Agroforestry Systems **50**: 199–241, 2000.

Pests and diseases in agroforestry systems of the humid tropics

G. SCHROTH[1, *], U. KRAUSS[2], L. GASPAROTTO[3], J. A. DUARTE AGUILAR[3] and K. VOHLAND[4]

[1] *University of Hamburg, Institute of Applied Botany, c/o Embrapa Amazônia Ocidental, C.P. 319, 69011-970 Manaus-AM, Brazil;* [2] *CABI Bioscience, c/o Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Unidad de Fitoproteccion, 7170 Turrialba, Costa Rica;* [3] *Embrapa Amazônia Ocidental, C.P. 319, 69011-970 Manaus-AM, Brazil;* [4] *Humboldt University, Institute of Systematic Zoology, 10099 Berlin, Germany (*Author for correspondence, E-mail: schroth@internext.com.br)*

Key words: cover crop, diversity, host range, microclimate, plant nutrition, shade, windbreak

Abstract. Few studies have included detailed investigations of the interactions of agroforestry techniques with pests and diseases, although the relevance of such interactions has long been recognized. The objectives of this review are to provide basic information on pests and diseases in tropical agroforestry systems and to develop concepts which can assist in the future in the systematic data collection and analysis in this field. The emphasis is on simultaneous agroforestry systems with annual and perennial crops, although rotational systems are also discussed. Crop rotation is an important pest and disease control strategy in annual cropping systems, and the principle of altering host with non-host plants can also be applied in improved fallow systems, provided that hosts of crop pests and diseases are avoided when selecting the fallow species. When annual cropping systems are transformed into simultaneous agroforestry, the control strategy of frequent disturbance of pest and disease populations is to some extent substituted for the strategy of increased stability and internal control mechanisms. However, reduced pest and disease risk is not automatically achieved by introducing perennial plants and increasing the plant diversity in a system. If plant species are introduced that harbor pests or diseases of other species in the system, the risk of pest and disease outbreaks may actually increase. For evaluating such risks, it is important to consider host-ranges of diseases on the pathovar instead of the species level. Beside the selection of compatible plant species, their spatial arrangement may be important for reducing the spread of pest and disease organisms through the system, although little information is available on such effects, and they may be largely irrelevant for organisms with efficient dispersal mechanisms such as wind-dispersed fungi. In addition to the species-specific, ‘biological’ effects of plants on pests and diseases, their unspecific, ‘physical’ effects can be of major relevance for pest and disease development as well as the susceptibility of the affected plant species. Increased pest and disease incidence has often been observed directly at the tree-crop interface, caused by the humid microclimate, physical protection of mammal and bird pests by the trees and eventually reduced pest and disease tolerance of competition-stressed crops. Linear tree plantings and hedgerows affect the wind transport of small insects and disease propagules, the active immigration and emigration of pest organisms as well as the populations of natural enemies. Similarly, overhead shade has a major effect on the micro-climatic conditions under which pest and disease organisms, their natural enemies and the crops themselves develop, and its optimization is a highly efficient control strategy for many pests and diseases. On infertile soils, the susceptibility of crops to pests and diseases is strongly affected by the availability of plant nutrients, which may be influenced by agroforestry techniques in various ways. Soil management measures such as mulching and planting cover crops may affect crop health by improving soil fertility and by directly acting on pest and disease populations. The importance of a more systematic collection of pest and disease related information for agroforestry, e.g., in a central database, and of the development of strategies for reducing pest and disease risks in agroforestry in cooperation with farmers is stressed.

Introduction

Although the relevance of pest and disease interactions with agroforestry measures has been recognized many years ago (Epila, 1986; Huxley and Greenland, 1989), few agroforestry studies have included detailed investigations on such interactions. A major review of the state-of-the-art of agroforestry science concluded only recently that 'next to nothing is known' in this area despite its potential importance for the sustainability of agroforestry systems (Sanchez, 1995). This situation is somewhat surprising, because on one hand, the replacement of monoculture crops by more diverse agroforestry systems is often seen as a strategy to reduce the risk of pest and disease outbreaks; and on the other hand, it has long been known that the effects of certain tree species on pest and disease incidence impose restrictions for their employment in associations with sensitive crop species. More recently, the devastations caused by the leucaena psyllid (*Heteropsylla cubana*) in agroforestry systems with *Leucaena leucocephala* have drawn the attention to the risks to which the tree component itself, and thus the investments into tree planting, may be exposed not only in plantation forestry (Evans, 1992), but also in agroforestry systems (Boa, 1998).

The present review was written with the objectives of providing basic information on pests and diseases in agroforestry and of developing some concepts which could assist in the future in a more systematic data collection in this field. It is obvious that in view of the vast number of tree and crop species of actual or potential interest for agroforestry with their numerous pests and diseases, completeness in the treatment of the subject could not have been our objective. We discuss characteristics of agroforestry systems which may affect the occurrence and development of pests and diseases and which may be manipulated through systems design and management, with the aim of a general improvement of crop health and a reduction of the pest and disease-related risks which are inherent in any agricultural activity. We also propose research directions which may lead to an improved understanding of the effects of certain characteristics of agroforestry systems on diseases and pests and to a refinement of management measures for their control.

In this review, 'pests and diseases' comprise all micro- and macrobiotic agents which damage crops and trees with the exception of weeds. 'Pests' refers to animals (arthropods, vertebrates, nematodes etc.), and 'diseases' or 'pathogens' refers to microorganisms, including fungi, bacteria, viruses etc. Agroforestry systems comprise both rotational (i.e., improved fallows) and simultaneous systems (Nair and Muschler, 1993), but we make a clear emphasis on permanent associations of trees and crops. We present information from agroforestry systems with annual and with perennial crops. Data from monoculture plantations of tree crops were included where the information seemed to be directly relevant for agroforestry associations (e.g., effects of cover crops or of shade on pest and disease relations). Due to the background of the authors, the emphasis is on the humid tropics, but the principles are valid for agroforestry system also in other regions and climates.

The following discussion of the interactions of agroforestry measures with pests and diseases has been subdivided into apparently separate areas such as microclimatic effects, nutritional effects or effects of increased diversity. It will become clear, however, that these factors do not act in isolation from each other and that it is often not easy to say which is the most important one in a given field situation. Epila (1986), Dix et al. (1995) (for the temperate zone), Mchowa and Ngugi (1994), Singh Rathore (1995) and Rao et al. (2000) have summarized much of the available information on insect pests in agroforestry. Mchowa and Ngugi (1994) and Singh Rathore (1995) provide lists of pest species associated with some widely used agroforestry trees. Reviews which provide an integrated view on both pests and diseases in agroforestry systems have so far not been available.

Crop rotations vs. simultaneous agroforestry: trading pest and disease control options for increased stability?

Before chemical pest and disease control became available, one of the phytosanitary cornerstones of agriculture with annual crops was crop rotation, and even nowadays it is an important way of controlling populations of nematodes, parasitic soil fungi and other pests and diseases in agricultural systems (Bullock, 1992). Perennial cropping systems, such as orchards, do not offer the possibility of annual crop rotation, but instead they are characterized by a greater stability in time of the system which allows the development of a certain equilibrium between pests/diseases and their natural enemies (e.g., predators, parasitoids). This equilibrium is an important component of biological and integrated pest control (Heitefuss, 1987). Fallows contribute to the control of pest and disease populations in a field if the fallow species are non-hosts, less suitable hosts than the main crops or if they inhibit the pests or disease agents in some way. For example, velvetbean (*Stizolobium deeringianum*), sesame (*Sesamum indicum*), castorbean (*Ricinus communis*), partridge pea (*Cassia fasciculata*), marigold (*Tagetes* spp.) and *Crotalaria* spp. possess properties antagonistic to nematodes and may be used to reduce nematode populations in the soil (Rodríguez-Kábana, 1992). On the other hand, certain tree species are hosts of nematodes which also attack crop species, and these species need to be excluded from rotations with sensitive crops. For example, *Sesbania sesban* is susceptible to the root-knot nematodes *Meloidogyne incognita* and *M. javanica* which makes this tree unsuitable for rotations with crops sensitive to these nematodes (see Table 2 below) and renders the establishment of the tree itself difficult both in nurseries and in the field (Mchowa and Ngugi, 1994; Desaeger and Rao, 1999). Several other woody species which are commonly used in agroforestry are also hosts for plant nematodes (*Meloidogyne* spp., *Pratylenchus* spp.), including pigeonpea (*Cajanus cajan*), *Leucaena leucocephala*, *Sesbania grandiflora*, *Tephrosia vogelii* and several *Acacia* species (Page and Bridge, 1993; Duponnois et al., 1999), and more research on the phytopathological implications of their use in fallow rotations (and associations with crops) is necessary. If host species of crop pests as well as excessive reliance on single tree species are avoided, improved fallows can certainly contribute to the control of pest and disease populations in crop rotations.

In simultaneous systems, the situation is more complicated. When trees are introduced into annual cropping systems, thereby transforming agriculture into agroforestry, the system is moved a step away from the pest and disease control principle of frequent disturbance (by crop rotation, tillage and sometimes burning) towards greater stability (due to the presence of the trees). This is both a risk and an opportunity. The possibilities of active pest and disease control by the farmer may decrease, but the internal control mechanisms of the system may increase. Crop rotation can also be practiced in a field bordered by woody shelterbelts or in a system with scattered trees, but the part of the field occupied by the trees will have to be excluded. Under the trees, perennial weeds get established which are absent from the annually tilled, and often burned, soil under the crops (Schroth and Zech, 1995). If either the trees or the new weed species are alternate hosts for crop pests or diseases, the efficiency of crop rotation on the remaining area of the system may be reduced. In exchange, the diversity of the system may increase, and a variety of permanent niches is created which may harbor predators and parasitoids of crop pests and diseases, but also new pest and disease organisms. Moreover, the microclimate of the system is changed, and this may affect the pest and disease agents, their natural enemies and also the susceptibility of the crops to pest and disease damage. The trees may affect nutrient cycling and soil organic matter content, and this may again affect the susceptibility of the crops and the survival of fungal propagules in the soil. Although the introduction of shade trees into a tree crop monoculture seems less drastic a change than tree planting in annual crop fields, the implications for pest and disease organisms can be severe, as will be seen below. The introduction of trees into a cropping system always entrains a number of interdependent changes, and the considerations which have to be given to species selection, arrangement and management are accordingly complex if the net result of the exchange of farmers' control options against internal control mechanisms is to be an overall reduced pest and disease risk.

Good diversity and bad diversity – effects of increasing numbers of plant species on pests and diseases

The effects of the diversity of plant species present in a field especially on crop pests has received considerable attention by intercropping specialists (Risch et al., 1983; Altieri, 1991; Vandermeer and Perfecto, 1998). Comparisons of species-rich and species-poor agroecosystems have often demonstrated lower populations of specialist herbivores in polyculture systems which contained both host and non-host plants than in monocultures of host plants. This characteristic of polycultures has been explained with the lower resource concentration for the pest and an increased abundance of predators and parasitoids due to the higher availability of alternate food sources and suitable microhabitats (Altieri, 1991; Power and Flecker, 1996; Stamps and Linit, 1998). In most cases, the mortality of herbivores from predation or parasitism is higher in diverse than in simple agroecosystems (Russell, 1989), contrary to the observation that high diversity may also render the search for prey more difficult for specialist predators (Sheehan, 1986). Similarly, fungal disease infection is often lower when the host plant density is lower (Burdon and Chilvers, 1982), which is usually the case in more diverse systems. It could thus be expected that a high plant diversity protects agroforestry systems to some extent from pest and disease outbreaks.

How diverse are agroforestry systems?

However, agroforestry systems differ widely in their plant diversity. As far as trees and crops are concerned, they are more diverse than monoculture crops. This is not necessarily the case if weed species are also considered, because weed control can be an objective of agroforestry measures, such as mulching or rotation with improved fallows for weed suppression (Rao et al., 1998). Weeds can either increase or reduce the populations of specialist herbivores in crop fields, depending on whether they are hosts or non-hosts of the pests (Schellhorn and Sork, 1997). If spontaneous vegetation is not considered (or effectively suppressed), some agroforestry systems have a rather low plant diversity: alley cropping or similar arrangements of woody erosion barriers on slopes may consist of only one tree species plus one or two crop species at a time, and shaded coffee (*Coffea* sp.) plantations may consist of one tree crop species and one shade tree species (e.g., *Erythrina* sp. or *Inga* sp.) (Beer et al., 1998). In plantations of cocoa (*Theobroma cacao*) or cupuaçu (*Theobroma grandiflorum*), the self-incompatibility of the crop plants with respect to pollination obliges to associate several clones within the same field, and this may sometimes increase the diversity of the system from a phytopathological point of view if the clones differ in their susceptibility to certain pests and diseases (see below). Traditional cocoa plantations in West Africa (de Rouw, 1987) and Brazil (Johns, 1999) often have a highly diverse shade tree stratum because the trees are retained from the original forest instead of being specifically planted. At the upper end of the diversity range of tropical agroforestry systems are the homegardens and ‘agroforests’ (Michon and de Foresta, 1999) which may contain several hundred plant species per hectare (Power and Flecker, 1996). The plant diversity of agroforestry systems thus ranges from rather low to very high, and rules on the effect of diversity on pests and diseases, if they exist, are unlikely to apply in the same way to all types of agroforestry.

Two further caveats have to be made to discourage unjustified expectations with respect to diversity as a pest and disease insurance strategy in agroforestry. The first is that pest and disease problems clearly also occur in highly diverse systems. For example, Ewel et al. (1982) did not find a significant difference in percent leaf area loss to herbivores between humid-tropical agroecosystems of widely differing diversity, including a homegarden system as well as annual and perennial monocultures. In the highly diverse rubber (*Hevea* sp.) agroforests of Indonesia, pigs and monkeys which inhabit this forest-like vegetation are a considerable threat to the regeneration of the rubber trees (van Noordwijk, 1999). Pest and disease outbreaks have also been reported from tropical rainforest (Augspurger, 1984; Newman, 1993) and sclerophyll *Eucalyptus* forest (Newman, 1991), indicating that such problems occur even in highly diverse natural vegetation.

The second caveat is that the use of high plant diversity as a strategy to reduce pest and disease risks in agroforestry systems not only meets considerable technical but also economic difficulties. Whereas a farmer is free to cultivate his or her crops either on separate fields or in association, the choice of the crops themselves (and thus the overall crop diversity of the farm) is strongly influenced by the availability of markets for the respective products and the needs of the household. The selection of timber and fruit trees also has to respect local market conditions, although more freedom of choice may exist for ‘service’ trees, e.g., trees grown for shade or wind protection.

Diversity as risk-avoidance strategy

The simplest way of employing diversity as a strategy to reduce pest and disease risks in agroforestry is by planting several species so that some survive and produce when others are damaged by pest and disease outbreaks. The devastations of *Leucaena leucocephala* plantings by the leucaena psyllid *Heteropsylla cubana* have drawn the attention to the pest and disease risks to which agroforestry trees are often exposed (Mchowa and Ngugi, 1994; Day and Murphy, 1998). The problem was particularly severe in this case because of the narrow genetic base of the *Leucaena* introductions (Rao et al., 2000). However, pest problems have also been reported for several other agroforestry trees (Rao et al., 2000). In Brazil, the shoot borer *Terastia meticolosalis* has become a limiting factor in the use of *Erythrina* spp. as cocoa shade (Duarte Aguilar et al., 1986). Serious damage was also caused by *Aphis craccivora* on *Gliricidia sepium* shade trees in Mexican cocoa plantations (Soto and

Madrigal, 1998). Diversification of the tree component of agroforestry systems by broadening the genetic base of the species and mixing different species can be used to reduce pest and disease risks.

These risks may be particularly high when trees are planted outside their native home range. According to Mitchell (1989), many tree species originating from Australia or the Neotropics experience elevated mortality when planted in Africa due to attack by fungus-growing termites, which are absent from the home range of these trees. In an experiment in Zimbabwe, termites caused mortality rates at 18 months of 66% for *Eucalyptus camaldulensis* and 51% for *Leucaena leucocephala*. In contrast, other exotic species such as the Australian *Acacia holosericea* and the central American *Enterolobium cyclocarpum* proved to be resistant to termite attack in this trial. The transferability of such results to other sites is problematic, as Mitchell (1989) mentioned much contradiction in reported susceptibility of the same tree species at different sites, possibly due to differences in site conditions and termite species present. However, not only exotic tree species undergo severe pest and disease risks. For example, the timber species of the Meliacea family (e.g., *Swietenia* spp., *Khaya* spp.) are notorious for their pest problem, the *Hypsipyla* shoot borers, within their native growth areas (Lamprecht, 1986). In this case, planting the trees outside their home range can help to reduce the risk, as illustrated by the successful planting of the Latin American *Cedrela odorata* in West Africa since 1922 (Centre Téchnique Forestier Tropical, 1989).

According to the mechanisms mentioned at the beginning of this section, a reduced development of pest and disease organisms in agroforestry systems compared with simpler agricultural systems would be expected if either the crop or tree species which are sensitive to certain pests or pathogens are effectively diluted by non-host species which form barriers to their propagation within the agroforestry system, or if pests and disease vectors are more effectively controlled by their natural enemies due to the greater complexity of the agroforestry compared with a purely agricultural system. For employing these diversity effects strategically in agroforestry design, more is required than simply adding more plant species to a species-poor system.

Firstly, the *choice of species* is critical. Together with a new plant species, ‘associated biodiversity’ is introduced into a system, consisting of the insects, microbes, birds and other organisms living on and in this plant (Vandermeer and Perfecto, 1998). If this ‘associated biodiversity’ includes pests of plant species already present, the risk of pest damage in the system may increase, despite the increased diversity. Plant species that are unsuitable hosts for pests already present in the system or that harbor parasitoids, on the other hand, may have a favorable effect. In western Amazonia, several insect pests of maize (*Zea mays*) and cowpea (*Vigna unguiculata*) occurred at higher densities when these crops were grown in association with tree crops than when grown alone. The pests were mainly associated with the two palm species in the system, peach palm (*Bactris gasipaes*) and açai (*Euterpe oleracea*), which apparently provided a favorable landing base and shelter for the insects (Fazolin and Estrela, 1999). On the other hand, planting coconut palms (*Cocos nucifera*) instead of the common shade tree *Gliricidia sepium* in Malaysian cocoa plantations increased the populations of ants by providing nesting sites and honeydew. The ants protected the cocoa from the important mirid pest, *Helopeltis theobromae* (Way and Khoo, 1991). As these examples demonstrate, the characteristics of a specific plant species can easily override the diversity effect. The importance of distinguishing between specific effects of certain (plant) species and the general effect of altered species diversity when studying diversity effects on ecosystem processes has recently been stressed by Huston (1997). In the practice of agroforestry, however, this distinction will often be difficult or impossible to make, as will be seen further below.

Furthermore, it is certainly relevant *how* the new species are added to the system. For example, how far apart should host species of the same pest or disease be planted, and with which other species should the interspaces be filled to form efficient barriers for the dispersal of pathogens? How should the plants be arranged to maximize the effect of natural enemies on pest and disease organisms in the system? Answering these questions requires a detailed understanding of the mechanisms through which species associations and their spatial arrangement influence the demography, movements and activity of pest and disease organisms as well as their natural enemies in the field. Unfortunately, these aspects have rarely been studied in an agroforestry context. Munro (cit. in Newman, 1993) found that the biological control of prickly pear (*Opuntia inermis*) with the moth *Cactoblastis cactorum* in eastern Australia led to mean distances between surviving *Opuntia* plants of 5 to 20 m, a distance range which was apparently effective in limiting the spread of the pest from one plant individual to the neighboring one. For diseases, the host plant density would especially influence the progress of the infection in a field when the mechanism of dispersal is only effective over short distances, as is the case for autonomous or nematode-dispersal (Burdon and Chilvers, 1982). Conidia of the fungal disease agent in coffee, *Colletotrichum gloeosporioides*, have been rain-dispersed as far as eight meters from infected coffee trees (Waller, 1972). Planting the coffee bushes further apart than this may reduce the spread of the disease through the plantation if the conidia fall on the soil or on non-host plants and die before they are further transported. *Phytophthora* species spread from one host to the next by rain splash, flowing water along soil pores and root channels etc., and their dispersal would thus also be expected to be slower in mixed plantations of host and non-host species than in host monocultures. Distances in the range of several meters between individuals (or small groups) of the same species are obviously unrealistic in monoculture plantations, but may not be so in agroforestry systems composed of several annual and perennial crop species interspersed with trees.

For wind-dispersed diseases, on the other hand, the host-plant density within a plantation may be of little importance because the propagules spread readily through the whole system. Associating cocoa clones differing in their susceptibility to the wind-dispersed fungus *Crinipellis perniciosa* (witches' broom disease) did not reduce the incidence of this disease (Evans, 1998), and associating rubber clones susceptible to different isolates of the wind-dispersed leaf blight fungus (*Microcyclus ulei*) in the same field was equally inefficient in controlling its spread (Junqueira et al., 1989). More research on the effect of spacing and planting patterns on pest and disease incidence in agroforestry systems and their applicability for different pests and pathogens is clearly warranted. It should also be recalled that even in cases where the presence of a non-host crop or tree species (or clone) in a system does not protect an associated crop or tree species from a given pest or disease, it may still reduce the risk for the system as a whole by spreading it over several different species.

Of host ranges and pathovars – the importance of combining the right species

As noted before, the effect of adding a new species to an agroforestry association on the pest and disease situation depends often more on the characteristics of the species than on the increase in species diversity. If the wrong species are chosen for an association, agroforestry systems are likely to experience equal or even higher pest and disease incidence than simpler agricultural systems. Of central importance for the employment of plant diversity for reducing pest and disease risks is that the associated species are not hosts and do not harbor the same pest and disease organisms. How to choose such species is the topic of the present section.

Pests and diseases shared by related plant species

There is a tendency for plants belonging to the same or closely related taxonomic groups to share insect pests and certain diseases (Table 1). This may result in the year-round maintenance of the pest populations, but also the populations of their natural enemies, in a system composed of annual crop species and taxonomically related trees. For example, bruchids, the pantropical seed pests of grain legumes, in general also feed on the seeds of tree legumes which are commonly used in agroforestry associations (Hill, 1997). In Kenya, the legume tree *Acacia mearnsii* shared several insect pests with the food legumes *Phaseolus vulgaris*, *Pisum sativum* and *Cajanus cajan*, but not with *Vigna unguiculata* (Epila, 1986). Ferreira et al. (1998) give many examples of insect pests that are shared by coconut palms and other palm species in Brazil, including both cultivated (oil palm – *Elaeis guineensis*, açai – *Euterpe edulis*) and spontaneous species. The obligate parasitic nematode *Bursaphelenchus cocophilus*, causing red ring disease, attacks 17 palm species, including coconut and oil palm (Ploetz et al., 1994). The nematode is transmitted by the major, pantropical insect pest, *Rhynchophorus palmarum* (Hill, 1997),

Table 1. Some important pests and diseases that mainly affect one group of taxonomically related crop and tree species.

Pest or disease	Principal group of affected plant species	Affected plant species from other families
Insects		
Bruchids[a]	Many herbaceous and woody legumes	
Rhynchophorus palmarum[b]	Many cultivated and wild palm species	Papaya (*Carica papaya*), Sugarcane (*Saccharum* sp.)
Erinnys ello[c]	Manioc (*Manihot esculenta*) and rubber trees (*Hevea* spp.)	Papaya
Sahlbergella and other mirids[d]	Cocoa (*Theobroma cacao*), cola (*Cola* spp.) and other Sterculiaceae	Bombacaceae
Conopomorpha cramerella[d]	Cocoa, *Cola nitida*	Rambutan (*Nephelium lappaceum*)
Hypsipyla spp.[e]	Meliaceae (many timber trees)	*Casuarina equisetifolia*
Viruses		
Cocoa swollen shoot virus (vector: many insects)[f]	Cocoa, *Cola chlamydantha* and, to a lesser extent, other Sterculiaceae	(Bombacaceae)
Fungi		
Moniliophthora roreri (moniliasis=frosty pod)[g]	Cocoa and other *Theobroma* species, *Herrania* spp.	
Crinipellis perniciosa (witches’ broom)[g]	Cocoa and other *Theobroma* species	Annatto (*Bixa orellana*)
Nematodes		
Bursaphelenchus cocophilus[h]	Red ring disease of coconut palm (*Cocos nucifera*), oil palm (*Elaeis guineensis*) and other palm species	
Phytoplasma		
Lethal yellowing[h]	Coconut palm, oil palm and other palm species	*Pandanus utilis*

[a] (Epila, 1986); [b] (Hogue, 1993; Ferreira et al., 1998); [c] (Martins and Marin, 1998); [d] (Mossu, 1990); [e] (Lamprecht, 1986); [f] (Lass, 1985); [g] (Evans, 1978; Evans, 1998); [h] (Ploetz et al., 1994).

which is strongly attracted to cut leaves and harvest residues of oil palm, coconut palm or peach palm. Although the insect causes little damage in peach palm, the large quantities of residues from the palmito harvest attract the insect, which may then affect other palms nearby. Also, coconuts share the phytoplasma that provokes lethal yellowing with 32 other palm species (Ploetz et al., 1994). It seems likely that the disease vector, the insect *Myndus crudus* (Homoptera), transmits the pathogen between different palm species when these are grown in association.

The genera *Cola* and *Theobroma* belong both to the Sterculiaceae. *Cola* species as well as other Sterculiaceae (and also Bombacaceae) are hosts of cocoa mirids (e.g., *Sahlbergella*) and should not be used as shade for this crop (Mossu, 1990). Numerous Sterculiaceae are also hosts for the cocoa swollen shoot virus, including the West African forest trees *Cola chlamydantha*, *Cola gigantea* and *Sterculia tragacantha* (as well as the Bombacaceae *Bombax buonopozense* and *Ceiba pentandra*), which is another reason why these trees are commonly removed from the shade layer of cocoa plantations. However, under field conditions, only *Cola chlamydantha* transmits the virus easily to cocoa (Lass, 1985), the other species present a much lower risk. In SE Asia and the Pacific, the attack of cocoa by the pod borer (*Conopomorpha cramerella*) is favored by the proximity of its alternate host, *Cola nitida* (as well as by rambutan – *Nephelium lappaceum*, Sapindaceae) (Mossu, 1990). Between different species of the genus *Theobroma*, such as cocoa and cupuaçu, cross-infection of the fungi *Moniliophthora roreri* (causing moniliasis=frosty pod) and *Crinipellis perniciosa* occurs readily (Evans, 1978; Evans, 1998), although *Crinipellis* isolates from cocoa which were not pathogenic to cupuaçu have also been described (Bastos, 1990). Both pathogens are important in parts of the American tropics. In eastern Brazil, monocropped cassava (*Manihot esculenta*) is commonly attacked by the caterpillar *Erinnys ello*. Planting rubber trees, which belong to the same family as cassava (Euphorbiaceae), in association with this crop increased the need for chemical control of the caterpillar on the rubber to once every year compared to once every four to five years when the rubber was grown alone (L. Gasparotto, pers. observation). Based on such evidence, Singh Rathore (1995) recommended the association of species in agroforestry systems that are taxonomically far apart.

Pests and diseases shared by unrelated plant species

There are however many examples of pest species shared by taxonomically unrelated plant species, especially when the various development stages of insects with their often differing feeding habits are considered (Singh Rathore, 1995) (Table 2). Smith (1981) reviewed the relationships between cocoa shade types used in Papua New Guinea and important cocoa pests and diseases, listing numerous pest and disease species shared by cocoa and (unrelated) legume trees such as *Leucaena leucocephala*, *Flemingia candida* and *Albizia* spp. For example, *Flemingia candida* and *Eucalyptus deglupta* are hosts of the important cocoa mirid, *Helopeltis clavifer*. Smith (1981) concluded that the frequent use as a shade tree of *Leucaena leucocephala* should be discouraged and instead the traditional association of cocoa with coconut palms be promoted which caused less pest and disease problems. Similarly, the use

Table 2. Some important pests and diseases that are shared by taxonomically unrelated crop and tree species (see also last column of Table 1).

Pest or disease	Affected crop species	Affected timber and service tree species
Insects and mites		
Helopeltis clavifer[a]	Cocoa (*Theobroma cacao*)	*Flemingia candida*, *Eucalyptus deglupta*
Planococcus citri[b]	Coffee (*Coffea arabica*), cocoa, *Citrus*	*Leucaena leucocephala*, *Erythrina*, *Tephrosia*
Myrmelachista ambigua[c]	Coffee	*Inga* spp.
Apate monachus[d]	Coffee	*Khaya ivorensis*
Cratosomus flavofasciatus[e]	*Citrus*	*Cordia verbenacea*[1]
Scirtothrips awemdii[f]	Orange (*Citrus sinensis*)	*Grevillea robusta*
Viruses		
Cucumber mosaic virus (vectors: mostly aphids)[g]	> 200 crop species from 40 families	Many legumes, e.g. *Robinia pseudoacacia*, *Sesbania exaltata*
Peanut bud necrosis virus (vectors: thrips)[h]	> 370 plant species from > 50 families	Many legumes
Fungi		
Phythophthora cinnamomi[g]	> 1000 species and varieties of plants, e.g. avocado (*Persea americana*), pineapple (*Ananas comosus*), peach (*Prunus persica*), macadamia (*Macadamia* spp.)	*Eucalyptus* spp., *Pinus* spp.
Pellicularia koleroga[i]	Many species, e.g. coffee, mango (*Mangifera indica*), orange (*Citrus sinensis*), rubber (*Hevea* sp.), carambola (*Averrhoa carambola*), rambutan (*Nephelium lappaceum*)	*Acacia mangium*
Sclerotium coffeicola[j]	Many species, e.g. coffee, soursop (*Annona muricata*), mango, carambola	*Ceiba pentandra*, *Khaya ivorensis*
Colletotrichum gloeosporioides[k]	Cassava (*Manihot esculenta*), melon (*Cucumis melo*)	*Gliricidia sepium*
Mycena citricolor (South American leafspot or cock's eye disease of coffee)[l]	> 150 species, e.g. coffee, *Annona reticulata*, citrus, mango, avocado, cocoa	Several native and introduced forest trees, e.g. *Inga* spp., *Ocotea* sp.
Many soil borne fungi, e.g. *Armillaria*, *Fomes*, *Ganoderma*, *Rosellinia*, *Verticillium*[m]	Many cultivated and wild tree species	Many cultivated and wild tree species

Table 2. (Continued).

Pest or disease	Affected crop species	Affected timber and service tree species
Nematodes		
Meloidogyne incognita, *M. javanica*[n]	Tobacco (*Nicotiana* spp.), bean (*Phaseolus vulgaris*), tomato (*Lycopersicon esculentum*), eggplant (*Solanum melongena*)	*Sesbania* spp., *Acacia* spp.
Radopholus similis[2, o]	Approx. 100 species, e.g. banana (*Musa* sp.), maize (*Zea mays*), sorghum (*Sorghum bicolor*), cowpea (*Vigna unguiculata*), pigeonpea (*Cajanus cajan*), groundnut (*Arachis hypogaea*)	*Cupressus* spp., *Podocarpus macrophyllus*, *Sesbania* spp., bamboos (*Bambusa* sp., *Gigantochloa apus*)

[1] Use as trap crop; [2] Some evidence for host-specific races, see text.
[a] (Smith, 1981); [b] (Le Pelley, 1973; Smith, 1981; Hogue, 1993); [c] (Le Pelley, 1973); [d] (Lamprecht, 1986); [e] (Nascimento et al., 1986); [f] (Grout and Richards, 1990); [g] (Ploetz et al., 1994; Brunt et al., 1997); [h] (Kokalis-Burelle et al., 1997); [i] (Gasparotto and Silva, 1999); [j] (Gasparotto and Veras, 1999); [k] (Amusa and Alabi, 1996); [l] (Sequeira, 1958; Lass, 1985); [m] (Lass, 1985; Ploetz et al., 1994; Muraleedharan and Chen, 1997); [n] (Mchowa and Ngugi, 1994; Duponnois et al., 1999); [o] (Price, 1994; Marín, 1997)

as coffee shade of *L. leucocephala* in Java and of *Inga laurina* and *Inga vera* in Puerto Rico were discouraged because these species were alternative hosts of coffee pests, in the former case of the mealybug *Planococcus citri* (which also attacks citrus and cocoa and is hosted by several other legume trees; Hogue, 1993; Smith, 1981), and in the latter case of the mite *Myrmelachista ambigua* (Le Pelley, 1973). The borer *Apate monachus* attacks the West African timber tree *Khaya ivorensis* as well as coffee plantations (Lamprecht, 1986). When planted in proximity to rubber or cassava, *Erinnys ello* also feeds on the unrelated papaya (*Carica papaya*) (Martins and Marin, 1998) (Table 1). Examples of insect pests that affect a wide variety of taxonomically unrelated species of fruit trees and annual crops in Brazil can be found in Sobrinho et al. (1998).

Trap crops

The attractiveness of a plant species for the pests of another species can be usefully employed in agroforestry associations in the form of trap crops which concentrate the pests or disease vectors at a place where they cause less damage or can be easier neutralized (e.g., by spraying or collecting). Such trap crops are an interesting option when they attract pests from the primary crop within the field (local attraction), but not when they attract pests from areas outside the field (regional attraction) (Mchowa and Ngugi, 1994). Nascimento et al. (1986) demonstrated the strong attraction of the *Citrus* pest

Cratosomus flavofasciatus by the small tree *Cordia verbenacea* in Bahia, Brazil, and recommended the inclusion of this tree at distances of 100 to 150 m in *Citrus* orchards. They speculated that pests of several other fruit crops could similarly be trapped by this tree species.

Host ranges of pathogens

As for pests, a principle of the management of diseases in agroforestry should be to associate plant species that do not share the same diseases so that one species is not affected by pathogen populations that have built up on an associated species. Also, spreading of pathogens through the system could in some cases be reduced by the presence of non-host plants (see above). It is thus essential to know how specific pathogens are for certain crops and if cross-infection between different plant species actually occurs in the field.

Pathogens differ widely in their host specificity (Tables 1 to 3). Some viral diseases have particularly wide host ranges, e.g., the cosmopolitan cucumber mosaic virus (Ploetz et al., 1994) and the Asian peanut bud necrosis virus (Kokalis-Burelle et al., 1997) (Table 2). Their vectors are often similarly non host-specific, which means that these viruses can be readily transmitted from one plant species to another one within an association. Other economically important viruses seem to be restricted to a single host, e.g., the banana bunchy top virus that occurs in the old world and Oceania (Kokalis-Burelle et al., 1997) (Table 3), and bananas infected with this virus would thus not present a risk to associated species. A particular danger are diseases which infect host plants without producing clear symptoms (or with long latent periods), but which can be transmitted to associated species. This is often the case with viruses. The behavior of the insect vectors of viruses can sometimes be influenced by species associations. For example, the presence of maize or weeds has been found to reduce the incidence of rosette virus (a very host-specific, mainly African virus, Table 3) on groundnut (*Arachis hypogaea*), apparently through modified behavior of the aphids which transmit the virus (Allen, 1983). Similar effects could be expected in associations of groundnut with woody plants (Schroth et al., 1995a). Extensive, up-to-date information on virus diseases and their host plants can be obtained online (Brunt et al., 1997).

Among fungal diseases, *Phytophthora cinnamomi* has a particularly wide host range (Table 2). It probably originated on cinnamon (*Cinnamomum zeylanicum*) in Sumatra and, when introduced to > 70 countries, proved capable of attacking > 1000 varieties and species of plants (Ploetz et al., 1994). The wide-spread fungal pathogens *Pellicularia koleroga* and *Sclerotium coffeicola* attack numerous cultivated plant species (both native and introduced) in Amazonia, especially during the rainy season (Gasparotto and Silva, 1999; Gasparotto and Veras, 1999). Both pathogens affect several species in the same area, suggesting that cross-infection actually occurs in the field (L. Gasparotto, pers. observation). *Colletotrichum gloeosporioides* isolated from

Table 3. Pest and disease species with narrow host range that present little or no risk for associated species.

Pest or disease	Affected crop and tree species
Viruses	
Banana bunchy top virus (vector: *Pestalonia nirgonervosa*)[a]	Banana and plantain (*Musa* sp.), enset (*Ensete* sp.)
Groundnut rosette virus (vectors: *Aphis craccivora*, *Aphis* spp.)[a]	Groundnut (*Arachis hypogaea*), unknown wild host
Fungi	
Phythophthora capsici, *P. citrophthora*, *P. palmivora*[b]	Several species, e.g. cocoa (*Theobroma cacao*; black pod=pod rot), rubber (*Hevea* spp.), black pepper (*Piper nigrum*), coconut (*Cocos nucifera*), but limited cross-infection between species
Mildews, rust and smut fungi (with few exceptions), many leafspots[c]	Many plant species, affected by different species of fungi; some rusts require two unrelated host species to complete their reproduction cycle
Fusarium oxysporum[d]	Many species, but specific on race level
Bacteria	
Most bacterial wilts, caused by *Pseudomonas*, *Erwinia*, *Xanthomonas*[e]	Many species, but specific on pathovar level

[a] (Kokalis-Burelle et al., 1997; Jones, 1999); [b] (Resnik et al., 1980; Virgens Filho et al., 1987; Ortíz, 1996); [c] (Müller and Loeffler, 1992); [d] (Stover and Simmonds, 1983); [e] (Ploetz et al., 1994; Thurston, 1998).

leaves and pods of *Gliricidia sepium* in Nigeria caused necrotic lesions on leaves of several annual crop species, with cassava and melon (*Cucumis melo*) being the most susceptible (Amusa and Alabi, 1996). *Crinipellis perniciosa* causes witches' broom not only in *Theobroma* species, but also in annatto (*Bixa orellana*) trees when associated with infected cocoa (Bastos and Andebrhan, 1986).

The important fungal disease agent of coffee in Latin America, *Mycena citricolor* (=*Omphalia flavida*, South American leafspot or cocks' eye disease), affects at least 150 alternative hosts from 45 families (Sequeira, 1958) (Table 2). However, *M. citricolor* does not sporulate on most of these species and has not been reported to cause economic damage to any species other than coffee, indicating that the proximity of these plants does neither increase nor reduce the disease risk for coffee.

Many soil-borne, parasitic fungi from the genera *Armillaria*, *Fomes*, *Ganoderma*, *Rosellinia* and *Verticillium* can build up inoculum on one host plant and spread to another, associated host (Lass, 1985; Ploetz et al., 1994; Muraleedharan and Chen, 1997). For coffee, cocoa and tea (*Camellia sinensis*), the initial infection foci of such fungi in a field are often moribund shade trees or tree residues left after clearing. *Verticillium* wilt of avocado is more severe when avocado is intercropped with alternative hosts such as solanaceous vegetables, olive (*Olea europaea*), cotton (*Gossypium* sp.), some stone fruits and berries (Ploetz et al., 1994). On the other hand, mortality of *Acacia mangium* trees due to *Rosellinia* sp. was higher in pure stands than in mixed agroforestry systems with annual and perennial crops, possibly because of wider spacing and faster growth of the trees in the association (Kapp and Beer, 1995).

Other fungal pathogens are rather host-specific and would not readily be transmitted from one plant to another, including most mildews, smuts, rusts and many leafspots (Table 3). Some fungal and bacterial pathogens have a broad host-range on the species level, but are host-specific on lower taxonomic levels and are therefore subdivided into *pathovars* or *formae speciales*, which are specific for individual plant species, and further into races, which are specific for varieties of plants. For example, the notorious generalist *Fusarium oxysporum* is in fact highly host-specific on lower taxonomic levels: *F. oxysporum* f. sp. cubense only attacks the genera *Musa* and *Heliconia*, and it is further subdivided into races which are specific for certain banana varieties (Stover and Simmonds, 1983). The three *Phytophthora* species *P. capsici*, *P. citrophthora* and *P. palmivora* attack both rubber and cocoa (where they cause *Phytophthora* pod rot=black pod disease), but individual strains isolated from one host did not infect the other one (Virgens Filho et al., 1987). In another study, cross-inoculations of *P. palmivora* isolates from cocoa, rubber and black pepper (*Piper nigrum*) gave variable results, but in general the aggressiveness of the pathogen was highest on its original host (Resnik et al., 1980). *P. palmivora* from cocoa did not infect coconut, although some coconut isolates elicited symptoms on cocoa at a slower rate than cocoa isolates (Ortíz, 1996). As mentioned before, *Phytophthora* is dispersed by soil and water, including wind-blown rain, and the chance that its propagation in a plantation is reduced by an alternation of host and non-host species should be higher than for wind-dispersed disease agents, although direct evidence for this is apparently lacking.

Nematodes often attack several host plants, although even generalists may show preferences for certain hosts (Fogain and Gowen, 1995) (Table 2). The problems caused by the root-knot nematode *Meloidogyne* spp. in fallow rotations with *Sesbania sesban* in southern Africa have already been mentioned. Another nematode, *Radopholus similis*, attacks approximately 100 crop plants, although more specific races seem to exist (e.g. banana and citrus race; Marín, 1997) (Table 2). Some 50 plant species are known non-hosts and could be used as rotation and association partners for susceptible species. These include tomato, sweet potato (*Ipomoea batatas*) and bitter orange (*Citrus aurantium*) (Tarte et al., 1981; Price, 1994; Marín, 1997).

Regional differences

The effect of a plant species on the pests and diseases of another species may change from one place to another, causing regional differences in recommendations for species associations. *Erythrina* species, which are widely used in Latin America as cocoa shade, have been reported to be hosts for cocoa tree borers in central Africa (Poncin, 1957). Zakra et al. (1986) observed higher mortality due to rodents (*agoutis*) of young coconut palms in association with rice (*Oryza sativa*) than in associations with several other food crops in the Côte d'Ivoire. The rice also increased the incidence of two diseases in the coconut palms, blast and dry bud rot, which are transmitted by insects living on rice, *Sogatella cubana*, *Sogatella kolophon* and *Recilia mica*. The authors stressed that in areas unaffected by these problems, rice could be one of the major crops associated with young coconut palms.

In conclusion, it is apparent that considerable specialized knowledge is necessary to avoid associating species that share some of their pests and diseases. Especially insect pests as well as nematodes and viruses often affect numerous crop and trees species (Table 2), whereas many fungal and bacterial diseases are too specific in their host range to pose a threat to other plant species that are associated with their primary host (Table 3). The probability that associated plant species share pests and diseases is increased for closely related species (Table 1), although the selection of unrelated species for agroforestry associations is no guarantee at all against the existence of common pests and diseases.

Biological and physical effects of plants on pests and diseases

When studying the effect of a certain plant species on the incidence of pests and diseases in agroforestry systems, it is important to distinguish between effects that are related to the biological characteristics of a certain plant species and those that are related to its physical properties and that depend on the life form and size of a plant rather than its species. This distinction is important because the appropriate action to reduce negative effects may vary accordingly. A biological (specific) effect would be if a tree species increases the pest or disease incidence in an associated crop because it is an alternative or intermediate host of the pest or pathogen. In this case, the appropriate management decision would be to remove this species from the system and to replace it by another one which does not serve as a host. Several examples for this situation have been given above. A physical (unspecific) effect, on the other hand, would be if the tree species increases the pest or disease incidence by creating a suitable (e.g., moist, shaded) microclimate for the respective organism. In this case, it may not be necessary to change the tree species, but rather to reduce its shade by a partial crown pruning, or to thin it to obtain a wider spacing. Both biological and physical effects can also be favorable, e.g., when the species encourages parasitoids and predators of pests present in the system by providing them with nectar and pollen (biological), or when its shade is unfavorable for the development of a pest (physical). The previous sections on diversity were concerned with biological effects, and it is now apparent that the possibility of generalizations with respect to these effects is rather limited. In the following sections, mainly physical effects will be discussed, which can be more easily transferred from one situation to the other. It will however be seen that the physical and the biological attributes of a plant or group of plants (e.g., a shade tree layer, a windbreak etc.) can often not be clearly separated.

Pest and disease incidence at the tree-crop interface

Heterogeneous land use systems such as agroforestry are characterized by a mosaic of biotic and abiotic factors which is a product of the spatial arrangement of the different plant species and their respective effects on soil conditions, litter, microclimate etc. As a consequence, the incidence of pests and diseases within agroforestry systems may also exhibit spatial patterns within agroforestry plots, and such patterns need to be known to the farmer so that he or she can look for pests and diseases where these are most likely to appear. Pronounced small-scale patterns in pest and disease incidence can often be observed near the ‘tree-crop interface’, i.e., the boundary between areas planted with trees and crops.

Several experimenters who compared crop development and yield at different distances from the tree-crop interface with the aim of quantifying the effects of shoot and root competition observed that these target effects were confounded with differences in pest and disease incidence. Such interactions may already start when seeding the crop. It was often found more difficult to establish an annual crop near the tree-crop interface than at greater distance from the trees because of increased seed predation. Increased damage to maize seedlings by birds and rodents necessitating reseeding in the vicinity of *Leucaena leucocephala* and *Gliricidia sepium* hedgerows has been reported from an alley cropping experiment in southern Nigeria (Lal, 1989). In a similar experiment with *G. sepium* in the forest zone of the Côte d’Ivoire, rodents also fed preferentially on maize and groundnut seeds close to the hedgerows. Mice had their burrows under the trees where the soil was not tilled, and during daytime they could sometimes be observed hiding under the trees. At harvest, the number of plants in the first crop row from the trees was reduced by 25% for maize and by 20% for groundnut, and there were more resown plants which were likely to produce reduced yields (Schroth et al., 1995a; Schroth et al., 1995b). The increase in mouse populations with increasing numbers of hedgerows in the landscape has been confirmed by Fitzgibbon (1997) in the temperate zone. Similar problems with chicken hiding in boundary plantings of *Senna siamea* trees and *Leucaena leucocephala* hedgerows between agricultural fields and feeding on maize seeds have also been observed in the savanna of central Togo (Schroth et al., 1995c).

These localized pest problems are not restricted to the establishment phase of the crop. Birds and mice hiding in the foliage of the *Gliricidia sepium* hedgerows and feeding on the grains of maturing rice have been observed in the Côte d'Ivoire (Schroth et al., 1995b), and grain-eating birds hiding in hedgerows of *Inga edulis* and presumably feeding on the rice crop have also been reported from an experiment in the Peruvian Amazon (Fernandes et al., 1993). Such problems are difficult to prevent even when the fields are continuously guarded.

Positions close to trees which are most affected by their shade may differ markedly in microclimatic conditions from more open positions, and this may influence the development of crop diseases. Where shading or root competition lead to reduced crop development, the plants may also become more susceptible to certain diseases. Rust (*Puccinia arachidis*) and late leafspot (*Phaeoisariopsis personata*) affected groundnut much more in the crop rows which were most shaded by the trees than in other positions in the aforementioned alley cropping experiment in Côte d'Ivoire (Schroth et al., 1995a). In this position, potential evapotranspiration was strongly reduced by the shade of the hedgerows, and the groundnut leaves dried later in the morning than in less shaded areas. This localized microclimatic effect counteracted a general reduction of the incidence of the two foliar diseases in the agroforestry system which was apparently mediated by the *Gliricidia* mulch as it also occurred in mulched plots without hedgerows. Delayed drying of leaves under tree shade near the field border also increased leaf blight (*Helminthosporium maydis*) of maize (Lukens and Mullamy, 1972).

In another alley cropping experiment with *Sesbania sesban* in the Rwanda highlands, the trees seemed to reduce the incidence of maize rust (*Puccinia sorghii*) at the tree-crop interface as measured by the proportion of infected leaves, the number of uredinia per plant and the area under the diseased leaf progress curve (Yamoah and Burleigh, 1990). The disease incidence was lower in alleys of 2, 4, 6 and 8 m width than in an adjacent field without hedgerows. Despite the higher proportion of maize plants close to the interface in narrow alleys than in wide alleys, there was no significant effect of alley width on disease incidence.

Quantitatively, the area affected by such interface phenomena may be of little importance in boundary plantings or other systems with wide distances between the trees, but it may be considerable in alley cropping or other intensively mixed systems. Field plots of small-holders may often consist to a large extent of border areas. It is important that such border situations are recognized in agroforestry research. Measurement plots which are placed in the central part of an agroforestry experiment to avoid border effects may not always be adequate in phytopathological research.

According to the information presented above, especially with respect to rodent and bird pests, it seems advisable to promote agroforestry techniques in which the percentage of crop plants directly neighboring trees is relatively low, e.g., boundary plantings of trees around fields instead of alley cropping systems with narrow alleys. On steep slopes, however, this advice may be contradicted by the needs of soil conservation.

Effects of linear tree plantings and hedgerows on pests and diseases

Line plantings of trees around fields of annual or perennial crops are a common component of agroforestry systems. In dry and wind-exposed areas, windbreaks are often planted for microclimate improvement and soil conservation. Boundary plantings of trees around fields are also a convenient way of producing firewood and poles without reducing too much the area available for cropping. Living fences may be a low-cost option for fencing pastures, and ‘box plots’ surrounded by tree rows have been proposed as an alternative to overhead shade for cocoa (Alvim and Alvim, 1980; Lim, 1980). In the following, the term hedgerow will be used irrespective of the height, spacing and management (e.g., pruning etc.) of the trees. Microclimatic effects of hedgerows have been reviewed by Norton (1988) and Brenner (1996).

Effects of hedgerows on pests and their natural enemies

Hedgerows are both a source of pest species and of their natural enemies. In the Cape Province of South Africa, the attack of orange trees (*Citrus sinensis*) by thrips (*Scirtothrips aurantii*) was increased in the proximity of *Grevillea robusta* windbreaks, whereas orange trees close to windbreaks of *Pinus radiata* and *Casuarina cunninghamiana* had increased populations of the mite *Euseius addoensis* which preys on thrips. The contrasting effects of the tree species was explained with the high nectar production of *Grevillea* which allowed the thrips to build up high population densities (Grout and Richards, 1990). However, flower-bearing plants that produce nectar and pollen are usually also most efficient in maintaining populations of the natural enemies of crop pests (Epila, 1986; Russell, 1989). The distance over which hedgerows on field borders influence populations of natural enemies of herbivores depends on the mobility of the respective species. Parasitoids that spend much time flying may extend farther from hedgerows than predators that follow a ‘sit-and-wait’ strategy (Russell, 1989).

In addition to their role as a perennial habitat for insects, linear tree plantings affect the active and passive movements of insects through the landscape. Permeable windbreaks reduce the wind speed below 80% for about twice their height to the windward side and for about 15 to 20 times their height to the leeward side (Webster and Wilson, 1980). The flight directions and landings of many flying insects is strongly determined by wind. Such insects may accumulate in the calmer air on the leeward side of windbreaks, at a distance which increases with windspeed and permeability of the windbreak (Pasek, 1988), or on trees from which they move into the crop fields (Singh Rathore, 1995). In this way, vegetation barriers such as hedgerows can trap pest species which are transported more or less passively by the wind and which would have been blown over the field in the absence of the trees (Baldy and Stigter, 1993). However, the physical 'windbreak effect' of a hedgerow is not the only factor influencing insect distribution. Bowden and Dean (1977) stressed the importance of vegetation diversity for the patterns of insect accumulation around hedgerows. Dean and Luuring (1970) observed differences between aphid species concerning their distribution in cereal fields relative to tree rows. To determine where a windbreak should be placed to provide maximum protection to a crop field from wind-transported insect pests, the most critical groups and the way their distribution is affected by windbreaks would thus have to be known for a specific situation.

Woody borders may also form barriers to the movements of insects out of a plot. This effect arises from the repelling effect of a non-host vegetation to the movements of specialist herbivore insects. The barrier effect increases with the height of the non-host vegetation and can enhance the local build-up of pest populations (Bhar and Fahrig, 1998). These authors see a trade-off between the enhancement of pest populations on the field scale and the reduction of pest populations on the landscape scale by hedgerows. The latter effect may arise from the barrier effect of the hedgerows for crop pests which may reduce the colonization of newly planted fields. They suggest that the reduction of pest populations by such woody barriers around fields is most efficient when the landscape is composed of many small fields on which crops are grown on a short rotation between host and non-host crops.

Effects of hedgerows on diseases

The effect of hedgerows on diseases is equally contradictory as that on pests. According to Norton (1988), protection from wind can reduce the susceptibility of crops to diseases, e.g., that of cherry trees (*Prunus* spp.) to brown rot (*Monilinia* sp.). On cocoa in SE Asia, windbreaks are a control measure against vascular streak die-back caused by *Oncobasidium theobromae* as nocturnal winds favor the development of this fungus, especially on young, malnourished and insect-infested plants (Mossu, 1990). Many fungal species are wind-dispersed, gusty winds being particularly effective in spore dissemination. By reducing air turbulence, windbreaks (or shade) can reduce both the spread of disease propagules from already infected plantations and their entry into healthy plantations, protecting especially plants in the lower canopy (Aylor, 1990). Planting of windbreaks around *Citrus* orchards has been recommended as a measure to reduce the influx of propagules of *Xanthomonas axonopodis* (syn. *X. campestris*) pv. *citri*, causal agent of citrus canker, in the state of São Paulo, Brazil (Fundecitrus, 1998).

However, wind-dispersed disease propagules can be transported over very large distances, thereby reaching even isolated fields with susceptible crops.

Ascospores of *Mycosphaerella fijiensis*, causing black Sigatoka of banana, have been monitored over distances exceeding 50 km and no significant dilution of inoculum was observed in a 4 km radius from a single inoculum source (Calvo and Romero, 1998). Basidiospores of *Crinipellis perniciosa* can be transported over at least 50 to 70 km (Evans and Solórzano, 1982), and several rust fungi are believed to have crossed the Atlantic ocean with the trade winds, e.g., coffee rust from Angola to Bahía and sugarcane rust from Africa to the West Indies (Nagarajan and Singh, 1990; Hamelin et al., 1995). Also, the number of propagules produced on infected plants may be immense: cocoa pods infected with moniliasis may produce fungal spores during nine months when suspended in the canopy (Evans et al., 1977), and still one or two months when on the ground (Evans, 1981). The number of spores produced in the former case may amount to 7 billion from a single pod (Evans et al., 1977). In view of the wide transport distances and the enormous quantity of disease propagules released into the air, windbreaks could be expected to delay the onset of an infection on susceptible crops through their effects on air circulation (Venturieri, 1993), although they are unlikely to prevent it.

Once the inoculum has reached the plots protected by hedgerows, reduced air movement may lead to prolonged leaf and fruit wetness, and this may enhance the build-up of microbial inoculum and facilitate the infection process, e.g., of witches' broom in cocoa and cupuaçu (Venturieri, 1993). Insufficient aeration and high humidity in cocoa plantations increase *Phytophthora* pod rot (black pod), especially when the temperature is relatively low (Mossu, 1990). The higher humidity behind windbreaks can also increase scab (*Venturia* spp.) on apple (*Malus sylvestris*) and pear trees (*Pyrus* sp.), and brown rot or *Botrytis* rot of stone fruits. These problems especially arise when the windbreaks are too dense (Norton, 1988).

As the microclimatic effect of linear tree plantings depends on the height of the trees, it may be rather small in systems where the trees are frequently coppiced, such as hedgerow intercropping. Monteith et al. (1991) measured no consistent difference in vapor pressure deficit between alley cropped and sole cropped millet in India. However, they noted that a smaller crop plant than millet may experience a more humid microclimate within the alleys. As noted before, this was confirmed for groundnut which experienced increased foliar disease incidence in alley cropping than in (mulched) sole cropping in the Côte d'Ivoire, despite frequent coppicing of the hedgerows (Schroth et al., 1995a).

Effects of overhead shade by trees on pests and diseases

In agroforestry associations, a certain degree of shading of smaller plants by associated trees is an almost universal phenomenon. In shaded coffee, cocoa and tea plantations, the provision of shade can be the main function of the trees which may either be planted for this purpose (e.g., *Inga*, *Gliricidia*, *Erythrina*) or be retained from previous forest vegetation (de Rouw, 1987; Beer et al., 1998). In other cases, the shade trees may serve a production function in addition to their service role for the smaller, shade-demanding crops, e.g., in associations of cocoa with coconut palms (Mossu, 1990) or of coffee with timber trees (Beer et al., 1998). In many cases, however, partial and temporary shading may occur as an unavoidable consequence of the association of tree and crop species of differing size, even if the smaller plant species are not shade-demanding. This would be the case in most agroforestry associations with annual crops.

Shade influence on pests

Shade and the accompanying increase in humidity and reduction in temperature affect both the insect pests and their predators and disease organisms (Tables 4 and 5). Most aphids prefer shady conditions in warm climates (Singh Rathore, 1995), whereas the density of herbivorous beetles on beans was higher in monoculture than under maize shade (Risch, 1981). Many hymenopteran parasitoids exhibit greater host-searching capacity under unshaded conditions, so that their efficiency as natural biocontrol agents should increase. On the other hand, entomopathogenic fungi may be more efficient as biocontrol agents under conditions of shade and increased humidity (Singh Rathore, 1995).

The effect of shade on pests and diseases in agroforestry has been studied quite intensively in systems with cocoa and coffee as part of attempts to cultivate these traditionally shaded crop species under unshaded conditions (Table 5). In cocoa plantations, insufficient overhead shade favors the development of numerous herbivorous insect species, including thrips (*Selenothrips rubrocinctus*) and mirids (*Sahlbergella*, *Distantiella* etc.) as well as diseases that follow mirid attack (tracheomycose, *Calonectria*, *Colletotrichum*) (Mossu, 1990). Even in shaded plantations, these insects concentrate at spots where the shade trees have been destroyed, e.g., by wind (Poncin, 1957). Bigger (1981) found an increase in the numbers of Lepidoptera, Homoptera, Orthoptera and the mirid *Sahlbergella singularis* and a decrease in the number of Diptera and Hymenoptera from the shaded towards the unshaded part of a cocoa plantation in Ghana. The first group includes many pest species, while many Hymenoptera are parasitoids.

Whereas a certain equilibrium develops between cocoa and its mirid pests under shaded conditions, unshaded cocoa degrades rapidly in the absence of anti-mirid treatments (Decazy, 1981). This has been experienced already in the early 1920s by cocoa farmers on the African islands of Fernando Pó and São Tomé, then among the leading cocoa producers in the world. These attempted to increase cocoa production by removing much of their shade canopy. ‘Shortly thereafter, however, most of these farms were wiped out by insect attacks’ (Gordon, 1976, cit. in Johns, 1999). When insecticides became available, spectacular yield increases due to shade removal and fertilization

Table 4. Overview of shade effects on crop pests and diseases.

Causal factor	Desirable effects	Undesirable effects
Reduced UV radiation	Reduced sporulation and spore release of fungi	Protection of pathogens from lethal UV radiation
Reduced temperature	Reduced activity of sun-loving herbivorous insects (e.g. beetles)	More favourable temperature for microbial growth, increased activity of shade-loving herbivorous insects (e.g. aphids), reduced activity of many hymenopteran parasitoids
Reduced temperature fluctuations	Reduced dew formation on plant surfaces	
Reduced air movements	Less dissemination of spores and propagules	Prolonged leaf and fruit wetness, favouring microbial growth and infection
Increased atmospheric humidity, slower drying of plant surfaces	Increased efficiency of entomopathogenic fungi	Increased release of fungal spores, spore germination and microbial growth
Interception of rainfall	Reduced spore dissemination by splash effects under small-leaved trees	Coalescence of raindrops and increased splash dispersal of spores under large leaves
Mechanical effects	Protection of crops from damage by hail storms which could create entry points for infection	Increased damage from falling branches etc.
‘Associated biodiversity’ of shade trees	Trees harbor natural enemies and antagonists of crop pests; non-host plants as dispersal barriers for pests, diseases and their vectors	Trees serve as alternate hosts or provide physical protection to crop pests, diseases and their vectors
Effects on soil fertility and water and nutrient supply	Increased soil organic matter content and nutrient availability enhance antagonistic potential of soil microorganisms against pests and diseases and crop vigor; improved nutritional status of certain tree crops under shade	Competition between crops and shade trees for water and nutrients reduces crop vigor
Susceptibility of crop plants to pests and diseases	Reduced stress from excessive temperature, radiation and transpirational demand; avoidance of excessive vigor favoring some biotrophic infections such as witches’ broom on cocoa	Etiolated and weak plants under excessive shade

were obtained in the shade-and-fertilizer experiment at Tafo, Ghana. However, the unshaded plots had to be sprayed against the cocoa mirids *Distantiella theobroma* and *Sahlbergella singularis* at frequent intervals. When spraying was reduced, the yields of these plots decreased continuously and fell below those of the shaded plots 14 years after shade removal (Bigger, 1981). For cocoa, shading is thus an effective insurance strategy against insect pests. Johns (1999) explained the resistance of many cocoa farmers in Bahía, Brazil, against government initiatives to reduce the shade canopy of rainforest remnant trees in their plantations during the 1970s and 1980s with a general aversion against risk (and thus changes in their customary practices), although only five out of 10 interviewed farmers were aware of the increased need for insecticides (and fertilizers) under unshaded conditions.

In coffee, the effect of shade on insect pests is less clear than in cocoa, as the leaf miner (*Leucoptera meyricki*) is reduced by shade, whereas the coffee berry borer (*Hypothenemus hampei*) may increase under shade (Willey, 1975). Similarly, unshaded tea suffers more from attack by thrips and mites, such as the red spider mite (*Oligonychus coffeae*) and the pink mite (*Acaphylla theae*), whereas heavily shaded and moist plantations are more damaged by mirids (*Helopeltis* spp.) (Muraleedharan and Chen, 1997). In Sri Lanka, a higher incidence of live-wood termites (*Glyptotermes dilatatus*), which attack mainly soft-wooded tea cultivars, has been observed in unshaded plantations compared with plantations shaded by *Gliricidia sepium*. However, this effect was not related to the microclimatic effects of the trees. The termites were frequently found in the rotted stumps of the shade trees which seemed to act as diversionary hosts by attracting the swarming termite alates, thereby reducing the colonization of the tea plants (Sivapalan et al., 1977). In other situations, rotting tree stumps can be a source of insect pests and diseases, and their removal when establishing plantations of perennial crops such as cocoa or coffee is often recommended (Cambrony, 1989; Mossu, 1990).

Shade influence on diseases

Published information on the influence of shade on plant diseases tends to be more contradictory than that on insect pests. One reason for this is that increased shade is almost necessarily associated with changes in other factors which affect disease development, such as increased plant density. Excessive plant density, leading to high humidity and disease proliferation has been reported from homegarden systems (Nair, 1979), and this may have outweighed any positive or negative shade effects. Also, quantitative shade levels and climatic data are not always presented in research reports, although these may be critical for understanding the results. Studies which provide this information tend to compare extreme levels to verify specific hypotheses rather than intermediate levels which would often be practically more relevant.

Shade can influence plant diseases through numerous mechanisms which

Table 5. Effect of different shade intensities on important pests and diseases of tropical crops.

Crop species	Severity of pest or disease attack		
	Increased under shade	Decreased under shade[1]	Least with moderate shade
Cocoa (*Theobroma cacao*)[a]	*Phytophthora* pod rot (*P. capsici*, *P. citrophthora*, *P. palmivora*), blight and shot hole (*Colletotrichum gloeosporioides*)	Thrips (*Selenothrips rubrocinctus*), mirids (*Sahlbergella*, *Distantiella*); witches' broom (*Crinipellis perniciosa*); *Verticillium dahliae*, anthracnosis and terminal die-back (*Colletotrichum gloeosporioides*), cocoa swollen shoot virus	Pink disease (*Corticum salmonicolor*), stem canker (*Phytophthora palmivora*), moniliasis (*Moniliophthora roreri*)[2]
Coffee (*Coffea arabica*)[b]	Coffee berry borer (*Hypothenemus hampei*); South American leafspot (*Mycena citricolor*), pink disease (*Corticium salmonicolor*), thread blight (*Pellicularia koleroga*), *Marasmius* spp.	Leaf miner (*Leucoptera meyricki*); leafspot (*Cercospora coffeicola*)	Rust (*Hemileia vastatrix*)[2]
Tea (*Camellia sinensis*)[c]	Mirids (*Helopeltis* spp.); blister blight (*Exobasidium vexans*)	Thrips, mites (*Oligonychus coffeae*, *Acaphylla theae*)	
Coconut (*Cocos nucifera*)[d]		Leafspot (*Drechslera incurvata*)	
Banana and plantain (*Musa* sp.)[e]		Black & yellow Sigatoka (*Mycosphaerella fijiensis* and *M. musicola*)	
Groundnut (*Arachis hypogaea*)[f]	Rust (*Puccinia arachidis*), late leafspot (*Phaeoisariopsis personata*)		
Maize (*Zea mays*)[g]	Leaf blight (*Helminthosporium maydis*)	Rust (*Puccinia sorghii*)	

[1] Disease problems may increase under excessive shade levels (> 50%), which may be caused by very dense plant stands, lack of shade management etc.; [2] Evidence contradictory, possibly not influenced by common shade levels.

[a] (Lass, 1985; Chandra Mohanan et al., 1989; Mossu, 1990; Beer et al., 1998; Evans, 1998); [b] (Willey, 1975; Cambrony, 1989; Beer et al., 1998; Guharay et al., 1999); [c] (Muraleedharan and Chen, 1997); [d] (Fagan, 1987); [e] (Vicente-Chandler et al., 1966); [f] (Schroth et al., 1995a); [g] (Lukens and Mullamy, 1972).

often act simultaneously (Table 4). Shading alters both the quantity and the quality of light. Light, in particular near UV frequencies around 350 nm, can stimulate sexual and asexual sporulation in many fungal species, whereas short and long wavelengths trigger spore release (Kranz, 1974; Aylor, 1990). These effects are partially counteracted by the lethal effect of strong UV-exposure on microorganisms. Shading also reduces air and soil temperatures and buffers against high and low temperature extremes (Barradas and Fanjul, 1986). Similar to windbreaks, shade trees reduce air movements within a plant stand whose repercussions on pests and diseases have been discussed above. Atmospheric humidity and consequently the surface wetness of plants are increased under shade. High humidity triggers the release of fungal spores in many species, and free moisture is required for spore germination. This explains reported increases of disease incidence at the tree-crop interface (see above) and in very dense plant stands (Ramachandran et al., 1998). Fungal and bacterial pathogens grow best at moderate temperature and high humidity, which are both provided by a shade canopy. A reduction of leafspot (*Drechslera incurvata*) on three varieties of dwarf coconut under 30% and even more so 50% artificial shade compared with full sunlight was attributed to the reduction of temperature fluctuations and consequently reduced dew formation on the leaves (Fagan, 1987). Shade trees also intercept rainfall and alter throughfall distribution (Schroth et al., 1999). Reduced impact of raindrops can reduce spore dispersal by splash effects (Evans, 1998), although large-leaved shade trees may coalesce rain drops which subsequently have increased impact (Beer et al., 1998). Mechanical damage to crops can create entry points for opportunistic pathogens. In areas with hail storms, the risk may be reduced by shade (Beer et al., 1998), but in other situations it may be increased. For example, falling coconut fronds and branches of shade trees increased thread blight caused by *Pellicularia koleroga* (syn. *Koleroga noxia*) and *Marasmius* spp. on cocoa in Malaysia (Lass, 1985).

Shade may also affect the susceptibility of plants for diseases by altering their physiological state. In general, stressed plants are more susceptible to diseases. Stress can be a result of overexposure to sunlight, resulting in drought stress and photo-oxidation. For example, intense evapotranspiration caused by insufficient shade favors tracheomycose caused by *Verticillium* sp. of cocoa (Mossu, 1990). On the other hand, excessive shade results in shortage of photosynthates and in delicate, etiolated plants. Shade effects on crop nutrition are discussed further below.

Given this multitude of interacting mechanisms, the interpretation and especially the prediction of shade effects on crop diseases in agroforestry is not always straight-forward. For example, the sporulation of *Exobasidium vexans*, the causal agent of blister blight in tea, is proportional to daily hours of sunshine, whereas the disease progress is negatively related to hours sunshine, because the basidiospores are sensitive to UV radiation, and the infection and lesion development require free moisture and high humidity (Kranz, 1974; Ventkata Ram, 1979; Muraleedharan and Chen, 1997). As a consequence, epidemics of blister blight of shaded tea have been reported from many countries (Muraleedharan and Chen, 1997).

The definition of the optimum shade intensity for a crop is particularly difficult when several important diseases differ in their response to shade. This is the case in coffee. High humidity caused by excessive shade favors the development of several fungal coffee diseases, including South American leafspot (*Mycena citricolor*), pink disease (*Corticium salmonicolor*), thread blight (*Pellicularia koleroga*, syn. *Corticium koleroga*), and *Marasmius* spp. (Cambrony, 1989; Beer et al., 1998). For coffee rust (*Hemileia vastatrix*), increased incidence under intensive shade has also been suggested (Guharay et al., 1999), although this disease affects coffee under both shaded and unshaded conditions (Beer et al., 1998). The incidence of *Cercospora coffeicola*, in contrast, is increased under unshaded conditions (Beer et al., 1998; Guharay et al., 1999). As a consequence, attempts in Nicaragua to control coffee rust by sudden and radical shade removal generated more serious problems, for example by increasing the severity of *Cercospora* (Guharay et al., 1999).

In the absence of chemical disease control, 50% *Inga* shade completely prevented the important banana disease, yellow Sigatoka (*Mycosphaerella musicola*), on relatively resistant plantains and reduced it by about one half on highly susceptible Cavendish bananas in Puerto Rico. Plantain yields were slightly depressed by shading due to a reduced number of fruits per bunch, but banana yields were approximately twice as high under shade than in the open as an effect of the disease control (Vicente-Chandler et al., 1966). Fagan (1987) suggested reduced dew formation on the leaves as an explanation for the effect of shade on Sigatoka. The same reasons may also explain reduced incidence of black Sigatoka (*M. fijiensis*) of banana at high planting density (Cordeiro et al., 1998).

In cocoa, adequate shading is not only an important measure to control insect pests, but affects also several diseases. Under marginal site conditions in Uganda, unshaded and consequently stressed cocoa succumbed to the weak parasite *Verticillium dahliae* (Trocmé, 1972). Incidence of pink disease in Bahía, Brazil, is proportional to relative humidity and is consequently increased under shade. However, disease severity is higher in unshaded fields (Lass, 1985), presumably due to the increased susceptibility of the plants. The reduction of the witches' broom disease in cocoa by shading is due to several mechanisms: shading reduces excessive vigor of the crop which would be favorable for the development of the fungus; it reduces fluctuations of air humidity which trigger sporulation of the fungus; and it reduces air currents within the stand which favor autoinfection (Mossu, 1990; Evans, 1998). Elevated humidity under excessive shade can enhance the development of the pathogen, but also of its natural antagonists which decompose brooms and mummified pods, thereby reducing the production of new inoculum (Evans, 1998).

The fungus *Colletotrichum gloeosporioides* causes various disorders on cocoa which apparently differ in their response to shade. The leaf diseases blight and shot hole were increased under excessive shade in India (Chandra Mohanan et al., 1989) and for anthracnose caused by the same pathogen Mossu (1990) recommended pruning of the cocoa trees to reduce humidity. However, in Costa Rica anthracnosis (Beer et al., 1998) and terminal die-back caused by the same fungus (U. Krauss, unpublished) were associated with unshaded fields. *Phytophthora* pod rot is increased already by intermediate shade levels (Lass, 1985; Beer et al., 1998), whereas stem canker caused by the same fungus is increased in fields exposed to full sunlight due to water stress. *Phytophthora* is frequently vectored by ants (Evans, 1973; de Medeiros et al., 1993), and whether or not it is increased by shade depends on the ant species involved (Evans, 1998). Ant distribution as influenced by shading and shade species has been studied in cocoa plantations in Ghana (Bigger, 1981) and Malaysia (Way and Khoo, 1991) and in coffee plantations in Costa Rica (Perfecto and Vandermeer, 1996).

The relationship between shade and moniliasis has been controversial for many decades (Evans, 1998). Fowler et al. (1956) and Krauss and Soberanis (1999) found the highest incidence of the disease under very dense shade. The reduction of excessive shade to reduce the humidity and increase the aeration of the plantation has been recommended as a prophylactic control measure (Mossu, 1990). Under moderate shade, moniliasis was somewhat lower than without shade but this trend could be reversed in very rainy years and failed to be statistically significant (Días, 1957). Lok and Sandino (1999) found no correlation between the disease and shade levels of 17 to 50%.

Decreased shade increased mistletoe infection of cocoa in West Africa. Mistletoe seeds are spread by birds which are most abundant at the forest edge. Since mealybug-tending ants have a preference for mistletoe, cocoa swollen shoot virus (CSSV) which is transmitted by mealybugs is most common where mistletoe infection is high, i.e., in unshaded cocoa at the forest edge (Lass, 1985).

Climatic dependence of shade-disease interactions

The influence of local climate and weather on shade-disease interactions is illustrated by verticillium wilt of cotton (*Gossypium hirsutum*) caused by *Verticillium dahliae* in Uganda (Hansford, 1940). In cool areas where shade by an associated crop decreased soil temperatures to below the optimum of the pathogen, the disease was reduced by shade, whereas in hot areas, the temperature of exposed soil was above the optimum of the fungus, so that shading favored its development. During the dry season in Cuba, shading of tomatoes reduced damage by *Alternaria solani* and *Phytophthora infestans* by alleviating water stress of the plants (Pino et al., 1994), whereas under wetter conditions, these pathogens would have been favored by shade and the concomitant increase in humidity.

Shade management

As other elements of agroforestry, shade management for pest and disease control is obviously a question of optimization. Which shade level is best for a certain crop depends on its management (e.g., fertilization), local environmental conditions (e.g., temperature, rainfall) and the principal pests and pathogens at the respective site. In some cases, shade management for pest control will be given priority over shade management for the control of diseases (e.g., cocoa in Africa and Asia). In other cases, diseases are the major threat for a crop (e.g., black and yellow Sigatoka in banana and plantain), and the shade level will be selected according to optimum control of the respective pathogens. An important principle is to manage shade for minimizing physiological stress of the crops themselves (e.g., avoid excessive irradiation, too high or low temperatures, drought stress), thereby increasing their resistance to pest and disease attack. Optimum shade usually has a range which is sufficiently wide to accommodate seasonal and year-to-year fluctuations of weather conditions. However, even if the overall shade level of a plot is in the optimum range, pathogens may develop in micro-niches of high humidity which are created by patches of dense shade, and these may subsequently act as inoculum sources. It seems likely that, from a phytopathological view, a homogeneous, intermediate shade is more favorable than a patchwork of heavily shaded and unshaded spots, although this requires further confirmation. The type of shade depends very much on the shade tree species and their management, e.g., leaf size, crown form and pruning regime, and recommendations for shade species selection and management would thus depend on the outcome of further research in this area.

Effects of plant nutrient availability on pests and diseases

It has repeatedly been mentioned in this review that environmental stress increases the susceptibility of plants to pests and diseases. Beside drought, one of the dominating stress factors at many tropical sites is nutrient deficiency, caused by inherently infertile or degraded soil conditions. Such conditions can affect crop health by reducing the resistance (i.e., ability to avoid damage) and tolerance (i.e., ability to compensate for damage) of crops against pests and diseases. Vigorously growing plants with an optimum nutritional status are better able to replace leaf area or roots lost to a pathogen than nutrient-limited, and thus slow-growing plants (Marschner, 1995). Agroforestry may affect crop nutrition both positively and negatively. Improved soil structure and root development, biological N_2 fixation by legume trees on N deficient soils or applications of animal manure produced on the basis of fodder trees may improve crop nutrition. Shading improves the nutritional status of perennial crops such as cocoa when grown on infertile soils (Alvim and Alvim, 1980; Ling, 1990). On the other hand, competition between trees and crops for nutrients and nutrient sequestration in the tree biomass can reduce the availability of nutrients for the crops and could increase their susceptibility to certain pests and diseases. Competition for water can affect crop vigor directly or by reducing the mobility of nutrients in the soil (Table 4).

Despite the prominence of soil fertility studies in agroforestry research, there is little mentioning in the literature of agroforestry effects on crop health via nutrient availability. This may mean that few observations were carried out because the topic had low research priority, or that agroforestry effects on nutrient availability are in most cases too slow and gradual to provoke pronounced effects on crop resistance and health. In a farm survey in SE Nigeria, plantain showed a significantly higher incidence of black Sigatoka on infertile than on fertile soils, and a higher incidence on fields than in homegardens which had a higher soil nutrient and organic matter content due to the regular application of household refuse. As mineral fertilizers are hardly available to small farmers in the region, intensification of farming techniques that increase soil organic matter and nutrient contents, such as planted fallows and the application of compost and animal manure (as in homegardens) were suggested as a control strategy for this disease (Mobambo et al., 1994). In an alley cropping experiment in Mindanao, Philippines, on the other hand, agroforestry seemed to increase the susceptibility of the crop to disease attack. Low harvest indices and an increased number of empty grains of rice in agroforestry plots as compared to the agricultural control were explained with increased incidence of blast (*Pyricularia oryzae*) (Maclean et al., 1992). The disease apparently counteracted positive effects of the hedgerow biomass on crop development as evidenced by increased tiller and panicle numbers and increased plant height. As the incidence of blast in upland rice is increased by high N supply, the authors concluded that the amount of N-rich biomass applied to this crop needs to be controlled.

This points to the valid concern that N, the nutrient whose availability is easiest to increase through agroforestry measures, may reduce crop resistance against pests and diseases when supplied in excessive quantities. High N supply especially increases the infection by obligate parasites such as rust fungi (*Puccinia* spp.), whereas the infection by facultative parasites such as *Fusarium* is reduced. High N and low K supply also favor the attack of field crops by insect pests, mainly because of increased contents of amino acids in the plant (Marschner, 1995). In certain agroforestry systems, such as alley cropping or systems with perennial crops and leguminous shade trees, relatively large quantities of N-rich biomass may be applied to the crops. However, N uptake from biomass during the year of application is usually less than 20%, and values close to 10% are not uncommon (Xu et al., 1993; Palm, 1995). Much of the N not taken up is incorporated into the soil organic matter and is only gradually released through mineralization. Therefore, luxury consumption of N and reduced pest and disease resistance of the crops as a consequence of biomass applications would not normally be expected. On N deficient sites, such as sandy savanna soils, additional N supply from leguminous biomass may markedly increase crop vigor and would thus be expected to increase their tolerance to pests and diseases. In trees, the relationship between N supply and pest incidence is less clear than in herbaceous crops, because repellents and toxic plant compounds also have a pronounced influence on pest attack. Beside increasing the nutritional value of the plant tissue for herbivorous insects, high N availability can also reduce the levels of defensive, carbon-based metabolites such as tannins and terpenoids and increase levels of defensive, N-containing metabolites such as alkaloids or cyanogenic glycosides (Kytö et al., 1996).

Beside N, K is the nutrient through which agroforestry techniques are most likely to affect crop health. A high K supply generally improves the resistance of plants to fungal and bacterial parasites up to the level required for optimum plant growth (Marschner, 1995). It also reduced nematode and borer damage in tea (Muraleedharan and Chen, 1997). Woody biomass may contain rather high concentrations of K which becomes readily available upon decomposition, and mulching with prunings from legume trees has been found to improve the K nutrition of maize (Schroth et al., 1995b) and yam (Budelman, 1990). On the other hand, trees which are grown for timber may accumulate considerable quantities of K in their stems and could thereby reduce the availability of this element for crops, especially on K-deficient sites (Beer, 1988). However, there seems to be no information in the literature relating crop health to effects of agroforestry techniques on K availability.

In many tropical soils, P deficiency is one of the factors most limiting crop growth (Smyth and Cassel, 1995; Buresh et al., 1997), and under these conditions increased P supply can greatly increase the vigor of the crops and thereby their ability to compensate for pest and disease damage by new growth. Unfortunately, biomass usually contains too little P to meet crop requirements (Palm, 1995; Schroth et al., 1995b), and the potential of agroforestry to affect crop health through P availability is therefore limited.

Agroforestry measures may also improve crop health by increasing farmers' income, e.g., through the integration of high-value tree crops (Sinclair et al., 1994; Sanchez and Leakey, 1997), and thus their access to mineral fertilizers (and pesticides). Although such indirect agroforestry effects on pests and diseases could easily become dominant over the effects mentioned before, they will not be discussed further here.

Effects of mulch and cover crops on pests and diseases

Certain soil management practices that are frequently employed in agroforestry, such as mulching and the use of cover crops, can also affect pest and disease development, either directly or by influencing the resistance of the plants. Beside providing nutrients during decomposition, mulch (or litter) layers can improve soil physical conditions, water availability and root development and thereby the water and nutrient status of the plants (Webster and Wilson, 1980). The maintenance of high levels of organic carbon in the soil, e.g., through mulching or the application of animal manures, also helps to increase the antagonistic potential of soil microorganisms against crop pests, such as the control of the nematodes *Meloidogyne javanica* and *M. incognita* by the fungus *Verticillium chlamydosporium* and the bacterium *Pasteuria penetrans* (Page and Bridge, 1993). More directly, mulch could act on pathogens near the soil surface through leachates with fungistatic properties, as has been suggested for *Gliricidia sepium* biomass (Inostrosa and Fournier, 1982). The water extracts of this biomass contain phenolic substances with known fungistatic properties, such as protocatechuic acid (Walker and Stahmann, 1955; Ramamoorthy and Paliwal, 1993). In an experiment in the Côte d'Ivoire, groundnut showed lower incidence of rust and late leafspot when mulched with *Gliricidia sepium* biomass than in unmulched control plots (Schroth et al., 1995a). Mulch effects on crop pests are discussed in more detail by Rao et al. (2000).

Cover crops are frequently employed in plantation agriculture, e.g., of oil palm and rubber, and they could play a similar role in many agroforestry systems based on perennial crops. Cover crops fix N_2 (if legumes are used), suppress weeds, protect the soil and improve its chemical and physical characteristics (Webster and Wilson, 1980; Giller and Wilson, 2000). In addition to these beneficial effects, cover crops may interact with pests and diseases. In young plantations, overgrowing of stumps from the previous forest or diseased older trees by a cover crop hastens their decay and thus neutralizes them as sources of pathogenic fungi (e.g., *Fomes lignosus* in rubber) and insect pests (e.g., *Oryctes* in coconut) (de Taffin, 1993). Liang and Huang (1994) reported a higher percentage of parasitoids and a lower percentage of phytophages in the ground cover than in the tree canopies of a citrus orchard in China. Parasitoids and predatory mites in ground cover and canopy tended to belong to the same species, suggesting the possibility of migration between the two habitats. In Californian apple orchards, cover crops were found to harbor large numbers of insect species which attracted predators, although this did not necessarily relate to higher predator numbers on the trees (Altieri et al., 1987). Similarly, legume ground covers in pecan (*Carya illinoinensis*) orchards had abundant coccinellid populations, but the coccinellid populations in the trees (and thus their predation on aphids) were rarely affected by the ground cover because the tree and ground cover populations consisted of different coccinellid species (Rice et al., 1998). Cover crops may also host pests, and this may preclude associations with certain crops. In an agroforestry system with annual and perennial crops in central Amazonia, cowpea was virtually destroyed by *Diabrotica speciosa* (Coleoptera) which had built up high populations in the *Pueraria phaseoloides* cover crop (AMSR Pamplona, unpublished results, 1993).

As mentioned before, certain plant species have a depressive effect on nematodes, and these may be used as cover crops in tree crop plantations

(Govindaiah et al., 1991; Rodríguez-Kábana, 1992). Other cover crop species are themselves hosts of nematodes, although this does not necessarily lead to increased attack of the main crop. Wielemaker and Quirós (1997) found ten times higher numbers of the nematode *Radopholus similis* on the roots of the cover crop *Arachis pintoi* than on those of banana, but counts on banana roots did not differ between plots with and without this cover crop. When after five years the ground cover died of severe defoliation by insects, the nematodes did not migrate to the banana roots but died equally of starvation. In another study, counts of *R. similis* (and, non-significantly, *Helichotylenchus* sp.) in banana and plantain were reduced by a factor of four in association with *A. pintoi* (Vargas, 1997). In a comparison of the non-hosts *Crotalaria juncea*, *Tagetes erecta* and *Raphanus sativus* as ground cover for banana, *R. similis* counts decreased most with *C. juncea*, presumably because of an allelopathic effect (Subramaniyan and Selvaraj, 1990).

In certain plant species such as *Citrus*, increased humidity at the stem base can increase foot rot (*Phytophthora* spp.), and this needs to be taken into account when managing the cover crop, which has to be cut back from the trees at regular intervals (L. Gasparotto, unpublished). Also, the increased humidity provided by a cover crop or mulch layer may increase the attack of weakened or injured tree crops, such as rubber and cupuaçu, by the fungus *Botryodiplodia theobromae* (Gasparotto et al., 1997).

Conclusions

The interactions of plant communities – natural or man-made – with their pests and diseases are invariably complex, and the complexity further increases with the diversity of the system. When a farmer adopts agroforestry instead of annual monocultures, the opportunities of relatively easy monitoring of the pest and pathogen populations and their frequent disturbance through crop rotation, tillage and burning are traded against a greater stability of the system with an increased potential for self-regulation, which is however also more complex and more difficult to control. For this trade to be successful in reducing pest and disease risks, agroforesters should not merely rely on increased diversity, but should attempt to integrate into their decisions the full range of traditional and scientific knowledge on the interactions between plant species, planting designs and management practices on one hand, and pests, diseases and their natural enemies on the other hand. This obviously requires that this knowledge is collected and organized in a more systematic way than up to now.

The effects of agroforestry plants (or techniques) on pests and diseases can be divided into biological (species-related) and physical components (e.g., microclimate). The former are highly specific for certain plant-pest or plant-disease combinations and have to be studied on a case by case basis. The latter are easier to generalize, but even they depend on the regional (pedo)climatic conditions and the ever-changing weather. It should be kept in mind that, even if a plant species does not influence the pests and diseases of an associated species, the fact of having several species in the same field may still reduce the probability of losing the whole harvest (or shade tree layer) to pest and disease outbreaks for simple reasons of probability. This, however, works only if the associated plant species do not share important pests and diseases, and knowledge on this is clearly required when designing agroforestry associations.

In the ideal case, however, associated plant species would mutually reduce their pest and disease risks, either by reducing the population build-up and dispersal of the organisms, by harboring their natural enemies, or by creating environmental conditions unfavorable to their development. The chances of achieving such facilitative effects through agroforestry associations are greatest with respect to specialist herbivores and diseases, especially when these possess relatively inefficient dispersal mechanisms which make them susceptible to barrier effects of non-host vegetation. Our knowledge of how to design agroforestry systems to make use of such effects is however grossly insufficient. In contrast, wind-dispersed fungi may often be too mobile to be much affected by the presence of non-host plants, and some generalist pests and disease agents affect wide ranges even of unrelated crop and tree species in an association. However, some disease agents that were believed generalists only recently are now known to be rather specific, and this increases the chances that agroforestry can contribute to their control.

A major potential of agroforestry against both specialist and generalist pests and diseases lies in the ability to create environmental conditions which are favorable for the crops and unfavorable for its enemies. Well-designed agroforestry techniques can reduce crop stress by providing the right amount of shade, reducing temperature extremes, sheltering off strong winds and improving soil fertility, thereby improving the tolerance of crops against pest and disease damage, while at the same time influencing the development conditions for pest and disease organisms and their natural enemies. Poorly designed systems, on the other hand, may increase the susceptibility of crops for pests and diseases through excessive competition for light and soil resources.

To increase the knowledge base in the wide and complex field of pest and disease interactions with agroforestry techniques, the more systematic inclusion of pest and disease observations in ongoing agroforestry research is necessary, but certainly not enough. Specialists should identify pest and disease problems that can potentially be alleviated through agroforestry measures, and should develop corresponding experimentation programs in cooperation with agroforesters. Problems as well as potential solutions should be identified in close interaction with farmers, following the example of pioneer projects in this field (Aguilar et al., 1999). Problems and solutions will obviously differ from region to region, and to keep track of the vast amount of relevant information on pest and disease interactions with agroforestry measures, it may be advantageous to collect it in a data base at an international center, which would then assist in the development of further research and extension activities, e.g., through the publication of local manuals for researchers, extension workers and farmers.

Acknowledgements

The idea for this review had been around for some time, but we would like to thank Fergus Sinclair for motivating us to write it up, and John Bridge and Harry Evans for much useful information. The editor-in-chief and two referees improved the manuscript with their comments. GS received funding from the German Ministry of Education and Research (0339457B7/ENV23), UK from the United States Department of Agriculture through CABI Bioscience, and JADA from the Brazilian Conselho National de Desenvolvimento Científico e Tecnológico (CNPq) while working on this paper.

References

Aguilar A, Calderón M, Guharay F, Jiménez C, Mendoza R, Monterrey J, Monterroso D and Staver C (1999) Coffee growers make improved pest management decisions through group learning and experimentation by crop stage. In: International Symposium on Multi-strata Agroforestry Systems with Perennial Crops, CATIE, Turrialba, 22–27 February 1999, Extended Abstracts, pp 86–89. CATIE, Turrialba

Allen DJ (1983) The pathology of tropical food legumes. Chichester, John Wiley and Sons, 413 pp

Altieri MA, Trujillo FJ and Farrell J (1987) Plant-insect interactions and soil fertility relations in agroforestry systems: implications for the design of sustainable agroecosystems. In: Gholz HL (ed) Agroforestry: Realities, Possibilities and Potentials, pp 89–108. Martinus Nijhoff Publishers, Dordrecht

Altieri MA (1991) Ecology of tropical herbivores in polycultural agroecosystems. In: Price PW, Lewinsohn TG, Fernandes GW and Woodruff WB (eds) Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions, pp 607–617. John Wiley and Sons, Chichester

Alvim PT and Alvim R (1980) Environmental requirements of cocoa with emphasis on responses to shade and moisture stress. In: Proceedings of the International Conference on Cocoa and Coconuts, Kuala Lumpur, 1978, pp 93–111. The Incorporated Society of Planters, Kuala Lumpur

Amusa NA and Alabi AA (1996) Host range of *Colletotrichum gloeosporioides* from *Gliricidia sepium* and its implication in crop production. Crop Research (Hisar) 11: 359–363

Augspurger CK (1984) Seedling survival of tropical tree species: interaction of dispersal distance, light gaps, and pathogens. Ecology 65: 1705–1712

Aylor DE (1990) The role of intermittent wind in the dispersal of fungal pathogens. Ann Rev Phytopathol 28: 73–92

Baldy C and Stigter CJ (1993) Agrométéorologie des cultures multiples en régions chaudes. Paris, INRA, 246 pp

Barradas VL and Fanjul L (1986) Microclimatic characterization of shaded and open-grown coffee (*Coffea arabica* L.) plantations in Mexico. Agric For Meteorol 38: 101–112

Bastos CN (1990) Patogenicidade e características do isolado de *Crinipellis perniciosa* procedente de Uruçuca, Bahia. Fitopatologia Brasileira 15: 344–346

Bastos CN and Andebrhan T (1986) Urucu (*Bixa orellana*): nova espécie hospedeira da vassoura-de-bruxa (*Crinipellis perniciosa*) do cacaueiro. Fitopatologia Brasileira 11: 963–965

Beer J (1988) Litter production and nutrient cycling in coffee (*Coffea arabica*) or cacao (*Theobroma cacao*) plantations with shade trees. Agrofor Syst 7: 103–114

Beer J, Muschler R, Kass D and Somarriba E (1998) Shade management in coffee and cacao plantations. Agrofor Syst 38: 139–164

Bhar R and Fahrig L (1998) Local vs. landscape effects of woody field borders as barriers to crop pest movement. Conserv Ecol (online) 2

Bigger M (1981) Observations on the insect fauna of shaded and unshaded Amelonado cocoa. Bull Entomol Res 71: 107–119

Boa E (1998) Diseases of agroforestry trees: do they really matter? Agroforestry Forum 9: 19–22

Bowden J and Dean GJW (1977) The distribution of flying insects in and near a tall hedgerow. J Appl Ecol 14: 343–354

Brenner AJ (1996) Microclimatic modifications in agroforestry. In: Ong CK and Huxley P (eds) Tree-Crop Interactions, pp 159–187. CAB International, Wallingford

Brunt AA, Crabtree K, Dallwitz MJ, Gibbs AJ, Watson L and Zurcher EJ (1997) Plant viruses online: description and lists from VIDE database, version 16. http://www.biology.anu.edu.au/groups/mes/vide.

Budelman A (1990) Woody legumes as live support systems in yam cultivation II.The yam-Gliricidia sepium association. Agrofor Syst 10: 61–69

Bullock DG (1992) Crop rotation. Crit Rev Plant Sci 11: 309–326

Burdon JJ and Chilvers GA (1982) Host density as a factor in plant disease ecology. Ann Rev Phytopathol 20: 143–166

Buresh RJ, Smithson PC and Hellums DT (1997) Building soil phosphorus capital in Africa. In: Buresh RJ, Sanchez PA and Calhoun F (eds) Replenishing Soil Fertility in Africa, pp 111–149. Soil Science Society of America, Madison

Calvo C and Romero R (1998) Evaluación del gradiente de dispersión de la enfermedad de la Sigatoka negra del banano (*Musa* AAA). Corbana 23: 51–56

Cambrony HR (1989) Le caféier. Le Technicien d'Agriculture Tropicale 11. Paris, Editions Maisonneuve et Larose, 166 pp

Centre Téchnique Forestier Tropical (1989) Mémento du Forestier. Paris, MinistËre de la Coopération et du Développement, 1266 pp

Chandra Mohanan R, Kaveriappa KM and Nambiar KKN (1989) Epidemiological studies of *Colletotrichum gloeosporioides* disease of cocoa. Ann appl Biol 114: 15–22

Cordeiro ZJM, Matos AP, Oliveira SL and Silva SO (1998) Estratégia para convivência e controle da Sigatoka negra no Brasil. Cruz das Almas, Embrapa Mandioca e Fruticultura, 6 pp

Day RK and Murphy ST (1998) Pest management in tropical agroforestry: prevention rather than cure. Agroforestry Forum 9: 11–14

de Medeiros M A, Fowler H G and Delabie H C (1993) Interaction of black pod disease (*Phytophthora* spp.) and the ant *Azreca chartifex spiritii* in Bahian cocoa plantations. Agrotrópica 5: 65–68

de Rouw A (1987) Tree management as part of two farming systems in the wet forest zone (Ivory Coast). Acta Oecol Oecol Appl 8: 39–51

de Taffin G (1993) Le cocotier. Le Technicien d'Agriculture Tropicale 25. Paris, Editions Maisonneuve et Larose, 166 pp

Dean GJ and Luuring BB (1970) Distribution of aphids in cereal crops. Ann appl Biol 66: 485–496

Decazy B (1981) Ombrage et traitements, anti-mirides sur les cacaoyers: leur influence sur la production. In: 7th International Cocoa Research Conference, 1979, Douala, Cameroon, pp 443–446. Cocoa Producers' Alliance, Lagos

Desaeger J and Rao MR (1999) The root-knot nematode problem in sesbania fallows and scope for managing it in western Kenya. Agrofor Syst 47: 273–288

Dix ME, Johnson RJ, Harrell MO, Case RM, Wright RJ, Hodges L, Brandle JR, Schoeneberger MM, Sunderman NJ, Fitzmaurice RL, Young LJ and Hubbard KG (1995) Influence of trees on abundance of natural enemies of insect pests: a review. Agrofor Syst 29: 303–311

Días J (1957) Observaciones sobre la incidencia de Monilia del cacao en Ecuador. Turrialba 7: 95–99

Duarte Aguilar JA, Parra JRP and Ferraz ECA (1986) Biologia de *Terastia meticulosalis* Guenée em dietas artificiais. In: X Congresso Brasileiro de Entomologia, 26–31 January 1986, Rio de Janeiro, p 39. Sociedade Entomológica do Brasil, Rio de Janeiro

Duponnois R, Senghor K, Thioulouse J and Bâ AM (1999) Susceptibility of several sahelian *Acacia* to *Meloidogyne javanica* (Treub) Chitw. Agrofor Syst 46: 123–130

Epila JSO (1986) The case for insect pest management in agroforestry research. Agric Syst 19: 37–54

Evans HC (1973) Invertebrate vectors of *Phytophthora palmivora*, causing black pod disease of cocoa in Ghana. Ann appl Biol 73: 331–345

Evans HC, Edwards DF and Rodríguez M (1977) Research on cocoa diseases in Ecuador: past and present. PANS 23: 68–80

Evans HC (1978) Witches' broom disease of cocoa (*Crinipellis perniciosa*) in Ecuador. I. The fungus. Ann appl Biol 89: 185–192

Evans HC (1981) Pod rot of cocoa caused by *Moniliophthora (Monilia) roreri*. Phytopathol. Papers 24. Kew, Commonwealth Mycological Institute, 44 pp

Evans HC (1998) Disease and sustainability in the cocoa agroecosystem. In: Proceedings of the First International Workshop on Sustainable Cocoa Growing, Panama City, 30 March to 2 April, 1998, p 12. Smithsonian Tropical Research Institute, Smithsonian Migratory Bird Center, http://www.si.edu/smbc/evans.htm

Evans HC and Solórzano GR (1982) Witches' broom disease: wrong experiment right result. In: de Laforest J (ed) 8th International Cocoa Research Conference, Cartagena, Colombia, 18–23 October 1991, pp 415–418.

Evans J (1992) Plantation forestry in the tropics. Oxford, Clarendon Press, 403 pp

Ewel J, Benedict F, Berish C, Brown B, Gliessman S, Amador M, Bermúdez R, Martínez A, Miranda R and Price N (1982) Leaf area, light transmission, roots and leaf damage in nine tropical plant communities. Agro-Ecosys 7: 305–326

Fagan HJ (1987) Influence of microclimate on *Drechslera* leaf spot of young coconuts: effect of desiccation on spore survival and of moisture and shade on infection and disease development. Ann appl Biol 111: 521–533

Fazolin M and Estrela JLV (1999) Population and levels of damages of the main pests of bean, corn and rice in an agroforestry system in the Amazon region. In: International Symposium on Multi-strata Agroforestry Systems with Perennial Crops, CATIE, Turrialba, 22–27 February 1999, Extended Abstracts, pp 107–111. CATIE, Turrialba

Fernandes ECM, Davey CB and Nelson LA (1993) Alley cropping on an acid soil in the upper Amazon: mulch, fertilizer, and hedgerow root pruning effects. In: Technologies for sustainable agriculture in the tropics. ASA Special Publication 56, pp 77–96. American Society of Agronomy, Madison

Ferreira JMS, de Lima MF, Santana DLQ and Moura JIL (1998) Pragas do coqueiro. In: Sobrinho RB, Cardoso JE and Freire FCO (eds) Pragas de Fruteiras Tropicais de Importância Agroindustrial, pp 81–118. Embrapa-SPI, Brasilia

Fitzgibbon CD (1997) Small mammals in farm woodlands: the effects of habitat, isolation and surrounding land-use patterns. J Appl Ecol 34: 530–539

Fogain R and Gowen S (1995) Pathogenicity on maize and banana among isolates of *Radopholus similis* from four producing countries of Africa and Asia. Fruits 50: 5–9

Fowler RL, Desrosiers R and Hopp H (1956) Evaluation of certain factors affecting yield of cocoa in Ecuador. Ecology 37: 75–81

Fundecitrus (1998) A maior citricultura do mundo n×o combina com o cancro cítrico. Araraquara, Fundação Paulista de Defesa da Citricultura, 18 pp

Gasparotto L, Santos AF, Pereira JCR and Ferreira AF (1997) Doenças da seringueira no Brasil. Brasília, Embrapa, 168 pp

Gasparotto L and Silva SEL (1999) Novos hospedeiros de *Pellicularia koleroga* no estado do Amazonas. Fitopatologia Brasileira 24: 469

Gasparotto L and Veras SM (1999) Hospedeiros de *Sclerotium coffeicola* no estado do Amazonas. Fitopatologia Brasileira 24: 93

Giller KE and Wilson KJ (2000) Nitrogen fixation in tropical cropping systems, 2nd edition. Wallingford, CAB International

Govindaiah, Dandin SB, Philip T and Datta RK (1991) Effect of marigold (*Tagetes patula*) intercropping against *Meloidogyne incognita* infecting mulberry. Indian J Nematology 21: 96–99

Grout TG and Richards GI (1990) The influence of windbreak species on citrus thrips (Thysanoptera: Thripidae) populations and their damage to South African citrus orchards. J Entomol Soc South Africa 53: 151–157

Guharay F, Monterroso D and Staver C (1999) Designing pest-suppressive multiple-strata crop systems. In: International Symposium on Multi-strata Agroforestry Systems with Perennial Crops, CATIE, Turrialba, 22–27 Feb 1999, Extended Abstracts, pp 80–84. CATIE, Turrialba

Hamelin RC, Beaulieu J and Plourde A (1995) Genetic diversity in populations of *Cronartium ribicola* in plantations and natural stands of *Pinus strobus*. Theor Appl Genet 91: 1214–1221

Hansford CG (1940) Vascular diseases of cotton in Uganda. E Afr Agric J 4: 279–282

Heitefuss R (1987) Pflanzenschutz. Stuttgart, Georg Thieme, 342 pp

Hill DS (1997) The economic importance of insects. London, Chapman and Hall, 395 pp

Hogue CL (1993) Latin American insects and entomology. Berkeley, University of California Press, 536 pp

Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110: 449–460

Huxley PA and Greenland DJ (1989) Pest management in agroforestry systems. A record of discussions held at CAB International, Wallingford, UK, 28–29 July 1988. Agrofor Abstr 2: 37–46

Inostrosa I and Fournier LA (1982) Efecto alelopático de *Gliricidia sepium* (Jacq.) Steud (madero negro). Rev Biol Trop 30: 35–39

Johns ND (1999) Conservation in Brazil's chocolate forest: the unlikely persistence of the traditional cocoa agroecosystem. Environ Manage 23: 31–47

Jones DR (ed) (1999) Diseases of banana, abacá and enset. Wallingford, CAB International, 544 pp

Junqueira NTV, Gasparotto L, Lieberei R, Normando MCS and Lima MIPM (1989) Physiological specialization of *Microcyclus ulei* on different *Hevea* species: identification of pathotype groups. Fitopatologia Brasileira 14: 147

Kapp GB and Beer J (1995) A comparison of agrosilvicultural systems with plantation forestry in the Atlantic lowlands of Costa Rica. Agrofor Syst 32: 207–223

Kokalis-Burelle N, Porter DM, Rodríguez-Kábana R, Smith DH and Subrahmanyam P (1997) Compendium of peanut diseases. St Paul, APS Press, 94 pp

Kranz J (1974) Epidemics of plant diseases. New York, Springer, 170 pp

Krauss U and Soberanis W (1999) A case study on the effect of biological disease control on the rehabilitation of abandoned cocoa (*Theobroma cacao*) farms under two shading regimes and with two application times in Tingo María, Peru. In: International Symposium on Multi-strata Agroforestry Systems with Perennial Crops, CATIE, Turrialba, 22–27 February 1999, Extended Abstracts, pp 116–119. CATIE, Turrialba

Kytö M, Niemelä P and Larsson S (1996) Insects on trees: population and individual response to fertilization. Oikos 75: 148–159

Lal R (1989) Agroforestry systems and soil surface management on a tropical alfisol. I. Soil moisture and crop yields. Agrofor Syst 8: 7–29

Lamprecht H (1986) Waldbau in den Tropen. Hamburg, Paul Parey, 318 pp

Lass RA (1985) Diseases. In: Wood GAR and Lass RA (eds) Cocoa, pp 265–365. Longman, Harlow

Le Pelley RH (1973) Las plagas del café. Barcelona, Labor, 663 pp

Liang W and Huang M (1994) Influence of citrus orchard ground cover plants on arthropod communities in China: a review. Agric Ecosys Environ 50: 29–37

Lim DHK (1980) New developments in shade for hybrid cocoa in Sabah. In: Proceedings of the International Conference on Cocoa and Coconuts, Kuala Lumpur, 1978, pp 122–142. The Incorporated Society of Planters, Kuala Lumpur

Ling AH (1990) Cocoa nutrition and manuring in Malaysia. Planter (Malaysia) 66: 302–312

Lok R and Sandino D (1999) Traditional cocoa agroforestry systems in Waslala, Nicaragua: adoption of technology and adaption to local environment and priorities. In: International Symposium on Multi-strata Agroforestry Systems with Perennial Crops, CATIE, Turrialba, 22–27 Feb 1999, Extended Abstracts, pp 251–255. CATIE, Turrialba

Lukens RJ and Mullamy R (1972) The influence of shade and wet soil on southern corn leaf blight. Plant Dis Rep 56: 203–206

Maclean RH, Litsinger JA, Moody K and Watson AK (1992) The impact of alley cropping *Gliricidia sepium* and *Cassia spectabilis* on upland rice and maize production. Agrofor Syst 20: 213–228

Marín DH (1997) Rotación de cultivos: una opción para el manejo de nemátodos fitoparásitos en la renovación de plantaciones bananeras. Corbana 22: 107–111

Marschner H (1995) Mineral nutrition of higher plants. London, Academic Press, 889 pp

Martins DS and Marin SLD (1998) Pragas do mamoeiro. In: Sobrinho RB, Cardoso JE and Freire FCO (eds) Pragas de Fruteiras Tropicais de Import‚ncia Agroindustrial, pp 143–153. Embrapa-SPI, Brasilia

Mchowa JW and Ngugi DN (1994) Pest complex in agroforestry systems: the Malawi experience. For Ecol Manage 64: 277–284

Michon G and de Foresta H (1999) Agro-forests: incorporating a forest vision in agroforestry. In: Buck LE, Lassoie JP and Fernandes ECM (eds) Agroforestry in Sustainable Agricultural Systems, pp 381–406. Lewis Publishers, Boca Raton

Mitchell MR (1989) Susceptibility to termite attack of various tree species planted in Zimbabwe. In: Boland DJ (ed) Trees for the tropics, pp 215–227. Australian Centre for International Agricultural Research, Canberra

Mobambo KN, Zuofa K, Gauhl F, Adeniji MO and Pasberg-Gauhl C (1994) Effect of soil fertility on the response to black leaf streak of plantain (*Musa* spp., AAB group) under traditional farming systems in southeastern Nigeria. Intern J Pest Manage 40: 75–80

Monteith JL, Ong CK and Corlett JE (1991) Microclimatic interactions in agroforestry systems. For Ecol Manage 45: 31–44

Mossu G (1990) Le cacaoyer. Le Technicien d’Agriculture Tropicale 14. Paris, Editions Maisonneuve et Larose, 160 pp

Muraleedharan N and Chen ZM (1997) Pests and diseases of tea and their management. J Plantation Crops 25: 15–43

Müller E and Loeffler W (1992) Mykologie, 5th edition. Stuttgart, Georg Thieme, 367 pp

Nagarajan S and Singh D V (1990) Long-distance dispersion of rust pathogens. Ann Rev Phytopathol 28: 139–153

Nair PKR (1979) Intensive multiple cropping with coconut in India. Berlin, Paul Parey

Nair PKR and Muschler RG (1993) Agroforestry. In: Pancel L (ed) Tropical Forestry Handbook, pp 987–1057. Springer, Berlin

Nascimento AS, Mesquita AL and Sampaio HV (1986) Planta-armadilha no controle de coleobroca em citros. Inf Agropec , Belo Horizonte 12: 13–18

Newman EI (1991) The role of root-inhabiting fungi in mixed-species plant communities. In: Atkinson D (ed) Plant root growth, pp 437–451. Blackwell Scientific Publications, Oxford

Newman EI (1993) Applied ecology. Oxford, Blackwell Science, 328 pp

Norton RL (1988) Windbreaks: benefits to orchard and vineyard crops. Agric Ecosys Environ 22/23: 205–213

Ortíz CF (1996) Étude de la Diversité Genetique de Populations de *Phytophthora* Pathogenes du Cacaoyer (*Theobroma cacao* L.) et du Cocotier (*Cocos nucifera* L.). PhD Thesis. Toulouse, Université Paul Sabatier, 85 pp

Page SLJ and Bridge J (1993) Plant nematodes and sustainability in tropical agriculture. Expl Agric 29: 139–154

Palm CA (1995) Contribution of agroforestry trees to nutrient requirements of intercropped plants. In: Sinclair FL (ed) Agroforestry: Science, Policy and Practice, pp 105–124. Kluwer Academic Publishers, Dordrecht

Pasek JE (1988) Influence of wind and windbreaks on local dispersal of insects. Agric Ecosys Environ 22/23: 539–554

Perfecto I and Vandermeer J (1996) Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. Oecologia 108: 577–582

Pino M, Dominí M, Terry E, Bertolí M and Espinosa R (1994) El maíz como cultivo protector del tomate en condiciones de estres ambiental. Cultivos Tropicales 15: 60–63

Ploetz RC, Zentmyer GA, Nishijima WT, Rohrbach KG and Ohr HD (1994) Compendium of Tropical Fruit Diseases. St Paul, APS Press, 88 pp

Poncin L (1957) The use of shade at Lukolela Plantations. In: Report of the Cocoa Conference, Grosvenor House, London, pp 281–288. The Cocoa, Chocolate and Confectionery Alliance, London

Power AG and Flecker AS (1996) The role of biodiversity in tropical managed ecosystems. In: Orians GH, Dirzo R and Cushman JH (eds) Biodiversity and Ecosystem Processes in Tropical Forests, pp 173–194. Springer, Berlin

Price NS (1994) Alternate cropping and the management of *Radopholus similis* and *Cosmopolites sordidus*, two important pests of banana and plantain. Intern J Pest Manage 40: 237–244

Ramachandran N, Sarma YR, Anandaraj M and Abraham J (1998) Effect of climatic factors on *Phytophthora* leaf infection in black pepper grown in arecanut-black pepper mixed cropping systems. J Plantation Crops 16: 110–118

Ramamoorthy M and Paliwal K (1993) Allelopathic compounds in leaves of *Gliricidia sepium* (Jacq.) Kunth ex Walp. and its effect on *Sorghum vulgare* L. J Chem Ecol 19: 1691–1701

Rao MR, Nair PKR and Ong CK (1998) Biophysical interactions in tropical agroforestry systems. Agrofor Syst 38: 3–50

Rao MR, Singh MP and Day R (2000) Insect pest problems in tropical agroforestry systems: Contributory factors and opportunities for management. Agrofor Syst (in press)

Resnik FCZ, Vale FXR and CampÍlo AMFL (1980) Patogenicidade de alguns isolados de *Phytophthora* sobre diferentes hospedeiros. Rev Theobr 10: 91–97

Rice NR, Smith MW, Eikenbary RD, Arnold DC, Tedders WL, Wood B, Landgraf BS, Taylor GG and Barlow GE (1998) Assessment of legume and nonlegume ground covers on Coleoptera: Coccinellidae density for low-input pecan management. Am J Altern Agric 13: 111–123

Risch S (1981) Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. Ecology 62: 1325–1340

Risch SJ, Andow D and Altieri MA (1983) Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. Environ Entomol 12: 625–629

Rodríguez-Kábana R (1992) Cropping systems for the management of phytonematodes. In: Grommers FJ and Maas PWT (eds) Nematology from Molecule to Ecosystem. Proceedings of the Second International Nematology Congress, 11–17 August 1990, Veldhofen, pp 219–233. European Society of Nematologists, Dundee

Russell EP (1989) Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environ Entomol 18: 590–599

Sanchez PA (1995) Science in agroforestry. In: Sinclair FL (ed) Agroforestry: Science, policy and practice, pp 5–55. Kluwer Academic Publishers, Dordrecht

Sanchez PA and Leakey RRB (1997) Land use transformation in Africa: three determinants for balancing food security with natural resource utilization. Eur J Agron 7: 15–23

Schellhorn NA and Sork VL (1997) The impact of weed diversity on insect population dynamics and crop yields in collards, *Brassica oleracea* (Brassicaceae). Oecologia 111: 233–240

Schroth G, Balle P and Peltier R (1995a) Alley cropping groundnut with *Gliricidia sepium* in Côte d'Ivoire: effects on yields, microclimate and crop diseases. Agrofor Syst 29: 147–163

Schroth G, Oliver R, Balle P, Gnahoua GM, Kanchanakanti N, Leduc B, Mallet B, Peltier R and Zech W (1995b) Alley cropping with *Gliricidia sepium* on a high base status soil following forest clearing: effects on soil conditions, plant nutrition and crop yields. Agrofor Syst 32: 261–276

Schroth G, Poidy N, Morshäuser T and Zech W (1995c) Effects of different methods of soil tillage and biomass application on crop yields and soil properties in agroforestry with high tree competition. Agric Ecosys Environ 52: 129–140

Schroth G, da Silva LF, Wolf MA, Teixeira WG and Zech W (1999) Distribution of throughfall and stemflow in multi-strata agroforestry, perennial monoculture, fallow and primary forest in central Amazonia, Brazil. Hydrol Process 13: 1423–1436

Schroth G and Zech W (1995) Root length dynamics in agroforestry with *Gliricidia sepium* as compared to sole cropping in the semi-deciduous rainforest zone of West Africa. Plant Soil 170: 297–306

Sequeira L (1958) The host range of *Mycena citricolor*. Turrialba 8: 136–147

Sheehan W (1986) Response by specialist and generalist natural enemies to agroecosystem diversification: a selective review. Environ Entomol 15: 456–461

Sinclair FL, Verinumbe I and Hall JB (1994) The role of tree domestication in agroforestry. In: Leakey RRB and Newton A (eds) Tropical trees: potential for domestication and the rebuilding of forest resources, pp 124–136. HMSO, London

Singh Rathore MP (1995) Insect pests in agroforestry. Working Paper No. 70. Nairobi, International Centre for Research in Agroforestry, 73 pp

Sivapalan P, Senaratne KADW and Karunaratne AAC (1977) Observations on the occurrence and behaviour of live-wood termites (*Glyptotermes dilatatus*) in low-country tea fields. PANS 23: 5–8

Smith ESC (1981) The interrelationships between shade types and cocoa pest and disease problems in Papua New Guinea. In: 7th International Cocoa Research Conference, Douala 1979, pp 37–43. Cocoa Producers' Alliance, Lagos

Smyth TJ and Cassel DK (1995) Synthesis of long-term soil management research on Ultisols and Oxisols in the Amazon. In: Lal R and Stewart BA (eds) Soil Management – Experimental Basis for Sustainability and Environmental Quality, pp 13–59. Lewis Publishers, Boca Raton

Sobrinho RB, Cardoso JE and Freire FCO ((1998) Pragas de fruteiras tropicais de importância agroindustrial. Brasilia, Embrapa-SPI, 209 pp

Soto SS and Madrigal HC (1998) Presencia de *Aphis craccivora* Koch (Homoptera: Aphididae) en plantaciones de cacao en Tabasco, Mexico. Agrotrópica 10: 47–48

Stamps WT and Linit MJ (1998) Plant diversity and arthropod communities: Implications for temperate agroforestry. Agrofor Syst 39: 73–89

Stover RH and Simmonds NW (1983) Bananas. Harlow, Longman, 468 pp

Subramaniyan S and Selvaraj P (1990) Effect of antagonistic intercrops on burrowing nematode in Robusta banana. South India Horticult 38: 216–217

Tarte R, Pinochet J, Gabrielli C and Ventura O (1981) Differences in population increase, host preference and frequency of morphological variants among isolates of the banana race of *Radopholus similis*. Nematrópica 11: 43–52

Thurston JL (1998) Tropical plant diseases, 2nd edition. St Paul, APS Press, 200 pp

Trocmé O (1972) Contribution à l'étude d'une maladie du cacaoyer en Ouganda: le dessèchement éco-fongique des branches. Café Cacao Thé 16: 219–235

van Noordwijk M (1999) Tree-tree interactions and regeneration strategies for rubber agroforests. In: International Symposium on Multi-strata Agroforestry Systems with Perennial Crops, CATIE, Turrialba, 22–27 February 1999, Extended Abstracts, pp 161–164. CATIE, Turrialba

Vandermeer JH and Perfecto I (1998) Biodiversity and pest control in agroforestry systems. Agroforestry Forum 9: 2–6

Vargas A (1997) Cultivo de banano (*Musa* AAA) y plátano (*Musa* AAB) en presencia y ausencia de una cobertura vegetal viva (*Arachis pintoi* CIAT-18748). Corbana 22: 23–29

Ventkata Ram CS (1979) Factors influencing germination, penetration and lesion development on tea leaves following deposition of *Exobasidium vexans* spores. Proc Placrosym 2: 193–204

Venturieri GA (1993) Cupuaçu: a especies, sua cultura, usos, e processamento. Belem, Clube do Cupu, 108 pp

Vicente-Chandler J, Abruna F and Silva S (1966) Effect of shade trees on five crops in the humid mountain region of Puerto Rico. J Agric Univ Puerto Rico 50: 218–225

Virgens Filho A C, Alvim R and Araújo A C (1987) Plantio de cacaueiros sob seringais adultos na região sul da Bahía. In: 10th International Cocoa Research Conference, Santo Domingo, Dominican Republic, 17–23 May, 1987, pp 33–38

Walker JC and Stahmann MA (1955) Chemical nature of disease resistance in plants. Ann Rev Plant Physiol 6: 351–366

Waller JM (1972) Water-borne dispersal of coffee berry disease and its relation to control. Ann appl Biol 71: 1–18

Way MJ and Khoo KC (1991) Colony dispersion and nesting habits of ants, *Dolichoderus thoracicus* and *Oecophylla smaragdina* (Hymenoptera: Formicidae), in relation to their success as biological control agents on cocoa. Bull Entomol Res 81: 341–350

Webster CC and Wilson PN (1980) Agriculture in the tropics. London, Longman, 640 pp

Wielemaker F and Quirós (1997) Banana production with ‘Pinto’s peanut’ (*Arachis pintoi* cv. Amarillo) and ‘oreja de raton’ (*Geophila repens*) as cover crops. In: Yglesias J (ed) Primer Taller Internacional sobre Control Biologico y Producción Integrada en el Cultivo de Banano, pp 84–99. EARTH, Guácimo, Costa Rica

Willey RW (1975) The use of shade in coffee, cocoa and tea. Hortic Abst 45: 791–798

Xu ZH, Myers RJK, Saffigna PG and Chapman AL (1993) Nitrogen cycling in leucaena (*Leucaena leucocephala*) alley cropping in semi-arid tropics II. Response of maize growth to addition of nitrogen fertilizer and plant residues. Plant Soil 148: 73–82

Yamoah CF and Burleigh JR (1990) Alley cropping *Sesbania sesban* (L) Merill with food crops in the highland region of Rwanda. Agrofor Syst 10: 169–181

Zakra N, Pomier M and de Taffin G (1986) Premiers résultats d’une expérience d’association cocotiers-cultures vivrières en Moyenne Côte d’Ivoire. Oléagineux 41: 381–389