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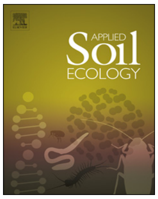

Review

Impacts of soil abiotic attributes on Fusarium wilt, focusing on bananas

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ABSTRACT

Production of many crops, including bananas, is threatened worldwide by the spread of pathogenic strains of *Fusarium oxysporum*, the causal agent of Fusarium wilt. Severity of the disease is related to soil biotic and abiotic attributes, which influence the plant, the pathogen and the other soil organisms. Across a variety of crops, soil temperature, redox potential, and extractable iron and manganese contents are generally positively correlated with disease severity, whereas pH, nitrate:ammonium ratio, organic matter content and extractable calcium, zinc, silicon, potassium, phosphorus and boron contents are negatively correlated, but less consensus exists for bananas. There are numerous incompletely understood interactions between soil abiotic attributes and disease severity, including those between pH- and redox-controlled micronutrient availability, buffering by organic matter and clay, and effects of nutrients on plant defence mechanisms. Though not all soil attributes can be managed, pH, organic matter content and availability of nutrients show promise for manipulation to reduce disease severity and mitigate risk.

1. Introduction

'Fusarium wilt', a vascular wilt disease, is caused by soil-borne pathogenic strains of *Fusarium oxysporum*, a diverse species complex of fungus including both pathogenic and non-pathogenic forms (Leslie and Summerell, 2008). The pathogenic strains are largely host specific and are responsible for yield losses in a variety of important crops such as tomato, cucumber, melons, flax, lettuce, strawberry, oil palm, tobacco, carnation, cotton, and banana (Table 1) and can even affect humans (Leslie and Summerell, 2008). *F. oxysporum* is currently subdivided into formae speciales based on host plant species rather than taxonomic distinctness (Kang et al., 2014; Leslie and Summerell, 2008). As a hemibiotroph, *F. oxysporum* attacks susceptible hosts, but it is a facultative saprophyte, able to survive on dead organic material for extended periods of time. It can also live as an endophyte in symptomless host plants, including common weed species (Altinok, 2013; Hennessy et al., 2005). While the impact of pathogenic strains has been geographically limited in the past, the rise of global transport has vastly increased their spread and importance (Desprez-Loustau et al., 2007). The relationship between soil properties and disease severity may differ between species and strains of *Fusarium* (Jarvis and Thorpe, 1980).

Several reviews (Dordas, 2008; Höper and Alabouvette, 1996; Janvier et al., 2007) outlined the effects of soil abiotic characteristics on severity of soil-borne diseases but did not focus on Fusarium wilts. Höper and Alabouvette's (1996) review did discuss Fusarium wilt, but subsequent research has furthered the understanding of several mechanisms. A recent review of management of Fusarium wilt of banana by Ploetz (2015b) only briefly addressed manipulation of soil properties. This review focuses on bananas due to the recent spread of Panama disease, but it also includes relevant results from a variety of other crops affected by *F. oxysporum*. We review the effects of soil abiotic attributes on Fusarium wilt, based on field surveys, manipulative trials and laboratory experiments.

This review focusses primarily on soil chemical characteristics, with special emphasis on micronutrient availability. The effects of soil physical characteristics are only briefly examined due to the limited number of studies that have been performed. Most physical properties are best measured in the field, but most research has focused on soil characteristics amenable to analysis in the laboratory. Many soil characteristics influence availability of micronutrients to organisms, and manipulation of micronutrient availability has been proposed as a method to reduce the severity of Fusarium wilt (Lemanceau, 1989). The relationships between Fusarium wilt severity and soil attributes are complex and far from being fully understood. However, a rapidly improving understanding of the mechanisms involved suggests that management interventions to mitigate effects of the disease may be possible in the future.

2. Fusarium wilt of bananas (Panama disease)

Bananas and plantains are a major source of food and income for people in many tropical and subtropical regions (Lescot, 2015). Nearly 50% of world production is of the Cavendish cultivar (*Musa* AAA), which is susceptible to a currently spreading pathogenic strain of *F. oxysporum*. Similarly susceptible cultivars cover a large proportion of remaining production (Lescot, 2015).

The causal agent of Panama disease, *Fusarium oxysporum* f.sp. *cubense* (Foc), is subdivided into 'races' based on the cultivars of banana

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Table 1
Previous studies correlating Fusarium wilt severity with soil physicochemical variables, bioavailability of essential elements and amendment with various materials. ‘Positive correlation’ refers to an increase in disease severity with increasing value of the variable. Underlining indicates hydroponic studies and superscripts indicate host plant species: ^{1}banana; ^{2}asparagus; ^{3}carnation; ^{4}chickpea; ^{5}chrysanthemum; ^{6}cotton; ^{7}cucumber; ^{8}flax; ^{9}lettuce; ^{10}lime; ^{11}muskmelon; ^{12}oil palm; ^{13}radish; ^{14}strawberry; ^{15}tomato; ^{16}watermelon; ^{17}wheat.

Variable	Positive Correlation* (manipulated)	Positive Correlation (observed)	Negative Correlation (observed)	Negative Correlation* (manipulated)
Temperature	Peng et al. (1999)^{1}, Ferrocino et al. (2013), Scott et al. (2010)^{9}, Fang et al. (2011)^{14}, Larkin and Fravel (2002)^{15}			
Reduction potential (eH)	Huang et al. (2015b), Peng et al. (1999), Wen et al. (2015)^{1}, Blok et al. (2000)^{2}, Bhatti and Kraft (1992)^{4}, Yao et al. (2016)^{8}, Jorge-Silva et al. (1989)^{11}, Oritsejafor (1986)^{12}, Ebihara and Uematsu (2014)^{14}, Ghaemi et al. (2011)^{15}, Cao et al. (2016)^{16}			
pH	Peng et al. (1999)^{1}, Cao et al. (2016)^{16}		Alvarez et al. (1981), Deltour et al. (2017), Domínguez et al. (1996), Domínguez et al. (1995), Rishbeth (1957), Román Jerí (2012), Stover (1956)^{1}, Yuen et al. (1983)^{3}	Fan and Li (2014), Shen et al. (2015a)^{1}, Duuff et al. (1995)^{3}, Jones et al. (1975)^{7}, Höper et al. (1995), Scher and Baker (1980), Senechkin et al. (2014)^{8}, Gatch and du Toit (2016)^{9}, Fang et al. (2012)^{14}, Borrero et al. (2004), Jones and Woltz (1969), Jones and Woltz (1968, 1970), Woltz and Jones (1973)^{15}, Everett and Blazques (1967), Jones et al. (1975)^{16}
Organic Matter Content			Alvarez et al. (1981)^{1}	Pérez Salas et al. (2013), Shen et al. (2015a)^{1}, Markakis et al. (2016)^{7}, van Bruggen et al. (2015)^{8}, Abadie et al. (1998)^{12}, Akhter et al., 2016; Castaño et al. (2011)^{15}, Cao et al. (2016), Yogev et al. (2011)^{16}
Nitrate:Ammonium ratio	Zhang et al. (2013)^{1}, López-Berges et al. (2010)^{15}, Cao et al. (2016)^{16}			Jones et al. (1975), Wang et al. (2016), Zhou et al. (2017)^{7}, Morgan and Timmer (1984)^{10}, Borrero et al. (2012), Duffy and Défago (1999), Woltz and Jones (1973), Woltz et al. (1992)^{15}, Jones et al. (1975)^{16}
Calcium content			Alvarez et al. (1981)^{1}	Peng et al. (1999)^{1}, Höper et al. (1995), Keane and Sackston (1970)^{8}, Gatch and du Toit (2016)^{9}, Spiegel et al. (1987)^{11}, Jones and Woltz (1969)^{15}
Iron & Manganese content	Peng et al. (1999)^{1}, Duijff et al. (1994), Duijff et al. (1993)^{3}, Saikia et al. (2005)^{4}, Scher and Baker (1982)^{7}, Höper et al. (1995), Kloepper et al. (1980), Lemanceau and Alabouvette (1993), Lemanceau et al. (1988), Scher and Baker (1982)^{8}, Leeman et al. (1996), Scher and Baker (1982)^{13}, Jones and Woltz (1969), Jones and Woltz (1970), Segarra et al. (2010)^{15}	Domínguez-Hernández et al. (2010), Domínguez et al. (1996), Domínguez et al. (1995)^{1}		Dong et al. (2016)^{1}, Duffy and Défago (1999)^{15}
Zinc content	Gatch (2013)^{9}, Duffy and Défago (1999)^{15}		Gutierrez Jerez et al. (1983)^{1}	Fernández-Falcón et al. (2004), Hecht-Buchholz et al. (1998)^{1}, Saikia et al. (2009)^{4}, Duffy and Défago (1997)^{15}
Silicon content	Smith et al. (2005)^{6}, Huang et al. (2011)^{15}			Fortunato et al. (2014), Fortunato et al. (2012a,b), Jones (2013), Kidane and Laing (2008), Wibowo et al. (2014)^{1}
Sodium content & Electrical Conductivity	Triky-Dotan et al. (2005), Woltz et al. (1992)^{15}		Dominguez et al. (2001), Domínguez et al. (1996)^{1}	
Potassium content		Domínguez-Hernández et al. (2010)^{1}		Ollagnier and Renard (1976), Renard and Franqueville (1991)^{12} Cao et al. (2016)^{16}
Phosphorus content	Woltz and Jones (1973)^{15}			Shen et al. (2015a,b)^{1}
Boron content				Dong et al. (2016)^{1}, Keane and Sackston (1970)^{8}

affected (Ploetz, 2015a). Race 1 (R1) affects Maqueno, Silk, Pome, Pisang Awak and Gros Michel cultivars, Race 2 affects cooking bananas, Race 3 does not affect bananas, and Race 4 affects Race 1- and 2-susceptible cultivars as well as Cavendish (Ploetz, 2015a). Race 4 is subdivided into Subtropical Race 4 (SR4), that affects susceptible cultivars under stressful growing conditions in the subtropics, and Tropical Race 4 (TR4), that affects susceptible cultivars in all conditions (Ploetz, 2015a).

Over the past hundred years Panama Disease has had devastating effects on global banana production (Ploetz, 2015a). The disease was originally described in 1874 in Brisbane, and again in 1890 in Central America. In the first half of the 20th century over 40,000 ha of commercial Gros Michel (Musa AAA) bananas, plus lesser amounts of other susceptible cultivars, were destroyed by Foc R1 (Pegg et al., 1996). The spread of Foc R1, subsequent production losses of Gros Michel, and associated economic drivers caused a large-scale transition to Cavendish, the most agronomically successful resistant cultivar. The clonal nature of bananas and reliance upon a single cultivar in large plantations means the industry is vulnerable to rapid spread of diseases.

Foc TR4, which was first identified in the 1990's, now poses a serious threat to global banana production due to its continual spread, and the widespread cultivation of susceptible cultivars (Ploetz and Pegg, 1997). Foc TR4 has now been confirmed throughout Southeast Asia (Chittarath et al., 2017; Hung et al., 2017; Mostert et al., 2017), and in China, South Asia, the Middle-East, Africa (García-Bastidas et al., 2013; Ploetz et al., 2015) (Ordonez et al., 2015) (Qi et al., 2008) (Thangavelu, 2016) and Australia (Cook et al., 2015; O'Neill et al., 2016). Future spread to growing regions in Latin America would make the impact global.

There is not yet a commercially effective method of controlling Panama disease (Ploetz, 2015b). Quarantine measures have slowed, but are unlikely to stop the spread of Foc TR4. Selection and breeding of Foc TR4-resistant varieties has generated some promising cultivars such as Goldfinger and Taiwanese GCTCV somaclones (Hwang and Ko, 2004), but a suitably productive alternative to Cavendish has not yet been found. Fungicides will not be able to control this soil-borne pathogen in the field, for a variety of reasons, but they have shown promise for disinfection of farm implements contaminated by *F. oxysporum* of tomato (Amini and Sidovich, 2010; Song et al., 2004), watermelon (Everts et al., 2014) and banana (Nel et al., 2007). The rotation of crops, or fallowing of fields is ineffective as Foc commonly persists in soil beyond 20 years (Stover, 1962). Recently, addition of microorganisms (Cha et al., 2016; Cotxarrera et al., 2002; Fu et al., 2017; Shen et al., 2015a; Wu et al., 2013) and chemical amendments (Fortunato et al., 2012a; Liu et al., 2016; Peng et al., 1999) have shown promise for reducing disease severity. In case of only partially resistant cultivars being found, continued large-scale production of bananas would rely upon agronomic management of the disease.

3. Mechanisms of soil-borne disease suppression

Suppressiveness or conduciveness is the tendency of a soil to inhibit or enhance soil-borne disease. Suppressive soils are those in which disease impact is low despite the presence of a susceptible host, pathogen and a suitable environment (Baker and Cook, 1974). This involves inhibition of the pathogen's growth or virulence, enhancement of plant defence mechanisms, enhancement of the abundance or activity of microorganisms antagonistic or competitive to the pathogen, or a combination of these mechanisms (Fig. 1).

Suppression is primarily a function of soil microbiology and can be classed as general or specific. General suppression involves competition between the pathogen and other soil microorganisms for limited resources (Janvier et al., 2007). Edaphic, climatic and management factors affect these microbial interactions (Weller et al., 2002). Specific suppression involves the direct effects of an antagonistic organism on the pathogen (Janvier et al., 2007). Specific suppression can be induced or enhanced through the introduction of a specific organism (Fu et al., 2017; Nel et al., 2006; Xue et al., 2015). General suppression is typically considered non-transferrable and must be enhanced in situ (Weller et al., 2002). General and specific suppression are not mutually exclusive; they can operate simultaneously and in varying degrees. The size and diversity of the soil microbial community strongly influences suppressiveness (Shen et al., 2015b), and soil microbial community composition depends on soil abiotic properties. Similarly the susceptibility and effectiveness of the host plant defence is dependent on soil characteristics. Therefore alteration of the soil properties can influence suppression and disease severity. By shifting environmental conditions to favour organisms competitive with, or antagonistic to, Foc, or enhancing host plant defence, the suppressiveness of the soil may be increased.

4. Impacts of soil abiotic attributes

A wide variety of abiotic soil attributes have been correlated with suppression of Fusarium wilt in a range of crops, including bananas (Fig. 2, Table 1). Effects on suppression are generally consistent across susceptible crops but there are exceptions. The effect of soil attributes on suppression is usually described in terms of a particular attribute, but it should be kept in mind that attributes and their associations with suppression are interrelated (Fig. 3). Studies may have manipulated a particular soil attribute and report results accordingly, but it is certain that other attributes would also have been altered, and the effect of the measured attribute may have been indirect. It is impossible to test the effect of individual attributes, due to the complexity of the soil environment. For example, manipulation of pH alters bioavailability of most nutrients. Furthermore, as suppressiveness is a relative measure, it is important to understand the differences between test and control treatments, as many factors may influence responses. Finally, translating results from one environment to another may not be wise because such conditions may influence the treatment effects. Nevertheless, examining multiple studies can give insights into the importance of various attributes. To explore the studied effects of soil attributes, each of the following sections identifies, as far as possible, the mechanisms of suppression, as well as links to related attributes, gaps in understanding, and possible implications for management.

4.1. Temperature

Fusarium wilt severity is positively correlated with soil temperature in pot trials of banana (Peng et al., 1999), tomato (Larkin and Fravel, 2002) and lettuce (Ferrocino et al., 2013; Scott et al., 2010). For example, an increase from a high/low diurnal temperature regime of 26/18 °C–28/20 °C substantially increased disease severity in a pot trial with lettuce (Scott et al., 2010). Similarly, an increase from 24 to 34 °C significantly increased disease severity in both conducive and suppressive soils in a pot trial with banana (Peng et al., 1999).

Controlling growing temperature for banana is difficult due to its perennial growth and large land coverage. Unlike short-season crops, whose growing season can be shifted to align with optimum seasonal temperature, banana is cultivated year-round. Soil temperature can be reduced by shading, with a denser planting or cultivation of ground cover. Ground cover has been shown to reduce Foc incidence and severity in a field trial with bananas (Pattison et al., 2014) and the effect may have been partially due to reduced soil temperature. Covering the ground with plant residues or mulch has also been shown to modulate daily temperature variation (Horton et al., 1994). Temperature-controlled greenhouses are not practical for large scale commercial cultivation of banana due to the large areas required.

4.2. Water and oxygen

Reductive soil disinfestation has been found effective as a potential

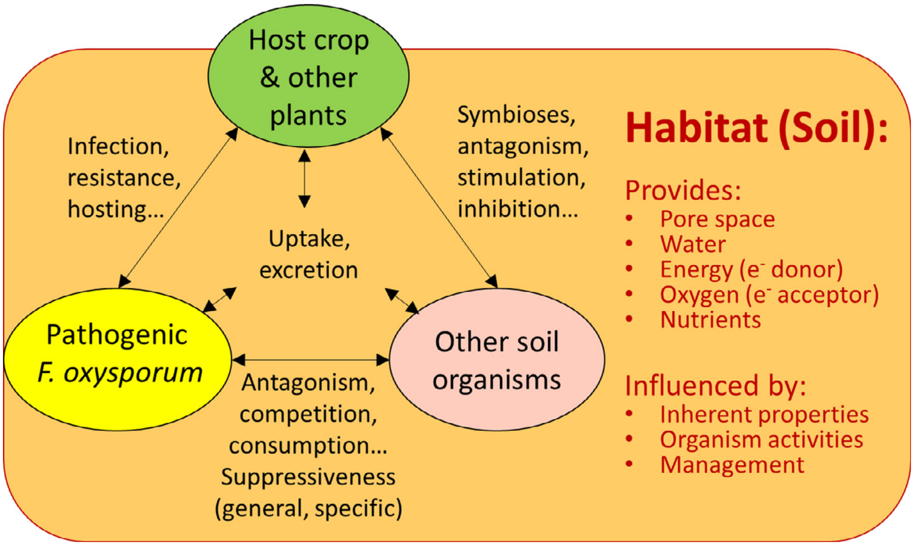

Fig. 1. Soil is the habitat for all organisms involved in soil-borne diseases such as Fusarium wilt. Soil physicochemical conditions govern the resources available for those organisms and can thereby influence severity of the disease.

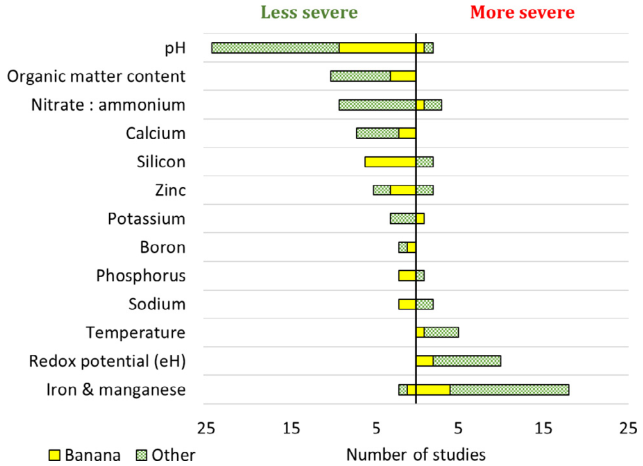

Fig. 2. Summary of the studies describing relationships between soil characteristics and severity of Fusarium wilt. More or less severe correspond to an increase in the listed characteristic. See Table 1 for references.

means of controlling Foc in field trials in China (Huang et al., 2015b). The procedure, initially developed in Japan and the Netherlands, was based on observations of soil-borne disease suppression in irrigated rice paddies, which are regularly flooded. A suppressive anaerobic environment is created by consumption of oxygen during decomposition of soil organic matter, as replenishment by diffusion is minimal in saturated soil (Huang et al., 2015b; Momma et al., 2013; Shrestha et al., 2016). This anaerobic decomposition generates antifungal acids and volatile organic compounds and shifts microbial community composition to being bacteria-dominated and suppressive to Fusarium wilt (Hewavitharana et al., 2014; Huang et al., 2015a; Liu et al., 2016; Momma, 2015). Once aerobic conditions resume, the suppressive community remains (Goud et al., 2004). It is worth noting that suppression did not occur when soil was saturated without organic matter addition in laboratory experiments (Wen et al., 2015), nor when oxygen was available to surface soil in field trials (Stover, 1955). This indicates that suppression is unlikely to occur during natural flood events that are typically short lived, with aerated water and variable addition of organic matter. Reductive soil disinfestation by flooding is generally not feasible for banana production due to the constraints of water

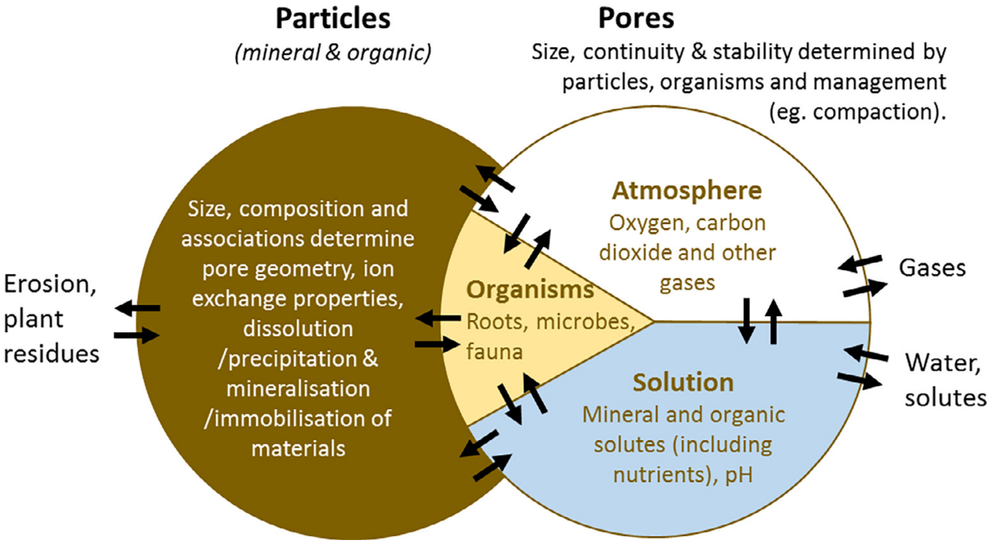

Fig. 3. Soil physical, chemical and biological properties and processes interact in many ways to influence severity of soil-borne diseases. Arrows indicate influences and fluxes.

availability, topography and fallow time required; waterlogging is detrimental to banana root development and functioning (Aguilar et al., 1998; Rishbeth, 1957).

Although reducing conditions have been shown to control Fusarium wilt, opposing processes may also occur. A reducing soil environment tends to increase the solubility and bioavailability of redox-sensitive micronutrients. Increased micronutrient bioavailability from reduced pockets within the crop root zone has been theorized to increase *F. oxysporum* pathogenicity (Dominguez et al., 2001). Furthermore, a reducing environment inhibits nitrification, increasing the concentration of soil ammonium, which is generally conducive to Fusarium wilt development. In the trials showing disinfestation by waterlogging, such effects were presumably overcome by the negative effects on the pathogen, such as an inability to function anaerobically, the release of antifungal bacterial exudates and the absence of a host crop to infect (Stover, 1954).

Low soil water content has been shown to be conducive to Fusarium wilt in several crops. In pot trials, soil water content below field capacity was conducive to Fusarium wilt of banana (Peng et al., 1999), tomato (Ghaemi et al., 2011), chickpea (Bhatti and Kraft, 1992) and melon (Jorge-Silva et al., 1989), possibly due to water stress of the host plant.

4.3. Mineralogy, texture and structure

A correlation between Fusarium wilt suppression and soil mineralogy was first identified in Central and South America (Rishbeth, 1957; Stotzky et al., 1961; Stotzky and Torrence Martin, 1963). As Foc R1 moved through the region, banana plantations that remained in production longer than 10 years before abandonment due to disease losses were all observed to have montmorillonite-like clays present (Stotzky and Torrence Martin, 1963). Pot trials with wheat and flax have also found montmorillonite more suppressive to Fusarium wilt than other clays (Amir and Alabouvette, 1993; Höper et al., 1995). Deltour et al. (2017) identified a positive correlation between clay content and suppression of Fusarium wilt of banana in a field survey in Brazil, but did not identify the types of clay involved.

Clay may influence suppression by altering oxygen diffusion (Dominguez et al., 2001; Stotzky and Rem, 1967), pH buffering (Rosenzweig and Stotzky, 1979) and availability of nutrients (Lavie and Stotzky, 1986). Early research suggested that reduced oxygen diffusion is harmful to pathogen growth (Stotzky and Rem, 1967). More recently however, it has been suggested that the formation of anaerobic micropores in soil aggregates actually promotes Foc SR4 pathogenicity, by increasing iron availability (Dominguez et al., 2001). Such anaerobic micropores are more likely to form in soils with higher clay content. The ability of clay to buffer pH and ion concentrations may reduce the impact of pH change on suppression (Siebner-Freibach et al., 2004). Smectite has been demonstrated to reduce the micronutrient acquisition effectiveness of siderophores produced by pathogenic fungi, through adsorption of the ferrisiderophore complex (Fig. 4) (Lavie and Stotzky, 1986; Siebner-Freibach et al., 2004). Conversely, *Pseudomonas* siderophores and the synthetic chelate EDDHA, both of which suppress Fusarium wilt (Lemanceau and Alabouvette, 1993; Scher and Baker, 1982), are highly successful at iron acquisition in the presence of smectite clays (Ferret et al., 2014). Siderophores are typically organism-specific, though some micronutrient piracy does occur (Harrington et al., 2015). Greater adsorption of fungal siderophores than competing chelates by clay could be expected to reduce micronutrient uptake by *F. oxysporum*. Thus the impacts of clay on suppression of fungal diseases may involve interactions with soil characteristics such as pH, redox state and micronutrient bioavailability.

Analysis of soil physical characteristics in suppression studies has almost exclusively focused on those that can be measured in the laboratory, such as texture and aggregation (Deltour et al., 2017; Dominguez et al., 2001). Only limited field research on the effects of hydraulic conductivity, porosity and structural stability on disease has been carried out. A field survey of bananas and Foc SR4 in the Canary islands found that hydraulic conductivity and macroporosity were negatively correlated with disease severity, and that structural stability was also important (Gutierrez Jerez et al., 1983). Further research is required to investigate the effect of soil structural characteristics on disease severity.

4.4. pH

Soil pH is often referred to as a master variable due to its substantial effect on biotic and abiotic processes (Brady and Weil, 2000), and effects on Fusarium wilt have been shown in several studies. A negative relationship between Fusarium wilt severity and soil pH has been demonstrated for banana and a variety of other hosts (Fig. 5). However, there have also been contradictory results demonstrating a positive relationship, with both banana (Peng et al., 1999) and other crops (Cao et al., 2016; Hopkins and Elmstrom, 1976; Huang et al., 2012). One possible reason for the difference may be related to the nature of the soils studied. Peng et al. (1999) studied a soil with pH 8, which they acidified, whereas most other studies examined mildly acidic soils, which they limed. Soil pH is a major determinant of microbial community composition (Rousk et al., 2010) and the soil organisms acclimatized to the naturally high pH in Peng et al.'s (1999) pot trial with banana may have responded differently to those found in acidic soils. In the case of the other anomalous studies, pH varied as a result of various treatments but was not deliberately manipulated; Cao et al. (2016), in pot and field experiments with watermelon, and Huang et al. (2012), in a pot trial with cucumber, varied organic amendment type, whereas Hopkins and Elmstrom (1976), in a field trial with watermelon, varied ammonium fertilizer rates. Although a correlation between pH and suppression was observed, it may have been coincidental. The inconsistency amongst results demonstrates the complexity of the response to changes in pH and the importance of directly versus indirectly manipulated variables.

Soil pH, in combination with redox state, modulates the bioavailability of essential elements, particularly redox-sensitive micronutrients such as iron, manganese, zinc and copper (Collins and Buol, 1970). Availability of nutrients influences health of the host plant, *F. oxysporum* and other soil microorganisms. To obtain micronutrients many organisms produce siderophores with stability constants differing in magnitude and pH dependence. Therefore, the relative ability of different species to obtain essential micronutrients differs with pH, due to the effect of pH on solubility of the metals and stability of the chelated forms (Boukhalfa and Crumbliss, 2002; Dhungana and Crumbliss, 2005).

Soil pH is also strongly positively correlated with bacterial diversity and abundance, with a doubling of bacterial diversity between pH 4 and 8 (Rousk et al., 2010), which encompasses the ideal soil pH range for most crops. Increased diversity of the bacterial population enhances general suppression and broadens the array of nutrient acquisition strategies, increasing the likelihood of a strong competitor to *F. oxysporum* being present. Increased competition, combined with reduced availability of nutrients, means *F. oxysporum* is less likely to meet its metabolic requirements at higher pH.

Soil pH can be altered by inputs and losses of materials, including cycling of nitrogen and carbon; this is particularly important in agricultural systems in which nitrogen fertilizer and organic matter are applied. Application of ammonium-based fertilizers or urea, or generation of ammonium from organic matter breakdown, leads to acidification of the rhizosphere due to excretion of protons by roots when ammonium is taken up, and to nitrification and leaching loss of nitrate. On the other hand, application of nitrate-based fertilizers tends to increase soil pH (Tinker and Nye, 2000). Organic matter, either produced in situ or imported from elsewhere, has a large cation exchange capacity, which buffers soil pH through adsorption of ions (Baldock and

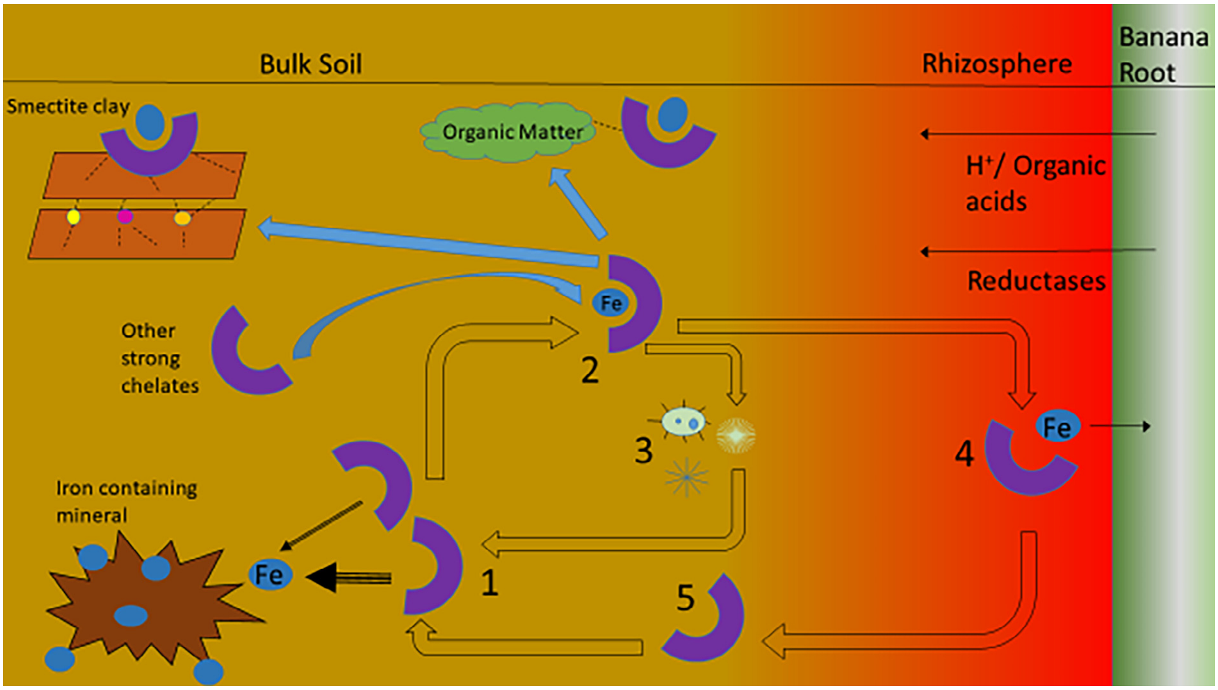

Fig. 4. Micronutrient acquisition by chelating ligand (purple 'c's). Step 1: Competition between microbially-produced chelating ligand (siderophores) of different stability (the more stable the greater the amount of iron chelated). Step 2: Bound iron is transported by diffusion, which is hampered by adsorption to organic matter and clay, and piracy of iron by more stable chelating ligands. Step 3: Microorganisms take up their specific siderophores with bound iron and siderophore is regenerated. Step 4: Loss of stability in acidic/reducing rhizosphere, freeing iron cation. Step 5: Chelating ligand leaves rhizosphere and regains structure and chelating ability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

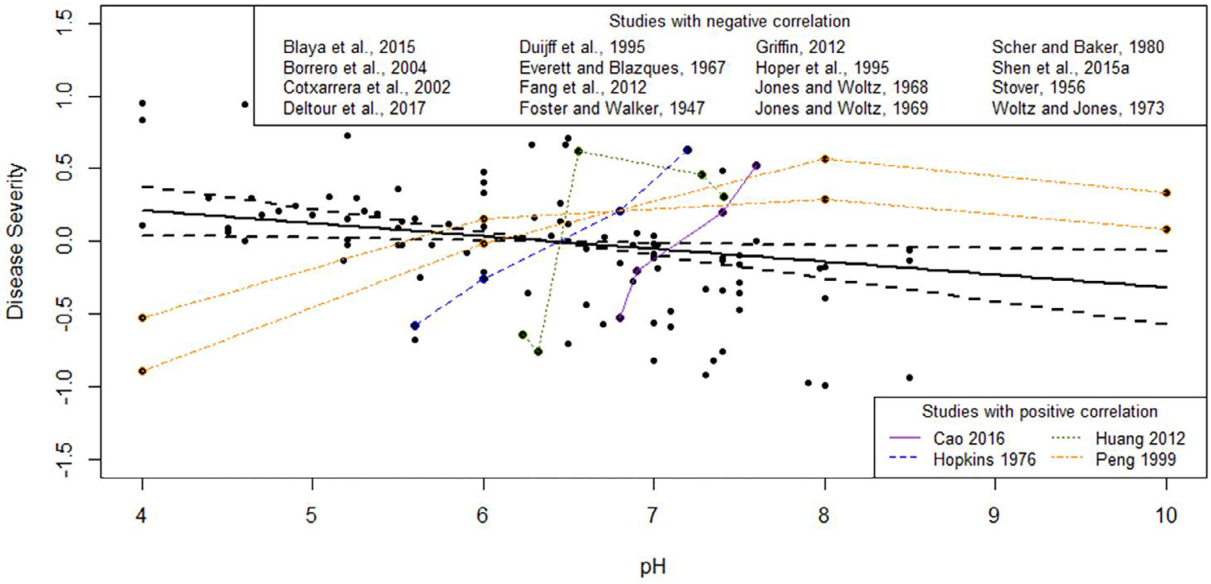

Fig. 5. Generalized additive model for the meta-analysis of pH and disease severity from 21 studies of Fusarium wilt across a variety of crops and regions (see Table 1 for crops). In the studies included, soil pH was measured but not necessarily deliberately manipulated. Disease severity values reported in studies were normalized for comparison, with 0 representing the average disease severity for all studies. The overall trend is negative (full line, p = 0.013), as is the trend for most of the individual studies. The four studies demonstrating a positive correlation have been individually identified. Dashed lines represent the 95% confidence interval.

Nelson, 2000). These changes to pH then initiate other changes in the soil environment, such as nutrient availability, influencing suppression.

Although there have been numerous studies on the effects of pH on *F. oxysporum,* our understanding of the relationship is far from complete. The optimum soil pH_{water} for growing bananas is approximately 5.0–7.5 (Weinert and Simpson, 2016). If pH modification were to be used as a means of reducing disease severity in the field, then the possible detrimental effect of raising pH above the optimum for bananas must be outweighed by the effect on disease suppression. For each combination of soil conditions and management regime there is presumably an optimum pH for plant growth and disease suppression. The relationship between pH and suppression requires in-field research to better understand these complex interactions.

4.5. Organic matter

Organic matter strongly affects plant health, the chemical, physical and biological characteristics of soil, and disease suppression. It is also one of the most commonly added (as organic amendment applications or via exudation and death of plant roots) and compositionally diverse soil amendments. Furthermore, the amount and composition of organic matter within soil depend upon the inputs, climate, mineralogy, organisms and management. It is difficult to identify the mechanisms of suppression attributable to organic matter versus what are unimportant or confounding factors. This, in combination with limited analytical characterization of organic matter, and variability of results, makes it difficult to identify consistent trends. Reviews linking organic matter characteristics to disease suppression have had mixed success at identifying unifying trends (Baum et al., 2015; Bonanomi et al., 2007; Griffin, 2012; Hoitink and Fahy, 1986; Janvier et al., 2007). That said, a meta-analysis has found at least some suppression from organic matter application in 74% of cases involving *Fusarium* across more than 150 studies (Bonanomi et al., 2007).

Suppression of Fusarium wilt associated with organic matter is generally attributable to a combination of interlinked biotic and abiotic characteristics (Baum et al., 2015). The biotic controls include total microbial community size, which creates competition for organic carbon, nutrients and space, and microbial antagonism by specific organisms (Baum et al., 2015). The importance of microbial populations to disease suppression has been demonstrated through a loss of suppressiveness when soil is sterilised (Cotxarrera et al., 2002; Noble and Coventry, 2005; Reuveni et al., 2002). The abiotic characteristics of the organic matter and soil influence the microbial population composition, both directly and indirectly affecting the pathogen (Figs. 1, 3). Physically, the organic matter impacts on the structure and structural stability of the soil, including pore spaces (Baldock and Nelson, 2000). Chemically, organic matter impacts the soil pH, pH buffering capacity, amounts, forms and bioavailability of carbon and nutrients, and concentrations of important molecules such as siderophores (Baum et al., 2015).

The decomposability of organic matter appears of principal importance for disease suppression, as it affects the balance between the pathogen and competitive microorganisms (Fig. 6) (Bonanomi et al., 2010). As decomposability declines, from fresh plant residues, through composts to different forms of peat, suppression tends to increase initially then decline steadily (Bonanomi et al., 2010). Application of compost has been demonstrated to generally increase suppression of Fusarium wilt of flax, melon and chrysanthemum in pot trials, though the effect varied with the type of compost (Chef et al., 1983; Saadi et al., 2010; van Rijn et al., 2007).

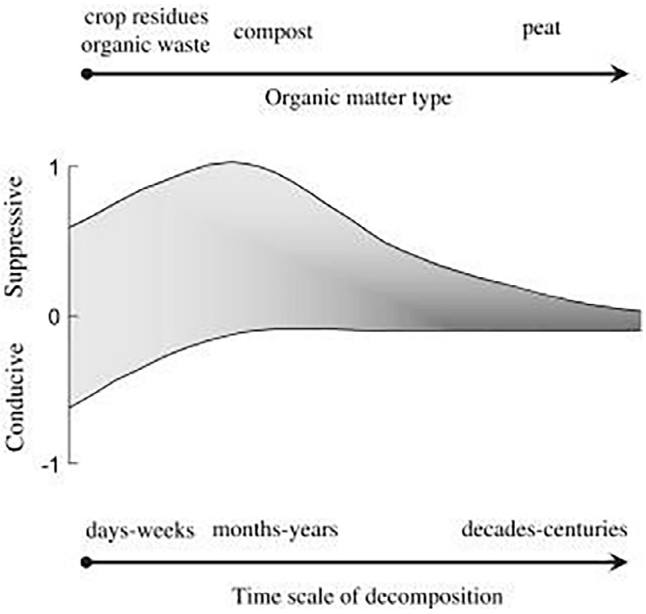

Fig. 6. Schematic representation of disease suppression dynamics during organic matter decomposition (Bonanomi et al., 2010).

During the process of decomposition labile carbon sources are preferentially converted to carbon dioxide by microbes, increasing the overall recalcitrance of the remaining organic matter. This progressive loss of carbon and increased competition has been demonstrated to play a central role in the suppressiveness of some soils to *F. oxysporum* (Elad and Baker, 1985b; Lemanceau, 1989; Mazurier et al., 2009). High concentrations of labile carbon sources such as sugars in fresh plant residues mean there is little competition for carbon when they are added and thus no suppression. Increasing levels of glucose addition increased Fusarium wilt severity in a pot trial with flax (Lemanceau, 1989). An increased proportion of more complex compounds such as carboxylic and amino acids in amendments, has been found to increase suppression in pot trials with tomato and field trials with flax (Borrero et al., 2006; Senechkin et al., 2014). Castaño et al. (2011) correlated hemicellulose concentration in organic amendments with suppression of *F. oxysporum* in tomato and carnation. Eventually, when decomposition has reduced carbon availability below that required to support a suppressive microbial community, suppression declines (Hoitink et al., 1997). In summary, if there is little competition and carbon is readily available to *F. oxysporum*, disease appears to increase, whereas if competition is strong, or carbon sources are more difficult for *F. oxysporum* to metabolise, suppression occurs.

The carbon-to-nitrogen (C:N) ratio of organic matter appears to be related to suppression. C:N ratio is a commonly measured characteristic of organic matter associated with the extent of decomposition (Brady and Weil, 2000), and it differs substantially amongst organic amendments and soils. C:N ratio is positively correlated with *F. oxysporum* suppression, primarily due to its control on microbial community dynamics and ammonium generation during decomposition (Griffin, 2012). A very high C:N ratio (> 70:1) generally lowers the mineral nitrogen concentration as microorganisms scavenge nitrogen; this reduces ammonium production, which can otherwise mitigate compost suppressiveness (Cotxarrera et al., 2002; Yogev et al., 2006). A C:N ratio above 20:1 also reduces plant-available nitrogen stressing the plant and likely increasing susceptibility to disease (De Ceuster and Hoitink, 1999). A full understanding of the relationship between C:N ratio and suppression will require further research and a better understanding of the relative importance of the effects on the host plant, pathogen and competing microorganisms.

Soil organic matter greatly affects pH and nutrient availability due to its cation exchange capacity and wide range of acidic and basic functional groups (Brady and Weil, 2000). Soil pH was found to strongly positively correlate with suppression in a field trial with flax where varying combinations of plant residues and animal dung were added (Senechkin et al., 2014), as well as in pot trials with tomato and carnation where various plant residues were added (Borrero et al., 2009; Borrero et al., 2004). In addition to supplying energy to heterotrophs, nutrients in organic matter can be important for plants and soil organisms (Brady and Weil, 2000). Finally, siderophores, molecules produced by microorganisms to acquire micronutrients, can adsorb to organic matter, affecting their acquisition effectiveness (Fig. 4) (Ahmed and Holmström, 2014). In summary, the substantial effects of organic matter on suppression are complex, varied and incompletely understood, though provide promise for future research.

4.6. Nitrogen

In addition to nitrogen in organic matter being important for disease severity and management, so is the nature of mineral nitrogen compounds in soil. Typically, the addition of nitrate fertilizer increases the suppressiveness of soils to *F. oxysporum*, whereas addition of ammonium decreases suppressiveness (Table 1), although results vary. Studies have shown ammonium to be disease conducive relative to nitrate in field trials with melon (Jones et al., 1975), in pot trials with lime, cucumber, tomato and chrysanthemum (Morgan and Timmer, 1984; Wang et al., 2016; Woltz and Engelhard, 1973; Woltz et al., 1992), and in hydroponics trials with tomato and cucumber (Borrero et al., 2012; Duffy and Défago, 1999; Wang et al., 2016; Zhou et al., 2017). On the contrary, ammonium application has been found suppressive relative to nitrate application in a pot trial with tomato (López-Berges et al., 2010), and a hydroponics trial with banana (Zhang et al., 2013). Also, soil ammonium concentration was negatively correlated with disease severity of watermelon in field and pot experiments with piggery waste (following anaerobic biogas generation) application (Cao et al., 2016). Finally, ammonium application has been reported to have no impact on disease severity on a field trial with cucumber (Jones et al., 1975) and pot trial with tomato (Jarvis and Thorpe, 1980). The effects of mineral nitrogen form on disease severity presumably occur through their effects on rhizosphere chemistry, plant defence mechanisms and fungal pathogenicity.

Ammonium and nitrate differ in their impact on rhizosphere chemistry. Nitrogen fertilizer is predominantly applied as ammonium, nitrate or urea, which rapidly hydrolyses to generate ammonium. When organic matter with a low C:N ratio decomposes ammonium is also generated, as nitrogen is surplus to the needs of the decomposers (Brady and Weil, 2000). Ammonium skews plant ion uptake to cations, hence altering the uptake of other ions such as potassium, chloride and nitrate (Hawkesford et al., 2012). Also, as the plant takes up ammonium, protons are excreted into the rhizosphere, acidifying the soil. Conversely, nitrate uptake increases relative cation uptake, and protons are removed from the rhizosphere for plant reduction of nitrate to ammonia (Tinker and Nye, 2000). This increases the pH of the rhizosphere (Neumann and Römheld, 2012), which has been shown to decrease Fusarium wilt severity.

Nitrogen supply and form affect plant defence, via the regulation of intracellular concentrations of cell sugars and amino acids, which provide nutrients for invading fungi upon cell apoptosis; polyamines, which act as defence signals; and nitric oxide (Mur et al., 2016). For an in-depth review of the role of nitrogen in plant defence against pathogens, see the recent work by Mur et al. (2016). The reduction of nitrate (NO_3^-) to nitrite (NO_2^-) generates nitric oxide (NO) through the nitrate reductase pathway (Gupta et al., 2005). A high concentration of ammonium inhibits this reaction, thereby reducing the concentrations of nitric oxide in the plant (Gupta et al., 2013). Nitric oxide is involved in plant defence both initially, as part of the pathogen-triggered immunity response (Zeidler et al., 2004), and upon cell death as a scavenger, reacting with superoxide (O_2^-) as part of the pathogen-induced hypersensitivity response (Delledonne et al., 1998; Delledonne et al., 2001; Swarupa et al., 2014). This scavenging function is particularly important in limiting cell death in relation to *F. oxysporum* infection. As a facultative saprophyte, *F. oxysporum* can survive on living or dead tissue and so can benefit from cell apoptosis due to the discharge of nutrient-rich cytoplasm (Anthony et al., 2017).

Nitrogen supply also affects pathogenicity of *F. oxysporum.* Most experiments have shown increased severity of Fusarium wilt with increasing supply of ammonium (Fig. 2), but López-Berges et al. (2010) found the opposite in a pot trial with tomato. Invasive growth, hyphal fusion and host adhesion were all suppressed by ammonium and increased in the presence of nitrate (López-Berges et al., 2010). When deprived of nitrogen in their preferred form (organic nitrogen or ammonium), saprophytic fungi entered a nutrient exploration mode resulting in rapid infection of the host (Walters and Bingham, 2007). Zhou et al. (2017) tested suppression both *in vitro* and *in vivo* to differentiate between the suppression of the pathogen and the disease. They determined that both the plant and pathogen grew better with addition of nitrate but it was the balance of the *F. oxysporum* pathogenicity mechanism against the opposing plant defence mechanism that determined infection success and disease severity (Zhou et al., 2017).

Nitrogen amount, as well as form, is important for Fusarium wilt suppression. Nitrogen deficiency stress in the plant is likely to increase susceptibility to disease, and increased nitrogen application has been shown to decrease disease severity in a field trial with fava bean (Dong et al., 2013), and a hydroponic trial with cucumber (Zhou et al., 2017) but was observed to increase disease severity in banana fields in Jamaica (Rishbeth, 1957). Despite this, research has shown no correlation between plant tissue nitrogen concentrations and suppression of Fusarium wilt of tomato in a pot trial (Hoffland et al., 2000). This may indicate that above the concentration that the plant can take up, further nitrogen fertilising has no benefit, or may even be detrimental. Further research is needed to identify the optimal level of nitrogen in each system, as well as understand better the effects of nitrogen form on *F. oxysporum*, particularly Foc TR4.

4.7. Calcium

The addition of calcium to soil has been shown to suppress Fusarium wilt across a wide variety of host plants and soil conditions (Table 1). Calcium supply has often been manipulated together with pH (Everett and Blazques, 1967; Gatch and du Toit, 2016; Jones and Overman, 1971; Jones and Woltz, 1969; Jones and Woltz, 1970). Soil pH is typically manipulated with calcium hydroxide ($Ca(OH)_2$) or limestone ($CaCO_3$). To manipulate calcium supply without altering pH, calcium sulphate has been used. An additive benefit from increasing both pH and calcium concentration has been identified in pot trials with tomato (Jones and Woltz, 1969).

Calcium, like silicon, stabilizes the cell structure, accumulating at the cell wall and the middle lamella (Hawkesford et al., 2012). Increased calcium concentration in the cell wall helps to reduce the loss of cytoplasmic compounds in the case of cellular penetration by fungi. Higher concentrations of calcium in the intercellular space can also inhibit attack by parasitic fungi (such as *F. oxysporum*) by inhibiting enzymes designed to degrade the middle lamella (Huber et al., 2012).

Calcium is also involved in intracellular mechanisms regulating plant defence and pathogen growth. In the plant cytosol, calcium concentration change has been identified as a key secondary messenger in defence against both biotic and abiotic stressors (Lecourieux et al., 2006). Plant cytosol calcium concentrations modulate response to both parasitic and symbiotic fungi, such as arbuscular mycorrhizal fungi (Johnson and Oelmüller, 2013; Navazio and Mariani, 2008; Sherameti et al., 2014). Inoculation with arbuscular mycorrhizal fungi has shown promise for Foc R1 suppression in bananas by increasing nutrient availability, and high calcium supply enhances this symbiosis (Smith, 2006). In the cytosol of *F. oxysporum,* calcium is involved in sporulation and in signalling pathways regulating hyphal growth rate and morphology (Hoshino et al., 1991; Kim et al., 2015) indicating that *F. oxysporum* may be controlled by limiting calcium. However, there is no evidence to suggest that calcium supply could be regulated at a level that benefits the host plant but not the pathogen, so future research would best focus on maximising the relative benefit for the host plant compared to the pathogen.

4.8. Iron and manganese

Iron and manganese are here discussed together, as they are similar with respect to environmental effects on their availability and mechanisms of suppression. The lower the supply of bioavailable iron or manganese in soil, the more successful host plants and beneficial bacteria appear to be in the presence of *F. oxysporum* (Table 1). Micronutrient requirements differ amongst organisms, and *F. oxysporum* has a particularly high requirement (Woltz and Jones, 1981). The bioavailability of metals essential for microorganisms and plants, particularly iron and manganese, is determined largely by their oxidation state, which is driven by soil pH and redox potential. These metals change from soluble, mobile and plant-available forms with low oxidation state to insoluble, immobile forms with high oxidation state as soil pH and redox potential increase (Lindsay and Schwab, 1982). The ability of soil organisms to obtain bioavailable micronutrients can be altered by manipulating the soil pH and redox state (Höper and Alabouvette, 1996; Jones and Woltz, 1970).

Organisms have developed specific acquisition strategies to compete for micronutrients, as naturally occurring concentrations of available forms in soil are typically below those required for continued growth (Fig. 4). Strategy 1 plants, such as bananas, excrete protons and organic acids to acidify the rhizosphere, and reduce insoluble Fe^{3+} to soluble Fe^{2+} with reductases (Marschner and Römheld, 1995). Strategy 2 plants, comprised entirely of grasses, excrete phytosiderophores that chelate Fe^{3+}, increasing its bioavailability (Marschner and Römheld, 1995). This acquisition strategy is similar to that of fungi and bacteria, which also produce siderophores (Lemanceau et al., 2009; Marschner and Römheld, 1995). Plants are able to take up iron bound by bacterially produced siderophores either directly, by taking up the entire siderophore-metal complex (Vansuyt et al., 2007; Xiong et al., 2013), or indirectly, by acidifying and reducing the rhizosphere, destabilising the complex (Bienfait, 1986). Once free of the siderophore, diffusion moves iron ions to the root, where they are taken up. Fungal and bacterial siderophores must compete with each other to make iron available. The higher the stability of a metal-chelate complex, the greater the proportion of available metal cations captured by the chelate.

Chelating agents with high chelate stability (K) have long been shown to induce suppression of *F. oxysporum*, as shown with application of 8-quinolinol to Fusarium wilt of cotton by Subramanian (1956). In later experiments the strong artificial chelating agent ethylenediaminedi-*O*-hydroxyphenylacetic acid (EDDHA, $K = 10^{33.9}$) (Lindsay, 1979) outcompeted the weaker *F. oxysporum* siderophore fusarinine ($K = 10^{29}$) for iron (Scher and Baker, 1982). Pseudobactin ($K = 10^{32}$) (Meyer and Abdallah, 1978), produced by *Pseudomonas fluorescens*, also outcompetes fusarinine for iron, leading to *F. oxysporum* suppression (Saritha et al., 2015; Scher and Baker, 1982; Van Peer et al., 1990). Both EDDHA, which binds free iron, and Fe-EDDHA have been shown to suppress *F. oxysporum* growth and Fusarium wilt severity in rhizosphere soil (Scher and Baker, 1982). The plant is able to take up iron from Fe-EDDHA and release the EDDHA to bind free iron (Fig. 4) (Elad and Baker, 1985a). In bulk soil, away from the roots, EDDHA but not Fe-EDDHA, decreases *F. oxysporum* chlamydospore germination (Elad and Baker, 1985a). EDDHA in bulk soil, unlike saturated Fe-EDDHA, sequesters available iron, decreasing *F. oxysporum* germination. EDDHA has also been shown to shuttle iron from clay-adsorbed fungal siderophores to the plant due to its low adsorption affinity, further enhancing plant growth at the expense of soil fungi (Siebner-Freibach et al., 2004). Lemanceau and Alabouvette (1993) provided a comprehensive (to that date) review of suppression by addition of chelate and production of siderophores by *Pseudomonas*.

Effects of iron availability on suppression of Fusarium wilt (*F. oxysporum)* have been attributed to the effect of the pathogen's iron status on virulence. Iron is essential for many processes in fungi, so it must be acquired at an adequate rate for growth and pathogenicity. Iron deficiency and toxicity can both occur, so organisms have complex processes to maintain specific internal concentrations. The deletion of Hap-X, a bZIP protein in *F. oxysporum* responsible for iron homeostasis, substantially reduces the virulence and growth of the pathogen under iron-depleted conditions (Gsaller et al., 2014; López-Berges et al., 2012; López-Berges et al., 2013). Virulence is further reduced if competition for iron is increased by the presence of siderophore producing antagonistic bacteria (López-Berges et al., 2013). The environmental concentration of iron required for *F. oxysporum* f. sp. *cucumerinum* chlamydospore germination has been identified in laboratory studies as between 10^{-22} and 10^{-27} M, and concentrations in the rhizosphere may fall below this value (Simeoni et al., 1987). The link between pathogenicity, propagation and iron status points to possible future management strategies. Reducing bioavailable micronutrient concentrations below the levels required by the pathogen may provide a means of reducing disease severity.

Manganese has similar effects to iron. It is essential for photosynthesis, nitrogen metabolism and the formation of variety of enzymes in plants (Millaleo et al., 2010). Manganese is also involved in the production of lignin, an important component for plant defence against fungal invasion (Broadley et al., 2012; Dordas, 2008; Gatch, 2013). Like iron, manganese is acquired by fungi and bacteria through chelation, and has similar vulnerabilities to treatment with chelates. Low available manganese has been shown to reduce Fusarium wilt disease severity in a pot trial with tomato (Jones and Woltz, 1970) and *F. oxysporum* chlamydospore germination in laboratory trials (Sneh et al., 1984).

4.9. Zinc and other trace elements

Zinc, like iron and manganese, is a redox-sensitive essential micronutrient, but it tends to have the opposite effect on Fusarium wilt, decreasing disease severity. In plants, zinc is involved in protein and starch synthesis, membrane stability and defence mechanisms, and as an enzyme cofactor (Siddiqui et al., 2015). Studies have shown zinc is important in the oxidative burst defence mechanism of plants (Cakmak, 2000; Kawano et al., 2002) which reduced disease severity of *F. solani* in wheat, except if zinc was deficient (Khoshgoftarmanesh et al., 2010).

Increased zinc bioavailability reduces production of fusaric acid by *F. oxysporum* (Duffy and Défago, 1997). Fusaric acid has been identified as a cause of phytotoxicity, a trigger for plant defence mechanisms, and a virulence factor in pathogenic *F. oxysporum*, but its effect is suppressed by the addition of zinc, copper and iron (López-Díaz et al., 2017). This indicates that fusaric acid is both a phytotoxin and a chelator, produced as part of a feedback loop to provide necessary micronutrients to pathogenic *F. oxysporum* (López-Díaz et al., 2017). However, increased bioavailability of zinc has shown mixed effects on Fusarium wilt in pot trials with tomato (Jones and Woltz, 1970), except in high concentrations where phytotoxicity is likely to be involved (Duffy and Défago, 1997). While most studies suggest that zinc has a suppressive effect on Fusarium wilt, its requirement for so many biological processes makes it difficult to identify mechanisms for the effects.

Other essential micronutrients also appear to influence Fusarium wilt severity. A molybdenum concentration < 20 mg/L decreased Fusarium wilt severity in hydroponic studies of tomato (Duffy and Défago, 1999). Molybdenum is necessary for the conversion of nitrate nitrogen to amino acids in plants (Siddiqui et al., 2015) and plant molybdenum requirements are highly dependent upon the nitrogen fertiliser form supplied (Broadley et al., 2012). However, molybdenum's role in plant defence and Fusarium wilt suppression is unclear. Copper suppressed Fusarium wilt of tomato at concentrations > 20 mg/L in hydroponic trials (Duffy and Défago, 1999). Copper is important for formation of a physical lignin barrier to disease, and for production of phenolic compounds, part of the plant response to pathogens (Siddiqui et al., 2015). Boron deficiency has also been demonstrated to increase Fusarium wilt disease severity in flax (Keane and Sackston, 1970), though no change was found in a hydroponic study of bananas (Dong et al., 2016). Like copper, boron plays a role in cell wall structure and the production of defence-related compounds. Other trace elements may also influence Fusarium wilt but their effects have not been reported.

4.10. Silicon

Although not qualifying as an essential element for plants (Arnon and Stout, 1939), silicon has long been identified as an important constituent in plant defence (Huber et al., 2012). Various pot trials have concluded that the addition of soluble silicon reduces Fusarium wilt severity (Foc R1 and TR4) in bananas (Fortunato et al., 2012a; Fortunato et al., 2012b; Jones, 2013; Kidane and Laing, 2008; Wibowo et al., 2014). The mechanisms of defence in bananas are not entirely clear but have been hypothesized to encompass both physical and biochemical factors (Sakr, 2016). For an in-depth review of silicon in plant defence against pathogens, see the recent reviews by Sakr (2016) and Wang et al. (2017).

Silicon fertilizer increases plant silicon uptake, allowing formation of a barrier in root cell walls that resists fungal penetration and ingress (Fortunato et al., 2012b; Jones, 2013). Research has shown silicon is most effective for defence, and is most efficiently absorbed, when applied to the roots (Liang et al., 2005), triggering both the biochemical and cell wall physical mechanisms (Dallagnol et al., 2015).

Biochemical defence mechanisms involving silicon include local and whole-plant responses to attack. A whole-of-plant response is evident from enhanced resistance to both root and foliar diseases when silicon supply to the roots is increased (Dallagnol et al., 2015). Plant defence responses include activation of the phenylpropanoid pathway (Fortunato et al., 2014) and silicon-mediated accumulation of phenolics and lignin at infection sites (Fortunato et al., 2012a; Whan et al., 2016).

Silicon is a major constituent of most soil minerals but little is available in soluble form. Accelerated mineral weathering by root exudates has been shown to increase bioavailable silicon in the rhizosphere, compared to bulk soil (Gattullo et al., 2016). This enhanced weathering was linked to phytosiderophore production in graminacious plants suffering iron deficiency (Gattullo et al., 2016). Bananas, as iron acquisition strategy 1 type plants (Marschner and Römheld, 1995), do not produce phytosiderophores, but they do exude protons, reductases and organic acids, and this is likely to increase mineral weathering and silicon availability. Bananas are also likely to benefit from fungal and bacterial siderophore-mediated weathering in the rhizosphere.

5. Conclusions

Fusarium wilt severity is influenced by numerous soil abiotic attributes and their interactions. Several promising avenues for mitigating Fusarium wilt are suggested by previous research with a variety of crops, however this research is mostly pot trials and field observations. These avenues have yet to be tested in field conditions and commercial production systems. We hypothesise that suppression will be maximised by: increasing soil pH to the highest value possible without impacting plant growth; maintaining soil water content, which largely controls the soil redox state, consistent and high to avoid stress on the plant; maintaining high concentrations of bioavailable calcium, silicon and zinc; keeping concentrations of bioavailable iron and manganese low to disadvantage the pathogen; and, when mineral nitrogen fertiliser is added, applying nitrate rather than ammonium. Addition of partially decomposed organic matter with C:N ratio between 20:1 and 70:1, amended with suppressive organisms, also appears to decrease disease severity. To assess their effectiveness these approaches need to be tested in manipulative field experiments, individually and in combination, in different regions, soil types, cultivars and management systems. For bananas, due to the semi-perennial nature of production, trials must be long term to examine possible accumulation or dissipation of effects over time. Despite the complexities and challenges involved, further elucidation of the mechanisms discussed here appears well worthwhile, with the ultimate goal of developing commercially feasible cultural techniques to reduce severity of Fusarium wilt.

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