

Effect of Nutrition and Soil Function on Pathogens of Tropical Tree Crops

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1. Introduction

Crops grown in the tropics are subject to different kinds of disease pressure from those produced in temperate regions. The greater biodiversity found in the tropics, including diversity of fungi, is reflected by the larger number of pathogen species in tropical regions (see Ploetz, 2007; Wellman, 1968, 1972). Perennial crops, and tropical perennials in particular, have features in common that may predispose them to pathogen infections. Pathogen inocula, such as microsclerotia, may build up from year to year in perennial crops (Pennypacker, 1989). Also, tropical conditions are usually suitable for the year-round survival and propagation of pathogen species, unlike temperate climates which have a cooler season when pathogen populations die off or are reduced. Tropical perennial crops often include susceptible genotypes on the farm and the presence of susceptible host material encourages the production of inoculum and the initiation of new infections (Ploetz, 2007). Ploetz (2007) remarks that the presence of susceptible hosts is a particularly important barrier to disease control in tropical perennials.

Diseases in the tropics may be complicated by interactions between different pathogens, or between pathogens and insect pests (Holliday, 1980; Ploetz, 2006; Vandermeer et al., 2010; Anonymous, 2010). Disease complexes involving a number of fungal pathogens or fungi and nematodes are common in tropical situations. Interactions between pathogens and environmental stress may also occur. Crops can become more susceptible to pathogen infections when weakened by environmental stress such as drought, temperature extremes, and exposure to sunlight or wind (Agrios, 2005). Stressed plants, or plants sustaining damage caused by insects or other pathogens, may also be susceptible to attack by secondary pathogens or pathogens that infect through wounds (Palti, 1981). Nutrient deficiencies may increase the susceptibility of crops to disease. In tropical perennial crops, poor plant nutrition is likely to be a particularly important contributing factor to production losses (Schroth et al., 2000). In addition to lower production due to nutrient deficiency, low nutrition may predispose plants to diseases, increasing losses further. Nutrient deficiency causes the plant to become weakened and generally more susceptible to infection. Under such conditions, infection by weakly pathogenic species that would normally cause few problems may become more serious. The incidence and severity of particular diseases may also be linked to deficiencies of particular nutrients. However, much more research has been

conducted on the relationships between particular nutrients and diseases in annual crops, than in perennial species, particularly tropical perennials.

Many tropical perennials are grown in an agroforestry situation with other crop species. Unlike the situation with annual cropping, there are fewer opportunities to include fallow periods or rotations in perennial systems during which inoculum loses its viability and the system can in general 'recover'. In tropical perennial systems, soil-borne pathogens, such as nematodes, may build up over time. An important aim in the management of these systems is to achieve a position of equilibrium between pests/diseases and the predators and parasites that keep them in check (Schroth et al., 2000). Furthermore, as perennial crops are present more or less permanently in the system, they remove nutrients on a continuous basis, without a fallow period during which soil fertility can be restored. In this light, the role of the nutrient status of tropical perennials in mitigating disease is an important topic and deserves attention from researchers.

Many diseases of tropical perennial crops are "new encounter" diseases which develop following production in new areas outside of the region of the crop's origin (Ploetz, 2007). At first, such plantings may enjoy a mainly disease-free period with high productivity. They are removed from the pressures of co-evolved pathogens and pests in their region of origin. However, such a 'honeymoon' period ends when new fungal pathogens (as well as other pathogens and pests) transfer from hosts indigenous to the region in which the crop is being produced (Keane and Putter, 1992). The indigenous hosts often remain unidentified. This is largely because the fungus causing the new disease often resides asymptotically on its original host plant (for example, as an endophyte) (Ploetz, 2007). New encounter diseases may cause devastating losses. Unlike co-evolved pathogens in the region of the crop's origin, new encounter pathogens have few antagonists that could reduce disease incidence or severity. Poor growing conditions and poor farm management may further exacerbate the situation.

2. Role of plant nutrition in mitigating disease

Most studies on the role played by individual nutrients in preventing or reducing disease have been conducted on temperate crop species, or on tropical annuals such as rice. Little attention has been paid to the role of nutrition in alleviating diseases of tropical tree crops. However, for some diseases of tropical perennial species, a link is often observed between a deficient nutrient status caused by low soil fertility or poor plant nutrition and disease severity (Desaeger et al., 2004). Generally, plants stressed by various environmental limitations may be weakened and more vulnerable to disease and these include nutrient-deficient plants. Nutrient-deficient plants may be particularly susceptible to infection by facultative pathogens (Palti, 1981). Pathogens that are mild in normal conditions of plant growth and exist mainly as saprophytes or endophytes, such as some *Fusarium* spp. and *Alternaria* spp., may cause severe disease under conditions of nutrient stress or aluminium toxicity (Desaeger et al., 2004).

Adequate nutrition helps to mitigate pest/disease damage by replacement of root and shoot tissues (Marschner, 1995). However, studies conducted on other crop species, especially temperate crops, have elucidated how particular nutrients, including micronutrients, may

enhance disease prevention. Further studies are needed to ascertain whether nutrient elements have similar roles in tropical perennial crops.

Macronutrient elements

In tropical perennials crops, as in annuals, disease is often a consequence of inadequate nutrition, particularly of *nitrogen* (N). Low supplies of N may predispose plants to infections by facultative parasites such as *Fusarium* spp. However, most research on the effect of N supply on disease has been conducted on temperate annuals (Agrios, 2005; Jones et al., 1989; Palti, 1981). For example, diseases in species of the Solanaceae family including *Fusarium* wilt, *Alternaria* early blight, *Pseudomonas solanacearum* wilt, *Sclerotium rolfsii* and *Pythium* damping off are increased under low N conditions (see Agrios, 2005). Vascular wilts caused by *F. oxysporum* in the annual crops tomato, cotton and pea, as well as *Alternaria* blights of a number of crops, may also be increased under low N conditions (Palti, 1981).

In contrast to cases where a low N supply predisposes crops to disease, research on annual crops has demonstrated that an excessive N supply increases disease or damage caused by some pests and pathogens (Jones et al., 1989; Palti, 1981 p.136). Pest and pathogen attack of above ground parts of the plant may be encouraged by high N in the presence of low K and P (Desaeger et al., 2004); a high N/K ratio encourages insect herbivory by increasing the content of free amino acids in plant tissues (Marschner, 1995). A number of studies with cereals and other crops have shown that obligate pathogens in particular, such as *Puccinia* spp. causing rust and other biotrophs, can be encouraged by a high N supply (see Palti, 1981). For example, an increase in rice blast disease (*Magnaporthe grisea*) was observed in upland rice, which had been treated with the green manure of an alley crop with a high N content (Maclean et al., 1992). Possibly excess N might also favour the development of infections by obligate fungal parasites in tropical perennials although there is little evidence for this. For example, a poor nutrient status in coffee plants has been reported to predispose them to rust infection (Waller et al., 2007 p. 302).

The form of N supplied can be a significant factor in plant disease. A supply of ammonium-N may predispose plants to certain diseases, while nitrate-N is favourable for the development of others (Palti, 1981). For example, *Fusarium* wilt severity in some crops is greater when N is supplied as ammonium, while *Verticillium* wilts are enhanced by a nitrate-N supply (see Section 4.1). Possibly this is connected to a pH effect in the rhizosphere. *Fusarium* wilts are favoured by acidic soils and *Verticillium* wilts by a higher soil pH (see Palti, 1981). Uptake of ammonium-N occurs in exchange for protons (H⁺ ions), causing a decrease in pH in the rhizosphere while nitrate uptake has the opposite effect on pH as OH⁻ ions are pumped out by roots in exchange for NO₃⁻ ions (Rice, 2007). Pathogenic fungi may be particularly sensitive to localised changes in the rhizosphere, such as pH fluctuations.

Some tropical perennial crops, notably banana, coffee, coconut and cocoa, have a high demand for *potassium* (K), suggesting that K deficiency may occur in areas that produce these crops over a long-term (see Section 3, below). This is particularly the case in areas planted with perennials that receive insufficient levels of fertiliser. In agroforestry farming systems, mulch from woody biomass (e.g. pruned branches) can be a good source of K and, conversely, as K is sequestered by woody species, this may create K-deficiency in sites which already have low levels of K in the soil (Beer et al., 1998). Potassium is a mobile

element with multiple functions in the plant. It acts as a counter-ion for anion transport, regulates stomatal aperture and the water potential of plant cells, affects cell wall plasticity, as well as other roles (Rice, 2007). It promotes wound healing and decreases frost injury (Palti, 1981). Potassium deficiency has been found to be linked to diseases in a number of temperate crops (see Palti, 1981) and a high K supply can improve resistance of plants to fungal and bacterial pathogens (Marscher, 1995; Perrenoud, 1977; 1990). The mechanism of resistance in some disease-resistant genotypes might be related to a greater efficiency in K uptake (Prabhu et al., 2007). The N/K ratio can affect resistance: if it is too high cells have thinner cell walls and weaker membranes and are more prone to pathogen attack (Perrenoud, 1990; Potash Institute, www.ipipotash.org). For similar reasons, cereals may become more prone to lodging. A low potassium/chlorine (K/Cl) ratio in plant tissues, which might result from the application of chloride-containing compounds such as ammonium fertilisers, may predispose plants to disease (e.g. wheat rust caused by *Puccinia* spp. or other diseases, see Prabhu et al., 2007; Jones et al., 1989). K-deficiency increases the concentration of soluble sugars in leaf tissues providing a substrate for many pathogens (Potash Institute, www.ipipotash.org). It is likely that the susceptibility of tropical perennial crops to some pathogens is also increased under conditions of K deficiency. In a study on tea plants, for example, a high K supply reduced nematode and borer damage (Muraleedharan and Chen, 1997). Another study showed that supplying K reduced Fusarium wilt in oil palm (Turner et al., 1970). However, few research studies have been conducted that could confirm a link between K nutrition and disease incidence or severity in tropical perennial crops.

Phosphorus (P)-deficiency is especially limiting to production of perennial crop in many tropical soils. Most P in the soil is in a fixed form (unavailable to plants) and the proportion of fixed P is increased at low soil pH levels (see Rice, 2007). Very low levels of available P are found in acid tropical soils (Mengel and Kirkby, 1982 p. 471). Woody biomass is very low in P, unlike K, and, therefore, external sources of P are often necessary in farm management (Beer et al., 1998). Phosphorus nutrition improves crop vigour and may decrease severity of diseases through new growth (Smyth and Cassell, 1995; Buresh, 1997). Improved root growth by P nutrition may allow the plant to 'escape' attack by soil-borne fungal pathogens or nematodes (Prabhu et al., 2007). Foliar application of phosphates may decrease diseases such as powdery mildew (Reuveni and Reuveni, 1998). Incidence of anthracnose (caused by *Colletotrichum lindemuthianum*) in susceptible cowpea cultivars was found to be higher in plants grown without applied P than in plants grown with P supplied at rates up to 80 kg of P fertiliser/ha (Adebiton, 1996). In the same study, disease severity in all of the cowpea cultivars tested was also decreased by P amendment and chickpea genotypes with resistance to *Ascochyta* blight had higher tissue concentrations of P and K than susceptible genotypes, which had a higher N content.

Mycorrhizal fungi, which form symbiotic associations with the roots of tropical perennials, such as coffee and banana, play a crucial role in accessing sources of P for their host plants. These fungi can access sources of P in the soil that are unavailable to non-mycorrhizal plant roots. As well as decreasing the impacts of plant pathogens (Azco'n-Aguilar and Barea, 1996), mycorrhizal plants have higher contents of certain nutrients, such as P. An example of this was demonstrated by greenhouse experiments conducted on coffee by Vaast et al. (1997). Coffee plants inoculated at an early stage with AM fungi had higher tissue P contents than non-mycorrhizal plants. High P tissue contents were maintained following inoculation with the nematode pathogen *Pratylenchus coffeae* and these plants also had fewer root lesions

than non-mycorrhizal plants inoculated with the nematode or mycorrhizal plants that had been inoculated with the AM fungi at a later stage. Care needs to be taken with supplying inorganic P to crops as an excessive external P supply can inhibit mycorrhizal development. This may lead to a shortage of other nutrients, such as zinc, that mycorrhizal roots are efficient at accessing for the plant (Andrade et al., 2009).

An adequate supply of calcium (Ca) has been demonstrated to enhance resistance to a number of diseases in annual crop species caused by pathogens such as *Rhizoctonia solani*, *Sclerotium* spp., *Botrytis* spp., *Fusarium oxysporum* and the nematodes *Meloidogyne* spp. and *Pratylenchus* sp. (Agrios 2005; Jones et al., 1989). Resistance of lucerne to nematodes was shown to increase with supplied Ca (see Palti, 1981 p. 142). A large proportion of Ca in plants is present in the apoplast and, influences cell structural properties, especially of the cell wall (Rice, 2007). Increased levels of Ca-pectate complexes in the cell wall are likely to increase resistance to vascular wilt pathogens because this form of pectate is resistant to breakdown by endopolygalacturonase enzymes produced by fungi to degrade pectin in the xylem vessel walls. Ca-pectin complexes might also impede the progress of wilt pathogens growing within the xylem (Corden, 1965; Pennypacker, 1989; Waggoner and Dimond, 1955). However, Ca also has metabolic functions within the symplast as a secondary messenger in signalling pathways (Rice, 2007). Calcium possibly plays a significant role in mechanism(s) of disease resistance in fruits. A relatively large proportion of Ca taken up by plants is distributed to fruits and low Ca has been linked to increased incidence of fruit diseases such as brown-eye spot in coffee berries (see Section 4.2). Groundnut pods have a high Ca demand and pod rot caused by *Pythium* and *Rhizoctonia* spp. has been linked to a low Ca content. High rates of magnesium and K application can reduce the Ca content of pods, increasing disease severity (Prabhu et al., 2007)

Sulphur (S) is a component of defense-related peptides and proteins such as glutathione and phytoalexins. Application of S to deficient soil reduced leaf spot, caused by *Pyrenopeziza* in oil seed rape and stem canker caused by *Rhizoctonia solani* in potato (Haneklaus, 2007). The effect of S nutrition on diseases of tropical perennials is largely unknown. However, deposits of elemental sulphur (S) were observed in the xylem of cocoa plants in response to infection with *Verticillium dahliae* (Resende et al, 1996; Cooper and Williams, 2004). Similar findings were made in tomato (Williams et al., 2002 – see Haneklaus, 2007). Elemental S is toxic to some fungal pathogens and may be considered to be a phytoalexin in its own right (Resende et al., 1996). Magnesium (Mg) is an essential component of chlorophyll and, therefore, the photosynthetic systems of plants. However, a direct relation between Mg and plant disease has been less commonly demonstrated than with the other macronutrient elements. Magnesium, with K, plays a role in phloem-loading of sugars (Cakmak et al., 1994). Magnesium also activates enzymes such as glutathione synthetase.

Micronutrient elements

Micronutrients have a diverse range of functions in plants: for example, as enzyme co-factors with redox roles and, in the case of elements such as boron and silicon, in tissue strengthening or structural functions. The numerous biochemical functions of micronutrients are reflected by their roles in a diverse range of mechanisms of disease resistance. Zinc (Zn) nutrition appears to be involved in resistance to many diseases. The mechanisms involving Zn in disease resistance are unclear but Zn acts as a co-factor for numerous enzymes (Rice, 2007). Stimulation of root growth by Zn may account for some

observed cases of disease resistance (Duffy, 2007). Zinc application to soils reduces attack by root pathogens of tomato, including *Fusarium solani*, *Rhizoctonia solani* and *Macrophoma phaseoli*, and also *Rhizoctonia* root rots of wheat, chickpea, cowpea and medicago (Duffy, 2007; Gaur and Vaidge, 1983; Kalim et al., 2003; Streeter et al., 2001). In tropical perennials, the role of Zn in disease resistance remains to be investigated. However, Zn-deficiency in rubber (*Hevea brasiliensis*) predisposes the tree to infection with *Oidium heveae* (Duffy, 2007). Zinc has been reported to alleviate *Phytophthora* diseases. Low Zn levels in soils and leaf tissues were associated with a high incidence of *Phytophthora* pod rot (or black pod) of cocoa in Papua New Guinea (Nelson et al., 2011). Supplying *Manganese* (Mn) has been shown to alleviate various diseases in a number of crop plant species (Palti, 1981; Thompson and Huber, 2007). Manganese occurs in different redox states and while it is present in healthy tissues as the Mn^{2+} ion, it accumulates at sites of pathogen attack in the Mn^{4+} form, for example in rice affected by blast (Thompson and Huber, 2007). *Iron* (Fe) has an essential role in plant cells as a co-factor in redox reactions and other functions. Fe is mainly available to plants as its reduced ion, Fe^{2+} . *Verticillium* wilt in mango caused by *V. albo-atrum*, and in groundnut caused by *V. dahliae* was mitigated in both cases by the application of Fe in chelated form (see Palti, 1981 p. 142). On the other hand, control of *Fusarium* wilt in tomato was favoured by low Fe (Woltz and Jones, 1981). Similarly, *Fusarium* wilt has been shown to be lower at low levels of Mn. *F. oxysporum* has a particularly high demand for some micronutrient elements, especially Mn, Fe and Zn (Jones et al., 1989; Woltz and Jones, 1981). The supply of Mn, Fe and possibly other nutrients, to *F. oxysporum* strains causing vascular wilt may therefore increase disease incidence and/or severity (see section 4.1, below).

The availability of other micronutrients to plants has been linked to disease alleviation in particular instances. *Copper* (Cu) deficiency decreases lignification in the xylem and has been linked to lodging in cereals (Evans et al., 2007). Copper has direct toxic effects on pathogens as well. A Cu supply protects grapes and hops from Downy mildew, caused by *Plasmopara viticola* and *Pseudoperonospora humuli*, respectively (see Evans et al., 2007). *Nickel* (Ni), like Fe and Zn, is a co-factor of some enzymes, such as ureases, which break down urea into less toxic forms (Rice, 2007). Nickel application has been shown to reduce brown spot in rice (caused by *Cochliobolus miyabeanus* syn. *Helminthosporium oryzae*). Supplying *molybdenum* (Mo) reduced late blight in potato and *Ascochyta* blight in beans and peas (Palti, 1989 p. 143). As a co-factor of nitrate reductase, this element plays a particularly important role in the reduction of nitrate to ammonium (Rice, 2007).

Silicon (Si), now regarded as an essential micronutrient, has been shown to enhance disease resistance in many instances (Datnoff et al., 2007). In sugar cane, ring spot was alleviated by Si amendments (see Datnoff et al., 2007). Low Si in rice has been linked to susceptibility to a number of pathogens including *Pyricularia*, *Sclerotium oryzae*, *Cochliobolus* and *Xanthomonas oryzae* (Palti, 1981 and references within). A supply of Si enhances resistance to rice blast (Datnoff et al., 2007). Supplying Si to coffee reduced leaf disease and nematode infections in roots (see Sections 4.2 and 4.5). Possibly Si, with other nutrients such as Ca and *boron* (B), influences cell wall properties and enhances mechanical strengthening of tissues (Rice, 2007). Shen et al. (2010) tested the effect of potassium silicate on *in vitro* growth of some plant pathogens, including *Fusarium oxysporum*, *Rhizoctonia solani* and *Pestalotiopsis clavispora*, finding no influence if the media pH was maintained at the same level as the control. They suggested that the mechanism by which Si confers resistance may be related to provision of a physical barrier to pathogen infection or to the induction of a defense

response in the host, rather than to a chemical effect. Silicon and other elements, including Ca and B, may be of particular importance in resistance to facultative pathogens, wound invading pathogens and nematode infections.

3. Management of soils supporting tropical perennial crops

Since many tropical soils are nutrient-poor and the replacement of nutrients by mineral or organic fertilisers is often inadequate, tropical perennial crops are particularly prone to nutrient stress. Growing perennial crops can lead to nutrient deficiencies if the soils in which they are grown are not adequately amended with mineral or organic fertilisers. Long-term cropping of one or a few species in tropical soils can also have other impacts on soil properties, such as the soil pH, that in turn may cause nutrient deficiencies. In addition, poor sanitation (e.g. removal of infected plant material), flooding (which may spread inoculum as well as causing plant stress) and inappropriate canopy management are common exacerbating factors leading to increases in disease incidence and severity on a farm (Kohler et al., 1997). Importantly, disease may also have the effect of reducing the plants' nutrient status or impairing water uptake. For example, coffee tree roots and the roots of other tree crops infected with nematodes or fungi may have impaired water and chemical uptake mechanisms causing wilting and nutrient deficiency (Nelson et al., 2002; Waller et al., 2007 p. 279).

Table 1 presents data on nutrient uptake by some tropical perennial crops based on previous studies. The data refer only to the nutrient content of marketable products; the nutrients contained in waste (e.g. discarded tea leaves and coffee or cocoa beans) are not included. In the case of nutrients removed by cocoa in Nigeria (reported by Wessel, 1985), it can be seen that the pod husks, which are normally discarded, remove high amounts of K (77 kg ha⁻¹y⁻¹ in the husks of pods producing one ton of dry beans). Substantial amounts of Ca are also removed with cocoa pods and other fruit products.

	Yield	Nutrients removed (kg ha ⁻¹ y ⁻¹)		
		N	P	K
Coffee	1000 kg beans	40	2	42
Rubber	Latex	6-36	1-7	5-31
Tea	1000 kg leaves (dry)	41	3	21
Banana	40 - 70 tonnes	225-450	20-40	800-1200
Coconut	6920 nuts	96	19	115
Cocoa	1000 kg beans (dry)	23	4	8
	Cocoa pod husks	17	2	77

Table 1. Estimated removal of N, P and K from the soil by the harvested products of some tropical tree crops. Yields indicated for each crop are estimates of the quantity of produce obtained per hectare each year (sources: Krauss, 2003; Wessel, 1985). Note that where the quantities removed were given for the oxides of P and K in the original data, these figures have been converted to indicate the respective quantities of the elements removed.

Soil acidity or low pH, common in the tropics, may be increased under particular crops, especially long-term perennial crops, or by the application of some kinds of mineral fertiliser (Jones et al., 1989). Soil pH decreases when forest soils are turned over to perennial crops, such as coffee and cocoa (Beer, 1988; Beer et al., 1998; Hartemink, 2005). Lowering soil pH decreases the availability of basic cations, particularly Ca and Mg. However, increased soil

acidity increases the availability of other cations to plant roots. These include the cations of Mn and aluminium (Al) which can reach toxic levels as their uptake by plants increases. The proportion of soil P that is fixed and unavailable for plant uptake increases in acid conditions (Mengel and Kirkby, 1982). Liming can reduce the severity of a number of diseases perhaps by increasing the availability of a number of nutrients to crops, as well as providing a source of Ca, reducing Al toxicity and improving soil structure (Palti, 1981 p. 142). The increase in pH in limed soils also favours the growth of bacteria, including actinomycetes, which include species that are antagonistic to fungal pathogens (Palti, 1981 p. 29; Jones et al., 1989).

Shade and nutrition

Tropical perennials produced in agroforestry systems are affected by other species on the farm, including shade trees in the case of shade-requiring tree crops such as cocoa and coffee (Schroth et al., 2001). Importantly for such shade-requiring species, managed shade can reduce incidence and severity of some pests and diseases. Shade may also reduce stress to tree crops by preventing extremes in temperature, water loss etc. that may result from exposure (Staver et al., 2001). This, in turn, mitigates diseases that become more severe in stressed plants. Removal of shade can increase photosynthesis and, therefore, raise the productivity of tree crops such as coffee and cocoa. The removal of shade from coffee farms, for example, can provide double the yields of shaded coffee in the short-term (Waller et al., 2007). However, this may be followed by impacts from other problems, including increased susceptibility to diseases such as brown-eye spot (see Section 4.2), wind and storm damage, frost damage at higher altitudes, increased evapotranspiration (and water loss) and lower levels of soil organic matter (Waller et al., 2007 p. 313). Conditions such as overbearing dieback and sunscorch of coffee (see Section 4.4) may result from shade removal. Other twig and leaf blights, such as anthracnose caused by *Colletotrichum gloeosporioides* on cocoa grown in Indonesia become more severe following shade removal (Agus Purwantara, pers. comm.). Conversely, excessive shade and inadequate pruning can provide suitable conditions for other coffee and cocoa pathogens, such as *Corticium* spp. (causing web blight and pink disease), *Phytophthora palmivora* (causing pod rot and other diseases in cocoa) and *Mycena citricolor* (causing South American leaf spot in coffee). Shade trees may be sources of other pathogens with wide host ranges such as the root pathogens *Armillaria* and *Ganoderma* spp.

Shade trees have a mixed effect on the plant nutrition of other crops in the agroforestry system (Schroth et al., 2001). They may compete with crops for water and nutrients in the soil and sequester nutrients in their biomass (Palm, 1995). However, they also provide inputs of nutrients to the system through leaf litter or by nitrogen-fixation. In Central America, *Cordia alliodora* shade trees on each hectare of coffee produce 5.7 tons of leaf litter per year, containing 114 kg N, 7 kg P and 54 kg K (Beer, 1988). Forest trees providing shade for cocoa in West Africa produced 5 tons of leaf litter per hectare each year, containing 79 kg N and 4.5 kg P (Murray, 1975). Legume shade trees in cocoa and coffee agroforestry systems provide approximately 60 kg N ha⁻¹y⁻¹ by biological fixation of N₂ (Beer, 1988). However, some legumes may cause decreases in soil pH. Somarriba and Beer (2011) reported that timber species grown with cocoa did not impact cocoa production. Shade trees with relatively deep roots can remobilise nutrients in the system (Schroth et al., 2001). Beer et al. (1998) cite reports of lower leaching rates of N under shaded coffee (9 kg ha⁻¹y⁻¹) than under unshaded coffee (24 kg ha⁻¹y⁻¹).

4. Diseases of tropical perennial crops in relation to nutrient and other growing conditions

The main types of disease that impact production and performance of major tropical perennials and the conditions that influence disease incidence and/or severity, particularly nutrition and soil function, are outlined below. Most of the diseases described are caused by new encounter pathogens, while some such as witches' broom disease of cocoa in South America and coffee wilt disease, which has caused severe losses and tree death in East Africa, are caused by co-evolved pathogens. While each group of diseases (e.g. dieback diseases) has common features that relate to their management and control, it should be noted that pathogens from widely separate taxonomic groups may cause similar symptoms common to a particular type of disease. Therefore, control measures to reduce plant diseases need to take into account the taxon of the pathogen as well as the type of disease it causes. Diseases of tropical crops are often complex being associated with more than one pathogen or pest, or transmitted by vectors. Conversely, a particular pathogen species may cause more than one disease. Therefore, the disease groupings outlined below may overlap with each other considerably.

4.1 Vascular wilts

Vascular wilts can cause serious losses for a number of tropical perennial crops. Vascular wilts may be soil-borne with infections initiated in the roots, as in many wilts caused by *Fusarium oxysporum*, or else they may be initiated in the phyllosphere, especially by infections via wounds as occurs in many *Ceratocystis* wilts, caused by *Ceratocystis fimbriata* and closely related species on a wide range of crop hosts. Coffee wilt (tracheomycosis) attributed to *Gibberella xylarioides* (anamorph: *Fusarium xylarioides*) has become a serious disease problem in Robusta coffee-growing areas of East Africa (Rutherford, 2006; Flood, 2010). An adequate nutrient supply to coffee trees is recommended as part of an integrated strategy to manage this disease (e.g. see www.nyruussell.com/all-about-coffee). Wounding caused by nematodes in the roots or by insects in aerial parts may increase the possibility of infection by fungi causing soil-borne diseases, including wilts. In coffee, for example, infection with nematodes can predispose plants to infection with *F. oxysporum* (Kohler et al., 1997; Nelson, 2002).

Insects may also transmit disease by carrying spores to wounded tissues or by producing insect frass containing spores that can be dispersed by wind. For example, species of *Ambrosia* beetles are attracted to cocoa tissues infected with *Ceratocystis* spp. and insect frass containing their spores may be disseminated to other plants by wind. Vascular wilts have in some cases been linked to environmental factors, such as drought stress. Drought-stressed plants are more susceptible to *Ceratocystis* wilt (Harrington, 2004). Vascular wilt diseases are complicated by the fact that plants may be more susceptible to the causal pathogen in conditions of water or nutrient deficiency but that, additionally, the pathogen may impair transport in the vascular tissues thus causing water or nutrient deficiency in the plant tissues.

Wilts caused by host-specific races of *F. oxysporum* occur in a number of crop species. Panama disease of banana caused by *F. oxysporum* f. sp. *cubense* is particularly devastating (Ploetz, 2006). Following infection of the root, the fungus enters the vascular system and impedes water and nutrient transport to the upper plant. The leaves of infected banana plants become yellow and dry and the plant eventually wilts. The pathogen can be spread through flooding and, therefore, drainage and prevention of over-irrigation are particularly

necessary. As the pathogen can be harboured by the bunch stalks, sanitation measures should be applied (Kohler et al., 1997). Some studies on *F.oxysporum* wilts suggest that nutrient availability to both the plant and the pathogen may affect the level of disease severity. The factor(s) causing the wilt are unclear: in Fusarium wilt of tomato it has been attributed to physical blockage or by the secretion of toxins (Walker, 1972 p. 300). Reducing soil acidity by liming is used to reduce *F. oxysporum* infection of coffee plants (Kohler et al., 1997). Possibly, liming reduces the availability of some micronutrients to the fungus. As mentioned previously, *F. oxysporum* has a particularly high demand for some micronutrients, including Mn, Fe and Zn. Mn may be in particular demand by the pathogen. Jones and Woltz (1972) showed that the control of Fusarium wilt of tomato by liming could be reversed by supplying Mn in chelated form to the limed soils. Liming may also help to control Fusarium wilts by changing the soil microbial populations. Under conditions of high pH, bacteria, including actinomycete, populations increase, including those of antagonistic species (Jones et al., 1989). Increased calcium supply to the plant has been shown to reduce the severity of Fusarium wilt of tomato (Walker, 1972 p. 303). The mechanism involved may be related to the increase in resistance conferred by Ca to enzymatic breakdown of pectate compounds by the fungus, which might also account for the effect of Ca supply on reducing Verticillium wilt (see below).

As mentioned previously, the form of N that is present in the soil, whether as nitrate or ammonium ions can influence the incidence and severity of vascular wilts (see Section 2). Application of N as ammonium fertiliser can increase Fusarium wilt: this has been suggested to be an effect of increased acidity or related to a reduction in the K/Cl ratio (Jones et al., 1989). A study on Fusarium wilt of banana by Nasir et al. (2003) suggested that the effect of the form of N supplied on disease severity is not related to the activity of the pathogen. When banana plantlets were transplanted into soils infested with *F. oxysporum*, an increase of wilt disease severity and the invasion of roots by the pathogen were found to be independent of *F. oxysporum* activity in the soil (Nasir et al, 2003). Amendment of soil with chicken manure increased disease severity, but not *F. oxysporum* activity; it appeared that the increase in disease and pathogen invasion was a consequence of supplying N as the ammonium-form but that this was not connected to pathogen activity in the soil. Another study demonstrated that a lower rate of germination of *F. oxysporum* chlamydospores occurred in soils that had an adequate supply of Ca, particularly in relation to other basic cations, Mg and K (Chuang, 1988; 1991). The same study indicated that higher soil pH values and populations of actinomycetes also decreased spore germination rates. Domingues et al. (2001) compared banana field plots which differed in their capacity to suppress Fusarium wilt. Soils that suppressed disease had a lower proportion by weight of water-stable aggregates, than conducive soils. They hypothesised that the higher proportion of water-stable aggregates in the conducive soils favoured anaerobiosis, which increased availability of reduced Fe ions for the pathogen, which as mentioned previously, has a high demand for micronutrients, such as Fe.

Verticillium wilt caused by *Verticillium dahliae* also occurs in some perennial crops. While Fusarium wilt is encouraged by acidic soils, Verticillium wilt is favoured by a higher soil pH. A build-up of inoculum can occur in perennial crop species affected by *V. dahliae*; in the case of Verticillium wilt of pistachio, new infections are initiated by microsclerotia, which can survive for long periods on pistachio roots. A higher incidence of Verticillium wilt has been found in pistachio trees under conditions of K deficiency (Pennypacker, 1989). This

may be a consequence of impaired root growth and, therefore, increased exposure to microslerotia (Pennypacker, 1989). K deficiency in cotton is enhanced by infection with *V. dahliae*, perhaps due to a decrease in the ability of the roots to take up K after infection with the fungus (Bell, 1989).

An increase in severity of Verticillium wilt of cotton in response to P supplied as superphosphate has been reported – possibly P promotes pathogen activity within the plant (Bell, 1989). A study on cocoa affected by Verticillium wilt in Nigeria indicated that P supply had no effect on infections (Emechebe, 1980). Calcium nutrition may enhance resistance to Verticillium wilt in some cases (Bell, 1989). This could be related to an increase in the levels of Ca-pectin complexes, which are resistant to breakdown by a pectin-degrading enzyme produced by the fungus (see Section 2). Possibly, Ca-pectin complexes are involved in impeding growth of the fungus through the xylem (Pennypacker, 1989).

4.2 Diseases causing lesions on leaves and fruits

Leaf and fruit spots

Some leaf/fruit diseases, e.g. infections by the Mycosphaerellaceae pathogen, *Cercospora mangiferae* (syn. *Stigmina mangiferae*), causing angular leaf spot in mango and other pathogens of mango are influenced by the growing conditions of the host. Similarly, brown-eye leaf spot in coffee caused by *Cercospora coffeicola*, becomes more serious under conditions of environmental stress. Brown-eye spot is encouraged if coffee is grown in unshaded conditions, particularly if the soil is nutrient-poor (see Kohler et al., 1997; Nelson, 2008a). Deficiency in N and K in particular, may accentuate brown-eye spot (Wrigley 1988). In an experiment with coffee seedlings grown in pots, Pozza et al. (2001) showed that supplying bovine manure to coffee trees, as well as other types of fertiliser reduced the severity of brown-eye leaf spot. Santos et al. (2008) compared the incidence of brown-eye spot on ten-year old coffee in neighbouring plots that were managed either conventionally using inorganic fertiliser applications, or by organic methods in which only organic amendments were applied to the soil. In a period of two consecutive years, disease incidence was higher in the plot under conventional management (28% and 29%) than in the plot managed using organic methods (9% and 12%), although higher berry yields were obtained in the conventionally managed plots. Possibly, the higher rates of disease in the conventionally-treated trees were a consequence of nutrient-deficiency, particularly of Ca and Mg. The leaf concentrations of Ca and Mg were lower in the conventionally-treated plants. Possibly this was due to the higher yields from the trees receiving conventional treatment (so that these trees had a higher nutrient requirement than the lower yielding organic trees).

Infections in citrus-growing areas in Cameroon and other tropical countries in Africa by the Mycosphaerellaceae pathogen, *Phaeoramularia angolensis*, causing leaf and fruit lesions creates serious losses for farmers. In a survey of disease-affected areas, Ndo et al. (2010) found that disease severity was lower in citrus species grown on volcanic soils in Cameroon than in other soil-types. Altitude was also a key factor affecting disease severity. Since volcanic soils are generally nutrient-rich, this suggests that plant nutrition plays a role in mitigating this disease. In the case of *Dothiorella gregaria*, a Botryosphaeriaceae pathogen that causes fruit spot on mandarin, Ca and Zn contents of plant tissues may influence disease severity. Isolates of this pathogen were inoculated into mandarin by da Silva Moraes et al. (2007) who found that the highest lesion rates were obtained on plants with the lowest Ca and Zn contents.

Particularly serious leaf diseases of banana include black sikatoga (or black leaf streak) caused by *Mycosphaerella fijiensis* (syn. *Paracercospora fijiensis*), yellow sikatoga (*Mycosphaerella musicola* syn. *Pseudocercospora musae*), freckle caused by *Guignardia musae* (syn. *Phyllosticta musarum*) and Black Cross (*Phyllachora musicola*) which may be associated with previous infections with *Cordana musae*. Black sikatoga disease is reduced under shade (Ploetz, 2003; Stover, 1972). The disease may increase under conditions of poor nutrition and, therefore, improved host nutrition is one recommended control measure (Nelson et al., 2006; Mobambo et al., 1994); adequate phosphorus nutrition may be particularly necessary for disease alleviation.

Algal leaf spot disease occurs on a number of tropical perennials including breadfruit, citrus, guava, cocoa, mango, soursop and black pepper. The causal agent is *Cephaleuros virescens* or other species of the same genus. Orange and green spots can be seen on leaves and young stems, particularly in trees weakened by stress or in periods of high rainfall (Nelson, 2008b). In avocado, poor plant nutrition, lack of soil drainage and still conditions (e.g. under dense canopies) are predisposing factors for algal infection (Nelson, 2008b).

A study in Brazil indicated a link between N nutrition and infection of citrus trees with the bacterial pathogen, *Xylella fastidiosa* causing variegated chlorosis disease (see Huber and Thompson, 2007). Nitrification increased disease severity but where a groundcover grass species was planted between rows of citrus trees, a decrease in the disease was demonstrated; this was explained by the inhibiting effect of the ground cover crop on nitrification. Nitrification decreases concentrations of ammonium ions in the soil and this, in turn, decreases Mn availability to the plant. Inhibition of nitrification caused an increase in Mn uptake by 50%. Thus in this case it appears that an increase in availability of Mn confers resistance to the host rather than favouring the pathogen, as in some *Fusarium* wilts.

Rusts

Rust in banana is caused by *Uredo musae* and in coffee by *Hemileia vastatrix*. In some annual crop species, rusts may be encouraged by high levels of N fertilisation (see Section 2). However, coffee rust has been reported to be more severe on plantations grown under nutrient poor conditions (Waller et al., 2007, p. 302). Applications of silicon (Si) have been shown to decrease the level of coffee rust on coffee seedlings. Martinati et al. (2008) found that the number of rust lesions on leaves of Si-treated coffee (*C. arabica*) seedlings was decreased in proportion to the dosage of Si (as potassium silicate) supplied to the soil by up to 66% compared to the control, which received no Si.

In an epidemiological study on coffee rust in Honduras, Avelino et al. (2006) reported that the intensity of coffee rust infection was dependent on the production situation, rather than regional differences in environmental parameters, such as rainfall levels. They showed that coffee rust was associated with acid soils, soils treated with mineral fertilisers and increased yields. Possibly, an acidifying effect of the mineral fertilisers was the main factor accounting for higher levels of disease.

Anthracnose

Anthracnose diseases affect leaves, shoots and fruit of a variety of tropical perennial crops on farms and can also create severe post-harvest problems. The Ascomycotina species, *Glomerella cingulata* (anamorph: *Colletotrichum gloeosporioides*), an endophyte on plant species

such as cocoa, *Theobroma cacao* (Rubini et al., 2005), is the most common causal pathogen, infecting a number of tropical tree crops such as avocado, mango, coffee and kauri (*Agathis* sp). Symptoms include blackened and sunken lesions on fruit, and marginal necrosis of young or flush leaves. On avocado, fruit and leaves are infected by *C. gloeosporioides*, the leaves developing large light brown lesions and, in wet weather, pink spore masses. Anthracnose is transmitted mainly by rainsplash (Kader, 2002) and heavy rainfall increases the severity of anthracnose in Robusta coffee. Rust infections can predispose Arabica coffee to anthracnose infection (Kohler et al., 1997). As an endophyte and facultative parasite, this pathogen may be asymptomatic in healthy plants of some crop species, only becoming pathogenic under conditions of stress, such as over-exposure to sun in the case of shade-requiring crops. As with other latent species (see Prakash, 2000; Kohler et al., 1997), the removal of dead twigs and branches before flowering is a crucial measure to control infection by the fungus. Possibly, nutrition plays a role in the control of anthracnose. Anthracnose in the orchid, *Cymbidium* sp., caused by *Colletotrichum orchidacearum*, for example, was reduced by applying macronutrients, especially K and P (Yi et al., 2003). Acosta-Ramos et al. (2003) took an integrated management approach, including soil and foliar application of nutrients, to mango trees in an orchard in Mexico and recorded decreases in the incidence of both anthracnose, caused by *C. gloeosporioides*, and stem end rot, caused by *Lasiodiplodia theobromae*.

In papaya and mango, a post-harvest problem caused by anthracnose infection of the fruit is particularly serious and can be controlled by dipping fruit in hot water or a fungicide (such as benomyl). Anthracnose infects all parts of the mango plant: new leaf flushes are particularly susceptible and, in wet weather, flowers are susceptible to blossom blight. In guava, which incurs serious losses from anthracnose disease, infections may be associated with fruit fly damage and with scab damage caused by *Sphaceloma perseae* (Ploetz, 2007). Passion fruit is also a host of anthracnose. Passion fruit produced under poor growing conditions may also be infected with *Alternaria* sp. causing brown spot.

4.3 Fruit rots

Conditions predisposing perennial crops to fruit rots include high rainfall, poor drainage and poor sanitation practices, whereby infected fruits (which provided sources of new inoculum) are not disposed of correctly. This is particularly relevant in the case of *Phytophthora palmivora*, the straminopile (formerly oomycete) pathogen, which is responsible for fruit rots in a wide range of host species in the tropics including breadfruit, cocoa, black pepper, papaya and vanilla. On coconut and betel nut trees it causes bud rot, inflicting serious losses to these crops. The pathogen is dispersed mainly by motile zoospores, which require the presence of external water and infection (Guest, 2007). Hence, incidence of fruit rots caused by *P. palmivora* increases dramatically under conditions of high moisture during heavy rainfall periods in the wet season, poor drainage or slightly cooler conditions at higher altitudes that reduce evapotranspiration rates. In many host species, it also infects other parts of the plant including leaves and stems. Inoculum from one infected part of the plant can initiate infections in other tissues. On cocoa farms, insects, including ants and beetles, also transmit disease, carrying spores from infected sites to initiate new infections (Konam and Guest, 2004). Therefore, sanitation is a crucial control measure for *Phytophthora* diseases. A link between low levels of zinc nutrition and pod rot incidence

was reported from Papua New Guinea (Nelson et al., 2011). Other *Phytophthora* species also cause fruit rots; particularly devastating losses in cocoa in West Africa are caused by *P. megakarya*, for example (Guest, 2007). Similarly devastating losses are caused in South America by the basidiomycete, *Moniliophthora roreri* that causes frosty pod. A fruit rot in cocoa is also caused by *Lasiodiplodia theobromae* in southern and Southeast Asia. On avocado, the same pathogen species causes browning of the fruit from the stem end (Kohler et al., 1997) and fruit rot in papaya (Kader, 2002). *L. theobromae* generally requires wounding to initiate infection (Kader, 2002). A possible relation to plant nutrition has been raised by studies of some *Phytophthora* fruit rots. For example, brown rot of citrus caused by *Phytophthora citrophthora*, is enhanced under when N fertiliser is provided as ammonium-N (Menge and Nemeč, 1997).

Verticillium theobromae causes cigar end rot of banana. Sanitation (including removal of dead flowers), canopy aeration and exposure to light are recommended management methods for this disease (Nelson et al. 2006). A serious fruit rot of guava is caused by *Pestalotiopsis disseminate* that infects the fruit from the stalk end producing white fruiting bodies that later become brown. This disease is linked with poor nutrition; hence proper soil amendment to improve fertility is a recommended control measure. Similarly, *Pestalotiopsis* sp. infection of coconut can be reduced by improved growing conditions through the application of fertiliser (Kohler et al., 1997). *Pestalotiopsis* (Fig. 1) has been isolated from cocoa leaves that have symptoms of vascular-streak dieback - possibly it is a secondary pathogen.

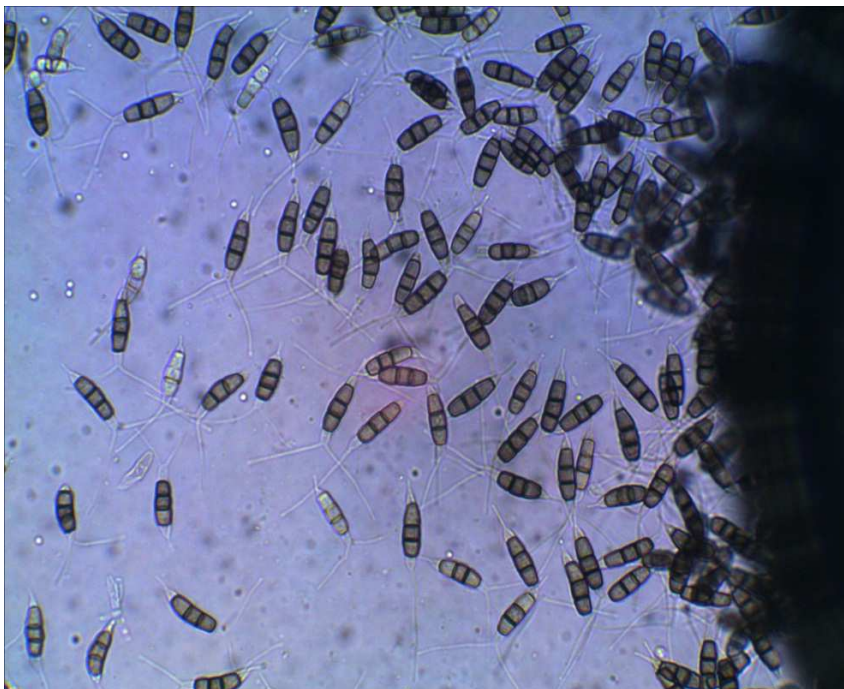


Fig. 1. Conidia of *Pestalotiopsis* sp. isolated from cocoa leaves in Sulawesi, Indonesia; magnified x400 (author's photo).

4.4 Dieback diseases

Dieback diseases are caused by a range of pathogens. Some diseases may involve the interaction of more than one pathogen species and may be prevalent in ageing trees or trees weakened by environmental stress (Ploetz, 2006). This is particularly the case for infections by facultative parasites, such as some Botryosphaeriaceae species which can survive in a latent form in dead wood or are wound invaders. Similarly, the weakly aggressive pathogen, *Fusarium decemcellulare* has been linked to dieback and cushion gall of cocoa. Other tree crops are also infected with this pathogen (see Ploetz, 2006). Infection is possibly facilitated by wounds caused by insects (Holliday 1980). The pathogen can interact with other pathogens such as *Lasiodiplodia theobromae* (syn. *Botryodiplodia theobromae*) and *Phytophthora palmivora* (Holliday, 1980).

In coffee, overbearing dieback is linked to poor nutrition, nitrogen-deficiency in particular, which has the effect of lowering soluble sugar reserves in the stem. Exposure to the sun, resulting in plant stress and excessive cropping, poor root function (e.g. resulting from pathogen attack) and weed competition can all be factors predisposing trees to this condition. Infection by opportunistic fungi such as *Colletotrichum gloeosporioides* and *F. oxysporum* follows, causing dieback of the stem (Flood, 2010; Waller et al., 2007). The disease can be managed by supplying shade, applying N and decreasing crop density (Waller et al., 2007 p 284). Sunscorch damage is also associated with infection of berries by pathogens such as *F. stilboides* and *Cercospora coffeicola* (Waller et al., 2007 p. 285).

In the case of pink disease caused by the basidiomycete, *Corticium salmonicolor* (syn. *Erythricium salmonicolor*), a lack of light caused by heavy shade and insufficient pruning, encourages infections in a number of species including citrus, cocoa, coffee, rubber, tea and black pepper. On cocoa, symptoms of the disease include a pink to creamy white crust on the bark and cracking of the bark with gum exudates. Sudden death of the whole branch may occur with the leaves remaining attached. A number of timber (forest) trees are also hosts to this pathogen. Wet conditions promote infections of tree crops.

The most severe dieback disease affecting cocoa in the Southeast Asian region is vascular-streak dieback (VSD) caused by another basidiomycete species, *Ceratobasidium theobromae* (syn. *Oncobasidium theobromae*). Infection is initiated in particularly wet conditions on young leaves by wind-borne spores, which are very short-lived (Keane et al., 1972; Keane, 1981; Prior, 1985; Guest and Keane, 2007). Following germination of the spores, the fungal hyphae penetrate the xylem in the leaf by a mechanism that remains unknown. The pathogen can grow via the xylem to lower parts of the branch causing leaf chlorosis and fall, and eventual dieback of the branch (Fig. 2). In susceptible varieties tree death may result, but most cocoa genotypes exhibit partial resistance to VSD. The identification of a second species, *C. ramicola*, in VSD-infected tissue (Samuels et al., 2011) raises the possibility that more than one pathogen is causing the disease. A significant and widespread change in VSD symptoms has occurred since 2004. After 2004, necrosis of infected leaves was observed (rather than only chlorosis as previously seen), with the infected leaves remaining attached to the branch longer; cracks in the midrib of the infected leaves were also observed, which allowed emergence and sporulation of the fungus from the leaves themselves, in addition to the petiolar scars on the stems as observed prior to 2004 (Purwantara et al., in process). Disease severity has also increased so that many farmers in Indonesia now identify VSD as their primary problem and the main reason given for changing their cocoa farms over to

other crops, including maize, neelam and oil palm (pers. comm. Ade Rosmana, Hasanuddin University). Possibly the change in symptoms and increased severity of the disease is the result of an environmental factor interacting with *C. theobromae* infections or VSD-infected trees have become susceptible to infection by a secondary pathogen(s); trees weakened by stress, such as poor nutrition, might be predisposed to such a secondary infection (Mossu, 1990 cited by Schroth et al., 2000). An alternative explanation for the change in symptoms and severity of the disease is that a new strain of the pathogen, *C. theobromae*, has emerged. Further work is underway to elucidate the pathogen-environmental relationship that might lie behind the changed VSD symptoms.

A devastating disease of cocoa is witches' broom, caused by a co-evolved pathogen of cocoa, a basidiomycete species, *Moniliophthora perniciosa*. The disease causes distortion of growth in the shoots, creating a broom-like appearance. Although the pathogen co-evolved with cocoa, it has caused most damage in plantations in Bahia, Brazil away from its centre of origin in the Amazon rainforest. Improved management, including the appropriate use of fertilisers, combined with the introduction of resistant cocoa genotypes has been effective in mitigating the impact of this disease (Keane and Putter, 1992). Dieback in cocoa caused by *L. theobromae* has been observed in the Cameroons (Mbenoun et al., 2008) and in India (Kannan et al. 2010). Vascular streaking has been observed in both cases. Kannan et al. (2010) isolated the pathogen and reinoculated seedlings, which showed disease symptoms after 20 days. Infection by *L. theobromae* is facilitated by



Fig. 2. Left: Cocoa tree in Sulawesi, Indonesia infected with VSD. Right: LS of a stem of infected cocoa showing hyphae of the causal organism, *C. theobromae*, in a xylem vessel, magnified x400 (author's photos).

wounding or insect damage. In passion fruit, for example, infection is facilitated by tunnelling by a species of beetle. Generally, preventing insect damage or other forms of wounding may reduce infection. Removal of dead twigs or branches is also a recommended control measure since *L. theobromae* is a facultative saprophyte (Kohler et al., 1997). Thread blight or black rot in coffee is caused by a basidiomycete, *Ceratobasidium noxium* (formerly *Pellicularia koleroga* syn. *Corticium koleroga*), which infects branches of coffee trees causing blackening and drying of leaves, leading to branch dieback. The pathogen also infects cocoa, citrus and woody species. *Marasmiellus scandens* causes white thread blight of cocoa. Infection by *M. scandens* is may be associated with stem borers, especially Scolytidae beetles (observation by Asman, Hasanuddin University).

Various causes of mango decline have been reported. Mango decline is associated with opportunistic fungi such as *Botryosphaeria ribis*, *Physalospora* sp. and others (see Zheng et al., 2002). *L. theobromae* has also been linked to mango decline (Shahbaz et al., 2009), while a form of mango decline in Brazil is caused by *Ceratocystis fimbriata* (Ploetz, 2007). Mango decline symptoms are reported to include interveinal chlorosis in leaves, stunting and terminal and marginal necrosis with dieback of young stems, internal softening of the fruit and even tree death; these symptoms may be linked to Mn and Fe deficiency (Crane and Campbell, 1994). Both Mn and Fe may be deficient in plants growing in high pH soil. Another mango disease that has recently become a serious problem in some regions (e.g. northern Australia) is mango malformation caused by *Fusarium* spp., which cause distortion in the growth of shoots and buds.

Many dieback diseases are caused by a combination of factors, including nutrient deficiency, drought and wounding or transmission of inoculum by insects. A fungus surviving in a host plant as an endophyte or as a saprophyte on dead tissue may switch to being a pathogen in stressed plants (Shulz and Boyle, 2005). Nutrient deficiency could be a key predisposing factor for this switch to occur. Generally, adequate host nutrition, as well as shade management and sanitation (such as adequate pruning and the removal of dead twigs), are crucial preventative measure for some forms of dieback.

4.5 Root and collar rots, cankers and nematode infections

Root and collar rots

Root and collar rots are particularly severe in soils with low organic matter content, poor soil structure with a high level of compaction and poor drainage (Desaeger et al., 2004). If roots are restricted to the upper soil layers due to claypans or hardpans, this results in a greater exposure of roots to soil-borne pathogens. Similarly, old roots may leave pathogen inocula in cracks and fissures in the soil, increasing contact with new roots; an example of this is found in cases of *Eucalyptus marginate* and other native Australian species infected by the soil-borne pathogen *Phytophthora cinnamomi* (see Desaeger et al., 2004).

The basidiomycete, *Marasmiellus inoderma* infects all parts of the banana plant causing stem rot in particular. The pathogen has a number of hosts and is encouraged in marginal, nutrient-poor, soils with a high clay content and by poor drainage; soil improvement by organic amendments and better plant nutrition are recommended for managing the disease (Nelson et al., 2006). In breadfruit, *Lasiodiplodia theobromae* (syn. *Botryodiplodia theobromae*) causes a collar rot characterised by external white strands. As mentioned above, this is a wound invading fungus and drought-stressed trees may be particularly predisposed to infection. *Phellinus noxius* (Basidiomycota) also infects bread fruit trees at the base of the trunk creating a brown encrustation (that includes soil particles) sometimes with a white margin and gum exudates. Other hosts of this pathogen include cocoa, coffee, *Leucaena* sp., mango, oil palm and forest trees, such as *Tectonia*, *Swietenia* and laurel (Kohler et al., 1997). Diseases caused by the fungus include brown root and collar rot in cocoa: the fungus may encircle the whole trunk, causing sudden death of the tree with leaves remaining attached. As the pathogen is dispersed between roots in the soil, adjacent trees may be infected and killed. Therefore, removal of tree stumps and all large roots before planting is a necessary preventative control measure. Rigidoporus root rot (or white root rot) caused by the basidiomycete, *Rigidoporus microporus* causes serious crop losses to rubber, mango, durian

and other tree crops. It is a serious pathogen of rubber trees in Malaysia. Red root disease caused by *Ganoderma philippii* (syn. *G. pseudoferreum*) another basidiomycete, is also an important rubber pathogen in Malaysia and India. The use of arsenic-containing sprays as a control method for root rots creates environmental concerns. As for other root pathogens, sanitation of areas prior to planting is a necessary control measure.

Ganoderma orbiforme (syn. *G. boninense*) is the most severe pathogen on oil palm in southeast Asia (Susanto et al., 2005; Flood et al., 2005; www.dfid.gov.uk). Sanitation is particularly important and diseased trees, including the roots, are dug out mechanically, and shredded for composting. In a recently established trial in Sumatra, Indonesia, shredded plant material and empty fruit bunches are being used to prepare compost using microbial promoters, particularly *Trichoderma* spp., which the trial aims to test by soil application in order to assess their effect on root rot disease (Agus Purwantara, pers. comm.). Srinivasulu (2003) reported a higher incidence of *Ganoderma* spp. infection of coconut growing on sandy and red soils (which had a low organic matter content) than on black soils (with a higher organic matter content). Amendment of soil with calcium nitrate has been used to reduce *Ganoderma* basal stem rot in coconut palms (Kandan et al., 2010). In a plot of coconut trees affected by this disease, Kharthikaya et al. (2006) demonstrated that a combined treatment of frequent irrigation, soil applications of neem cake, *Trichoderma viride*, *Pseudomonas fluorescens* and a fungicide prevented the spread of the pathogen, *G. lucidum*, and led to the recovery of 42% of diseased palm trees.

Phytophthora spp. cause root rots in crops such as avocado and citrus. Root rot in avocado caused by *P. cinnamomi* becomes particularly severe under conditions of flooding (Ploetz, 2007). *Phytophthora* root rot in citrus is associated with citrus leaf miner damage and *Diaprepes* root weevil (Ploetz, 2007). The form of nitrogen available to citrus trees appears to affect the severity of this disease. Root rot of citrus was shown to increase in the presence of ammonium-N but decreased by supplying nitrate-N (Menge and Nemeč, 1997). Root rots are also caused by *Rosellinia* spp. on crops such as avocado, citrus and banana – they are favoured by acidic soil conditions (Ploetz, 2007).

Nematodes

Nematodes are generally favoured by coarse-textured soils that are low in organic matter and biological activity (Desaeger et al., 2004). For example, bananas became more susceptible to nematodes when grown in degraded soil that had lost much of its original organic matter (Page and Bridges, 1993) and nematode attack on maize was more damaging in unfertilised, than in fertilised plots (Desaeger et al., 2004). The intensity of crop production can also influence nematode populations. In Costa Rica, Avelino et al. (2009) examined the conditions that influence populations of two nematode species, *Meloidogyne exigua* (root-knot nematode) and *Pratylenchus coffeae* colonising roots of coffee. The two species had specific preferences of altitude and soils, with low *M. exigua* populations being associated with non-sandy soils with a high K and Zn content, but high populations of both species occurred on farms which had inter-row planting distances of less than 0.9 m, irrespective of environmental conditions. This, the authors suggest, indicates that intensification of coffee production provides conditions favourable for nematode reproduction and transmission.

Nutrient supply and organic amendments can have direct impacts on nematode populations and infection. In a guava growing area of Brazil, the numbers of juveniles of the root-knot

nematode of guava, *M. enterolobii* (syn. *M. mayaguensis*) in naturally infested areas, were decreased by manure application to the soil (Souza et al., 2006). As mentioned above (Section 4.2), silicon (Si) supplied to coffee plants was shown to decrease the number of rust lesions on leaves; Si also has an effect on resistance to nematodes. Silva et al. (2010) found that a lower number of *M. exigua* galls and eggs occurred in the roots of coffee (*C. arabica*) plants that had been inoculated with the nematode and provided with Si, compared to control plants which were not supplied with Si.

Nematode infections may predispose tree crops to infections by other pathogens creating disease complexes (Desaeger et al., 2004). Generally, nematodes may have a number of roles in facilitating disease development acting as vectors and wounding agents. They may affect the susceptibility of the host to other pathogens, or influence rhizosphere ecology (Desaeger et al., 2004). Melendez and Powell (1969) reported that nematode infection of roots of tobacco plants caused a soil-inhabiting *Trichoderma* sp. to become pathogenic. Vascular wilt pathogens are particularly encouraged by endoparasitic nematodes, while cortical root pathogens are encouraged by ectoparasitic nematodes (Hillocks and Waller, 1997). The nematode species, *Radopholus similis* causes root rot in, among other crops, banana, avocado, coconut, coffee and sugar cane. In banana, *Fusarium oxysporum* infections of the root were associated with roots infested with *R. similis* (Blake, 1966). Gomes et al. (2011) reported that the causes of root rot in guava decline in Brazil included colonisation by nematodes (*M. enterolobii* syn. *M. mayaguensis*) and a *Fusarium* sp., identified upon isolation as *F. solani*. Infestation of roots by the nematode appeared to predispose roots to infection by *F. solani*, as the latter species was only isolated from nematode-infected roots. The authors found that *F. solani* isolates inoculated into the roots of guava plants initiated infections in trees that had been pre-inoculated with the nematode, but not those that had been physically damaged using a knife. Therefore, it appears that physical damage alone by the *M. enterolobii* did not account for the predisposition of guava colonised by the nematodes to *F. solani* infection. Khan et al. (1995) had earlier shown that inoculation of papaya with both the nematode *M. incognita* and *F. solani* caused a greater decrease in plant growth than inoculation with either species alone. They also showed that the level of root rot (caused by *F. solani*) could be decreased by the application of NPK fertiliser.

Phytophthora stem canker

Canker infections are initiated on species such as cocoa and durian by the same causal pathogen of fruit rots and leaf blights, *Phytophthora palmivora*. Other *Phytophthora* species may be associated with cankers, but *P. palmivora* is the most prevalent species of the genus on tropical tree crops. On cocoa, cankers are moist, wine-red lesions under the bark that expand in diameter during the wet season (Guest, 2007; McMahon et al., 2010). If cankers girdle the whole stem, sudden death results with the leaves still attached to the tree. Particularly wet conditions encourage *Phytophthora* stem canker, which can be a serious problem in areas prone to water logging or flooding. The presence of susceptible hosts, lack of pruning or management to enhance air circulation and lack of sanitation of sources of inoculum, such as infected pods can all lead to increased incidence of the disease. Since old and apparently weaker trees are more susceptible (author's observation) it is possible that poor nutrition might encourage cankers to develop. Low zinc (Zn) nutrition has been suggested to predispose plants to *Phytophthora* infection (Nelson et al., 2011).

5. Soil amendments with microbial species to control disease

Application of composts to soils has been shown to have a suppressive effect on soil-borne diseases such as damping off, root rots and wilts, both in controlled glasshouse experiments and in the field (Noble and Coventry, 2005). Loss of disease suppression occurs if the composted materials are sterilised indicating that their suppressive effect is mainly biological (Bonanomi et al., 2010; Noble and Coventry, 2005). In Papua New Guinea, the time in which *P. palmivora* inoculum remained viable was found to be shorter in soils under cocoa leaf litter mulch than under grass litter: possibly conditions in the soils under leaf litter were more favourable to microorganisms antagonistic to the pathogen (Konam and Guest, 2002). McDonald et al. (2007) showed that the factor(s) conferring disease suppression of *P. cinnamomi* in avocado orchards can be transferred from suppressive to conducive soils. Suppressive soils may be effective in reducing disease due to either a high total microbial activity or to the presence of particular antagonistic species (Weller et al., 2002). Reeleder et al. (2003) identified biological parameters as being the best predictors of the capacity of soils for disease suppression. These include microbial biomass, substrate respiration, fluorescein diacetate (FDA) activity and populations of bacteria, including fluorescent pseudomonads, and of antagonist fungi, particularly *Trichoderma* spp. But the mechanisms leading to pathogen suppression and the antagonistic organisms involved remain little understood. The employment of molecular techniques to track changes in microbial communities in amended soils and to select potential biocontrol agents has been proposed by some researchers (Noble and Coventry, 2005; Reeleder et al, 2003).

Various studies have demonstrated disease suppression following soil amendments with organic materials or by treatments with antagonist microorganisms isolated from soils (Table 2). Root rot caused by *P. nicotianae* in Florida citrus orchards was reduced by treatments with composted municipal waste (Widmer et al., 1998). However, the suppressive activity of the compost was lost after storage for three months or more. Also, some sources of waste contained toxins that impaired plant growth. Vawdrey et al (2002) tested different soil amendments for their effect on root rot of papaya, caused by *Phytophthora palmivora*. They found in both pot and field experiments that a sawdust/urea preparation was more effective in reducing disease and *P. palmivora* populations, than the other organic materials tested, such as molasses. A lower soil moisture level in sawdust/urea treated soils might partly explain the suppressive effect of this treatment (Vawdrey et al., 2002). Organic amendments based on preparations from the neem tree (*Azadirachta indica*) have been shown to be effective in disease suppression, and to have nemitocidal properties (Agbenin, 2004). Applications of neem cake and other organic materials in combination with *Trichoderma harzianum*, reduced both the populations of *P. meadii* and their infection of cardamon plants (Bhai and Sarma, 2009). Peng et al. (1999) compared the effect of conducive and suppressive soils on disease severity of Fusarium wilt in Cavendish banana plantlets. The conducive soil had higher populations of filamentous fungi than the suppressive soil, which had greater numbers of bacteria and actinomycetes. They reported that, compared to the conducive soil, the suppressive soil reduced *Fusarium oxysporum* chlamydospore germination by 41% and decreased disease severity by over 50%. However, supplying Ca compounds or Fe in a chelated form to both suppressive and conducive soils decreased Fusarium wilt in the plantlets by 33-50%.

A number of studies have been conducted reporting the isolation of potential microbial biocontrol agents from the soils in which tropical perennials are grown. Examples are the identification of five *Trichoderma* species, selected from 25 isolates from mango orchards in Mexico, which had an inhibitory effect on the growth of *Fusarium* spp. *in vitro* (Michel-Acevedo et al., 2001), the isolation of *Trichoderma* spp. demonstrated to have *in vitro* inhibitory effects on the cocoa pathogen, *Moniliophthora perniciosa* (Rivas-Cordero, 2010), on *Ganoderma orbiforme* (syn. *G. boninense*) (Siddiquee et al., 2009) and on *Lasiodiplodia theobromae* and *Colletotrichum musae*, isolated from infected banana (Samuels, 2006; Sangeetha 2009). Lower levels of disease caused by *G. orbiforme* in infected oil palm seedlings were recorded

Crop	Disease (causal pathogen)	Type of treatment	Impact on disease	Notes	Source
Oil palm	Basal stem rot (<i>G. orbiforme</i>)	<i>T. harzianum</i> conidia spray	Disease severity index 5% cf. 95% (control)	Oil palm seedlings treated	Izzati et al., 2008
Banana	Nematode infection (<i>R. similis</i>)	Non-pathogenic <i>F. oxysporum</i> isolate	No. of root lesions reduced	Defence-related genes upregulated	Paparu, 2008
Coffee	Nematode infection (<i>P. coffea</i>)	Pre-inoculation of coffee with AM fungi	Reduce number of lesions	High P tissue level in mycorrhizal plants	Vaast and Craswell, 1997
Tea	Rot (<i>Armillaria</i> sp.)	<i>T. harzianum</i> applied to detached tea stems	Reduce incidence by 52% up to 100%	Four <i>T. harzianum</i> isolates effective	Otieno et al., 2003
Papaya	Root rot (<i>P. palmivora</i>)	Sawdust/urea mix	Root rot severity index 1.2 compared to 5 (control)	Treatment also lowered soil moisture content	Vawdrey et al., 2002
Cardamon	Root rot (<i>P. meadii</i>)	Neem cake plus <i>T. harzianum</i>	Reduced infection	<i>T. harzianum</i> applied with manure also effective	Bhai and Sarma, 2009
Citrus	Root rot (<i>P. nicotianae</i>)	Composted municipal waste	Reduce incidence from 95% to 5%	But some wastes toxic to plants	Widmer et al., 1998
Mango	Leaf spot (<i>P. mangiferae</i> , <i>L. theobromae</i> , <i>M. mangiferae</i>)	Apply <i>B. subtilis</i> isolate <i>in vivo</i>	Reduce leaf spot diameter by over 70%	<i>In vitro</i> inhibition by <i>B. subtilis</i> also verified	Okigbo and Osuinde, 2003

Table 2. Examples of impacts on diseases by soil amendments and other treatments applied to tropical trees crops.

following treatment of the seedlings with *T. harzianum* conidia (Izzati et al. 2008). Tea stems inoculated with *T. harzianum* demonstrated resistance to infection by *Armillaria* sp. (Otieno et al., 2003). Muleta et al. (2007) found that among isolates of rhizobacteria isolated from soils under coffee, some *Pseudomonas* and *Bacillus* species strongly inhibited the *in vitro* growth of *Fusarium* spp., including *F. stilboides* and *F. oxysporum*. Such rhizobacteria have potential as biocontrol agents of coffee wilt diseases. Using an integrated approach to management of *Fusarium* spp. and the citrus nematode, *Tylenchulus semipenetrans*, in Egypt, Abd-Elgawad et al. (2010) showed that the application of bacterial isolates contributed to a reduction of populations of these pathogens.

In a study of leaf spot disease of mango in Nigeria, Okigbo and Osuinde (2003) demonstrated the pathogenicity of three fungi species isolated from the leaf lesions (*Pestalotiopsis mangiferae*, *Lasiodiplodia theobromae* and *Macrophoma mangiferae*) by inoculating them individually onto healthy mango leaves. In addition, the authors isolated a bacterium identified as *Bacillus subtilis* from soil under mango trees and showed that it inhibited growth *in vitro* of the three causal pathogens and also reduced disease severity *in vivo* when applied to soil in the field. In tea plants infected with *L. theobromae*, *in vivo* control of the disease was demonstrated by pre-treatment of the plants with bacteria that had been isolated from the tea rhizosphere and shown to have *in vitro* antagonistic activity (Purkayastha et al., 2010). Stirling et al. (1992) isolated fluorescent pseudomonads from avocado soils suppressive to *P. cinnamomi* (causing root rot) and demonstrated their *in vitro* antagonism to the pathogen. *In vivo* control of the root-knot nematode on coffee roots, *Meloidogyne incognita*, by the application of an obligate bacterial parasite of the nematode, a strain of *Pasteuria penetrans*, was demonstrated by Carneiro et al. (2007). The colonisation of banana roots by the nematode *Radopholus similis* could be decreased by inoculation of the banana plants with a non-pathogenic isolate of *F. oxysporum* (Paparou et al., 2008). The authors demonstrated that inoculation of the fungus caused the up-regulation of a number of defence-related genes in the host plant (the expression of some of these genes was also increased by inoculation with the nematode). However, the means by which biocontrol agents exert antagonistic effects towards pathogens may include a variety of other mechanisms, including direct antibiosis and competition.

Role of mycorrhizae

Most plants form symbiotic associations with fungi, forming mycorrhizae. In tropical perennial crop species such associations mainly occur with arbuscular mycorrhizal (AM) fungi, but associations with other taxonomic groups of fungi, forming ectomycorrhizae, are also found. In fact, it could be said that, under natural conditions, plants have mycorrhizae rather than roots (Azco'n-Aguilar and Barea, 1996). Mycorrhizal fungi have an irreplaceable role in supplying nutrients to the plants, particularly of phosphorus (P), which is often unavailable for direct uptake by plant roots. They can also reduce disease severity, particularly of diseases caused by soil-borne pathogens, such as nematodes, in addition to conferring tolerance to drought and salinity (Andrade et al., 2009). Increased tolerance to nematodes has been reported in perennial crop species inoculated with mycorrhizal fungi. Vaast et al. (1997) reported enhanced resistance to *Pratylenchus coffeae* in coffee plants inoculated with AM fungi, with fewer lesions occurring in the AM fungi-inoculated roots (see Section 2). Similarly, an increase in resistance to nematodes was reported in banana plants that

had been inoculated with mycorrhizal fungi (Elsen et al., 2003). In a study in citrus orchards in Thailand, increased growth, P uptake and resistance to root rot caused by *Phytophthora nicotianae* was shown to result from the inoculation of citrus trees with a species of AM fungus, *Glomus etunicatum*, isolated from local citrus orchard (Watanarojanaporn et al., 2011). A second AM fungus isolate, identified as *Acaulospora tuberculata*, also conferred resistance to *P. nicotianae* disease. Mycorrhizal fungi may compete for infection sites with the pathogen and/or they may impede access to nutrients by the pathogen (Azco'n-Aquila and Barea, 1996).

6. Conclusion

Soil function, plant nutritional status and cultural management practices have a strong influence on the incidence and severity of many diseases of tropical perennials. Diseases are influenced, not only by the general nutritional status of the plant (i.e. by an adequate supply of macronutrients), but also by individual nutrients. Soil pH is particularly important for a number of reasons, including its effect on availability of cations to the plant, pathogen or antagonists. It also influences microbial ecology, with a number of potential antagonists among bacterial and actinomycete species being favoured by a higher soil pH. Since tropical perennial crops and the use of inorganic fertiliser can lower soil pH, liming and/or compost treatments are strategies that can be adopted for disease mitigation in these crops. Composting farm waste, not only returns nutrients to the farm, but also improves farm sanitation as it kills larvae of pests and pathogen spores and other forms of inoculum. Nutrient elements supplied in mineral fertilisers can interact and care needs to be taken in their application. As mentioned earlier, some fertilisers can increase concentrations of Cl in plant tissues and decrease the K/Cl ratio. Also mentioned previously (Section 2), applications of Mg or K in excess can reduce the uptake of other basic cations, particularly Ca. To complement the use of soil amendments as a way to increase production and decrease pest and pathogen damage, it is important that tropical perennial crops are managed properly with cultural methods such as pruning, shade regulation, soil drainage and sanitation.

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8. References

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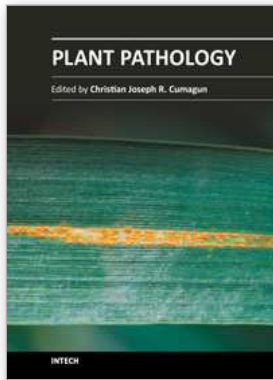
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