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INVITED REVIEW

DISEASES CAUSED BY SOILBORNE PATHOGENS: BIOLOGY, MANAGEMENT AND CHALLENGES

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SUMMARY

Soilborne pathogens cause severe diseases in many crops. They have common features based on their close connection with the soil, which has a strong influence on their survival and capacity to cause disease. The latter stems from interactions between the pathogen and the host, which both in turn interact with the biotic and abiotic components of the environment. Soilborne pathogens produce resting structures which, in the absence of a host, are inactive, and are therefore protected from the soil's hostile activities due to fungistasis. However, in the presence of root exudates of a susceptible host in the rhizosphere, or an adequate nutrient source, they germinate and infect the plant, pending suitable conditions. In addition, soilborne pathogens may colonize the roots of plants that are not their major host, without inducing visible symptoms. Soilborne pathogens have many mechanisms for their spatial dispersal, e.g., through infected propagation material. Basic management strategy involves disruption of one or more of the disease components, at any stage of disease development, to achieve an economic reduction in disease with minimal disturbance to the environment. This is achieved by chemical, physical, biological, cultural, physiological and genetic approaches, using soil disinfestation (fumigation, soil solarization, biofumigation, anaerobic soil disinfestation), biocontrol, organic amendments, resistant cultivars and grafting, fungicides, cultural practices, induced resistance and others. These should be carried out in the framework of integrated pest-management programs. Many challenges remain. We need to study the gap between the promising results obtained under controlled conditions and the modest results obtained under realistic ones. A better understanding of the mechanisms and modes of action of the involved processes should provide new tools for disease management.

Keywords: biocontrol, disease control, disease management, soil, soilborne pathogen, soil disinfestation.

INTRODUCTION

Diseases caused by soilborne pathogens (DSBP) cause heavy losses to many crops; they include seedling, vascular and root rot diseases. Soilborne pathogens include fungi, oomycetes, nematodes, viruses (carried by nematodes or other organisms) and parasitic plants, e.g., *Phelipanche* (*Orobanche*). Although they are very diverse, these pathogens share some basic features related to being soilborne. They survive and act in the soil, at least during part of their lives. Consequently, they are heavily influenced by the soil's abiotic and biotic components, as well as by agricultural practices which are applied to the soil, such as irrigation, tillage, manure application and fertilization. They invade the plants through belowground organs but may also reach the upper parts of the plant. All of these features affect their management, as detailed herein.

DSBP differ from foliar diseases, although the line between these two groups is not always clear-cut. Foliar diseases are very common in natural habitats. For example, rusts, powdery mildews and other foliar diseases can be frequently seen on cereals and legumes in the wild; in contrast, soilborne pathogens are extremely rare in natural habitats – *Phytophthora cinnamomi* in *Eucalyptus* forests in Australia is one such exceptional case (Cook and Baker, 1983). Therefore, outbreaks of DSBP in agricultural systems are an unusual magnification of a natural phenomenon that is enhanced by agricultural practices, such as frequent cropping of susceptible crops in soils (Park, 1963). Consequently, the soil becomes enriched with pathogen inocula, and their populations are built up (Katan, 2002). Foliar diseases are polycyclic, whereas DSBP are considered monocyclic, although there are exceptions (Pfender, 1982). Foliar pathogens are directly exposed to temperature and humidity fluctuations in the ambient environment. In contrast, in the soil, and especially with irrigated crops, the soil mass dampens such fluctuations (Garett, 1970). The soil environment (both natural and agricultural) is the major, but not sole factor determining whether a disease will occur and at what intensity.

Research on DSBP is hindered by the following conditions: (1) the soil is opaque, preventing examination of the pathogen *in situ*. Methods to overcome this have been

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devised (Scher and Baker, 1983; Cytryn and Minz, 2012); (2) pathogen propagules differ in their resistance to hostile conditions and in their longevity. These include conidia, mycelia, sclerotia, chlamydospores, rhizomorphs and oospores, among others. Thus, both the quantity and quality of the inoculum affect pathogen survival and pathogenicity. Inoculum quality is generally difficult to assess and is frequently overlooked; (3) the soil is a heterogeneous medium consisting of many microhabitats that differ in size, microbial activity, nutrient availability, and toxicant concentrations. This results in a non-uniform distribution of pathogen populations in the soil or the root zone (Mihail and Alcorn, 1987; Campbell and Van der Gaag, 1993); (4) there are large populations of established microorganisms in the soil that are not necessarily connected to a host plant. Such microorganisms mask the population of disease-causing soilborne pathogens, although they may significantly affect those pathogens. The use of culture-based assessments of microbial populations in soils can only reveal a small fraction of the existing populations. However, continuous improvements in molecular techniques have enabled the detection of uncultivable microorganisms, raising doubt as to the significance of data based only on classical culture methods, using various agar media.

Typical soilborne pathogens cause visible and distinct symptoms, such as lesions, rots and wilt, which may lead to plant mortality. They are therefore considered major pathogens. In contrast, "minor pathogens" act as parasites on root tips or root cortical cells, resulting in suppression of plant growth and stunting (Sewell, 1984; Schippers *et al.*, 1987; Gamliel and Katan, 1991). However, under certain conditions, a major pathogen may cause only partial stunting, whereas a minor pathogen may become highly destructive. Minor pathogens and deleterious microorganisms are also involved in cases of growth decline, such as "soil sickness", monoculture and replant diseases (Mazzola and Strauss, 2014), phenomena which may be regarded as various types of plant health disturbances.

Revealing the life cycle of soilborne pathogens and their hosts' responses can provide potential tools for their management. There are numerous publications and books on issues related to DSBP, and not all of these issues can be covered in one article. Also, there are books which deal with specific soilborne pathogens, e.g., *Rhizoctonia* (Sneh *et al.*, 1997), *Verticillium* (Pegg and Brady, 2002) and *Fusarium* (Gullino *et al.*, 2012). Therefore, in this review, selected topics, which have the potential to provide additional approaches for better combating soilborne pathogens, are addressed.

LIFE CYCLE, ECOLOGY AND EPIDEMIOLOGY OF SOILBORNE PATHOGENS

The activities of disease-causing soilborne pathogens depend heavily on the presence of the host as well as other biotic and abiotic agents. In the zone of influence of the plant roots (rhizoplane and rhizosphere), the pathogen, the host and surrounding microorganisms are continuously affected by one another as well as by the biotic and abiotic components of the environment (Fig. 1). If the pathogen and the host are compatible and the environmental conditions are suitable, sequential infection processes occur. The pathogen propagules germinate and then penetrate the belowground plant organs, the plant becomes infected, morphological and physiological changes take place in both the host and the pathogen, and a disease syndrome is produced. Later, pathogen resting structures are formed in the infected host tissues. Plant residues containing the resting structures are incorporated into agricultural field soils after plant death. Then, intensive microbial activity occurs and successions of microorganisms of various groups develop in the decomposing plant tissues. The balance between pathogen production of resting structures and saprophytic activity on the one hand, and the decline in the pathogen population due to antagonistic and other hostile activities and death due to natural causes on the other, ultimately determines the pathogen's ability to survive in the absence of a host. Planting a new host in such soils, or enabling contact between the pathogen and roots of a new plant, will initiate a new cycle (Lockwood, 1988; Katan, 2002).

Two phenomena that occur in the root zone and determine the fate of the pathogen and its ability to initiate infection are fungistasis and the production of root exudates. Fungistasis is a property of natural soils whereby germination of propagules is inhibited (Dobbs and Hinson, 1953; Lockwood, 1977). Fungistasis (mycostasis) consists of an exogenous, temporary dormancy imposed on the propagules by the natural soil which can be nullified by various means. It is a universal phenomenon, widespread in soils with normal biological activity, and has been shown to prevent the germination of many fungi. This phenomenon occurs with other soil microorganisms as well, such as soil bacteria (soil microbiostasis) (Ho and Ko, 1985). Dormant propagules are less vulnerable to the soil's antagonistic activity, and fungistasis prevents the propagule from germinating in the absence of potentially colonizable substrates such as plant roots. Therefore, fungistasis has a great survival value for soil fungi. It is associated with normal microbial activity in the soil. It can be nullified by soil sterilization, addition of organic nutrients (e.g., glucose and amino acids) to the soil or the presence of root exudates. There are several fungistatic mechanisms mediated by soil microorganisms, including the presence of volatile or soluble inhibitory substances, which prevent germination, and deficiencies in nutrients that are essential for germination (Ko and Lockwood, 1967; Liebman and Epstein, 1992).

Root exudates (also termed root excretions) are substances that are released by plant roots into the surrounding medium (Curl, 1986). As nutrient and microbiological compounds follow a decreasing gradient from the root surface into the soil, the influence of the roots diminishes with distance. Root exudates contain sugars, amino acids, and many other substances that affect the activities of soil microorganisms and pathogens (Gamliel and Katan, 1992). The enhanced microbial activity in the rhizosphere (R), as compared with the bulk (non-rhizosphere) soil (S), is expressed as the R:S ratio of microbial populations. This ratio is usually in the range of 10:1 to 20:1.

The rhizosphere is the arena in which fungistasis is nullified and pathogen propagules germinate. Under suitable conditions, germination will result in root infection. However, the rhizosphere is also an area with intensive activity of antagonistic biological processes that may control the pathogen. Root exudates may affect the pathogen propagules by inducing their germination in the presence of the host, attracting motile propagules (e.g., zoospores and bacteria) to the roots, stimulating pathogen growth, or causing the formation of infection structures. On the other hand, root exudates that are deficient in nutrients or that contain toxic substances affect the pathogens adversely. The quantity and quality of the root exudates are determined by the plant's characteristics and by environmental factors such as temperature, soil moisture, root injury, presence or absence of minerals, and even foliar sprays. Volatile seed exudates were found to stimulate germination of *Pythium* sporangia (Nelson, 1987). These included acetaldehyde, ethanol and ethane, among others. Exudates also leak from the germinating seeds – the spermosphere – and these too affect the pathogens (Nelson, 2004).

The mechanisms of fungistasis and root exudate production should continue to be the focus of future studies since they play a major role in the ecology of soilborne pathogens and their antagonists. As such, their elucidation may provide additional tools for the management of DSBP, especially with regard to biocontrol of soilborne pathogens.

Under normal agricultural conditions, soilborne pathogens have to survive for various lengths of time in the absence of their major hosts. This survival can be passive, via the production of resting structures that are resistant to biotic and abiotic agents and that have the capacity to remain inactive in the absence of the host, but can germinate near its roots. Survival can be active, for example by colonizing organic matter in the soil or the roots of plants which are not major hosts without causing visible symptoms or damage to the plant; such plants can be regarded as symptomless carriers or asymptomatic plants (Katan, 1971; Malcolm *et al.*, 2013). The term "non-host" for such plants is not appropriate because "non-host" plants are infected, namely, they host the pathogen, but without expressing disease symptoms.

The active movement of most soilborne pathogens in soils is very limited. Nevertheless, the spread of these pathogens in the field and to other fields or regions is remarkable, indicating that they have effective means for dispersal. The most effective is by means of infected plant propagation material, e.g., seeds, tubers, transplants, cuttings, etc. In an era of globalization and rapid movement of trades and passengers, this tool has become even more threatening. Other means of pathogen dispersal are via infested soil, or by being carried by cars, agricultural tools and machines, water and wind, as well as through root-to-root contact (Rekah *et al.*, 1999); infected plant debris can also be carried by machines or cars, and dispersal can also be carried out by aerial spores (Rowe *et al.*, 1977; Katan *et al.*, 1997) and infested manure.

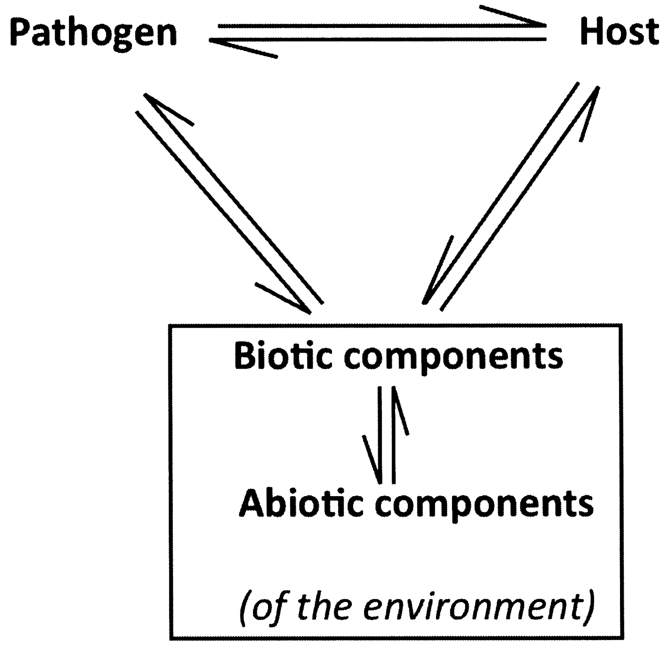

Fig. 1. Interactions among the pathogen, host and biotic and abiotic components of the environment that are connected with plant disease.

There are many methods for assessing soilborne pathogen populations. A classic technique is the use of plate counts based on selective media that are specific for each pathogen (Dhingra and Sinclair, 1995). In certain cases, macroscopic propagules, e.g., *Sclerotium rolfsii* or nematodes, can be counted directly. Serological methods have been developed for some specific pathogens. The vegetative compatibility grouping approach is a biological tool for identifying pathogenic forms based on genetic relatedness, and it is especially helpful in distinguishing between pathogenic and non-pathogenic forms of *Fusarium* (Leslie, 2012). In recent years, many reliable and rapid molecular tools have been developed for soilborne pathogen assessments and their use is on the rise (Cytryn and Minz, 2012; Lievens *et al.*, 2012). There are numerous approaches to disease assessment, with increasing interest in remote-sensing tools for this purpose.

The relationships between inoculum density (ID) and disease incidence (DI), and between DI and yield, have been much investigated, and numerous models have been proposed to describe it (van der Plank, 1963; Campbell and Benson, 1994). DI increases upon increasing ID but the relationship is usually not linear. There are many approaches to describing ID–DI relationships, e.g., log-log, probit transformation and others. Many epidemiological aspects of plant diseases are discussed in detail by Gilligan (1983) and by Campbell and Benson (1994).

Under different edaphic and other environmental conditions, a similar ID can result in different levels of DI. In addition, soil suppressiveness greatly influences the level of DI. Since inoculum in soil may consist of different resting structures or be of different qualities, e.g., single propagules vs. pieces of infected plants containing huge amounts of inoculum, ID does not necessarily reflect inoculum efficiency. Therefore, the use of ID to predict disease levels has its limitations. Although the term inoculum potential has been used in the literature for various purposes, its use as equivalent to ID should be avoided.

Many studies on the effects of environmental factors, e.g., temperature, have been carried out in pure pathogen cultures. However, the pathogen's response to temperature (or other factors) does not necessarily reflect the effect of temperature on DI, because the plant and biotic environment's responses to this factor might be totally different from that of the pathogen.

MANAGEMENT OF SOILBORNE PATHOGENS

The unique features of soilborne pathogens, in particular their existence in soil, present both difficulties and options for their management. The pathogens' presence in soil makes the application of control tools difficult but on the other hand, the presence of inoculum in soil prior to planting enables predicting the disease level when suitable tools are available (Katan *et al.*, 2012). However, soil inoculum is not the only source of infestation and in some cases, it is not even the major one. This makes management more complicated because all sources of inoculum have to be managed.

Disease is the result of interactions among the host, the pathogen and each of the biotic and abiotic components of the soil and ambient environment. The basic management strategy should involve interference, disturbance or manipulation of one or more of these components, or their interactions, to achieve an economic reduction of the disease. However, this has to be done with minimal disturbance to the environment and natural resources. Thus, suppressing or eradicating the pathogen is only one of many potential disease-management options. A holistic approach to management is therefore essential. The basic approaches for disease management (strategies) are chemical, physical, biological, cultural, and by induction or incorporation of physiological or genetic resistance in the host. The measures (tactics) are numerous, including soil disinfestation (SD), breeding for resistant cultivars and grafting, organic amendments (OA), biocontrol, sanitation, pesticides, induced resistance, crop rotation, biofumigation, and many others. Only some of these measures are effective against post-planting inoculum of soilborne pathogens originating from external sources, e.g., contaminated water, aerial propagules, or reinfestation of the soil.

Effective disease management has to be performed at every disease site throughout the disease cycle. It should prevent pathogen invasion of non-infested fields, e.g., by using pathogen-free propagation material and by enforcing quarantine measures. Sanitation, namely, removal or eradication of infected plant residues or other sources of inoculum, as well as containment of invading inocula, are complementary measures. In the infested field, inoculum eradication or reduction is achieved by SD prior to planting. During the cropping season, the diseased plants can be treated with biocontrol agents (BCA), resistance-inducing agents, fungicides or cultural methods, e.g., adjusting fertilization and irrigation. Finally, formation of pathogen resting structures in the diseased plants should also be prevented by eradication, flaming or removing the diseased plants to reduce inoculum for the next season. Some of these measures will be referred to below.

Integrated pest management (IPM) of soilborne pathogens should aim to combine control methods in an environmentally optimal manner for rational and sustainable disease reduction. IPM aims to achieve an economic reduction of DI with minimal negative effects on environmental and natural resources, while reducing pesticide use. IPM also enables benefiting from control measures which are only partially effective, e.g., cultural methods or certain BCA, by combining them to achieve an additive or even synergistic effect (Katan *et al.*, 2012; Chellemi *et al.*, 2016). All sources of inoculum, at all sites, must be managed during the entire life cycle of the pathogen, namely, before, at and after planting. In addition, crop-management practices, compatibility with other control measures of all pests of the crop, technological, economic, social and regulatory aspects, as well as knowledge transfer, should be considered. Decision-support systems, when available, enable achieving rational management which responds appropriately at the right time and location with minimal disturbance of the environment, in contrast to routine control. Combining methods of control is more than merely mixing two or more methods; for example, the application sequence should also be considered (Eshel *et al.*, 2000). Moreover, some control measures may not be compatible with others and cannot be combined.

A system approach to sustainable pest management has been suggested by various authors. Lewis *et al.* (1997) suggested that long-term resolutions for pest management can only be achieved by restructuring and managing these systems in ways that maximize the array of built-in preventive strengths, with therapeutic tactics. Chellemi *et al.* (2016) suggested four pillars for the system approach to managing soilborne pathogens: preventing the introduction and spread of pathogens into the crop system, reducing pathogen population to levels that can be managed through natural biological feedback, improving soil suppressiveness and minimizing the impact of destructive actions, e.g., pesticides, through an integrated approach to pest management.

Crop and soil health should also be considered (van Bruggen and Semenov, 2000; Katan and Vanachter, 2010). Doran *et al.* (1996) defined soil health as the soil's continued capacity to function as a vital living system to sustain biological productivity and promote plant, animal and human health. Thus, a healthy soil should be as free as possible from biotic and abiotic stresses, enabling optimal crop productivity without intolerable environmental costs, maintaining optimal recycling activity and having the capacity for resilience, namely, the capacity to recover, for example, by means of soil suppressiveness. The concept of root health in connection with pest management has been reviewed (Cook, 2000).

In the following, selected potential tools for management are briefly discussed.

1. *Soil disinfestation* (SD)

SD was first established at the end of the 19th century for eradication of the soil pest *Phylloxera* in vineyard soils in France. The basic idea of SD is to eradicate soil pests *before planting* by using drastic tools; for decades this was carried out by either physical means - steaming the soil, or other means of heating - or treating the soil with highly toxic volatile or soluble chemicals. The chemical approach is still predominant (Gamliel and Katan, 2012b). In 1976, soil solarization was introduced (Katan *et al.*, 1976; Gamliel and Katan, 2012a) and later, biofumigation and anaerobic SD (ASD) were adopted, all of which have to be performed pre-planting since SD tools are harmful to plants. SD should aim to achieve effective reduction of soil pest populations with minimal harm to soil microbial and beneficial activities, including mycorrhizae and other elements of the environment, without leaving phytoxic residues. This is a difficult task since the disinfestants are drastic and non-selective. Combining SD with OA reduces the harmful effect on soil microbial activities. SD should be carried out in wet soil since pests are more vulnerable to killing agents under wet conditions.

SD has to control pests to the desired soil depth, usually 30-50 cm. It can only control existing populations of the pest; it does not protect the soil from contamination from outside sources, except when soil suppressiveness is induced. Therefore, recontamination of the disinfested soil should be absolutely avoided.

Carbon disulfide is a mild fumigant which was introduced in the 19th century. The fumigant chloropicrin was introduced for SD in the first part of the 20th century and is still in use for certain purposes, alone or in combination with other fumigants. For several decades, starting in the 1950s, methyl bromide (MB) was the major soil fumigant, since it is very effective against a wide spectrum of soil pests, including many weeds, and because of its high vapor pressure. It can also be used at relatively lower temperatures and it dissipates rapidly from the soil. However, its inclusion in the ozone-depleting layer resulted in its phase out in 2005 in developed countries (Katan, 1999; Gullino *et al.*, 2003; Porter *et al.*, 2010). Since then, much effort has been invested in developing chemical and non-chemical alternatives to this effective fumigant. Additional fumigants, for use alone or in combination with other methods, are available or are undergoing experimental trials. However, none of them has the wide spectrum of MB. They include nematicides, fumigants based on the generation of methyl isothiocyanate (MITC) such as metam sodium, iodomethane (methyl iodide), formaldehyde, dimethyl disulfide and others. When MITC-based fumigants are frequently applied to the soil, enhanced biodegradation develops in the soil, resulting in reduced control effectiveness (Triky-Dotan *et al.*, 2009).

Soil solarization is carried out by means of solar heating of the soil, which is covered with transparent plastic material during the appropriate hot and dry season for about 4-6 weeks, thereby controlling a variety of soilborne pathogens, weeds and certain arthropods. There are thermotolerant pathogens, e.g., *Macrophomina phaseolina* and *Monosporascus*, which are not controlled by soil solarization (Katan, 1981; Stapleton, 2000; Gamliel and Katan, 2012a).

Because soil solarization involves mild soil heating, to around 45-55°C in the upper soil layers and 35-40°C in the lower layers, it has no drastic effect on the soil's biotic components. It results in physical thermal killing of pathogens in the upper, hotter soil layers and frequently induces a beneficial microbial shift in the less heated soil layers, which contributes to pathogen control (Stapleton and DeVay, 1984; Gamliel and Katan, 1991; Culman *et al.*, 2006; Gelsomino and Cacco, 2006; Ozylmaz *et al.*, 2016). Moreover, it frequently induces soil suppressiveness (Greenberger *et al.*, 1987). This non-chemical SD technique has advantages but also limitations: it is dependent on climate and on maintaining the land with no crop for several weeks. There are various ways to improve its effectiveness, e.g., by combining it with other methods, including fumigants at reduced dosage or OA. It frequently involves a beneficial shift in microbial activities as well as induced resistance in the host (Okon-Levy *et al.*, 2015).

Structural solarization of the greenhouse by closing it and raising space temperatures to 60°C or higher is used for sanitation of the greenhouse structure from pathogens that are left on it (Shlevin *et al.*, 2003).

The incorporation of OA of plant origin, e.g., green manure or other sources, into the soil for the purpose of improving plant growth and health upon their decomposition has been practiced for centuries. For example, ancient Sanskrit texts from 14th century in India or even earlier recommend the use of botanicals as OA, including crucifers which are known to release toxic antifungal volatiles upon their decomposition. This disease-management approach has the advantage of not harming the environment while recycling waste materials. However, the use of OA for disease control, especially for SD, also involves difficulties due to irreproducibility and lower success rate under farm conditions, especially due to inconsistency in the OA composition. The use of compost as an OA for inducing soil suppressiveness and managing root diseases has been shown (Hoitink and Fahy, 1986; Hoitink *et al.*, 1997; Yogev *et al.*, 2006). The classic works on the control of potato scab by green manure in the 1920s (Millard, 1923) were followed by numerous similar studies with OA and pathogens, with varying levels of success. Important fundamental work on the use of OA for disease management was carried out by G. Papavizas' group in Beltsville, MD, USA. The OA approach to disease management led to the development of biofumigation (biosolarization), which is another SD method. It is based on combining an OA, which upon decomposition releases volatile and non-volatile substances that are toxic to pathogens, with plastic mulching which retains the volatiles and increases their toxicity; when it is performed under the appropriate solarization conditions, heating increases its effectiveness. Crucifers are frequently used as OA (Lewis and Papavizas, 1970), and the effectiveness of biofumigation in controlling various pathogens has been demonstrated (Gamliel and Stapleton, 1993, 2012; Klein *et al.*, 2007; Guerrero *et al.*, 2005).

ASD is another approach to SD that combines OA with plastic tarping of the soil to create anaerobic conditions. The method involves addition of a labile carbon source to stimulate microbial growth and respiration, tarping with plastic to limit gas exchange, and irrigation to fill the soil pore space with water, which allows for diffusion of decomposition by-products through the soil solution and reduces soil oxygen levels. Anaerobic conditions are created as the rapid growth of aerobic microorganisms depletes the remaining soil oxygen and the microbial community shifts to facultative and obligate anaerobes (Butler *et al.*, 2012; Shennan *et al.*, 2012). Anaerobic conditions are maintained for a period that varies with soil temperature and carbon sources used before the tarp is either removed or planting holes punched through it to allow oxygen back into the soil and stimulate the degradation of the remaining by-products of anaerobic decomposition. Different mechanisms may prove to be critical for suppressing specific organisms, but production of organic acids via anaerobic decomposition of the added carbon, release of volatile compounds, and biocontrol by microorganisms that flourish during the process are all potentially important.

2. *Resistant cultivars and grafting*

Breeding for resistance to pests is a very effective tool for controlling them with no negative effect on the environment. However, it takes many years to develop a cultivar which combines resistance with the desired commercial traits. Resistance might be controlled by a dominant, semi-dominant, or recessive gene (oligogenic), but multigene (polygenic) and cytoplasmic control is also known. Single dominant genes for resistance can be easily introduced into commercial cultivars using marker-assisted breeding methods (Guimaraes *et al.*, 2007). Indeed, when present, single genes that code for resistance strongly dominate plant breeding, despite the fact that they are prone to and provide selection pressure for the evolution of new races of pathogens. When vertical resistance is available, many plant breeders tend to ignore the option of horizontal resistance (Rabinowitch and Cohen, 2012). Partial resistance can be effectively used by combining it with other methods, resulting in effective control. There is intensive research regarding the possible use of genetic engineering, bioinformatics, gene editing and other technologies in breeding for resistance, but acceptance of some of these tools is still pending.

Grafting scions of commercially desirable but susceptible cultivars on rootstocks resistant to soilborne pathogens often provides plants with functional resistance that is equal to that of non-grafted cultivars that carry genes for resistance. The grafting approach provides flexibility because it is relatively easier and faster to replace a rootstock (when a new physiological race appears, for example) than to breed a new cultivar. Increasing effort is being invested in this approach for crops such as tomato, melon and watermelon as an alternative to MB. Grafting provides a rapid solution to acute pathological problems, in contrast to the long and expensive breeding programs. In addition, the scion–rootstock interaction may result in enhanced tolerance to abiotic stresses, improved efficiency of water and nutrient use, ameliorated growth and development, and improved fruit yield and quality (Lee and Oda, 2003; Cohen *et al.*, 2007; Rabinowitch and Cohen, 2012).

3. *Additional management measures*

The use of BCA as antagonists for control of soilborne pathogens began in the first half of the 20th century and it is certainly a very exciting topic. *Trichoderma* spp. have been thoroughly studied by many researchers as BCA, and it seems that this fungus has many traits that can control pathogens (Chet, 1987). Additional BCA have been studied and some commercialized, including *Talaromyces*, *Gliocladium*, streptomycetes, fluorescent pseudomonads, nematicidal BCA and many others. Use of BCA by farmers is still relatively small scale, but they can be successfully incorporated into IPM programs. There are numerous publications on BCA for disease management (e.g., Chet, 1987; Paulitz and Belanger, 2001; Fravel, 2005).

Soil fungicides are used mainly with seedling diseases because the plants only need to be protected for a relatively short period. Controlling wilt diseases, which requires protection of the crop for long periods, is a much more difficult task. Nevertheless, there are some cases of fungicide effectiveness, e.g., benomyl for control of *Fusarium* or *Sclerotinia sclerotiorum*, although it is no longer available for many crops (Chase, 2012).

There is increasing interest in control by cultural practices (CP), whereby agricultural practices are harnessed to create an environment that is favorable for the host and hostile to the pathogen (Palti, 1981; Walters, 2009; Katan, 2010; Elmer, 2012). We now realize that although CP do not have a dramatic effect as a disease-management tool, they can, nevertheless, contribute to disease reduction when combined with other control methods in IPM programs. There are many reports on the potential of CP for disease reduction, including sanitation, mineral fertilization, irrigation, tillage, adjusting time of sowing, adjusting soil temperature by plastic mulch, crop rotation, deep ploughing, flooding, weed control and others. The use of CP as management tools, especially sanitation, warrants more attention.

Induced resistance has been widely investigated using chemicals or beneficial microorganisms (Kuc, 1982; Reslinski and Walters, 2009; Cohen *et al.*, 2016). This is certainly a promising management tool which should play a more significant role in disease management under farm conditions. Certain chemicals that induce disease resistance are in commercial use.

Disease management in organic agriculture is based only on non-chemical management tools. This issue is thoroughly discussed in a recent book on the topic (Finckh *et al.*, 2015).

CHALLENGES AND CONCLUDING REMARKS

Every stage in the pathogen's life cycle and in disease development, as well as its interactions with biotic and abiotic components of the environment have the potential to become effective disease-management tools through disease intervention or disruption, or through activation of beneficial processes. In addition, every currently used disease-management measure should be reexamined and reassessed in light of continuously accumulating knowledge, toward its further improvement and reduction of negative side effects. There is also the difficult question of why only a small proportion of the many disease-management measures that are found promising under controlled conditions ultimately reach the application stage (Katan, 1993; Mazzola and Freilich, 2017). Below, these issues, as well as some potentially promising options for disease management, are discussed.

A typical example of the large gap between promising results under laboratory or greenhouse conditions and limited successes under realistic conditions can be found in the field of biological control using BCA or OA. This field of research started at the beginning of the 20th century but frequently yielded irreproducible results. One reason for this might be that the research systems that were used under controlled conditions did not adequately represent the real conditions (Katan, 1993). For example, the natural fluctuations in ambient conditions, e.g., temperature and soil moisture, and their combinations, are difficult to simulate. It is especially difficult to weigh and mandate the different values. Improved simulation and research systems will provide more representative and reliable results on control effectiveness and eliminate unnecessary field experiments. The genetic and physiological quality of the BCA has to be continuously assessed. Another reason for the gap between the laboratory/greenhouse and field results is connected with the fact that in many cases, adequate technologies and delivery systems for implementation of each specific BCA were not developed, or were not adequately adapted (Katan, 1993). BCA are living agents, and as such are very complex and influenced by the environment. All of the above is relevant, either wholly or in part, to other management tools.

Research on biocontrol mechanisms could provide new approaches for their improvement and implementation. As with any management measure, basic and applied research should be carried out closely and interactively. Emphasis should be placed on the implementation of BCA via propagation materials, e.g., by coating seeds or loading transplants with BCA. This approach will enable reducing economic and environmental costs while improving control effectiveness. However, this can only be successful if the control agent (including pesticides) protects the plant for the entire necessary period of plant growth. Therefore, chances of its success are higher with seedling diseases than with the long-term vascular diseases. The authorities might promote the introduction of BCA, or other agents that are in harmony with the environment, by subsidizing them in the first period of their introduction.

Regarding the use of OA for disease management, elucidating their mode of action and identifying the chemical substances and/or microorganisms that are involved in pathogen control could provide tools for assessing OA quality for disease management and enhancing reproducibility. It is important to use OA that are waste materials and an environmental burden, e.g., products from the food industry (Lazarovitz, 2004). Although in most studies OA were chosen by trial and error, there are some important exceptions in which OA selection was based on a concept, for example: the use of chitin as an OA in an attempt to promote chitinolytic microorganisms as BCA (Mitchell and Alexander, 1962), or the use of nitrogenous materials that release toxic volatiles (Lazarovitz, 2004). Management of the indigenous soil microbial community, though possessing limitation, would appear to provide a more sustainable means to meet the goal of biological soilborne disease control (Mazzola and Freilich, 2017).

The pathogen resting structures, which are resistant to biotic and abiotic factors and are produced in large quantities in the soil and in the infected plant tissues, enable soilborne pathogens to survive for long periods. Their temporary dormancy in the absence of a host protects them from hostile soil activities. Therefore, attempts should be made to prevent their formation, or increase their susceptibility, by suppressing the melanization of microsclerotia (Tjamos and Fravel, 1995), eradicating them through the application of chemicals to the soil at the end of the production season (Radewald *et al.*, 2004), or enhancing their germination in the absence of a host, e.g., using an appropriate OA. Revealing the mechanisms of resting-structure formation, fungistasis and root exudation could provide tools for achieving these goals. Sanitation and crop rotation, which aim to reduce soil inoculum, are additional and complementary tools.

Suppressive soils constitute a natural treasure that should be better exploited. We certainly need innovative approaches to make better use of them (Kinkel *et al.*, 2011). We need to develop tools such as biological indicators to identify the level of soil suppressiveness (van Bruggen and Semenov, 2000). Suppressive soils should be treated differently from regular soils, especially with respect to SD, to maintain their suppressiveness or even increase it. We should find ways to increase suppressiveness of non-suppressive soils. The possibility of enriching such soils with antagonistic microorganisms, originally isolated from suppressive soils, to render them suppressive remains an open question.

Rapid and sensitive diagnostic tools must be developed to detect and prevent the introduction of new pests. In this era of precision agriculture, remote-sensing tools will hopefully become a common working approach.

Breeding for disease resistance will continue to be a major tool in plant protection. Hopefully, continuing developments in genetics and genomics for the investigation of both hosts and pathogens will provide lasting plant resistance. In most cases of newly emerging soilborne pathogens, the original source - whether they come from the hosts' natural habitat or via genetic routes - is unknown. Moreover, we still cannot predict when a new virulent physiological race or fungicide-resistant strain will appear. This is learned the hard way, by trial and error. Further emphasis should be placed on investigating the coevolution of hosts and pathogens before and during the crop domestication process.

MB was the major SD fumigant for decades, but was phased out in 2005 due to its harmful effect on the ozone layer. Means for optimal and effective use of MB had been developed in the past, but major mistakes were also made. There were no attempts to reduce MB dosages, e.g., by using films that are less impermeable to gas, and no alternatives were developed, despite the fact that potential alternatives, e.g., grafting and the use of OA, were known (Katan, 1999; Gullino *et al.*, 2003). We are in the process of developing effective alternatives to MB. The MB crisis taught us a painful lesson which should not be repeated. We have to remember that every management tool, especially pesticides, might be removed from use for any of a variety of reasons. Therefore, developing new tools and approaches for disease management should be a continuous task, rather than one that is taken on only under emerging conditions.

It has been a long and exciting journey in soil microbiology and soilborne pathogen research, from the 1920s when S. Waksman concluded that fungi play an important role in soil microbial activities, until today, with molecular tools providing a wealth of information on the composition, diversity and biological activities of soil organisms and pathogens. In the present review, several lines of investigation are suggested. However, totally new and unexpected developments will hopefully arise and open new doors. We need to be aware of their appearance and should warmly adapt and adopt them.

REFERENCES

Butler D.M., Kokalis-Burelle N., Muramoto J., Shennan C., McCollum T.G., Rosskopf E.N., 2012. Impact of anaerobic soil disinfestation combined with soil solarization on plant-parasitic nematodes and introduced inoculum of soilborne plant pathogens in raised-bed vegetable production. *Crop Protection* **39**: 33-40.

Campbell C.L., Benson D.M., 1994. Epidemiology and Management of Root Diseases. Springer Verlag, Berlin.

Campbell C.L., Van der Gaag D.J., 1993. Temporal and spatial dynamics of Microsclerotia of *Macrophomina phaseolina* in three fields in North Carolina over four to five years. *Phytopathology* **83**: 1434-1440.

Chase A.R., 2012. Chemical control of Fusarium wilt in greenhouse crops. In: Gullino M.L., Katan J., Garibaldi A. (eds). Fusarium Wilts of Greenhouse Vegetable and Ornamental Crops, pp. 117-120. APS Press, USA.

Chellemi D.O., Gamliel A., Katan J., Subbarao K.V., 2016. Development and deployment of system-based approaches for the management of soilborne plant pathogens. *Phytopathology* **106**: 216-225.

Chet I., 1987. *Trichoderma* application, mode of action, and potential as a biocontrol agent of soil-borne plant pathogenic fungi. In: Chet I. (ed). Innovative Approaches to Plant Disease Control, pp. 137-160. John Wiley and Sons, NY, USA.

Cohen R., Burger Y., Horev C., Koren A., Edelstein M., 2007. Introducing grafted cucurbits to modern agriculture. *Plant Disease* **91**: 916-923.

Cohen Y., Vaknin M., Mauch-Mani B., 2016. BABA-induced resistance: milestones along a 55-year journey. *Phytoparasitica* **44**: 513-538.

Cook R.J., 2000. Advances in plant health management in the twentieth century. *Annual Review of Plant Pathology* **38**: 95-116.

Cook R.J., Baker K.F., 1983. The Nature and Practice of Biological Control of Plant Pathogens. American Phytopathological Society, USA.

Culman S., Duxbury J., Lauren J., Thies J., 2006. Microbial community response to soil solarization in Nepal's rice-wheat cropping system. *Soil Biology and Biochemistry* **38**: 3359-3371.

Curl E.A., 1986. The Rhizosphere. Springer Verlag, Berlin.

Cytryn E., Minz D., 2012. Approaches to assess microbial activities in soil. In: Gamliel A., Katan J. (eds). Soil Solarization. Theory and Practice, pp. 15-22. APS Press, USA.

Dhingra O.D., Sinclair J.B., 1995. Basic Plant Pathology Methods. CRC Press, Boca Raton.

Dobbs C.G., Hinson W.H., 1953. A widespread fungistasis in soils. *Nature* **172**: 197-199.

Doran J.W., Sarratonino M., Liebeg M.A., 1996. Soil health and sustainability. *Advances Agronomy* **56**: 1-54.

Elmer W.H., 2012. Cultural practices. In: Gullino L.M., Katan J., Garibaldi A. (eds). Fusarium Wilts of Greenhouse Vegetable and Ornamental Crops. pp. 67-74. APS Press, USA.

Eshel D., Gamliel A., Grinstein A., Di Primo P., Katan J., 2000. Combined soil treatments and sequence of application in improving the control of soilborne pathogens. *Phytopathology* **90**: 751-757.

Finckh M.R., van Bruggen A.H.C., Tamm L., 2015. Plant Diseases and their Management in Organic Agriculture. APS Press, USA.

Fravel D.R., 2005. Commercialization and implementation of biocontrol. *Annual Review of Phytopathology* **43**: 337-359.

Gamliel A., Katan J., 1991. Involvement of fluorescent pseudomonads and other microorganisms in increased growth response of plants in solarized soils. *Phytopahology* **81**: 494-502.

Gamliel A., Katan J., 1992. Influence of seed and root exudates on fluorescent pseudomonads and fungi in solarized soils. *Phytopahology* **82**: 320-327.

Gamliel A., Katan J., 2012a. Soil Solarization: Theory and Practice. APS Press, USA.

Gamliel A., Katan J., 2012b. Soil and substrate disinfestation in protected structures. In: Gullino M.L., Katan J., Garibaldi A. (eds). Fusarium Wilts of Greenhouse Vegetable and Ornamental Crops, pp. 121-131. APS Press, USA.

Gamliel A., Stapleton J.J., 1993. Effect of chicken compost or ammonium phosphate and solarization on pathogen control, rhizosphere microorganisms and lettuce growth. *Plant Disease* **77**: 886-891.

Gamliel A., Stapleton J.J., 2012. Combining soil solarization with organic amendments. In: Gamliel A., Katan J. (eds). Soil Solarization: Theory and Practice, pp. 109-120. APS Press, USA.

Garrett S.D., 1970. Pathogenic Root-Infecting Fungi. Cambridge University Press, London.

Gelsomino A., Cacco G., 2006. Compositional shifts of bacterial groups in a solarized and amended soil as determined by denaturating gel electrophoresis. *Soil Biology Biochemistry* **38**: 91-102.

Gilligan C.A., 1983. Modelling soilborne pathogens. *Annual Review of Phytopathology* **21**: 45-64.

Greenberger A., Yogev A., Katan J., 1987. Induced suppressiveness in solarized soils. *Phytopathology* **77**: 1663-1667.

Guerrero M.M., Ros C., Guirao P., Martínez M.A., Martínez M.C., Barceló N., Bello A., Lacasa A., López J.A., 2005. Biofumigation plus solarization efficacy for soil disinfestation in sweet pepper greenhouses in the Southeast of Spain. *Acta Horticulturae* **698**: 293-297.

Guimarães E.P., Ruane J., Scherf B.D., Sonnino A., Dargie J.D., 2007. Marker-assissted selection: current status and future perspectives in crops, livestock, forestry and fish. FAO Working Group on Biotechnology Rome.

Gullino M.L., Camponogara A., Gasparrini G., Rizzo V., Clini C., Garibaldi A., 2003. Replacing methyl bromide for soil disinfestation: The Italian experience and implications for other countries. *Plant Disease* **87**: 1012-1021.

Gullino M.L., Katan J., Garibaldi A., 2012. Fusarium Wilts of Greenhouse Vegetable and Ornamental Crops. APS Press, USA.

Ho W.C., Ko W.H., 1985. Soil microbiostasis: effects of environmental and edaphic factors. *Soil Biology Biochemistry* **17**: 167-170.

Hoitink H.A.J., Fahy P.C., 1986. Basis for the control of soilborne plant pathogens with composts. *Annual Review Phytopathology* **24**: 93-114.

Hoitink H.A.J., Stone A.G., Han D.Y., 1997. Suppression of plant diseases by composts. *HortScience* **32**: 184-187.

Katan J., 1971. Symptomless carriers of tomato Fusarium pathogen. *Phytopathology* **61**: 1213-1217.

Katan J., 1981. Solar heating (solarization) of soil for control of soil-borne pests. *Annual Review Phytopathology* **19**: 211-236.

Katan J., 1993. Replacing pesticides with nonchemical tools for the control of soilborne pathogens – a realistic goal? *Phytoparasitica* **21**: 91-99.

Katan J., 1999. The methyl bromide issue: problems and potential solutions. *Journal of Plant Pathology* **81**: 153-159.

Katan J., 2002. Interactions of soilborne pathogens with roots and aboveground plant organs. In: Weizel Y., Eshel A., Kafkafi V. (eds). Plant Roots: the Hidden Half (third edition), pp. 949-959. Marcel Dekker, USA.

Katan J., 2010. Cultural approaches for disease management: present status and future prospects. *Journal of Plant Pathology* **92**: S4.7-S4.9.

Katan J., Greenberger A., Alon H., Ginstein A., 1976. Solar heating by polyethylene mulching for the control of diseases caused by soilborne pathogens. *Phytopathology* **66**: 683-689.

Katan J., Shtienberg D., Gamliel A., 2012. The integrated management concept in the context of soilborne pathogens and soil disinfestation. In: Gamliel A., Katan J. (eds). Soil Solarization: Theory and Practice, pp. 91-97. APS Press, USA.

Katan J., Vanachter A., 2010. Soil and crop health following soil disinfestation. *Acta Horticulturae* **883**: 25-36.

Katan T., Shlevin E., Katan J., 1997. Sporulation of *Fusarium oxysporum* f. sp. *lycopersici* on stem surfaces of tomato plants and aerial dissemination of inoculum. *Phytopathology* **87**: 712-719.

Kinkel L.L., Bakker M.G., Schlatter D.C., 2011. A coevolutionary framework for managing disease-suppressive soils. *Annual Review of Phytopathology* **49**: 47-67.

Klein E., Katan J., Austerweil M., Gamliel A., 2007. Controlled laboratory system to study soil solarization and organic amendments effects on plant pathogens. *Phytopathology* **97**: 1476-1483.

Ko W.H., Lockwood J.L., 1967. Soil fungistasis: relation to fungal spore nutrition. *Phytopatho*logy **57**: 894-901.

Kuc J., 1982. Induced immunity to plant disease. *Bioscience* **32**: 854-860.

Lazarovitz G., 2004. Managing soilborne plant diseases through selective soil disinfestation by a knowledge-based application of soil amendments. *Phytoparasitica* **32**: 427-431.

Lee J.M., Oda M., 2003. Grafting of herbaceous vegetable and ornamental crops. *Horticultural Review*s **28**: 61-124.

Leslie J.E., 2012. Genetics of *Fusarium oxysporum*. In: Gullino M.L., Katan J. Garibaldi A. (eds). Fusarium Wilts of Greenhouse Vegetable and Ornamental Crops, pp. 39-46. APS Press. USA.

Lewis W.J., van Lenteren J.C. , Phatak S.C., Tumlinson III J.H., 1997. A total system approach to sustainable pest management. *Proceedings National Academy Sciences USA* **94**: 12243-12248.

Lewis J.A., Papavizas G.C., 1970. Evolution of volatile sulfur-containing compounds from decomposition of crucifers in soil. *Soil Biology and Biochemistry* **2**: 239-246.

Liebman J.A., Epstein L., 1992. Activity of fungistatic compounds from soil. *Phytopathology* **82**: 147-153.

Lievens B., Hansseen I.M., Rep M., 2012. Recent developments in the detection and identification of *formae speciales* and races of *Fusarium oxysporum*: from pathogenicity testing to molecular diagnostic. In: Gullino M.L., Katan J., Garibaldi A. (eds). Fusarium Wilts of Greenhouse Vegetable and Ornamental Crops, pp. 47-55. APS Press, USA.

Lockwood J.L., 1977. Fungistasis in soil. *Biological Reviews* **51**: 1-43.

Lockwood J.L., 1988. Evolution of concepts associated with soilborne pathogens. *Annual Review of Plant Pathology* **26**: 93-121.

Malcolm G.M., Kuldau G.A., Gugino B.K., Jimenez-Gasco M., 2013. Hidden host plant associations of soilborne fungal pathogens: an ecological perspective. *Phytopathology* **103**: 538-544.

Mazzola M., Freilich S., 2017. Prospects of biological soilborne disease control: application of indigenous versus synthetic microbiomes. *Phytopathology* **107**: 256-262.

Mazzola M., Strauss S.L., 2014. Replant disease control and system resilience to pathogen re-infestation in response to *Brassica* seed meal amendment. *Acta Horticulturae* **1044**: 105-112.

Mihail J.D., Alcorn S.H., 1987. *Macrophomina phaseolina*: spatial patterns in a cultivated soil and sampling strategies. *Phytopathology* **77**: 1126-1137.

Millard W.A., 1923. Common scab of potatoes. *Annals of Applied Biology* **10**: 70-88.

Mitchell R., Alexander M., 1962. Microbiological processes associated with the use of chitin for biological control. *Proceedings of the Soil Science Society of America* **26**: 556-558.

Nelson E.B., 1987. Rapid germination of sporangia of *Pythium* species in response to volatiles from germinating seeds. *Phytopathology* **77**: 1108-1112.

Nelson E.B., 2004. Microbial dynamics and interactions in the spermosphere. *Annual Review of Phytopathology* **42**: 271-389.

Okon-Levy N., Meller Y., Haile Z.M., Elad Y., Rav-David E., Jurkevitch E., Katan J., 2015. Induced resistance to foliar diseases by soil solarization and *Trichoderma harzianum*. *Plant Pathology* **64**: 365-374.

Ozylmaz U., Benlioglu K., Yildis A., Benlioglu H.S., 2016. Effects of soil amendments combined with solarization on the soil microbial community in strawberry cultivation using quantitative real-time PCR. *Phytoparasitica* **44**: 661-680.

Palti J., 1981. Cultural Practices and Infections Crop Diseases. Springer Verlaz, Berlin.

Park D., 1963. The ecology of soilborne fungal disease. *Annual Review of Phytopathology* **1**: 241-258.

Paulitz T.C., Belanger R.R., 2001. Biological control in greenhouse systems. *Annual Review of Phytopathology* **39**: 103-133.

Pegg G.F., Brady B.L., 2002. Verticillium Wilts. CABI Publishing, UK.

Pfender W.F., 1982. Monocyclic and polycyclic root diseases: distinguishing between the nature of the disease cycle and the shape of the disease progress curve. *Phytopathology* **72**: 31-32.

Porter I., Banks J., Mattner S., Frazer P., 2010. Global phase out of methyl bromide under the Montreal Protocol: implications for bioprotection, biosecurity and the ozone layer. In: Gisi U., Chet I., Gullino M.L. (eds). Recent Developments in Management of Plant Disease, pp. 293-309. Springer, New York, USA.

Rabinowitch H.D., Cohen R., 2012. Genetics and breeding for resistance and grafting for protection against *Fusarium oxysporum* wilts. In: Gullino M.L., Katan J., Garibaldi A. (eds). Fusarium Wilts of Greenhouse Vegetable and Ornamental Crops, pp. 83-100. APS Press, USA.

Radewald K.C., Ferrin D.M., Stanghellini M.E., 2004. Sanitation practices that inhibit reproduction of *Monosporascus cannonballus* in melon roots left in the field after crop termination. *Plant Pathology* **53**: 660-668.

Rekah Y., Shtienberg D., Katan J., 1999. Spatial distribution and temporal development of Fusarium crown root rot of tomato and pathogen dissemination in field soil. *Phytopathology* **89**: 831-839.

Reslinski T., Walters D., 2009. Induced resistance for plant disease control. In: Walters D. (ed.). Disease Control in Crops, pp. 62-92. Wiley Blackwell, Oxford, UK.

Rowe R.C., Farley J.D., Coplin D.L., 1977. Airborne spore dissemination and recolonization of steamed soil by *Fusarium oxysporum* in tomato greenhouses. *Phytopathology* **67**: 1513-1517.

Scher F.M., Baker R., 1983. Fluorescent microscopic technique for viewing fungi in soil and its application to study of *Fusarium* suppressive soil. *Soil Biology and Biochemistry* **15**: 715-718.

Schippers B., Bakker A.W., Bakker P.A.H.M., 1987. Interactions of deleterious and beneficial rhizosphere microorganisms and the effect of cropping practices. *Annual Review of Phytopathology* **25**: 339-358.

Sewell G.W.F., 1984. Replant diseases: etiology and importance. *Proceedings of the British Crop Protection Conference*, pp. 1175-1182. Brighton.

Shennan C., Muramoto J., Lamers J., Mazzola M., Rosskof E.N., Kokalis-Burelle N., Momma N., Butler D.M., Kobora Y., 2012. Anaerobic soil disinfestation for soil-borne disease control in strawberry and vegetable systems. *Acta Horticulturae* **1044**: 165-175.

Shlevin E., Saguy I.S., Mahrer Y., Katan J., 2003. Modeling the survival of two soilborne pathogens under dry structural solarization. *Phytopathology* **93**: 1247-1277.

Sneh B., Jabaji-Hare S., Neate S.M., Dijst G., 1997. *Rhizoctonia* Species: Taxonomy, Molecular Biology, Ecology, Pathology and Disease Control. Kluwer, London.

Stapleton J.J., 2000. Soil solarization in various agricultural production systems. *Crop Protection* **19**: 837-841.

Stapleton J.J., DeVay J.E., 1984. Thermal components of soil solarization as related to changes in soil and root microflora and increased growth response. *Phytopathology* **74**: 255-259.

Tjamos E.C., Fravel D., 1995. Detrimental effects of sub-lethal heating and *Talaromyces flavus* on microsclerotia of *Verticillium dahliae. Phytopathology* **85**: 388-392.

Triky-Dotan S., Austerweil M., Steiner B., Peretz-Alon Y., Katan J., Gamliel A., 2009. Accelerated degradation of metamsodium in soil and consequences for root disease management. *Phytopathology* **99**: 362-365.

van Bruggen A.H.C., Semenov A.M., 2000. In search of biological indicators for soil health and disease suppression. *Applied Soil Ecology* **15**: 13-24.

van der Plank J.E., 1963. Plant Diseases: Epidemics and Control. Academic Press, New York, USA.

Walters D., 2009. Managing crop diseases through cultural practices. In: Walters D. (ed.). Disease Control in Crops: Biological and Environmentally Friendly Approaches, pp. 7-26. Wiley-Blackwell, UK.

Yogev A., Raviv M., Hadar Y., Cohen R., Katan J., 2006. Plant waste-based composts suppressive to disease caused by pathogenic *Fusarium oxysporum. European Journal of Plant Pathology* **116**: 267-278.