Received: 18 March 2022 | Accepted: 22 August 2022

DOI: 10.1111/ppa.13641

Plant Pathology An International Journal edited by the British Society for Plant Pathology WILEY

REVIEW ARTICLE

Back to the roots: Understanding banana below-ground interactions is crucial for effective management of Fusarium wilt

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Funding information
University of Hohenheim; German Academic Exchange Service

Abstract

Global banana production is affected by Fusarium wilt, a devastating disease caused by the soilborne root-infecting fungus, *Fusarium oxysporum* f. sp. *cubense* (Foc). Fusarium wilt is notoriously difficult to manage because infection arises through complex below-ground interactions between Foc, the plant, and the soil microbiome in the root–soil interface, defined as the rhizosphere. Interactions in the rhizosphere play a pivotal role in processes associated with pathogen development and plant health. Modulation of these processes through manipulation and management of the banana rhizosphere provides an auspicious prospect for management of Fusarium wilt. Yet, a fundamental understanding of interactions in the banana rhizosphere is still lacking. The objective of this review is to discuss the state-of-the-art of the relatively scant data available on banana below-ground interactions in relation to Fusarium wilt and, as a result, to highlight key research gaps. Specifically, we seek to understand (a) the biology of Foc and its interaction with banana; (b) the ecology of Foc, including the role of root-exuded metabolites in rhizosphere interactions; and (c) soil management practices and how they modulate Fusarium wilt. A better understanding of molecular and ecological factors influencing banana below-ground interactions has implications for the development of targeted interventions in the management of Fusarium wilt through manipulation of the banana rhizosphere.

KEYWORDS
banana, chlamydospore, exudates, *Fusarium oxysporum* f. sp. *cubense*, rhizosphere, root

1 | INTRODUCTION

Banana (*Musa* spp.) is a giant perennial herb with a pantropical distribution (Heslop-Harrison & Schwarzacher, 2007). Bananas originated in South-east Asia following interspecific and intraspecific hybridization between two wild diploid species, *Musa acuminata* (AA) and *M. balbisiana* (BB). These two species contributed the A and B genomes, respectively, resulting in more than 1000 banana varieties comprising diploids (AA, AB, BB), triploids (AAA, AAB, ABB) and tetraploids (ABBB) (Heslop-Harrison & Schwarzacher, 2007). Most of the cultivated bananas are triploids, which include sweet dessert bananas such as Cavendish (AAA), Gros Michel (AAA), Apple (Silk AAB), Pome (AAB) and Pisang Awak (ABB), and cooking bananas such as Matooke bananas (*Musa* spp. genomic group AAA), plantains (AAB) and Bluggoe (ABB) (Heslop-Harrison & Schwarzacher, 2007).

Bananas are cultivated in more than 135 countries and on approximately 11 million ha. In 2020, the global banana production quantity reached 163 million tonnes, an increase from 154.4 million tonnes in 2015 (FAOSTAT, 2022). Commercial production is done on large-scale monoculture plantations, with considerable agricultural inputs such as inorganic fertilizers, pesticides and irrigation. In contrast, subsistence production is done on small plots (0.2–4 ha) in mixed-cultivar systems, or intercropped with other perennial and annual crops, and with minimal or even no inputs (Bellamy, 2013; Kimunye et al., 2020). Bananas play an important role in food security and provide income for over 400 million people globally. About 87% of bananas produced globally are consumed locally or sold in informal markets. Cavendish (AAA) cultivars such as Grande Naine, Williams and Valery constitute almost half of the bananas cultivated in the world and dominate banana exports (Heslop-Harrison & Schwarzacher, 2007).

Globally, bananas are threatened by Fusarium wilt disease caused by the notorious soilborne, root-infecting fungus, *Fusarium oxysporum* f. sp. *cubense* (Foc; Figure 1a) (Viljoen et al., 2020). Three physiological races of Foc are pathogenic to banana (Ploetz, 2015). The strain that caused significant losses of Gros Michel bananas in Latin America in the 20th century is Foc race 1, which is also pathogenic to other dessert bananas such as Apple (Silk AAB), Pome (AAB) and Pisang Awak (ABB) bananas. Foc race 2 affects Bluggoe (ABB) and other cooking bananas. Foc races 1 and 2 are not virulent to Cavendish bananas. Cavendish bananas are affected by Foc race 4, which can also cause disease to banana cultivars susceptible to Foc races 1 and 2 (Ploetz, 2015). Foc race 4 is subdivided into Foc "subtropical" race 4 (STR4) and "tropical" race 4 (TR4). Foc STR4 causes disease in Cavendish bananas in the subtropics due to predisposition to abiotic stresses such as low temperatures (Moore et al., 1993; Viljoen, 2002). However, unlike Foc STR4, Foc TR4 is virulent to Cavendish bananas under all environmental conditions (Ploetz, 2015). Like other *F. oxysporum* species, Foc produces three kinds of asexual spores: microconidia, macroconidia and chlamydospores (Figure 1b–e) (Leslie & Summerell, 2006). Chlamydospores serve as the source of primary Foc inoculum in soil, whereas micro- and macroconidia are responsible for colonization and multiplication of Foc in vascular tissues of the plant (Ploetz, 2015).

The process by which Foc infects banana roots occurs in the rhizosphere, a narrow zone of soil approximately 2 mm immediately adjacent to the roots, and is influenced by roots primarily through root exudates (Beckman, 1987; Li et al., 2011). Root exudates stimulate the germination of Foc chlamydospores, producing hyphae that infect host roots and subsequently colonize the plant vascular tissues, which results in water stress, severe leaf chlorosis and wilting of the plant (Beckman, 1987; Ploetz, 2015; Stover, 1962). Chlorosis and wilting progress from the older to younger leaves, after which the leaves droop at the petiole (Figure 1f) (Viljoen et al., 2020). Pseudostems of infected plants are sometimes characterized by longitudinal splits in the lower portion of the outer leaf sheaths (Figure 1g,h). When split open, the pseudostems reveal numerous yellow to dark red strands caused by infected xylem vessels (Viljoen et al., 2020). In the field, infected plants show symptoms as early as 3 months after planting but are most severely affected at the flowering stage (Viljoen et al., 2020). Depending on the phase and magnitude of infection, infected plants may die before producing fruit (Rishbeth & Naylor, 1957; Viljoen et al., 2020). As the plant dies, it decomposes releasing masses of chlamydospores into the soil. Chlamydospores remain quiescent in soils, thereby limiting the cultivation of susceptible banana varieties in Foc-infested soils for decades (Rishbeth & Naylor, 1957).

Losses associated with Fusarium wilt during the era of Gros Michel were estimated at $2 billion (Ploetz, 2015) while losses caused by Foc TR4 are very considerable. Annual economic losses due to Foc TR4 were estimated at $253 million in Taiwan (Aquino et al., 2013) and $121 million in Indonesia (Hermanto et al., 2009). In 2013, Foc TR4 was detected in Africa on a commercial banana plantation in Mozambique (Viljoen et al., 2020). The pathogen destroyed the commercial banana plantation, killing nearly a million plants at a rate of about 15,000 plants per week, which prompted measures to be instituted to curb the spread of Foc TR4 (Viljoen et al., 2020). In China, Li et al. (2013) reported a fourfold increase (40,000 hectares) in banana production area infested by Foc within a period of years from 2002. Scheerer et al. (2018) projected that by 2040, 17% of the current banana-growing area could be infested by Foc TR4. This could result in losses worth about $10 billion. Foc TR4 has continued to spread inexorably throughout the world's banana-growing regions (Drenth & Kema, 2021) causing very considerable damage and impact on banana production.

Banana varieties resistant to Foc are the most effective and efficient strategy to reduce the impact of Fusarium wilt (Viljoen et al., 2020; Zorrilla-Fontanesi et al., 2020). However, disease resistant hybrids are undermined by inferior fruit characteristics such as taste and postharvest properties (Viljoen et al., 2020). For instance, FHIA-01 (Goldfinger), FHIA-02 and FHIA-18 hybrids are resistant to Foc TR4, but not popular among consumers because they have a lower pulp-to-peel ratio and are not as sweet as Grand Naine or Williams (Dadzie, 1998; Smith et al., 2014). Similarly, variants of Giant Cavendish (GCTCVs) developed in Taiwan were shown to be partially resistant to Foc TR4 (Hwang & Ko, 2004), but have a longer cycle time than Cavendish cultivars. The majority of disease-resistant hybrids are produced through conventional breeding, which is a tedious and slow process that can take more than 15 years (Tenkouano et al., 2011).

Genetic engineering may provide multiple and durable resistance to plant pathogens (Collinge & Sarrocco, 2022). Genetic engineering has been shown to provide resistance to Foc in commercial banana cultivars without altering the desired fruit and agronomic traits (Dale et al., 2017; Paul et al., 2011). However, a key challenge facing genetically modified bananas is the concern of regulators and consumers regarding the possible adverse effects of transgenes on human health and/or the environment (Ishii & Araki, 2016). More recently, technologies such as gene-editing using the CRISPR/Cas9 system are profoundly revolutionizing the ability to precisely engineer the banana genome by introducing genetic modifications to

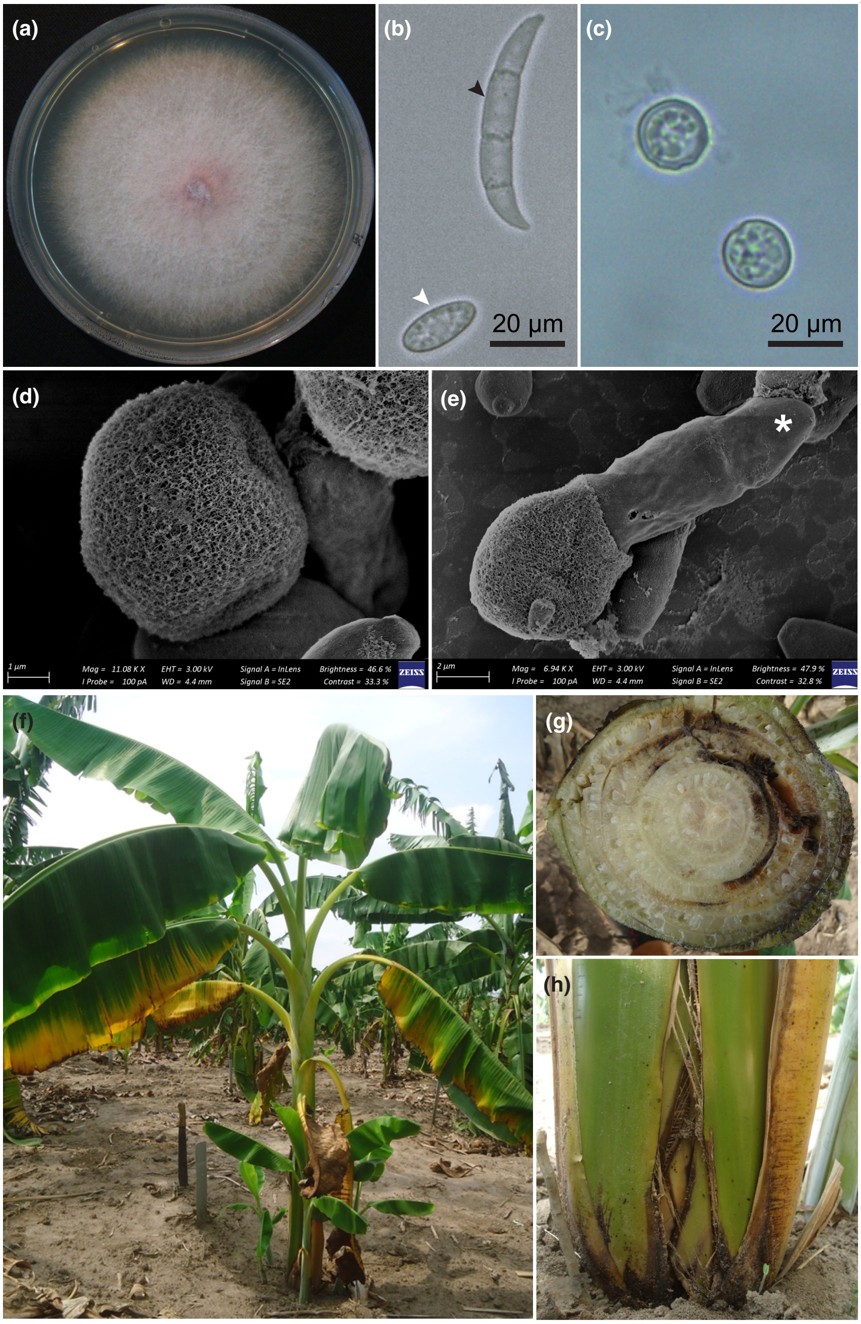

FIGURE 1 A colony of *Fusarium oxysporum* f. sp. *cubense* (Foc) growing on potato dextrose agar medium (a); bright-field microscopy micrographs of spore types produced by Foc: microconidium (white arrowhead) and macroconidium (black arrowhead) (b), and chlamydospores (c). Scanning electron microscopy micrographs of a dormant (d) and germinating (e) chlamydospore with a protruding germ tube (white asterisk). Typical symptoms of banana Fusarium wilt disease: wilting and drooping of leaves (f), and rotting and splitting of the pseudostem (g, h). [Colour figure can be viewed at wileyonlinelibrary.com]

favour a desired trait in a relatively short time (Tripathi et al., 2020). However, it remains uncertain if banana modified with gene-editing will be acceptable to consumers. Moreover, the current regulatory uncertainties may further impact research and development of genome-edited crops, which could interfere with international trade in commodity crops including banana (Conko et al., 2016).

Infection of host roots by Foc arises through complex interactions in the banana rhizosphere, including interactions with the microbiome, parasitic nematodes and soil physicochemical factors (Dita et al., 2018; Stover, 1962). Moreover, management of Fusarium wilt is particularly difficult because (a) Foc is a soilborne pathogen that can persist in infested soils for decades even in the absence of the host; (b) Foc can spread easily, for instance through contaminated soil, farm machinery, irrigation water or via infected planting material; and (c) Foc is a vascular pathogen that, once established within the plant vascular tissues, becomes inaccessible to control measures such as nonsystemic fungicides and non-endophytic biological control agents (BCAs) (Bubici et al., 2019; Dita et al., 2018; Rishbeth, 1955; Stover, 1962; Viljoen et al., 2020). Because of this, containment (exclusion and early quarantine) measures are the only effective strategy for the control of Fusarium wilt when disease-resistant varieties are not available (Dita et al., 2018; Viljoen et al., 2020). However, once the disease is established in a field, containment becomes impractical and management must focus

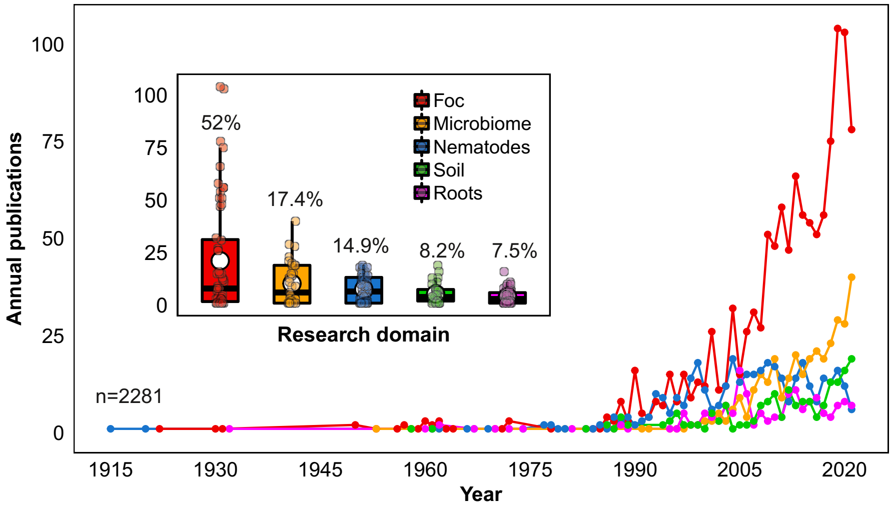

FIGURE 2 Temporal trend of publications on major research domains of banana rhizosphere and *Fusarium oxysporum* f. sp. *cubense*. Research articles retrieved from the databases AGRIS, CAB Direct, SciVerse Scopus and ProQuest published from 1915 to 2021. Boxplots (inset) show the upper and lower quartile, median (bold horizontal bar), mean (white circle) and whiskers (vertical lines). The points represent the cumulative number of articles for each research domain, and percentages, per year. [Colour figure can be viewed at wileyonlinelibrary.com]

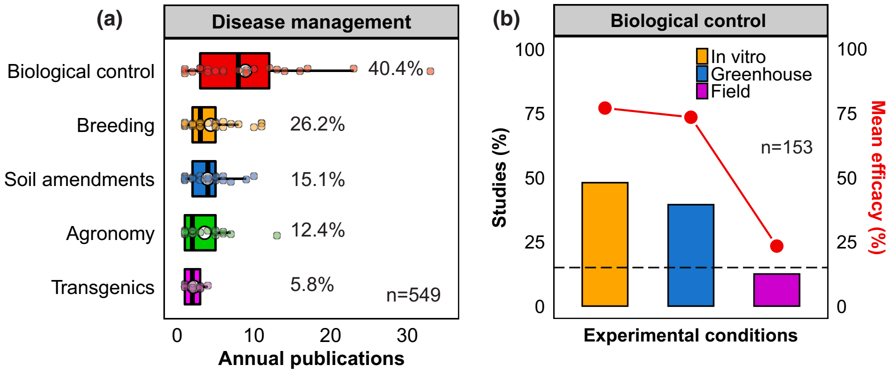

FIGURE 3 Publication on strategies for management of banana Fusarium wilt. (a) Boxplots show the upper and lower quartile, median (bold horizontal bar), mean (white circle) and whiskers (vertical lines). The points represent the cumulative number of articles for each category and percentages. (b) Studies on biological control of Fusarium wilt are conducted under in vitro laboratory conditions, greenhouse (or pot) trials and in the field, and exhibit varying efficacies. [Colour figure can be viewed at wileyonlinelibrary.com]

on integrating the available disease management strategies (Dita et al., 2018; Pattison et al., 2018).

Previous studies showed that manipulation of the banana rhizosphere can suppress Fusarium wilt (Fernández-Falcón et al., 2004; Nowembabazi et al., 2021; Peng et al., 1999). This includes alteration or supplementation of soil microbiota into the rhizosphere along with adjustment of soil physicochemical properties. For the former case, Fusarium wilt was suppressed by application of microbial inoculants such as strains of *Bacillus*, *Pseudomonas* and *Trichoderma* (Catambacan & Cumagun, 2021; Fu et al., 2016; Yadav et al., 2021). For the latter case, increasing the bioavailability of nutrients such as calcium, phosphorus and zinc, or decreasing iron bioavailability was shown to alleviate the impact of Fusarium wilt and to promote plant growth and vigour (Fernández-Falcón et al., 2004; Nowembabazi et al., 2021; Peng et al., 1999).

Integrating rhizosphere manipulation with existing disease management strategies could thus be suggested as an option to reduce the build-up of Foc inoculum in soil, prevent pathogen spread and alleviate the impact of Fusarium wilt on susceptible banana varieties. However, the prospect of rhizosphere manipulation has been compromised largely by inconsistent efficacy in the field (Orr et al., 2021; Thangavelu & Mustaffa 2010; Wibowo et al., 2013). This is attributed to several factors arising from interactions in the banana rhizosphere including interactions with the microbiome, parasitic nematodes and soil physicochemical factors (Belgrove et al., 2011; Orr & Nelson, 2018; Peng et al., 1999). The rhizosphere is intriguingly complex and dynamic (Sasse et al., 2018). As a result, ecological interactions in the banana rhizosphere in relation to Fusarium wilt remain poorly understood. Therefore, realizing the potential of rhizosphere manipulation for suppression of Fusarium wilt requires a comprehensive understanding of the versatile interactions and mechanisms in the banana rhizosphere.

The objective of this review is to bring together the relatively scant data available to date on the subject of banana below-ground interactions in relation to Fusarium wilt and to highlight the key research gaps. Specifically, we sought to understand (a) the biology of Foc and its interaction with banana; (b) the ecology of Foc, including the role of root-exuded metabolites in rhizosphere interactions; and (c) soil management practices and how they modulate Fusarium wilt. First, we summarize the scope of research on the banana rhizosphere by showing the key research domains. Then, we describe abiotic and biotic interactions and how they potentially influence Fusarium wilt. In so doing, we illustrate how the known mechanisms involved in these interactions can yield distinct effects on Fusarium wilt. Details related to the epidemiology of Fusarium wilt and pathogen genomics are covered to a lesser extent in this review because these have been thoroughly reviewed elsewhere (Dita et al., 2018; Pegg et al., 2019; Viljoen et al., 2020).

2 | LITERATURE SEARCH AND ARTICLE SELECTION

A literature search was conducted in four electronic databases: AGRIS, CAB Direct, SciVerse Scopus and ProQuest, which represent the main comprehensive databases for research in agricultural and life sciences. Databases were searched from their first entries up to 15 November 2021. The search strategy consisted of compiling four search strings, one for each category (banana, Foc, Fusarium, rhizosphere), while combining these with the Boolean operator "AND" to obtain only the intersection. Due to limited resources for translation, publications in languages other than English were excluded. Duplicates were identified using queries targeting identical digital object identifiers, titles, authors or first 50 characters of the abstract. Articles without an abstract or articles clearly indexed either as review, editorial or errata were excluded. Frequencies and percentages were used to summarize the nominal data.

A total of 3409 titles and abstracts were retrieved from the databases, of which 2281 studies on the banana rhizosphere were eligible for data extraction. Through synthesis of the data, four general research domains were identified: (a) studies on Foc (n = 1186); (b) studies on nematodes (n = 396); (c) studies on the microbiome (n = 341); (d) studies on soil physicochemical properties (n = 187); and (e) studies on banana roots (n = 171). Publications on Foc mainly focused on pathogen biology, host–pathogen interactions and disease management and showed a continuous increase over time (Figure 2). This could be attributed to the increased importance of Foc and the increased digitalization of information. Management of Fusarium wilt is a dominant element of banana rhizosphere research (Figure 3a). Biological control dominates the strategies for management of Fusarium wilt with 222 (40.4%) publications. This was followed by studies on breeding or screening bananas for resistance to Foc with 144 publications (26.2%). Studies on soil amendments, agronomic practices and genetic modification accounted for 83 (15.1%), 68 (12.4%) and 32 (5.8%) of the publications, respectively (Figure 3a). Nearly half (48.0%) of the studies on biological control have been conducted under in vitro laboratory conditions, while 39.5% were pot (greenhouse) trials, and less 15% were field studies (Figure 3b). Generally, BCA strains were highly effective in vitro and in the greenhouse, with a mean efficacy of 77.1% and 73.5%, respectively, whereas efficacy was less than 25.0% in the field (Figure 3b). In the field, the majority of studies reported only a delay in the development of disease symptoms and plants still succumbed to Fusarium wilt.

3 | INTERACTIONS IN THE BANANA RHIZOSPHERE

3.1 | The rhizosphere

The characteristics of the rhizosphere, a narrow volume of soil surrounding plant roots, may be drastically different from those of the bulk soil (i.e., soil without roots). Generally, the rhizosphere consists of three distinct regions: the rhizosphere per se (the soil closely adhered to the root), the rhizoplane (root surface) and the root (Sasse et al., 2018). The banana plant consists of a subterranean corm from which new suckers and more than 500 adventitious main roots (cord roots) emerge and branch to form numerous smaller secondary and tertiary lateral roots (Blomme, 2000). Cord roots originate from the corm in groups of about four and can grow up to a length of about 5 m. Cord roots are 4–10 mm in diameter, relatively straight and cylindrical, and possess a prominent root cap of up to 10 mm thick at the root tip (Blomme, 2000; Lecompte et al., 2002). Cord roots possess root hairs that occur 4–6 cm behind the root tip and can grow over 2 mm long. Secondary and tertiary lateral roots are the most active portion of the banana root system (Blomme, 2000; Lecompte et al., 2002). Functionally, the banana root system is important for anchorage, acquisition of nutrients and water, and for the synthesis and storage of some plant hormones (Blomme, 2000; Lecompte et al., 2002).

Generally, the cytoarchitecture of banana cord roots and lateral roots is similar and consists of concentric cell layers (Figure 4). The outermost epidermis/rhizodermis is followed by the cortex, endodermis, pericycle and the central cylinder (stele), which contains phloem and xylem vascular tissues (Lecompte et al., 2002). Because of this internal structure, it can be anticipated that root cell layers respond to infection by Foc or nonpathogenic soil microorganisms and symbionts in a transcriptionally distinctive manner. Yet, the functional significance of the banana root cytoarchitecture remains elusive and little is known about the biochemical and structural contribution of particular cell layers in the establishment of pathogenic, nonpathogenic and beneficial interactions with microorganisms in the banana rhizosphere.

Plant roots influence the rhizosphere primarily through root exudates and rhizodeposits, which can attract or deter soil microorganisms (Sasse et al., 2018). Rhizodeposits include volatile compounds, sloughed root cap cells and debris (Sasse et al., 2018). On the other hand, root exudates include an assortment of primary and secondary metabolites of both low (<1 kDa) and high (>1 kDa) molecular weight (Badri & Vivanco, 2009). Root exudation and rhizodeposition in banana with regard to Fusarium wilt remain largely unexplored. Moreover, assessment of the mechanisms and effective concentration of root-secreted metabolites in the banana rhizosphere under field conditions presents a substantial challenge.

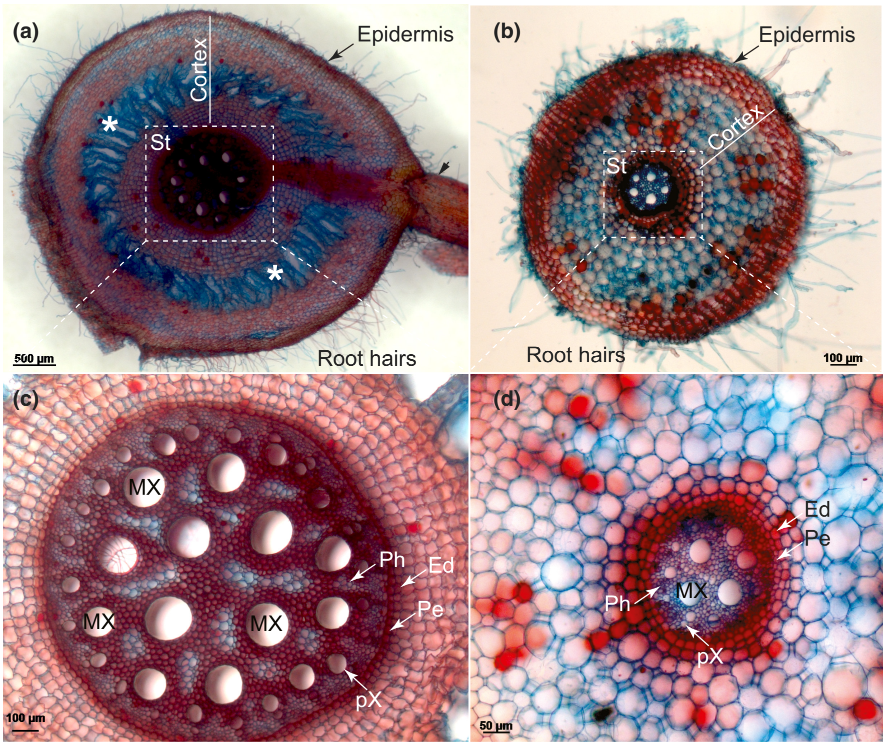

FIGURE 4 Bright-field microscopy micrographs showing the structural organization of a primary root (about 7 cm from the root tip) and a secondary root of Cavendish banana cultivar Grande Naine stained with Safranin O and Alcian blue 8GX. Lignified tissues are stained in red while celluloses are stained in blue. Transverse section of a primary root (a) with an emerging secondary root (black arrowhead; b). Transverse sections of a primary (c) and secondary (d) root focusing only on the root stele. The root layers are marked: epidermis; cortex; Ed, endodermis; Pe, pericycle; St, stele. Aerenchyma is marked by asterisks. MX, metaxylem; pX, peripheric xylem vessel; Ph, phloem cells. [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Interactions of Foc and host roots

Infection of banana roots by Foc occurs in two phases: a primary determinative phase and a secondary determinative phase (Beckman, 1987). The primary determinative phase occurs in the rhizosphere and entails germination of Foc chlamydospores, hyphal growth, penetration of host roots and colonization of the root cortex and endodermis. These events are followed by the secondary determinative phase in which the fungus colonizes and establishes in the vascular bundles leading to disease (Beckman, 1987). While the secondary determinative phase has been extensively studied, little is known about the primary determinative phase. The source of primary Foc inoculum is hardy thick-walled asexual spores called chlamydospores, which can remain quiescent in soil for decades (Rishbeth, 1955). Generally, the thick wall surrounding a chlamydospore is tacitly agreed upon to confer resistance to adverse conditions that are often encountered in the soil. Foc can also survive in soil by saprophytic colonization of plant debris, or by commensal colonization of nonhost plants without apparent disease symptoms (Hennessy et al., 2005; Pittaway et al., 1999). Generally, the factors that contribute to the formation, quiescence and persistence of chlamydospores in soil remain elusive.

When suitable conditions are encountered, chlamydospores in soil undergo a revival cellular process called germination (Figure 1d,e) and produce hyphae that infect host roots (Ploetz, 2015; Rishbeth, 1955). Chlamydospore germination is a crucial step in the life cycle of Foc, yet this process remains largely uncharacterized. Moreover, most of the studies on spore germination in Foc have been conducted using conidia (Deng et al., 2015; Li et al., 2011), which may not be appropriate substitutes for chlamydospores. Previous studies suggest that chlamydospore germination is stimulated by metabolites related to amino acids or sugars in root exudates of banana (Buxton, 1962; Li et al., 2011) or when in contact with pieces of fresh uncolonized plant residue (Stover, 1962). However, a direct underpinning of root exudate metabolites that can stimulate chlamydospore germination is still lacking. In the study of Buxton (1962), root exudates of the susceptible banana cultivar Gros Michel did not inhibit spore germination, whereas root exudates of the resistant cultivar Lacatan had an inhibitory effect, which diminished with the age of the plant. Further analysis revealed a higher composition of sugars in root exudates of Gros Michel than Lacatan. Moreover, only 13 of the 18 amino acids identified were common in root exudates of both cultivars. Buxton (1962) therefore suggested that the differences in root exudate metabolites may contribute to host resistance against Foc race 1 in the rhizosphere through their effects on chlamydospore germination.

After germination, hyphae grow and colonize the rhizoplane prior to infection of roots (Li et al., 2017). This is followed by the secondary determinative phase in which hyphae penetrate host roots and subsequently establish in the vascular bundles (Beckman, 1987; Stover, 1962). Penetration of roots occurs mostly directly through the tips (cap region) of lateral roots at distances of about 5–15 cm from the corm (Li et al., 2017; Pegg et al., 2019; Rishbeth, 1955; Wardlaw, 1961). Infection rarely occurs through cord roots, and the radial spread of the pathogen by direct root-to-root contact is unlikely (Rishbeth, 1955). Upon infection, roots undergo extensive transcriptome reprogramming (Bai et al., 2013). In particular, transcripts of genes associated with defence such as cell wall lignification are highly and more rapidly expressed in roots of tolerant/resistant plants compared to susceptible plants (Bai et al., 2013). Invasion of host tissues is facilitated by a repertoire of carbohydrate-active enzymes, which degrade the host cell wall (Qin et al., 2017).

Inside host roots, hyphae colonize the cortex and endodermis, and invade the xylem vessels of lateral roots through pits. The root xylem acts as a barrier that mounts defence responses to intercept pathogen ingress (Rishbeth & Naylor, 1957). Other host defence responses include the production of antifungal compounds, suberization and lignification of the plant cell wall, production of gels and tyloses, and the accumulation of gums (Beckman, 1987; Mace & Wilson, 1964; Rishbeth & Naylor, 1957). Paratracheal cells (parenchyma cells surrounding the xylem vessels) as well as the surrounding tissue exude gums containing mostly polysaccharides and phenolic metabolites (Mace, 1963; Mace & Wilson, 1964). Phenolic metabolites may possess limited toxicity, but their oxidation products are both toxic and denaturants of fungal enzymes (Beckman, 2000). Successful colonization of roots is followed by colonization of the corm, which marks a key stage in pathogen establishment (Beckman, 1987; Stover, 1962). Foc penetrates the stele and invades the xylem vessels. Mycelia remain within xylem vessels and produce conspicuous masses of microconidia, which germinate and produce more hyphae that further colonize the plant, spreading within the cell apoplast and causing profound cytological distortions (Beckman, 1987). Consequently, the pathogen's mycelium and conidia, as well as the gels and gums produced by the plant in response to infection, clog the host's xylem vessels. The activated host resistance responses lead to crushing of xylem vessels by the proliferating adjacent parenchyma cells via callose deposition (Beckman, 1987). Ultimately, this results in the blockage of water and nutrient transport, leading to plant wilting and death (Li et al., 2017). Wilting is further exacerbated by fusaric acid, a toxin produced by Foc (Liu et al., 2020).

3.3 | Interactions with the rhizosphere microbiome

Communities of plant-associated microorganisms such as bacteria, fungi, archaea and protists constitute the plant microbiome (Compant et al., 2019). The plant and its microbiome function together physically and have intertwined metabolism such that they are together termed the holobiont (Compant et al., 2019). Plants rely on the rhizosphere microbiome to facilitate nutrient acquisition, in exchange for carbon-rich root exudates for nutrition (Compant et al., 2019; Sasse et al., 2018). Furthermore, interactions between beneficial microorganisms and plant roots can result in systemic host resistance to pathogens, due to activation of induced systemic resistance (Bakker et al., 2013). As a result, there is growing interest to elucidate how banana-associated microbial communities impact Fusarium wilt. However, a large proportion of bacteria and fungi associated with banana remain unidentified and their functional potential unknown (Kaushal, Swennen, et al., 2020a; Köberl et al., 2015). Traditional culture-dependent approaches and advanced culture-independent approaches, such as next-generation sequencing and DNA metabarcoding (Table 1), have been used to profile microbial assemblages associated with banana under different management practices (Kaushal, Swennen, et al., 2020a; Köberl et al., 2015; Yuan, Hong, et al., 2021a; Yuan, Wang, et al., 2021b).

Soil management practices, such as the application of organic amendments, intercropping or crop rotation, have been shown to modulate the structure and composition of banana-associated microbial communities (Yuan, Hong, et al., 2021a; Yuan, Wang, et al., 2021b) that can be harnessed for effective disease suppression (Tables 2 and 3). Generally, bulk soil harbours diverse bacterial and fungal communities, which progressively decline in the rhizosphere and roots of the banana plant, suggesting that bulk soil serves as the pool of microbial communities (Kaushal, Mahuku, et al., 2020b). Nevertheless, the majority of the bacterial and fungal communities present in bulk soil have also been frequently found in the rhizosphere, and as endophytes inside the roots and corm of the banana plant (Kaushal, Swennen, et al., 2020a; Köberl et al., 2015).

Kaushal, Swennen, et al. (2020a) reported that the rhizosphere, roots and corm of Sukari Ndizi (AAB) with symptoms of Fusarium wilt exhibited lower bacterial and fungal diversity compared to symptomless plants. It was suggested that the impact of disease stress on banana plants may have altered the quality and/or quantity of available root exudates in the rhizosphere (Kaushal, Swennen, et al., 2020a). In support of this, Yuan et al. (2018) reported that Cavendish banana challenged with Foc exhibited enhanced exudation of phenolics such as phthalic acid, salicylic acid (SA) and cinnamic acid. The phenolics stimulated the expression of genes associated with antibiotic production and biofilm formation in the biocontrol bacterium *Bacillus amyloliquefaciens* NJN-6 (Yuan et al., 2018). Organic acids and plant hormones are key components of root exudates known to stimulate chemotaxis, a phenomenon in which cell movement is directed in response to an extracellular chemical gradient (Li et al., 2012). Fumaric acid in root exudates of banana stimulated biofilm formation and colonization of banana roots by the plant growth-promoting bacterium *Bacillus subtilis* N11 (Zhang et al., 2014). Similarly, in chemotaxis in vitro assays, bacterial species from the genera *Bacillus*, *Brevibacillus*, *Paenibacillus*, *Providencia* and *Pseudomonas*, isolated from the banana rhizosphere, were attracted by SA (Li et al., 2012). Chemotaxis is an essential component of bacterial aggregation and biofilm formation, which are crucial for establishing and maintaining intimate spatial association with the plant, thereby improving plant growth and health (Li et al., 2012). Moreover, biofilm formation in bacterial BCAs may provide protection from predation and fluctuating environmental conditions (Li et al., 2012).

In Cavendish banana, inoculation with an incompatible Foc race 1 showed enhanced resistance to a compatible Foc TR4, when subsequently inoculated in the roots (Wu et al., 2013). The enhanced resistance to Foc TR4 was associated with elevated levels of SA and expression of *PR-1* and several other defence-related genes in roots compared to the roots of plants not pre-inoculated with Foc race 1 (Wu et al., 2013). However, how these host defences may affect the banana rhizosphere microbiome is largely unknown. Studies in the model plant *Arabidopsis thaliana* have demonstrated that the fungal endophyte *Trichoderma* T-78 colonized an SA-impaired mutant faster

TABLE 1 Summary and study methods for articles assessing banana-associated microbiome

Reference	Banana cultivar	Study description and target microbial communities	Microbiome characterization approach		Most relevant remarks/key findings
			Culture-dependent[a]	Culture-independent[b]	
Rossmann et al. (2012)	Diverse cultivars, including East African Highland bananas (AAA)	Field study on smallholder farms with varying management; community structure and function of bacteria and fungi in bulk soil, rhizosphere and pseudostem microhabitats	SNA, PDA, MacConkey, TSM, King's B media	PCR-SSCP fingerprinting of bacterial 16S rRNA and fungal ITS genes; pyrosequencing of bacterial 16S rRNA gene; qPCR quantification of *Enterobacteriaceae* targeting 16S rRNA gene; ARDRA; FISH-CLSM	Microhabitat-specific microbial communities were noted across sites and management practices; antagonistic bacteria enriched in plant tissues whereas fungi were predominant in soil; the pseudostem contained abundant and diverse bacteria genera of *Enterobacteriaceae*
Kaushal, Swennen, et al. (2020a)	Sukari Ndizi (AAB)	Field study on smallholder farms with varying management; community structure, diversity and assemblage of bacteria and fungi in the rhizosphere, roots and corms of plants with and without symptoms	–	Illumina MiSeq sequencing of V3-V4 region of bacterial 16S rRNA gene and fungal ITS2	High bacterial and fungal diversity and richness noted in the rhizosphere, decreasing in root and corm; bacteria and fungi in roots and corm primarily originate from the rhizosphere; disease status was a key driver of fungal community composition
Kaushal, Mahuku, et al. (2020b)	Mchare (AA), Sukari Ndizi (AAB)	Root endophytic bacteria of plants with and without symptoms	–	Illumina MiSeq sequencing of V3-V4 region of bacterial 16S rRNA gene	*Proteobacteria*, *Bacteroidetes*, and to a lesser extent *Actinobacteria*, dominated root endophytic bacteria; root endophytic bacteria were greatly impacted by disease
Deltour et al. (2017)	Maçã (AAB)	Field sites under agroforestry management and mixed cultivars; culturable and nonculturable bacterial communities of bulk soil	LB agar, Komada media	DGGE analysis of V3 region of bacterial 16S rRNA gene amplicons; sequencing of V3 region of bacterial 16S rRNA gene	Soil suppressiveness could not be linked to culturable bacterial communities; soil suppressiveness was linked to clay content, pH, cultivar diversity, and negatively correlated with silt, sand, the density of cv. Maçã and soil cover by graminoids
Shen et al. (2014)	Cavendish cv. Brazil (AAA)	Field sites with organic amendments including bio-organic fertilizer (BIO); bacterial communities of bulk soil	–	Pyrosequencing of V1-V3 region of 16S bacterial rRNA gene	Disease suppression after BIO application linked to a shift within soil bacterial community (e.g., specific enrichment of genera *Gemmatimonas* and *Sphingomonas*)
Zhou et al. (2019)	Cavendish cv. Brazil (AAA)	Field study; bacterial and fungal communities of diseased and disease-free plants	Komada medium	Illumina MiSeq sequencing of V3-V4 region of bacterial 16S rRNA gene and fungal ITS1	Abundance of bacteria genera *Bacillus*, *Lactococcus* and *Pseudomonas* in disease-free soils was twice that of diseased soils; fungal genus *Mortierella* was the most abundant (34.6%) in disease-free soils, compared to 15.4% in diseased soils

TABLE 1 (Continued)

Reference	Banana cultivar	Study description and target microbial communities	Microbiome characterization approach		Most relevant remarks/key findings
			Culture-dependent[a]	Culture-independent[b]	
Fu et al. (2016)	Cavendish cv. Brazil (AAA)	Field study with continuous application of bio-organic fertilizer (BIO); rhizosphere culturable bacterial communities	R2A agar; Biolog EcoPlate (for community-level physiological profiling based on the carbon source utilization)	DGGE analysis of V3 region of bacterial 16S rRNA gene amplicon	BIO application reduced disease incidence by stabilizing metabolic potential and community structure of culturable bacteria genera (e.g., *Bacillus* and *Pseudomonas*)
Sudarma and Suprapta (2011)	–	Culturable actinomycetes, bacteria, fungi and Foc antagonists in bulk soil of diseased and disease-free fields	PDA, NA, Kenknight media	–	Actinomycete genera (e.g., *Actinomyces* and *Streptomyces*), bacteria genera (e.g., *Bacillus* and *Pseudomonas*) and fungal genera (e.g., *Trichoderma*, *Aspergillus*, *Penicillium*) were abundant in soils of disease-free compared to diseased fields
Huang et al. (2015)	–	In vitro study; changes in *F. oxysporum*, bacterial and fungal communities of bulk soil after reductive soil disinfestation (RSD)	–	Illumina MiSeq sequencing of the V4 hypervariable region of bacterial 16S rRNA gene and fungal ITS1; qPCR quantifation of total bacteria, fungi, and Foc; DGGE analysis of bacterial 16S rRNA gene and fungal ITS amplicons	Bacterial genera (e.g., *Ruminococcus*, *Coprococcus*), and to a lesser extent *Clostridium* were dominant and increased while *F. oxysporum* decreased during RSD; after RSD, fungal genera (e.g., *Podospora* and *Zopfiella*) increased but *Fusarium* decreased further
Fu et al. (2017)	Cavendish cv. Brazil (AAA)	Field study; temporal effects of bio-organic fertilizer (BIO) and compost application on composition and abundance of rhizosphere bacterial and fungal communities	–	Pyrosequencing of V4-V5 region of bacterial 16S rRNA gene and fungal ITS; qPCR quantification of total bacteria, fungi, Foc, and biocontrol agent NJN-6 (*Bacillus amyloliquefaciens*) in BIO	BIO amendment increased abundance of bacteria, but decreased abundance of fungi and *F. oxysporum*; BIO amendment enriched bacterial genera (e.g., *Sphingobium*, *Gp6*, *Gp4*, *Lysobacter*, *Sphingopyxis* and *Dyadobacter*), but depleted *Gp1*, *Ralstonia*, *Burkholderia* and *Mucilaginibacter*

(Continues)

TABLE 1 (Continued)

Reference	Banana cultivar	Study description and target microbial communities	Microbiome characterization approach: Culture-dependent[a]	Microbiome characterization approach: Culture-independent[b]	Most relevant remarks/key findings
Köberl et al. (2015, 2017)	Gros Michel (AAA)	Field study of impact of biogeography and agroforestry on gammaproteobacterial microbiome in the rhizosphere, roots, pseudostem and leaves of healthy plants and plants with symptoms	–	Illumina MiSeq sequencing of hypervariable V4 region of bacterial 16S rRNA gene	Diversity and community members gammaproteobacterial identified as potential indicators of healthy banana plants; bacterial genera (e.g., *Pseudomonas* and *Stenotrophomonas*) increased in healthy plants; *Enterobacteriaceae* preferentially increased in diseased plants
Shen et al. (2018)	Cavendish cv. Brazil (AAA)	Field study on sites under varying lengths of banana monoculture; bacterial and fungal communities of bulk soil	–	Illumina MiSeq sequencing of the V4 region of bacterial 16S rRNA gene and fungal ITS1	Monocropping increased Foc accumulation; disease incidence and high fungal richness were significantly correlated with successive cropping; fungal genus *Mortierella* dominated soil fungal communities
Effendi et al. (2019)	–	Field study; bacterial communities from rhizosphere of Foc-infected and uninfected banana plants	–	Illumina MiSeq sequencing of the V4 region of bacterial 16S rRNA gene	Bacteria phyla *Acidobacteria* and *Verrucomicrobia* were associated with healthy rhizosphere soil
Fu et al. (2019)	Cavendish (AAA)	Field study; bacterial and fungal communities of rhizosphere of healthy and diseased plants	–	Illumina MiSeq sequencing of the V4 region of bacterial 16S rRNA gene and fungal ITS1 region; qPCR quantification of bacteria and fungi	Bacterial and fungal diversity was not different between the rhizosphere of healthy and diseased plants; diversity of microbial communities markedly more stable in rhizosphere of healthy plants than diseased plants
Sun et al. (2013)	Foc-susceptible cultivar Baxi and tolerant cultivar Fj01	Field study; rhizosphere bacterial communities and activities of soil phosphatase and urease	Biochemical analysis of soil enzymes (phosphatase and urease)	T-RFLP and qPCR analysis of bacterial 16S rRNA gene	Higher bacterial diversity, abundance and urease activity noted in the rhizosphere of Fj01 compared to Baxi
Cabanás et al. (2021)	Dwarf Cavendish (AAA)	Field and pot studies; endophytic bacterial and fungal communities from roots of mother plants and suckers; Foc antagonists	NA, PDA media	Illumina MiSeq sequencing of V3-V4 region of bacterial 16S rRNA gene and fungal ITS2 region	Relative abundance of bacterial genus *Pseudomonas* was higher (but not significant) in suckers than in mother plants; *Rhizobium*, *Streptomyces* and *Actinophytocola* were higher (but not significant) in mother plants than suckers
Xia et al. (2011)	–	Epiphytic and endophytic *Trichoderma* associated with banana roots	TSM and its modified form	AFLP analysis of ITS and translation elongation factor (*tef1*)	*T. asperellum*, *T. virens*, *T. koningiopsis*, *H. lixii*, *T. atroviride* were identified as key epiphytes; *T. asperellum*, *T. virens*, *T. brevicompactum*, *H. lixii* were identified as key endophytes; *T. asperellum*, *H. lixii*, *T. virens* were found in both niches

TABLE 1 (Continued)

Reference	Banana cultivar	Study description and target microbial communities	Microbiome characterization approach		Most relevant remarks/key findings
			Culture-dependent[a]	Culture-independent[b]	
Shen, Ruan, Chao, et al. (2015a)	Cavendish cv. Brazil (AAA)	Field study; bacterial communities as an indicator of Fusarium wilt-suppressive soils in orchards with differing disease incidences	–	Pyrosequencing of V4-V5 region of bacterial 16S rRNA gene	Bacteria genera exhibited significant difference among orchards; bacteria genera (e.g., *Chthonomonas*, *Pseudomonas* and *Tumebacillus*) were significantly enriched in suppressive soils, whereas *Gp2* was significantly reduced; enrichment of *Gp5* and *Pseudomonas* together with soil available phosphorus were significantly correlated with disease suppression
Rames et al. (2018)	Ducasse banana (syn. Pisang Awak, ABB)	Field study; changes in the soil microbiome in banana under ground cover management compared to bare soil	Soil biochemical analysis (β-glucosidase activity, fluorescein diacetate hydrolysis, labile C)	T-RFLP and qPCR analysis of bacterial 16S rRNA gene	Disease suppression tended to increase over time under ground covers compared to bare soil; fungal richness was correlated with disease suppression and activity of β-glucosidase in soils under ground covers
Shen, Ruan, Xue, et al. (2015b)	Cavendish cv. Brazil (AAA)	Field study; response of rhizosphere microbial community soil application of bio-organic fertilizer (BIO), compost and chemical fertilizer over time	–	Pyrosequencing of V4-V5 region of bacterial 16S rRNA gene and fungal ITS region	BIO application induced disease suppression via manipulation of microbial community composition; *Acidobacteria* (*Gp1* and *Gp3*) were significantly enriched whereas abundance of *Rhizobium* and *Fusarium* decreased
Thangavelu and Jayanthi (2009)	Variety of commercial cultivars and wild bananas	Field sampling and pot study; nonpathogenic *Fusarium oxysporum* (np*Fo*) isolates from banana rhizosphere	Komada, PDA media	RFLP analysis of the fungal ITS region	In a pot trial, np*Fo* isolates promoted plant growth and reduced severity of Fusarium wilt by up to 89.4% (in tissue culture plants) and 77.8% (in sucker-derived plants) compared to controls; in the field, np*Fo* isolates (Ra-1 and Ro-3) reduced disease by up to 84% compared to controls

(Continues)

TABLE 1 (Continued)

Reference	Banana cultivar	Study description and target microbial communities	Microbiome characterization approach		Most relevant remarks/key findings
			Culture-dependent[a]	Culture-independent[b]	
Chou et al. (2017)	Cavendish (AAA)	Field sampling; functional diversity and dominant populations of bacteria in bulk soils of long-term organic and conventional farms	TSA, NFA, TPA, SMA media; community-level physiological profiling using Biolog EcoPlate	16S rRNA sequencing	Diversity and dominant soil bacterial population (β-*proteobacteria*, *acidobacteria* and α-*proteobacteria*) was significantly higher in organic than conventional farms
Sánchez-Zúñiga et al. (2021)	Gros Michel (AAA)	Field study; farms under different management (organic, organic intermediate conventional, abandoned)	Community-level physiological profiling using Biolog EcoPlate	Sanger sequencing of species-specific amplicons	Farm under conventional management had the greatest presence of beneficial indicator microorganisms

[a] Culture media: PDA, potato dextrose agar; SNA, synthetic nutrient agar; TSM, *Trichoderma*-selective medium; LB, Luria-Bertani medium; TSA, tryptic soy agar; NFA, nitrogen-free agar; TPA, tricalcium phosphate agar; SMA, skimmed milk agar; R2A, Reasoner's 2A medium; NA, nutrient agar.

[b] Molecular techniques: AFLP, amplified fragment length polymorphism; ARDRA, amplified rDNA restriction analysis; DGGE, denaturing gradient gel electrophoresis; FISH-CLSM, fluorescence in situ hybridization coupled with confocal laser scanning microscopy; qPCR, quantitative polymerase chain reaction; SSCP, single-stranded conformational polymorphism; T-RFLP: terminal restriction fragment length polymorphism. Marker genes: conserved genes (commonly 16S ribosomal RNA [rRNA], internal transcribed spacer [ITS] and 18S rRNA) that typically contain a highly variable region that can be used for detailed identification. The variable region is flanked by highly conserved regions that can serve as binding sites for the PCR primers.

TABLE 2 Soil nutrient management practices, their effect on Fusarium wilt disease of banana, and proposed mechanisms

Soil parameter	Effect on disease	Proposed mechanisms	References
Iron (Fe)	High Fe bioavailability increases disease severity	Fe promotes chlamydospore germination leading to root infection	Domínguez et al. (2001), Peng et al. (1999)
Soil pH	Low (acidic) pH increases disease severity. High (neutral or slightly alkaline) pH decreases disease severity	pH influences nutrient bioavailability (e.g., Fe) in the rhizosphere by altering the cation exchange capacity of the soil	Segura-Mena et al. (2021), Stover (1962)
		pH profoundly influences metabolic activity of rhizosphere microorganisms	Komada (1975), Peng et al. (1999)
		Low pH (pH 3.8–4.0) is ideal for in vitro culture of Foc from soils and may stimulate chlamydospore germination. Low pH increases bioavailability of micronutrients (e.g., Fe) and Mg, which are known to influence host susceptibility to Fusarium wilt	
Potassium (K)	High K decreases disease severity	K is essential for strengthening plant cells, thereby limiting Foc infection and ingress; K is essential for expression of host defence-related proteins	Navajothy et al. (2011), Nowembabazi et al. (2021)
Nitrogen (N)	Nitrate (NO_3^-) fertilizers decrease disease severity	NO_3^- enhances host resistance by increasing lignification of plant tissues; improves absorption of other nutrients required for host resistance thereby maintaining a higher photosynthetic rate	Delvaux et al. (2005), Epp (1987), Nasir et al. (2003)
	Ammonium (NH_4^+) fertilizers increase disease severity	Selective absorption of NH_4^+ over NO_3^- coupled with a high demand and uptake of K results in acidification of the rhizosphere due to extrusion of protons from banana roots	
Phosphorus (P)	High P is associated with disease suppression	P is important for root development	Shen, Ruan, Xue, et al. (2015b)
Magnesium (Mg)	High Mg reduces disease severity	Mg is a cofactor for enzymes in many cellular process in the plant including photosynthesis	Hu et al. (2021), Wu et al. (2020)
Zinc (Zn)	Zn deficiency is associated with high disease severity	Zn supposedly improves formation of tyloses in the xylem th occlude Foc and limit pathogen ingress	Borges-Pérez et al. (1991), Fernández-Falcón et al. 2004), Hecht-Buchholz et al. (1998)
Silicon (Si)	Si application reduces disease severity	Si stimulates defence responses of the phenylpropanoid pathway (e.g., lignin, phenylalanine ammonia-lyase, polyphenoloxidase, peroxidase, β-1,3-glucanase and chitinase)	Fortunato et al. (2012, 2014)
Calcium (Ca)	Ca application reduces disease severity; high Ca increases susceptibility	Ca is involved in cellular signalling processes that are essential for defence plant response; Ca is an important component of plant cell walls	Peng et al. (1999)

than the wild type (Martínez-Medina et al., 2017). Similarly, involvement of jasmonic acid signalling in the assembly of the rhizosphere microbiome was reported in jasmonic acid-defective *A. thaliana* mutants (Carvalhais et al., 2015).

Microbiome interactions typically occur via complex networks consisting of a plethora of interdependent individuals that interact in a mutualistic, synergistic or parasitic mode. Ou et al. (2019) highlighted the importance of constructing microbial networks in the soil to manage banana Fusarium wilt. Microbial network analysis can be highly instrumental to zoom into specific microbial consortia such as communities of beneficial microorganisms. However, in-depth insight in plant metabolites and traits that shape and sustain the rhizosphere microbiome, which in turn contribute to defence, could emerge through carefully designed experiments in which metagenomics, metatranscriptomics and root metabolomics approaches are integrated (Hultman et al., 2015). Given the decreasing cost of metagenome sequencing, adoption of high-throughput sequencing and network analysis may reveal the role of microbiome variability across field sites and banana genotypes. Metagenome-wide association studies, coupled with machine-learning predictions of both bulk soil and the rhizosphere, could enable the prediction of plant productivity at different field sites based on site-specific microbiome data (Yuan et al., 2020). This information could inform plant pathologists and banana breeders to make well-informed choices regarding field sites for variety testing, selection and performance in soils infested with Foc. Thus, in future, analysis of interactions involving genotype × environment × microbiome will probably emerge.

TABLE 3 Common plant species reported to suppress Fusarium wilt disease of banana and the proposed mechanisms of suppression

Plant species	Banana cropping system	Effect on Fusarium wilt	Proposed mechanism	Reference
Cassava (*Manihot esculenta*)	Rotation/intercrop	Reduced disease incidence	Lowering of Foc inoculum in soil	Buddenhagen (2009)
Chinese leek (*Allium tuberosum*)	Intercrop/rotation	Suppressed Fusarium wilt	Antifungal organic volatiles (e.g., 2-methyl-2-pentenal) and organosulphur compounds (e.g., dimethyl trisulfide) in root exudates inhibit chlamydospore germination and mycelial growth	Li et al. (2020), Zhang et al. (2013)
			Antifungal metabolites in root exudates suppress Foc through induction of reactive oxygen species; decreasing mitochondrial transmembrane potential; decreasing ergosterol biosynthesis; induction of autophagy	Zuo et al. (2015, 2017)
Pinto peanut (*Arachis pintoi*), carpet grass (*Axonopus affiinis*), greenleaf desmodium (*Desmodium intortum*)	Intercrop/ groundcover	Reduced disease severity and incidence by 20%; delayed onset of symptoms	Augmentation of the diversity and activity of soil microbial communities; reduction of Foc inoculum in soil	Pattison et al. (2014), Rames et al. (2018)
Pineapple (*Ananas comosus*), maize (*Zea mays*)	Rotation	Pineapple–banana rotation was more effective than maize–banana rotation	Reduction of Foc inoculum in soil; augmentation of beneficial soil microorganisms (e.g., *Acidobacteria*, *Planctomycetes*, *Burkholderia*, *Talaromyces* and *Clonostachys*)	Wang et al. (2015), Yuan, Wang, et al. (2021b)
Rice (*Oryza sativa*)	Rotation	Reduced disease incidence from initial 30%–50% to 8.1%–17.6% in the first year, and 0.8%–6.3% in the subsequent 2.5–3 years	–	Hwang (1985)
Coffea spp.; Fabaceae trees (*Inga* spp. and *Erythrina poeppigiana*)	Intercrop/ agroforestry	–	–	Köberl et al. (2015, 2017)
Chilli pepper (*Capsicum frutescens*)	Rotation	Reduced disease incidence and Foc inoculum in soil	Reduction of Foc inoculum through stimulation of the abundances of antagonistic bacterial genera (e.g., *Gemmatimonas*, *Pseudomonas*, *Sphingobium* and *Sphingomonas*)	Hong et al. (2020)

3.4 | Interactions with parasitic nematodes

Banana is affected by parasitic nematodes that differ in their lifestyle and feeding habits, and often occur in mixed populations (Coyne et al., 2018). Parasitic nematodes of banana include the root-knot nematode (*Meloidogyne* spp.), root-lesion nematodes (*Pratylenchus* spp.), spiral nematode (*Helicotylenchus multicinctus*) and the burrowing nematode *Radopholus similis*, which is considered the nematode of major concern (Coyne et al., 2018). Interactions between parasitic nematodes and Foc seem to vary considerably across banana genotypes. For example, in the field, Epp (1987) found no association between the incidence and severity of Fusarium wilt and the infestation of Cavendish with nematodes (*R. similis*, *Meloidogyne* spp.). Conversely, Loos (1959) reported that *R. similis* aggravated the severity of Fusarium wilt and early expression of disease symptoms in Gros Michel. Similarly, Almeida et al. (2018) found that banana fields severely affected by Fusarium wilt were heavily infested with *Pratylenchus* spp.

In pot trials, synergistic albeit inconsistent interactions between Foc and *R. similis* have been reported (Chaves et al., 2014; Dinesh et al., 2014; Rocha et al., 2020). Unlike *R. similis*, *Meloidogyne* spp. are sedentary endoparasites that infect host roots resulting in abnormal vessel elements and disruption of the arrangement and continuity of the vascular tissues (Coyne et al., 2018). Moreover, giant cells associated with the feeding of *Meloidogyne* spp. serve as a nutrient sink, which may predispose the roots to infection by Foc. Collectively, as parasitic nematodes and Foc occupy a similar ecological niche in the banana rhizosphere, they may develop complex interactions depending on the species of nematode. While there are far fewer reports so far, concomitant infection with Foc and parasitic nematodes may aggravate Fusarium wilt, for instance, through nematode-induced wounds, which can provide a portal for root entry by Foc (Almeida et al., 2018). Future studies are needed to untangle the mechanisms underlying the interactions between parasitic nematodes and races of Foc, for example, by analysis of metabolites secreted by nematode-infected roots in relation to the lifestyle of the nematode. Such information would foster appropriate use of the Fusarium wilt-resistant or tolerant banana cultivars in soils infested with both Foc and nematodes.

3.5 | Interactions with physicochemical soil properties

Optimal supply of nutrients is essential for optimal growth and health of banana plants (Nowembabazi et al., 2021; Shen, Ruan, Chao, et al., 2015a). The nutritional status can affect plant metabolic activity including the expression of host defences against invading pathogens (Marschner et al., 2011). Several studies have demonstrated that manipulation of the bioavailability of nutrients in soil (e.g., nitrogen, phosphorus, potassium, magnesium, manganese, iron, zinc) and soil pH can reduce the incidence and severity of Fusarium wilt (Table 2). However, the mechanisms by which nutrient bioavailability and soil chemical properties may impact Fusarium wilt are complex and poorly understood. Moreover, assessing the impact of the infinitely varied forms of nutrients on Fusarium wilt remains a challenge due to the influence of other abiotic and biotic factors in the soil environment. Further studies are needed to assess the independent effects of physicochemical soil factors on Foc, the banana plant and the banana microbiome.

Bioavailability of iron in soil is one of the critical factors that has been linked to the severity of Fusarium wilt (Domínguez et al., 1996; Orr & Nelson, 2018). Although iron is abundant in soil, its bioavailability is generally limited (c.10^{-18} M), and well below the optimal requirement for plants (10^{-9}–10^{-4} M) and microorganisms (10^{-7}–10^{-5} M) (Robin et al., 2008). In a pot trial, Peng et al. (1999) reported that application of the synthetic iron chelator EDDHA reduced disease severity and germination of Foc chlamydospores by one-third to one-half. Iron chelators with a high stability constant (K), such as HBED ($K = 10^{39.7}$) and EDDHA ($K = 10^{33.9}$), sequester iron with high affinity (Robin et al., 2008). This limits iron bioavailability and can thereby cause iron starvation to Foc (Peng et al., 1999). However, in a field study, Orr et al. (2021) suggested that the iron nutrition of Foc is not effectively altered by chelators, as no decrease in disease severity was observed when HBED and EDDHA were applied to Foc-infested soils. Studies are needed to establish the requirement of iron in the germination of Foc chlamydospores and to determine if Foc can subvert iron chelators and thereby evade iron starvation.

Soil pH is another factor that has been reported to modulate Fusarium wilt (Table 2). The optimum soil pH for growing bananas is approximately 5.0–7.5, while soil pH values of 5.6–6.0 have been recommended for management of Fusarium wilt (Dita et al., 2018; Domínguez et al., 2001). A high incidence of Fusarium wilt has been associated with lower soil pH, whereas soils suppressive to Fusarium wilt have a neutral or slightly alkaline pH (Deltour et al., 2017; Stover, 1962). In a pot trial, Peng et al. (1999) found that disease progression was slower in acidic soils than alkaline soils (pH 8). This was attributed to the influence of pH on chlamydospore germination, as high pH favoured chlamydospore germination. The effects of pH on Fusarium wilt are multifaceted and complex as pH also controls the bioavailability of nutrients and trace elements and affects the activities of extracellular enzymes and the reactivity of soil organic matter (Paul et al., 2006). Future studies are needed to further understand the impact of soil pH on banana root exudation, chlamydospore germination and growth of Foc, and the rhizosphere microbiome.

Other abiotic soil factors, such as soil type, temperature and water content have been shown to affect the severity of Fusarium wilt, but the precise mechanisms are not well known (Pattison et al., 2014). Regarding soil water content, Aguilar et al. (2000) reported that waterlogged soils result in hypoxia or anoxia, which greatly restricts oxygen to banana roots. Under oxygen-deficient conditions, the activities of enzymes involved in phenol metabolism are enhanced, resulting in the formation of lysigenous aerenchyma in the mid cortex (Figure 4a) from about 50 mm behind the root tip. Lysigenous aerenchyma is a gas space created by death of cells in the root cortex that enables efficient diffusion of oxygen within plants and thereby reduces the energy costs associated with root cells. Aguilar et al. (2003) suggested that aerenchyma may also provide a by-pass for Foc hyphae around barriers in the stele. Collectively, manipulation of physicochemical soil properties is a promising strategy for management of Fusarium wilt. Understanding the interplay between the soil and banana-associated microbiota will expand our knowledge on the impact of soil abiotic factors on biological control of Fusarium wilt.

Soil management practices, such as crop rotation and intercropping, have been reported to suppress Fusarium wilt (Table 3). Disease suppression has been linked to root-secreted metabolites, which in part target the early stages of Foc development (Table 3), yet the underlying mode of inhibition remains unclear. Zuo et al. (2015) suggested that the inhibitory effect of *Allium tuberosum* volatiles could be intensified by root-secreted phenolic compounds, but the effect of phenolic compounds on the early development of Foc is not completely understood. Phenolic compounds are abundantly secreted by legumes (Fabaceae), such as *Desmodium uncinatum* and *Mucuna pruriens* (Hooper et al., 2015). Accordingly, legumes could be useful intercrops when developing sustainable banana production systems (McIntyre et al., 2001; Ocimati et al., 2019). In this line, it will be relevant to identify legumes with root-secreted metabolites that can suppress Foc development and disease incidence in the field.

4 | CONCLUSION AND FUTURE OUTLOOK

Research on banana Fusarium wilt has a long history. However, it is remarkable how little progress has been made towards understanding the rhizosphere ecology of Foc. Research is needed to integrate previous advancements with consideration of disease management, host genetics and the biology of Foc to synthesize a clarified view of how banana below-ground interactions influence Fusarium wilt. The rhizosphere is a complex adaptive environment of closely interacting biological, chemical and physical components. Management and manipulation of the banana rhizosphere has great potential for improving plant growth and suppression of Fusarium wilt. To realize the potential of rhizosphere manipulation for suppression of Fusarium wilt, a comprehensive understanding of banana below-ground interactions and the mechanisms involved is required.

ACKNOWLEDGEMENTS

We thank Dr Mary K. Musyoki for the helpful discussions. This work was supported with funding from the German Academic Exchange Service (DAAD) through the Food Security Centre (FSC) of the University of Hohenheim. Open Access funding enabled and organized by ProjektDEAL

CONFLICTS OF INTEREST

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed.

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REFERENCES

Aguilar, E.A., Turner, D.W., Gibbs, D.J., Armstrong, W. & Sivasithamparam, K. (2003) Oxygen distribution and movement, respiration and nutrient loading in banana roots (*Musa* spp. L.) subjected to aerated and oxygen-depleted environments. *Plant and Soil*, 253, 91–102.

Aguilar, E.A., Turner, D.W. & Sivasithamparam, K. (2000) *Fusarium oxysporum* f. sp. *cubense* inoculation and hypoxia alter peroxidase and phenylalanine activities in nodal roots of banana cultivars (*Musa* sp.) differing in their susceptibility to Fusarium wilt. *Australian Journal of Botany*, 48, 589–596.

Almeida, N.O., Teixeira, R.A., Carneiro, F.A., de Oliveira, C.M., Ribeiro, V.A., Lobo Júnior, M. et al. (2018) Occurrence and correlations of nematodes, *Fusarium oxysporum* and edaphic factors on banana plantations. *Journal of Phytopathology*, 166, 265–272.

Aquino, A.P., Bandoles, G.G. & Lim, V.A.A. (2013). *R&D and policy directions for effective control of Fusarium wilt disease of Cavendish banana in the Asia-Pacific region*. Taipei: FFTC-AP. Available at: https://ap.fftc.org.tw/article/598 [Accessed 1 September 2022].

Bai, T.T., Xie, W.B., Zhou, P.P., Wu, Z.L., Xiao, W.C., Zhou, L. et al. (2013) Transcriptome and expression profile analysis of highly resistant and susceptible banana roots challenged with *Fusarium oxysporum* f. sp. *cubense* tropical race 4. *PLoS One*, 8, e73945.

Beckman, C.H. (1987) *The nature of wilt diseases of plants*. St Paul MN, USA: APS Press.

Beckman, C.H. (2000) Phenolic-storing cells: keys to programmed cell death and periderm formation in wilt disease resistance and in general defence responses in plants? *Physiological and Molecular Plant Pathology*, 57, 101–110.

Badri, D.V. & Vivanco, J.M. (2009) Regulation and function of root exudates. *Plant, Cell & Environment*, 32, 666–681.

Bakker, P.A.H.M., Doornbos, R.F., Zamioudis, C., Berendsen, R.L. & Pieterse, C.M.J. (2013) Induced systemic resistance and the rhizosphere microbiome. *Plant Pathology Journal*, 29, 136–143.

Belgrove, A., Steinberg, C. & Viljoen, A. (2011) Evaluation of nonpathogenic *Fusarium oxysporum* and *Pseudomonas fluorescens* for Panama disease control. *Plant Disease*, 95, 951–959.

Bellamy, A.S. (2013) Banana production systems: identification of alternative systems for more sustainable production. *Ambio*, 42, 334–343.

Blomme, G. (2000) *The interdependence of root and shoot development in banana (*Musa *spp.) under field conditions and the influence of different biophysical factors on this relationship*. PhD thesis. Katholieke Universiteit Leuven: Leuven.

Borges-Pérez, A., Fernández Falcón, M., Bravo Rodrigues, J.J., Pérez-Francés, J.F. & López-Carreño, I. (1991) Enhanced resistance of banana plants (Dwarf Cavendish) to *Fusarium oxysporum* f. sp. *cubense* by controlled Zn nutrition under field conditions. *Banana Newsletter*, 14, 24–26.

Bubici, G., Kaushal, M., Prigigallo, M.I., Gómez-Lama Cabanás, C. & Mercado-Blanco, J. (2019) Biological control agents against Fusarium wilt of banana. *Frontiers in Microbiology*, 10, 616.

Buddenhagen, I. (2009) Understanding strain diversity in *Fusarium oxysporum* f. sp. *cubense* and history of introduction of "Tropical Race

4" to better manage banana production. *Acta Horticulturae*, 828, 193–204.

Buxton, E.W. (1962) Root exudates from banana and their relationship to strains of the Fusarium causing Panama wilt. *Annals of Applied Biology*, 50, 269–282.

Cabanás, C.G.-L., Fernández-González, A.J., Cardoni, M., Valverde-Corredor, A., López-Cepero, J., Fernández-López, M. et al. (2021) The banana root endophytome: differences between mother plants and suckers and evaluation of selected bacteria to control *Fusarium oxysporum* f. sp. *cubense*. *Journal of Fungi*, 7, 194.

Carvalhais, L.C., Dennis, P.G., Badri, D.V., Kidd, B.N., Vivanco, J.M. & Schenk, P.M. (2015) Linking jasmonic acid signaling, root exudates, and rhizosphere microbiomes. *Molecular Plant-Microbe Interactions*, 28, 1049–1058.

Catambacan, D.G. & Cumagun, C.J.R. (2021) Weed-associated fungal endophytes as biocontrol agents of *Fusarium oxysporum* f. sp. *cubense* TR4 in Cavendish banana. *Journal of Fungi*, 7, 224.

Chaves, N., Staver, C. & Dita, M. (2014) Interaction of *Radopholus similis* and *Fusarium oxysporum* f. sp. *cubense* in banana. In: *Abstract retrieved from 29th International Horticultural Congress (Brisbane)*, Available at: https://www.researchgate.net/profile/Nancy-Chaves/ [Accessed 8 September 2022]

Chou, Y.M., Shen, F.T., Chiang, S.C. & Chang, C.M. (2017) Functional diversity and dominant populations of bacteria in banana plantation soils as influenced by long-term organic and conventional farming. *Applied Soil Ecology*, 110, 21–33.

Collinge, D.B. & Sarrocco, S. (2022) Transgenic approaches for plant disease control: status and prospects 2021. *Plant Pathology*, 71, 207–225.

Compant, S., Samad, A., Faist, H. & Sessitsch, A. (2019) A review on the plant microbiome: ecology, functions, and emerging trends in microbial application. *Journal of Advanced Research*, 19, 29–37.

Conko, G., Kershen, D.L., Miller, H. & Parrott, W.A. (2016) A risk-based approach to the regulation of genetically engineered organisms. *Nature Biotechnology*, 34, 493–503.

Coyne, D.L., Cortada, L., Dalzell, J.J., Claudius-Cole, A.O., Haukeland, S., Luambano, N. et al. (2018) Plant-parasitic nematodes and food security in sub-Saharan Africa. *Annual Review of Phytopathology*, 56, 381–403.

Dadzie, B.K. (1998) Post-harvest characteristics of black Sigatoka resistant banana, cooking banana and plantian hybrids. In: *Technical Guidelines INIBAP 4*. Rome, Italy: International Plant Genetic Resources Institute. Available at: https://pdf.usaid.gov/pdf_docs/Pnack067.pdf [Accessed 8 September 2022]

Dale, J., James, A., Paul, J.Y., Khanna, H., Smith, M., Peraza-Echeverria, S. et al. (2017) Transgenic Cavendish bananas with resistance to Fusarium wilt tropical race 4. *Nature Communications*, 8, 1496.

Deltour, P., França, S.C., Pereira, O.L., Cardoso, I., De Neve, S., Debode, J. et al. (2017) Disease suppressiveness to Fusarium wilt of banana in an agroforestry system: influence of soil characteristics and plant community. *Agriculture, Ecosystems & Environment*, 239, 173–181.

Delvaux, B., Rufuikiri, G. & Dufey, J. (2005) Ion absorption and proton extrusion by banana roots. In: Turner, D.W. & Rosales, F.E. (Eds.) *Banana root system: towards a better understanding for its productive management*. Montpellier: INIBAP, pp. 114–121.

Deng, G.M., Yang, Q.S., He, W.D., Li, C.Y., Yang, J., Zuo, C.W. et al. (2015) Proteomic analysis of conidia germination in *Fusarium oxysporum* f. sp. *cubense* tropical race 4 reveals new targets in ergosterol biosynthesis pathway for controlling Fusarium wilt of banana. *Applied Microbiology and Biotechnology*, 99, 7189–7207.

Dinesh, B.M., Ravichandra, N.G., Reddy, B.M. & Somasekhara, Y.M. (2014) Interactions between *Radopholus similis* and *Fusarium oxysporum* f. sp. *cubense* causing wilt complex on Banana. *International Journal of Advanced Research (Indore)*, 2, 976–985.

Dita, M., Barquero, M., Heck, D., Mizubuti, E.S. & Staver, C.P. (2018) Fusarium wilt of banana: current knowledge on epidemiology and research needs toward sustainable disease management. *Frontiers in Plant Science*, 9, 1468.

Domínguez, J., Negrin, M.A. & Rodriguez, C.M. (1996) Soil chemical characteristics in relation to Fusarium wilts in banana crops of Gran Canaria Island (Spain). *Communications in Soil Science and Plant Analysis*, 27, 2649–2662.

Domínguez, J., Negrín, M.A. & Rodríguez, C.M. (2001) Aggregate water-stability, particle-size and soil solution properties in conducive and suppressive soils to Fusarium wilt of banana from Canary Islands (Spain). *Soil Biology and Biochemistry*, 33, 449–455.

Drenth, A. & Kema, G. (2021) The vulnerability of bananas to globally emerging disease threats. *Phytopathology*, 111, 2146–2161.

Effendi, Y., Pambudi, A. & Pancoro, A. (2019) Metagenomic analysis of *Fusarium oxysporum* f. sp. *cubense*-infected soil in banana plantation, Sukabumi, Indonesia. *Biodiversitas Journal of Biological Diversity*, 27, 1939–1945.

Epp, M.D. (1987) Somaclonal variation in bananas: a case study with Fusarium wilt. *Banana and Plantain Strategies Cairns, Australia: ACIAR Proceedings*, 21, 140–150.

FAOSTAT (2022) *Production and trade statistics*. Available at: https://www.fao.org/faostat/en/#data. [Accessed 4 July 2022].

Fernández-Falcón, M., Borges, A.A. & Borges-Pérez, A. (2004) Response of Dwarf Cavendish banana plantlets to inoculation with races 1 and 4 of *Fusarium oxysporum* f. sp. *cubense* at different levels of Zn nutrition. *Fruits*, 59, 319–323.

Fortunato, A.A., Rodrigues, F.Á., Baroni, J.C.P., Soares, G.C.B., Rodriguez, M.A.D. & Pereira, O.L. (2012) Silicon suppresses Fusarium wilt development in banana plants. *Journal of Phytopathology*, 160, 674–679.

Fortunato, A.A., da Silva, W.L. & Rodrigues, F.Á. (2014) Phenylpropanoid pathway is potentiated by silicon in the roots of banana plants during the infection process of *Fusarium oxysporum* f. sp. *cubense*. *Phytopathology*, 104, 597–603.

Fu, L., Ou, Y., Shen, Z., Wang, B., Li, R. & Shen, Q. (2019) Stable microbial community and specific beneficial taxa associated. *Journal of Microbiology and Biotechnology*, 29, 1624–1628.

Fu, L., Penton, C.R., Ruan, Y., Shen, Z., Xue, C., Li, R. et al. (2017) Inducing the rhizosphere microbiome by biofertilizer application to suppress banana Fusarium wilt disease. *Soil Biology and Biochemistry*, 104, 39–48.

Fu, L., Ruan, Y., Tao, C., Li, R. & Shen, Q. (2016) Continuous application of bioorganic fertilizer induced resilient culturable bacteria community associated with banana Fusarium wilt suppression. *Scientific Reports*, 6, 27731.

Hecht-Buchholz, C., Borges-Pérez, A., Fernández Falcón, M. & Borges, A.A. (1998) Influence of zinc nutrition on Fusarium wilt of banana - an electron microscopic investigation. *Acta Horticulturae*, 490, 277–284.

Hennessy, C., Walduck, G., Daly, A. & Padovan, A. (2005) Weed hosts of *Fusarium oxysporum* f. sp. *cubense* tropical race 4 in northern Australia. *Australasian Plant Pathology*, 34, 115–117.

Hermanto, C., Sutanto, A., Edison, H.S., Daniells, J.W., O'Neill, W., Sinohin, V.G. et al. (2009) Incidence and distribution of Fusarium wilt disease of banana in Indonesia. *V International Symposium on Banana: ISHS-ProMusa Symposium on Global Perspectives on Asian Challenges*, 897, 313–322.

Heslop-Harrison, J.S. & Schwarzacher, T. (2007) Domestication, genomics and the future for banana. *Annals of Botany*, 100, 1073–1084.

Hong, S., Jv, H., Lu, M., Wang, B., Zhao, Y. & Ruan, Y. (2020) Significant decline in banana Fusarium wilt disease is associated with soil microbiome reconstruction under chilli pepper–banana rotation. *European Journal of Soil Biology*, 97, 103154.

Hooper, A.M., Caulfield, J.C., Hao, B., Pickett, J.A., Midega, C.A.O. & Khan, Z.R. (2015) Isolation and identification of *Desmodium* root exudates from drought tolerant species used as intercrops against *Striga hermonthica*. *Phytochemistry*, 117, 380–387.

Hu, W., Yang, B., He, Z. & Li, G. (2021) Magnesium may be a key nutrient mechanism related to Fusarium wilt resistance: a new banana cultivar (Zhongjiao No. 9). *PeerJ*, 9, e11141.

Huang, X., Liu, L., Wen, T., Zhu, R., Zhang, J. & Cai, Z. (2015) Illumina MiSeq investigations on the changes of microbial community in the *Fusarium oxysporum* f. sp. *cubense* infected soil during and after reductive soil disinfestation. *Microbiological Research*, 181, 33–42.

Hultman, J., Waldrop, M.P., Mackelprang, R., David, M.M., McFarland, J., Blazewicz, S.J. et al. (2015) Multi-omics of permafrost, active layer and thermokarst bog soil microbiomes. *Nature*, 521, 208–212.

Hwang, S.C. (1985) Ecology and control of fusarial wilt of banana. *Plant Protection Bulletin*, 27, 233–245.

Hwang, S.C. & Ko, W.H. (2004) Cavendish banana cultivars resistant to Fusarium wilt acquired through somaclonal variation in Taiwan. *Plant Disease*, 88, 580–588.

Ishii, T. & Araki, M. (2016) Consumer acceptance of food crops developed by genome editing. *Plant Cell Reports*, 35, 1507–1518.

Kaushal, M., Mahuku, G. & Swennen, R. (2020) Metagenomic insights of the root colonizing microbiome associated with symptomatic and non-symptomatic bananas in Fusarium wilt infected fields. *Plants*, 9, 263.

Kaushal, M., Swennen, R. & Mahuku, G. (2020) Unlocking the microbiome communities of banana (*Musa* spp.) under disease stressed (Fusarium wilt) and non-stressed conditions. *Microorganisms*, 8, 443.

Kimunye, J.N., Were, E., Mussa, F., Tazuba, A., Jomanga, K., Viljoen, A. et al. (2020) Distribution of *Pseudocercospora* species causing Sigatoka leaf diseases of banana in Uganda and Tanzania. *Plant Pathology*, 69, 50–59.

Köberl, M., Dita, M., Martinuz, A., Staver, C. & Berg, G. (2015) Agroforestry leads to shifts within the gammaproteobacterial microbiome of banana plants cultivated in Central America. *Frontiers in Microbiology*, 6, 91.

Köberl, M., Dita, M., Martinuz, A., Staver, C. & Berg, G. (2017) Members of Gammaproteobacteria as indicator species of healthy banana plants on Fusarium wilt-infested fields in Central America. *Scientific Reports*, 7, 45318.

Komada, H. (1975) Development of a selective medium for quantitative isolation of *Fusarium oxysporum* from natural soil. *Review of Plant Protection Research*, 8, 114–124.

Lecompte, F., Vaucelle, A., Pages, L. & Ozier-Lafontaine, H. (2002) Number, position, diameter and initial direction of growth of primary roots in *Musa*. *Annals of Botany*, 90, 43–51.

Leslie, J.F. & Summerell, B.A. (2006) *The Fusarium laboratory manual*. Iowa: Blackwell Publishing.

Li, C., Chen, S., Zuo, C., Sun, Q., Ye, Q., Yi, G. et al. (2011) The use of GFP-transformed isolates to study infection of banana with *Fusarium oxysporum* f. sp. *cubense* race 4. *European Journal of Plant Pathology*, 131, 327–340.

Li, C., Yang, J., Li, W., Sun, J. & Peng, M. (2017) Direct root penetration and rhizome vascular colonization by *Fusarium oxysporum* f. sp. *cubense* are the key steps in the successful infection of Brazil Cavendish. *Plant Disease*, 101, 2073–2078.

Li, C.Y., Mostert, G., Zuo, C.W., Beukes, I., Yang, Q.S., Sheng, O. et al. (2013) Diversity and distribution of the banana wilt pathogen *Fusarium oxysporum* f. sp. *cubense* in China. *Fungal Genomics & Biology*, 3, 2–3.

Li, P., Ma, L., Feng, Y.L., Mo, M.H., Yang, F.X., Dai, H.F. et al. (2012) Diversity and chemotaxis of soil bacteria with antifungal activity against Fusarium wilt of banana. *Journal of Industrial Microbiology and Biotechnology*, 39, 1495–1505.

Li, Z., Wang, T., He, C., Cheng, K., Zeng, R. & Song, Y. (2020) Control of Panama disease of banana by intercropping with Chinese chive (*Allium tuberosum* Rottler): cultivar differences. *BMC Plant Biology*, 20, 432.

Liu, S., Li, J., Zhang, Y., Liu, N., Viljoen, A., Mostert, D. et al. (2020) Fusaric acid instigates the invasion of banana by *Fusarium oxysporum* f. sp. *cubense* TR4. *New Phytologist*, 225, 913–929.

Loos, C.A. (1959) Symptom expression of Fusarium wilt disease of 'Gros Michel' banana in the presence of *Radopholus similis* (Cobb, 1893) Thorne, 1949, and *Meloidogyne incognita* acrita Chitwood, 1949. *Proceedings of the Helminthological Society of Washington D.C*, 26, 103–111.

Mace, M.E. (1963) Histochemical localization of phenols in healthy and diseased banana roots. *Physiologia Plantarum*, 16, 915–925.

Mace, M.E. & Wilson, E.M. (1964) Phenol oxidases and their relation to vascular browning in Fusarium infected banana roots. *Phytopathology*, 54, 840–842.

Marschner, P., Crowley, D. & Rengel, Z. (2011) Rhizosphere interactions between microorganisms and plants govern iron and phosphorus acquisition along the root axis-model and research methods. *Soil Biology and Biochemistry*, 43, 883–894.

Martínez-Medina, A., Appels, F.V. & van Wees, S.C. (2017) Impact of salicylic acid-and jasmonic acid-regulated defences on root colonization by *Trichoderma harzianum* T-78. *Plant Signaling & Behavior*, 12, e1345404.

McIntyre, B., Gold, C., Kashaija, I., Ssali, H., Night, G. & Bwamiki, D. (2001) Effects of legume intercrops on soil-borne pests, biomass, nutrients and soil water in banana. *Biology and Fertility of Soils*, 34, 342–348.

Moore, N.Y., Pegg, K.G., Allen, R.N. & Irwin, J.A.G. (1993) Vegetative compatibility and distribution of *Fusarium oxysporum* f. sp. *cubense* in Australia. *Australian Journal of Experimental Agriculture*, 33, 797–802.

Nasir, N., Pittaway, P.A. & Pegg, K.G. (2003) Effect of organic amendments and solarisation on Fusarium wilt in susceptible banana plantlets, transplanted into naturally infested soil. *Australian Journal of Agricultural Research*, 54, 251–257.

Navajothy, F.A., Narayanaswamy, R., Ponniah, D. & Trudayaraj, V. (2011) Spectroscopical differences among soil samples of selected susceptible and resistant varieties of banana in relation to wilt disease. *International Multidisciplinary Research Journal*, 1, 20–28.

Nowembabazi, A., Taulya, G., Tinzaara, W. & Karamura, E. (2021) Effect of integrated potassium nutrition on Fusarium wilt tolerance in apple bananas. *African Journal of Plant Science*, 15, 257–265.

Ocimati, W., Ntamwira, J., Groot, J.C., Taulya, G., Tittonell, P., Dhed'a, B. et al. (2019) Banana leaf pruning to facilitate annual legume intercropping as an intensification strategy in the East African highlands. *European Journal of Agronomy*, 110, 125923.

Orr, R. & Nelson, P.N. (2018) Impacts of soil abiotic attributes on Fusarium wilt, focusing on bananas. *Applied Soil Ecology*, 132, 20–33.

Orr, R., Pattison, A., Northfield, T. & Nelson, P.N. (2021) Fe chelates have little to no effect on the severity of Fusarium wilt of bananas in soils of the humid tropics. *Journal of Plant Pathology*, 103, 595–604.

Ou, Y., Penton, C.R., Geisen, S., Shen, Z., Sun, Y., Lv, N. et al. (2019) Deciphering underlying drivers of disease suppressiveness against pathogenic *Fusarium oxysporum*. *Frontiers in Microbiology*, 10, 2535.

Pattison, A.B., Molina, A.B., Chao, C.P., Viljoen, A. & Lindsay, S.J. (2018) Integrating management practices to support banana production in the presence of Fusarium wilt. *Acta Horticulturae*, 1196, 129–136.

Pattison, A.B., Wright, C.L., Kukulies, T.L. & Molina, A.B. (2014) Ground cover management alters development of Fusarium wilt symptoms in Ducasse bananas. *Australasian Plant Pathology*, 43, 465–476.

Paul, A., Stösser, R., Zehl, A., Zwirnmann, E., Vogt, R.D. & Steinberg, C.E. (2006) Nature and abundance of organic radicals in natural organic matter: effect of pH and irradiation. *Environmental Science & Technology*, 40, 5897–5903.

Paul, J.Y., Becker, D.K., Dickman, M.B., Harding, R.M., Khanna, H.K. & Dale, J.L. (2011) Apoptosis-related genes confer resistance to Fusarium wilt in transgenic 'Lady Finger' bananas. *Plant Biotechnology Journal*, 9, 1141–1148.

Pegg, K.G., Coates, L.M., O'Neill, W.T. & Turner, D.W. (2019) The epidemiology of Fusarium wilt of banana. *Frontiers in Plant Science*, 10, 1395.

Peng, H.X., Sivasithamparam, K. & Turner, D.W. (1999) Chlamydospore germination and Fusarium wilt of banana plantlets in suppressive and conducive soils are affected by physical and chemical factors. *Soil Biology and Biochemistry*, 31, 1363–1374.

Pittaway, P.A., Nasir, N. & Pegg, K.G. (1999) Soil receptivity and host-pathogen dynamics in soils naturally infested with *Fusarium oxysporum* f. sp. *cubense*, the cause of Panama disease in bananas. *Australian Journal of Agricultural Research*, 50, 623–628.

Ploetz, R.C., Kema, G.H.J. & Ma, L.J. (2015) Impact of diseases on export and smallholder production of banana. *Annual Review of Phytopathology*, 53, 269–288.

Qin, S., Ji, C., Li, Y. & Wang, Z. (2017) Comparative transcriptomic analysis of race 1 and race 4 of *Fusarium oxysporum* f. sp. *cubense* induced with different carbon sources. *G3: Genes, Genomes, Genetics*, 7, 2125–2138.

Rames, E.K., Pattison, A.B., Czislowski, E. & Smith, M.K. (2018) Soil microbial community changes associated with ground cover management in cultivation of Ducasse banana (*Musa* sp. ABB, Pisang Awak subgroup) and suppression of *Fusarium oxysporum*. *Australasian Plant Pathology*, 47, 449–462.

Robin, A., Vansuyt, G., Hinsinger, P., Meyer, J.M., Briat, J.F. & Lemanceau, P. (2008) Iron dynamics in the rhizosphere: consequences for plant health and nutrition. *Advances in Agronomy*, 99, 183–225.

Rocha, A.J., dos Ferreira, M.S., de Rocha, L.S., Oliveira, S.A.S., Amorim, E.P., Mizubuti, E.S.G. et al. (2020) Interaction between *Fusarium oxysporum* f. sp. *cubense* and *Radopholus similis* can lead to changes in the resistance of banana cultivars to Fusarium wilt. *European Journal of Plant Pathology*, 158, 403–417.

Rishbeth, J. (1955) Fusarium wilt of bananas in Jamaica: I. Some observations on the epidemiology of the disease. *Annals of Botany*, 19, 293–328.

Rishbeth, J. & Naylor, A.G. (1957) Fusarium wilt of bananas in Jamaica: III. Attempted control. *Annals of Botany*, 21, 599–609.

Rossmann, B., Müller, H., Smalla, K., Mpiira, S., Tumuhairwe, J.B., Staver, C. et al. (2012) Banana-associated microbial communities in Uganda are highly diverse but dominated by Enterobacteriaceae. *Applied and Environmental Microbiology*, 78, 4933–4941.

Sánchez-Zúñiga, K., Tapia-Fernández, A. & Rivera-Méndez, W.E. (2021) Effect of three different agronomic conditions on biochemical profile and diversity in the rhizosphere of banana plantations infected with *Fusarium oxysporum* Race 1. *Revista Chapingo Serie Horticultura*, 27, 55–70.

Sasse, J., Martinoia, E. & Northen, T. (2018) Feed your friends: do plant exudates shape the root microbiome? *Trends in Plant Science*, 23, 25–41.

Scheerer, L., Pemsl, D.E., Dita, M., Perez Vicente, L. & Staver, C. (2018) A quantified approach to projecting losses caused by Fusarium wilt tropical race 4. *Acta Horticulturae*, 1196, 211–218.

Segura-Mena, R.A., Stoorvogel, J.J., García-Bastidas, F., Salacinas-Niez, M., Kema, G.H.J. & Sandoval, J.A. (2021) Evaluating the potential of soil management to reduce the effect of *Fusarium oxysporum* f. sp. *cubense* in banana (*Musa* AAA). *European Journal of Plant Pathology*, 160, 441–455.

Shen, Z., Penton, C.R., Lv, N., Xue, C., Yuan, X., Ruan, Y. et al. (2018) Banana Fusarium wilt disease incidence is influenced by shifts of soil microbial communities under different monoculture spans. *Microbial Ecology*, 75, 739–750.

Shen, Z., Ruan, Y., Chao, X., Zhang, J., Li, R. & Shen, Q. (2015) Rhizosphere microbial community manipulated by 2 years of consecutive biofertilizer application associated with banana Fusarium wilt disease suppression. *Biology and Fertility of Soils*, 51, 553–562.

Shen, Z., Ruan, Y., Xue, C., Zhong, S., Li, R. & Shen, Q. (2015) Soils naturally suppressive to banana Fusarium wilt disease harbor unique bacterial communities. *Plant and Soil*, 393, 21–33.

Shen, Z., Wang, D., Ruan, Y., Xue, C., Zhang, J., Li, R. et al. (2014) Deep 16S rRNA pyrosequencing reveals a bacterial community associated with banana Fusarium wilt disease suppression induced by bio-organic fertilizer application. *PLoS One*, 9, e98420.

Smith, M.K., Langdon, P.W., Pegg, K.G. & Daniells, J.W. (2014) Growth, yield and Fusarium wilt resistance of six FHIA tetraploid bananas (*Musa* spp.) grown in the Australian subtropics. *Scientia Horticulturae*, 170, 176–181.

Stover, R.H. (1962) Studies on Fusarium wilt of bananas: VIII. Differentiation of clones by cultural interaction and volatile substances. *Canadian Journal of Botany*, 40, 1467–1471.

Sudarma, I.M. & Suprapta, D.M. (2011) Diversity of soil microorganisms in banana habitat with and without Fusarium wilt symptom. *Journal of the International Society for Southeast Asian Agricultural Sciences*, 17, 147–159.

Sun, J., Peng, M., Wang, Y., Li, W. & Xia, Q. (2013) The effects of different disease-resistant cultivars of banana on rhizosphere microbial communities and enzyme activities. *FEMS Microbiology Letters*, 345, 121–126.

Tenkouano, A., Pillay, M. & Ortiz, R. (2011) Breeding techniques. In: Pillay, M. & Tenkouano, A. (Eds.) *Banana breeding: constraints and progress*. Boca Raton, FL, USA: CRC Press, pp. 181–202.

Thangavelu, R. & Jayanthi, A. (2009) RFLP analysis of rDNA-ITS regions of native non-pathogenic *Fusarium oxysporum* isolates and their field evaluation for the suppression of Fusarium wilt disease of banana. *Australasian Plant Pathology*, 38, 13–21.

Thangavelu, R. & Mustaffa, M. (2010) A potential isolate of *Trichoderma viride* NRCB1 and its mass production for the effective management of Fusarium wilt disease in banana. *Tree and Forestry Science and Biotechnology*, 4, 76–84.

Tripathi, L., Ntui, V.O. & Tripathi, J.N. (2020) CRISPR/Cas9-based genome editing of banana for disease resistance. *Current Opinion in Plant Biology*, 56, 118–126.

Viljoen, A. (2002) The status of Fusarium wilt (Panama disease) of banana in South Africa. *South African Journal of Science*, 98, 341–344.

Viljoen, A., Ma, L.-J. & Molina, A.B. (2020) Fusarium wilt (Panama disease) and monoculture banana production: resurgence of a century-old disease. In: Ristaino, J.B. & Records, A. (Eds.) *Emerging plant diseases and global food security*. St Paul, MN, USA: APS Press, p. 184.

Wang, B., Li, R., Ruan, Y., Ou, Y., Zhao, Y. & Shen, Q. (2015) Pineapple–banana rotation reduced the amount of *Fusarium oxysporum* more than maize–banana rotation mainly through modulating fungal communities. *Soil Biology and Biochemistry*, 86, 77–86.

Wardlaw, R.C. (1961) *Banana diseases including plantains and abaca*. London, UK: Longmans, Green and Co. Ltd.

Wibowo, A., Santosa, A.T., Subandiyah, S., Hermanto, C. & Taylor, M.F.P. (2013) Control of fusarium wilt of banana by using *Trichoderma harzianum* and resistant banana cultivars. *Acta Horticulturae*, 975, 173–178.

Wu, X., Shan, Y., Li, Y., Li, Q. & Wu, C. (2020) The soil nutrient environment determines the strategy by which *Bacillus velezensis* HN03 suppresses Fusarium wilt in banana plants. *Frontiers in Plant Science*, 11, 1801.

Wu, Y., Yi, G., Peng, X., Huang, B., Liu, E. & Zhang, J. (2013) Systemic acquired resistance in Cavendish banana induced by infection with an incompatible strain of *Fusarium oxysporum* f. sp. *cubense*. *Journal of Plant Physiology*, 170, 1039–1046.

Yadav, K., Damodaran, T., Dutt, K., Singh, A., Muthukumar, M., Rajan, S. et al. (2021) Effective biocontrol of banana Fusarium wilt tropical race 4 by a bacillus rhizobacteria strain with antagonistic secondary metabolites. *Rhizosphere*, 18, 100341.

Yuan, J., Wen, T., Zhang, H., Zhao, M., Penton, C.R., Thomashow, L.S. et al. (2020) Predicting disease occurrence with high accuracy based on soil macroecological patterns of Fusarium wilt. *The ISME Journal*, 14, 2936–2950.

Yuan, J., Wu, Y., Zhao, M., Wen, T., Huang, Q. & Shen, Q. (2018) Effect of phenolic acids from banana root exudates on root colonization and pathogen suppressive properties of *Bacillus amyloliquefaciens* NJN-6. *Biological Control*, 125, 131–137.

Yuan, X., Hong, S., Xiong, W., Raza, W., Shen, Z., Wang, B. et al. (2021) Development of fungal-mediated soil suppressiveness against Fusarium wilt disease via plant residue manipulation. *Microbiome*, 9, 200.

Yuan, X., Wang, B., Hong, S., Xiong, W., Shen, Z., Ruan, Y. et al. (2021) Promoting soil microbial-mediated suppressiveness against Fusarium wilt disease by the enrichment of specific fungal taxa via crop rotation. *Biology and Fertility of Soils*, 57, 1137–1153.

Xia, X., Lie, T.K., Qian, X., Zheng, Z., Huang, Y. & Shen, Y. (2011) Species diversity, distribution, and genetic structure of endophytic and epiphytic *Trichoderma* associated with banana roots. *Microbial Ecology*, 61, 619–625.

Zhang, H., Mallik, A. & Zeng, R.S. (2013) Control of Panama disease of banana by rotating and intercropping with Chinese chive (*Allium tuberosum* Rottler): role of plant volatiles. *Journal of Chemical Ecology*, 39, 243–252.

Zhang, N., Wang, D., Liu, Y., Li, S., Shen, Q. & Zhang, R. (2014) Effects of different plant root exudates and their organic acid components on chemotaxis, biofilm formation and colonization by beneficial rhizosphere-associated bacterial strains. *Plant and Soil*, 374, 689–700.

Zhou, D., Jing, T., Chen, Y., Wang, F., Qi, D., Feng, R. et al. (2019) Deciphering microbial diversity associated with Fusarium wilt-diseased and disease-free banana rhizosphere soil. *BMC Microbiology*, 19, 161.

Zorrilla-Fontanesi, Y., Pauwels, L., Panis, B., Signorelli, S., Vanderschuren, H. & Swennen, R. (2020) Strategies to revise agrosystems and breeding to control fusarium wilt of banana. *Nature Food*, 1, 599–604.

Zuo, C., Li, C., Li, B., Wei, Y., Hu, C., Yang, Q. et al. (2015) The toxic mechanism and bioactive components of Chinese leek root exudates acting against *Fusarium oxysporum* f. sp. *cubense* tropical race 4. *European Journal of Plant Pathology*, 143, 447–460.

Zuo, C., Zhang, W., Chen, Z., Chen, B. & Huang, Y. (2017) RNA sequencing reveals that endoplasmic reticulum stress and disruption of membrane integrity underlie dimethyl trisulfide toxicity against *Fusarium oxysporum* f. sp. *cubense* tropical race 4. *Frontiers in Microbiology*, 8, 1365.

How to cite this article: Were, E., Viljoen, A. & Rasche, F. (2023) Back to the roots: Understanding banana below-ground interactions is crucial for effective management of Fusarium wilt. *Plant Pathology*, 72, 19–38. Available from: https://doi.org/10.1111/ppa.13641