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Interactions between Aerial and Soil-borne Pathogens: Mechanisms and Epidemiological Considerations

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ABSTRACT

Aerial and soil-borne pathogens can simultaneously attack different parts of the same plant. The latter can alter the susceptibility of hosts to infection by aerial pathogens and vice versa. Normally the effects are via the host plant. The studies related to the interactions among soil-borne and aerial pathogens generally do not emphasize epidemiological aspects. Most of them are merely descriptive. Even for the most studied interactions, the mechanisms involved are rarely described. Although pathogen interaction phenomenon still remains poorly studied, it is evident in many situations that appropriate strategies of disease management may take into account the possibility of pathogen infection of different parts of the same plant. In this review, we discuss the current literature regarding the mechanisms and epidemiology of interactions between soil-borne and aerial pathogens. Examples of interactions between both soil-borne fungi and aerial pathogens and nematodes and aerial pathogens are given considering effects on the disease or pathogen dynamics and the crop yield loss.

Keywords: epidemiology, foliar diseases, integrated control, root diseases

CONTENTS

INTRODUCTION

In spite of the olden observation of Fawcett (1931) that "nature does not work with pure cultures alone but most frequently with associations", the history of plant pathology has been dominated by the search for single agents of disease, how they can be identified and how they can be shown to cause a distinctive set of symptoms in a particular crop (Jeger 2001). The interactions among plant diseases have been neglected in epidemiological studies, although more than one disease usually occur in the field at the same time (Kranz and Jörg 1989; Campbell and Madden 1990).

Interacting pathogens usually affect the same plant organ (Powell 1971a), but aerial and soil-borne pathogens can attack simultaneously different parts of the same plant. Actually, there are examples in the literature demonstrating that soil-borne pathogens can alter the susceptibility of the host to infection by aerial pathogens and *vice versa*. Many leaf spot diseases are more severe on tropical crops grown under stress (often caused by root diseases) than under favorable conditions (Waller and Bridge 1984).

Most studies on combined effects of diseases emphasize the examination and interpretation of interactions and what they mean with regard to crop loss. According to Johnson (1990), the objectives of studies on the interactions among diseases can usually be divided into understanding and defining the combined effects on crop yield and providing recommendations or decision aids to manage multiple-pest problems. Discerning the importance of effects of root and shoot diseases on the same plant is difficult even when one disease does not clearly affect the susceptibility of the plant to the other diseases (Waller and Bridge 1984). The aerial parts are more readily seen and therefore damage is generally attributed to aerial diseases. However, root diseases can, for example, reduce the capacity of plants for compensatory growth (Waller and Bridge 1984).

The effects of combined infections depend upon pathogen-host combinations as well as weather conditions (Campbell and Madden 1990), particularly temperature (Reyes and Chadha 1972). Experimentation and assessment methods affecting results of interaction studies have been discussed by Hyde (1981) and Sikora and Carter (1987).

In this review, we will present some considerations about mechanisms and epidemiology of interactions between soil-borne and aerial pathogens.

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Review

DISEASE INTERACTIONS, PATHOGEN DYNAMICS AND CROP LOSS

Interactions among diseases can be categorized according to the disease or pathogen dynamics and the crop yield loss. A more detailed explanation about this subject can be found in Paula Júnior *et al.* (2003). The definitions of Odum (1953) can be helpful to interpret interactions related to the dynamics of pathogens. This author suggested the following classifications for associations between organisms: neutralism (neither population is affected by association), competition (each population adversely affects the other in the struggle for food, nutrients, living space, or other common need), mutualism (growth and survival of both populations are improved, but neither can survive under natural conditions without the other), protocooperation (both populations benefit from the association, but the relationship among them is not obligatory), commensalism (one population benefits from the association, but the other is not affected), amensalism (one population is inhibited by the association and the other is not affected), parasitism and predation (one population adversely affects the other by direct attack, but depends on the other).

Otherwise, there are three outcomes of combined diseases on crop yield that can result in either more or less yield loss than the additive effects (no interaction) of the individual diseases. Without interaction, the effects of multiple diseases on crop yield are independent, although the lack of interaction among diseases seems to be rare in nature. In general, one pathogen may influence the resistance of a host to infection and colonization by another. The presence of one parasite species may cause a host to become less vulnerable to an attack by a second species (for example, as a result of inducible responses in plants), or more vulnerable (simply because of the host's weakened condition) (Begon *et al.* 2006). Thus, an infected plant is altered, somehow, in its physiological functions and susceptibility to invasion by other pathogens. It may result in a synergistic interaction in terms of combined effect of the pathogens, or in an antagonistic interaction in terms of competitive exclusion (Zacheo 1993). The interactions are termed synergistic if the host-yield reduction caused by the interacting diseases is higher than the sum of the yield reduction caused by each disease individually. On the other hand, if the yield reduction is lower than the sum of the yield reduction caused by each disease individually, the interaction is termed antagonistic.

Synergistic interactions are important because the economic damage threshold for each disease can be significantly lowered by the presence of another disease. Conversely, antagonistic interactions can increase the economic damage threshold of a disease in the presence of another (Johnson 1990).

The classification of interactions is sometimes a difficult task. For the same disease combinations and conditions, different effects can be observed on the dynamics of diseases and on the crop loss. Bookbinder and Bloom (1980) found a predisposing effect of *Uromyces appendiculatus* and *Meloidogyne incognita* on bean plant weight; however, concerning the pathogen dynamics, an antagonistic effect was observed. Similarly, the effects of the co-inoculation of *Rhizoctonia solani* and *Colletotrichum lindemuthianum* or *U. appendiculatus* on beans on the dynamics of root rot and anthracnose or rust were different from those observed on the plant growth (Paula Júnior 2002).

INTERACTION MECHANISMS

As stated, infection by one pathogen may alter the host response to subsequent infection by another. However, even for the most studied interactions, the mechanisms involved are rarely described.

The effect of a multiple infection depends on the behavior of each one of the involved pathogens. The trophic interaction of the fungi with the host plant seems to play an important role in determining the type of interaction among multiple pathogens (Vollmer 2005). Plant pathogens can be divided into biotrophic and necrotrophic, according to their lifestyles. Biotrophs feed on living host tissue, whereas necrotrophs kill host tissue and derive nutrients from dead or dying cells. A biotrophic pathogen depends on the host organism as a source of nutrients, i.e. it is an obligate parasite. Biotrophic plant pathogenic fungi typically infect host plants without causing cell death for several days. The infection process often involves the formation of specialized feeding structures (e.g. haustorium) in infected plant cells (Perfect and Green 2001). There are different groups of biotrophic fungi. The obligate biotrophs, such as the powdery mildews, the downy mildews and the rusts, cannot be extensively cultured *in vitro* and form specialized haustoria within host plant cells. The facultative biotrophs, e.g. the smut fungus *Ustilago maydis*, can survive saprophytically, but require a successful biotrophic infection of plants for the completion of their life cycles (Perfect and Green 2001). In general, to survive in the absence of the host, the biotrophic pathogens depend on long-lived spores and other propagules that may remain viable for long time waiting for a suitable host (Friberg *et al.* 2005). Biotrophic plant pathogenic microbes, such as downy or powdery mildews and rusts, are generally accepted to have an intricate biological interaction with their host plant, presumably as a result of co-evolution (van Kan 2006).

On the other hand, necrotrophic (non-obligate) pathogens blur the tidy distinctions between parasites, predators and saprotrophs. As the death of host tissues is often inevitable and sometimes quite rapid, necrotrophic parasites are really predators, and once the host is dead, they are saprotrophs. But while the host is alive, necroparasites share many features with other types of parasite (Begon *et al.* 2006). Necrotrophs kill host cells by means of toxic molecules and lytic enzymes and they subsequently decompose the plant tissue and consume it for their own growth. The toxins produced by necrotrophic pathogens can be either specific to the host or non-specific. Non-specific toxins are involved in a broad range of plant-fungus or plant-bacterial interactions. There are necrotrophic fungal pathogens with a broad host range, particularly those in the order of Moniliales, including *Monilinia fructicola*, *Sclerotinia sclerotiorum* and *Botrytis cinerea* (van Kan 2006). If the toxic molecule presents differential activity to one or a few plant species, the pathogen has a limited host range and the metabolite is referred to as a host-selective toxin (HST), such as in the case of *Cochliobolus* and *Alternaria* spp. (van Kan 2006). Necrotrophs often enter the plant through wounds causing immediate and severe disease symptoms on it.

Some pathogens can be clearly assigned as biotrophic or necrotrophic. However, many others behave as both biotrophic and necrotrophic, depending on the conditions to which they are submitted or on the stages of their life cycles (Glazebrook 2005). Such pathogens are called hemi-biotrophics. Many fungi which are commonly considered necrotrophic may be, in fact, hemi-biotrophic, as they have a biotrophic stage in the beginning of the infection process. The infection strategies of this group of fungi are characterized by an initial period of biotrophy followed by the development of secondary necrotrophic hyphae, which ramify through host tissues, killing them before spreading (e.g. some *Colletotrichum* species) (Perfect and Green 2001).

Foliar diseases caused by non-obligate pathogens seem to increase when the host is simultaneously infected with a destructive pathogen. Nicholson *et al.* (1985) found that corn plants infected by *Pratylenchus hexincisus* developed significantly more leaf blight, caused by *Colletotrichum graminicola*. These authors proposed that nematode infection hastened leaf senescence and favored anthracnose leaf blight. Alternaria leaf blight was more severe on sunflower infected with *R. solani* (Bhowmik and Singh 1977). Similarly, Verticilium wilt reduced plant vigor and caused premature senescence on potato plants, which increased early blight severity caused by *Alternaria solani* (Harrison 1974).

During the process of colonization of plant tissues by *C. lindemuthianum*, the phase of slow senescence and of eventual death of infected cells was apparently accelerated in *R. solani*-infected plants (Paula Júnior 2002). Conversely, a decrease in foliar diseases caused by obligate pathogens has been reported (Bookbinder and Bloom 1980; Paula Júnior 2002). Disease severity caused by obligate parasites generally decreases when the host is also infected with virus (Paula Júnior *et al.* 2003). On the other hand, stem, stalk, and root rots caused by less specialized fungi commonly increase when the host is also infected with virus (Beute and Lockwood 1968).

Antagonistic interactions

Antagonistic interactions are explained either as a direct effect of an organism on another or as an indirect effect through changes in the host physiology (Waller and Bridge 1984). The mechanisms of antagonistic interactions among pathogens include antibiosis, competition, hyperparasitism, predation and stimulation of the active defense mechanisms in the host (Cook 1981). In the case of interactions among pathogens that infect simultaneously different plant organs, the most important mechanisms are competition, antibiosis and induced host plant resistance. The competition among pathogens in this case is probably mediated through the host and is related to the use of plant foliage and/or reductions in plant vigor (Harrison 1974; Johnson *et al.* 1986).

Antibiosis can be defined as the interaction among organisms in which one or more metabolites produced by one organism have detrimental effects on the other. The stimulation of active defense mechanisms in the host by one interacting pathogen or its metabolites has a direct action on the host plant and not on the other pathogen. Many pathogens or their metabolites can induce changes in the biochemical mechanisms of host resistance response, which results in an improvement of the resistance against other pathogens. Examples of induction of resistance involving foliar and soil-borne pathogens can be found in McIntyre and Dodds (1979) and Gessler and Kúc (1982).

Synergistic interactions

According to Powell (1971b), three theoretical mechanisms of bio-predisposition are involved in the interacting among pathogens: (1) the primary pathogen may make the host more susceptible to the secondary pathogen; (2) the primary pathogen may enhance the activity of the secondary pathogen; and (3) the secondary pathogen may even enhance the activity of the primary pathogen. Although it is possible to classify theoretically these mechanisms of bio-predisposition, it is very complicated to do this practically, because the cause-effect relationships are not always obvious. For example, the time of pathogen arrival on host is an important factor in the response of a multiple pathogen system, along with fungus nutritional association with the host (Vollmer 2005).

In the case of the interactions between aerial and soil-borne pathogens, the signal transmission by the host (which causes metabolic or systemic changes, such as modifications in the level of growth regulators, exudates and other substances), the shortening of the incubation period, the changes of the nutritional status and the composition of the host cell (Powell 1971b; Evans and Haydock 1993) can explain increments of the host susceptibility and the enhancement of the activity of the interacting pathogens.

Inherent susceptibility of root tissues to root rot may be increased by virus infection (Beute and Lockwood 1968). Possible mechanisms by which a virus infection can increase root rot have been proposed: virus infection leads to an increased exudation from roots of virus-infected plants, with an increased leakage of nutrients, including carbohydrates and amino acids. This may result in an increase in the inoculum level of the pathogens in the rhizosphere (Beute and Lockwood 1968; Evans and Stephens 1989). The ability of roots to synthesize lignin barriers against soil-borne fungi infection is reduced when plants are infected by virus (Evans and Stephens 1989).

SELECTED EXAMPLES

Some selected examples of interactions between soil-borne and aerial pathogens will be presented in two topics considering fungi and nematodes as soil-borne interacting pathogens. Further examples involving these two groups of soil-borne pathogens are also shown in **Tables 1** and **2**. Some comments of the authors are presented, as well as a general classification of the response observed in the population dynamics or in crop loss.

Soil-borne fungi and aerial pathogens

Most of the research on associations of soil-borne fungi and systemic viruses has indicated increases in fungus infection or acceleration of the infection process (Nitzany *et al.* 1973; Chant and Gbaja 1986). Similarly, the presence of a fungus can predispose the host plant to increased viral multiplication (Gbaja and Chant 1985; Chant and Gbaja 1986).

Increasing the host susceptibility to other pathogens caused by virus can be explained by a number of factors, since viruses can have considerable influence on host metabolic activities (Pieczarka and Zitter 1981). Bateman (1961) suggested that the movement of materials from the roots to the cotyledons infected with *Cucumber mosaic virus* (CMV) increased the susceptibility of cucumber seedlings to *Rhizoctonia* damping-off (Bateman 1961). The enhancement of root exudation in virus-infected plants increased the severity of diseases caused by soil-borne pathogens (Beute and Lockwood 1968; Diaz-Polanco *et al.* 1969; Tu and Ford 1971; Pieczarka and Zitter 1981; Pratt *et al.* 1982; Evans and Stephens 1989). The increased permeability of the cell membrane may explain the enhancement of root exudation of different compounds, including nutrients utilizable by fungi. The augmented supply of amino acids increases the inoculum potential of root pathogens in the rhizosphere, favoring pathogens that cause root rot (Beute and Lockwood 1968).

The maize smut causes a decrease of sugar in the stalks and an increase of maize susceptibility to stalk rot caused by *Gibberella zeae*. The latter is a low-sugar disease (Michaelson 1957). The reduced ability of virus-infected asparagus plants to wall-off and lignify infection courts of pathogenic *Fusarium* spp. may contribute to the increase in disease severity in these plants (Evans and Stephens 1989). The influence of PVX on the growth of *Verticillium dahliae* in potato stems seems to be due to an increased disease susceptibility resulting from a general loss of vitality in the PVX-infected plants (Goodell *et al.* 1982). According to Chant and Gbaja (1986), metabolic changes induced by *F. oxysporum* in plant tissues lead to more favorable conditions for CPMV (*Cowpea mosaic virus*) multiplication on cowpea seedlings. On the other hand, increase in exudation induced by SMV (*Squash mosaic virus*) infection does not directly reduce the inoculum potential of *Fusarium solani* f. sp. *cucurbitae* (Magyarosy and Hancock 1974). Exudation seems to indirectly affect inoculum potential via its influence on the soil microflora. It exerts a competitive influence on the causal agent of the stem rot disease during the initial phase of pathogenesis (Magyarosy and Hancock 1974). According to Diaz-Polanco *et al.* (1969), the effect of host exudation upon fungal development may be direct or indirect. They associated the protective effect of viruses on *F. solani* f. sp. *cucurbitae* to changes in the rhizosphere of virus-infected squash plants. The mechanism for the reduction of *Fusarium*-infection may involve spore germination.

The deleterious effect of PVX on plant nutritional levels was apparently detrimental to *Colletotrichum atramentarium* colonization of potato plants (Goodell *et al.* 1982). These unexpected results are not in keeping with the characterization of *C. atramentarium* as a saprophyte or weak

Table 1 Selected examples of interactions between soil-borne fungi and aerial pathogens.

Host	Soil-borne fungus	Aerial pathogen	Author's comments	General response	References
Alfafa	*Phytophthora megasperma*	*Alfafa mosaic virus* (AMV)	Combined infection of alfalfa by AMV and *P. megasperma* greatly exceeding the effect of either pathogen alone during the winter, but not during the summer	Predisposition	Gold and Ashcraft 1972
Anoda cristata	*Fusarium lateritium*	*Alternaria macrospora*	Combinations of *F. lateritium* and *A. macrospora* are more effective than either pathogen used alone for the control of this weed	Predisposition	Crawley *et al.* 1985
Arrowleaf clover	*Phytophthora megasperma* f. sp. *trifolii*, *P. erythroseptica*	*Bean yellow mosaic virus* (BYMV)	Simultaneous dual inoculations, and prior inoculations with BYMV, greatly increased the severity of symptoms, in comparison to those caused by virus and *Phytophthora* species individually	Predisposition	Pratt *et al.* 1982
Asparagus	*Fusarium oxysporum.* f. sp. *asparagi*	*Asparagus virus II* (AV-II)	Asparagus seedlings infected with AV-II became more diseased when inoculated with *F. oxysporum* f. sp. *asparagi* than did virus-free seedlings	Predisposition	Evans and Stephens 1989
Barley	*Fusarium oxysporum* f. sp. *radicis-lycopersici*	*Blumeria graminis* f. sp. *hordei*	*Fusarium oxysporum* f. sp. *radicis-lycopersici* reduced the primary infection frequency of *Blumeria graminis* f. sp. *hordei* (BGH) on the first leaves. The resistance mechanism seems to be based on a dysfunction of the haustorium and/or its interface with the host cell	Induction of resistance	Nelson 2005
Bean	*Fusarium oxysporum* f. sp. *tracheiphilum*, *F. oxysporum* f. sp. *phaseoli*	*Sunn-Hemp mosaic virus* (SHMV)	Co-infection by SHMV with either of the vascular wilt pathogens caused greater losses in total fresh weight and leaf area, compared with uninfected plants or plants infected singly with any one of these pathogens	Predisposition	Gbaja and Chant 1985
Bean	*Thielaviopsis basicola*	*Uromyces appendiculatus*	Rust predisposes bean plants to infection by the soil inhabitant pathogen *Thielaviopsis basicola*	Predisposition	Yarwood 1969
Brassica sp.	*Fusarium oxysporum* f. sp. *conglutinans*	*Turnip mosaic virus* (TuMV)	Fungus-infected plants inoculated with the virus were more severely yellowed and weighed less than plants infected with the fungus alone. Similarly, when inoculated with the fungus, mosaic-infected plants were more severely stunted than plants with the virus alone	Predisposition	Reyes and Chadha 1972
Corn, wheat	*Pythium graminicola*, *Diplodia zeae*, *Fusarium moniliforme*, *F. oxysporum*, *F. roseum*, *Helminthosporium pedicellatum*	*Maize dwarf mosaic virus* (MDMV)	The soil-borne pathogens caused more severe root rot in MDMV-infected plants than in virus-free seedlings	Predisposition	Mwanza and Williams 1966
Cowpea	*Fusarium oxysporum* f. sp. *tracheiphilum*, *F. oxysporum* f. sp. *phaseoli*	*Cowpea mosaic virus* (CPMV)	Combined infections of cowpea seedlings by CPMV and *F. oxysporum* induced greater losses in leaf area, fresh and dry weights than infection by either pathogen alone	Predisposition	Chant and Gbaja 1986
Cucumber	*Fusarium* spp.	*Cucumber mosaic virus* (CMV)	Virus infection increased susceptibility of cucumber to *Fusarium* spp.	Predisposition	Nitzany *et al.* 1973
Cucumber	*Fusarium oxysporum* f. sp. *cucumerinum*	*Colletotrichum lagenarium*, *tobacco necrosis virus* (TNV)	Resistance to cucumber wilt was induced in cucumber plants inoculated with *C. lagenarium* or TNV	Induction of resistance	Gessler and Kúc 1982
Cucumber	*Rhizoctonia* sp.	*Cucumber mosaic virus* (CMV)	Post-emergence damping-off caused by *Rhizoctonia* sp. was increased from 10-15% to 60-87% by CMV infection	Predisposition	Bateman 1961
Cucumber	*Pythium ultimum*	*Cucumber mosaic virus* (CMV)	Much less mortality was caused by the fungus alone	Predisposition	Nitzany 1966
Lupine	*Fusarium solani* f. sp. *lupini*	*Bean yellow mosaic virus* (BYMV)	The intensity of root and stem rot was greater in plants inoculated with BYMV and *F. solani* f. sp. *Lupini*, compared to the fungus alone	Predisposition	Patil 1973
Maize	*Gibberella zeae*, *Helminthosporium pedicellatum*	*Maize dwarf mosaic virus* (MDMV)	Corn seedlings infected with MDMV were more susceptible to root rot diseases incited by *G. zeae* and *H. pedicellatum* than virus-free seedlings	Predisposition	Tu and Ford 1971
Maize	*Fusarium moniliforme*	*Aspergillus flavus*	*Fusarium moniliforme* inhibited kernel infection by *A. flavus* in inoculated maize ears and led to reduced aflatoxin contamination of kernels	Competition	Zummo and Scott 1992
Maize	*Fusarium moniliforme*	*Aspergillus flavus*	*Fusarium moniliforme* can inhibit kernel infection by *A. flavus* and aflatoxin contamination of other uninjured kernels on the same ear	Competition	Wicklow *et al.* 1988
Maize	*Gibberella zeae*, *Diplodia zeae*	*Ustilago maydis*	Corn smut predisposed corn to stalk rot caused by both *G. zeae* and *D. zeae*	Predisposition	Michaelson 1957
Pea	*Pythium* sp.	*Bean yellow mosaic virus* (BYMV), *pea mosaic virus* (PMV)	Pythium root rot of peas was much more severe in plants previously infected with the viruses	Predisposition	Escobar *et al.* 1967
Pea	*Aphanomyces euteiches*, *Fusarium solani*	*Pea mosaic virus* (PMV), *alfafa mosaic virus* (AMV), b*ean yellow mosaic virus* (BYMV), *pea enation mosaic virus* (PEMV)	A combined virus-fungus infection resulted in more severe symptoms of disease, compared to the effects of a fungus infection alone	Predisposition	Farley and Lockwood 1964

Table 1 (Cont.)

Host	Soil-borne fungus	Aerial pathogen	Author's comments	General response	References
Pea	*Fusarium solani* f. sp. *pisi*, *Aphanomyces euteiches*	*Bean yellow mosaic virus* (BYMV), *common pea mosaic virus* (PMV)	The exudates from virus-infected plants may increase the inoculum potential of the root rot fungi	Predisposition	Beute and Lockwood 1968
Pepper	*Rhizoctonia solani*	*Tobacco mosaic virus* (TMV-P), *pepper mottle virus* (PeMV)	Plants infected with TMV-P and PeMV were more susceptible to *R. solani*	Predisposition	Pieczarka and Zitter 1981
Potato	*Fusarium roseum*	*Potato virus X* (PVX)	PVX decreases the susceptibility of potato tubers to *F. roseum*	Induction of resistance	Jones *et al.* 1968; Jones and Mullen 1974
Potato	*Verticillium dahliae*, *Colletotrichum atramentarium*	*Potato virus X* (PVX)	1) PVX had no effect on the incidence of infection by *V. dahliae*, but increased the level of host colonization by *V. dahliae.* 2) Infection and stem colonization by *C. atramentarium* was inversely correlated with PVX infection	1) Predisposition 2) Competition	Goodell *et al.* 1982
Potato	Verticillium dahliae	*Alternaria solani*	Concurrent infestations of potato leafhopper, *A. solani* and *V. dahliae* result in yield and foliage reductions that are less than the sum of the losses caused by a solitary infestation of each organism	Competition	Johnson *et al.* 1987; Johnson *et al.* 1986; Johnson 1990
Potato	*Verticillium dahliae*, *Colletotrichum atramentarium*	*Potato virus X* (PVX)	1) The severity of *V. dahliae* was greater in the presence of PVX. 2) The severity of *C. atramentarium* was lower in the presence of PVX	1) Predisposition 2) Antagonism	Jellison *et al.* 1979
Potato	*Verticillium albo-atrum*	*Alternaria solani*	The reduction of *Verticillium* wilt by soil fumigation could explain the increased effectiveness of early blight control on fumigated soil	Predisposition	Harrison 1974
Red clover	*Fusarium oxysporum, F. roseum, F. solani, F. moniliforme*	*Red clover vein mosaic virus* (RCVMV)	Only *F. oxysporum* and *F. solani* caused a faster decline of plants in combination with RCVMV	Predisposition	Dennis and Elliott 1967
Squash	*Fusarium solani* f. sp. *cucurbitae*	*Squash mosaic virus* (SMV)	Protection to Fusarium stem rot was induced by SMV indirectly via its influence on the soil microflora, through the increase in exudation.	Competition	Magyarosy and Hancock 1974
Squash	*Fusarium solani* f. sp. *cucurbitae*	*Squash mosaic virus* (SMV), *watermelon mosaic virus* (WMV), *wild cucumber mosaic virus* (WCM)	Virus-infected plants survived longer than virus-free plants when they were inoculated with *F. solani* f. sp. *cucurbitae*. Protection was reduced by increasing inoculum level	Induction of resistance	Diaz-Polanco *et al.* 1969
Sunflower	*Rhizoctonia solani*	*Alternaria* sp.	Alternaria leaf blight of sunflower was more severe on plants infected with *R. solani*	Predisposition	Bhowmik and Singh 1977
Tobacco	*Phytophthora parasitica* var. *nicotianae*	*Tobacco mosaic virus* (TMV)	TMV systemic induced protection against race 3 of *P. parasitica* var. *nicotianae*	Induction of resistance	McIntyre and Dodds 1979
Tomato	*Fusarium oxysporum* f.sp. *lycopersici* race 2	*Oidium* sp.	Root infection by *Fusarium* reduced the severity of *Oidium* on leaves	Antagonism	Silva *et al.* 2001
Tomato	*Verticillium dahliae*, *Fusarium* spp.	*Tobacco mosaic virus* (TMV)	Severity of symptoms on plants infected by either *V. dahliae* or *Fusarium* spp. increased in the presence of TMV	Predisposition	Thanassoulopoulos 1976
Wheat	*Gaeumannomyces graminis* var. *tritici*	*Erysiphe graminis f.* sp. *tritici, Septoria nodorum*	1) *G. graminis* var. *tritici* suppressed *E. graminis* f. sp. *tritici* and 2) increased the infection by *S. nodorum*	1) Not clear 2) Predisposition	Jörg 1987
Wheat	*Pseudocercosporella herpotrichoides*	*Erysiphe graminis f.* sp. *tritici, Septoria nodorum*	*P. herpotrichoides* increases the severity of *E. graminis* f. sp. *tritici* and *S. nodorum*	Predisposition	Jörg 1987
Wheat	*Pseudocercosporella herpotrichoides*	Puccinia recondita	The formation of pustules of *P. recondita* was delayed, the rust severity was 20% lower, and the newly formed pustules were smaller in plants infected by *P. herpotrichoides*	Antagonism	Grigorév 1981
Wheat	*Gaeumannomyces graminis*	Septoria nodorum	Germ-tubes of *S. nodorum* grew more rapidly and host tissue was more rapidly colonized on leaves from take-all plants	Predisposition	Jenkins and Jones 1980
Wheat	*Pseudocercosporella herpotrichoides*	Septoria nodorum	Significantly higher levels of *S. nodorum* developed on the leaves of eyespot infected plants, but there was no significant interaction in terms of grain yield. Eyespot infection markedly predisposed the developing seed to infection by *S. nodorum*	Predisposition	Jones and Jenkins 1978
White clover	*Fusarium. oxysporum*, *F. roseum*, *Rhizoctonia solani*, *Sclerotium bataticola*	*Bean yellow mosaic virus* (BYMV)	When both a fungus species and BYMV were present, no significant increase in pathogenicity was observed, compared with the corresponding fungus alone	Additive	McCarter and Halpin 1961

pathogen, which would lead to the expectation of a high level of *C. atramentarium* infection in the less vigorous virus-infected plants (Goodell *et al.* 1982). Virus-induced protection has been also observed by McIntyre and Dodds (1979) and Gessler and Kúc (1982).

Many leaf spot diseases caused by necrotrophic pathogens are more severe under stress caused by root diseases (Waller and Bridge 1984). For example, *Verticilium* wilt reduced plant vigor, led to premature senescence of potato plants and increased early blight severity caused by *A. solani* (Harrison 1974).

On the other hand, the stress caused by root diseases may reduce the development of biotrophic pathogens on the aerial part of the plants. Silva *et al.* (2001) found that the

Table 2 Selected examples of interactions between nematodes and aerial pathogens.

Host	Nematode	Aerial pathogen	Author's comments	General response	References
Bean	*Meloidogyne incognita*	*Uromyces appendiculatus*	Infection of plants with both pathogens suppressed plant weights significantly more than did infection by either pathogen alone, but when the pathogens were together, fungal uredia were reduced in size and sporulation capacity and *M. incognita* produced fewer root galls, and fewer eggs per egg mass	Predisposition, competition (pathogen dynamics)	Bookbinder and Bloom 1980
Bean, tomato	*Meloidogyne javanica*	*Tobacco ringspot virus* (TRSV), *tobacco mosaic virus* (TMV)	Nematodes enter TRSV infected bean plants in higher number, compared to uninfected controls. Nematodes grow more rapidly in TMV infected tomatoes than in uninfected controls	Predisposition	Bird 1969
Cardamom	*Meloidogyne incognita*	*Cardamom mosaic virus* (CarMV)	*Meloidogyne incognita* produced five to ten times more individuals on cardamon plants infected with katte mosaic virus than on healthy plants	Predisposition	Ali 1988
Cotton	*Meloidogyne* spp.	*Alternaria tenuis*	Infection by *Meloidogyne* spp. increased the susceptibility of cotton seedlings to *A. tenuis*	Predisposition	Cauquil and Shepard 1970
Eggplant	*Tylenchorhynchus brassicae, Rotylenchulus reniformis*	*Brinjal mosaic virus* (BMV)	The population build-up of both the ectoparasite *T. brassicae* and the semi-endoparasite *R. reniformis* on eggplant (*Solanum melongena*) was promoted when plants were infected with brinjal mosaic virus	Predisposition	Naqvi and Alam 1975
Gladiolus	*Meloidogyne javanica*	*Pseudomonas marginata*	*Meloidogyne javanica* greatly increased the severity of gladiolus scab caused by *P. marginata*	Predisposition	El-Goorani *et al.* 1974
Maize	*Pratylenchus hexincisus*	*Colletotrichum graminicola*	Severity of anthracnose leaf blight increased significantly in plants that were also infected with the nematode	Predisposition	Nicholson *et al.* 1985
Maize	*Meloidogyne incognita*	*Maize mosaic virus* (MMV)	The interaction between the virus and the root-knot nematode was synergistic	Predisposition	Khurana *et al.* 1970
Maize	*Meloidogyne incognita*	*Tobacco mosaic virus* (TMV)	The host-parasite relationship of tobacco and the root-knot nematode was influenced synergistically by TMV	Predisposition	Goswami and Raychaudhuri 1973
Peach orchards	*Criconemella xenoplax*	*Pseudomonas syringae* pv. *syringae*	The nematode was a predisposing agent for the bacterial spot	Predisposition	Lownsbery *et al.* 1973, 1977
Peach orchards	*Criconemella xenoplax*	*Xanthomonas campestris* pv. *campestris*	Defoliation resulting from bacterial spot was greater in nonfumigated, nematode-infested soil than in fumigated soil	Predisposition	Nesmith and Dowler 1975
Peach trees	*Criconemella xenoplax*	*Xanthomonas campestris* pv. *pruni*	Bacterial spot damage was more severe on peach trees when the soil was infested with *C. xenoplax* than when nematodes have been suppressed	Predisposition	Shepard *et al.* 1999
Petunias, cucumber	*Ditylenchus dipsaci*	*Arabis mosaic virus* (AMV), *cucumber mosaic virus* (CMV)	AMV inhibited *D. dipsaci* in petunias and CMV in cucumber	Antagonism	Fritzsche 1970
Prune	*Macroposthonia xenoplax*	*Pseudomonas syringae*, *Cytospora leucostoma*	*Macroposthonia xenoplax* increased the susceptibility of young French prune trees to *P. syringae* and *C. leucostoma*	Predisposition	English *et al.* 1982
Solanum khasium	*Meloidogyne* sp.	*Tobacco mosaic virus* (TMV)	The root-knot index was higher on plants inoculated with TMV than on healthy plants	Predisposition	Ismail *et al.* 1979
Soybean	*Meloidogyne incognita*	*Tobacco ringspot virus* (TRSV)	Plants with both the virus and the nematode had a much reduced root system	Predisposition	Ryder and Crittenden 1962
Tobacco	*Ditylenchus dipsaci*	*Tobacco mosaic virus* (TMV), *tobacco rattle virus* (TRV), *belladona mottle virus* (BeMV), *arabis mosaic virus* (ArMV), *tomato blackring virus* (ToBRV)	*Ditylenchus dipsaci* was 1) inhibited by TMV and TRV, but 2) favored by BMV, AMV and ToBRV	1) Antagonism 2) Predisposition	Weischer 1975
Tomato	*Meloidogyne incognita*	*Alternaria solani*	Part of the yield reduction in plants infected with *M. incognita*, as compared to the controls, was apparently due to the nematodes interacting with the early blight fungus	Predisposition	Barker 1972
Tomato	*Meloidogyne* spp.	*Clavibacter michiganensis*	Bacterial canker of tomato was increased when the roots were infected with *Meloidogyne* spp.	Predisposition	De Moura *et al.* 1975
Tomato	*Meloidogyne incognita*	*Tomato mosaic virus* (ToMV)	When virus infection preceded nematode inoculations, nematodes were suppressed, and when nematodes were the first agent, the virus was inhibited	Antagonism	Alam *et al.* 1990
Tomato	*Meloidogyne incognita*	*Tobacco mosaic virus* (TMV)	In two of three tomato varieties, the egg production of *M. incognita* was significantly increased by the presence of TMV	Predisposition	De Moura and Powell 1977
Vigna sinensis	*Meloidogyne incognita*	*Cowpea mosaic virus* (CPMV)	Plants inoculated with nematodes and virus (10 days later) were stunted 50 days after the inoculation, whereas those in all other treatments grew well. Plants inoculated with virus early had more severe symptoms of nematode attack than those inoculated with virus 10 days later	Predisposition	Goswami *et al.* 1974

Table 2 (Cont.)

Host	Nematode	Aerial pathogen	Author's comments	General response	References
White clover	*Meloidogyne incognita*	*Peanut stunt virus* (PSV)	*Meloidogyne incognita* and PSV acted independently in reducing forage productivity and persistence	Additive	McLaughlin and Windham 1996
Zinnia elegans	*Meloidogyne incognita*	*Zinnia mosaic virus* (ZiMV)	Plants infected with zinnia mosaic virus were better hosts for *M. incognita* than healthy plants	Predisposition	Jabri *et al.* 1985
Zucchini	*Meloidogyne javanica*	*Watermelon mosaic virus* (WMV)	Inhibitory effects on *M. javanica* were observed in plants infected with watermelon mosaic virus. Virus infection retarded the establishment of these nematodes in the roots, as compared with healthy plants	Antagonism	Huang and Chu 1984

severity of *Oidium* on tomato plants coinoculated with *Fusarium oxysporum* f. sp. *lycopersici* (race 2) was inversely proportional to the inoculum concentration of the wilt pathogen in the soil (0 to 10^6). In the non-infested soil treatment, plants presented better growth and *Oidium* severity increased. The mechanism proposed for the reduction of *Oidium* severity in the presence of *Fusarium* is that the root infection may result in physiological changes of leaves that affect the capacity of the tissues to support the development of the obligate parasite.

Similar results were obtained by Nelson (2005), who reported that drench inoculation of the undisturbed roots of barley seedlings with *Fusarium oxysporum* f. sp. *radicis-lycopersici* significantly reduced the primary infection frequency of the causal agent of the powdery mildew *Blumeria graminis* f. sp. *hordei* on the first leaves. The length of secondary hyphae and subsequent conidial production by *B. graminis* were reduced by pre-inoculation with *Fusarium*. The reduction in infection frequency was observed as early as 48 h after the plants were challenge-inoculated with *B. graminis*, immediately following inoculation with *Fusarium*. The induced resistance continued up to 16 d after treatment, as indicated by the reduction in the infection frequency; up to 22 d when evaluated as a reduction in the length of secondary hyphae; and up to 35 d when evaluated as a reduction in conidial production. According to the author, the resistance mechanism did not seem to be based on the death of the haustorium or of the host cell, but on the dysfunction of the haustorium and/or its interface with the host cell.

Root damage caused by *R. solani* on bean is commonly magnified if biological stresses are present, such as other pathogens (Abawi and Pastor-Corrales 1990). The effects of the co-inoculation of *R. solani* and the aerial pathogens *C. lindemuthianum* or *U. appendiculatus* at different inoculum levels on the disease dynamics and on the growth of bean plants under greenhouse conditions were investigated (Paula Júnior 2002). Bean seeds were sown in soil infested with *R. solani* inoculum produced on rice grains. Additional experiments in which bean seedlings were transplanted to infested soil were also carried out. Conidial suspensions of *C. lindemuthianum* and uredospores of *U. appendiculatus* were inoculated onto leaves at the plant developmental stages V2 and V3, respectively. Interactions between root rot and the aerial diseases were observed, depending on the inoculum levels and on the timing of *R. solani* inoculation. Anthracnose severity was higher on plants infected by *R. solani*. On the other hand, *R. solani* infection reduced the diameter of pustules and rust severity. Root rot severity and population density of the soil-borne pathogen in the soil were magnified at high levels of *C. lindemuthianum* or *U. appendiculatus* on shoot when seedlings were transplanted to soil infested with *R. solani* at low levels. In these experiments, a synergistic interaction between root rot and anthracnose affected the plant dry weight. Thus, root rot is a stress factor that increases anthracnose severity on beans. Antagonistic effects on the plant dry weight were seen for the combination root rot/rust only when bean seeds were sown in infested soil.

Inoculation of bean plants with *Fusarium oxysporum* f. sp. *phaseoli* before *U. appendiculatus* inoculation reduced the severity, the number and the size of rust pustules. However, when *U. appendiculatus* was inoculated first, the development of the rust was not affected by the inoculation of *F. oxysporum* f. sp. *phaseoli*. In both situations, the development of Fusarium wilt was not affected by rust (Admassu 2002).

Effects of rust on other bean diseases have been described (Yarwood 1977; Stavely and Pastor-Corrales 1984). Rust predisposes bean plants to infection by the soil inhabitant pathogen *Thielaviopsis basicola* (Yarwood 1977). The mechanisms involved in this interaction were not determined.

Nematodes and aerial pathogens

Plant-parasitic nematodes often play a major role in disease interactions. Interactions involving nematodes are important because they contribute substantially to change the crop growth (Zadoks and Schein 1979). Nematodes participate in disease complexes in different ways. They can create portals of entry for other pathogens and modify the host rhizosphere, favoring the growth of other pathogens. Nematodes can be efficient vectors for viruses, bacteria and fungi; they can also alter the host susceptibility to other pathogens, by inducing physiologic changes in the host (Bergeson 1971). Effects of nematode infection in different host organs are also expected, since they can induce systemic responses in host plants (Friedman and Rohde 1976; Sitaramaiah and Pathak 1993).

Indirect effects of plant viruses on nematodes via the host plant are well-documented (Weischer 1975, 1993). They are based on changes in host plant metabolism caused by both organisms. Favorable or detrimental effects occur or are more pronounced when nematode inoculation is preceded by virus infection for two to three weeks (Alam *et al.* 1990; Weischer 1993).

Although many interactions involving nematodes and other plant pathogens are well-documented, there are several contradictory results, mainly due to unsuitable methodologies for determining the full extent of interactions (Sikora and Carter 1987).

Maize infected with *P. hexincisus* developed more leaf blight, caused by *C. graminicola*, compared to those without nematode infection. One explanation proposed for this increase in disease severity is that infection with the nematode hastens leaf senescence, and this would be expected to favor anthracnose leaf blight (Nicholson *et al.* 1985). The predisposing effect of *Tobacco ringspot virus* (TRSV) on *M. javanica* penetration may be associated with the presence of the virus in the meristematic region of the root whereto nematodes are attracted. Moreover, the influence of *Tobacco mosaic virus* (TMV) on the growth of *M. javanica* may be an indirect effect of the decreased amount of nitrogen available, which increases the rate of nematode growth (Bird 1969). Changes in free amino acid levels in sugarcane caused by *Sugarcane mosaic virus* (SCMV) were responsible for population changes in various nematodes (Showler *et al.* 1990).

Criconemella xenoplax affects the susceptibility of plum and peach to *Pseudomonas syringae* directly through feeding damage to roots, which results in water stress throughout the tree (Lownsbery *et al.* 1973; Mojtahedi *et al.*

1975). Shepard *et al.* (1999) suggested an additional host response to deeding by *C. xenoplax*, which allows extensive development of bacterial spot symptoms even when there is no evidence of water stress.

There is an interaction between *U. appendiculatus* and *M. incognita* on beans. The pathogens interact with each other through their influence on the host plant. The infection of plants with *U. appendiculatus* and *M. incognita* simultaneously suppressed plant weights more than did infection by either pathogen alone. Both pathogens on the same plant influenced the reproduction of each other, probably through effects on the host. Nematode infections reduced the uredial diameter, which resulted in a decreased sporulation capacity of uredia on leaves of nematode-infected plants. The mechanism by which *M. incognita* caused this response was not determined, but it may be related to the suppression of shoot growth caused by this pathogen or to the suppression of host photosynthesis (Bookbinder and Bloom 1980). The lower weight of root knot nematodes-infected tomato plants is correlated with retarded photosynthetic rate (Wallace 1974). The number of root galls per gram of root was reduced by *U. appendiculatus* infection when both pathogens were applied simultaneously and when the fungus was applied first. This response may be related to the suppression of translocation of photosynthates to roots of *U. appendiculatus*-infected plants, resulting in reduced root growth, which caused less egg production (Bookbinder and Bloom 1980).

M. incognita predisposes plants to infection by the Fusarium wilt fungus, and this complex further predisposes plants to infection by *Alternaria tenuis*. Root-knot nematodes (*M. incognita acrita*), *A. tenuis*, *F. oxysporum* f. sp. *vasinfectum*, *Glomerella gossypii*, and *R. solani* caused synergistic effects on the severity of cotton seedling diseases. *A. tenuis* and *F. oxysporum* f. sp. *vasinfectum* alone caused slight symptoms or no disease. However, when these fungi were combined with nematodes, disease was severe. In combination with nematodes, *R. solani* or *G. gossypii* killed or damaged the seedlings faster. Besides, less fungal inoculum was required for infection (Powell 1971a).

EPIDEMIOLOGICAL APPROACHES

In a previous review (Paula Júnior *et al.* 2003), we discussed some aspects related to the epidemiology of interactions among pathogens. However, there are only few studies related to the interactions among soil-borne and aerial pathogens which emphasize epidemiological aspects and are not merely descriptive (Nicholson *et al.* 1985; Johnson *et al.* 1986, 1987; McLaughlin and Windham 1996).

The presence or absence of interactions depends on the initial pathogen population densities and plant species and varieties (Tu and Ford 1971; De Moura and Powell 1977; Sikora and Carter 1987; Weischer 1993). Under conditions where significant alterations in the normal balance occur, an interaction between the various factors can lead to disease complex etiology and synergistic interactions (Sikora and Carter 1987).

The nature of the interaction between soil-borne and aerial pathogens on a given host may indicate the type of disease control required. For example, when a virus enhances the severity of a root disease, the control of the virus is relevant (Reyes and Chadha 1972). According to Jones and Jenkins (1978), the predisposing effect of eyespot caused by *Pseudocercoporella herpotrichoides* on wheat seed infection by *Septoria nodorum* has considerable epidemiological significance, since seed treatments are partially effective in controlling *S. nodorum*.

The assessment of plant susceptibility to aerial pathogens can be limited by interactions with soil-borne pathogens, particularly in interactions involving low levels of root infection (Jenkins and Jones 1980). The type of interaction between soil-borne and aerial pathogens on a given host may indicate the strategy of disease control required, since the simultaneous infection of plants by soil-borne and aerial pathogens can modify the severity of diseases caused by either of the pathogens alone. For example, when a virus enhances the severity of a root disease, the control of the virus is relevant (Reyes and Chadha 1972). Although studies involving pathogen interaction still remain quite new, it is obvious for many pathosystems that significant progress in recommending the implementation of appropriate strategies of disease management can only be achieved by careful consideration of all implications related to the interactions.

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