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Review

Plants and Phytoplasmas: When Bacteria Modify Plants

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Abstract: Plant pathogen presence is very dangerous for agricultural ecosystems and causes huge economic losses. Phytoplasmas are insect-transmitted wall-less bacteria living in plants, only in the phloem tissues and in the emolymph of their insect vectors. They are able to manipulate several metabolic pathways of their hosts, very often without impairing their life. The molecular diversity described (49 '*Candidatus* Phytoplasma' species and about 300 ribosomal subgroups) is only in some cases related to their associated symptomatology. As for the other plant pathogens, it is necessary to verify their identity and recognize the symptoms associated with their presence to appropriately manage the diseases. However, the never-ending mechanism of patho-adaptation and the copresence of other pathogens makes this management difficult. Reducing the huge impact of phytoplasma-associated diseases in all the main crops and wild species is, however, relevant, in order to reduce their effects that are jeopardizing plant biodiversity.

Keywords: plant diseases; bacterium; symptoms; pathogenicity; molecular classification

Citation: Bertaccini, A. Plants and Phytoplasmas: When Bacteria Modify Plants. *Plants* **2022**, *11*, 1425. https://doi.org/10.3390/plants11111425

Academic Editors: Milan S. Stankovic, Paula Baptista and Petronia Carillo

Received: 3 May 2022
Accepted: 24 May 2022
Published: 27 May 2022

1. Introduction

Plant pathogen presence is usually known as a very dangerous component of agricultural ecosystems and is associated with huge economic losses. The world history was also often shaped by dangerous plant epidemics or pandemics such as the wheat rust that was among the main causes of the Roman empire failure, the potato late blight by *Phythophthora infestans* producing the Irish migration to America due to the famine, and the coffee rust obliging to stop the coffee cultivation is several areas, mainly in islands. Recently plant pathogenic bacteria have played an important role in reducing kiwi cultivation, due to the canker by *Pseudomonas syringae* pv. *actinidiae* [1], and citrus, through the greening ('*Candidatus* Liberibacter' species) [2] diseases. Moreover, there are bacteria hosted by plants and insects that are both associated with severe epidemic or with useful changes in plant behavior. While their presence in apple trees causes severe losses in production and kills millions of coconut palm trees in the Caribbean, the presence of a poinsettia branching bacterium is allowing its commercial production as pot plant (Figure 1).

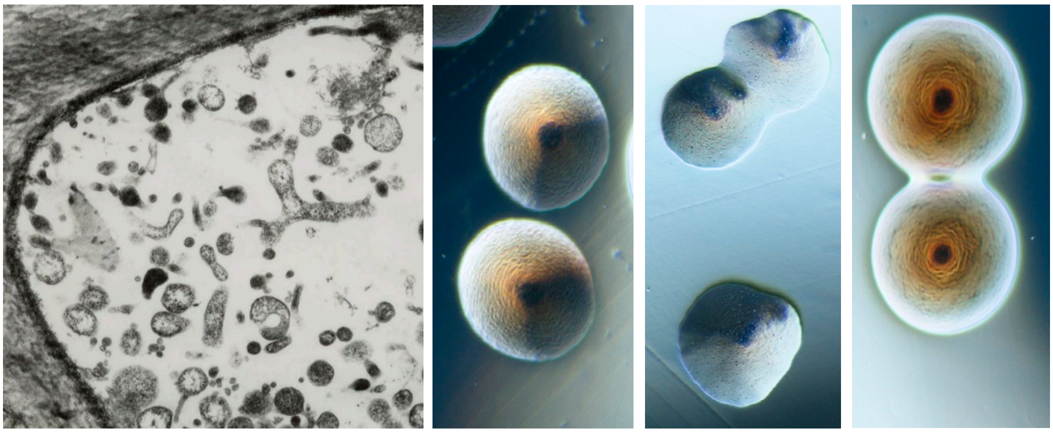
(**a**) (**b**) (**c**)

Figure 1. Coconut (**a**), aster (**b**), and poinsettia (**c**) infected by phytoplasmas.

Phytoplasmas are insect-transmitted wall-less bacteria provisionally classified to be the '*Candidatus* Phytoplasma' species [3,4]. They live only in the plant phloem tissues and in the emolymph of their insect vectors, especially concentrated in the salivary glands. Their relationship with both plants and insects is very intimate and they are able to manipulate several metabolic pathways, very often without impairing the host's life [5].

2. Phytoplasma Discovery

The phytoplasma presence in plants historically dates back about 1000 years, when special tree peonies exhibiting green flowers were given to the Chinese court during the Song dynasty (900 BC) as the most precious and beautiful flower of the empire. However, scientific records of phytoplasma-associated plant diseases started when, in 1967, mulberry dwarf, rice yellow dwarf, and sweet potato witches' broom, long considered to be caused by viruses, using electron microscopy, were found to be colonized by small pleomorphic bodies (80–800 nm in diameter) resembling mycoplasmas (bacterial pathogens of humans and animals) and were named mycoplasma-like organisms (MLOs) [6]. Their discovery stimulated worldwide investigation and numerous plant diseases were associated with the consistent presence of MLOs. These bacteria were long considered unculturable, but about 10 years ago, colonies containing molecularly different phytoplasmas began to be obtained in artificial media from different infected plant species (Figure 2) [7–11].



(**a**) (**b**)

Figure 2. Transmission electron microscopy picture of a thin section in the phloematic tissue of a phytoplasma infected gladiolus plant showing the presence of strong pleomorphism (×8000) (**a**). Tree morphotypes of colonies containing phytoplasmas under binocular microscope (×40) (**b**).

3. Phytoplasma Classification

The '*Candidatus* Phytoplasma' genus provisional classification is highly relevant due to its application in epidemiological and ecological studies, mainly aimed at keeping the severe phytoplasma plant diseases under control worldwide. The updated proposed guidelines accommodate those '*Ca*. Phytoplasma' species strains sharing > 98.65% sequence identity of their full or nearly full 16S rRNA gene sequences, obtained with at least 2-fold coverage of the sequence, compared with those of the reference strain of such species [4]. The officially published '*Candidatus* Phytoplasma' species are 49; however, they do not cover all the relevant biodiversity, especially in reference to differential geographic distribution and/or host species. Therefore, the differentiation in ribosomal groups and subgroups [12] is still valuable and should be used to be able to work on their epidemiology and prevention in the different areas of the world. The main distribution of strains is tightly related to the geographic areas and to the dissemination performed by propagation materials, such as cuttings and seeds, that are also infected, even if only in low percentages (1–3%).

4. Relationship between Phytoplasma Symptomatology and Classification

Together with the study on the diseases associated with the presence of these bacteria, the first step was to give them a name according to the diverse disease in which the association was detected with specific phytoplasmas. Today, 30 years after this exercise started it appears clear that the molecular diversity described in phytoplasmas (49 '*Candidatus* Phytoplasma' species and about 200 ribosomal subgroups) using the 16S ribosomal gene as basic standard is only in some cases related to a differential symptomatology. Identical symptoms are associated with different phytoplasmas and vice versa. Moreover, phytoplasmas associated with decline symptoms in some species could be associated with phyllody/virescence in others, such as '*Ca.* P. solani' infecting potatoes, tomatoes, and grapevine. Therefore, contrary to the other plant pathogens it is necessary to verify the pathogen identity by molecular tools on a case-by-case basis; however, at the same time, it is of utmost importance to also recognize the symptoms associated with the presence of the phytoplasmas in order to appropriately manage the disease. This review of the main symptoms and several associated phytoplasmas worldwide is aimed at helping the recognition of the presence of these bacteria in plants, further clarifying their relationship with the host plants. This feature is, however, not stable over time also in the same plant species, considering the never-ending mechanism of patho-adaption that is part of life also in microorganisms; pathogens are special microorganisms that are simply looking for new ecological niches to ensure their survival and do not aim to destroy or kill the hosts.

4.1. Shoot Proliferation and Witches' Broom

Diseases with symptoms of witches' broom can be caused by basidiomycetes but could also be associated with the presence of phytoplasmas. In both cases they are economically important in a number of crop plant species, including the cocoa tree, jujube, citrus, and apple and timber trees, such as poplar, *Melia azedarach*, and paulownia (Figure 3). Among woody species, this malformation is almost always associated with the presence of specific phytoplasmas, such as in apple ('*Ca.* P. mali), lime ('*Ca.* P. aurantifolia'), lilac ('*Ca.* P. fraxini'), paulownia ('*Ca.* P. asteris'), almond ('*Ca.* P. phoenicium'), *Juniperus* (16SrIX-E), walnut (16SrIII-G), *Balanites triflora* ('Ca. P. balanites'), spartium ('*Ca.* P. spartii'), black alder (16SrX-E), hibiscus ('*Ca.* P. brasiliense'), *Guazuma* spp. (16SrXV-B), chestnut ('*Ca.* P. castaneae'), *Cassia italica* ('*Ca.* P. omanense'), and salt cedar ('*Ca.* P. tamaricis'). In herbaceous host plants, the presence of witches' broom was reported in diverse species, some of them as hosts of new phytoplasma strains (Table 1), such as strawberry, peanut, cactus, tabebuja, tomatillo, chayote, black raspberry, erigeron, alfalfa, and pigeon pea.

(**a**) (**b**) (**c**) (**d**)

Figure 3. Cactus pear (*Opuntia ficus-indica*) proliferation (**a**), apple proliferation (**b**), citrus witches' broom (**c**), and jujube witches' broom (**d**) are associated with the presence of phytoplasmas in diverse areas of the world.

Table 1. Molecular diversity and geographic distribution of selected phytoplasmas belonging to different ribosomal groups/'*Candidatus* Phytoplasma' species (marked by different color) associated with witches' broom symptoms.

Disease (Acronym)	Continent	16Sr Subgroups	'*Candidatus* Phytoplasma' Species	GenBank Accession Number	References
Aster yellows w. b. (AY-WB)	America	16SrI-A	'*Ca*. P. asteris'	NC_007716	[13]
Paulownia w. b. (PaWB)	Asia	16SrI-D		AY265206	[14]
Strawberry witches' broom (STRAWB1), (STRAWB2)	America	16SrI-I / -K		U96614, U96616	[15]
Peach rosette-like (PRU0382)	America	16SrI-W		HQ450211	[16]
Peanut witches' broom (PnWB)	America	16SrII-A		L33765	[17]
Lime witches' broom (WBDL)	Asia	16SrII-B	'*Ca*. P. aurantifolia'	U15442	[18]
Cactus witches' broom (CWB)	Asia	16SrII-G to -L		EU099568, EU099552, EU099569, EU099572, EU099551, EU099546, EF647744	[19]
Tabebuia witches' broom	America	16SrII-O			[20]
Tomatillo witches' broom	America	16SrII-T		U125185	[21]
Walnut witches' broom (WWB)	America	16SrIII-G		AF190226, AF190227	[22]
Poinsettia branch-inducing (PoiBI)	Europe, America	16SrIII-H		AF190223	[22]
Chayote w. b. (ChWBIII)	America	16SrIII-J		AF147706	[23]
Black raspberry w. b. (BRWB7)	America	16SrIII-Q		AF302841	[24]
Conyza witches' broom	America	16SrIII-X		KC412026	[25]
Jujube witches' broom (JWB-G1)	Asia	16SrV-B	'*Ca*. P. ziziphi'	AB052876	[26]
Balanites triflora w. b. (BltWB)	Asia	16SrV-F	*Ca*. P. balanitae'	AB689678	[27]
Korean jujube witches' broom	Asia	16SrV-G		AB052879	[26]
Bischofia polycarpa witches' broom	Asia	16SrV-H		KJ452547	[28]
Blackberry witches' broom	Europe	16SrV-I		KR233473	[29]
Clover proliferation (CP)	America	16SrVI-A	'*Ca*. P. trifolii'	AY390261	[30]
Erigeron witches' broom (ErWB)	America	16SrVII-B		AY034608	[31]
Argentinian alfalfa w.b. (ArAWB)	America	16SrVII-C		AY147038	[32]
Erigeron w. b. (EboWB-Br0)	America	16SrVII-D		KJ831066	[33]
Loofah witches' broom (LufWB)	Asia	16Sr VIII-A	'*Ca*. P. luffae'	AF086621	[34]
Pigeon pea w. b. (PPWB)	America	16SrIX-A		AF248957	[35]
Almond witches' broom (AlWB)	Asia	16SrIX-B/-D	'*Ca*. P. phoenicium'	AF515636, AF515637	[36]
Juniperus witches' broom	America	16SrIX-E		GQ925918	[37]
Almond and stone fruit witches' broom (N27-2), (A1-1)	Asia	16SrIX-F/-G	'*Ca*. P. phoenicium'	HQ407532, HQ407514	[38]
Apple proliferation (AP)	Europe, Asia	16SrX-A	'*Ca*. P. mali'	AJ542541	[39]
Spartium witches' broom (SpaWB)	Europe	16SrX-D	'*Ca*. P. spartii'	X92869	[40]

Table 1. *Cont.*

Disease (Acronym)	Continent	16Sr Subgroups	'*Candidatus* Phytoplasma' Species	GenBank Accession Number	References
Black alder w. b. (BAWB, BWB)	Europe	16SrX-E		X76431	[41]
Hibiscus witches' broom (HibWB)	America, Asia	16SrXV-A	'*Ca.* P. brasiliense'	AF147708	[42]
Guazuma w. b. (GWB)	America	16SrXV-B		HQ258882	[43]
Chestnut witches' broom	Asia	16SrXIX-A	'*Ca.* P. castaneae'	AB054986	[44]
Rhamnus witches' broom	Europe	16SrXX-A	'*Ca.* P. rhamni'	AJ583009	[40]
Weeping tea witches' broom	Oceania	16SrXXV-A *		AF521672	[45]
Cassia w. b. (CaWB)	Asia	16SrXXIX-A	'*Ca.* P. omanense'	EF666051	[46]
Bindweed witches' broom (RBiWB)	Asia	16SrXXIX-B		KY047493	[47]
Salt cedar witches' broom	Asia	16SrXXX-A	'*Ca.* P. tamaricis'	FJ432664	[48]

w. b., witches' broom; *, described as sequence deposited in GenBank only.

The excessive shoot proliferation results in poor or no fruit production and severely reduces the cultivation of some of these crops. Citrus in the Arabian Peninsula, jujube in China, and apple proliferation in Europe are some of the most severe cases that greatly reduce the possibility to produce and commercialize popular fruits. This modification is due to the loss of apical dominance of the shoots linked to disorders in the hormone balance.

4.2. Stunting and Little Leaf

Stunting in plants could be due to virus or phytoplasma presence; however, it must also be verified that glyphosate or similar pesticides were not applied in the area in which these malformations are present in plants in the past years, since this can produce indistinguishable symptoms (Figure 4). The presence of phytoplasmas is reported in several plant species enclosing small fruits, vegetables, corn, and soybean; in some cases, these bacteria were associated with the presence of little leaf or stunting also in trees, such as cherry, eucalyptus, and *Sophora japonica* [49] (Table 2). In strawberries the case *Fragaria multicipita* was discovered to be not a true species, but just a cloned phytoplasma-infected genotype [15]. The hormone imbalance, according with the diverse infected species, is usually present and the transportation of starch and other metabolites for the appropriate development is very often impaired.

(**a**) (**b**) (**c**) (**d**)

Figure 4. *Sophora japonica* stunting and yellows (**a**); *Eucalyptus* little leaf (**b**), periwinkle little leaf (**c**), and corn stunting (**d**).

Table 2. Molecular diversity and geographic distribution of selected phytoplasmas belonging to different ribosomal groups/'*Candidatus* Phytoplasma' species (marked by different color) associated with little leaf and stunting symptoms.

Disease (Acronym)	Continent	16Sr Subgroups	'*Candidatus* Phytoplasma' Species	GenBank Accession Number	References
Blue dwarf wheat (BDW)	Asia	16SrI-C	'*Ca.* P. tritici'	DQ078304	[50]
Blueberry stunt (BBS3)	America	16SrI-E		AY265213	[14]
Cherry little leaf (ChLL)	Europe	16SrI-Q		AY034089	[51]
Pepper little leaf (PeLL)	America	16SrI-S		DQ092321	[52]
Tomato little leaf (ToLL)	America	16SrI-T		DQ375238	[52]
Vasconcellea cundinamarcensis little leaf	China	16SrII-U		KP057205	[53]
Spiraea stunt (SP1)	America	16SrIII-E		AF190228	[23]
Heterothalamus little leaf (HetLL)	America	16SrIII-W		KC412029	[26]
Broccoli stunt (BSP-21)	America	16SrIII-Z		JX626327	[22]
Rubus stunt (RuS)	Europe	16SrV-E	'*Ca.* P. rubi'	AY197648	[54]
Fragaria multicipita, multiplier disease	America	16SrVI-B		AF190224	[15]
Periwinkle little leaf (PLL-Bd)	Asia	16SrVI-D		AF228053	[55]
Portulaca little leaf (PLL-Ind)	Asia	16SrVI-H		EF651786	[56]
Soybean stunt (SoyST1c1)	America	16SrXXXI-A	'*Ca.* P. costaricanum'	HQ225630	[57]

4.3. Phyllody and Virescence

The transformation of different plant organs into leaves is a very relevant symptom among those associated with phytoplasma presence and is known as phyllody; this type of malformation could also be due to the application of pesticides based on hormone-like molecules. The virescence is the change of the color of flowers to green, which is due to phytoplasma presence, but in some cases the diagnostics can be tricked by the existence of flowers that are green and the presence of genetic factors modifying the anthocian distribution in the plant, as can be seen in a Chinese variety of rose and in some special clones of periwinkle (Figure 5). The most relevant phytoplasma-associated diseases are reported in flowering species for commercialization; however, virescence is also present in horticultural and seed crops, such as tomatoes, cabbages, strawberries, and clover, among several other species (Table 3).

(**a**) (**b**) (**c**) (**d**) (**e**)

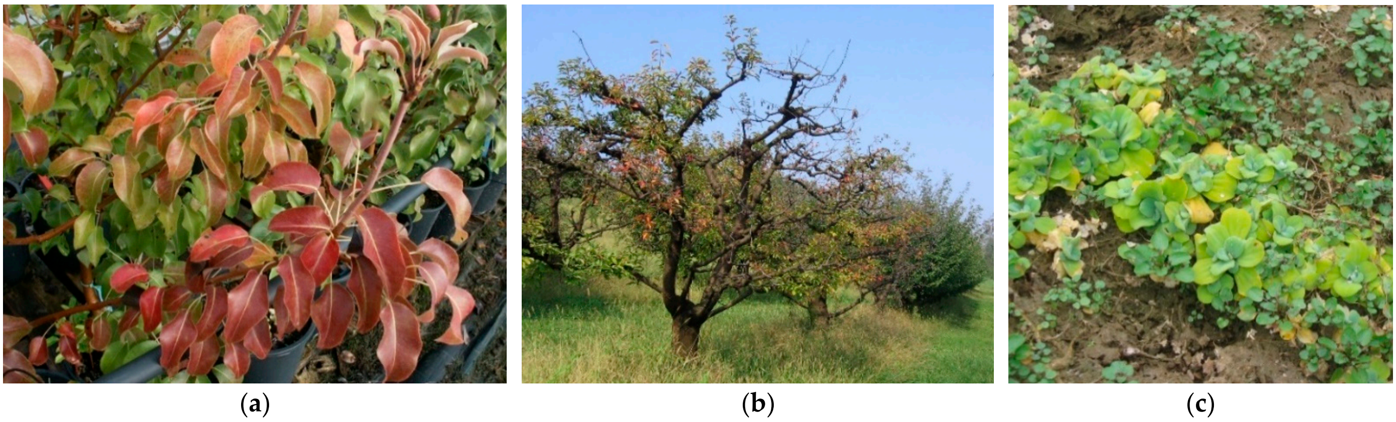
Figure 5. Virescence in gladiolus (**a**) and in periwinkle (**b**); phyllody in echinaea (**c**), rose (**d**), and strawberry (**e**). The rose flowers are showing virescence and phyllody due to genetics, rather than the phytoplasma presence in all the others.

Table 3. Molecular diversity and geographic distribution of selected phytoplasmas belonging to different ribosomal groups/'*Candidatus* Phytoplasma' species (marked by different color) and associated with phyllody and virescence symptoms.

Disease (Acronym)	Continent	16Sr Subgroups	'Candidatus Phytoplasma' Species	GenBank Accession Number	References
Clover phyllody (CPh)	America	16SrI-C		AF222065	[15]
Faba bean phyllody (FBP)	Asia, Africa	16SrII-C		X83432	[58]
Pichris echioides phyllody (PEY)	Europe	16SrII-E		Y16393	[58]
Cotton phyllody (CoP)	Africa	16SrII-F		EF186827	[59]
Strawberry leafy fruit (SLF)	America	16SrIII-K		AF274876	[15]
Dandelion virescence (DanVir)	Europe	16SrIII-O/-P		AF370120, AF370119	[60]
Heterothalamus little leaf (HetLL)	America	16SrIII-W		KC412029	[26]
Centarurea solstitialis virescence (CSVI)	Europe	16SrVI-E		AY270156	[61]
Catharanthus phyllody (CPS)	Africa	16SrVI-F		EF186819	[59]
Naxos periwinkle virescence (NAXOS)	Europe, Asia, America	16SrIX-C		HQ589191	[62]
Sarsoon phyllody	Asia	16SrIX-H		KU892213	[63]
Japanese hydrangea phyllody	Asia	16SrXII-D	'*Ca.* P. japonicum'	AB010425	[64]
Mexican periwinkle virescence (MPV)	America	16SrXIII-A	'*Ca.* P. hispanicum'	AF248960	[65]
Strawberry green petal (STRAWB2)	America	16SrXIII-B		U96616	[15]
Malaysian periwinkle virescence (MaPV)	Asia	16SrXXXII-A	'*Ca.* P. malaysianum'	EU371934	[66]

4.4. Yellowing and Decline

One of the main symptoms associated with the presence of phytoplasmas is the yellowing, in several cases these bacteria are also known as agents of yellows diseases. Generally, the yellowing of the aerial portions of the plant is complemented by a general decline that led to a huge, and in several cases complete, loss of production (Figures 6 and 7). However, these symptoms can also be due to lack of nutrients, poor fertilization, and the presence of other pathogens infecting the root apparatus. The presence of phytoplasmas in plants exhibiting decline and yellowing must be considered together with these other factors in complex syndromes. The phytoplasmas associated with these symptoms are detected in some of the most economically relevant woody species, such as grapevine, fruit trees, and palms (especially coconut and other species for nut production) (Table 4). The metabolic basis for these symptoms is still very poorly understood, but the excessive consumption of sugar and the lack of its mobilization to the sink organs are involved.



(**a**) (**b**) (**c**)

Figure 6. Reddening in pear decline (**a**), yellowing in plum (**b**) and watercress (**c**).

(**a**) (**b**) (**c**)

Figure 7. Grapevine yellows (**a**), coconut lethal yellowing (**b**), and elm yellows (**c**) associated with the presence of diverse phytoplasmas.

Table 4. Molecular diversity and geographic distribution of selected phytoplasmas belonging to different ribosomal groups/'*Candidatus* Phytoplasma' species (marked by different color) associated with yellows and decline symptoms.

Disease (Acronym)	Continent	16Sr Subgroups	'*Candidatus* Phytoplasma' Species	GenBank Accession Number	References
Aster yellows (MAY)	America	16SrI-B	'*Ca.* P. asteris'	M30790	[14]
Aster yellows apricot Spain (A-AY)	Europe, America	16SrI-F		AY265211	[14]
Aster yellows (AV2192	Europe	16SrI-L		AY180957	[67]
Aster yellows (AVUT)	Europe	16SrI-M		AY265209	[17]
Aster yellows (IoWB)	America	16SrI-N		AY265205	[17]
Aster yellows from *Populus* (PopAY)	Europe	16SrI-P		AF503568	[68]
Papaya mosaic (PpM)	Oceania	16SrII-D	'*Ca.* P. australasia'	Y10096	[69]
Echinopsis yellow patch	America	16SrII-R		DQ535900	[21]
Peach X-disease (PX11CT1)	America	16SrIII-A	'*Ca.* P. pruni'	JQ044393	[22]
Clover yellow edge (CYE)	America, Europe	16SrIII-B		AF173558	[22]
Goldenrod yellows (GR1)	America	16SrIII-D		GU004372	[22]
Milkweed yellows (MW1)	America	16SrIII-F		AF510724	[22]
Virginia grapevine yellows (VGYIII)	America	16SrIII-I		AF060875	[70]
Western peach X-disease (WX)	America	16SrIII-S		L04682	[71]
Coconut lethal yellowing (LYJ-C8)	America	16SrIV-A	'*Ca.* P. palmae'	AF498307	[4]
Yucatan coconut lethal decline (LDY)	America	16SrIV-B		U18753	[72]
Tanzanian coconut lethal decline (LDT)	Africa	16SrIV-C	'*Ca.* P. cocostanzaniae'	X80117	[72]
Texas phoenix decline (TPD	America	16SrIV-D		AF434969	[73]
Coconut lethal yellowing (LYDR-B5)	America	16SrIV-E		DQ631639	[74]
Washingtonia robusta decline	America	16SrIV-F		EU241512	[73]
Elm yellows (EY)	Europe, America	16SrV-A	'*Ca.* P. ulmi'	AY197655	[75]
'Flavescence dorée' (FD-C)	Europe	16SrV-C		X76560	[76]
'Flavescence dorée' (FD-D)	Europe	16SrV-D		AJ548787	[76]
Illinois elm yellows (EY-IL1)	America	16SrVI-C		AF409069	[77]

Table 4. *Cont.*

Disease (Acronym)	Continent	16Sr Subgroups	'*Candidatus* Phytoplasma' Species	GenBank Accession Number	References
Ash yellows (AshY)	America, Europe, Asia	16SrVII-A	'*Ca.* P. fraxini'	AF092209	[78]
European stone fruit yellows (ESFY)	Europe, Asia	16SrX-B	'*Ca.* P. prunorum'	AJ542544	[39]
Pear decline (PD)	Europe, America	16SrX-C	'*Ca.* P. pyri'	AJ542543	[39]
Rice yellow dwarf (RYD)	Asia	16SrXI-A	'*Ca.* P. oryzae'	AB052873	[79]
"Stolbur" (STOL11)	Europe, America, Asia, Africa	16SrXII-A	'*Ca.* P. solani'	AF248959	[80]
Australian grapevine yellows (AUSGY)	Oceania	16SrXII-B	'*Ca.* P. australiense'	L76865	[81]
Strawberry lethal yellows (StrawLY)	Oceania	16SrXII-C		AJ243045	[82]
Yellows diseased strawberry (StrawY)	Europe	16SrXII-E	'*Ca.* P. fragariae'	DQ086423	[83]
"Bois noir" (BN-Op30), (BN-Fc3)	Europe	16SrXII-F /-G		EU836652, EU836647	[84]
Bindweed yellows (BY-S57/11)	Europe	16SrXII-H	'*Ca.* P. convolvuli'	JN833705	[85]
Chinaberry yellows (CBY1)	America	16SrXIII-C		AF495882	[86]
Chinaberry yellowing (ChTY)	America	16SrXIII-G	'*Ca.* P. meliae'	KU850940	[86]
Sugarcane yellow leaf syndrome	America	16SrXVI-A	'*Ca.* P. graminis'	AY725228	[87]
Pinus phytoplasma (PinP)	Europe, America, Africa	16SrXXI-A	'*Ca.* P. pini'	AJ310849	[88]
Lethal yellowing Mozambique (LYDM 178)	Africa	16SrXXII-A	'*Ca.* P. palmicola'	KF751387	[89]
Cape Saint Paul Wilt Ghana (LDG)	Africa	16SrXXII-B		Y13912	[90]
Buckland valley grapevine yellows	Oceania	16SrXXIII-A *		AY083605	[45]
Malayan yellow dwarf (MYD)	Asia	16SrXXXII-B		EU498727	[66]
Malayan oil palm (MOP)	Asia	16SrXXXII-C		EU498728	[66]
Allocasuarina phytoplasma	Oceania	16SrXXXIII-A	'*Ca.* P. allocasuarinae'	AY135523	[40]
Bogia coconut syndrome (BCS)	Oceania	Not determ.	'*Ca.* P. noviguineense'	LC228755	[91]
Palm decline (RID7692)	Oceania	Not determ.	'*Ca.* P. dypsidis'	MT233886	[92]
Not described	Oceania	Not determ.	'*Ca.* P. stylosanthis'	MT431550	[93]
Palm decline	Oceania	16SrXXXVI	'*Ca.* P. wodyetiae'	KY069029	[94]

*, described as sequence deposited in GenBank only.

4.5. White Leaf

The white leaf symptomatology (Figure 8) is limited to a small range of species, monocotyledonous, and is reported to be associated with phytoplasma presence only in Asia and Europe (Table 5). The main economically relevant disease is the sugarcane white leaf that is severely infecting this crop in all Asian countries. The presence of diverse phytoplasmas is associated in sugarcane also with other symptoms, such as yellow leaf and grassy shoots. These diseases are insect- and cutting-transmitted and in some cases also transovarially [95]. The lack of chlorophyl in the leaves is the main modification, which is often accompanied by a strong shortening of the cycle span and early drying; inappropriate photosynthesis is the mechanism involved in this modification of plants.

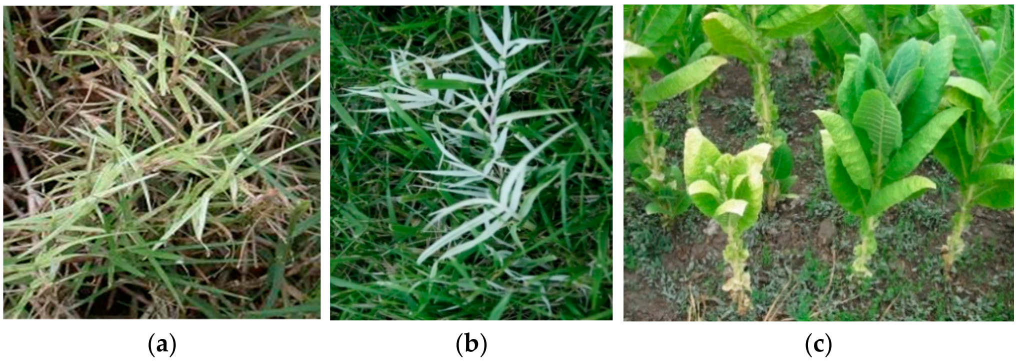


Figure 8. Bermudagrass white leaf in *Cynodon dactilon* (**a**,**b**) and yellow and stunting in tobacco (**c**).

Table 5. Molecular diversity and geographic distribution of selected phytoplasmas belonging to different ribosomal groups/'*Candidatus* Phytoplasma' species (marked by different color) associated with white leaf symptoms.

Disease (Acronym)	Continent	16Sr Subgroups	'*Candidatus* Phytoplasma' Species	GenBank Accession Number	References
Cirsium white leaf (CirWL)	Europe	16SrIII-R		AF373105	[72]
Cirsium white leaf (CWL)	Europe	16SrIII-U		AF373105, AF373106	[81]
Sugarcane white leaf (SCWL)	Asia	16SrXI-B	'*Ca.* P. sacchari'	X76432	[96]
Sugarcane white leaf (SCWL)	Asia	16SrXI-D		KR020685	[97]
Bermudagrass white leaf (BGWL)	Europe	16SrXIV-A	'*Ca.* P. cynodontis'	AJ550984	[98]
Bermudagrass white leaf Iran	Asia	16SrXIV-B		EF444485	[99]
Bermudagrass white leaf (RS304/13)	Europe	16SrXIV-C		KP019339	[100]

4.6. Purple Top and Other Malformations

The presence of phytoplasmas in the sieve tube also interferes with the composition of the phloem sap and is associated with hormone imbalance; therefore, several diverse malformations in roots, flowers, tubers, and leaves can be observed in infected plants (Figure 9). Phytoplasmas that induce these malformations infect mainly herbaceous crops (Table 6).

Figure 9. Cassava frog skin (**a**), tomato (**b**) and potato "stolbur" (**c**), potato purple top (**d**), and carrot reddening (**e**).

Table 6. Molecular diversity and geographic distribution of selected phytoplasmas belonging to different ribosomal groups/'*Candidatus* Phytoplasma' species (marked by different color) associated with purple top and other malformations.

Disease (Acronym)	Continent	16Sr Subgroups	'*Candidatus* Phytoplasma' Species	GenBank Accession Number	References
Soybean purple stem (SPS)	America	16SrI-O		AF268405	[101]
Mexican potato purple top (JAL8), (SON18)	America	16SrI-U/-V		FJ914650, FJ914642	[53]
Papaya bunchy top (BTS)	America	16SrI-X		JF781308	[102]
Tomato "brote grande"	America	16SrI-Y	'*Ca.* P. lycopersici'	EF199549	[103]
Papaya bunchy top (BTS)	America	16SrI-Z		JF781311	[104]
Potato purple top	Asia	16SrII-M		FJ914643	[105]
Papaya BTSp	America	16SrII-N		JF781309	[102]
Cuban papaya	America	16SrII-P		DQ286948	[22]
Papaya bunchy top (TSpHav02-IIA)	America	16SrII-Q		JF78131	[22]
Echinopsis yellow patch	America	16SrII-R		DQ535900	[22]
Amaranthus hypochondriacus 52A	America	16SrII-S		FJ357164	[22]
Pecan bunch (PB)	America	16SrIII-C		GU004371	[23]
Cassava frog skin (CFSD)	America	16SrIII-L		EU346761	[106]
Potato purple top (MT117)	America	16SrIII-M		FJ226074	[23]
Potato purple top (AKpot6)	America	16SrIII-N		GU004365	[23]
Sweet and sour cherry (ChD)	Europe	16SrIII-T		FJ231728	[107]
Passion fruit phytoplasma (PassWB-Br4)	America	16SrIII-V		GU292082	[108]
Cranberry false-blossom	America	16SrIII-Y		KF62652	[109]
Passionfruit (WB-Br4)	America	16SrVI-I	'*Ca.* P. sudamericanum'	GU292081	[110]
Leafhopper-borne (BVK)	Europe	16SrXI-C		X76429	[13]
Cirsium phytoplasma	Europe	16SrXI-E	'*Ca.* P. cirsii'	KR869146	[111]
Sugarcane grassy shoot (SCGS)	Asia	16SrXI-F		HF586636	[112]
Potato (169/Hezuo 88)	Asia	16SrXII-I		EU338445	[112]
Mexican potato purple top (SINPV)	America	16SrXIII-D		FJ914647	[53]
Papaya apical curl necrosis (PACN)	America	16SrXIII-E		EU719111	[113]
Strawberry red leaf	America	16SrXIII-F		KJ921641	[114]
Papaya bunchy top	America	16SrXVII-A	'*Ca.* P. caricae'	AY725234	[88]
American potato purple top wilt	America	16SrXVIII-A	'*Ca.* P. americanum'	DQ174122	[115]
Sorghum bunchy shoot	Oceania	16SrXXIV-A *		AF509322	[45]
Sugarcane phytoplasma D3T1	Africa	16SrXXVI-A *		AJ539179	[45]
Sugarcane phytoplasma D3T2	Africa	16SrXXVII-A *		AY539180	[45]
Derbid phytoplasma	Africa	16SrXXVIII-A *		AY744945	[45]

*, described as sequence deposited in GenBank only.

5. Phytoplasma Genomics

Unlike common bacteria and many other organisms, including animals and plants, mycoplasmas use the UGA stop codon as a tryptophan-encoding codon; moreover, a gene encoding peptide chain release factor 2 that recognizes UGA as a termination codon is present in the phytoplasma genome [116]. The first complete genome sequence of 860,631 bp of the mutant OY-M that was reported in 2004 with a GC content of 28% [117]. Gene annotation analysis revealed that although the genome encoded basic cellular functions including DNA replication, transcription, translation, and protein translocation, the genes required for amino acid and fatty acid biosynthesis, the tricarboxylic acid cycle, and electron transport/oxidative phosphorylation were not present. Although metabolic genes were few in number, the OY-M genome contained many transporter genes. The phytoplasma genome is also rich in repeat regions with duplicated genes and transposon-like elements called potential mobile units; these features are similar to genes and organized in a conservative manner and are thought to play roles in the regulation of gene expression and serve as drivers for phytoplasma interaction with insects and plants [13,118–120].

6. Mechanisms to Infect Plants and Insects

The longtime search for pathogenicity factors still did not elucidate this important aspect and very little clarification is available about a basic question, which is: are phytoplasmas always pathogenic? The finding of several cases of phytoplasma presence in asymptomatic plants do not allow to answer to this question yet. Phytoplasmas are spread between plants by phloem-feeding insects, such as leafhoppers, planthoppers, and psyllids [121]. Due to their wide range of plant hosts, phytoplasmas are often detected in various crops and wild plants [122]. Because phytoplasmas are transmitted transovarially in several cases [123], the presence or absence of insect hosts is a critical determinant of their survival in the natural environment. When phytoplasmas invade insects, their extracellular membrane proteins play important roles for host interactions. Notably, antigenic membrane protein (AMP), a representative of phytoplasma membrane proteins that is predominantly detected on the phytoplasma cell surface, was found to form a complex with host microfilaments determining whether an insect can transmit a phytoplasma [124–127]. Furthermore, microarray and gene expression patterns analyses revealed that phytoplasmas dramatically alter the expression of approximately one-third of their genes using transcription factors to establish host switching between plants and insects [128].

7. Genetic Factors Determining Symptom Development

Some of the molecular mechanisms by which phytoplasmas induce their most typical symptoms were elucidated. Comparing the genome sequences of OY-W and OY-M revealed the duplication of glycolytic gene clusters in the OY-W genome. It has been suggested that this difference is responsible for the high consumption of carbon sources, resulting in high growth rates and severe symptoms, such as yellowing, dwarfism, and decline, at least in the case of the OY-W phytoplasma strain [129]. Furthermore, the mechanisms of purple top symptoms have been revealed. Phytoplasma infection activates the anthocyanin biosynthetic pathway. The increased accumulation of anthocyanin not only changes the color of the leaves to purple, but also acts as an antioxidant that protects plant cells from damage caused by reactive oxygen species, which results in leaf cell death [130].

A comprehensive search for pathogenicity-related genes, in which phytoplasma genes encoding secreted proteins were expressed. In 2009, the first phytoplasma effector protein, TENGU, a secreted peptide of 38 amino acids, was identified as an inducer of witches' broom [131]. It is conserved among various phytoplasma strains. Following secretion from the phytoplasma cell, TENGU is cleaved in planta to a peptide of 12 amino acids, which is then transported to the shoot apical meristem, wherein it inhibits the signaling pathway of the plant hormone auxin and induces witches' broom symptoms [132]. TENGU also induces the sterility of male and female flowers by inhibiting the signaling pathway of jasmonic acid (JA) [133]. The reduction in endogenous JA levels is thought to contribute to attracting insect vectors. Similarly, another secreted protein, SAP11, downregulates JA synthesis and increases the fecundity of insect vectors.

In phytoplasma-infected plants, phyllody often affects sepals, and abnormal expression patterns of MTFs genes were found in all floral organs except stamens in phytoplasma-infected petunias [134,135]. Recently, SAP54 and PHYL1 were found to be homologous proteins that induce phyllody in the floral organs of *Arabidopsis thaliana.* The proteins interact with and then degrade A- and E- class MTFs via the ubiquitin–proteasome pathway and are genetically and functionally conserved among phytoplasma strains and species. Therefore, the phyllody-inducing gene/protein (phyllogen) family was demonstrated to induce flower phyllody and related malformations (virescence and proliferation). Phyllogens induce flower phyllody in various angiosperms and MTF degradation in non-flowering plants. These molecules induce virescence, phyllody, and proliferation symptoms, indicating that these flower symptoms are not independent symptoms induced by distinct effectors but a series of gradually changing phenotypes. Flower virescence can be considered just a mild form of phyllody, and the loss of flower meristem determinacy can be considered a severe form of phyllody [136–139].

Why do phytoplasmas induce symptoms accompanied by unique morphological changes, such as witches' broom and phyllody? Both symptoms increase the prevalence of short branches and small young leaves, which are preferred by sap-feeding insects. Furthermore, phyllody flowers remain green even when healthy flowers wither. These features are likely to enhance the attraction of insect vectors and thus the spread of phytoplasmas. Such manipulations of the morphology of host plants appear to be a common strategy for the survival of phytoplasmas.

8. Management

Because phytoplasmas are difficult to culture, electron microscopy observation using ultrathin sections of sieve elements and plant recovery after tetracycline treatment were the only diagnostic methods available when phytoplasmas were discovered. Subsequently, several DNA-based technologies to detect phytoplasmas have been developed and applied routinely [140] to detect and correctly identify the phytoplasmas present in diseased crops and devise appropriate management strategies [141]. Although treatment using tetracycline-class antibiotics suppresses phytoplasma multiplication in infected plants cultured *in vitro*, high concentrations of antibiotics damage the plant tissues [142–145]. Recently, a comprehensive screening of 40 antibiotics showed that phytoplasmas were eliminated from infected plants not only by the application of tetracycline but also by using rifampicin. Diverse alternative and more sustainable methods were tested and are under trial for practical application; however, the production of phytoplasma-free nursery stocks is still the basis of a friendly and sustainable management, since curing plants is time- and money-consuming, considering that this pathogens are insect- and seed-transmitted. Methods to eliminate phytoplasmas from crops using diverse molecules and resistance inducers showed increased plant performances but not pathogen elimination, and in many cases the scaling up of these systems has not yet been exploited.

9. Concluding Remarks

In the last quarter century, although there have been many barriers to the study of phytoplasmas, such as the difficulty of culturing them and the necessity of producing plant or insect hosts to maintain them for scientific purposes, several phytoplasma molecular and biological properties have been elucidated. Further research work, including the development of effective and ecofriendly strategies to control phytoplasma-associated diseases, will greatly contribute to both the understanding of phytoplasma biology and their physiopathological role in agricultural productions.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Acknowledgments: The author thanks their colleagues, Nicoletta Contaldo, Bojan Duduk, Alberto Calari, Carmen Castillo Carrillo, Luciano Rovesti, Gian Luigi Rana, and Giovanni Granata, for kindly providing some of the pictures.

Conflicts of Interest: The author declares no conflict of interest.

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