Chapter 15.

Nematodes and other soilborne pathogens in agroforestry

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Key questions

1. What are the main factors that govern the build-up of soilborne pathogens?
2. Which strategies can be followed to avoid outbreaks of soilborne diseases?
3. How can agroforestry be a tool in the management of soilborne disease problems?

15.1. Introduction

Soilborne organisms (such as plant parasitic nematodes, fungi, bacteria, phytoplasma, protozoa and viruses) are among the most underestimated of the factors which affect plant productivity in tropical regions. Because of their microscopic size and the non-specific symptoms of an infection, these organisms live out of sight and, generally, out of mind of the growers and plant protection workers. Root-knot nematodes are an exception in that they cause distinctive symptoms in the form of root galls, which are sometimes referred to as 'root elephantiasis' by subsistence farmers in central Kenya (Fig. 15.1a). Otherwise, most farmers and extension staff are not able to identify nematodes and other soilborne diseases (Sharma *et al*., 1997). Moreover, interactions commonly occur between nematodes and other soil pathogens, complicating any quick recognition of the problem and assessment of the damage done. Soilborne plant pathogens affect plants primarily through the infection of roots. These organisms occur as complexes in soils and in plant tissues, the nature of which are generally poorly understood and little quantified. In addition to pathogenic and parasitic organisms[1], the soil contains a wide range of competitor saprobes, antagonists, beneficial organisms, yeasts, bacteria and nematodes (Fig. 15.2). The population size of each of these groups is determined by edaphic and environmental factors, as well as by the availability of host roots.

Fig. 15.1. Negative and positive nematode associations with *Sesbania sesban*: A. Root-knot nematode (*Meloidogyne* spp.) causing 'elephantiasis' in *Sesbania* roots, B. Entomoparasitic nematode (*Hexamermis* spp.), emerging from larvae of a defoliating insect pest (*Mesoplatys ochroptera*) on *Sesbania*.

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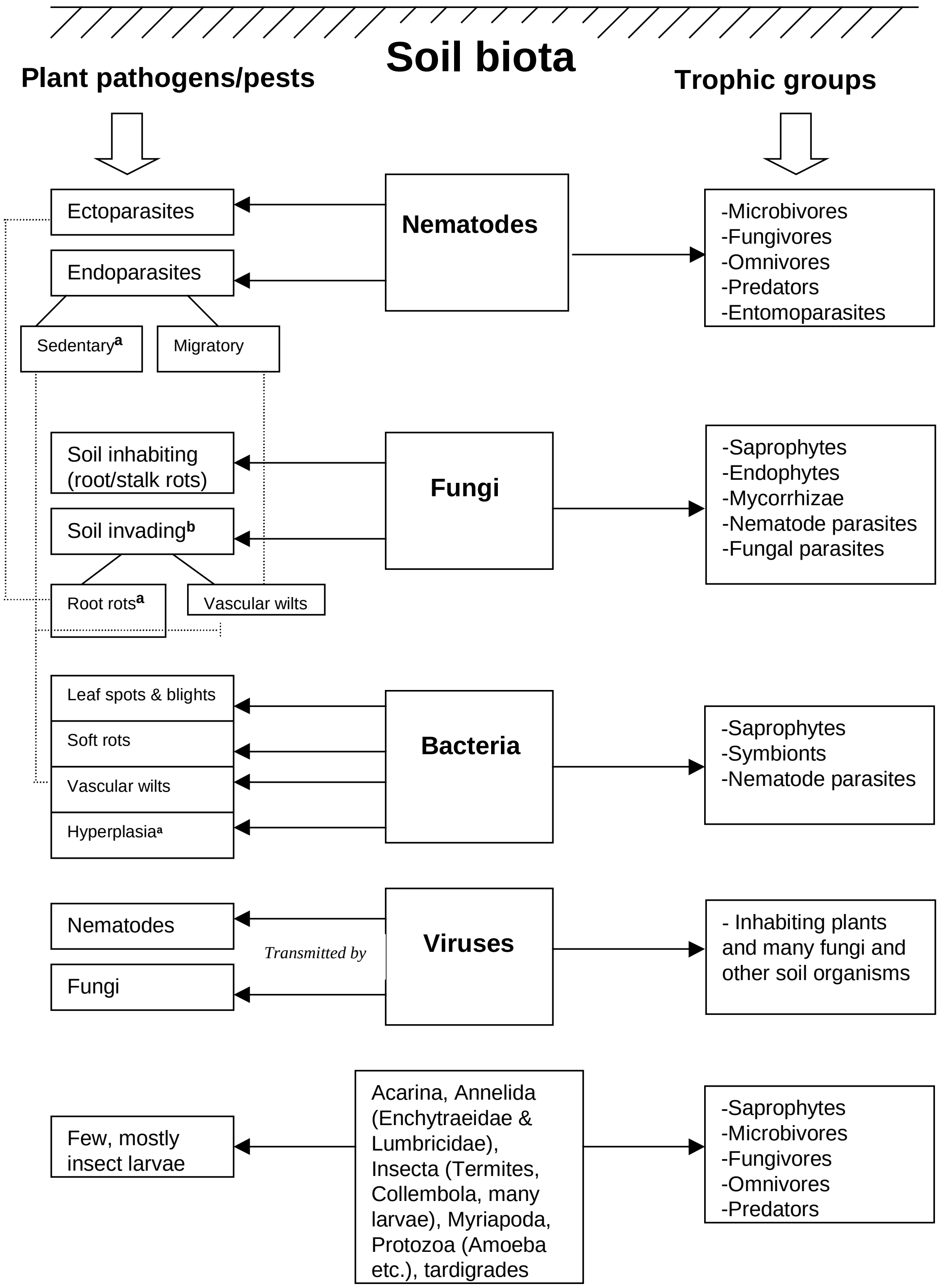
[1] 'Pathogenic' indicates the ability to cause disease, whereas 'parasitic' means that one organism obtains its food from another organism, with or without causing disease.



[a] Galls or tumors on roots are usually due to root-knot nematodes (see also Fig. 1a); on crucifers, however, they may be caused by clubroot fungus (*Plasmodiophora brassicae*); also crown gall bacteria (*Agrobacterium tumefaciens*) cause galls on the crown (and roots) of fruit seedlings.

[b] Most soilborne fungal pathogens are categorized as soil invaders, which indicates their ability to be facultative saprophytes; *Rhizoctonia* and *Pythium* are two important pathogens that are soil inhabitants.

Fig. 15.2. Pathogenic and beneficial groups of soil biota and interactions among pathogenic groups (indicated by broken lines).

Soilborne plant pathogenic and beneficial organisms are one of the key factors which determine crop health and productivity. The mechanisms that keep these organisms in check are influenced by environmental conditions and by the cropping practices used. Soil management practices greatly affect the dynamics of soil biota in managed ecosystems. While considerable attention has been paid to aspects of soil fertility and water management, research on soil health and its relation to ecosystem productivity has been neglected. Little attention has been paid to less obvious disease problems, where suppression of the causal pathogens may be due to a particular cropping environment and/or to the activity of competing organisms in the soil. Instead of focusing only on individual pathogens, it is important to take a holistic view of the soil environment and examine the total soil fungi and nematode populations, etc. and the ways in which they are affected by changing the management practices.

The growing emphasis placed on agroforestry as a means of producing tree products on farm constitutes a recognition of the need to reduce the pressure being placed on forests and natural vegetation. As a result of the intensive cultivation of selected trees on farms (agroforestry), many pest problems have come to the fore; it is now accepted that unless these pest problems are solved, the potential benefits of improved agroforestry cannot be realized. Not only is research on insects and diseases in tropical agroforestry limited, the linkage between farmers and extension services in the area of plant health is also poorly developed. There exist certain general misconceptions, which hold that trees have no, or limited, pests and that diversified systems based on trees reduce pests (insects and diseases).

In this chapter, we discuss the factors governing the build-up of soilborne pathogens, and the opportunities which exist for their management in tropical agroforestry ecosystems (see ‘Key questions’, above). The agroforestry systems considered are rotational systems, tree/crop combinations and complex multistrata systems and home gardens.

15.2. Factors contributing to soilborne pests and diseases

The development and severity of disease in plants can be visualized as a triangle, which is the result of interactions between the host, the environment and the pathogen (Fig. 15.3). The size of the epidemic or the amount of disease is proportional to the sum total of these factors, as long as none of the factors are zero. In the following sections, we will discuss the role of each of these components, namely the importance of agroforestry systems (15.2.1. Cropping systems), the impact of soil and climate (15.2.2. Soil and climate) and the extent and impact of interactions between soil biota in the build up of soilborne diseases (15.2.3. Interactions among soil biota).

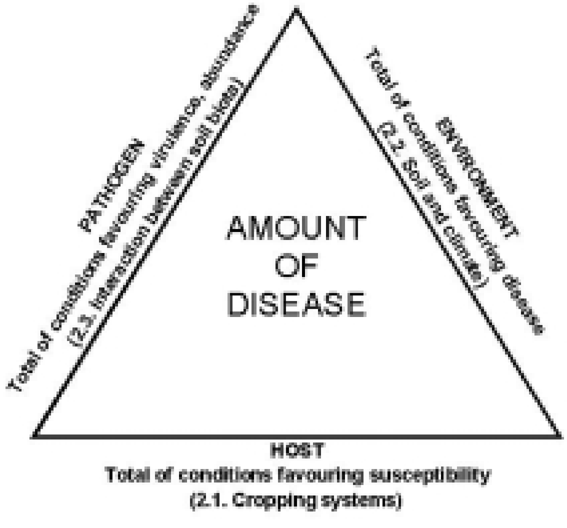


Fig. 15.3. The disease triangle. The amount of disease is proportional to the quantities of favourable host, pathogen and environmental conditions converging at a given time and space (after Agrios, 1997).

15.2.1. Cropping systems

Cropping systems in tropical regions are generally more diverse and less reliant on chemical inputs than are those in temperate regions. There is also a greater diversity of nematodes and other pests in tropical regions (Luc *et al.*, 1990). Pest outbreaks are considered to be more frequent in the tropics, although crop damage by soilborne pests is usually masked by many other, more visible, limiting factors (Smart and Perry, 1968; Wellmann, 1972). The reasons for the more serious pest problem in the tropics are the generally favourable climatic conditions, the greater pathogenicity of pest species and the more severe disease complexes (Mai, 1986). Table 15.1 lists some of the most common soilborne pathogens in the tropics and the crops and trees that may be affected in different systems.

Table 15.1. Common soilborne nematode, fungal and bacterial pathogens on agroforestry trees and shrubs, herbaceous cover crops, and major field crops in the tropics

Pest/pathogen	**Food and cash crops**	**Herbaceous cover crops**	**Trees/shrubs for planted fallows**	**Trees for boundaries**	**Trees in croplands and home gardens**
Nematodes					
Meloidogyne spp. (Root-knot nematodes)	Many vegetables, legumes, tubers, coffee and other cash and utility crops	*Desmodium distortum;* *Tithonia diversifolia*; *Vicia* spp.; *Vigna* spp.	*Sesbania* spp.; *Tephrosia* spp.	*Acacia* spp.; *Albizia* spp.; *Faidherbia albida*; *Prosopis juliflora*	*Adansonia digitata*; *Carica papaya*; *Ficus* spp.; *Phoenix dactylifera*; *Psidium guava*; *Vitis* spp.
Pratylenchus spp. (lesion nematodes)	Cereal crops, root and tuber crops, banana, coffee, tea	*Arachis* spp., forage grasses	*Crotalaria* spp.; *Senna* spp.	*Pinus* spp.	*Hevea* spp.
Radopholus similis (Burrowing nematode)	Banana, citrus, pepper				Palms; *Persea americana*
Rotylenchulus spp. (Reniform nematodes)	Vegetables, cotton, pineapple	*Indigofera hirsuta*	*Cajanus cajan*		*C. papaya*; *Passiflora edulis*
Fungi					
Fusarium spp. (wilt and rot)	Banana, bean, coffee, cotton, melon, potato, tomato	*Vicia* spp.	*C. cajan*; *Crotalaria juncea;* *Sesbania sesban*		Palms
Phytophthora spp. (rots)	Many vegetables, cocoa, citrus, tobacco	*Lupinus* spp.		*Eucalyptus* spp.; *Pinus* spp.	*P. americana* ; *Macadamia* spp.; citrus
Armillaria mellea (root rot)	Coffee, tea, root and tuber crops		*C. cajan*	*Acacia* spp.; *Erythrina* spp.; *Grevillea robusta*	*Annona* spp.; *Macadamia* spp.; *Vitis* spp.

Sclerotium rolfsii (southern blight)	Solanaceous crops, root and tuber crops, legumes, rice	*Mucuna* spp.	*S. sesban*		*P. americana* and many other fruit trees
Verticillium dahliae (wilt)	Cocoa, cotton, potato, tomato			*Dalbergia sissoo*	Anacardiaceae (mango, cashew, pistachio); *P. americana*
Bacteria					
Ralstonia solanacearum (bacterial wilt)	Solanaceous crops, banana, ginger, groundnut			*Casuarina equisetifolia*; *Eucalyptus* spp.	*Annona* spp.

NB Blank table cells probably indicate lack of knowledge rather than lack of hosts.

Sources: Desaeger and Rao, 1999a; Desaeger, 2001; Dommergues, 1990; Lenné and Boa, 1994; Mayers and Hutton, 1987; Mc Sorley, 1981; USDA, 1960; Waller and Hillocks, 1997.

15.2.1.1 Fallow–crop rotational systems

Planted or 'improved' fallows, which use fast-growing leguminous trees and shrubs (also referred to as cover crops), are being promoted in east and southern Africa, in order to replenish soil fertility in nitrogen-depleted soils and to increase crop yields (ICRAF, 1998). However, a disadvantage of growing *Tephrosia vogelii* and *Sesbania sesban*, two of the most promising species for short-duration (6–12 months) planted fallows, is that they are susceptible to root-knot nematodes (*Meloidogyne* spp.), and markedly increase the nematode's population in the soil (Desaeger and Rao, 1999a; 2001b). Root-knot nematodes (Table 15.1) are by far the most devastating nematode pest in the tropics. Maize (*Zea mays*) yields which follow *S. sesban* or *T. vogelii* fallows are not affected, as maize is a poor host to most isolates of root-knot nematodes, but yields of highly susceptible crops, such as bean (*Phaseolus vulgaris*), are severely reduced.

A number of herbaceous and shrubby cover crops are good hosts to root-knot nematodes (Table 15.1), although some of them, such as *Tithonia diversifolia,* do not show the typical root gall symptoms. *Crotalaria* species effectively suppress populations of root-knot nematodes, and those of most other sedentary plant-parasitic nematodes (Good *et al.,* 1965; Sukul, 1992; Wang *et al*., 2002), but instead they host lesion (*Pratylenchus* spp.) and spiral nematodes (*Helicotylenchus* spp. and *Scutellonema* spp.). In western Kenya, maize yield reductions of up to 10–50% were ascribed to damage caused by lesion nematodes (Desaeger, 2001).

Very little is known about the importance of soilborne fungal or bacterial diseases in rotational systems involving crops and planted fallows. In western Kenya, *Fusarium oxysporum,* which causes wilt in *Crotalaria juncea* (Hillocks, 1997), is suspected of being responsible for the severe early wilting of a number of *Crotalaria* spp. used as cover crops (e.g. *C. grahamiana*). *S. sesban* experienced wilt caused by *Sclerotium rolfsii* under dry conditions in Hawaii (Evans and Rotar, 1987) and root rot and wilt caused by *F. oxysporum* f. sp. *sesbaniae* in India (Lenné and Boa, 1994). Root rots caused by *Macrophomina phaseolina, Armillaria mellea* and *Ganoderma* spp. may seriously affect the growth of several *Acacia* species (Lenné and Boa, 1994).

15.2.1.2 Mixed systems

Multiple cropping systems are still the norm amongst traditional and subsistence farmers in the tropics, and are estimated to provide as much as 15–20% of the world's food supply (Altieri, 1991). Trees or shrubs can be planted together with crops in different arrangements and for different purposes. They may be dispersed, in order to provide shade to the understorey crop(s); they may be planted along field boundaries, to act as a windbreak or fence; they may be managed as hedgerows, for mulch and/or fodder and for soil conservation; they may be grown to support climbing crops such as beans, betel vine (*Piper betle*) and black pepper (*Piper nigrum*), or under-sown with herbaceous covers, as is the case in plantation crops. Unless the correct choice of tree species is made, there is a danger that they will promote soil pests by serving as alternative hosts. If two or more species in a system have a common pest (or disease), the chances that it will spread and have a severe effect are greater in a mixed system than they are in a rotational system, because species are in close proximity and because there is continuous interaction among the species.

The typical 'under-forest' shrub crops - coffee (*Coffea arabica*), cocoa (*Theobroma cacao*) and tea (*Camellia sinensis*) - are often combined with shade trees of the genera *Erythrina, Albizia, Gliricidia* and *Leucaena*. Shading is an effective insurance strategy against aboveground insect pests, as well as against diseases in cocoa and coffee plantations. Intercropped coffee suffers less damage from coffee rust than pure coffee, as the latter experiences greater physiological stress (Waller, 1984). Belowground pathogens may also be affected, either by reducing the host’s stress and predisposition, or by altering the soil microclimate. In Uganda, solar radiation stress predisposed unshaded cocoa to attack by *Verticillium dahliae* (Palti, 1981). Disease damage will be aggravated, however, if any of the shade trees host the soilborne pathogens that infect the understorey crops. The use of banana as a shade crop in coffee or cocoa could increase infection by *Pratylenchus coffeae*, as banana is a good host for this nematode. In south Asia, the burrowing nematode *Radopholus similis* and the reniform nematode *Rotylenchulus reniformis* may become more damaging when tea is intercropped with crops such as coffee, cloves (*Syzygium aromaticum*) and pepper, all being good hosts for both nematodes (Sivapalan, 1972; Campos *et al.* 1993).

No major nematode problems were noted on trees employed for hedgerow intercropping, such as *Leucaena leucocephala*, *Calliandra calothyrsus, Gliricidia sepium* and *Inga edulis*, but root rots caused by species of *Fusarium* and *Ganoderma* have been reported to kill *Leucaena* in Asia and Australia (Lenné and Boa, 1994). Many soilborne pathogenic fungi of the genera *Armillaria, Fomes, Ganoderma, Verticillium* and *Rosellinia* have been found to spread to alternate hosts, such as coffee, cocoa and tea, from moribund shade trees or tree residues left after clearing (Schroth *et al*., 2000b). However, *Gliricidia sepium* (also called, because of its toxic seeds, bark, leaves and roots, *mata ratón* in Spanish, meaning ‘rat’ or ‘mouse killer’) is free of soilborne diseases, despite the fact that it has been grown widely throughout the tropics. In mixed fallows of *S. sesban* and *G. sepium* in eastern Zambia, there was greater mortality of the *Sesbania*-defoliating beetle *Mesoplatys ochroptera* than in pure *S. sesban* fallows. This was probably due to the beetles feeding on the poisonous *G. sepium* leaves in the mixed stand (Sileshi and Mafongoya, 2000).

Home gardens and multistrata systems typically occur in the humid and sub-humid tropics, and resemble the local tropical forest ecosystems. Fruit trees and palms, such as areca nut (*Areca catechu*), coconut (*Cocos nucifera*), oil palm (*Elaeis guineensis*) and peach palm (*Bactris gasipaes*), are often the major components of home gardens. With the exception of the commercially important plantation crops, little research has been done on the soilborne diseases of perennial crops or on other economically valuable tree species.

It is common for taxonomically related plants to share the same pests and diseases. Among plant-parasitic nematodes, the semi-endoparasitic *Tylenchulus semipenetrans* is often found to infect many tropical fruits belonging to the families Rutaceae (*Citrus* spp.), Rosaceae (*Eriobotrya japonica*), Oleaceae (*Olea europea*), and Ebenaceae (*Diospyros* spp.). *Citrus* spp. and *Diospyros* spp. are also good hosts for *Radopholus similis.* Species of *Meloidogyne* and *Rotylenchulus,* on the other hand, commonly infect fruit trees belonging to the Caricaceae, Passifloraceae and Moraceae (*Artocarpus* spp.) (McSorley, 1981). The nematode *Rhadinaphelenchus cocophilus*, which causes red ring disease in coconut, attacks 17 other palm species, including oil palm. This nematode is transmitted by the pantropical palm weevil *Rhynchophorus palmarum.*

Radopholus similis is a widespread nematode, and infects many crops, including coconut and areca nut. It is known to infect crops such as betel vine, black pepper, banana (*Musa paradisiaca*), ginger (*Zingiber officinale*) and turmeric (*Curcuma longa*) in the multispecies cropping systems of southern India (Griffith and Koshy, 1993).

Verticillium dahliae and *V. albo-atrum* are extremely polyphagous soilborne fungi, and affect many species in home gardens, including fruit trees, such as mango (*Mangifera indica*) and avocado (*Persea americana*), and vegetables, such as aubergine (*Solanum melongena*) and tomato (*Lycopersicon esculentum*) (Palti, 1981). Moreover, the fungus *Sclerotium rolfsii,* as well as root-knot nematodes, attacks both vegetables and fruit crops. Planting orchards on old vegetable land therefore often warrants soil disinfection prior to planting.

15.2.2. Soil and climate

Many abiotic factors and physical and chemical soil properties interact with soilborne diseases, and may enhance or reduce the impact they have on economic plants. The susceptibility of crops to pathogens is often greater in the case of those grown on infertile soils than in the case of those grown under fertile soil conditions, and many mild pathogens may cause severe disease under conditions of nutrient stress or aluminium toxicity. The damage caused by lesion nematodes was relatively greater in unfertilized maize than was the case in the fertilized crop (Desaeger, 2001). The increased susceptibility of many solanaceous plants to *Fusarium* wilt, *Alternaria solani* early blight, *Pseudomonas solanacearum* wilt, *Sclerotium rolfsii* and *Pythium* damping-off of seedlings was ascribed to nitrogen deficiency (Agrios, 1997). Excessive nitrogen supply, however, especially in the absence of adequate potassium and phosphorus may reduce crop resistance to (mainly aboveground) pests and diseases, implying the need for careful consideration when planting fallows and using cover crops to input nitrogen into the systems.

Calcium reduces the severity of several diseases, such as the fungi *Rhizoctonia*, *Sclerotium*, *Botrytis* and *F. oxysporum* and the nematodes *Meloidogyne* spp. and *Ditylenchus dipsaci* (stem nematode). However, it increases the severity of black shank disease in tobacco (caused by *Phytophthora parasitica* var. *nicotianae*) and of the common scab in potato (caused by *Streptomyces scabies*; Agrios, 1997). The effect calcium has on disease resistance seems to be a result of its effect on the composition of cell walls and on their resistance to penetration by pathogens. As most crops have broad pH tolerances, manipulating the soil reaction could potentially be a means of combating certain diseases. Among fungal diseases, *Fusarium* wilt and clubroot of crucifers are more severe in low pH soils, whereas *Verticillium* is more damaging in high pH soils (Palti, 1981). Similarly, in the case of nematodes, lower pH levels increased galling by root-knot nematode (Steinmüller, 1995), but decreased infection by cyst nematodes (Grau, 2001).

The damage potential of many plant-parasitic nematodes is higher in coarse-textured soil than it is in fine-textured soil, because of higher nematode activity as a result of better soil porosity and oxygenation and because of generally lower inherent soil fertility and biological activity. Root rots are most severe in soils with a low organic matter content, poor soil structure and high compaction with inadequate drainage. Soil degradation due to the loss of organic carbon was reported to increase the vulnerability of banana to major pests, including nematodes, causing huge declines in yield (Page and Bridge, 1993). Many tropical soils contain subsurface zones of dense and/or hard materials, such as claypans and hardpans. Such soils result in an abnormal root distribution, with a large portion of the roots being locked up in the upper parts of the profile where most of the pathogens also reside. In high strength soils, aggregation of roots in cracks or voids may lead to inoculum aggregation if the roots become infected and decay. New roots may grow through the channels left by old roots, virtually assuring contact with very large numbers of pathogens. *Phytophthora cinnamomi* devastated *Eucalyptus marginata* in Australia on shallow lateritic soils, as the fungal zoospores were easily dispersed into cracks in the hard layer that had previously been penetrated by the trees' sinker roots (McDonald, 1994).

High temperatures in the tropics provide favourable growth conditions for pathogens, and also induce heat and/or drought stress in host plants, which further increases both their susceptibility to, and rapid development of, disease (Liddell, 1997). Rainfall and soil moisture affect the host–pathogen interaction in several conflicting ways. Symptom expression tends to be more severe under hot and dry conditions, and 'dryland' pathogens, such as *Fusarium* stalk rots and *Macrophomina* charcoal rots, are typical examples of diseases which appear on crops under stress (Palti, 1981). Drought stress weakens the host plant's resistance and tolerance (the former term indicates the ability of the plant to resist pathogen infection and the latter the ability of the plant to withstand infection without apparent damage). Root endoparasites, such as root-knot nematodes, often cause considerably more damage when soil water becomes limiting for plant growth, as they are protected from environmental stress by the root tissue. In western Kenya, root-knot nematodes caused less damage to *S. sesban* on deep and heavy soils under good rainfall conditions (despite high nematode reproduction) than they did in Malawi. There, the same nematodes caused high mortality and poor growth of *Sesbania* on shallow and light soils under drought conditions. Although the semi-arid tropical region is infested with hordes of deadly pathogens, the majority of plant pathogens and severity of disease outbreaks is closely correlated with high humidity and rainfall. In fungal diseases, formation, liberation, germination and movement of spores, mycelial growth, and root invasion are always greater under moist conditions. Diseases such as *Sclerotium* and bacterial blight, *Phytophthora* and *Pythium* rots, and ectotrophic root diseases such as *Armillaria* and *Fomes* rots are predominantly found in humid and sub-humid agroecological zones (Hillocks and Waller, 1997). Damping-off diseases of seedlings are generally more common in relatively cooler climates.

Few functional linkages between soilborne pathogens and edaphic factors have yet been found (Campbell and Benson, 1994). Still, in spite of its complexity, the spatial and temporal heterogeneity of the soil environment in agroforestry systems presents a unique research opportunity in terms of elucidating interactions which occur between environmental factors and assessing and predicting the impacts of agricultural practices. A great deal of insight could be gained if more quantitative information were to be available on the interactions between soil type, root growth and pathogen epidemiology.

15.2.3. Interactions among soil biota

An understanding of the interactions which occur among different groups of soil flora and fauna will help us to manipulate them in a manner which achieves favourable effects. Direct interactions occur when microorganisms compete for space or nutrients, or when one group antagonizes another by producing toxic metabolites. Indirect interactions are mediated through the root system; for instance, one pathogen may increase or decrease the susceptibility of the host plant to another pathogen. Interactions may work either way - there are probably as many organisms favouring pathogens as there are antagonists, and often the quality and degree of the interactions change as soil conditions are altered (Khan, 1993).

15.2.3.1 Synergistic interactions

Several reviews have discussed the role of nematodes in disease complexes, and numerous nematodes have been associated with viral, bacterial and fungal diseases (Khan, 1993; Abawi and Chen, 1998). Nematodes can play different roles in disease complexes; they act as (1) vectors (e.g. for several viruses), (2) wounding agents (e.g. *Meloidogyne arenaria* and *Cylindrocladium crotalariae* on groundnut), (3) host modifiers (e.g. *Pratylenchus penetrans* and *Verticillium dahliae* on potato), (4) rhizosphere modifiers (e.g. *Meloidogyne incognita* and *Rhizoctonia solani* on tomato and okra), and (5) resistance breakers (e.g. *M. incognita* and *Phytophtora parasitica* on tobacco) (Hussey and McGuire, 1987). Several longidorid and trichodorid nematode species transmit a range of economically important viruses, which cause diseases of fruits, vegetables and ornamentals in temperate climates. However, there is no evidence yet of nematode-transmitted viruses in the tropics, even though tropical Africa is regarded as the place of origin of these nematodes (Hillocks and Waller, 1997). Information on soilborne viruses, and on related mycoplasms in the tropics in general is very scarce, due to the fact that these organism are difficult to study and also to a lack of adequate resources.

The most common synergistic (or positive) interactions are those which occur between plant-parasitic nematodes and root fungi, such as species of *Fusarium, Rhizoctonia,* *Pythium, Sclerotium,* and *Verticillium*. *F. oxysporum* readily establishes itself in the feeder roots of banana when they are invaded by the nematode *R. similis*, but the fungus has seldom been recovered from nematode-free roots (Blake, 1966). In general, endoparasitic nematodes tend to increase diseases caused by vascular wilt fungi, while ectoparasitic nematodes increase infection by cortical rot pathogens (Hillocks and Waller, 1997; Fig. 15.2). Positive interactions between *Meloidogyne javanica* and *Fusarium* spp. have been observed on pigeonpea (*Cajanus cajan*), coffee and mimosa, as well as on a wide range of annual crops. *Verticillium* species often form disease complexes with species of the *Pratylenchus* and *Globodera* nematodes. Interactions between nematodes and root-rot and wilt-inducing fungi have been reported for at least 45 crops, mainly from the tropics, and have involved over 15 nematode genera and more than 20 fungal genera (Evans and Haydock, 1993; Francl and Wheeler, 1993). Disease complexes between nematodes and bacteria are less common; the best-known example is probably the interaction between the root-knot nematode and *Ralstonia* (*Pseudomonas*) *solanacearum*, which causes bacterial wilt. The latter is widely considered as the most important soilborne bacterial pathogen, and has a broad host range and different pathovars (indicating a subspecies or group of strains that can infect only plants within a certain genus or species).

➔ Fig. 15.2 here

Soil fungi may reduce plant resistance to pest infection and promote, or reduce (several examples exist of either occurrence), nematode root penetration (Freckman and Caswell, 1985). Occasionally, moreover, non-pathogenic soil-inhabiting microorganisms (such as *Trichoderma* spp.) may become pathogenic when roots are infected by nematodes (Melendez and Powell, 1969). Some authors have questioned the importance of organism interrelationships in disease complexes involving nematodes and pathogens, and have suggested that the perceived synergism may be caused instead by alterations in the abiotic soil environment (Sikora and Carter, 1987). The latter theory stresses the need for more effort to be made to unravel the complex nature of these interactions.

Not much is known about the role played by saprophytic fungi and non-parasitic or free-living (bacterial- and fungal-feeding) nematodes in disease epidemiology. Free-living nematodes are usually dominant over their plant-feeding counterparts in the soils, and are also commonly found inside plant roots as secondary feeders. They play a major role in soil organic matter decomposition and in nutrient cycling processes in the soil, and are most abundant in soils that are rich in organic matter (Sharma and Sharma, 1999). Although free-living nematodes may cause reductions in the populations of pathogenic bacteria and fungi, they may also aid in the dispersal of the same fungi and bacteria, as well as of mycorrhizae and rhizobia (Hillocks and Waller, 1997). As they can also disrupt plant health by interfering with symbionts, some of them need to be considered as facultative parasites. Some fungivorous nematodes have been observed to suppress ectomycorrhizae on pines and endomycorrhizae on many plants, and some bacterivorous nematodes have been observed to inhibit nitrogen fixation (Freckman and Caswell, 1985; Huang, 1987). However, with regard to symbionts, plant-parasitic nematodes (such as root-knot nematodes) are more damaging than free-living nematodes[2]. Although the majority of interactions are negative (Taha, 1993), nodulation in some *Acacia* spp. was stimulated by root-knot nematodes, possibly by facilitating the entry of the bacteria or by physiological mechanisms that favour the initiation of rhizobial symbiosis (Duponnois *et al*., 1997). Nodulation of *S. sesban* in western Kenya was greatly reduced by high levels of root-knot nematodes, but was slightly stimulated by low levels of the same nematodes (Desaeger, 2001). However, using a *Rhizobium* strain from northern Kenya, nodulation of *S. sesban* was not reduced even at the highest nematode population (Desaeger, 2001), indicating the need to select *Rhizobium* inoculum appropriate to nematode-infested soils. Alternatively, the result may have been exacerbated by the often low numbers of compatible rhizobia for *S. sesban* in these soils (see Chapter 13, this volume).

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[2] Root galls and *Rhizobium* nodules look very similar to the untrained eye, but unlike galls, which are an integral part of the root, nodules are distinct structures and can easily be rubbed off.

15.2.3.2 Antagonistic interactions

Antagonistic interactions among soil organisms reduce the risk of soilborne diseases. ‘Antagonist’ is an umbrella term for parasites, predators, pathogens, competitors, and other organisms (such as rhizobacteria, mycorrhizae, fungal endophytes, bacterial and fungal parasites, nematode-trapping fungi and predatory nematodes) that repel, inhibit or kill pathogens (Table 15.2). The antagonistic potential of soils has been defined as the capacity of a soil ecosystem to prevent or reduce the introduction and/or spread of plant pathogens or other deleterious agents. Considering that more than 90% of soil microorganisms have not been cultured and studied, the potential of antagonistic interactions within the soil is probably greatly underestimated (Sikora, 1992).

Table 15.2. Parasitic and antagonistic potential of soil organisms to kill or inhibit plant-parasitic nematodes and soilborne pathogens.

Hyperparasites[a]	**Target pathogen**
Bacterial	
• *Pasteuria* spp.	Nematodes
Fungal	
• Nematode-trapping: *Arthrobotrys* spp.	Nematodes
• Nematode-parasitic: *Paecilomyces lilacinus*, *Verticillium chlamydosporium*, *Dactylella oviparasitica*	Nematodes
• Fungal parasites: *Trichoderma* spp.	Damping-off and root rot fungi (*Rhizoctonia, Pythium, Fusarium*)
• Insect parasites: *Beauveria* spp.	White grubs and cockchafers
Other	
• Predatory amoeba, nematodes, tardigrades and mites	Nematodes; fungi
• Entomopathogenic nematodes	Various insects (adults and larvae)
Antagonists[a]	
Bacterial	
• *Agrobacterium radiobacter*	*Agrobacterium tumefaciens*
• Fluorescent *Pseudomonas* spp.	Nematodes; fungi
• Rhizobacteria, *Bacillus subtilis*	Several fungal diseases
Fungal	
• Non pathogenic *Fusarium* spp.	*Fusarium* wilts
• Mycorrhizae: *Glomus, Gigaspora, Endogone* spp.	Root-knot nematodes
• *Trichoderma* spp.	Wide range of soilborne and foliar fungal pathogens
Others	
• Actinomycetes (*Streptomyces* spp.)	Fungi

[a] ‘Hyperparasites’ use their host directly as food, whereas ‘antagonists’ act by substrate invasion or modification, or by excreting agents such as antibiotics, siderophores and bacteriocins. The distinction between hyperparasites and antagonists is not always clear (certain agents, such as *Trichoderma virens* may behave in both ways, depending on the pathogen parasitized or antagonized).

Sources: Baker and Cook, 1974; Cook and Baker, 1983; Sikora, 1992; Stirling, 1990; Tjamos *et al*., 1991; Copping and Menn, 2000.

Interesting case studies of so-called suppressive soils have been reported which, typically, show low disease incidence on a susceptible host, even in the presence of adequate inoculum and abiotic factors favourable to the pathogen (Rouxel, 1991). For example, the *Chinampa* soils in Mexico, which date back to the Aztec era, and which are characterized by large inputs of aquatic mud, plant residues and manures, are well known for the suppression of pathogens such as *Pythium* spp. and *Meloidogyne* spp. (Zuckerman *et al.*, 1989; Garcia-Espinosa, 1998). Although low pest incidence in suppressive soils is, in general, linked to physicochemical properties associated with the fine texture of these soils (Bruehl, 1987), evidence also points to biological factors, particularly rhizobacteria and species of *Fusarium* and *Trichoderma,* being determinants. The fluorescent pseudomonads, aggressive bacterial root colonizers that sometimes produce antibiotics, are often cited as being the major biological factors.

Many examples exist of fungal hyperparasitism, a well-known case being the use of *Trichoderma* spp. as biocontrol agents against soilborne fungal pathogens (Baker and Cook, 1974). Another example is the delayed development of symptoms caused by fungal diseases in seedlings inoculated with non-pathogenic fungi or hypovirulent strains of the pathogen (Gindrat, 1979). Despite numerous attempts, however, only limited success has been recorded with biocontrol in the field, and most of the agents tested remain as ‘petri-dish antagonists’. The successful introduction and establishment of chosen antagonists or hyperparasites in the soil requires either an empty ecological niche or an abundant food/resource base large enough for there not to be competition with existing soil inhabitants. Both situations are difficult to achieve in the real world. Instead of inoculating the soil with antagonists, the practical option is to stimulate the growth of natural antagonists in the soil through the incorporation of organic matter and other soil amendments (see sections 15.2.3. Interactions among soil biota and 15.4.2. Plant tolerance/resistance). However, few attempts have been directed at investigating the actual effects of amendments on antagonists.

In addition to the nutritional benefits they offer, rhizobia and mycorrhizae offer protection against certain root diseases. *Rhizobium japonicum* prevented the development of root diseases caused by *Fusarium oxysporum* and *Phytophthora megasperma* on soybean (*Glycine max*) and lucerne (*Medicago sativa*), except when pathogens had already infected these legumes, in which case the pathogens interfered with rhizobial activity (Palti, 1981). When an ectomycorrhizal mantle develops on fine roots, pathogens are rarely able to penetrate such roots, as is the case with *Phytophthora cinnamomi* on pines (Marx, 1975). Also, endomycorrhizae such as *Endogone* spp. and *Glomus* spp. have been shown to give protection against several soilborne pests and pathogens (Gindrat, 1979).

Competition among different taxa of plant-parasitic nematodes often has a negative effect on at least one of the competitors, especially when their feeding habits are similar. Tomato roots had lower populations of lesion nematodes when root-knot nematodes were present (Estores and Chen, 1972). Mechanisms of competition may include mechanical destruction, physical occupation of feeding sites or induced physiological changes in the host’s suitability or attractiveness (Eisenback and Griffin, 1987; Khan, 1993). Nematode interactions are often difficult to explain, and the knowledge base, especially with regard to tropical systems, is small.

A huge amount of information is available on nematodes that parasitize insects (Poinar, 1975; Nickle, 1984). Entomoparasitic nematodes may kill their host by feeding and entomopathogenic nematodes vector a bacterium, which actually causes the insect’s death. The entomoparasitic nematode *Hexamermis sp.* was found inside the larvae and adults of the *Sesbania*-defoliating beetle *Mesoplatys ochroptera,* causing their death in Zambia (Kenis *et al.*, 2001; Fig. 15.1b). In Florida, the mole cricket nematode *Steinernema scapterisci* is used in pastures to keep populations of mole crickets, of the genus *Scapteriscus,* under control (Smart *et al.*, 1991).

15.3. Strategies for the management of soil pests based on general sanitation

The aims of sanitation are to prevent the introduction of the pathogen inoculum into cultivated fields and to reduce or eliminate the inoculum from fields that are already infected. Pathogens can be introduced through seed and through vegetative propagation material, such as cuttings, tubers and seedlings. Vegetatively propagated crops - such as bananas and plantains, ginger, cassava (*Manihot esculenta* Crantz), potatoes (*Solanum tuberosum*), yams (*Dioscorea* spp.), sugarcane (*Saccharum officinarum* L.), taro (*Colocasia esculenta* (L.) Schott) and sweet potatoes (*Ipomoea batatas* (L.) Poir) - are frequently infected by pathogens, especially viruses, systemic pathogens, and nematodes.

Aphids and whiteflies transmit many seedborne viruses. As these insects become more scarce as altitude increases, traditional potato growers in the Andes, and cassava farmers in the Kenyan highlands, obtain their seed from high-altitude areas where insect-transmitted virus diseases are minimal (Thurston, 1992). Similarly, the seed of different legumes and cucurbits affected by seedborne diseases should be grown and harvested during dry seasons or in arid areas under irrigation, in order to avoid the high scope for disease infection provided by wet weather. The use of disease-free banana suckers, which can be obtained by meristematic tissue culture, is one of the main practices used to reduce nematode damage to banana.

Soil quality, soil water status and choice of shade trees all affect the incidence and severity of soilborne diseases in nurseries. It is advisable not to plant bananas or plantains for shade in a nursery, as they host many nematode pests. Root-knot nematodes are among the most common soilborne pests in tropical nurseries, and account for poor rooting and seedling quality.

Many strategies exist to rid nursery beds of soilborne pathogens: in the tropics they are often based on heat therapy. Burning plant debris, such as dry tobacco stalks, maize stover, rice husk and wood, on the surface of seedbeds is a practice commonly used in Africa to ward off root-knot infestation. To be effective, a sufficiently hot burn, which causes heat to penetrate the soil, is required: this requires the use of wood or woody stalks rather than grass, for example. Root-knot is very effectively controlled in seedbeds by turning soil broken up into a fine tilth at regular intervals during the dry season. Nematodes are killed as they are exposed to high temperatures, solar rays and drying (Bridge et al., 1990; Bridge 1996, 2000b). Soil solarization, or heating the soil by covering the seedbed with transparent polyethylene, is one of the most practical and efficient means used to reduce soilborne pathogens in nursery beds. Solarization will be effective provided the soil is moist, the plastic is properly sealed at the edges, and the solar radiation is high. Heat therapy is also used to kill nematodes inside the corm tissue of banana suckers by immersing them in hot water (55°C) for 15-25 min (Stover, 1972).

It is extremely difficult to eradicate soilborne pathogens once they are established in the field. Cultural and physical methods, such as crop rotation, use of resistant cultivars, removal or burial of infected plants and crop debris, adjusting crop density, and depth and time of planting, are only effective against certain diseases. However, these measures may not be effective if the pathogen pressure is too high: in such a case they can only be controlled by chemical soil disinfection, generally fumigation.

Chemical control of soilborne diseases is impractical for most small-scale farmers in the tropics, because of cost considerations and a lack of knowledge concerning chemical use. The use of chemicals is, in general, directly related to farmers' economic situations, and very few farmers in the tropics consider ecological considerations to be a reason for not using them. In reality, chemical pesticides are, unfortunately, the preferred option for most farmers, if they are available and affordable, as farmers often (wrongly in many cases) believe that chemicals are the best pest-control solution. Farmers who consider alternatives to pesticides generally expect instant results similar to those provided by chemicals (Bridge, 1998). Apart from their high cost, some of the problems associated with the use of chemicals on small-scale farms in the tropics are a lack of knowledge regarding the use of correct chemicals (farmers often use insecticides to try and control fungal diseases, for example), their own safety, and the correct application rate and frequency. Many of the broad spectrum and highly persistent pesticides, which have been banned in most developed countries, are still being marketed in many developing countries.

Many weed species serve as alternative hosts to soilborne pathogens (such as *Meloidogyne* and *Verticillium* spp.) with or without being seriously affected themselves. If such weeds are not properly controlled, they may reduce the effectiveness of break crops employed in crop rotation to eliminate soilborne pathogens. In western Kenya, *Striga hermonthica*, a parasitic weed in maize, was found to be a good host for root-knot nematodes, which nullifies the effectiveness of maize as a rotation crop used to reduce root-knot nematodes in *Striga*-infested fields (Desaeger, 2001). Planted fallows of *Crotalaria* were more effective in reducing *Meloidogyne* populations in researcher-managed plots than in farmer-managed fields, probably because of poorer weed control in the latter (Desaeger, 2001).

The soil's physical, chemical and biological environments impose restrictions on the dispersal of soilborne pathogens. Unlike windborne pathogens, these do not spread by means of movement at the landscape level; nematodes, for example, only move a few metres per year. However, the exception to this rule are some systemic fungi, which may spread with seeds, and certain facultative soil-inhabiting insects, which may disperse over long distances at the adult stage. Foraging rhizomorphs of *Armillaria* spp. are also capable of spreading over several acres.

Of greater significance is the indirect spread of nematodes and pathogens through water and soil movement (erosion and sandstorms) and human interventions (irrigation and movement of machinery). Nematodes were spread by the wind in the groundnut growing area of Senegal (Baujard and Martiny, 1994) and an entire field of pepper was lost to *Phytophthora capsici* downstream of windblown rain and floodwater in the USA (Bowers and Mitchell, 1990). Within a field, a disease inoculum often accumulates and causes high infection rates in the lowest parts of the field, especially when the field is irrigated. At the landscape level, various pathogens (such as nematodes, wilts and blights) may spread to distant fields by means of irrigation channels, drainage ditches and even rivers. The spread, from isolated foci to a whole plantation, of *F. oxysporum* f. sp. *albedinis,* which causes wilt ('bayoud') in oil palm, was attributed to flood irrigation (Kranz *et al.*, 1977). Flooding can also be advantageous, however, as most parasitic nematodes and fungi such as *Verticillium* and *Fusarium* can be controlled by flooding the soil for at least two months (Sumner, 1994). This is particularly interesting in areas where flooding occurs either naturally or as part of the farming system (paddy rice or fish ponds).

Many of the sanitary measures mentioned here do not require a great deal of technology and/or money. Small-scale farmers in the tropics can gain a lot by incorporating the relevant sanitation practices into their farming systems.

15.4. The avoidance approach to the management of soil pests

15.4.1. Crop rotation

Historically, crop rotation has been a major tactic for the control of soilborne pests and diseases. Crop rotations suppress soilborne pathogens if the crops employed in rotation are poor hosts, if they act as trap crops for the pathogens, if they produce toxic or inhibitory allelochemicals (Table 15.3), and/or if they provide niches for antagonistic flora and fauna (Table 15.2). Evidence for utilizing specific crop rotations to ward off soilborne pathogens and enhance productivity can be found in ancient Chinese and Indian literature: the system was used in the pre-Columbian Inca culture, and in Medieval and Renaissance Europe (Rodríguez-Kábana and Canullo, 1992). In Peru, potato cyst nematodes (*Globodera* spp.) have traditionally been managed by rotating potato with other Andean tubers, such as oca (*Oxalis tuberosa*), mashua (*Tropaeolum tuberosum*) and ullucu (*Ullucus tuberosus*). Inca law demanded that potatoes must not be grown on the same land more than once in 7 years (Thurston, 1990). Mashua was recently found to contain isothiocyanates - nematicidal compounds that are commonly found in cruciferous plants and that are related to methyl isothiocyanate, which is the active ingredient of the soil fumigant metam sodium.

Besides directly reducing the main pathogen, crop rotation can act against a predisposing pathogen, as is the case in the reduction of *Fusarium* wilt which results when the predisposing agents (root-knot nematodes) are controlled. A potential exists for exploiting rotations as a control for soilborne diseases. However, the use of such a technique requires the existence of a knowledge base regarding the disease incidence and host status of the component species. Generally, closely related crops and trees are more likely to support the same diseases than unrelated species are (see section 15.2.1.2 Mixed systems). In particular, continuous

Table 15.3. Trap and antagonistic crops and organic amendments with potential for control of plant-parasitic nematodes and soilborne pathogens

Trap and antagonistic crops	**Target pest/pathogen**
Cover crops	
• *Arachis* spp. (wild groundnut); *Brassica* spp. (mustard); *Cassia fasciculata* (partridge pea); *Crotalaria* spp.; *Macroptilium* spp. (siratro); *Mucuna* spp. (velvetbean); *Pueraria* spp.; *Stylosanthes gracilis*	Root-knot nematodes
• *Indigofera hirsuta* (hairy indigo)	Root-knot and lesion nematodes
• *Crotalaria* spp.; *Mucuna* spp. (velvetbean)	Root-knot and reniform nematodes
Flower crops	
• *Gaillardia* spp., *Helenium* spp., *Tagetes* spp. (marigold)	Nematodes; *Verticillium* wilt
Oil crops	
• *Arachis hypogaea* (groundnut)	Root-knot nematodes
• *Ricinus communis* (castor); *Sesamum indicum* (sesame)	Root-knot and lesion nematodes
Pasture crops	
• *Chloris gayana* (Rhodes grass); *Eragrostis curvula* (weeping lovegrass); *Panicum maximum* (panic grass)	Root-knot nematodes
• *Cynodon dactylon* ('coastal' bermudagrass)	Root-knot nematodes; *Fusarium* wilt
• *Sorghum bicolor* x *S. sudanense* (Sorghum-sudangrass)	Root-knot nematodes; bacterial wilt; *Striga*
Tree crops	
• *Azadirachta indica* (neem)	Root-knot nematodes; various soil pests
• *Sesbania rostrata*	*Hirschmanniella* spp. (rice root nematodes)
Organic amendments	
Agricultural wastes/residues	
• Lucerne and cereal straw, cassava peelings, cocoa pods, coffee husks, sugarcane residue, tea waste, tree bark, wood ash, etc.	Nematodes; fungal root rots; *Verticillium* wilt; *Sclerotium* blight
Animal wastes	
• Bonemeal, crab chitin, farmyard manure, poultry manure, etc.	*Phytophthora* root rot; *Verticillium* wilt; *Fusarium* wilt; nematodes
Green manure	
• *Aeschynomene* spp. (jointvetch); *Azolla* spp.	Nematodes
• Asparagus, clover, crucifers, neem, sudangrass, velvet bean, water hyacinth, etc.	Nematodes; *Pythium* rot; *Fusarium* wilt; fungal root rots
Oil cakes	
• Castor, cotton, mustard, neem, groundnut, sesame, soybean, etc.	Nematodes; fungal root rots; bacterial blight

Sources: Abawi and Chen, 1998; Bridge, 1987; Egunjobi, 1985; Gamliel, 2000; McSorley, 2001; McSorley *et al*., 1994; Noe, 1998; Saka, 1985; Sumner, 1994; Thurston, 1997; Wang *et al*., 2002.

cropping of legumes, crucifers, cucurbits and other vegetables should be avoided; the rotation of unrelated crops, for instance legumes with cereals, is recommended. Still, this principle is not a guarantee against soilborne diseases, as there are many examples of soilborne diseases that are shared by taxonomically unrelated plant species.

Many soilborne pathogens, such as *Meloidogyne* spp., *Verticillium* spp., *S. rolfsii* and *Armillaria* spp., have wide host ranges and are difficult to control. They require carefully designed cropping systems. By contrast, many cyst nematodes and pathogens that cause bacterial wilts and root-rots are more host specific and are easier to control by crop rotation. In general, while the same nematodes and viruses often affect numerous crops and trees, many fungal and bacterial pathogens are more specific in their host ranges and do not pose so great a threat to other plant species associated or rotated with their primary hosts. Some fungal and bacterial pathogens have a broad host range at the species level, but are host specific at lower taxonomic levels. They are, therefore, subdivided into *pathovars* or *formae speciales*, and are then further divided into races.[3] *Fusarium oxysporum* is an example of a well-known generalist that is actually highly host specific at lower taxonomic levels.

Both the duration of the fallow phase and the number of 'break crops' that need to be grown in rotation in order to control soilborne diseases depend on the length of time that the pathogen can survive. Cyst nematodes resist disintegration in the soil for long periods, so rotations of three or more years may be required. Also, many fungal pathogens (for example, *Fusarium* spp. and *Verticillium* spp.) may survive for several years in the soil. In western Kenya, planted fallows of *S. sesban* and *T. vogelii* require a one-season rotation with pure maize, instead of the traditional maize–bean intercrop, in order to avoid root-knot nematode damage to susceptible beans (Desaeger and Rao, 2000). Table 15.2 gives several cover crops and pasture grasses that can be used, in crop rotations, to reduce root-knot nematodes and other soilborne plant pathogens (either by acting as trap crops or through some other mechanism).

Many *Crotalaria* species have proved to be excellent rotation crops for the control of root-knot nematodes throughout the world (Wang *et al*., 2002). Cassava, pineapple, sweet potato, sugarcane, tomato and bitter orange are good rotation crops for banana, for which *Radopholus similis* (a burrowing nematode) is the main parasite (Loos, 1961; Luc *et al*., 1990). Although these crops may increase root-knot nematodes, banana is not affected greatly by root-knot nematodes, except in a few special production areas outside normal growing regions (Bridge, 2000a; Gowen and Quénéhervé, 1993). *Phaseolus aureus* (mung bean), *Vigna mungo* (black gram), *Vigna unguiculata* (cowpea), *Sesamum indicum* (sesame) and the cover crop *Indigofera hirsuta* (hairy indigo) were reported to be good rotation crops for the control of *Pratylenchus* spp. in rice (Bridge *et al*., 1990).

Much of the information available regarding crop rotations is highly site-specific. The effects of environment and season on the effectiveness of rotations are poorly understood, as are the effects that rotations have at a regional level and on non-target pests. An example of a rotation that aggravated a non-target pest is that of a sorghum rotation, for managing root-knot nematodes, which increased problems with wireworms in a subsequent potato crop (McSorley, 2001). There is no such thing as a 'miracle plant', and whether a certain crop or tree species is 'good' or 'bad' when used in a rotation depends on its proper use. *S. sesban* fallows, for instance, increase the risk of root-knot nematode damage to susceptible crops, but they also act as a false host to the parasitic weed *Striga* (*Striga asiatica* and *S. hermonthica*) and deplete its seed in the soil (Gacheru *et al*., 2000). Therefore, *S. sesban* should be considered an excellent rotation crop for maize in East Africa in terms of soil fertility replenishment as it reduces *Striga* infestation of maize. Although it increases the number of root-knot nematodes present, the latter do not significantly affect maize in the area.

15.4.2. *Plant tolerance/resistance*

Developing plant material that is tolerant/resistant to soilborne diseases is a continuing process, although some progress has been made in the case of some crops (Waller

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[3] *pathovars* or *formae speciales* are specific to certain plant species, whereas races are specific to a certain variety of a plant species.

and Hillocks, 1997). Resistance within a species is mainly against highly specific pathogens, such as the different *Fusarium* wilts; resistance against generalists, such as root-knot nematodes or *Sclerotium rolfsii,* is less common. However, alternative crops can be chosen which have high levels of resistance even to these generalist pathogens.

Increasing genetic uniformity in our major food crops is a dangerous trend, especially with regard to major disease outbreaks. Of the 3000 or so plant species that humans have used for food, about 150 have entered into world commerce; today humans are fed primarily by only about 15 plant species (Thurston, 1992). Therefore, at the very least it seems, maintaining the genetic diversity of these plant species appears crucial, as this would offer some kind of insurance against large-scale crop failures. The disastrous potato blight epidemic that occurred in Ireland in the 1840s, and which was caused by the introduced soilborne fungus *Phytophthora infestans*, was favoured by the genetic uniformity of the crop (Bezdicek and Granatstein, 1989).

Many local races or cultivars show remarkable tolerance to certain soilborne pathogens. Although these races are not necessarily high yielding under optimal conditions, they yield some harvest even under the worst conditions. As many as 50 different cultivars of potato are grown by Andean farmers in South America, a figure which should be compared to the use of only four main cultivars in the United States (Altieri, 1991).

Several comprehensive reviews have been written on the mechanisms, genetics and breeding behind resistance or tolerance (Robinson, 1976; Lamberti *et al*., 1983). In addition to traditional breeding methods, genetic engineering is becoming more and more important, especially with regard to resistance against pests and diseases. The potential of biotechnological advances is vast. However, the possible risks (such as the creation of new weeds, the amplification of existing weeds and harm to non-target species) should not be disregarded. Biosafety measures (including against certain biocontrol agents) should be put in place to restrict or prevent the spread and introduction of pests of plants and plant products (Schumann, 1991).

15.5. The confrontational approach to the management of soil pests

15.5.1. Mixed systems

Mixed systems, involving plant species that host different pathogens, provide a continuous food source for the reproduction of these pathogens and may aggravate disease incidence. On the other hand, lower density of host species and mutual competition among species in mixed systems reduces the chance for pathogens to increase to damaging levels. The presence of permanent hosts in the system ensures continuous food for predators and antagonists of the pathogen. The control strategy of frequent disturbance of pest and disease populations in crop rotations is, to some extent, substituted for by the strategy of increased stability and internal control mechanisms used in mixed systems (Schroth *et al*., 2000b).

15.5.2 Tree/crop intercrops

Considerable documentary evidence exists to suggest that the reduction of both aboveground and belowground insect pests is greater in annual intercrops than it is in pure crops (Altieri and Liebman, 1986). This is usually explained by the lower resource concentration for the pest and an increased abundance of predators and parasitoids due to greater availability of alternative food sources and suitable microhabitats in annual intercrops (Risch, 1981). In addition, the trap-crop principle is often cited as a mechanism of reduced pest attack: one component in the system attracts the pest and serves as a trap or decoy, preventing the infection of the host species. The secretion, by one of the species of the system, of harmful substances into the rhizosphere may be detrimental to the pathogen of the other species. This is the mechanism put forward to explain the fact that the occurrence of *Fusarium* wilt is lower in pigeonpea intercropped with sorghum than it is in pure pigeonpea (ICRISAT, 1984). The nematicidal activity of root exudates has been shown for certain plants, such as marigolds (*Tagetes* spp.) and neem (*Azadirachta indica*).

Antagonistic (trap- or pesticidal) crops have been fairly well documented thus far (Table 15.2). Interplanting of neem *(Azadirachta indica*) seedlings in chickpea (*Cicer arietinum*) or mung bean reduced the incidence of root-knot nematodes (Narwal, 2000). Guinea arrowroot or topinambour (*Calathea allouia*) has been reported to be antagonistic to

Meloidogyne spp. Its preference for shade also makes it an interesting species for association with trees, as with coffee in Puerto Rico (Noda *et al*., 1994).

Cover crops are often sown in plantation crops and orchards as a means of suppressing weeds and providing grazing for cattle. It is also common to grow agricultural crops between commercial tree crops, especially during the establishment phase. Such systems offer great opportunities for managing the soilborne diseases of the plantation crops, either through the growing of trap crops, or through the stimulation of antagonists and predators of the pathogen. In Florida and California, cover crops, such as vetch, clovers, grasses and forage groundnut (*Arachis pintoi* and *A. glabrata*), are planted inside vineyards and citrus orchards in order to control nematodes and weeds (Porazinska, 1998). Also *Crotalaria* species (such as *C. spectabilis* and *C. ochroleuca*) have been successfully used to control sedentary plant-parasitic nematodes in peach and banana orchards. In Nicaragua, *A. pintoi* and *Desmodium ovalifolium,* respectively, reduced the populations of *R. reniformis* and *M. incognita* when grown together with coffee (Herrera and Marbán-Mendoza, 1999). Carpets of creeping legumes stimulated the action of saprophytes and antagonistic microflora which worked to eliminate *Armillaria mellea* root rot inside infested stumps of rubber trees (Liyanage, 1997).

15.5.3. Multistrata complex systems and homegardens

Home gardens in West Java, and the Chagga multistorey gardens on Mt. Kilimanjaro, in Tanzania, have been in use for centuries without any major disease problems being apparent. High species diversity, combined with the individual care of each plant, generally results in a minimum incidence of insects and pathogens. Soils in these systems contain highly diverse biota, which reduce the risk of any one soil pathogen becoming predominant. It is generally accepted that a close relationship exists between species diversity and performance stability, although merely increasing diversity will not necessarily increase the stability of all ecosystems. One of the goals of pest management should be the identification of those elements of diversity that should be retained or added and those that should be eliminated (Nickel, 1972). The incidence of *R. similis* in multispecies systems in southern India decreased when coconut and areca nut palms were interplanted with cocoa, in comparison with when they were interplanted with banana, black pepper and cardamom (Griffith and Koshy, 1993).

An important aspect of multistrata systems is the physical, nonspecific effect that a plant species may have on pest and disease incidence - as opposed to the more obvious, specific biological effects. Although physical effects on microclimate (for example increased shade, moisture, or other physical factors) would mainly be significant in terms of the effect they have on aboveground insects and pathogens, biological activity below ground could also be affected by means of changes in the moisture, structure and porosity of the soil environment. Mortality of *Acacia mangium* trees due to species of the fungal pathogen *Rosellinia* was greater in pure stands than it was in mixed agroforestry systems, a fact attributed to the wider spacing and faster growth of the trees in the mixed agroforestry systems (Kapp and Beer, 1995).

15.5.4 Multispecies fallows

Natural fallows, which have a mixed vegetation, are less likely to experience damaging levels of soilborne pathogens. Desaeger and Rao (2000) found that short-duration (≤1 year) natural fallows did not increase populations of the parasitic nematodes *Meloidogyne* and *Pratylenchus* to damaging levels in western Kenya. Long-duration fallows (10 years or more) were found to decrease plant-parasitic nematodes in western Kenya (Kandji *et al*., 2001) and to increase nematode species diversity in Senegal (Pate, 1998). Therefore, increasing species diversity in planted fallows, in order to mimic the functions of natural fallows, is a technique that can limit the build-up of pathogens and their potential to damage susceptible crops in a rotation. Use of such a practice would increase the flexibility that farmers have in terms of choosing crops for rotation. However, practising rotations strictly for the purpose of controlling soilborne diseases may conflict with farmers' preferences for certain crops and with the suitability of certain crops in relation to the soil and climate.

Bean crops that followed mixed improved fallows of *S. sesban* + *C. grahamiana* and *T. vogelii* + *C. grahamiana* did not experience yield losses due to root-knot nematodes (Desaeger and Rao, 2001b). This result should be compared with the result gained when bean followed pure *S. sesban* or *T. vogelii* fallows. Inclusion of *C. grahamiana* in the fallows - a poor host for root-knot nematodes - had reduced the build-up of root-knot nematode and had increased the populations of lesion and spiral nematodes, as well as the populations of other less pathogenic nematodes. Similarly, the presence of the weakly pathogenic spiral nematode, *Helicotylenchus dihystera*, reduced the pathogenic impact of the nematode community in millet (*Pennisetum typhoides*; Villenave and Cadet, 1997). Not all mixed fallows guarantee the reduction of pests and diseases; quite the opposite may occur if the component species happened to host the same pathogen. An *S. sesban* + *T. vogelii* mixed fallow resulted in very high root-knot nematode damage to bean in rotation, in comparison with pure fallows of the respective species (Desaeger and Rao, 2001b).

Multi-species fallows may have other advantages, such as greater biomass production and greater resilience against environmental stresses than mono-species fallows (Khanna, 1998). Another advantage of multispecies planted fallows is that better synchrony exists between crop nutrient demand and mineralization of plant residues, especially when the foliage of component species has different chemical characteristics (Mafongoya *et al*., 1998).

15.5.5 Soil amendments/mulching

Maintaining high soil organic matter - by regularly incorporating organic materials, farmyard manure, crop residues and composts - usually improves a plant's ability to withstand pathogens (Linford *et al*., 1937; Palti, 1981). Several mechanisms may be responsible for the suppressive effect of organic matter on root pathogens:

1. Germination and lysis of propagules,
2. Competition for nutrients,
3. Release of toxic compounds - such as sulphur-containing volatiles and high concentrations of ammonia (Stirling, 1990),
4. Stimulation of antagonists, or parasitic or predacious biological control agents - e.g. chitin amendments increase populations of nematophagous fungi,
5. Interference with inoculum dissemination - e.g. mulch reduces soil splashing and the spread of bean web blight (Galindo *et al*., 1983),
6. Modification of soil environment (temperature and moisture).
7. Some examples of soilborne pathogens that can be controlled by using soil amendments are given in Table 15.3.

Organic materials and mulches offer many agronomic benefits: lowering soil temperature, maintaining soil moisture, protecting the soil against erosion, providing nutrients and organic matter to the soil, improving soil structure and reducing weeds. Probably because of this, they are seldom used with plant health as the primary consideration. Mulches may have a negative effect on crop health, as in certain cases they increase the incidence of plant diseases and shelter other pests, such as insects, slugs and rodents, as well as venomous snakes. Fresh plant material may initially be colonized by pathogens rather than by saprophytes. The application of green manures having a low C/N ratio may increase the incidence of pathogens such as *Rhizoctonia solani* and *Pythium* spp. and *Fusarium* spp. It has been found that, although fresh crop residues controlled *Pythium ultimum* on lettuce, they increased the incidence of *Fusarium solani* f. sp. *phaseoli* on bean (Palti, 1981). Therefore, dead plant residues are generally safer where infection by fungi such as *Pythium* spp. or *Phytophthora* spp. is expected. Manure applications increased the severity of *Fusarium* wilt and of *Rhizoctonia solani* in the USA (Shipton, 1977). Mulching in banana crops reduced populations of the nematode *R. similis*, but increased the populations of *Pratylenchus goodeyi*, as the latter prefers soils rich in organic matter (Kashaija *et al.,* 2001). A practice that is widespread in Uganda is the use, in banana plantations, of the leaves, the chopped corms and the pseudostems of banana as a mulch. This denies the banana weevil its major breeding sites in whole corms and pseudostems (Karamura and Gold, 2000).

Seasonal incorporation for several years of the quickly decomposing leaves of *T. diversifolia* and *S. sesban* did not reduce the parasitic nematode populations in maize, but greatly increased free-living nematodes (bacterivores and fungivores). By contrast, the slowly decomposing leaves (high in polyphenols) of *Calliandra calothyrsus* resulted in a much lower level of free-living nematodes, a level similar to that achieved through chemical fertilizer applications (Desaeger and Rao, 1999b).

One of the major limitations of the use of organic amendments and mulches is the large amount of organic material necessary, and consequently the high level of human labour required for its application. The use of organic residues for managing certain soilborne pathogens would be feasible in the humid and subhumid tropics where plant growth is rapid and luxurious but of questionable value in the semiarid tropics. The practice may have an advantage in the tropics over temperate regions, as the higher temperatures lead to faster decomposition, greater activity of saprophytes and build-up of potential biocontrol agents.

15.6 Conclusions

Many soilborne pathogens account for production losses in tropical agroecosystems. The impact such pests have on the small-scale farms of the tropics is not well recognized, because of a dearth of knowledge about the economic losses caused by them and because of the complexity of those systems practised by farmers in the tropics. One of the main reasons that small-scale farmers practise multiple cropping is to reduce or spread the risks they face, including the risks posed by soilborne pests. Management of soilborne pathogens in these systems requires an integrated approach, which will, in most cases, be based on cultural, physical and biological methods. Chemical means of controlling soilborne pests are expensive, non-remunerative and hazardous in most situations. Four basic approaches for soilborne pest management are suggested here: (1) preventing the introduction of new pests and diseases, which is a basic quarantine procedure; (2) preventing or avoiding the build-up of diseases to damaging levels, which is the major tactic underlying crop rotations; (3) reducing pathogen populations by increasing populations of agents antagonistic to the pathogens, for instance through use of organic amendments; (4) increasing biodiversity, as in, for example, the use of multiple cropping systems and multiple cultivars (see ‘Conclusions’ list below).

The success of non-chemical approaches in the management of soilborne pests and diseases in the tropics is often hampered by the absence of regional or site-specific information. While it is true that knowledge about soilborne pests and diseases in the tropics is growing, and is beginning to include subsistence crops such as maize, bean and cassava, it is also true to say that as more research is done more new problems are disclosed. One of the objectives of this chapter was to show that agricultural diversification, through agroforestry systems, does not by definition exclude soilborne disease problems. A lack of knowledge should not be mistaken for a lack of pests; the potential that newly introduced trees and shrubs have to aggravate such problems is probably equal to their potential to improve the soil pest situation. Many research issues, especially in relation to the tree component, have not been investigated and offer promising opportunities for disease management (see ‘Future research needs’, below).

Soilborne pests have a long history of institutional neglect in the IARCs, and corrective measures are required to increase stakeholders’ awareness of the existence and potential significance of soil pests (Sharma *et al*., 1997). With regard to farmers, few of the efforts that have been made to improve farming techniques have focused on the adoption of basic pest management technologies, in spite of the fact that many such practices do exist and could easily be applied. Improving the development and extension of pest management and control tools should, therefore, become a priority, not only in order to increase farmers’ awareness, but also to stimulate interest among all the other stakeholders.

Conclusions

1. The major principles for reducing the risk of soilborne pathogen problems are:
2. Applying sound sanitary practices;
3. Avoiding pathogen build-up by applying proper rotations (breaking the pathogen cycle);

4. Confronting pathogens - by employing biological agents such as antagonists, parasites and/or predators, by diversifying the cropping systems and by the addition of organic soil amendments.

Note that the use of multi-species fallow systems is a ‘hybrid’ tactic, using the potential of both rotation and diversification.

Future research needs

1. To determine the economic importance of, and identify major biosecurity concerns for, agroforestry systems in different ecoregions.
2. To understand the ecological relations and interactions that exist between pathogenic and beneficial microorganisms and different components of agroforestry systems.
3. To relate associated microbiological diversity to soil health in different ecosystems.

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