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Phytoplasmas and Phytoplasma Diseases: A Severe Threat to Agriculture

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Abstract

Several economically relevant phytoplasma-associated diseases are described together with an update of phytoplasma taxonomy and major biological and molecular features of phytoplasmas. Outlook about persepectives and future work to contain spread of these diseases are also reported.

Keywords

Phytoplasma Diseases, Detection, Prevention

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1. Introduction

The evidence that numerous yellows-type diseases of plants, believed to be caused by viruses, were associated with phloem colonization by prokaryotes morphologically resembling mycoplasmas (mycoplasma-like organisms: MLO) was first shown in 1967 [1]. During the last three decades ribosomal rDNA sequencing has provided a wealth of evidence that these wall-less prokaryotes that parasitize plants and insects, constitute a large monophyletic group within the class *Mollicutes*, and the trivial name "phytoplasma" followed by designation of '*Candidatus* Phytoplasma', were adopted to denote this taxon of plant pathogens [2]. Indirect biological proof, such as electron microscopy observation, phytoplasma and symptoms elimination after tetracycline treatments [3], insect and dodder transmission confirmed phytoplasma association with numerous plant diseases worldwide [4] [5]. Phytoplasmas have sizes variable from 200 to 800 nm, they are polymorphic because of the lack of cell wall (**Figure 1**), and survive and multiply in the isotonic environments provided by plant phloem and insect hemolymph. The phytoplasma chromosome is very small (680 - 1600 kb) and sequence analysis of 16S rDNA and other housekeeping genes suggest that they are most closely related to the *Acholeplasma* spp. than to spiro-

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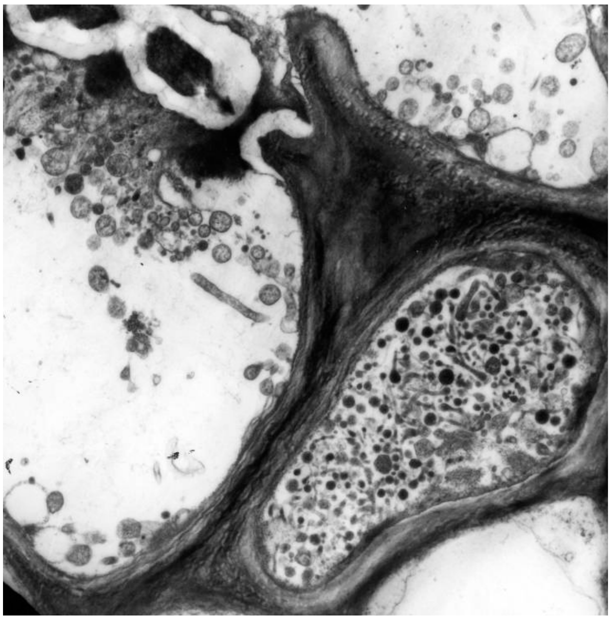

Figure 1. Elecron microscopy picture of cross section of sieve tubes with phytoplasmas (6000×).

plasmas, that are the other mollicutes reported as plant pathogen [6] [7]. The entire genome sequence has been completed for two strains of aster yellows ('*Candidatus* Phytoplasma asteris'), two strains of '*Ca*. P. australiense', and a strain of '*Ca*. P. mali' [8]-[12], providing the first opportunity to understand molecular mechanisms underlying pathogen-host interaction and also virulence [13]-[15].

The application of PCR and nested-PCR assays allow to broadly detect phytoplasma presence, also in mixed infection, in field collected samples [16] [17]. The use of conserved sequences has been a major breakthrough in detection, identification, and classification of phytoplasmas [18]-[26], and very recently a barcode system was applied also to phytoplasma detection and identification [27]. The introduction of diagnostic tests based on quantitative PCR assays (qPCR) showed to be highly sensitive, and reduced the risk of amplicon contamination, eliminating also the need for a gel-based post PCR product analysis, and making this technique a reliable alternative method to nested PCR assays in routine testing [28]-[30]. On the other hand, the possibility of phytoplasma maintenance in micropropagated shoots [31]-[33] make it possible to organize and maintain a collection of phytoplasma strains that can be provided upon request for general taxonomic identification purposes or other scientific studies worldwide.

2. Symptomatology and Economic Impact

Phytoplasmas are associated with diseases in several hundreds of plant species, including many economically important food, vegetable, and fruit crops; ornamental plants, timber and shade trees. Typical symptoms include virescence/phyllody (development of green leaf like structures instead of flowers) (**Figure 2**), sterility of flowers, proliferation of axillary buds resulting in a witches' broom growth, abnormal internodes elongation and generalized stunting. Phytoplasmas may induce many other nonspecific symptoms resulting from stress to which the infected plants are subjected. Hovewer not all infections are necessarily deleterious. For example, the free branching form of poinsettia has been widely used in commercial production of this popular seasonal ornamental, as this trait results in smaller potted plants with numerous showy bracts; these plants are infected by a phytoplasma strain not found up to now in other plant species [34] [35].

Phytoplasmas substantially undistinguishable on 16S rDNA gene can be associated with diseases inducing different symptoms and/or affecting different plant species, but different phytoplasmas can be associated with similar symptoms in the same or in different plant host(s). This oblige on one hand to search for more accurate molecular markers, ideally associated with pathogenicity features, to carry out phytoplasma identification on multi locus typing (MLT) basis and, on the other hand, to avoid assuming phytoplasma identity just from symp-

(a) (b)

(c) (d)

(e) (f)

Figure 2. Symptoms associated with phytoplasma presence, (a) apple proliferation: reddening of apical leaves and witches' broom appearance in an infected orchard in Italy; (b) European stone fruit yellows in plum: lost of apical dominance and abnormal leaf sprouting in the branches in a Japanese plum in Italy; (c) iujube witches' broom: shoots of jujube infected tree showing small leaves and witches' broom proliferation in a germoplams collection of jujube in China (photo by B. Duduk); (d) *Sophora japonica* yellows: trees showing yellows between others with normal foliage coloration located along a street in China where the phytoplasma-infected trees are graft inoculated and used as decorative varieties (photo by B. Duduk); (e) lime witches' broom showing typical leaf symptoms of small leaves and dry branches in a lime field in Oman (photo by B. Duduk); (f) strawberry green petals in which virescent and malformed fruits are present in a field in Italy (courtesy A. Calari).

toms and host species. This situation requires molecular identification of the pathogen in order to study its host range and insect vector(s) in the different agricultural or forestry ecosystems. Most damaging and studied phytoplasma diseases are described below in some details.

2.1. Grapevine Yellows (GY)

(GY) represent a collection of widespread diseases in grapevine displaying similar symptoms that are associated with molecularly distinguishable phytoplasmas. The most important diseases in the main viticultural areas of Europe are "flavescence dorée" (FD) and "bois noir" (BN). FD is prevalent in the some of the main grapevine growing countries and it is a quarantine pathogen [36]-[38]. Molecular studies have indicated the presence of phytoplasmas belonging to 16SrV-C and 16SrV-D, respectively and that these subgroup strains differ in their geographical distributions. Both FD types are experimentally transmissible by the same leafhopper vector *Scaphoideus titanus* [39]. Subgroup 16SrV-D strains were detected in northern Italy [38], France and Spain [40] [41] where severe disease outbreaks are most frequent. In other grapevine producing areas such as north-central Italy and Serbia the strains associated with FD disease outbreaks are associated with subgroup 16SrV-C strains [42] [43]. Disease symptoms mainly involve plant decline, leaf rolling, shrivelled grapes, unripened shoots and reddening or yellowing of leaves on red or white cultivars respectively. The severity and increasing presence of this disease has prompted extensive efforts for specific phytoplasma detection. One of the major problem viticulturists are facing is the variability of FD phytoplasma strains, therefore further FD strain identification is necessary and it is achieved by studying the polymorphisms in rpS3, SecY gene sequences as well as other genes [24] [40] [44] [45]. Since the majority of "new" discovered strains are very often associated with low epidemic spreading to achieve an effective disease control, with the lowest environmental impact, it is necessary to elucidate the FD strain once the phytoplasma is detected in a new areas or in infected areas after some years from an epidemic outbreak. This information is helpful to reduce and localize the pesticide application against the insect vector and can also help to decide about the need of localized or generalized uprooting of the symptomatic plants in the vineyard in which the FD is detected.

The BN disease is associated with phytoplasmas belonging to ribosomal subgroup 16SrXII-A that induce symptoms undistinguishable from FD. BN is prevalent in all viticultural areas worldwide and is transmitted to grapevine by the planthopper *Hyalesthes obsoletus* Signoret (Homoptera, Cixiidae) from field bindweed (*Convolvulus arvensis* L.) [46] and common nettle (*Urtica dioica* L.) as recognized sources of inoculum. In this case the disease management is very difficult since both phytoplasma and insect vectors are non-host specific, however, the usefulness of tuf gene polymorphism for rapid and cheap phytoplasma detection in epidemiological studies of BN was clearly shown [47] [48]. GY diseases occur in other areas of the world where affected plants exhibit syndromes that are seemingly indistinguishable from those of FD or BN but are associated with different phytoplasmas such as aster yellows (16SrI-B) in Italy and South Africa [49] [50], ash yellows (16SrVII-A) in Chile [51], and Australian grapevine yellows in Australia (16SrXII-B) [52] therefore specific local studies are necessary to devise the best management after identification of the insect vector.

2.2. Fruit Trees Declines

Economically important phytoplasma diseases of fruit trees in Europe include apple proliferation (AP), pear decline (PD) and European stone fruit yellows (ESFY). These phytoplasmas are quarantine pest and phylogenetic analyses indicate that the 16S rDNA sequences of the phytoplasmas associated with these disesases are identical or nearly identical. Psyllid vector transmission and host range specificity, clearly distinguish however the associated pathogens as separate species to which the names '*Ca*. P. mali', '*Ca*. P. pyri' and '*Ca*. P. prunorum', respectively, have been assigned [53] (**Table 1**). Apple proliferation is present in almost all European countries and its major impact on apple (*Malus domestica* Borkh) cultivars is that the affected trees produce small and unmarketable fruits. The disease reduces size (by about 50%), weight (by 63% - 74%) and quality of fruit, reduces also tree vigour, increasing susceptibility to powdery mildew. Typical AP symptoms are the witches' broom at the end of shoots, leaves are generally smaller and more dented, with unusually enlarged stipules. Fruits are smaller and flattened, and with elongated peduncles. Early leaf reddening is a good indication of the disease (**Figure 2**), but it can be induced also by other factors. Very recently a link was demonstrated between the diverse '*Ca*. P. mali' strains colonizing apple trees and the severity of disease expression [54]. Although apple is the main host of '*Ca*. P. mali', additional hosts including wild and ornamental *Malus* species, hazelnut (*Corylus* spp.), cherry (*Prunus avium*), apricot (*P. armeniaca*) and plum (*P. domestica*) have been identified. The

Table 1. Classification of phytoplasmas based on RFLP analyses and/or sequencing of 16S rDNA (based on 91).

16Sr subgroup	Strain (acronym) **‘*Candidatus* sp.’**	Genbank number	Reference
16SrI: Aster yellows (America, Europe, Asia, Africa)			
I-A	Aster yellows witches’ broom (AYWB)	NC_007716	[9]
I-A	Tomato big bud (BB)	L33760	[145]
I-B	Onion yellows mild strain (OY-M)	NC_005303	[11]
I-B	Aster yellows (MAY) **‘*Ca.* P. asteris’**	M30790	[146]
I-C	Clover phyllody (CPh)	AF222065	[146]
I-D	Paulownia witches’ broom (PaWB)	AY265206	[146]
I-E	Blueberry stunt (BBS3)	AY265213	[146]
I-F	Aster yellows apricot-Spain (A-AY)	AY265211	[146]
I-I	Strawberry witches’ broom (STRAWB1)	U96614	[147]
I-K	Strawberry witches’ broom (STRAWB2)	U96616	[147]
I-L	Aster yellows (AV2192)	AY180957	[148]
I-M	Aster yellows (AVUT)	AY265209	[146]
I-N	Aster yellows (IoWB)	AY265205	[146]
I-O	Soybean purple stem (SPS)	AF268405	[149]
I-P	Aster yellows from *Populus* (PopAY)	AF503568	[150]
I-Q	Cherry little leaf (ChLL)	AY034089	[151]
I-R	Strawberry phylloid fruit (StrawbPhF)	AY102275	[152]
I-S	Mexican potato purple top phytoplasma (COAH10)	FJ914654	[153]
I-U	Mexican potato purple top phytoplasma (JAL6)	FJ914650	[153]
I-V	Mexican potato purple top phytoplasma (SON18)	FJ914642	[153]
I-W	Peach rosette-like disease (PRU0382)	HQ450211	[154]
I-Y	“Brote grande” of tomato **‘*Ca.* P. lycopersici’**	EF199549	[155]
16SrII: Peanut witches’ broom (America, Africa, Europe, Asia, Australia)			
II-A	Peanut witches’ broom (PnWB)	L33765	[156]
II-B	Lime witches’ broom (WBDL) **‘*Ca.* P. aurantifolia’**	U15442	[157]
II-C	Faba bean phyllody (FBP)	X83432	[158]
II-D	Papaya mosaic (PpM) **‘*Ca.* P. australasia’**	Y10096	[159]
II-E	Pichris echioides phyllody (PEY)	Y16393	[159]
II-F	Cotton phyllody (CoP)	EF186827	[25]
16SrIII: X-disease (America, Europe, Asia)			
III-A	Peach X-disease (PX11CT1) **‘*Ca.* P. pruni’**	JQ044392/JQ044393	[160]
III-B	Clover yellow edge (CYE)	AF173558	[160]
III-C	Pecan bunch (PB)	GU004371	[160]
III-D	Goldenrod yellows (GR1)	GU004372	[160]

Continued

III-E	Spiraea stunt (SP1)	AF190228	[160]
III-F	Milkweed yellows (MW1)	AF510724	[160]
III-G	Walnut witches’ broom (WWB)	AF190226/AF190227	[160]
III-H	Poinsettia branch-inducing (PoiBI)	AF190223	[160]
III-I	Virginia grapevine yellows (VGYIII)	AF060875	[161]
III-J	Chayote witches’ broom (ChWBIII)	AF147706	[162]
III-K	Strawberry leafy fruit (SLF)	AF274876	[147]
III-L	Cassava frog skin disease (CFSD)	EU346761	[163]
III-M	Potato purple top (MT117)	FJ226074	[160]
III-N	Potato purple top (AKpot6)	GU004365	[160]
III-P	Dandelion virescence (DanV)	AF370119/AF370120	[152]
III-Q	Black raspberry witches’ broom (BRWB7)	AF302841	[164]
III-T	Sweet and sour cherry (ChD)	FJ231728	[165]
III-U	Cirsium white leaf (CWL)	AF373105/AF373106	[152]
III-V	Passion fruit phytoplasma (PassWB-Br4)	GU292082	[166]
16SrIV: Coconut lethal yellows (America, Africa)			
IV-A	Coconut lethal yellowing (LYJ-C8)	AF498307	[167]
IV-B	Yucatan coconut lethal decline (LDY)	U18753	[168]
IV-C	Tanzanian coconut lethal decline (LDT)	X80117	[168]
16SrV: Elm yellows (Europe, America, Asia, Africa)			
V-A	Elm yellows (EY) **‘*Ca*. P. ulmi’**	AY197655	[169]
V-B	Jujube witches’ broom (JWB-G1) **‘*Ca*. P. ziziphi’**	AB052876	[170]
V-C	“Flavescence dorée” (FD-C)	X76560	[171]
V-D	“Flavescence dorée” (FD-D)	AJ548787	[41]
V-E	Rubus stunt (RuS) **‘*Ca*. P. rubi”**	AY197648	[172]
V-F	Balanite witches’ broom (BltWB) **‘*Ca*. P. balanitae’**	AB689678	[173]
16SrVI: Clover proliferation (Europe, America, Asia)			
VI-A	Clover proliferation (CP) **‘*Ca*. P. trifolii’**	AY390261	[174]
VI-B	Strawberry multiplier disease (MC)	AF190224	[147]
VI-C	Illinois elm yellows (EY-IL1)	AF409069/AF409070	[175]
VI-D	Periwinkle little leaf (PLL-Bd)	AF228053	[176]
VI-E	*Centarurea solstitialis* virescence (CSVI)	AY270156	[177]
VI-F	Catharanthus phyllody phytoplasma (CPS)	EF186819	[25]
VI-H	Portulaca little leaf phytoplasma (PLL-Ind)	EF651786	[178]
VI-I	Passionfruit (WB-Br4) **‘*Ca*. P. sudamericanum’**	GU292081	[165]

Continued

16SrVII: Ash yellows (America, Europe)			
VII-A	Ash yellows (AshY) **‘*Ca.* P. fraxini’**	AF092209	[179]
VII-B	Erigeron witches’ broom (ErWB)	AY034608	[180]
VII-C	Argentinian alfalfa witches’ broom (ArAWB)	AY147038	[181]
16SrVIII: Loofah witches’ broom (Asia)			
VIII-A	Loofah witches’ broom (LufWB)	AF086621	[182]
16SrIX: Pigeon pea witches’ broom (Europe, Asia, America)			
IX-A	Pigeon pea witches’ broom (PPWB)	AF248957	[19]
IX-B	Almond witches’ broom (AlWB) **‘*Ca.* P. phoenicium’**	AF515636	[183]
IX-C	Naxos periwinkle virescence (NAXOS)	HQ589191	[184]
IX-D	Almond witches’ broom (AlWB)	AF515637	[183]
IX-E	*Juniperus* witches’ broom	GQ925918	[185]
IX-F	Almond and stone fruit witches’ broom (N27-2)	HQ407532	[60]
IX-G	Almond and stone fruit witches’ broom (A1-1)	HQ407514	[60]
16SrX: Apple proliferation (Europe, America)			
X-A	Apple proliferation (AP) **‘*Ca.* P. mali’**	AJ542541	[53]
X-B	European stone fruit yellows (ESFY) **‘*Ca.* P. prunorum’**	AJ542544	[53]
X-C	Pear decline (PD) **‘*Ca.* P. pyri’**	AJ54254	[53]
X-D	Spartium witches’ broom (SpaWB) **‘*Ca.* P. spartii’**	X92869	[186]
X-E	Black alder witches’ broom (BAWB(BWB))	X76431	[187]
16SrXI: Rice yellow dwarf (Europe, Asia, Africa)			
XI-A	Rice yellow dwarf (RYD) **‘*Ca.* P. oryzae’**	AB052873	[188]
XI-B	Sugarcane white leaf (SCWL)	X76432	[187]
XI-C	Leafhopper-borne (BVK)	X76429	[187]
16SrXII: Stolbur (Europe, Asia, America, Africa, Australia)			
XII-A	Stolbur (STOL11) **‘*Ca.* P. solani’**	AF248959	[189]
XII-B	Australian grapevine yellows (AUSGY) **‘*Ca.* P. australiense’**	L76865	[190]
XII-C	Strawberry lethal yellows (StrawLY)	AJ243045	[191]
XII-D	Japanese hydrangea phyllody **‘*Ca.* P. japonicum’**	AB010425	[192]
XII-E	Yellows diseased strawberry (StrawY) **‘*Ca.* P. fragariae’**	DQ086423	[193]
XII-F	“Bois noir” (BN-Op30)	EU836630	[194]
XII-G	“Bois noir” (BN-Fc3)	EU836647	[194]
XII-H	Bindweed yellows (BY-S57/11) **‘*Ca.* P. convolvuli’**	JN833705	[195]
16SrXIII: Mexican periwinkle virescence (America)			
XIII-A	Mexican periwinkle virescence (MPV)	AF248960	[156]
XIII-B	Strawberry green petal (SGP)	U96616	[147]

Continued

16SrXIV: Bermudagrass white leaf (Europe)			
XIV-A	Bermudagrass white leaf (BGWL) **'*Ca*. P. cynodontis'**	AJ550984	[196]
XIV-B	Bermudagrass white leaf Iran	EF444485	[197]
16SrXV: Hibiscus witches' broom (America)			
XV-A	Hibiscus witches' broom (HibWB) **'*Ca*. P. brasiliense'**	AF147708	[198]
XV-B	Guazuma witches' broom (GWB)	HQ258882	[199]
16SrXVI: Sugarcane yellow leaf syndrome (America)			
XVI-A	Sugarcane yellow leaf syndrome **'*Ca*. P. graminis'**	AY725228	[200]
16SrXVII: Papaya bunchy top (America)			
XVII-A	Papaya bunchy top **'*Ca*. P. caricae'**	AY725234	[201]
16SrXVIII: American potato purple top wilt (America)			
XVIII-A	American potato purple top wilt **'*Ca*. P. americanum'**	DQ174122	[201]
16SrXIX: Chestnut witches' broom (Asia)			
XIX-A	Chestnut witches' broom **'*Ca*. P. castaneae'**	AB054986	[202]
16SrXX: Rhamnus witches' broom (Europe)			
XX-A	Rhamnus witches' broom **'*Ca*. P. rhamni'**	AJ583009	[186]
16SrXXI: Pinus phytoplasmas (Europe)			
XXI-A	Pinus phytoplasma (PinP) **'*Ca*. P. pini'**	AJ310849	[203]
16SrXXII: -			
XXII-A	Lethal yellow disease Mozambique (LYDM) **'*Ca*. P. palmicola'**	KF751387	[204]
XXII-B	Cape St. Paul wilt disease (CSPW)	Y13912/JQ868442	[204]
16SrXXIII: -			
16SrXXIII-A	Buckland valley grapevine yellows	AY083605	[205]
16SrXXIV: -			
16SXXIV-A	Sorghum bunchy shoot	AF509322	[205]
16SrXXV: -			
16SXXV-A	Weeping tea witches broom	AF521672	[205]
16SrXXVI: -			
16SXXVI-A	Sugarcane phytoplasma D3T1	AJ539179	[205]
16SrXXVII: -			
16SXXVII-A	Sugarcane phytoplasma D3T2	AY539180	[205]
16SrXXVIII: -			
16SXXVIII-A	Derbid phytoplasma	AY744945	[205]
16SXXIX: Cassia witches' broom (Asia)			
16SXXIX-A	Cassia witches' broom (CaWB) **'*Ca*. P. omanense'**	EF666051	[206]

Continued

16SXXX: Salt cedar witches' broom (Asia)			
16SXXX-A	Salt cedar witches' broom **'*Ca.* P. tamaricis'**	FJ432664	[207]
16SXXXI: Soybean stunt (America)			
16SXXXI-A	Soybean stunt (SoyST1c1) **'*Ca.* P. costaricanum'**	HQ225630	[208]
16SXXXII: Malaysian periwinkle virescence and phyllody (Asia)			
16SXXXII-A	Malaysian p. virescence (MaPV) **'*Ca.* P. malaysianum'**	EU371934	[71]
16SXXXII-B	Malayan yellow dwarf phytoplasma (MYD)	EU498727	[70]
16SXXXII-C	Malayan oil palm phytoplasma (MOP)	EU498728	[70]
16SXXXIII: *Allocasuarina muelleriana* phytoplasma (Australia)			
XXXIII-A	Allocasuarina phytoplasma **'*Ca.* P. allocasuarinae'**	AY135523	[186]

-The ribosomal group has no designation since only Genbank sequences were employed for its determination.

psyllid *Cacopsylla picta* (Forster) is AP principal vector in northeastern Italy and in Germany, respectively, while in north-western Italy, *C. melanoneura* is the most abundant psyllid, and overwintering adults, are the responsible for its diffusion in apple orchards. Also the leafhopper *Fieberiella florii* Stal (Homoptera: Cicadellidae) has been demonstrated as vector of '*Ca*. P. mali' at least occasionally in Germany. Pear decline (PD) was first reported after 1945 in western regions of North America, but today it is of greater economic importance in European pear orchards. Main symptoms enclose poor shoot and spur growth, dieback of shoots, premature reddening and upper rolling of leaves, reduced leaf and fruit size and fewer fruits on trees. Symptoms of pear decline on trees are a very slow decline and a progressive weakening of the tree. Symptoms similar to those of pear decline can be produced by other factors, such as rootstock-scion incompatibility, poor drainage conditions, malnutrition, and drought. In North America and UK the known vector is the psyllid *Cacopsylla pyricola* (Foerster), but *Cacopsylla pyri* (L.) has been found as the main vector in European countries. Studies have indicated that '*Ca*. P. pyri' is able to overwinter in the body of *C. pyri* [55] and occurs seasonally during the vegetative stage of tree growth. While age of the tree and scion variety does not seem to influence the occurrence of the disease, differences in susceptibility among varieties and rootstocks have been reported.

European stone fruit yellows (ESFY) affects several stone fruit species inducing apricot, plum, and peach as well as several other *Prunus* species. Apricot (*Prunus armeniaca* L.) and Japanese plum (*P. salicina* Lindl.) are most susceptible; symptom severity on both affected species can be quite variable. Trees exhibit foliar yellowing, accompanied by leaf roll, followed by leaf reddening, reduction or suppression of dormancy with the consequent risk of frost damage, severe and progressive necroses, decline and mortality (**Figure 2**). European plum is generally tolerant to ESFY, some cultivars however, can show weak symptoms [56]. Wild or cultivated *Prunus* species, such as *P. cerasifera*, *P. mahaleb*, *P. padus*, *P. spinosa*, *P. tomentosa*, are tolerant to the disease, while *P. avium* demonstrated a high level of resistance. *Cacopsylla pruni* has been identified as the vector of ESFY [57]; the species completes one generation per year and adults overwinter on shelter plants (conifers). Tolerant *Prunus* species can also serve as sources for pathogen spread. In contrast to phytoplasma diseases of stone fruits in North America and Europe, where '*Ca*. P. pruni' was mainly identified [58] [59], epidemic outbreaks on almond and stone fruits in the Middle East (Lebanon and Iran) were attributed to '*Ca*. P. phoenicium' [60]-[63], whereas in China and India '*Ca*. P. ziziphi' was identified as the causal agent of severe declines of trees in both cherry and peach orchards [64].

2.3. Citrus Witches' Broom

Witches' broom disease of lime (WBDL), associated with the presence of '*Ca*. P. aurantifolia' (**Table 1**), is responsible for major losses of Mexican lime trees (*Citrus aurantifolia* L.). The disease was first observed more than 30 years ago in Oman, where the destruction of 98% of Mexican lime trees occurred and has since spread to the United Arab Emirates, Iran and India [65]. The infected Mexican lime trees in the early disease stages shows a number of witches' brooms, bearing small new pale green leaves. In advanced stages, leaves of the older witches' brooms dry up and eventually fall away leaving behind dead twigs, shoots and dried witches' broom (**Figure 2**). At this stage, the tree is unproductive bearing very few small fruits, which die quickly. The period from the first formation of witches' broom to the mortality of affected trees takes about five to six years. The natural host range of '*Ca*. P. aurantifolia' includes *Citrus aurantifolia*, *C. medica*, *C. limetta*, *C. lemon* and *C. jambhiri*. Phytoplasmas belonging 16SrI and 16SrIX have been detected in a devastating citrus disease known as huanglongbing (HB) in Brazil mainly attributed to three species of Gram negative bacteria in the genus '*Candidatus* Liberibacter', that is seriously threatening global citrus production [66] [67]. The pathogenic role of phytoplasmas was not clearly elucidated, but they can be detected in symptomatic plants in cases in which HB is not detected (R. Bassanezi, personal communication).

2.4. Palm Lethal Yellowing

Lethal yellowing (LY) is a quickly fatal disease that affects coconut (*Cocos nucifera* L.) and at least 36 other palm species in the Americas [68]. The phytoplasmas associated with devastating outbreaks of LY have been classified as members of group 16SrIV (**Table 1**). LY disease occurs elsewhere in the humid tropics under a variety of names depending on location, collectively, these diseases are known as "lethal yellowing-type diseases" (LYD) because they induce symptoms similar to or indistinguishable from those associated with LY. They threaten global coconut production because they kill palms quickly and are incurable. For tall-type coconuts, the onset of visible symptoms begins with a premature shedding of most or all fruit regardless of developmental stage. Aborted fruit usually develop a brownish black calyx-end rot reducing seed viability. The next symptom is inflorescence necrosis (blackening), which is most readily observed on newly opened inflorescences. Leaf discoloration (yellowing or bronzing) begins on the older, lowermost leaves, and progresses to involve successively younger leaves nearest the center of the crown. Affected leaves eventually turn brown, dessicate and hang down forming a skirt around the trunk for several days before falling to the ground. Worldwide this disease affects at least 30 species of palm, including *Phoenix dactylifera* (date palm), *Veitchia merrilli* (manila palm), *Caryota rumphiana* (fishtail palm), *Phoenix canariensis* (Canary Island date palm), and *Elaeis guineensis* (African oil palm) [69]-[71]. The disease is vectored by *Haplaxius* (*Myndus*) *crudus* (American palm cixiid) and possibly also by *Cedusa* species of derbid planthoppers [72]. More recently, phytoplasmas from other 16S ribosomal groups have been associated with diseases showing similar symptoms in palms in other parts of the world. In Saudi Arabia, a 16SrI group was found associated with the Al-Wijam disease of date palm [73] while in North Sudan, 16SrXIV group phytoplasmas were found (**Table 1**) in this species showing white tip die back and in mature palms with slow decline symptoms [70] [74] [75]. Recently, a 16SrVI phytoplasma was associated with coconut yellow decline and oil palm decline in Malaysia [70] [71]. Similarly, the Weligama wilt disease of coconut in Sri Lanka was associated with phytoplasmas belonging to the 16SrXI group (**Table 1**) [76]. Phytoplasmas belonging to groups 16SrXI and 16SrXIII are associated with Kalimantan wilt disease in Indonesia [77], and aster yellows phytoplasmas could be consistently associated with a lethal wilt of oil palm in Colombia [78].

2.5. Corn and Vegetables Phytoplasma Diseases

Many different vegetable species are seriously affected by molecularly differentiable phytoplasmas worldwide, however symptomatology is very similar for the same species regardless of the infecting phytoplasma strain. Potato witches' broom and maize bushy stunt are among the most widespread diseases in herbaceous hosts causing severe yield losses. While symptomatic potatoes are associated with the presence of phytoplasmas belonging to diverse 16Sr groups, mainly according to different geographic areas [80]-[84]; corn is consistently infected in America by aster yellows (16SrI-B) phytoplasmas [85] [86], while phytoplasma producing a similar disease in Europe belong to the "stolbur" group (16SrXII) and is vectored by *Repatuls panzeri* and *H. obsoletus* [79] [87]-[89]. The majority of cultivated vegetable or annual crops were reported as infected by phytoplasma diseases and phytoplasma identification usually is mainly linked to phytoplasmas that are endemic or epidemic to the surrounding areas, indicating that phytoplasma infecting herbaceous plant hosts exhibit very little host/insect vector species specificity [90].

3. Phytoplasma Classification and Identification

Over the last few years, phytoplasmas have been discovered at an increasingly rapid pace in emerging diseases worldwide and the 16S rDNA study by RFLP (restriction fragment lemght polymorphim) analyses [91] and sequencing has produced a detailed picture of phytoplasma diversity and of their phylogenetic relationships with other prokaryotes. The '*Candidatus* Phytoplasma' genus was described together with 19 '*Candidatus* species' [92] and formal descriptions for 35 '*Ca*. Phytoplasma species' total have since been published. Still others warranting formal description have been recognized, but remain to be published: '*Ca*. P. vitis', '*Ca*. P. palmae', '*Ca*. P. luffae', '*Ca*. P. cocostanzianae' and '*Ca*. P. cocosnigeriae'.

There are many more than 1000 16S rRNA gene sequences of phytoplasmas archived in the GenBank database, and it is now clear that additional conserved DNA sequences markers should be used as supplemental tools for finer phytoplasma differentiation [93], to better identify phytoplasma strains in order to correlate them to their differences in pathogenicity, vector relationships and host susceptibility. The rp gene sequences reveal more variation than 16S rDNA, the analyses conducted by RFLP or sequencing on *tuf* and/or *SecY* genes show also clear indications of phytoplasma strains relationships at least with their geographic distribution [20]-[23] [25] [26] [94] [95] and are now employed for epidemiologic studies in order to devise management control strategies for the main phytoplasma-associated diseases.

4. Biology and Genomics

Phytoplasmas are introduced by insect vectors during feeding activity into plant sieve tube elements, from which they spread systemically through the plants. Studies on the translocation of phytoplasmas after localized inoculation [96] or the re-colonization of trees [97], provide evidence that the translocation of phytoplasmas cannot be explained solely by assimilate flow, although active movement by the phytoplasmas seems unlikely, considering the lack of genes coding for cytoskeleton elements or flagella [98]. Phytoplasmas are mainly spread between plants by insects in the families Cicadellidae (leafhoppers), Fulgoridae (planthoppers), and Psyllidae (psyllids), which feed on the phloem sap of infected plants, therefore their host range is strongly dependent upon feeding preferences of their insect vectors [99]. Phytoplasmas may overwinter in insect vectors or in perennial plant hosts, and interact in various ways with insect hosts, and examples of both reduced and enhanced fitness of the vectors, have been reported [98]. There is mounting evidence of transovarial transmission of phytoplasmas occurring in certain insect based on studies of several phytoplasma-vector combinations that include: *Scaphoideus titanus*/aster yellows [99]; *Hishimonoides sellatiformis/*mulberry dwarf [100], *Matsumuratettix hiroglyphicus* (Matsumura)/sugarcane white leaf [101], and *Cacopsylla melanoneura/*plum [102]. The possibility of seed transmission has also been investigated following *in situ* detection of phytoplasma DNA in embryos from coconut palms with lethal yellowing disease [103]. Studies on *in vitro* growing commercial seedlings of alfalfa (*Medicago sativa*) firstly showed evidence of seed phytoplasma transmission, data were further confirmed by molecular testing of seedlings from phytoplasma-infected lime (*Citrus aurantiaca*), tomato (*Lycopersicum esculentum*), corn and winter oil seed rape maintained *in vitro* or under insect-proof conditions [104]-[106]. Phytoplasmas can also be efficiently spread via vegetative propagation such as the grafting of infected plant tissues as shoots onto healthy plants, by vegetative propagation through cuttings, and by micropropagation practices and any other method used to multiply plant material that avoids sexual reproduction.

Phytoplasmas possess the smallest genome of any plant pathogenic bacteria, only some bacterial symbionts of insects have smaller genomes, however many core housekeeping genes are present in multiple copies; they contain two rRNA operons that in several cases show sequence heterogeneity. Gene duplication and redundancy are also well represented: it was estimated that in the genome of the onion yellows (OY) phytoplasma the 18% of gene complement is represented by multiple redundant copies of only five genes, that are generally present in single copy (if they exist at all), in the other *Mollicutes* whose genomes have been sequenced [11]. Phytoplasma genomes contain relatively large numbers of transposon genes and insertion sequences that are unique to these bacteria, have similar compositions and contain similar genes; they are referred to either as variable mosaics (SVM) [107]-[109] or potential mobile units, (PMUs) [9]. Extrachromosomal DNA (EC-DNA) (1.7 - 7.4 kb) or plasmids of various sizes have been found in all members of the aster yellows (16SrI) and stolbur (16SrXII) phytoplasma groups as well as in some members of the X-disease (16SrIII) and clover proliferation (16SrVI) groups [110]-[114]. In the '*Ca*. P. asteris', onion yellows strain (OY), a mildly pathogenic, insect-transmitted line (OY-M) contains two types of plasmids (EcOYM and pOYM), each of which possesses a gene encoding the putative transmembrane protein ORF3. Likewise, a non-insect-transmissible line (OY-NIM), has the corresponding plasmids (EcOYNIM and pOYNIM), but pOYNIM lacks ORF3. It was shown that in OY-M, ORF3 was transcribed from two putative promoters, while on EcOYNIM one of the promoter sequences was mutated and the other deleted. ORF3 was not expressed in the OY-NIM-infected plants. Moreover, ORF3 protein seemed more specifically expressed in OY-M-infected insects than in plants. These results suggest that ORF3 may play an integral role in the interactions of OY with the insect host of this phytoplasma [2].

Phytoplasma genomes contain many genes encoding transporter systems, such as malate, metal-ion and amino-acid transporters, some of which are present as multiple copies. This feature suggests that phytoplasmas import many metabolites from their host cells, and this probably disturbs the metabolic balance, and causes disease symptoms in plants. Analysis of the genome sequence of the OY-M phytoplasma indicates lack of APT synthase genes, and suggests that these phytoplasmas import host ATP as yet unknown mechanisms and ATP synthesis may be strongly dependent on glycolysis. That hypothesis is supported by analysis of ca. 80-kb genomic DNA sequence derived from '*Ca*. P. asteris' OY-W, a strain which causes severe disease symptoms [115]. Interestingly, an approximately 30-kb region was found to be duplicated in the '*Ca*. P. asteris' OY-W genome [14]. Two sets of 5 glycolytic enzymes were encoded in this genomic region, which is a unique gene structure that has not been identified so far in any other bacterial genomes. The organization of glycolytic genes of '*Ca*. P. asteris' AY-WB [9] is similar to that of '*Ca*. P. asteris' OY-M, rather than '*Ca*. P. asteris' OY-W, suggesting the duplication of glycolytic genes is unique to '*Ca*. P. asteris' OY-W. Glycolysis seems to be an important metabolic pathway in some, but not all, phytoplasmas as these genes are completely absent in '*Ca*. P. mali' [10], the latter phytoplasma possesses a gene encoding 2-dehydro-3-deoxyphosphogluconate aldolase (*eda*) leading to he hypothesis that in this phytoplasma pyruvate is formed independently from glycolysis [116].

5. Interaction with Hosts

The occurrence of major surface epitopes, that are unique to each phytoplasma species, suggests that these proteins are key participants in specific interactions with host cells. Genes encoding these proteins have been isolated from several phytoplasma groups and are classified into three types: 1) immunodominant membrane protein (Imp), detected in the phytoplasmas associated with sweet potato witches' broom (SPWB) [98], apple proliferation (AP) [117], European stone fruit yellows (ESFY), pear decline (PD), and peach yellow leaf roll (PYLR) [118]; 2) immunodominant membrane protein A (IdpA), detected in phytoplasmas associated with western X-disease (WX) [119]; and 3) antigenic membrane protein (Amp), detected in the aster yellows (AY), clover phyllody (CPh), and onion yellows (OY) phytoplasmas [118] [120]. A high expression of the Amp protein was confirmed in AY, CPh, and OY phytoplasmas and this protein was shown to be exported via the Sec protein secretion system, accompanied by the cleavage of its N-terminal signal sequence. The Amp protein of the OY phytoplasma forms a complex with insect microfilament composed by actin and myosin that was correlated with the phytoplasma-transmitting capacity of leafhoppers, suggesting that the interaction between Amp and microfilament complexes plays a major role in determining the transmissibility of phytoplasmas [15]. Morton *et al*. [118] isolated genes encoding Imps and found that the sequence identities of these genes in several phytoplasmas were not correlated with that of the 16S rDNA gene suggesting that the variability of immunodominant membrane proteins reflects factors other than evolutionary time. Although the gene encoding the immunodominant membrane protein of the WX phytoplasma is idpA, however a gene homologous to Imp was also present in the WX genomic fragment in which the idpA gene was identified [121]. This observation suggests that Imp may be a common ancestor of phytoplasma immunodominant membrane proteins. The sequence identity of Imp was found to be low among the different phytoplasma groups, however the gene organizations flanking Imp were well conserved in most phytoplasmas, and the Imp genes studied thus far are orthologous because of their similar gene organization and conserved transmembrane structure [122]. In contrast, neither the orthologue of idpA, in the complete genomic sequences of OY-M [122], AY-WB [9], '*Ca*. P. australiense' [12], or '*Ca*. P. mali' [10] nor the orthologue of Amp, in the complete genomic sequence of '*Ca*. P. mali' have been found. Imp may serve an important role in host-phytoplasma interactions, like many positively selected proteins. The accumulation of Amp was calculated as about 10-fold greater than that of Imp, and this level was consistent with the "immunodominant" property of Amp in AY-group phytoplasmas. Detection of Imp in phytoplasma-infected plants is also possible however, and therefore the protein amount of Imp must also be high. Western blot analysis of Imp from OY-W suggested that the signal sequence of Imp was uncleaved, and that Imp was retained in the phytoplasma cell membrane. This result agrees with previous reports that Imp is an immunodominant membrane protein in several phytoplasmas, including AP [120] and since expression of Imp in OY-W is clearly shown, antibodies against Imp could be useful for the detection of phytoplasmas as was recently shown for Amp [123].

Since phytoplasmas are intracellular parasites of both plants and insects, their ability to adapt to two diverse environments is of considerable interest. Microarray analysis of '*Ca*. P. asteris' OY-M revealed that expression of approximately 33% of the genes changes during host switching between plant and insect, suggesting phytoplasma dramatically alters gene expression in response to its host [124] and may use transporters, secreted proteins, and metabolic enzymes in a host-specific manner. The genes encoded in the PMUs of '*Ca*. P. asteris' AY-WB are more highly expressed in insects than in plants, most likely due to increased production of the extrachromosomal circular type of PMU during insect infection [125]. Differential gene expression between plant and insect hosts has been also reported in '*Ca*. P. asteris' OY-M, in which TENGU, a small secreted protein identified in the phytoplasma genome, was shown to induce in transgenic *Arabidopsis thaliana* symptoms similar to those induced by phytoplasma presence, and is more highly expressed in plant than in insect hosts [13].

6. Virulence and Pathogenicity

Very little is known about phytoplasma virulence. Because they lack most of the common metabolic pathways, it has been speculated that they must assimilate a wide range of materials from the host cells, probably with detrimental effects to the hosts, such as differential symptom expression correlated with differences in genome size. In onion yellows (OY) phytoplasma mild proliferation and yellowing symptoms are present in infection by mild strain (OY-M), while yellowing, stunting, proliferation and witches' broom are induced by a severe strain (OY-W) and the two phytoplasmas has different chromosome size (OY-W, 1000 kbp and OY-M chromosome, 860 kbp). Further analysis showed that five glycolytic genes were duplicated in the severe strain and the phytoplasma population of OY-W had a higher titer than OY-M. In view of these findings, the higher consumption of the carbon source (because of the duplication of the glycolytic genes) may affect the growth rate of the OY-W phytoplasma and tourn in directly or indirectly produce more severe symptoms [14]. It was also shown that a virulence factor, "tengu-su" inducer (TENGU), induces witches' broom and dwarfism when expressed in transgenic plants of *Nicotiana benthamiana* and *A. thaliana*. Although the localization of phytoplasma is restricted to the phloem, TENGU protein was detected in the apical buds by immunohistochemical analysis, suggesting that it was transported from the phloem to other cells. Microarray analysis detected that auxin-responsive genes were down-regulated in the "tengu"-transgenic plants as compared to control plants [13].

Since phytoplasmas have no cell wall and reside inside of host cells, their membrane proteins and secreted proteins are exposed to the cytoplasm of the host plant or insect cell, and may play important roles in host-parasite interactions and/or virulence. Thus, the identification of genes comprising a secretion system in phytoplasma genomes is important for understanding their biology. Phytoplasmas possess two known secretion systems, the YidC system for the integration of membrane proteins, and the Sec system for the integration and secretion of proteins into the host cell cytoplasm. Genes encoding SecA, SecY, and SecE have been identified in the '*Ca*. P. asteris' OY-M genome, the SecY [126] [127], and SecA expression has been confirmed in phytoplasma-infected plants [128]. These genes have also been identified in three other phytoplasma genomes [9] [10] [12], and *secY* genes have been cloned from numerous phytoplasma strains [20]-[22]. These results strongly suggest that a functional Sec system is common to most or all phytoplasmas. Antigenic membrane protein [120], has been reported to be a substrate of the Sec system. Amp has a Sec signal sequence at its N-terminus, which is cleaved in '*Ca*. P. asteris' OY-M [126], suggesting that the phytoplasma Sec system utilizes recognition and cleavage of a signal sequence, as in other bacterial Sec systems.

In the '*Ca*. P. asteris' strain AY-WB genome, at least 56 genes encode predicted secreted proteins. One of these, SAP11, contains eukaryotic nuclear localization signals and accumulates in plant cell nuclei [9]. SAP11-expressing plants exhibit crinkled leaves and produce many stems. Moreover, the fecundity of insect vectors was increased after feeding upon SAP11-expressing plants when compared to those that fed upon nontransformed plants [129]. In addition to SAP11, SAP54 protein encoded by '*Ca*. P. asteris' AY-WB was reported to cause morphological changes in *A. thaliana* floral organ development, which resembled symptoms observed on phytoplasma-infected plants [130]. Although the molecular mechanisms contributing to these changes remain unknown, it is assumed that proteins secreted by phytoplasmas may interfere with the function of genes involved in flower development [131] [132]. The identification of TENGU, SAP11, and SAP54 suggest that phytoplasma could induce symptoms by secretion of effector proteins and modification of plant-gene activity [13] [129] [133].

Energy metabolism is certainly a key topic for understanding phytoplasma biology and pathogenesis. It has been reported that altered levels of oxygen and carbon dioxide affect phytoplasma abundance in *Oenothera* leaf tip cultures, and concentrations of carbohydrates in the phloem, roots and leaves of phytoplasma-infected plants differ from those in healthy plants [134]-[136]. Because of the wide array of symptoms expressed by diseased plants, nutrient depletion is probably not restricted to sugars, but also includes other compounds. A reduction in the concentration of photosynthetic pigments [137] and of total soluble proteins [137]-[139], as well as alterations in the hormone balance [135] [140], amino-acid transport [134] and the occurrence of folate and endopetidase gene homologues in phytoplasma genomes [141] were described as potentially affecting host plants infected with different phytoplasmas.

7. What Is New in the Field?

Many workers, mainly plant pathologists rather than mycoplasmologists, took up the challenge to culture these organisms. An early outcome of these efforts was successful axenic culture of spiroplasmas: this distinct group of organisms grew readily in media formulations whereas the phytoplasmas did not. The preliminary evidence that phytoplasmas can be grown in or on cell free laboratory media has been reported [142]-[144]. This is an important breakthrough in the study of their biology since, despite a reduced genome size in comparison to their ancestors, phytoplasmas retain an independent metabolism that allows them to survive as parasites in environments as diverse as plant phloem and insect haemolymph. This versatility is a unique property among microbes, shared only with some animal- or plant-infecting viruses and with a few other microorganisms such as the causal agent of malaria.

Employing specific commercially available media, it was possible to achieve growth of phytoplasmas belonging to diverse ribosomal groups from micropropagated periwinkle shoots, infected with phytoplasmas, as an initial source of inoculum. In spite of the relatively long time required for incubation in liquid medium, colony growth of phytoplasmas on agar usually occurs within two to five days, as for the majority of cultured bacteria. Although further research is needed and is in progress in order to optimize the culture system, the prospect of routine cultivation is now a real option for researchers. When observed with a binocular microscope, the phytoplasma colonies on the surface of agar medium are comparable in size and appearance to those of mycoplasmas (**Figure 3**). PCR assays using phytoplasma specific primers confirmed that phytoplasma DNA was present in those cultured cells used as a source of DNA template. Identification using RFLP analysis and direct sequencing of selected amplicons also confirmed phytoplasma identity [143].

From the preliminary cultivation work a patent has been submitted to cover the commercial exploitation of the methodology, however, research carried out for scientific purposes is not restricted by the patent. A major advantage of the procedure is that it may now be possible to build a comprehensive culture collection of diverse phytoplasmas without the need to maintain these strains by micropropagation methods. One of the most immediate benefits is a genome sequencing to compare and contrast gene complement and metabolic pathways of

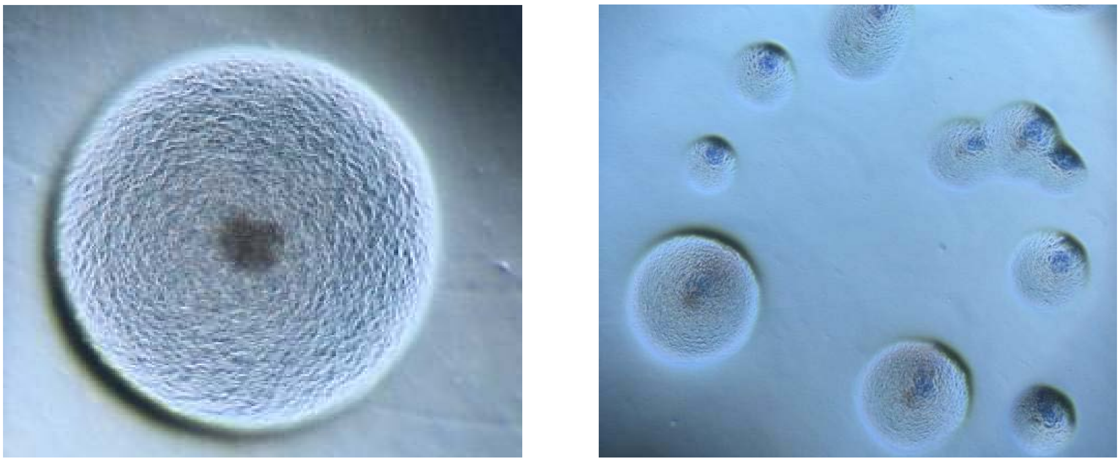
(a) (b)

Figure 3. Phytoplasma colonies under optical microscope [(a) magnification 50×, (b) magnification 20×].

strains representative of each phytoplasma 16Sr group. Currently genome sequencing is very inefficient, largely because of the intimate association of phytoplasmas with their respective host plants and insect vectors, therefore the availability of phytoplasma colonies should help. It is likely that whole genome comparisons will emerge as the premier tool for phytoplasma identification in the near future.

As a consequence, strategies targeting treatment or prevention of phytoplasma diseases could be better defined and more effective. In addition, more detailed knowledge about basic mechanisms that regulate the survival of phytoplasmas, which are among the smallest known self replicating organisms, should be obtained. These researches are urgently needed because the use of tetracycline is forbidden in some agricultural areas (Europe) since it is perceived to endanger human health. The recognition of durable resistance to phytoplasma diseases is the only effective long term mean of controlling these diseases. Selection and screening of plants resistant to phytoplasma infection as well as the study of the modes of colonization by phytoplasmas of plant and insect vectors are other possible applications. As a consequence strategies aiming to treat and/or prevent phytoplasma related plant diseases could be better defined and more effective. The hoped-for result would be enhanced ability to reduce the socio-economic impact that phytoplasma diseases have in all agricultural areas of the world.

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