limited impact on root morphology compared to root-knot nematode species, it does have vital impacts on soybean root and plant physiology (Barker et al., 1993; Hussey and Williamson, 1998). The modified roots infected with soybean cyst nematode may function as metabolic sinks (Poskuta et al., 1986) and the photosynthetic process may be altered (Barker et al., 1993). These changes, along with growth suppression of the plant, undoubtedly alter the relationship of plant with associated organisms. In this chapter, interrelationships between soybean cyst nematode and selected fungi, nematodes, bacteria, insects and weeds will be discussed.

INTERACTIONS WITH FUNGI

The relationship of the nematode with fungi comprise the greatest body of information on disease complexes of soybean involving soybean cyst nematode (Table 1). Most of the fungi evaluated in these nematode-fungus interactions are soil-borne, especially those that cause wilt or root disease. The associations with soybean cyst nematode, besides affecting the plant, also can affect the development and reproduction of the organisms involved.
Table 1. Summary of interactions between soybean cyst nematode and plant pathogenic fungi on soybean.

<table>
<thead>
<tr>
<th>Associated Fungus</th>
<th>Result</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Calonectria crotalariae</em></td>
<td>Activity of both pathogens increased</td>
<td>Overstreet and McGawley, 1988; Overstreet et al., 1990</td>
</tr>
<tr>
<td><em>Diaporthe phaseolorum var. caulivora</em></td>
<td>Reduction in canker length, additive effects on plant growth</td>
<td>Russin et al., 1989; Russin et al., 1990</td>
</tr>
<tr>
<td><em>Fusarium oxysporum</em></td>
<td>Increased vascular wilt</td>
<td>Ross, 1965</td>
</tr>
<tr>
<td><em>Fusarium solani f. sp. glycines</em></td>
<td>Increased foliar symptoms of sudden death syndrome; nematode reproduction reduced</td>
<td>McLean and Lawrence, 1993a; Roy et al., 1989; Rupe et al., 1991; Rupe and Gbur, 1995</td>
</tr>
<tr>
<td><em>Macrophomina phaseolina</em></td>
<td>Synergistic effect on yield</td>
<td>Wrinkler et al., 1994</td>
</tr>
<tr>
<td><em>Macrophomina phaseolina</em></td>
<td>No effect on yield</td>
<td>Francl et al., 1988</td>
</tr>
<tr>
<td><em>Phialophora gregata f. sp. sojae</em></td>
<td>Increased severity of root rot</td>
<td>Sugawara et al., 1997; Tabor et al., 2001</td>
</tr>
<tr>
<td><em>Phytophthora megasperma var. sojae</em></td>
<td>Root rot not affected</td>
<td>Abawi and Jacobsen, 1984</td>
</tr>
<tr>
<td><em>Rhizoctonia solani</em></td>
<td>Reduction in nematode reproduction</td>
<td>Dave, 1975</td>
</tr>
</tbody>
</table>
Plant damage

Several wilt and root rot diseases of soybean caused by fungi are enhanced by infection with soybean cyst nematode. In susceptible soybean, wilt symptoms caused by *Fusarium oxysporum* were more pronounced in plants also infected by soybean cyst nematode than in plants infected only with the fungus (Ross, 1965). Besides enhancing the wilt disease in a susceptible cultivar, the nematode can alter the wilt resistance in soybean. For example, Fusarium wilt resistance in the cultivar Yelredo was lost when it was infected by soybean cyst nematode (Ross, 1965).

In most cases, root rot is intensified by soybean cyst nematode. Simultaneous infections by *Phytophthora sojae* and the nematode resulted in additive effects on a susceptible soybean cultivar (Adeniji *et al.*, 1975). Incidence of soybean plants in Michigan fields exhibiting symptoms of disease induced by *P. sojae* was greater in areas with high population densities of soybean cyst nematode (Kaitany *et al.*, 2000). Plant nutrient stress may have been an additional factor in exacerbating the root rot. Disease expression of brown stem rot caused by *Phialophora gregata* f. sp. *sojae* was also more severe in association with soybean cyst nematode (Sugawara *et al.*, 1997). This increased severity of disease may be related to the greater amount of colonization of soybean stems by *P. gregata* when both pathogens infected the plant (Tabor *et al.*, 2001). Based on anecdotal evidence in soybean fields in Iowa, brown stem rot-resistant soybean infected with soybean cyst nematode become susceptible to the fungus (G. L. Tylka, personal communication). Additional loss of yield is probably occurring in fields with plants infected with one of the fungi discussed and soybean cyst nematode as demonstrated in Kansas with *Macrophomina phaseolina* (causal agent of charcoal rot) and the soybean cyst nematode. Soybean yield losses were greater when roots were infected by both pathogens than by either one alone (Todd *et al.*, 1987).

There are situations in which synergism between wilt or root rot
fungi and soybean cyst nematode is not evident. For example, the amount and severity of root rot of kidney bean, caused by *F. oxysporum*, was similar on plants infected with the fungus alone and those infected with the fungus and the nematode (Abawi and Jacobsen, 1984). Likewise, there was no evidence of an interaction of *Macrophomina phaseolina* and soybean cyst nematode in Missouri (Francl *et al.*, 1988).

Soybean sudden death syndrome, caused by *Fusarium solani* f. sp. *glycines*, can be more severe when the crop is infected with soybean cyst nematode as documented in Mississippi and Arkansas (McLean and Lawrence, 1993a; McLean and Lawrence, 1993b; Rupe *et al.*, 1991). In some fields and experiments, when susceptible soybean is infected by both pathogens, foliar symptoms of sudden death syndrome appear earlier and the incidence and severity are greater than on soybean infected with only the fungus (McLean and Lawrence, 1993a; Roy *et al.*, 1989; Rupe and Gbur, 1995). Since soybean cyst nematode-resistant cultivars that are susceptible to *F. solani* f. sp. *glycines* exhibited fewer symptoms of sudden death syndrome than cultivars susceptible to both pathogens, the nematode most likely enhances the disease (Hershman *et al.*, 1990). There are instances when the relationship between sudden death syndrome severity and soil populations of soybean cyst nematode is weak. In Iowa, sampling transects were located across areas of six fields with sudden death syndrome disease severity ranging from 0% to 100% (Scherm *et al.*, 1998). There was a weak but consistently positive correlation between sudden death syndrome disease severity and cyst numbers. Still, this weak but positive correlation of cyst numbers and disease severity of sudden death syndrome adds credibility to the premise that this nematode enhances sudden death syndrome. These data were collected when soybean had six trifoliate leaves. At this time, the numbers of cysts would include a mixture of newly produced cysts and residual cysts from previous years. Thus, soil samples should be collected multiple times to more clearly demonstrate the causal relationship of the fungus and disease severity.
Figure 1. Areas in the USA reporting sudden death syndrome and infested with soybean cyst nematode. Solid shading = States with soybean cyst nematode, but no documented sudden death syndrome. Line pattern = States documented to be infested with soybean cyst nematode and to have sudden death syndrome.

(Scherm et al., 1998). The role of the nematode could likewise be more clearly elucidated with multiple samplings throughout the growing season.

In Illinois, where soybean cyst nematode is present in almost every field, epidemics of sudden death syndrome occur annually. Disease is present even in soybean fields with low population densities of the nematode (< 50 eggs/100 cm³ soil) (Bond, unpublished). In this case, the population density of fungus propagules may be high. This population density factor, as measured in Iowa, needs to be characterized to better understand the relationship between population densities of both pathogens and the resulting crop response.

Management of sudden death syndrome is critical because of the potential economic loss over a large area (Fig. 1). This management will require the control of both pathogens. Since some
soybean cultivars have linkage between resistance genes for soybean cyst nematode and *F. solani* f. sp. *glycines* (Chang *et al.*, 1997; Meksem *et al.*, 1999), their use may reduce the disease and increase soybean seed production. Other tactics, such as crop rotation and cultural methods, should also be a part of the overall strategy for managing sudden death syndrome.

**Nematode and pathogen development and reproduction**

Populations of organisms attempting to occupy the same niche are competing for available space and resources. Some niches, such as roots, are ephemeral. The outcome is often the dominance of an organism within that niche. In many soil samples, soybean cyst nematode occurs in larger population densities than other nematodes within that sample. In spite of this apparent dominance of soybean cyst nematode in many soil samples, many biological and soil physical factors regulate its population size (See Chapters 6 and 11). Most certainly, predators, parasites and diseases of soybean cyst nematode will reduce its population density (See Chapter 11). There are many other biological factors occurring in niches occupied by soybean cyst nematode that determine the carrying capacity of that niche.

The influence of plant pathogenic fungi and soybean cyst nematode populations upon each other is probably mediated through the plant. Based on selected examples, this plant mediated response of the plant pathogenic organisms will be demonstrated. In some instances, infection of soybean by a pathogenic fungus apparently provides conditions favoring population increase of the nematode. Populations of soybean cyst nematode were larger on the soybean cyst nematode susceptible cultivar Lee infected with *Fusarium oxysporum* than on fungus-free plants (Ross, 1965). This nematode also increased to larger population densities on soybean cyst nematode susceptible and resistant soybean infected with *Calonectria crotalariae* (Overstreet and McGawley, 1988;
Overstreet et al., 1990). In these experiments, more juveniles penetrated roots of the fungus-infected plants than roots of fungus-free plants. In other experiments utilizing different fungi, the results were just the opposite. Populations of soybean cyst nematode were suppressed on plants infected with Phytophthora sojae (Adeniji et al., 1975), Macrophomina phaseolina (Todd et al., 1987) and Rhizoctonia solani (Dave, 1975). These differences may be a consequence of several factors, including differences in fungal pathogens or experimental conditions.

The biological interactions of plant-pathogenic fungi and soybean cyst nematode are related to food source, but some interactions are not such an obvious food relationship. Also, physiological and molecular events occur in the infected plant that may indirectly affect one or more of the associated microorganisms (Abawi and Chen, 1998). Several modes of interactions are possible. The invasion of a niche (e.g., root) by one or more fungal pathogens may reduce the activity of antagonists of soybean cyst nematode, thereby removing some of the resistance factors for nematode reproduction (See Chapter 11). The first organism to occupy a niche may be sufficient to prevent ingress of other organisms into that space. However, the situation is probably more complex. The early invader may produce allelopathic substances that inhibit the nematode antagonist.

Another potential means enabling reproductive success of soybean cyst nematode involves more successful root penetration. Root pathogenic fungi could cause soybean roots to leak exudates that may enhance egg hatching and attraction of juveniles to infection sites. On the other hand, if the fungal pathogen severely damages the food source of the nematode, the nematode population will be diminished. The plant may not be able to support feeding and reproduction of the nematode because of less root biomass, poorer root quality and reduced plant vigor. With more subtle damage by root-pathogenic fungi, the plant roots may not produce the quantity or quality of attractant needed for a high level of nematode invasion. Negative impacts on nematode reproduction may
result from fungal infection that renders the plant less attractive to nematode infection.

Interactions of organisms and their impacts become more complex for pathogens with diverse hosts. *F. solani* f. sp. *glycines* is an example of such an organism that may function as a pathogen of both the plant and soybean cyst nematode. As already discussed, it is the primary causal agent of sudden death syndrome (McLean and Lawrence, 1993a; McLean and Lawrence, 1995; Roy et al., 2000). As with other root pathogenic fungal species, damage to the roots, plus the reduced plant vigor, simply makes the plant a less suitable host for the nematode (McLean and Lawrence, 1995). In addition, the fungus is a parasite of soybean cyst nematode. This interaction has recently received renewed attention because of the importance and spread of sudden death syndrome. During the growing season, this persistent fungus infects soybean roots and various life stages of the nematode. Being present in the cysts is advantageous for dissemination of the fungus since cysts are readily transported from field to field by machinery and by soil erosion factors (wind and water).

Population densities of soybean cyst nematode can decrease significantly within a single growing season in a soybean crop severely affected by sudden death syndrome (Bond, unpublished). This reduction in nematode population densities may result from severely weakened plants unable to support the nematode population, fungal parasitism of the eggs or a combination of both factors. More research is needed to elucidate the interaction between these two pathogens.

INTERACTIONS WITH BACTERIA

Most of the published information on the interaction of bacteria and soybean cyst nematode has emphasized the beneficial relationships of nitrogen-fixing Rhizobia. HG Type 2- (race 1) suppresses nodulation and nitrogen fixation of soybean (Barker et al.,
1972; Huang and Barker, 1983; Huang et al., 1984; Ko et al., 1986). This interaction results in plants that are nitrogen deficient. Other HG Types have less affect on this detrimental response of the plant (See Chapter 6). As an example of a pathogenic bacterium interacting with the soybean cyst nematode, the relationship between *Xanthomonas axonopodis* pv. *glycines* (= *Xanthomonas campestris* pv. *glycines*) and soybean cyst nematode was neutral (Appel et al., 1984).

**INTERACTIONS WITH OTHER NEMATODES**

Soybean cyst nematode rarely occurs as the only nematode species in a soybean field, although it is frequently the dominant species. Feeding sites depend on the feeding habit of the nematode species. Conceptually, an ectoparasitic nematode would not affect soybean cyst nematode nor would the cyst nematode inhibit the ectoparasite. In reality, cyst nematodes usually inhibit the development and reproduction of non-cyst species (Eisenback, 1993). The practical or economic question involves the consequences to the plant or crop as a result of cohabitation in soybean roots by two or more species of nematodes.

Although soybean cyst nematode inhibits reproduction of associated species, its reproduction can be inhibited as well (See Chapter 6). One of the first documented studies on nematode-nematode interaction was between soybean cyst nematode and southern root-knot nematode (*Meloidogyne incognita*) (Ross, 1964). Population change of soybean cyst nematode in microplots in North Carolina was adversely affected only by high initial population densities of root-knot nematode (Ross, 1964). This effect was attributed to severe root-knot damage that retarded root growth. At the medium population levels of both species, the number of soybean cyst nematode second-stage juveniles were greater at several sampling times. In a recent study, the infection rate of these two nematode species was reduced by simultaneous
infestation of soil (Melakeberhan and Dey, 2003). Likewise, lesion nematode (*Pratylenchus penetrans*) inhibited the infection of soybean cyst nematode and the highest inoculum level of soybean cyst nematode adversely affected root invasion by the lesion nematode (Melakeberhan and Dey, 2003). Conversely, medium levels of soybean cyst nematode inoculation enhanced root infection by lesion nematode.

The impact of competition for food on plant damage caused by soybean cyst nematode and at least one other nematode species is typically additive or less than additive. There was no interaction between soybean cyst nematode and southern root-knot nematode on plant growth during the first two weeks after infestation in Georgia (Niblack *et al.*, 1986b). With combinations of low numbers of soybean cyst nematode and root-knot nematode, soybean yield suppression was additive (Ross, 1964). The suppression was less than additive in plots with high initial population densities of both nematodes. The affect of these two nematode species on the seed yield of cultivar Coker 237, susceptible to both species, was additive (Niblack *et al.*, 1986a). Soybean cyst nematode did not affect root-knot nematode resistance in root-knot resistant cultivars nor did the root-knot nematode affect the soybean cyst nematode resistance in soybean cyst nematode resistant cultivars (Niblack *et al.*, 1986a). Yield loss caused by soybean cyst nematode in Florida was not altered by southern root-knot nematode and/or sting nematode (*Belonolaimus longicaudatus*) (Dickson and McSorley, 1990).

Hybridization between soybean cyst nematode and other species of cyst-forming nematodes has been documented. Soybean cyst nematode can hybridize with sugar beet cyst nematode (Miller, 1988; Potter and Fox, 1965) and brassica cyst nematode (Miller, 1989). The biological significance of these hybridizations and the potential impact on plant health and management is unknown (Barker and McGawley, 1998).
MULTIPLE PEST INTERACTIONS

Crop management involves managing an array of interacting factors. The number of pests have increased in response to the intensification of soybean production. Several species of insects and numerous species of weeds constrain the crop from achieving its real yield potential. Management of pests is primarily directed at individual species. However, these organisms influence each other in most cases.

Multiple pest and/or pathogen interactions involving soybean cyst nematode result in additive effects or no effects in damage to the soybean crop compared to the damage caused by individual organisms. In interactions between the brown spot pathogen (*Septoria glycines*), the causal agent of bacterial pustule (*Xanthomonas axonopodis* pv. *glycines*) and soybean cyst nematode, soybean yield losses were additive for plants infected with *S. glycines* and soybean cyst nematode (Appel *et al.*, 1984). In combinations of soybean cyst nematode and the threecornered alfalfa hopper (*Spissitilus festinus*) with common cocklebur (*Xanthium strumarium*), sicklepod (*Cassia obtusifolia*) or pitted morningglory (*Ipomoea lacunose*), yields of soybean in field plots in Arkansas were generally additive (Robbins *et al.*, 1990). In this case, the damage thresholds established for these pests, individually, are applicable to fields infested with all of them. The impact of certain weeds, corn earworm (*Helicoverpa zea*) and soybean cyst nematode was also additive on suppressing soybean yields in North Carolina (Alston *et al.*, 1991a; Alston *et al.*, 1993). This study reveals that the situation is probably more complex because of plant growth modification induced by soybean cyst nematode. Parasitism by this nematode leads to stunting of the host, which reduces the ability of the soybean to compete with a wide spectrum of weed species (Alston *et al.*, 1991a; Alston *et al.*, 1991b; Chen *et al.*, 1995; Russin *et al.*, 1990). In addition, large population densities of soybean cyst nematode resulted in reduced soybean canopy closure, rendering the crop to be more attractive to corn
earworm (Alston et al., 1991a). Mortality of corn earworm larvae was less in the open canopy soybean than in the closed canopy crop (Alston et al., 1991b). These additive effects of multiple pests in field studies was also confirmed by a short-term greenhouse study (Russin et al., 1989). The total effect of soybean cyst nematode, *Diaporthe phaseolorum* var. *caulivora* (causal agent of stem canker) and soybean looper (*Psuedoplusia includens*) was less than the combined effect of each pest alone.

**MANAGEMENT CONSIDERATIONS**

Multiple stress factors are the norm in soybean crops. Wide arrays of pests are responsible for many of these stresses. The challenge is in integrating all of them into pest management programs as part of crop management programs. The seemingly additive effects lead to targeting all of the individual pests for management. However, managing soybean cyst removes one of the most restrictive stresses on the crop. This aspect may reduce the level of management for some of the other pests.

Managing populations of soybean cyst nematode in the context of managing multiple pests in the future will require a better understanding of the biology and ecology of the pests and the epidemiology of a disease or diseases. In most pest complexes on soybean, the combination of soybean cyst nematode with other pests results in additive losses of seed yield. These interactions are likely to affect the behavior of most of the interacting organisms. The population densities of soybean cyst nematode are often modified, directly and/or indirectly by the interrelationships.

Management options and recommendations need to account for the number and variety of pests within the same soybean field. Host resistance is available for several pathogens, but combining resistance to soybean cyst nematode and several other pathogens is challenging. It is especially a concern if resistance to several pathogens is developed at the cost of yield potential (“yield drag”).
The weed and arthropod components of the pest populations need to be managed by other tactics. A complex situation is created by the interactive impact of each pest on the crop, the impact of each pest on each other and the response of the pest and the crop to management. Much research will be required to understand pest behavior in complexes and also their behavior in response to pest management tactics.

Research methods used to study complex interactions have employed greenhouse, field and microplot approaches. The common approaches have been to add the organisms individually and in all combinations to the experimental system or to use chemicals to reduce the population densities of selected organisms. Each of these methods has advantages and disadvantages. Isolines that vary by only one gene for resistance to a specific pathogen would be an improvement when evaluating interactions at the organismal level. Because of the inherent variability in pathogens and other pests, well characterized and unique isolates would further aid in the refinement of the experimental protocol. Available molecular tools should aid in the assessment of interactions at the genomic level.

Pests are a natural part of the cropping system and their impact will likely intensify in modern agroecosystems. Because of the economic importance of soybean and the potential losses in production from pest damage, continued research in pest complexes is crucial. The rapid spread and importance of soybean sudden death syndrome, brown stem rot and other soybean diseases and the role that soybean cyst nematode plays in these diseases underscores the research needs. In addition, herbicide resistant soybeans are likely to alter the weed composition because of the kinds of herbicides being used. Thus, managing pest complexes will continue to be a challenge and will probably be more important as additional genetically modified plants are used in production. The challenges of understanding the biological interactions of the plant and the pests are tremendous. The social, environmental and economic aspects add greatly to that challenge.
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**PATHOGEN INTERACTIONS**


