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Threats to global food security from emerging phytoplasma crop diseases

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Abstract

Extensive damage to over 1000 plant species, including food crops, oil and industrial crops, vegetables, fruit trees, ornamentals, fodder species and weeds, has been caused by emerging phytoplasma-mediated diseases, thereby posing significant threat to global food security. Multiple factors, including environmental changes, invasion pathways, vector transmission and the emergence of new pathogen lineages, contribute to the spread of these diseases. Effective management requires stable, long-term strategies to safeguard plant health. Key approaches include comprehensive loss assessments, integration of climate change impacts, predictive modelling, enhanced disease surveillance, and improved detection techniques targeting phytoplasmas. This review highlights phytoplasma-associated plant diseases, emerging pathogen threats, and the factors facilitating their spread, alongside methods for surveillance and detection. In addition, case studies and global collaborative efforts are discussed. Finally, we outline future research priorities aimed at improving the management of phytoplasma-induced plant diseases.

Introduction

The United Nations Department of Economic and Social Affairs, Population Division, projected in 2017 that the world's population, currently 7.6 billion, will rise to 8.6 billion in 2030, 9.8 billion in 2050 and 11.2 billion in 2100 (UN Department of Economic and Social Affairs, 2021). A meta-analysis revealed that global food demand will increase by 35–56% from 2010 to 2050, while the number of people at risk of hunger could fluctuate between −91% and +8% (van Dijk *et al.*, 2021). Substantial yield reductions due to crop pests and diseases are evident, with average losses of approximately 40% in wheat, rice, maize, potato, and soybean, significantly contributing to food insecurity (Savary *et al.*, 2019).Yield losses of up to 100% are possible without effective control measures, leading to widespread destruction. Globally, plant diseases caused by viruses, nematodes, bacteria, and fungi result in annual losses of approximately $220 billion (Savary *et al.*, 2019). In addition, Germany lost €25 million, and Italy lost approximately €100 million due to a phytoplasma epidemic in apple trees in 2001 (Strauss, 2009).

Phytoplasmas are wall-less bacteria belonging to the class Mollicutes that reside in the phloem sieve elements of diseased plants (Lee *et al.*, 1998). Taxonomy and identification of phytoplasmas rely on molecular methods and gene sequences, as these pathogens cannot be cultured in cell-free conditions. Currently, 48 '*Candidatus* Phytoplasma' species have been named based on several criteria, including <98.65% sequence identity in the 16S rRNA gene, <95–96% whole genome similarity, or ecological separation (Bertaccini *et al.*, 2022; Wei and Zhao, 2022). Wei and Zhao (2022) classified genetically diverse phytoplasmas into 37 groups and over 150 subgroups using restriction fragment length polymorphism (RFLP) profiles of the F2nR2 region of the 16S rRNA gene. Many phytoplasmas have been linked to newly emerging diseases worldwide in recent years (Huang *et al.*, 2023).

Phytoplasmas-associated diseases affect over 1000 plant species worldwide (Hiruki and Wang, 2004; Maejima *et al.*, 2014; Wang *et al.*, 2024). As a threat to food security, their infestation may cause substantial yield losses of up to 100% in cucumber, tomato, pepper, potato and Navratil crops (Bogoutdinov *et al.*, 2008; Rao and Kumar, 2017). Over the last four decades, millions of coconut palm trees in the Caribbean have been wiped out by a deadly lethal yellowing disease (LYD) associated with phytoplasmas (Brown *et al.*, 2006). In Jamaica alone, more than seven million palm trees died by 1980 due to LYD (Roca de Doyle, 2001). In Africa, similar diseases were observed and collectively referred to as lethal yellowing-like disease (Eden-Green, 1997). Eight million coconut palms, or 38 % of Tanzania's total hectarage, have been destroyed due to phytoplasma-associated-lethal disease since the 1960s (Mugini, 2002). Furthermore, an outbreak of LYD in Côte d'Ivoire damaged 350 hectares of coconut and destroyed 12,000 metric tonnes of copra annually, with an additional 7,000 hectares at risk (Arocha-Rosete *et al.*, 2014).

The incidence of phytoplasmas-associated plant diseases has been on the rise (Kumari *et al.*, 2019). Experts predict that this trend will continue in the future due to climate change in the geographic distribution of phytoplasmas and the increased international trade of host plants for planting (Al Ruheili *et al.*, 2021; Aidoo *et al.*, 2021; EFSA Panel on Plant Health (PLH), 2020). Moreover, efficient management of phytoplasmas can improve and sustainably increase agricultural yields (Bertaccini, 2021), thereby contributing to global food security. This review sheds light on phytoplasmas as plant pathogens, the threats they pose, factors contributing to their spread, global collaborative research efforts, management strategies and surveillance and detection. We present case studies that highlight management practices, lessons learned, and future research directions for phytoplasma-mediated diseases.

Understanding phytoplasma plant pathogens

Phytoplasmas, previously identified as mycoplasma-like organisms (MLOs) are one of the smallest known pathogens infecting several plant species worldwide. They are prokaryotic plant pathogenic bacteria, with size ranging from 200 to 1000 nm (McCoy *et al.*, 1989). The phytoplasma's cell lacks a wall and their outer covering is made up of a triple layered single unit membrane (Lee and Davis, 1992). They have genomic sizes ranging from 0.53 to 1.2 kb (Bai *et al.*, 2006; Oshima *et al.*, 2004), with a low G+C content (Kollar and Seemuller, 1989), being descended from an ancestral Gram-positive bacteria in the Bacillus – Clostridium group (Zhao *et al.*, 2009). They live and multiply in the functional phloem sieve tube elements of their hosts, producing disease symptoms such as virescence, phyllody and witches' broom (Bertaccini *et al.*, 2022; Lee *et al.*, 2000). Until their first isolation in pure culture, they were previously thought to be obligate parasites. Moreover, there is a gradual improvement in the methods for applicability to a wider range of '*Ca.* Phytoplasma' species (Contaldo *et al.*, 2012; Contaldo *et al.*, 2016).

The inability to obtain axenic culture of phytoplasmas in the past made their identification using cultural, morphological and biochemical methods challenging (Makarova *et al.*, 2012). Consequently, their identification has relied primarily on molecular methods (Bertaccini and Duduk, 2009) particularly using the 16S ribosomal RNA (16S rRNA) gene. This approach has been used to create two parallel classification systems. In one system all strains of the pathogen are placed in the provisional genus '*Ca.* Phytoplasma' and are separated into species based on variations in the nucleotide sequences of the 16S rRNA gene (IRPCM, 2004; Harrison *et al.*, 2011). In the second system, phytoplasmas are classified into groups and subgroups based on RFLP patterns obtained from PCR-amplified products of unknown isolates (Zhao *et al.*, 2009; Lee and Davis, 1992). Other investigators prefer to first sequence the PCR-amplified 16S rRNA-encoding gene products of the phytoplasma, after which the assembled nucleotides are used in a BLAST search to identify the species and phylogenetic analysis used to assign them to groups and sub-groups. In some instances, the gene sequences can be digested *in silico* and computer programs such as the *i*Phyclassifier can be used to delineate the 16Sr group and subgroups of the unknown isolates (Zhao *et al.*, 2009; Wei *et al.*, 2008). Multilocus analysis involving the 16S ribosomal gene, the 16S–23S intergenic spacer region and *secA* and *groEL* genes have been used to identify the species status of some phytoplasma isolated from palms in Florida (Soto *et al.*, 2021).

Phytoplasmas can infect a wide range of plant species (Seemüller *et al.*, 2002; Lee *et al.*, 2000; Olivier *et al.*, 2009). According to Hemmati *et al.* (2021a), more than 164 plant species made up of fruit crops, vegetables, cereal and oilseed crops, trees, ornamental plants and weeds in the Middle East region have been associated with fourteen 16Sr phytoplasma strains. In Mexico, phytoplasmas have been associated with diseases of different species of palm causing wilting of fronds and eventual death of plants (Hernandez *et al.*, 2020).

Transmission of phytoplasmas occurs via vegetative propagation, dodder (*Cuscuta* spp.), and insect vectors (Aryan *et al.*, 2016; Kaminska and Korbin, 1999). There have been studies on possible transmission of phytoplasma through alfafa seeds and the embryo of coconut fruits obtained from infected palms (Kahn *et al.*, 2002; Cordova *et al.*, 2003). Though some studies could not confirm seed transmission of phytoplasmas (Nipah *et al.*, 2007; Cordova *et al.*, 2003), recent studies have confirmed seed transmission of phytoplasmas in coconut (Narvaez *et al.*, 2022). Worldwide, leafhoppers, planthoppers and psyllids are known to transmit phytoplasmas (Weintraub and Beanland, 2006). These insects feed on plant phloem, ingest the pathogen, which then colonizes their guts and salivary glands, multiplies, and is subsequently released into new hosts during feeding (Ammar and Hogenhout, 2006). Demonstrating insect transmission of phytoplasmas has been challenging due to the difficulty of producing pure cultures. However, recent methodological advances have enabled transmission studies linking specific insect species to pathogen spread. For example, *Austroagallia sinuata* collected from infected fields transmitted '*Ca.* Phytoplasma aurantifolia' to *Aerva javanica* in periwinkle cages (Hemmati *et al.*, 2019). Similarly, the pathogen responsible for lethal bronzing disease (LB) of palm was successfully transmitted from infected spear leaves to a sucrose medium by *Haplaxius crudus* (Mou *et al.*, 2022), and *H. crudus* has recently been experimentally confirmed to transmit LYD (Narvaez *et al.*, 2022). As axenic culture methods for phytoplasmas continue to improve, more studies on insect transmissibility are expected in the future.

Threats posed by emerging phytoplasma pathogens

Evidence first appeared in 1967 linking prokaryotes that morphologically resembled mycoplasmas colonising phloem tissue (then termed mycoplasma-like organisms, MLOs) to yellowing-type plant diseases previously assumed to be caused by viruses (Doi *et al.*, 1967). Today, phytoplasmas are recognised as major plant pathogens associated with diseases that have serious environmental and economic consequences. A wide range of plant species, including ornamentals, timber trees, shade trees, and economically important food, vegetable, and fruit crops, are affected by phytoplasma-associated diseases (Bertaccini *et al.* 2014; Gasparich, 2010). Varying degrees of phytoplasma incidence on vegetables have been documented in 47 nations, spanning five continents (Kumari *et al.*, 2019). Phytoplasmas have been linked to 164 plant hosts, including feed crops, cereals, fruit crops, medicinal plants and shade trees. Fourteen of the 34 identified phytoplasma ribosomal groups have been reported across the Middle East and other regions worldwide (Hemmati *et al.*, 2021b). While specific phytoplasmas may have limited host ranges, phytoplasma-related disorders impact a diverse range of crops worldwide. Examples include pigeon pea witches' broom (16SrIX) in Brazil (Chen *et al.*, 2008) and the citrus huanglongbing disease in China, which is linked to the aster yellows phytoplasmas (16SrI) (Teixeira *et al.*, 2009). Over 300 different plant diseases that have been connected to phytoplasmas have impacted hundreds of plant taxa (Bertaccini and Duduk, 2009). Woody plant diseases such as coconut lethal yellowing, peach X-disease, grapevine yellows (GY) and apple proliferation, are particularly important due to their commercial significance. Notable phytoplasma diseases that have been recorded in Southeast Asia include rice yellow dwarf, peanut witches' broom, Bermuda grass white leaf and sugarcane white leaf and grassy shoot (Win and Jung, 2012). The phytoplasma group 16SrIX, which affects almond crops, is particularly problematic in the Middle East. Since the 1990s, almond production in Lebanon and Iran has been severely impacted by a fatal disease associated with this group. Thousands of almond trees have been lost in Lebanon since the initial outbreak in the south of the country 15 years ago (Abou-Jawdah *et al.*, 2003). Diseases linked to phytoplasma have long been known to cause significant financial harm to a range of domestic and wild plants. The threat posed by phytoplasma diseases is growing on a global scale due to two main causes: severe epidemics in the rest of the world that affect grapevines, citrus, forest trees, oil-seed crops, alfalfa, stone and pome fruits; and emerging diseases in Latin America, Asia, Africa and the Caribbean that primarily affect sugarcane, corn, cassava, coconuts, papaya and vegetables. In both scenarios, these diseases have the potential to expand to new crop species and significantly affect international trade. Although phytoplasmas are highly metabolically dependent on their host plant, they generally do not cause rapid death. However, in exceptionally cold climates, infected plants die, while in tropical climates, asymptomatic plant presence is common and can have serious epidemiological repercussions (Bertaccini, 2008).

Similar to the identification of phytoplasma strains on the American continent, which comprised strains from 12 subgroups within 10 ribosomal groups, strains from ten (10) ribosomal groups and 16 subgroups on the Asian continent have been documented. The phytoplasma group 16SrIII affects 10 types of vegetable crops, whereas the group 16SrI affects 14. Apart from the few incidences of the pathogen on tomatoes in Mexico, the 16SrIII phytoplasma group seems to be limited to countries such as Bolivia, Brazil, Argentina, Chile and Costa Rica. The 16SrI phytoplasmas group of the aster yellows category is the most common in various genera, followed by '*Ca.* Phytoplasma solani' (Stolbur phytoplasma) (16SrXIIA), clover proliferation (16SrVI) and the 16SrII group of peanut witches' broom (Kumari *et al.*, 2019). Analyses of NCBI database records show that phytoplasma groups 16SrI, 16SrII, 16SrIV, 16SrV, 16SrVI, 16SrIX, 16SrXI, 16SrXII, and 16SrXIV are prevalent in India (Ayman *et al.*, 2010; Priya *et al.*, 2010). In both Iran and India, 16SrI and 16SrII phytoplasmas significantly reduce squash yields (Salehi *et al.*, 2015; Rao *et al.*, 2017b).

Phytoplasmas also represent a major limiting factor for several economically important crops in Europe and North America. For instance, in North America and Europe, the aster yellow phytoplasma significantly reduces the value of ornamental plants such as gladiolus, hydrangea, purple coneflower and China aster, as well as vegetable crops such as lettuce, carrots and celery (Bertaccini and Duduk, 2009). Apple proliferation, European stone fruit yellows and pear decline are fruit tree phytoplasma diseases that are economically significant in Europe (Marcone *et al.*, 2023). Interestingly, in some cases, phytoplasmas infection in ornamental plants may provide desirable and valuable traits, such as the free-branching phenotypes in most commercial poinsettia varieties resulting from infection by phytoplasmas (Lee *et al.*, 2021).

Apple proliferation is widespread across Europe, where affected *Malus domestica* Borkh. trees produce undersized, unmarketable apples. Fruit quality is diminished, size is reduced by approximately 50%, and weight losses range from 63% to 74%. Additionally, reduced tree vigour increases susceptibility to powdery mildew. Three subgroups (16SrII-A, -C and -D) are widely distributed over the African continent and infect faba beans, squash, tomatoes, brinjal and chiles (Omar and Foissac, 2012; Alfaro-Fernández *et al.*, 2011, 2012). In Australia, only three (16SrII, 16SrV and 16SrXII) out of the seven phytoplasma groups (16SrI, 16SrII, 16SrIII, 16SrV, 16SrX, 16SrXI and 16SrXII) have been recorded, and these are known to infect vegetable crops. Nevertheless, there are few reports of phytoplasma disease affecting vegetable crops in Australia. The global analysis of phytoplasma and their threat to food security around the globe is presented in Table 1.

Factors contributing to spread of phytoplasma

Biotic and abiotic factors contribute immensely to phytoplasma transmission. The biotic factors transmit phytoplasma in persistent-propagative mechanism through multiplication within the vector after acquisition (Christensen *et al.*, 2005; Weintraub and Beanland, 2006; Jarausch and Weintraub, 2013; Mou *et al.*, 2022). The transmission of phytoplasmas by insect vectors begins with the acquisition of the pathogen from an infected plant via feeding. The pathogen spreads from the vector's gut to its salivary glands and reproduces within the vector. After reproduction, the vector transfers the pathogen to another plant via feeding thereby infecting the plant. Insects, specifically the phloem-feeding insects such as leafhoppers, planthoppers and psyllids are major vectors of phytoplasma spread (Weintraub and Beanland, 2006). For example, the planthopper *Haplaxius crudus* is a confirmed vector of '*Ca.* Phytoplasma aculeata', a phytoplasma responsible for lethal bronzing of palms in Mexico and Florida (Halbert *et al.*, 2014; Narváez *et al.*, 2018; Mou *et al.*, 2020a; Dzido *et al.*, 2020). Recent studies have also demonstrated transovarial transmission, where offspring of infected vectors carry the pathogen. For instance, the progeny of *Matsumuratettix hiroglyphicus* were found to harbour the sugarcane white leaf phytoplasma and could transmit it to healthy plants (Hanboonsong *et al.*, 2002; Weintraub and

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Table 1. The global analysis of phytoplasma and their threat to food security

Strains of phytoplasma	Host range	Distribution of phytoplasma (Country)	References
16SrII,16SrVI	Cabbage	China Iran	Salehi *et al.*, 2007; Cai *et al.*, 2016
16SrIV-D	Canary Island Date palms	USA	Harrision *et al.*, 2008
16SrIV-D	Edible date palms	USA	Harrision *et al.*, 2008
16SrIV-D	Wild date palms	USA	Harrision *et al.*, 2008
16SrIV-D	Pygmy date palms	USA	Jeyaprakash *et al.*, 2011
16SrII, 16SrVI, 16SrI, 16SrIX, and 16SrXII	Tomato	Iran	Zibadoost *et al.*, 2016; Salehi *et al.*, 2016
16SrVI, 16SrII	Cucumber	Iran	Zibadoost *et al.*, 2016
16SrII, 16SrVI	Potato	Iran	Zibadoost *et al.*, 2016
16SrII, 16SrVI	Chili	Iran	Zibadoost *et al.* 2016
16SrII, 16SrVI	Lettuce	Iran	Zibadoost *et al.*, 2016
16SrII, 16SrVI	Spinach	Iran	Zibadoost *et al.* 2016
16SrII, 16SrVI	Squash	Iran	Zibadoost *et al.*, 2016
16SrXIV	Bermuda grass	Iran, Turkey, Iraq, Saudi Arabia	Salehi *et al.*, 2009; Çağlar *et al.*, 2013; Omar, 2016; Alkuwaiti *et al.*, 2017
16SrII-D	Squash	Egypt	El-Sisi *et al.*, 2017

Beanland, 2006). In addition, phytoplasma can spread through agricultural and horticultural planting materials such as rootstocks, cuttings and grafting materials, especially in woody plants. Plant shoots and roots, such as basal shoots, stems, rhizomes, tubers, stolons, corms, buds and bulbs, can all vegetatively spread phytoplasma (Caglayan *et al.*, 2019; 2023). Seed transmission has been reported in both herbaceous and woody plant species (Satta *et al.*, 2019). The seeds from phytoplasma-infected alfalfa (*Medicago sativa*), lime (*Citrus aurantiaca*) and tomato (*Lycopersicum esculentum*) from Oman and Italy were found to contain phytoplasmas belonging to ribosomal groups 16SrI, 16SrXII and 16SrII (Khan *et al.*, 2002; Botti and Bertaccini, 2006).

Abiotic factors also facilitate the spread and prevalence of phytoplasmas. The weather influences the life cycle, behaviour and abundance of insect vectors responsible for phytoplasma transmission. Galetto *et al.* (2011) found that two phytoplasma – chrysanthemum yellows (vector: Euscelidius variegatus, host: daisy) and 'Flavescence dorée' (vector: *Scaphoideus titanus*, host: broad bean) multiplied faster in insects when it was cooler and in plants when it was warmer. Similarly, Maggi *et al.* (2014) discovered that the epidemics of chrysanthemum yellows phytoplasma in *Chrysanthemum carinatum* plants were faster at higher temperatures, with a linear increase in spreading rate from 0.2 plants infected per day at 15°C to about 0.7 plants per day at 30° *Ca.* Phytoplasma infections are also influenced by prevailing winds and geographical factors, such as mountain ranges, which determine their spread and direction of lethal yellowing of coconut palm (Mpunami *et al.*, 2000; Mora-Aguillera, 2002).

Surveillance and detection of phytoplasmas

The surveillance of phytoplasmas encompasses various techniques aimed at monitoring their presence and distribution in plant populations. Historically, methods like symptom profiling, microscopy, serology and dodder transmission studies have been employed for disease detection (Nair and Manimekalai, 2021; Gupta *et al.*, 2023). However, recent advances in molecular techniques, such as PCR and loop-mediated isothermal amplification (LAMP), have revolutionized early detection capabilities (Jawhari *et al.*, 2015; Parnell *et al.*, 2017). Additionally, biosensing techniques and innovative surveillance methods like remote sensing and citizen science initiatives have enhanced the ability to monitor phytoplasma populations (Dyussembayev *et al.*, 2021; Parnell *et al.*, 2017). These developments have significantly improved early detection and monitoring strategies. Various surveillance strategies, such as airborne surveillance and habitat monitoring, offer valuable insights into vulnerable plant hosts and habitats, aiding in resource allocation and decision-making for habitat restoration and biosecurity (Mitchell, 2024). Moreover, effective monitoring and surveillance methods, informed by statistical analyses such as geographic information systems (GIS), are critical for timely detection and management of phytoplasma diseases (Mitchell, 2024; Parnell *et al.*, 2017).

The implementation of PCR and nested-PCR assays enables the broad detection of phytoplasma presence, including instances of mixed infection, in field-collected samples (Bertaccini *et al.*, 2014). Utilizing conserved gene sequences has represented a significant breakthrough in detecting, identifying and categorizing phytoplasmas. A barcode system was previously utilized for the detection and identification of phytoplasmas (Bertaccini *et al.*, 2014). Additionally, the introduction of diagnostic tests based on quantitative PCR assays (qPCR) has proven highly sensitive, reducing the risk of amplicon contamination and eliminating the need for gel-based post-PCR product analysis, thus establishing qPCR as a reliable alternative method to nested-PCR assays in routine testing (Pérez-López *et al.*, 2017). PCR assays employing primers sourced from phytoplasma-specific DNA probes or sequences from the 16S rRNA gene have demonstrated superior sensitivity in detecting phytoplasmas within infected plant or insect hosts. Identification and classification have typically involved the use of RFLP analysis of this genetic locus, leading to the delineation of over thirty 16Sr groups designated as 16SrI –

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16SrXXXIII (Pérez-López *et al.*, 2017). Using a primer pair (P1/Tint) identified in a portion of the tRNA^{Ile} region within the spacer region resulted in a universal phytoplasma detection involving a secondary PCR product of approximately 200 bp (Smart *et al.*, 1996). Universal PCR primers targeting the 16S rRNA gene have also facilitated the detection of known phytoplasma strains (Gundersen and Lee, 1996; EPPO, 2018). However, alternative genes, such as *groEL* which is also known as *cpn60*, have been utilized as supplementary markers for phytoplasma identification and classification (Pérez-López *et al.*, 2017). The *cpn60* universal target (cpn60 UT), spanning approximately 550 bp, resides within the Cpn60-encoding gene, recognized as a molecular barcode for the Bacteria domain, and serving as a taxonomic marker for characterizing microbial communities (Pérez-López *et al.*, 2017).

Despite significant progress, persistent limitations primarily stem from the intricate nature of phytoplasma infections and their accelerated spread through global plant trade (Pierro *et al.*, 2019). Agricultural practices face substantial consequences due to challenges in early identification (Dyussembayev *et al.,* 2021). Statistical methodologies play a crucial role in guiding surveillance endeavours, aiding in resource allocation and decision-making for habitat restoration and establishment (Mitchell, 2024; Parnell *et al.*, 2017). Nonetheless, the challenge of detecting phytoplasmas in late spring may be attributed to their proliferation time on stems, branches and new foliage (Gupta *et al.*, 2023). Addressing these constraints necessitates ongoing research and innovative detection technologies to mitigate the impact of phytoplasma diseases on agriculture and ecosystems. Despite advancements in surveillance and detection techniques, several challenges persist, particularly in early identification due to inconspicuous symptoms and the erratic distribution of phytoplasmas within infected plants (Dyussembayev *et al.*, 2021; Gupta *et al.*, 2023). Moreover, predicting phytoplasma effectors remains challenging, hindering effectorome comparisons (Carreón-Anguiano *et al.*, 2023). Table 2 shows techniques and principles of phytoplasma detection. The difficulty in detecting phytoplasmas during late spring may be attributed to their proliferation on stems, branches and new leaves (Gupta *et al.*, 2023). When examining a pear tree, symptoms indicative of pear decline might easily be misinterpreted as signs of other problems like graft-incompatibility, chlorosis, virus-related diseases, or even drought (Errea *et al.*, 2002). However, enhancing early detection capabilities necessitates reliable detection methods and a deeper comprehension of phytoplasma biology. Table 3 depicts the challenges and solutions for early detection of phytoplasma.

Case studies on selected phytoplasma-related disease outbreaks

The global impact of phytoplasma diseases on crops and other environmentally significant plants is profoundly concerning (Bertaccini, 2021). These pathogens have caused substantial economic losses and continue to pose significant threats to agricultural sustainability (Pierro *et al.*, 2019). Multiple cases of devastating consequences of these diseases on various categories of crop species including tree crops (e.g. grapevines, apples, coconuts), vegetables (tomatoes, potatoes, carrots), cereals (maize) and legumes have been reported across different regions of the world (Pierro *et al.*, 2019; Siampour *et al.*, 2019). The outbreak of phytoplasma-related diseases highlights the high vulnerability of global cropping sysems and stresses the importance of continuous research in developing resistant varieties and innovative control methods (Hemmati *et al.*, 2021a). Currently, there is a continuous effort to control the impact of phytoplasma diseases in several crop cultivation areas across the globe (Wang *et al.*, 2024). Knowledge about previous outbreaks of the disease, management practices and current status of these diseases is essential in facilitating research and development efforts. A case study of selected phytoplasma diseases is briefly presented below:

Grapevine yellows diseases

The Grapevine yellow (GY) diseases are a group of phytoplasma-associated diseases affecting grapevines worldwide. Twelve '*Ca.* Phytoplasma' species, distributed across 17 16SrRNA subgroups, are reported to be associated with these diseases (Bertaccini *et al.*, 2022). In Europe, the most significant GY diseases are Flavescence dorée and Bois noir (BN), both of which have caused severe damage to viticulture over several decades (Jarausch *et al.*, 2021; Belli *et al.*, 2010). Flavescence dorée is linked to phytoplasmas belonging to the 16SrV-C and 16SrV-D subgroups, while BN disease is associated with phytoplasmas of the 16SrXII-A subgroup (Bertaccini *et al.*, 2007; 2014). GY outbreaks, particularly in Europe, have led to significant economic losses, reduced grape, apple, and peach yields, and quality deterioration, adversely affecting the wine industry (Ember *et al.*, 2018). Severe outbreaks in Italy, France, and Spain have produced symptoms such as leaf rolling, vine decline, shrivel.

Management strategies

Effective management of GY disease involves a comprehensive approach, including cultural practices such as removing infected vines planting disease-resistant cultivars, and implementing rigorous monitoring using molecular diagnostic tools (Oliveira *et al.*, 2019). Chemical control is limited due to the feeding behaviour of insect vectors (primarily leafhoppers), but integrated pest management strategies, incorporating biological controls such as predatory insects, are being explored, though further research is needed for widespread application (Bianco *et al.*, 2019; Belli *et al.*, 2010; Boudon-Padieu, 2003). Early detection and removal of infected vines, combined with strict quarantine measures, remain crucial for preventing further spread (Krüger *et al.*, 2022). Current research focuses on pathogen diversity, vector ecology, and host-pathogen interactions, aiming to develop sustainable management strategies and resilient grape cultivars through coordinated global efforts (Krüger *et al.*, 2022; Zambon *et al.*, 2018; Abu Alloush *et al.*, 2023; Bertaccini, 2021).

Witches' broom disease of lime

Witches' broom disease of lime (WBDL), caused by '*Ca.* Phytoplasma aurantifolia' (16Sr II-B), has severly affected Mexican lime production. The disease originated in Oman and subsequently spread to Brazil, the Middle East, and India (Hemmati *et al.*, 2021a; Al-Yahyai *et al.*, 2015). The outbreak destroyed over 50% of lime cultivation in some areas, leading to significant economic losses. Early symptoms include proliferation of multiple small pale-green leaves, which later dry and drop, leaving dead twigs (Donkersley *et al.*, 2018a).

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Table 2. Techniques and principles of phytoplasma detection

Detection techniques	Advantages/Principles	Reference
Symptom profiling, electron microscopy, DAPI (4',6-diamidino-2-phenylindole) staining, serology (monoclonal and polyclonal antisera)	Earlier and simple methods for phytoplasma detection.	Gupta *et al.*, 2023
Loop-mediated isothermal amplification (LAMP)	Early detection, rapid and sensitive identification of phytoplasma DNA. Minimal equipment requirement and amenable to in-field use.	Jawhari *et al.*, 2015; Nair and Manimekalai, 2021; Mitchell, 2024
Quantitative real-time PCR (QPCR)	High-throughput, rapid and sensitive detection of phytoplasmas; low concentration of phytoplasma detection is possible.	Satta *et al.*, 2017
Electrochemical and optical techniques such as the use of pathogen biosensors, anti-body biosensors, and DNA probe.	High sensitivity	Khater *et al.*, 2017; Dyussembayev *et al.*, 2021
Remote sensing	Phytoplasma surveillance	Parnell *et al.*, 2017
Citizen science initiatives	Phytoplasma surveillance	Parnell *et al.*, 2017
Diagnostic networks	Phytoplasma surveillance	Parnell *et al.*, 2017

Management strategies

Control measures for WBDL involve a combination of cultural, biological, and chemical approaches (Donkersley *et al.*, 2018b). Cultural measures include pruning infected branches, removing severely affected trees, and controlling weed hosts. Biological control methods, including the use of natural enemies of the psyllid vector and entomopathogenic fungi, have shown promise (Siampour *et al.*, 2019). However, insecticide-based chemical control is challenging due to the rapid reproduction of psyllids. Complete removal of infected trees in endemic areas is recommended to reduce disease spread (Hemmati *et al.*, 2021a). WBDL management underscores the importance of early detection and rapid response. The persistence of '*Ca.* Phytoplasma aurantifolia' in alternative hosts and wild plant species complicates eradication efforts (Bertaccini, 2023). Despite extensive control strategies, challenges persist due to the pathogen's wide host range, difficulty in controlling psyllid populations, and its capacity to infect multiple citrus species (Golmohammadi *et al.*, 2023). Research on WBDL focuses on understanding pathogen epidemiology, transmission dynamics, and genetic diversity (Bertaccini, 2023). Studies of psyllid vector behaviour also support efforts to breed resistant cultivars and develop biocontrol agents (Mankin and Rohde, 2020). Advances in diagnostic tools and epidemiological modelling are contributing to improved management strategies (Santos *et al.*, 2023). Collaboration among researchers, growers, and regulatory agencies remains essential in combating WBDL.

Lethal yellowing diseases

Lethal yellowing disease (LYD) is a devastating phytoplasma-mediated condition affecting about 35 palm species and characterized by similar symptoms (Gurr *et al.*, 2016). LYD was first observed in the Caribbean Island at the end of the 19th century. In Jamaica and the Americas, the disease is simply referred to as LYD, and as lethal yellowing-like diseases in other parts of the globe. LYD poses major impacts on palm trees, especially coconut trees, thus affecting global coconut production (Oropeza-Salín *et al.*, 2020). LYD and related diseases lead to rapid palm death, causing premature fruit shedding, necrosis, and leaf yellowing, with no known cure (Gurr *et al.*, 2016; Dollet *et al.*, 2009). These outbreaks, spanning over five decades in various countries worldwide, have caused extensive losses, even affecting previously resistant coconut cultivars in some regions, threatening coconut cultivation globally (Gurr *et al.*, 2016; Eziashi and Omamor, 2010). The disease is associated with '*Ca.* Phytoplasma palmae' (16SrIV-A, -B, -D, E and -F) in the Caribbeans and Americas (EFSA PLH Panel, 2017). '*Ca.* Phytoplasma palmicola' (16SrXXII-A, -B) in West Africa and Mozambique (Harrison *et al.*, 2014) and '*Ca.* Phytoplasma cocostanzaniae' (16SrIV-C) in Kenya and Tanzania. In Papua New Guinea, '*Ca.* Phytoplasma noviguineense' (16SrIV) is associated with Bogia Cococnut Syndrome (Miyazaki *et al.*, 2018).

Management strategies

LYD outbreaks have had devastating impacts on coconut palms and other susceptible species (Gurr *et al.*, 2016). Management of LYD involves various approaches, including removal and destruction of infected palms to reduce spread of disease, controlling insect vectors and employing resistant palm species or varieties (Gurr *et al.*, 2016). The persistence of phytoplasmas in alternative hosts and weed reservoirs complicates disease management. Application of antibiotics such as oxytetracycline and cultural practices via trunk injections have been attempted, though with limited success (Soto *et al.*, 2021).

'*Candidatus* Phytoplasma solani'

The outbreak of '*Ca.* Phytoplasma solani' in Serbia and neighbouring regions posed a severe threat to crops, such as potatoes and tomatoes, causing stunting and leaf deformation (Mitrović *et al.*, 2022; Kosovac *et al.*, 2018). The pathogen's prevalence in Europe results in substantial economic losses, despite control efforts involving quarantine measures, crop rotation and insecticides application (Kosovac *et al.*, 2023; Jakovljević *et al.*, 2020; Quaglino *et al.*, 2013). Challenges persist due to its varied host range, making vector control complex and necessitating separate disease management strategies in affected regions (Kosovac *et al.*, 2023; Pierro *et al.*, 2020).

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Table 3. Challenges and solutions for early detection of phytoplasma

Challenges of early detection	Solutions	References
Lack of visible symptoms during initial stages	Molecular techniques such as PCR and LAMP for rapid and sensitive identification	Parnell *et al.*, 2017; Dyussembayev *et al.*, 2021
Low concentration in woody hosts	Proper sampling techniques and reliable nucleic acid extraction methods	Jawhari *et al.*, 2015; EPPO, 2018
Erratic distribution within infected plants	Use of biosensing techniques and advanced tools for plant pathogen detection	Nair and Manimekalai, 2021; Gupta *et al.*, 2023
Diverse range of plant hosts	Universal PCR primers designed for the amplification of the 16S rRNA gene of any known phytoplasma	EPPO, 2018
Phytoplasmas disguising in plant's vascular system	New forms of surveillance, including remote sensing, citizen science initiatives and diagnostic networks	Parnell *et al.*, 2017
Difficulty in predicting effectors	Efforts towards reliable comparison of effectoromes, overcoming prediction challenges	Carreón-Anguiano *et al.*, 2023
Late spring detection challenges	Understanding the duration required for phytoplasma growth on stems, branches and new leaves	Gupta *et al.*, 2023

Management strategies

Managing outbreaks of '*Ca.* Phytoplasma solani' involves integrated pest management practices, including the removal and destruction of infected plants, controlling insect vectors and implementing strict quarantine measures to limit disease spread (Carminati *et al.*, 2021). Cultural practices such as crop rotation, planting disease-resistant cultivars and the use of healthy planting material, contribute to disease reduction (Sémétey *et al.*, 2018). Chemical control targeting insect vectors may be employed, but effectiveness varies due to the diverse nature of the vectors and their habitats (Mitrović *et al.*, 2022). Lessons learned from '*Ca.* Phytoplasma solani' outbreaks stress early detection, rapid response and preventive measures (Nutricati *et al.*, 2023). Understanding vector behaviour aids in targeted control. Quarantine and biosecurity are crucial (Chalam *et al.*, 2023). The current situation regarding '*Ca.* Phytoplasma solani' outbreaks varies across affected regions, with sporadic occurrences reported in some areas while persistent outbreaks continue in others (Mitrović *et al.*, 2022). Despite control efforts, challenges remain due to the complexity of vector-pathogen interactions, multiple potential reservoir hosts and environmental factors influencing disease spread (Kosovac *et al.*, 2023). Research on '*Ca.* Phytoplasma solani' emphasizes pathogen diversity, genetic studies and rapid diagnostics (Nutricati *et al.*, 2023; Çağlar *et al.*, 2021).

Focus areas includes vector biology, biocontrol agents and breeding resistant plants. The outbreak highlights the critical importance of proactive disease management through surveillance, early detection, and eradication. Integrated methods and collaborations have proven crucial for successful control in vineyards (Kosovac *et al.*, 2023; Mitrović *et al.*, 2022). Figure 1 indicates representative phytoplasma diseases, countries of major reported occurrence, management strategies, lessons learnt, and current situations and research efforts. The integration of various control methods, including both cultural practices and chemical treatments, was vital for effective disease management. Furthermore, collaboration between researchers, vineyard owners and governmental agencies was essential to implement and sustain these control measures, successfully.

International cooperation for phytoplasma disease control

The International Plant Protection Convention (IPPC) has outlined measures to curb the global outbreak of plant pests, aiming to mitigate negative impacts on food security, biodiversity, and economic prosperity. Currently, there is no effective curative treatment for LYD; however, thanks to the efforts of Michael Black, outbreaks have been maintained at manageable levels. As a palm grower in Jamaica, Black has significantly reduced the incidence of the disease on his farm by employing an integrated pest management approach. This includes on-farm quarantine measures, rigorous weekly surveillance, the removal and burning of palms exhibiting LYD symptoms, and the replanting of disease-resistant varieties. Also, by managing weeds and applying fertilizers effectively, as shown in the studies by Myrie *et al.* (2011), Serju (2012), and CARDI (2013), farmers can improve the health and yield of palm crops.

A large group of plant pests threaten global food production, forest productivity, biodiversity, and natural flora. Therefore, preventing the spread and establishment of these harmful pests in new countries and regions is the main task of national plant protection organizations (NPPOs) and the IPPC. These NPPOs are reliable entities entrusted with responsibilities to provide and receive government-to-government phytosanitary assurances, and should be resourced to accomplish this core mandate successfully. Myrie *et al.* (2011) and Serju (2012) documented that an extensive comparison of seven selected farms over several years revealed a significant reduction in LYD incidence on four farms that implemented Black's management practices. In contrast, three farms that did not adopt any management strategies continued to suffer severe losses due to the disease. Globally, it is recommended that infected palms be promptly removed and destroyed. Eradication programs should be enhanced with natural barriers to prevent vector movement, along with the application of insecticides and antibiotic treatments via trunk injection using tetracycline products (McCoy *et al.*, 1976; Eziashi and Omamor, 2010; Wang *et al.*, 2024). Figure 2 shows a network diagram showing international research collaboration under EU-funded TROPICSAFE Project (Adapted from Final Handbook with Innovation Factsheets).

Research initiatives and funding

Phytoplasma research projects have received a substantial amount of financial support from funding agencies to study pathogen identification on different crops across the globe. The European Union's Horizon 2020 programme (2014–2020) allocated nearly €80 billion to research and innovation. The TROPICSAFE Project, involving 22 partners from 12 countries, received €4 million of this

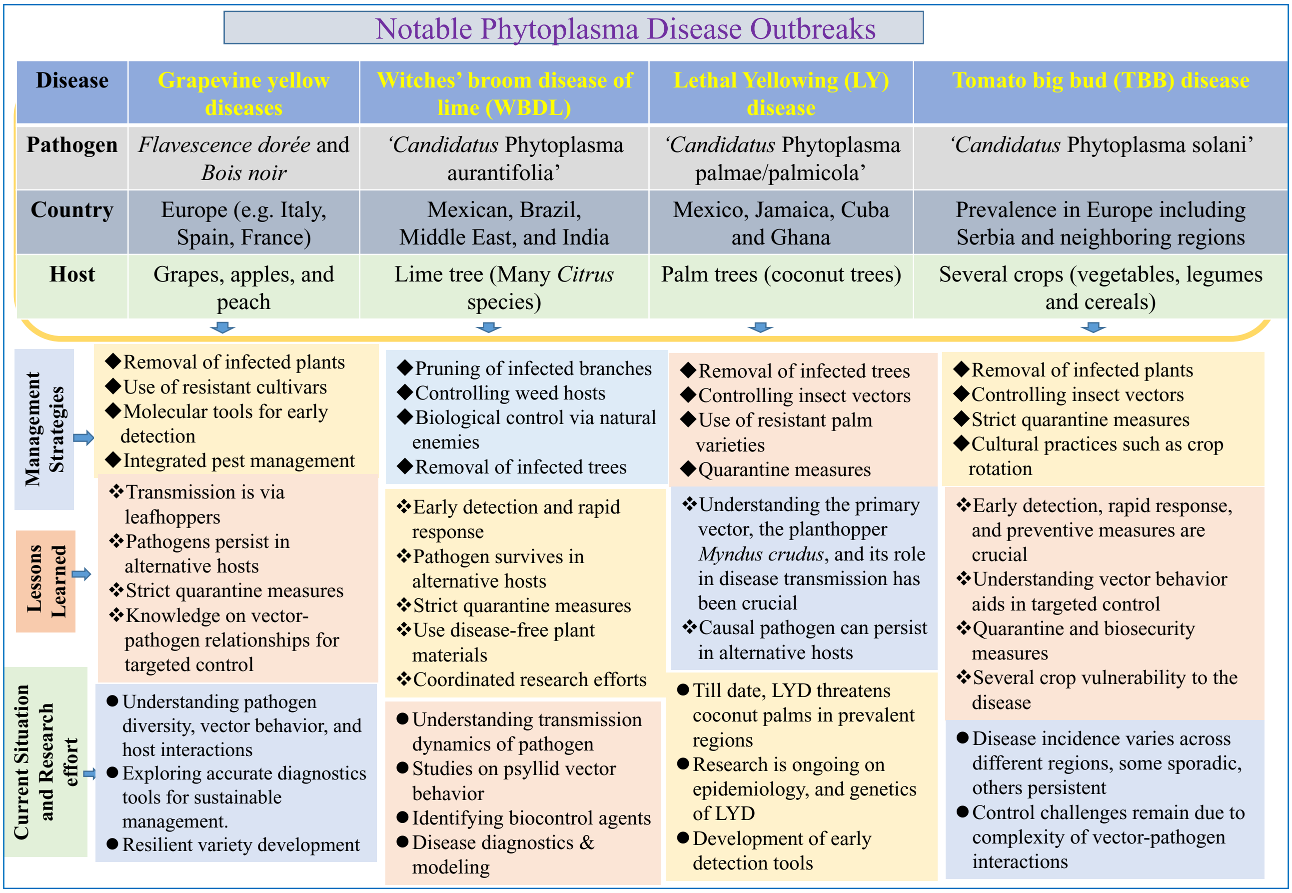

Figure 1. Representative phytoplasma diseases, countries of major reported occurrence, management strategies, lessons learnt and current situation and research effort.

funding. The project focuses on identifying insect-borne prokaryote-associated diseases in tropical and subtropical perennial crops (www.tropicsafe.eu). Major diseases under this funding include lethal yellowing in palms ('*Ca.* Phytoplasma' species), yellows in grapevines ('*Ca.* Phytoplasma' species), and Huanglongbing in citrus ('*Ca.* Liberibacter' species). The aims include: (1) generating data on epidemiological cycles, insect vectors, and alternative host plants; (2) developing rapid, reliable detection methods and holistic management approaches; and (3) scaling up demonstration activities and field trials to improve farmers' livelihoods. Researchers from Canada and Côte d'Ivoire are also exploring ways to reduce coconut crop losses from lethal yellowing, which devastates plantations in West Africa. Improved understanding of the disease, plant breeding, and replanting efforts will help preserve the livelihoods of Côte d'Ivoire's coconut farmers. Table 4 shows funding allocation for phytoplasma research. The Canadian International Food Security Research Fund (CIFSRF) has contributed CA$2.57 million to this work.

Management strategies of phytoplasma-mediated diseases

The lack of a cell wall by phytoplasmas makes them difficult to target with traditional bactericides (Hogenhout *et al.*, 2008). Consequently, managing phytoplasma-mediated diseases primarily involves targeting the insect vectors responsible for transmitting these pathogens, rather than directly treating infected plants (Bianco *et al.*, 2019). As there is currently no effective cure, mitigation strategies emphasize preventive cultural practices (Kumari *et al.*, 2019). Cultural practices play a pivotal role in managing phytoplasma diseases and include adopting resistant plant varieties, rogueing (removing and destroying infected plants), ensuring the use of clean propagating material, and controlling insect vectors known to transmit phytoplasmas (Bertaccini, 2021).

Antibiotics and other molecules

Even though antibiotics such as tetracyclines have been used in the field to control phytoplasma diseases in some high-value crops, their extensive use is limited by costs, emergence of resistant microbial strains, potential hazards to humans and concerns with environmental pollution (Tanno *et al.*, 2018). Other molecules such as ribosome-inactivating proteins, plant hormones and resistance inducers have been tested and shown to exhibit some level of efficacy (Bertaccini, 2021). Additionally, essential oils and ribosome-inactivating proteins have demonstrated promising results in eliminating phytoplasmas in micro-propagated infected plant shoots (Bertaccini, 2021). In vitro systems have also been utilized to produce phytoplasma-free germplasm, which can be further propagated in insect-proof conditions before deployment in open fields (Hogenhout, 2009). These diverse strategies offer a multifaceted approach to mitigate the impact of phytoplasma diseases on crops while minimizing reliance on traditional antibiotics.

Resistant plant varieties

Resistant plant varieties play a crucial role in reducing the susceptibility of crops to phytoplasma infections (Gorshkov and Tsers, 2022). Several species have been identified for their resistance

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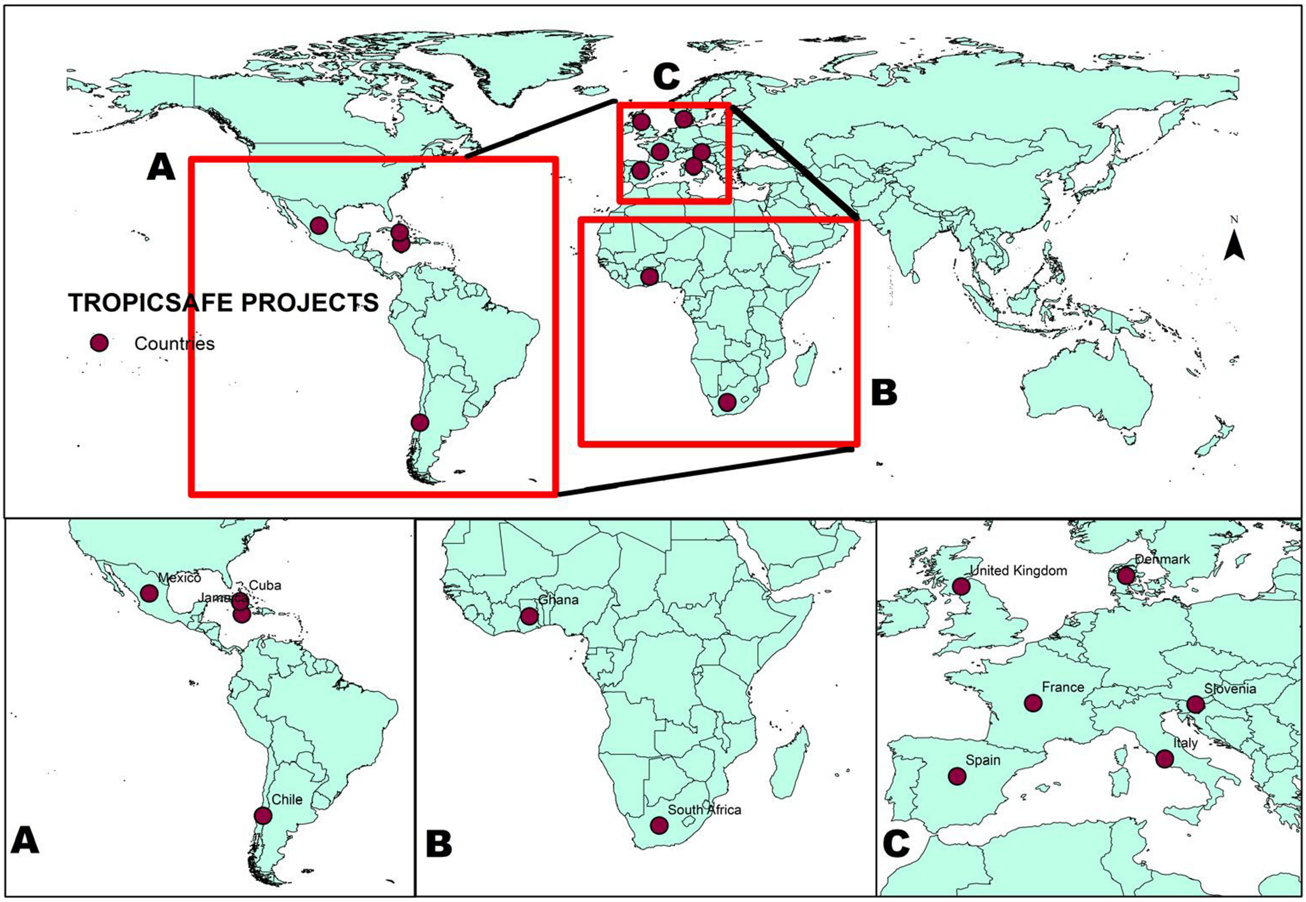

Figure 2. A Network Map showing international research collaboration involved in the TROPICSAFE Project (Adapted from Final Handbook with Innovation Factsheets, www.tropicsafe.eu). A=The Americas, B=Africa, C=Europe.

to specific phytoplasma infections, contributing to crucial insights for disease management and breeding programs (Wei *et al.*, 2021). For example, *S. mulayanum* and *S. alatum* have been identified as being resistant to sesame phyllody, with *S. alatum* specifically noted for possessing a dominant gene linked to phyllody resistance (Yadav *et al.*, 2022). In temperate fruit trees, various *Prunus* species, including European plum, sour and sweet cherry, demonstrated reduced susceptibility to European Stone Fruit Yellows (ESFY) phytoplasma infections, with some exhibiting tolerance and resistance (Cieślińska, 2011). Additionally, several *Prunus* species, such as *P. betulifolia, P. calleryana, P. nivalis, P. elaeagrifolia, P. syriaca, P. pashia* and *P. dimorphophylla,* were found to be resistant to Pear Decline phytoplasma infections (Marcone *et al.*, 2023). These resistant cultivars are essential for long-term disease management and breeding efforts aimed at developing elite plant lines with enhanced resistance (Roy *et al.*, 2023). Natural resistance mechanisms, including non-host resistance, are also valuable in managing phytoplasma diseases (Hogenhout, 2009). While resistant plant varieties play a crucial role in reducing the susceptibility of crops to phytoplasma diseases, their effectiveness may diminish over time. This may can be due to the emergence of new phytoplasma strains or changes in environmental conditions that can overcome these resistance mechanisms.

Use of disease-free materials

The use of disease-free planting material is crucial to minimizing phytoplasma contamination (Kumari *et al.*, 2019). This approach aligns with the principles of integrated pest management, emphasizing sustainable and holistic practices in agriculture (Deguine *et al.*, 2021). Ongoing research and adaptive strategies remain crucial to staying ahead of evolving challenges posed by phytoplasma diseases and their vectors.

Rogueing

Rogueing, the removal and destruction of infected plants, helps prevent the spread of phytoplasmas to healthy plants (Jeger and Gilligan, 2007). The primary objective of rogueing is twofold. Firstly, it aims to suppress the disease by preventing the dissemination of phytoplasmas (Bertaccini, 2021). In doing so, it disrupts the transmission cycle, especially considering the common mode of transmission through insect vectors. Secondly, rogueing serves as a vigilance monitoring tool, enabling the early detection of infected plants (Sisterson and Stenger, 2013). Early identification is crucial for swift action, preventing the disease from establishing and spreading extensively within the crop. However, rogueing is labour-intensive and costly, especially for small-scale farmers (Welbaum, 2017). Training and awareness programmes are therefore essential to ensure accurate symptom recognition.

Control of insect vectors

Phytoplasma diseases are primarily transmitted by insect vectors, particularly leafhoppers, planthoppers and psyllids (Kumari *et al.*,

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Table 4. Funding allocation for Phytoplasma research

	Funding agency	Amount	Time span	Location of collaborators	Reference
1.	European Union (TROPICSAFE)	€4 million	2014–2020	Global	www.tropicsafe.eu
2.	CIFSRF-IDRC	CA$2.57 million	2014–2017	West Africa & Canada	idrc-crdi.ca
3.	Citrus Research and Development Foundation	US$124 million	2010–2017	Florida, USA	The National Academies Press. https://doi.org/10.17226/25026
4.	European Union	€52.3 million	2013–2015	Europe	https://www.hrpub.org/download/20160930/UJAR5-10407286.pdf
5.	Kaken	¥7.9 Million	1995–1996	Asia	https://kaken.nii.ac.jp/en/grant/KAKENHI-PROJECT-07456026/
6.	Washington Tree Fruit Research commission	$230,561	2024–2027	North America	https://treefruit.wsu.edu/article/2024-washington-tree-fruit-research-commission-grant-awards-for-cherry

2019). Identification of vector species transmitting specific phytoplasma strains is essential for targeted control strategies. For example, the cixiid planthopper *Hyalesthes obsoletus* is the main vector of the 16SrI-B phytoplasma strain causing sesame phyllody (Kosovac *et al.*, 2018). In the case of ESFY, the psyllid *Cacopsylla pruni* is the primary vector transmitting the 16SrX-B phytoplasma to temperate fruit trees (Riedle-Bauer *et al.*, 2019). The control of insect vectors in the context of phytoplasma diseases requires a multifaceted and integrated approach (Weintraub and Beanland, 2006). By combining insect vector surveillance, biological control, and when necessary, targeted chemical interventions, farmers can effectively manage vector populations and minimize the risk of phytoplasma transmission (Skendžić *et al.*, 2021). Sustainable and environmentally friendly strategies are essential to protect agricultural ecosystems. Chemical vector control should be used cautiously due to potential ecological and environmental impacts (Gurr *et al.*, 2015). Nevertheless, in certain situations, specific classes of pesticides may be considered. These include neonicotinoids, pyrethroids, organophosphates, insect growth regulators (IGRs) and botanical insecticides (Lalah *et al.*, 2022). Important considerations include managing resistance, minimizing harm to non-target organisms, environmental impact, adherence to legal regulations and precise application timing (Damalas and Eleftherohorinos, 2011).

Good Agricultural Practices (GAPs)

Good sanitation practices, such as proper pruning and propagation techniques, are important in preventing the spread of phytoplasma diseases (Bertaccini, 2021). Timely planting is also critical, as susceptibility can vary with planting dates (Marcone *et al.*, 2023). To effectively manage phytoplasma diseases, it is crucial to combine multiple cultural practices, as relying on a single method may prove insufficient. Figure 3 is an infographic showing phytoplasmas disease management approaches.

Future perspectives

Human activities, such as monoculture farming and global trade, facilitate the rapid evolution of phytoplasmas, posing significant threats to global food security. Monitoring genetic diversity, mutation rates and potential host shifts is crucial for understanding and tackling emerging challenges. Expected trends include the development of more virulent strains and changes in host ranges (Venbrux *et al.*, 2023). Research into vector ecology, particularly the role of insect species, is essential to understand the factors influencing pathogen evolution and gene flow.

Technological advancement is vital for enhancing detection and control of phytoplasma infections (Carvajal-Yepes *et al.*, 2022). The collective employment of rapid and reliable diagnostic tools, molecular techniques such as PCR-based assays, advanced imaging technologies and omics Sciences such as genomics and proteomics offer promise for improved and accurate detection (Carvajal-Yepes *et al.*, 2022). Control strategies should explore new antimicrobial agents, resistant crop varieties and environmentally sustainable practices. Collaboration among researchers, agriculturists and industry players is crucial for practical solutions.

Developing resilient agricultural systems is imperative to mitigate the impact of emerging phytoplasma on global food security (Altieri, 1999). Integrated pest management, crop diversification and rotation practices are essential for enhancing crop resilience. Fostering resilient farming communities through education and extension services, empowering farmers with knowledge on disease prevention and sustainable practices; these contribute to building a robust defence against phytoplasma threats.

Recent breakthroughs in machine learning, geospatial analytics and big data mining, present exciting possibilities in battling phytoplasma-mediated diseases (Buja *et al.*, 2021; Kasinathan *et al.*, 2021; Ristaino *et al.*, 2021; Silva *et al.*, 2021; Zhang *et al.*, 2019). AI-driven monitoring systems can provide real-time alerts, contributing to proactive responses. Precision agriculture, guided by AI, optimizes resource use and enhances farm efficiency, providing adaptive management strategies against phytoplasma threats. These technologies also have the capacity to establish and strengthen global surveillance networks for phytoplasma for early detection and timely response (Carvajal-Yepes *et al.*, 2019). International collaboration, standardized surveillance protocols and remote sensing technologies are essential to prevent transboundary spread and ensure coordinated control measures.

In the long term, climate change may influence the spread of plant diseases, including phytoplasma infections (Chaloner *et al.*, 2021; Delgado-Baquerizo, 2020; Dudney *et al.*, 2021). Understanding the potential impact of climate change on the distribution and prevalence of phytoplasmas and their vectors is

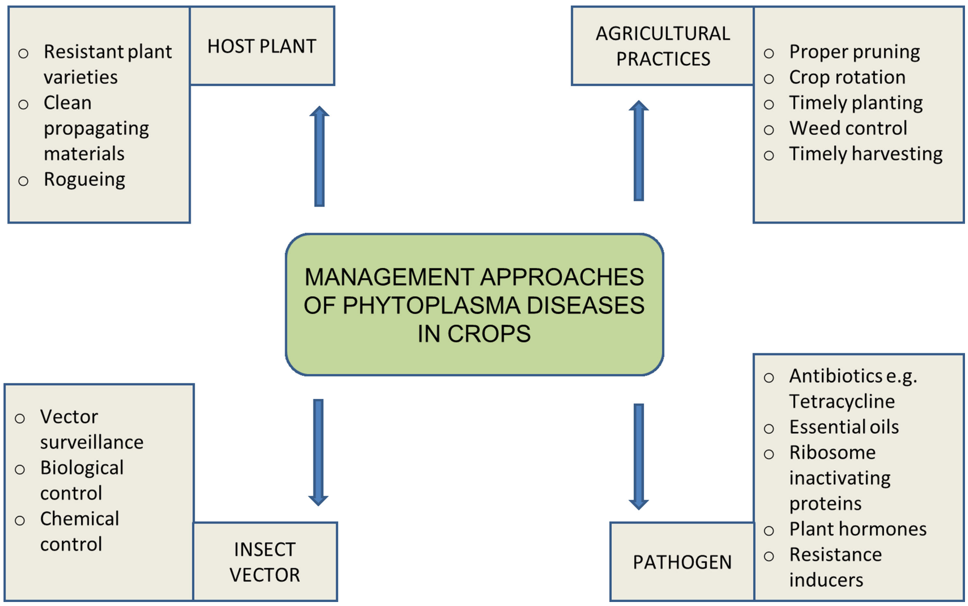

Figure 3. An infographic showing Integrated Pest Management Approaches.

critical. Climate modelling combined with epidemiological studies can predict areas at heightened risk, enabling proactive mitigation strategies.

Public–private partnerships are effective for accomplishing extension and outreach objectives in plant pathology (Markell *et al.*, 2020). Collaboration between academia, government, NGOs and agribusinesses expedites the development and implementation of new technologies and control strategies. Public-private collaborations enhance the accessibility and affordability of diagnostic tools, treatments and preventive measures, benefiting farmers globally.

Investing in capacity building and education programs is fundamental for building resilience plant protection (Gervais, 2004). Empowering individuals with knowledge and skills to identify, manage and prevent phytoplasma infections ensures a robust and adaptive agricultural sector. Training initiatives that cover integrated pest management, sustainable agriculture, and responsible technology use ensure a robust and adaptive agricultural sector capable of responding effectively to phytoplasma threats.

Conclusion

This review highlights the rising incidence of phytoplasma infections across diverse crops, ranging from staple grains to high-value cash crops, and their potential impact on food production. The adaptability of phytoplasmas to new environments and hosts, coupled with climate change, underscores the urgency of addressing this emerging agricultural challenge. The immediate and long-term implications for global food security necessitate a collaborative, multi-faceted approach to mitigate phytoplasma threats and safeguard future food supplies.

Data availability statement. All the data used and generated in the study can be found in this manuscript.

Author contributions. OFA: Study-conceived and designed, Writing-original draft, Review & Editing; AKD, JOH: Writing-original draft, Review & Editing; FKA, JO, AM, AFO, KO, FLS, NEY, HL: Writing-original draft; BAO: Formatting, Review & Editing.

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