

## INVITED REVIEW

## CURRENT STATUS OF MOLECULAR CLASSIFICATION OF THE PHYTOPLASMAS

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## SUMMARY

Phytoplasmas for which 16S rDNA sequences are available have been classified into 20 major phylogenetic groups or subclades. Further phytoplasmas have been assigned to these groups, according to other molecular data such as RFLP analysis of PCR-amplified ribosomal DNA, nucleic acid hybridization, and serological comparison. A total of 75 phytoplasmas were distinguishable among the molecularly characterized phytopathogenic mollicutes.

## RIASSUNTO

**STATO ATTUALE DELLA CLASSIFICAZIONE MOLECOLARE DEI FITOPLASMI.** I fitoplasmi, dei quali la sequenza nucleotidica del 16S rDNA era nota, sono stati classificati in 20 gruppi filogenetici principali. Sulla base di dati ottenuti mediante analisi di RFLP del DNA ribosomale amplificato mediante PCR, ibridazione di acidi nucleici e sierologia, altri fitoplasmi sono stati assegnati ai gruppi suddetti. Un totale di 75 distinti taxa è stato individuato tra tutti i mollicuti fitopatogeni caratterizzati con metodiche molecolari.

*Key words:* phylogeny, taxonomy, phytoplasmal diseases.

## INTRODUCTION

Phytoplasmas are nonhelical mollicutes associated with diseases of several hundred plant species (McCoy *et al.*, 1989). These disorders are characterized by flower malformation, other growth aberrations, yellowing and/or decline and are collectively referred to as yellows diseases. They were thought to be caused by viruses until a group in Japan (Doi *et al.*, 1967) recognized in diseased plants wall-less, pleomorphic bodies

which resembled in morphology and ultrastructure mycoplasmas known to be pathogens of humans and animals. Due to this similarity the structures detected in plants were called mycoplasma-like organisms (MLOs), but the failure of all attempts to culture phytoplasmas under axenic conditions made their characterization difficult and prevented their definitive classification.

A new era in phytoplasma research began when DNA-based methods were introduced about a decade ago, following the development of procedures to extract and enrich phytoplasmal DNA from infected plants or insects (Kirkpatrick *et al.*, 1987; Lee and Davis, 1988; Sears *et al.*, 1989; Kollar *et al.*, 1990). Phytoplasmal DNA could then be cloned and sequenced, and methods applied for amplification of this DNA using PCR. A wealth of molecular data on phytoplasma diversity and on the relationships of the phytoplasmas was generated. In several comprehensive studies on phylogeny and taxonomy of the phytoplasmas, many phytoplasmas from several phylogenetic groups have been examined, using either sequence or RFLP analysis of ribosomal DNA. However, there is no recent publication in which the available data are combined to present a comprehensive classification scheme. Thus, the aim of this review is to compile the results of both DNA-based and serological studies and present a picture of the current status of phytoplasma differentiation and classification. This will be done by grouping the phytoplasmas phylogenetically and assigning other molecularly characterized phytoplasmas, for which full-length 16S rDNA sequences were not available, to the groups delineated.

## PHYTOPLASMA PHYLOGENY

The first molecular indication of the mycoplasmal nature of the phytoplasmas was obtained by estimating the G+C content of highly enriched phytoplasmal DNA. The very low values obtained (23.0 to 26.2 mol %) suggested a close relationship to the culturable mollicutes (Kollar and Seemüller, 1989). More evidence came from

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estimation of genome size, found by Neimark and Kirkpatrick (1993) to lie between 600 and 1150 kb, which is within the range for culturable mollicutes.

Evidence on the phylogeny of phytoplasmas can be obtained using comparative sequence analysis of the conserved 16S rRNA gene, which was proposed by Woese (1987) as a universal phylogenetic marker for classifying major groups of prokaryotes. This approach has been used to determine relationships of culturable mollicutes with each other and with walled bacteria (Weisburg *et al.*, 1989).

Lim and Sears (1989) and Kuske and Kirkpatrick (1992) were the first to clone and completely sequence 16S rRNA genes of phytoplasmas. Sequence comparisons indicated that the two aster yellows (AY) phytoplasmas which were examined are more closely related to culturable mollicutes than to other bacteria. When the 16S rRNA gene became readily accessible by PCR amplification, Namba *et al.* (1993), Gundersen *et al.* (1994), and Seemüller *et al.* (1994) sequenced full-length or nearly full-length 16S rRNA genes of 37 representative strains. Comparison showed that these were more closely related to each other than to any other prokaryote, and indicated that the phytoplasmas represent a monophyletic clade of organisms more closely related to other mollicutes than to walled bacteria. The closest relatives of the phytoplasmas are some achleoplasmas such as *A. palmae* and *A. modicum* (Davis *et al.*, 1997a) of the anaeroplasma clade as defined by Weisburg *et al.* (1989). These relationships have been largely confirmed by sequence analysis of two conserved ribosomal protein genes (Lim and Sears, 1992; Gundersen *et al.*, 1994).

As a consequence of these studies, the International Committee of Systematic Bacteriology (ICSB) Subcommittee on the Taxonomy of *Mollicutes* (1993, 1997) has agreed to replace the trivial name MLO by the term phytoplasma. This name will also, under the provisional taxonomic status *Candidatus* (Murray and Schleifer, 1994), become the genus name of the plant pathogenic mycoplasmas.

#### METHODS TO DIFFERENTIATE AND CLASSIFY PHYTOPLASMAS

**SYMPTOMATOLOGY AND HOST RANGE.** Differentiation and classification of the culturable mollicutes is based on both phenotypic and genotypic characteristics (ICSB Subcommittee on the Taxonomy of *Mollicutes*, 1995).

Since phytoplasmas have not been grown in axenic culture, genotypic data are difficult to obtain and most of the phenotypic traits are still not applicable for their classification. Thus phytoplasmas were for a long time described and differentiated according to the symptoms they induce, the host plant affected, and sometimes also the geographic area where they occur (*e.g.* European aster yellows). A particular role in symptomatologic classification was played by the experimental host *Catharanthus roseus* (periwinkle), to which many phytoplasmas have been experimentally transmitted and in which they induce specific symptoms. A classification of phytoplasmas maintained in periwinkle was attempted by Marwitz (1990), and his grouping shows some similarities to the current genetic classification. However, in several cases phytoplasmas were grouped together, which are genetically distinctly different (*e.g.* the apple proliferation and X-disease agents), whereas others considered to be different are genetically closely related (*e.g.* the agents of AY and paulownia witches'-broom).

The specificity of insect vectors of phytoplasmas has also been used as a means of differentiation. For example, the two symptomatically similar phytoplasmoses affecting grapevine in France, flavescence dorée and bois noir, were correctly thought to be caused by two different agents because the vector of flavescence dorée (*Scaphoideus titanus*) did not transmit bois noir (Caudwell *et al.*, 1971). However, vector transmission is a complex process, being a three-way interaction between pathogen, vector and host (Chiykowski and Sinha, 1990), and is thus a difficult tool for use in taxonomy.

**SEROLOGY.** Polyclonal antisera and monoclonal antibodies have been produced against various phytoplasmas (for reviews see Kirkpatrick, 1991; Lee and Davis, 1992). Immunogens were usually extracted and enriched from infected plants, less often from infested insect vectors. As antisera prepared with plant-derived immunogens often showed strong cross reactivity with plant antigens, and as insect-derived immunogens were rarely available, the production of specific, high-titer antisera proved to be difficult. Thus most of the antibodies available were prepared against isolates maintained in high-titer hosts such as periwinkle or herbaceous plants, and were suited to detect and identify phytoplasmas in samples from hosts with a sufficiently high titer. However, due to the comparatively high specificity of antibodies, serology has provided only limited information about the interrelatedness of phytoplasmas and none about relationships with culturable mollicutes and walled bacteria. Thus, the future role of serological methods will mainly be the differentiation of

closely related strains that were difficult to distinguish at the level of rDNA or other conserved sequences.

**DOT AND SOUTHERN BLOT ANALYSIS.** Randomly cloned fragments of chromosomal phytoplasmal DNA have been widely used in dot blot hybridization assays (Kirkpatrick *et al.*, 1987; Lee and Davis, 1988; Bonnet *et al.*, 1990; Lee *et al.*, 1991). The probes usually showed a considerably broader detection range than antibodies. Depending on the sequence selected, the probes varied in specificity and allowed definition of wider or narrower relationships. In particular by using probes from different phytoplasmas and with different specificity, it was possible to identify groups of genetically different phytoplasmas and to distinguish phytoplasmas within the groups.

Southern blot hybridization and analysis of the resulting RFLP patterns provided more information on genetic relationships than dot blot assays, which are rarely used now. Strains that were indistinguishable by dot hybridization could be differentiated by RFLP analysis (Bonnet *et al.*, 1990). This method also revealed considerable genetic variation between AY strains (Kuske *et al.*, 1991; Lee *et al.*, 1992a; Schneider and Seemüller, 1994b) and between apple proliferation isolates (Kison *et al.*, 1994), and could further distinguish fruit tree phytoplasmas within the apple proliferation group (Kison *et al.*, 1997). Thus, using appropriate restriction enzymes and probes, Southern blot analysis is still an important tool in phytoplasma differentiation. Especially for the distinction of closely related strains, it may allow finer differentiation than RFLP analysis of PCR-amplified conserved sequences. Beside the limited hybridization range of most probes, the major disadvantage of Southern blotting is the insufficient sensitivity of the probes in comparative work with phytoplasmas from low-titer hosts.

**RFLP ANALYSIS OF PCR-AMPLIFIED CONSERVED DNA.** In contrast to antibodies and hybridization probes, the 16S rRNA gene is universal in prokaryotes and possesses both conserved and variable regions that make it useful for taxonomic studies. After 16S rDNA became readily accessible by PCR amplification, RFLP analysis of PCR-amplified rDNA was employed to comprehensively classify the phytoplasmas on a molecular basis for the first time. This work showed that similar phytoplasmas, e. g. from the same host, exhibit similar profiles whereas isolates from different hosts or different geographic areas differ in their RFLP patterns. Using frequently cutting restriction endonucleases, such as *AluI*, *RsaI* and others, approximately 12 major groups

and several subgroups were distinguishable (Lee *et al.*, 1993c; Schneider *et al.*, 1993). At present, RFLP analysis of PCR-amplified rDNA is the method of choice for routine differentiation and classification of phytoplasmas. As the information increases with the number of restriction sites, a large fragment is often preferred that comprises the entire 16S rRNA gene and the 16S-23S rDNA spacer region (Schneider *et al.*, 1995b). Differentiation can also be improved by increasing the number of restriction enzymes. Lee *et al.* (1993c) used 15 enzymes for the classification of many diverse phytoplasmas.

However, from the data available, it appears that classification based on RFLP analysis of the 16S rRNA gene alone does not reflect the full range of phenotypic diversity. This gene does not always seem sufficiently variable to allow distinction of phytoplasmas that differ in plant host or vector specificity. More variable are nucleic acid sequences of ribosomal protein genes, which have enabled identification of more RFLP groups than 16S rDNA data. The combined RFLP analysis of both sequences resulted in the most detailed differentiation of the AY and X-disease group phytoplasmas so far (Gundersen *et al.*, 1996). Another less conserved sequence, recently examined, is the gene encoding the elongation factor Tu (*tuf* gene). Due to its variability, a more detailed subdivision of AY group phytoplasmas was obtained than by 16S rDNA analysis (Schneider *et al.*, 1997a). RFLP analysis of randomly cloned chromosomal DNA fragments has also been employed, mainly to differentiate closely related phytoplasmas (Jarausch *et al.*, 1994; Daire *et al.*, 1997).

**SEQUENCE ANALYSIS OF CONSERVED DNA.** Sequence analysis of the 16S rRNA gene is the standard method for the phylogenetic classification of prokaryotes. Major efforts were undertaken by Namba *et al.* (1993), Gundersen *et al.* (1994), and Seemüller *et al.* (1994) in sequencing full-length or nearly full-length 16S rRNA genes of representative strains from major phytoplasma groups established by RFLP analysis of 16S rDNA. In these and other studies, in which more than 40 phytoplasmas were included, approximately 12 groups could be identified as distinct subclades of the phytoplasma clade. These subclades are considered to represent the equivalent of distinct species (ICSB Subcommittee on the Taxonomy of *Mollicutes*, 1997). The classification based on sequence analysis largely corresponds to the grouping obtained by RFLP analysis of PCR-amplified 16S rDNA. The few differences observed indicate that the sequence of a large molecule, such as the 16S rRNA gene, reflects phylogenetic distance more accurately than restriction patterns which depend on significantly

fewer genetic characters. The two 16S rRNA genes which occur in phytoplasmas (Schneider and Seemüller, 1994a), seem to differ little from each other and do not markedly affect the results of sequence analysis. The only pair of heterogeneous 16S rRNA genes, which has been sequenced, differed at four nucleotide positions (Liefsting *et al.*, 1996).

Analysis of another conserved sequence, the spacer region between the 16S and 23S rRNA genes, results in a classification scheme similar to that derived from 16S rDNA data. Although the spacer region is less commonly used in phylogenetic studies, it is an attractive molecule because it is considerably shorter than the 16S rRNA gene (220-250 bp versus *ca.* 1530 bp) and thus easier to sequence. In addition, the spacer region is, apart from the highly conserved tRNA<sup>Leu</sup> gene that is apparently present in all phytoplasmas, less conserved than the 16S rDNA. For this reason, more detailed differentiation is possible. More than 60 phytoplasma strains have been differentiated and classified by analysing the sequence of their 16S-23S spacer region (Kirkpatrick *et al.*, 1994; Schneider *et al.*, 1995b). Nucleotide sequence analysis of the conserved ribosomal protein L22 gene has also been used. This fragment supported the designation of subclades and their phylogenetic positions within the phytoplasma clade as obtained by 16S rDNA sequence analysis (Gundersen *et al.*, 1994).

#### DIFFERENTIATION AND CLASSIFICATION OF PHYTOPLASMAS

**PHYLOGENETIC GROUPING.** The taxonomy of the unculturable phytoplasmas is a particular problem because many criteria important in the taxonomy of culturable bacteria are only attainable with difficulty or not at all. This applies mainly to suitable phenotypic information. Thus, the criteria of modern bacterial taxonomy as a polyphasic approach to classification, in which genotypic, phylogenetic, and phenotypic information is integrated (Stackebrandt and Goebel, 1994), cannot be employed in phytoplasmaology. As similar problems exist with other nonculturable prokaryotes, a formal classification of such bacteria, which are extensively characterized by molecular techniques, has been proposed, using a *Candidatus* prefix (Murray and Schleifer, 1994). The Working Team on Phytoplasmas of the International Research Programme of Comparative Mycoplasmaology (IRPCM) of the International Organization for Mycoplasmaology (IOM) has, at its meetings in 1994 and 1996 at Bordeaux (France) and Orlando (Florida), proposed to adopt this new classification based on 16S rRNA gene sequences and describe each subclade (ma-

ior group) defined to the tentative species level as *Candidatus* Phytoplasma species. The ICSB Subcommittee on the Taxonomy of *Mollicutes* (1993, 1997) has agreed to this proposal and adopted the policy of basing phytoplasma taxonomy on phylogeny. So far, two phytoplasmas have been described, *Candidatus* Phytoplasma aurantifolia (Zreik *et al.*, 1995) and *Candidatus* P. australiense (Davis *et al.*, 1997a) (see also Table 2).

In our attempt at classification, 48 full-length or nearly full-length phytoplasma 16S rDNA sequences available from the EMBL databank were examined. In addition, the 16S rRNA gene sequence of nine other phytoplasmas was determined as described by Seemüller *et al.*, (1994) and included in the analysis. These phytoplasmas were strains ALY, BGWL, EVY, IAWB, IBS, PDI, PEP, PYLR, and RuS (see Fig. 1 for abbreviations). Analysis of the 57 phytoplasmas revealed a greater diversity than known from previous work, in which fewer phytoplasmas were examined. By including all strains and by defining some groups in a narrower sense than previously, twenty distinct subclades consisting of groups of related phytoplasmas or single phytoplasmas were recognized (Fig. 1). The single-phytoplasma subclades are in the following also referred to as groups. The subclades delineated include the Australian grapevine yellows (AUSGY), Italian bindweed stolbur (IBS), stolbur (STOL), aster yellows (AY), buckthorn witches'-broom (BWB), spartium witches'-broom (SpaWB), apple proliferation (AP), X-disease (WX), Italian alfalfa witches'-broom (IAWB), faba bean phyllody (FBP), pigeon pea witches'-broom (PPWB), cirsium phyllody (CirP), sugarcane white leaf (SCWL), Bermuda grass white leaf (BGWL), Tanzanian lethal decline (TLD), lethal yellowing (LY), loofah witches'-broom (LfWB), ash yellows (AshY), clover proliferation (CP), and elm yellows (EY) groups. Groups AUSGY, IBS, BWB, SpaWB, IAWB, CirP, BGWL, and TLD were newly defined on the basis of branching patterns and by differences in the 16S rDNA sequence homology of at least 2.3% (AUSGY group) and 2.4% (IAWB group), or greater. The IRPCM Working Team on Phytoplasmas had earlier agreed to a threshold of 2.5% to separate the stolbur phytoplasma group from the AY agents (Meetings 1994 and 1996 at Bordeaux and Orlando, respectively).

Due to the finer subclade differentiation, the groups as delineated here are less heterogeneous than in previous schemes. Of the larger subclades, the AY, apple proliferation, and elm yellows groups are relatively homogenous, differing in their levels of 16S rDNA sequence homology by not more than 1.7%, 1.6%, and 1.2%, respectively. Other subclades such as the sugar-

cane white leaf, faba bean phyllody, and X-disease groups are still relatively heterogeneous. This applies in particular for the sugarcane white leaf group, in which the evolutionary distance between the members varies between 2.3 and 2.7%. Thus, each of the group members may eventually be considered to be sufficiently different from the others to be distinguished at the species level. Within the X-disease and faba bean phyllody groups the greatest differences in the 16S rDNA sequence homology levels are 2.2 and 2.5%.

**COMPREHENSIVE CLASSIFICATION AND DIFFERENTIATION.** A total of 246 phytoplasmas (Tables 1 and 2) examined using DNA-based and/or serological methods were divided into major phylogenetic groups or subclades as described above. Table 1 shows 103 phytoplasmas placed within the largest subclade, the AY group, grouped according to a scheme proposed by Lee *et al.* (1993c) and Gundersen *et al.* (1994, 1996), based on 16S rDNA RFLP or putative restriction site analysis. In this scheme, 8 subgroups (I-A through I-I) are distinguished. The number of phytoplasmas placed in various subgroups varies from only one (I-D, I-E, I-F, I-H) to several or many, I-B being by far the largest subgroup. All phytoplasmas of a subgroup are considered to be very similar or identical, because they did not differ in the comparisons made. However, within subgroup I-A, I-B, and I-C, a total of nine additional phytoplasmas can be distinguished from the other subgroup members by combined RFLP analyses of 16S rRNA and ribosomal protein gene sequences (Gundersen *et al.*, 1996), Southern blot analysis, and/or serological comparison. Some of the AY phytoplasmas included in Table 1 were not sufficiently characterized to be assigned to one of the established subgroups.

The 143 non-AY phytoplasmas are classified in a similar way, except that the major groups and the phytoplasmas within the groups are named according to the diseases the phytoplasmas are associated with. Sometimes a geographic attribute is included into the name to further specify the pathogen (*e.g.* Tanzanian coconut lethal decline phytoplasma). The non-AY phytoplasmas are divided into 19 major groups (Table 2). In most groups there were one or more phytoplasmas that were not distinguishable from the taxon preceding them in the list so that they were treated as identical or very similar. Among the non-AY phytoplasmas, 58 taxonomic units were distinguishable, unevenly distributed among the groups. There are several groups consisting of only one taxon whereas in other groups, up to 11 taxa (X-disease group) were differentiated. In Table 2, ten phytoplasmas were included which were only partially characterized, so that only group assignment was possible.

## GEOGRAPHIC DISTRIBUTION AND PLANT ASSOCIATION

Phytoplasmas occur worldwide, but there are significant differences in the distribution of the various groups and subgroups. For example, AY subgroup I-A phytoplasmas have only been reported in North America whereas members of subgroup I-B are widespread in North America, Europe and Japan. Phytoplasmas of the stolbur and ash yellows groups have only been identified in Europe and North America, respectively, whereas phytoplasmas of the faba bean phyllody group are only known from Asia and Australia. Apple proliferation group phytoplasmas have only been reported in Europe with the exception of the peach yellow leaf roll agent, which occurs in western USA. However, the current information about distribution is likely to be just a temporary picture subject to change with further research. There is still very little known about the occurrence of phytoplasmas in vast areas including the former Soviet Union, Africa, and South America.

Tables 1 and 2 suggest that phytoplasmas may differ considerably in host specificity. In the AY group, members of subgroup I-B appear to have a wide host range since this group occurs in many plant species. In contrast, paulownia witches'-broom (subgroup I-D), blueberry stunt (subgroup I-E), and maize bushy stunt phytoplasmas (rr-rp variant of subgroup I-B) have each been identified only in one plant species. The fruit tree phytoplasmas of the apple proliferation group also seem to preferentially infect one host. The apple proliferation (Seemüller *et al.*, 1994), pear decline, and European stone fruit yellows phytoplasmas, from which more than one 16S rRNA gene has been sequenced, show nearly 100% homology whereas between the various pathogens clear differences exist. The ash yellows phytoplasma also seems to have a narrow host range. Similarly, phytoplasmas of the lethal yellowing and Tanzanian lethal decline groups appear to infect only palms. On the other hand, phytoplasmas of the faba bean phyllody group, in particular the sunn hemp witches'-broom phytoplasma, occur in many plant species. The well-defined stolbur phytoplasma has also been identified in many plant species.

However, host specificity is still not well understood and thus differentiation of phytoplasmas at the host specificity level difficult. Also, it seems not always be possible to distinguish phytoplasmas differing in host specificity by RFLP analysis of PCR-amplified conserved sequences. It is thus conceivable that the numer-

ous isolates of AY subgroup I-B and the sunn hemp witches'-broom phytoplasma are not as homogeneous as they appear at present. Additional work using other molecular markers or other methods might reveal greater genetic diversity. It may then become possible to correlate genotype and host specificity more closely. However, as most or all phytoplasmas grow in periwinkle and induce specific symptoms in this host, there may be no strict host specificity in phytoplasmas. Host range may also depend on the interaction with insect vectors.

### CONCLUSIONS AND OUTLOOK

This review reflects the tremendous progress made in the last decade in differentiating and classifying the phytoplasmas and elucidating their genetic diversity. It was possible to divide the phytoplasmas examined into 20 major groups, in which a total of 75 phytoplasmas could be distinguished. The major groups are distinctly different and are planned, according to the consensus reached, to be delineated to the species level. Such a formal description as *Candidatus* species will undoubtedly improve the current situation, complicated by confusing historical and preliminary classification schemes. However, the numbers of distinct taxa within the groups is constantly increasing. Therefore, despite the narrower definition of some major groups proposed in this paper, some of the subclades, in particular the AY, faba bean phyllody, X-disease, sugarcane white leaf, and apple proliferation groups, are genetically and/or pathologically still too diverse, and they cannot each be described as a single taxon, in a satisfactory working sense.

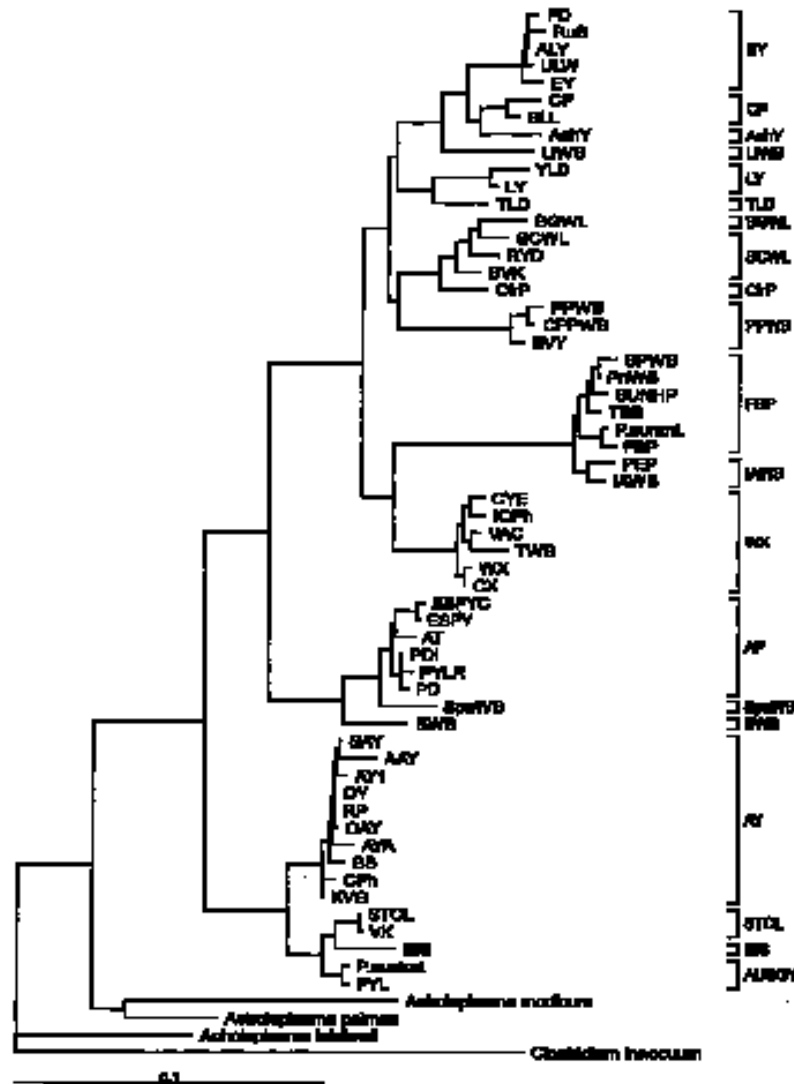
Therefore, the current concept for phytoplasma classification should be expanded and adapted to the existing diversity. One possibility would be to define each group as narrowly as possible. We also propose to describe only those major groups as *Candidatus* species that consist of only one taxon, or of phytoplasmas that are very closely related. For the other groups, consisting of several distinct phytoplasmas, all clearly different taxonomic units within the groups should be described separately, preferably as species. Examples of such additional putative taxa within subclades are the rice yellow dwarf phytoplasma and strain BVK of the sugarcane white leaf group, the European stone fruit yellows and pear decline phytoplasmas of the apple proliferation group, and the tsuwabuki witches'-broom phytoplasma of the X-disease group. Other taxa which are more closely related to a phytoplasma described as a tentative species may be distinguished as a subspecies although distinction at the species level or the use of infrasubspec-

ific ranks such as pathovar, serovar and strain is preferred (ICSB Subcommittee on the Taxonomy of *Mollicutes*, 1995). However, at the moment it is unclear how many of the molecularly distinguishable phytoplasmas will eventually be considered to be sufficiently different to be described at one of the levels discussed. One marker, such as a single conserved restriction site, may not always be sufficient to define a useful taxonomic unit.

According to the criteria recommended by the ICSB, bacteria belonging to the same species should exhibit at least 70% homology of their total DNA (Wayne *et al.*, 1987). However, DNA homologies between the nonculturable phytoplasmas are difficult to determine, and so the sequence of the conserved 16S rRNA gene was selected as the basis for phytoplasma classification. Unfortunately, there is no clear correlation between sequence homology of the 16S rDNA gene and that of the entire genome, and there is no threshold level defined for designating species on the basis of 16S rDNA sequence similarity. Comparisons show that bacteria sharing 16S rDNA similarity of about 99% may vary in the homology of their total DNA between 23.5 and 93%. However, most of the species that have been examined differ in their 16S rDNA sequence from related species of the same genus in at least 1.5% of the sequence positions, and usually more (Fox *et al.*, 1992). Thus, threshold levels of less than 2.5% for defining species may be appropriate to classify the pathologically diverse but phylogenetically coherent phytoplasmas, which differ in their 16S rDNA sequence by not more than 14.0%. This evolutionary distance corresponds to that within the phylogenetic groups of the culturable mollicutes as defined by Weisburg *et al.* (1989), which consist of much fewer taxonomic units. Thus, differences in the 16S rDNA sequence may not be sufficient to be the sole basis for phytoplasma classification, in which many distinct taxonomic units are phylogenetically closely related. For their differentiation, additional criteria may have to be included such as less conserved genes, pathological aspects, and geographical distribution. However, only such phylogenetically closely related taxa should be delineated which are genetically and pathologically adequately characterized. Any taxonomic work should be done with caution, keeping the conservative nature of any classification system in mind and taking practical considerations into account.

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**Fig. 1.** Phylogenetic dendrogram of the phytoplasmas examined, generated by using the Phylogeny Inference Package (PHYLIP), Version 3.57c (J. Felsenstein, Department of Genetics, University of Washington, Seattle, WA 98195). The bar represents a phylogenetic distance of 10%. Phylogenetic groups defined are shown in the right hand column. Group abbreviations correspond to the acronyms of the representative strains of the groups (see also text). Phytoplasma strain abbreviations and sequence accession numbers (from bottom): PYL, phormium yellow leaf (U43569); P. austral., *Candidatus* *Phytoplasma australiense* (AUSGY) (L76865); IBS, Italian bindweed stolbur (Y16391); VK, Vergilbungskrankheit (grapevine yellows) (X76428); STOL, stolbur of pepper (X76427); KVG, clover phyllody/Germany (X83870); CPh, clover phyllody/Canada (L33762); BB, tomato big bud/Arkansas (L33760); AYA (formerly ACLR), aster yellows from apricot (X68338); OAY, *Oenothera* aster yellows (M30790); RP, rape phyllody (U89378); OY, onion yellows (D12569); AY1, Maryland aster yellows (L33767); AAY, American aster yellows (X68373); SAY, western severe aster yellows (M86340); BWB, buckthorn witches'-broom (X76431); SpaWB (formerly SPAR), spartium witches'-broom (X92869); PD, pear decline/Germany (X76425); PYLR, peach yellow leaf roll (Y16394); PDI, pear decline/Italy (Y16392); AT, apple proliferation (X68375); ES-FY, European stone fruit yellows/Germany (X68374); ESFYC, European stone fruit yellows/Czech Republic (Y11933); CX, Canadian X-disease (L33733); WX, western X-disease (L04682); TWB, tsuwabuki witches'-broom (D12580); VAC, vaccinium witches'-broom (X76430); ICPh, Italian clover phyllody (X77482); CYE, clover yellow edge (L33766); IAWB, Italian alfalfa witches'-broom (Y16390); PEP, picris echioides phyllody (Y16393); FBP, faba bean phyllody (X83432); P.aurant., *Candidatus* *P. aurantifolia* (WBDL), (U15442); TBB, tomato big bud/Australia (Y08173); SUNHP, sunn hemp witches'-broom (X76433); PnWB, peanut witches'-broom (L33765); SPWB, sweet potato witches'-broom (L33770); EVY, echium vulgare yellows (Y16389); CPPWB, Caribbean pigeon pea witches'-broom (U18763); PPWB, pigeon pea witches'-broom (L33735); CcP, cirsim phyllody (X83438); BVK, from leafhopper *Psammotettix cephalotes* (X76429); RYD, rice yellow dwarf (D12581); SCWL, sugarcane white leaf (X76432); BGWL, Bermuda grass white leaf (Y16388); TLD, Tanzanian lethal decline of coconut (X80117); LY, coconut lethal yellowing (U18747); YLD, Yucatan lethal decline of coconut (U18753); LfWB, loofah witches'-broom (L33764); AshY, ash yellows (X68339); BLL, brinjal little leaf (X83431); CP, clover proliferation (L33761); EY, elm yellows/USA (L33763); ULW, elm yellows/France (X68376); ALY, alder yellows (Y16387); RuS, rubus stunt (Y16395); FD, flavescence dorée (X76560). *Clostridium innocuum* was used as an outgroup and three *Acholeplasma* species were included for comparison. See Tables 1 and 2 for further information about the phytoplasmas examined.

Table 1. Classification of phytoplasmas of the aster yellows (AY) group indentified and differentiated on the basis of molecular data and divided into subgroups.

Subgroup <sup>1</sup>	Strain/phytoplasma acronym(s)	Evidence of identity or similarity <sup>2</sup>	Disease	Plant or insect host	Geographic area	Selected references
I-A	BB	FS, rRFLP, cRFLP, S	Tomato big bud	<i>Lycopersicon esculentum</i> (tomato)	Arkansas	Lee <i>et al.</i> , 1992a, 1993a, 1993c; Gundersen <i>et al.</i> , 1996
I-A	OKAY1, NJAY, EAY	rRFLP, cRFLP, S	Aster yellows	<i>Lactuca sativa</i> (lettuce)	North America	Lee <i>et al.</i> , 1993a, 1993c; Gundersen <i>et al.</i> , 1996
I-A	AY27	rRFLP, cRFLP, S	Alberta aster yellows	<i>Callistephus chinensis</i> (China aster)	Canada	Lee <i>et al.</i> , 1992a, 1993a, 1993c; Gundersen <i>et al.</i> , 1996
I-A	CNI	rRFLP, cRFLP, S	Periwinkle little leaf	<i>Catharanthus roseus</i> (periwinkle)	USA	Lee <i>et al.</i> , 1992a, 1993a, 1993c; Gundersen <i>et al.</i> , 1996
I-A		rRFLP	Purple coneflower yellows	<i>Echinacea purpurea</i> (purple coneflower)	Wisconsin	Stanosz <i>et al.</i> , 1997
I-A	GD1	rRFLP, S	Dogwood stunt	<i>Cornus racemosa</i> (gray dogwood)	New York State	Griffiths <i>et al.</i> , 1994a
I-A	ErY4	rRFLP	Erigeron yellows	<i>Erigeron canadensis</i> (horseweed)	Maryland	Lee <i>et al.</i> , 1994
I-A	GSI	rRFLP	Goldenrod stunt	<i>Solidago</i> spp. (goldenrod)	Maryland	Lee <i>et al.</i> , 1994
I-A (rr-rrp)		rRFLP	Multiplier disease	<i>Fragaria x ananassa</i> (strawberry)	Florida	Harrison <i>et al.</i> , 1997
I-B	AY1	FS, rRFLP, cRFLP	Maryland aster yellows	<i>Catharanthus roseus</i> (periwinkle)	Maryland	Lee <i>et al.</i> , 1992a, 1993c; Gundersen <i>et al.</i> , 1996
I-B	DAY	rRFLP, cRFLP	Dwarf western aster yellows	<i>Trifolium</i> sp. (clover)	California	Kuske <i>et al.</i> , 1991; Lee <i>et al.</i> , 1993c; Gundersen <i>et al.</i> , 1996
I-B	TLAY2	rRFLP, cRFLP	Tulelake western aster yellows	<i>Solanum tuberosum</i> (potato)	California	Lee <i>et al.</i> , 1992a, 1993c; Gundersen <i>et al.</i> , 1996
I-B	OKAY3	rRFLP, cRFLP	Western aster yellows	<i>Daucus carota</i> (carrot)	Oklahoma	Lee <i>et al.</i> , 1992a, 1993c; Gundersen <i>et al.</i> , 1996
I-B	CY2, MY	rRFLP, cRFLP	Marguerite yellows	<i>Chrysanthemum frutescens</i> (marguerite)	Japan, Italy	Gundersen <i>et al.</i> , 1996; Vibio <i>et al.</i> , 1996; Okuda <i>et al.</i> , 1997
I-B	SL5, SL7, SL8, FPV	rRFLP	Periwinkle yellows	<i>Catharanthus roseus</i> (periwinkle)	USA	Lee <i>et al.</i> , 1993c; Harrison <i>et al.</i> , 1996
I-B	IPWB, SL1, SIPY, IPS, FE1	rRFLP, cRFLP	Periwinkle witches' broom and virescence	<i>Catharanthus roseus</i> (periwinkle)	Italy	Vibio <i>et al.</i> , 1996; Marccone <i>et al.</i> , 1997b
I-B	NYAY	rRFLP, cRFLP	New York aster yellows	<i>Lactuca sativa</i> (lettuce)	New York	Lee <i>et al.</i> , 1992a, 1993a, 1993c; Gundersen <i>et al.</i> , 1996
I-B	ILY	rRFLP, cRFLP	Italian lettuce yellows	<i>Lactuca sativa</i> (lettuce)	Italy	Vibio <i>et al.</i> , 1994; Marccone <i>et al.</i> , 1997b
I-B	HyPh1, BHy, LHV	rRFLP, cRFLP	Hydrangea phyllody	<i>Hydrangea macrophylla</i> (French hydrangea)	Europe	Lee <i>et al.</i> , 1993c; Vibio <i>et al.</i> , 1996; Marccone <i>et al.</i> , 1997b

I-B	AAV	FS, rRFLP,	American aster yellows	<i>Allium cepa</i> (onion)	Florida	Schneider <i>et al.</i> , 1993; Seemüller <i>et al.</i> , 1994; Marcone <i>et al.</i> , 1997a
I-B	OY	PS, SS, rRFLP	Onion yellows and virescence	<i>Gladiolus</i> hybrid ( <i>gladiolus</i> )	Japan, Italy	Namba <i>et al.</i> , 1993; Semüller <i>et al.</i> , 1994; Vibio <i>et al.</i> , 1995b
I-B	GIY	rRFLP, cRFLP	Gladiolus yellows	<i>Brassica oleracea</i> var. <i>capitata</i> (cabbage)	Europe	Bertaccini and Vibio, 1996; Vibio <i>et al.</i> , 1996
I-B	ICY	rRFLP	Italian cabbage yellows	<i>Brassica oleracea</i> var. <i>italica</i> (sprouting broccoli)	Italy	Marcone <i>et al.</i> , 1997b
I-B	IBP	rRFLP	Broccoli phyllody	<i>Brassica oleracea</i> var. <i>palmifolia</i> (kale)	Italy	Bertaccini and Vibio, 1996
I-B	SIKP	rRFLP	Kale phyllody	<i>Brassica rapa</i> var. <i>rapifera</i> (turnip)	Italy	Marcone <i>et al.</i> , 1997b
I-B	TPV	rRFLP	Turnip virescence	<i>Lycopersicon esculentum</i> (tomato)	Italy, Japan	Marcone <i>et al.</i> , 1997b; Okuda <i>et al.</i> , 1997
I-B		rRFLP	Big bud	<i>Calendula officinalis</i> (pot marigold)	Italy	Marcone <i>et al.</i> , 1997a
I-B	SICV	rRFLP	Calendula virescence	<i>Papaver rhoeas</i> (corn poppy)	Italy	Marcone <i>et al.</i> , 1997c
I-B	PV	rRFLP	Papaver virescence	<i>Raphanus raphanistrum</i> (wild radish)	Italy	Marcone <i>et al.</i> , 1997c
I-B	WRY	rRFLP	Wild radish yellows	<i>Portulaca oleracea</i> (purslane)	Italy	Marcone <i>et al.</i> , 1997c; Schneider <i>et al.</i> , 1997b
I-B	POY	rRFLP	Portulaca yellows	<i>Cyclamen persicum</i> (cyclamen)	Germany	Schneider <i>et al.</i> , 1997b
I-B		rRFLP	Cyclamen virescence	<i>Erigeron canadensis</i> (horseweed)	USA	Lee <i>et al.</i> , 1994
I-B	ErY	rRFLP	Erigeron yellows	<i>Alstroemeria</i> sp. ( <i>alstroemeria</i> )	Italy	Bertaccini and Vibio, 1996
I-B		rRFLP	Alstroemeria decline	<i>Ranunculus asiaticus</i> (Persian buttercup)	Italy	Vibio <i>et al.</i> , 1997
I-B		rRFLP	Ranunculus phyllody	<i>Mahva</i> sp. (mallow)	Italy	Vibio <i>et al.</i> , 1997
I-B		rRFLP	Mallow yellows	<i>Ambrosia artemisiifolia</i> (common ragweed)	Florida	Harrison <i>et al.</i> , 1996
I-B		rRFLP, cRFLP	Ragweed yellows	<i>Eupatorium capillifolium</i> ( <i>dogfennel</i> )	Florida	Harrison <i>et al.</i> , 1996
I-B		rRFLP, cRFLP	Dogfennel yellows	<i>Populus nigra</i> 'Italica' (Lombardy poplar)	France	Berges <i>et al.</i> , 1997
I-B		rRFLP	Poplar witches'-broom	<i>Cryptotaenia japonica</i> (Japanese honeysuckle)	Japan	Okuda <i>et al.</i> , 1997
I-B	JHW	rRFLP	Mitsuba witches'-broom	<i>Morus bombycis</i> (mulberry)	Japan	Namba <i>et al.</i> , 1993
I-B	MD	FS	Mulberry dwarf	<i>Chrysanthemum coronarium</i> (crown daisy)	Japan	Okuda <i>et al.</i> , 1997
I-B	GCW	rRFLP	Chrysanthemum witches'-broom	<i>Solanum melongena</i> (eggplant)	Japan	Okuda <i>et al.</i> , 1997
I-B	ED	rRFLP	Eggplant dwarf	<i>Prunus armeniaca</i> (apricot)	Italy	Lee <i>et al.</i> , 1995a
I-B		rRFLP	Unknown			

(continued)

Table 1 (continued)

Subgroup <sup>1</sup>	Strain/phytoplasma acronym(s)	Evidence of identity or similarity <sup>2</sup>	Disease	Plant or insect host	Geographic area	Selected references
I-B		rRFLP	Unknown	<i>Prunus persica</i> var. <i>nectarina</i> (nectarine)	Italy	Lee <i>et al.</i> , 1995a
I-B		rRFLP	Unknown	<i>Prunus salicina</i> (Japanese plum)	Italy	Lee <i>et al.</i> , 1995a
I-B		rRFLP	Unknown	<i>Trifolium pratense</i> (red clover)	Canada	Lee <i>et al.</i> , 1994
I-B		rRFLP	Unknown	<i>Solanum tuberosum</i> (potato)	Canada	Lee <i>et al.</i> , 1994
I-B		rRFLP	Unknown	<i>Celtis australis</i> (European hackberry)	Italy	Bertaccini <i>et al.</i> , 1996b
I-B		rRFLP	Unknown	<i>Ulmus</i> sp. (elm)	Italy	Lee <i>et al.</i> , 1995b
I-B		rRFLP	Grapevine yellows	<i>Vitis vinifera</i> (grapevine)	Italy	Alma <i>et al.</i> , 1996
I-B		rRFLP	Unknown	<i>Metacalfa pruinosa</i> (planthopper)	Italy	Dantelli <i>et al.</i> , 1996a
I-B		rRFLP	Mosaic, Free-branching, asymptomatic	<i>Euphorbia pulcherrima</i> (Christmas poinsettia)	Italy	Bertaccini <i>et al.</i> , 1996a, 1996c
I-B		rRFLP	Olive witches'-broom	<i>Olea europaea</i> (olive)	Italy	Danielli <i>et al.</i> , 1996b
I-B		rRFLP	Eucalyptus yellows	<i>Eucalyptus</i> spp. (eucalypt)	Italy	Bertaccini and Vibio, 1996
I-B		rRFLP	Myrtle yellows	<i>Myrtus communis</i> (myrtle)	Italy	Bertaccini and Vibio, 1996
I-B (rr-rr)	IOWB	rRFLP, cRFLP	Ipomoea obscura witches'-broom	<i>Ipomoea obscura</i>	Taiwan	Lee <i>et al.</i> , 1993c; Gundersen <i>et al.</i> , 1996
I-B (rr-rr)	MBS	rRFLP, cRFLP	Maize bushy stunt	<i>Zea mays</i> (corn)	Mexico, Ohio	Gundersen <i>et al.</i> , 1996
I-B (cRFLP)	OAY	FS, SS, rRFLP, cRFLP	Oenothera virescence	<i>Oenothera hookeri</i> (evening primrose)	Michigan	Lim and Sears, 1989; Kuske <i>et al.</i> , 1991; Gundersen <i>et al.</i> , 1996
I-B (cRFLP, S-a)	CL, RV	rRFLP, cRFLP, S	Chlorantia	<i>Brassica napus</i> (rape)	France	Kuske <i>et al.</i> , 1991; Keane <i>et al.</i> , 1996; Vibio <i>et al.</i> , 1996;
I-B (S-a)	SAY	FS, SS, rRFLP, cRFLP, S	Severe western aster yellows	<i>Apium graveolens</i> (celery)	California	Kuske and Kirkpatrick, 1992; Lee <i>et al.</i> , 1993c; Keane <i>et al.</i> , 1996
I-B (S-a)	CC	rRFLP, cRFLP, S	Cactus virescence	<i>Opuntia</i> sp. (cactus)	UK	Keane <i>et al.</i> , 1996; Vibio <i>et al.</i> , 1996
I-B (S-b)	PY	rRFLP, cRFLP, S	Primula yellows	<i>Primula</i> sp. (primrose)	Germany	Keane <i>et al.</i> , 1996; Vibio <i>et al.</i> , 1996
I-B (S-c)	KD	rRFLP, cRFLP, S	Koolsard	<i>Brassica</i> sp. (cabbage)	UK	Keane <i>et al.</i> , 1996; Vibio <i>et al.</i> , 1996
I-B (cRFLP, S-d)	EAY, AV2192	rRFLP, cRFLP, SS, S	European aster yellows	<i>Callistephus chinensis</i> (China aster)	Germany	Kuske <i>et al.</i> , 1991; Keane <i>et al.</i> , 1996; Vibio <i>et al.</i> , 1996
? I-B		rRFLP	Cardaria phyllody	<i>Cardaria draba</i> (hoary cress)	Germany	Schneider <i>et al.</i> , 1997b
? I-B		rRFLP	Bunias phyllody	<i>Bunias orientalis</i> (hill mustard)	Germany	Schneider <i>et al.</i> , 1997b
? I-B		rRFLP	Stellaria yellows	<i>Stellaria media</i> (common chickweed)	Germany	Schneider <i>et al.</i> , 1997b
? I-B		rRFLP	Carrot proliferation	<i>Daucus carota</i> (carrot)	Germany	Schneider <i>et al.</i> , 1997b
? I-B	AKV	rRFLP, cRFLP	Columbine virescence	<i>Aquilegia alpina</i> (columbine)	Germany	Schneider <i>et al.</i> , 1993; Schneider and Seemüller, 1994b
? I-B	DEV	rRFLP, cRFLP	Larkspur virescence	<i>Delphinium</i> hybrid (larkspur)	Germany	Schneider <i>et al.</i> , 1993; Schneider and Seemüller, 1994b

? I-B	DIV	rRFLP, cRFLP	Diplotaxis virescence	<i>Diplotaxis erucoides</i> (rocket)	Spain	Schneider <i>et al.</i> , 1993; Schneider and Seemüller, 1994b
? I-B	PVM, PVW	rRFLP, cRFLP	Plantain virescence	<i>Plantago</i> spp. (plantain)	Germany	Schneider <i>et al.</i> , 1993; Schneider and Seemüller, 1994b
I-C	CPh	FS, rRFLP, cRFLP	Clover phyllody	<i>Trifolium sativum</i> (red clover)	Canada	Lee <i>et al.</i> , 1992a, 1993c; Gundersen <i>et al.</i> , 1996
I-C	KVG, KV, KVF, KVE	FS, rRFLP, cRFLP, S	Clover phyllody	<i>Trifolium repens</i> (white clover)	Europe	Clark <i>et al.</i> , 1983; Firrao <i>et al.</i> , 1996a; Schneider <i>et al.</i> , 1997b
I-C	SGP	rRFLP, cRFLP, S	Strawberry green petal	<i>Fragaria x ananassa</i> (strawberry)	North America, Europe	Clark <i>et al.</i> , 1983; Gundersen <i>et al.</i> , 1996; Honet Hégrová <i>et al.</i> , 1996
I-C		rRFLP	Anemone virescence	<i>Anemone coronaria</i> (poppy anemone)	Italy	Vibio <i>et al.</i> , 1995a
I-C	SP1	rRFLP	Spirea stunt	<i>Spiraea tomentosa</i> (spirea)	USA	Lee <i>et al.</i> , 1994
I-C		rRFLP	Alstroemeria decline	<i>Alstroemeria</i> sp. (alstroemeria)	Italy	Bertaccini and Vibio, 1996
I-C		rRFLP	Unknown	<i>Celtis australis</i> (European hackberry)	Italy	Bertaccini <i>et al.</i> , 1996
I-C		rRFLP	Unknown	<i>Meibomia pruinoso</i> (planthopper)	Italy	Danielli <i>et al.</i> , 1996a
I-C		rRFLP	Mosaic, asymptomatic	<i>Euphorbia pulcherrima</i> (Christmas poinsettia)	Italy	Bertaccini <i>et al.</i> , 1996c
I-C		rRFLP	Olive witches'-broom	<i>Olea europaea</i> (olive)	Italy	Danielli <i>et al.</i> , 1996b
I-C		rRFLP	Eucalyptus yellows	<i>Eucalyptus</i> sp. (eucalypt)	Italy	Bertaccini and Vibio, 1996
I-C (rr-rr)	RPy	rRFLP, cRFLP	Ranunculus phyllody	<i>Ranunculus</i> sp. (buttercup)	Italy	Gundersen <i>et al.</i> , 1996
I-D	PaWB	PS, rRFLP	Paulownia witches'-broom	<i>Paulownia tomentosa</i> (paulownia)	Taiwan	Lee <i>et al.</i> , 1993c; Gundersen <i>et al.</i> , 1996
I-E	BBS	PS, rRFLP, cRFLP	Blueberry stunt	<i>Vaccinium</i> spp. (blueberry)	USA	Lee <i>et al.</i> , 1993c; Gundersen <i>et al.</i> , 1996
I-F	AYA (ACLR)	FS, rRFLP	Unknown	<i>Prunus armeniaca</i> (apricot)	Spain	Schneider <i>et al.</i> , 1993; Seemüller <i>et al.</i> , 1994
I-H	CYb	rRFLP, cRFLP	Chrysanthemum yellows	<i>Chrysanthemum frutescens</i> (marguerite)	Italy	Gundersen <i>et al.</i> , 1996
Subgroup <sup>1</sup>	Strain/phytoplasma acronym(s)	Evidence of identity or similarity <sup>2</sup>	Disease	Plant or insect host	Geographic area	Selected references

(continued)

Table 1 (continued)

Subgroup <sup>1</sup>	Strain/phytoplasma acronym(s)	Evidence of identity or similarity <sup>2</sup>	Disease	Plant or insect host	Geographic area	Selected references
I-I Mexican periwinkle virescence phytoplasma	MPV	rRFLP, cRFLP	Periwinkle virescence	<i>Catharanthus roseus</i> (periwinkle)	Mexico	Gundersen <i>et al.</i> , 1996
I-I		rRFLP	Strawberry green petal, stunting	<i>Fragaria x ananassa</i> (strawberry)	Florida	Jomantiene <i>et al.</i> , 1996; Harrison <i>et al.</i> , 1997
I-I	FWB	rRFLP	Periwinkle witches'-broom	<i>Catharanthus roseus</i> (periwinkle)	Florida	Harrison <i>et al.</i> , 1996
Subgroup unclear	COL	rRFLP, cRFLP	Latent	<i>Cuscuta odorata</i> (dodder)	Germany	Schneider <i>et al.</i> , 1993; Schneider and Seemüller, 1994b
	CVL	rRFLP, cRFLP	Periwinkle virescence	<i>Catharanthus roseus</i> (periwinkle)	Peru	Schneider <i>et al.</i> , 1993; Schneider and Seemüller, 1994b
	CVT	rRFLP, cRFLP	Periwinkle virescence	<i>Catharanthus roseus</i> (periwinkle)	Thailand	Schneider <i>et al.</i> , 1993; Schneider and Seemüller, 1994b
	MPY	DB	Periwinkle yellows	<i>Catharanthus roseus</i> (periwinkle)	Malaysia	Khew <i>et al.</i> , 1991
	SAS	rRFLP, cRFLP	Sandal spike	<i>Santalum album</i> (sandalwood)	India	Schneider <i>et al.</i> , 1993; Schneider and Seemüller, 1994b
	SAFP	SS, rRFLP, cRFLP, S	Safflower phylloxy	<i>Charthamus tinctorius</i> (safflower)	Israel	Schneider <i>et al.</i> , 1993; Schneider and Seemüller, 1994b
		DB	Pumpkin yellows	<i>Cucurbita pepo</i> (pumpkin)	Italy	Minucci <i>et al.</i> , 1995
		rRFLP	Monarda yellows	<i>Monarda fistulosa</i> (wild bergamot)	Canada	Khadhair <i>et al.</i> , 1997
		S	Lotus yellows	<i>Lotus corniculatus</i> (bird's-foot trefoil)	USA	Griffiths <i>et al.</i> , 1994a
		S	New England aster yellows	<i>Aster novae-angliae</i> (New England aster)	USA	Griffiths <i>et al.</i> , 1994a
		rRFLP	Poplar yellows	<i>Populus</i> spp. (poplar)	Europe	Berges <i>et al.</i> , 1997

<sup>1</sup> All subgroup members appear identical or very similar. Differing phytoplasmas within the subgroups are marked as follows:

(rr-rr), distinguishable on the basis of combined RFLP analyses of 16S rRNA and ribosomal protein genes, (cRFLP), distinguishable on the basis of cRFLP patterns (see under <sup>2</sup>),

S-a to S-d, serotypes according to Keane *et al.*, 1996.

<sup>2</sup> Nature of evidence: FS, full-length 16S rDNA sequence; PS, partial 16S rDNA sequence; SS, 16S/23S rDNA spacer sequence; rRFLP, RFLP patterns of PCR-amplified ribosomal DNA; cRFLP, RFLP patterns of nonribosomal DNA (PCR-amplified or Southern analysis); DB, dot blot analysis.

**Table 2.** Classification of non-aster yellows phytoplasmas identified and differentiated on the basis of molecular data and divided into major phylogenetic groups.

Phytoplasma group and group members associated with the diseases listed <sup>1</sup>	Acronym(s) of phyto-plasma	Evidence of identity or similarity <sup>2</sup>	Plant or insect host	Geographic area	Selected references
<b>AUSTRALIAN GRAPEVINE YELLOWS (AUSGY) GROUP</b>					
Australian grapevine yellows ( <i>Cand. Phytopl. australiense</i> ) = Papaya dieback	AUSGY	FS, rRFLP, cRFLP	<i>Vitis vinifera</i> (grapevine)	Australia	Padovan <i>et al.</i> , 1996; Davis <i>et al.</i> , 1997a
Phormium yellow leaf	PYL	rRFLP	<i>Carica papaya</i> (papaya)	Australia	Gibb <i>et al.</i> , 1996
		FS, cRFLP	<i>Phormium tenax</i> (New Zealand flax)	New Zealand	Liefing <i>et al.</i> , 1996
<b>ITALIAN BINDWEED STOLBUR (IBS) GROUP</b>					
Italian bindweed stolbur	IBS	FS, rRFLP	<i>Convolvulus arvensis</i> (field bindweed)	Italy	Marcone <i>et al.</i> , 1997a
<b>STOLBUR (STOL) GROUP</b>					
Stolbur of pepper	STOL	FS, SS, RFLP, cRFLP, S	<i>Capsicum annuum</i> (pepper)	France, Serbia	Fos <i>et al.</i> , 1992; Seemüller <i>et al.</i> , 1994; Marcone <i>et al.</i> , 1997a
= Tomato stolbur	STOL	SS, rRFLP, cRFLP, S	<i>Lycopersicon esculentum</i> (tomato)	Europe	Fos <i>et al.</i> , 1992; Boudon-Padieu <i>et al.</i> , 1996; Marcone <i>et al.</i> , 1997b
= Tobacco stolbur	STOL	rRFLP, S	<i>Nicotiana tabacum</i> (tobacco)	France, Italy	Fos <i>et al.</i> , 1992; C. Marcone, unpublished
= Eggplant stolbur		S	<i>Solanum melongena</i> (eggplant)	France	Fos <i>et al.</i> , 1992
= Strawberry yellows		S	<i>Fragaria x ananassa</i> (strawberry)	France	Fos <i>et al.</i> , 1992
= Porcelain disease		S	<i>Apium graveolens</i> (celery)	France	Fos <i>et al.</i> , 1992
= Periwinkle yellows		S	<i>Catharanthus roseus</i> (periwinkle)	France	Fos <i>et al.</i> , 1992
= Nightshade proliferation		S	<i>Solanum dulcamara</i> (bittersweet nightshade)	France	Fos <i>et al.</i> , 1992
= Lycopersicon hirsutum little leaf		S	<i>Lycopersicon hirsutum</i>	France	Fos <i>et al.</i> , 1992
= Leafhopper-borne		S	<i>Hyalosthes obsoletus</i> (planthopper)	France	Fos <i>et al.</i> , 1992
= Bindweed yellows		rRFLP, S	<i>Convolvulus arvensis</i> (field bindweed)	France, Germany	Fos <i>et al.</i> , 1992; Maixner <i>et al.</i> 1995; Schneider <i>et al.</i> , 1997b
= Bois noir, Vergilbungs-krankheit, other grapevine yellows	BN, VK	FS, SS, rRFLP, cRFLP	<i>Vitis vinifera</i> (grapevine)	Europe	Seemüller <i>et al.</i> , 1994; Marcone <i>et al.</i> , 1996a; Daire <i>et al.</i> , 1997
<b>BUCKTHORN WITCHES'-BROOM (BWB) GROUP</b>					
Buckthorn witches'-broom	BWB, BABW	FS, rRFLP	<i>Rhamnus catharticus</i> (buckthorn)	Germany	Seemüller <i>et al.</i> , 1994; Mäurer and Seemüller, 1996
<b>SPARTIUM WITCHES'-BROOM (S pa WB) GROUP</b>					
Spartium witches'-broom	SpaWB	FS, rRFLP	<i>Spartium junceum</i> (Spanish broom)	Italy	Marcone <i>et al.</i> , 1996b
Sarothamnus witches'-broom	SSWB	rRFLP	<i>Sarothamnus scoparius</i> (broom)	Italy	Marcone <i>et al.</i> , 1997f

(continued)

Table 2 (continued)

Phytoplasma group and group members associated with the diseases listed <sup>1</sup>	Acronym(s) of phyto-plasma	Evidence of identity or similarity <sup>2</sup>	Plant or insect host	Geographic area	Selected references
<b>APPLE PROLIFERATION (AP) GROUP</b>					
Apple proliferation	AP	FS, SS, rRFLP, cRFLP	<i>Malus domestica</i> (apple)	Europe	Kirkpatrick <i>et al.</i> , 1994; Seemüller <i>et al.</i> , 1994; Lorenz <i>et al.</i> , 1995
= Hazel decline		rRFLP	<i>Corylus avellana</i> (hazel)	Italy	Marcone <i>et al.</i> , 1996c
= Bindweed yellows		rRFLP	<i>Convolvulus arvensis</i> (field bindweed)	Germany	Schneider <i>et al.</i> , 1997
Pear decline	PD	FS, SS, rRFLP	<i>Pyrus communis</i> (pear)	Europe, North America	Kirkpatrick <i>et al.</i> , 1994; Seemüller <i>et al.</i> , 1994; Kison <i>et al.</i> , 1997
= Peach yellow leaf roll	PYLR	FS, rRFLP	<i>Prunus persica</i> (peach)	North America	Kirkpatrick <i>et al.</i> , 1994; Kison <i>et al.</i> , 1997
= Hazel decline		rRFLP	<i>Corylus avellana</i> (hazel)	Italy	Marcone <i>et al.</i> , 1996c
European stone fruit yellows of peach	ESFY	FS, SS, rRFLP, cRFLP	<i>Prunus persica</i> (peach)	Europe	Kirkpatrick <i>et al.</i> , 1994; Seemüller <i>et al.</i> , 1994; Kison <i>et al.</i> , 1997
= European stone fruit yellows of apricot (Apricot chlorotic leaf roll)	ESFY (ACLR)	SS, rRFLP, cRFLP	<i>Prunus armeniaca</i> (apricot)	Europe	Kirkpatrick <i>et al.</i> , 1994; Lorenz <i>et al.</i> , 1994; Kison <i>et al.</i> , 1997
= European stone fruit yellows of Jap. plum (Plum leptonecrosis)	ESFY (PLN)	rRFLP, cRFLP	<i>Prunus salicina</i> (Japanese plum)	Europe	Lorenz <i>et al.</i> , 1994; Marcone <i>et al.</i> , 1996c
= European stone fruit yell. of flowering cherry	ESFY	rRFLP, cRFLP	<i>P. serrulata</i> (flowering cherry)	Germany	Schneider <i>et al.</i> , 1993; Lorenz <i>et al.</i> , 1994
= European stone fruit yellows of Europ. plum	ESFY	rRFLP, cRFLP	<i>Prunus domestica</i> (European plum)	Europe	Lorenz <i>et al.</i> , 1994
= European stone fruit yellows of almond	ESFY	rRFLP, cRFLP	<i>P. amygdaliformis</i> (almond)	Europe	Lorenz <i>et al.</i> , 1994
= Hazel decline		rRFLP	<i>Corylus avellana</i> (hazel)	Italy	Marcone <i>et al.</i> , 1996c
<b>X-DISEASE (WX) GROUP</b>					
Western X-disease	WX	FS, SS, rRFLP, cRFLP, S	<i>Prunus persica</i> (peach)	Western USA	Seemüller <i>et al.</i> , 1994; Schneider <i>et al.</i> , 1995b; Gundersen <i>et al.</i> , 1996
= Disease unknown	PDX	SS, rRFLP, cRFLP	<i>Pyrus communis</i> (pear)	California	Gundersen <i>et al.</i> , 1996
= Erigeron yellows	ErY4	rRFLP	<i>Erigeron canadensis</i> (horseweed)	USA	Lee <i>et al.</i> , 1994
= Goldenrod stunt	GSI	rRFLP	<i>Solidago rugosa</i> (goldenrod)	USA	Lee <i>et al.</i> , 1994
= Free-branching of Christmas poinsettia		rRFLP	<i>Euphorbia pulcherrima</i> (Christmas poinsettia)	USA	Abad <i>et al.</i> , 1997
Canadian peach X-disease	CX	FS, rRFLP, cRFLP, S	<i>Prunus persica</i> (peach)	Canada	Lee <i>et al.</i> , 1992b, 1993c; Gundersen <i>et al.</i> , 1996
= Chokecherry X-disease	CCX	PS, rRFLP, cRFLP, S	<i>Prunus virginiana</i> (choke cherry)	USA	Gundersen <i>et al.</i> , 1996; Guo <i>et al.</i> , 1996
Clover yellow edge	CYE	FS, rRFLP, cRFLP, S	<i>Trifolium repens</i> (white clover)	Canada	Shina and Benhamou, 1983; Lee <i>et al.</i> , 1992b; Gundersen <i>et al.</i> , 1996

= Gentian witches'-broom = Grapevine yellows	GW FDVA, FDU	rRFLP rRFLP, cRFLP, S	<i>Gentiana</i> sp. (gentian) <i>Vitis vinifera</i> (grapevine)	Japan USA, Italy	Okuda <i>et al.</i> , 1997 Prince <i>et al.</i> , 1993; Chen <i>et al.</i> , 1993; Marcone <i>et al.</i> , 1996a Firrao <i>et al.</i> , 1996a
= Oxeye phyllody	OxP	rRFLP, cRFLP	<i>Chrysanthemum leucanthemum</i> (oxeye daisy)	Italy	Firrao <i>et al.</i> , 1996a
= Taraxacum yellows = Crepis yellows = Free-branching of Christmas poinsettia Milkweed yellows	= TaY = CreY	rRFLP, cRFLP rRFLP, cRFLP rRFLP	<i>Taraxacum officinale</i> (dandelion) <i>Crepis biennis</i> (rough hawk's beard) <i>Euphorbia pulcherrima</i> (Christmas poinsettia)	Italy Italy USA	Firrao <i>et al.</i> , 1996a Firrao <i>et al.</i> , 1996a Abad <i>et al.</i> , 1997
	MWY	rRFLP, cRFLP	<i>Asclepias syriaca</i> (milkweed)	USA	Griffiths <i>et al.</i> , 1994c; Gundersen <i>et al.</i> , 1996
Italian clover phyllody	ICPh	FS, rRFLP, cRFLP, S	<i>Trifolium</i> sp. (clover)	Italy	Firrao <i>et al.</i> , 1996a, 1996b
Pecan bunch	PB	rRFLP, cRFLP	<i>Carya illinoensis</i> (pecan)	USA	Gundersen <i>et al.</i> , 1996
Goldenrod yellows	GR1	rRFLP, cRFLP	<i>Solidago rugosa</i> (goldenrod)	USA	Griffiths <i>et al.</i> , 1994c; Gundersen <i>et al.</i> , 1996
Walnut witches'-broom	WWB	SS, rRFLP, cRFLP, S	<i>Juglans nigra</i> (black walnut)	USA	Kirkpatrick <i>et al.</i> , 1994; Gundersen <i>et al.</i> , 1996; Firrao <i>et al.</i> , 1996b
Spirea stunt	SP1	rRFLP, cRFLP	<i>Spiraea</i> sp. (spirea)	USA	Griffiths <i>et al.</i> , 1994c; Gundersen <i>et al.</i> , 1996
Free-branching of Christmas poinsettia Vaccinium witches'-broom	VAC	rRFLP	<i>Euphorbia pulcherrima</i> (Christmas poinsettia)	USA	Lee <i>et al.</i> , 1997a
	TWB	FS, SS, rRFLP, S	<i>Vaccinium myrtilus</i> (blueberry)	Germany	Schneider <i>et al.</i> , 1993; Kirkpatrick <i>et al.</i> , 1994; Seemüller <i>et al.</i> , 1994
Tsuwabuki witches'-broom	TWB	FS, rRFLP	<i>Farfugium japonicum</i> (tsuwabuki)	Japan	Namba <i>et al.</i> , 1993; Kirkpatrick <i>et al.</i> , 1994; Okuda <i>et al.</i> , 1997
? Green Valley X-disease ? Peach yellows ? Peach rosette ? Brazilian tomato big bud ? Dodonea yellows ? Horseweed phyllody	GVX PY PR BTBB DoY	rRFLP, cRFLP cRFLP SS, cRFLP, S rRFLP, S SS, DB rRFLP	<i>Prunus avium</i> (cherry) <i>Prunus persica</i> (peach) <i>Prunus persica</i> (peach) <i>Lycopersicon esculentum</i> (tomato) <i>Dodonea viscosa</i> <i>Erigeron canadensis</i> (horseweed)	California USA USA Brasil Hawaii USA	Ahrens <i>et al.</i> , 1993 Kirkpatrick, 1991 Kirkpatrick, 1991; Firrao <i>et al.</i> , 1996b Boudon-Padieu <i>et al.</i> , 1996 Borth <i>et al.</i> , 1995 Schneider <i>et al.</i> , 1997b
<b>ITALIAN ALFALFA WITCHES'-BROOM (IAWB) GROUP</b>					
Italian alfalfa witches'-broom Pisiris echinoides phyllody	IAWB PEP	FS, rRFLP FS, rRFLP	<i>Medicago sativa</i> (alfalfa) <i>Pisiris echinoides</i> (bristly ox tongue)	Italy Italy	Marcone <i>et al.</i> , 1997b Marcone <i>et al.</i> , 1997a
<b>FABA BEAN PHYLLODY (FBP) GROUP</b>					
Faba bean phyllody	FBP	FS, SS, rRFLP	<i>Vicia faba</i> (faba bean)	Sudan	Kirkpatrick <i>et al.</i> , 1994; Schneider <i>et al.</i> , 1995a
= Crotalaria phyllody = Crotalaria saltiana phyllody = Soybean phyllody Cotton phyllody	CtP (CJP) CSP SoyP CoP	rRFLP, S rRFLP, S rRFLP, S rRFLP, S	<i>Crotalaria juncea</i> (sunn hemp) <i>Crotalaria saltiana</i> <i>Glycine max</i> (soybean) <i>Gossypium hirsutum</i> (cotton)	Thailand Sudan Thailand Burkina Faso	Saeed <i>et al.</i> , 1994; Schneider <i>et al.</i> , 1995a Saeed <i>et al.</i> , 1994; Schneider <i>et al.</i> , 1995a Saeed <i>et al.</i> , 1994; Schneider <i>et al.</i> , 1995a Saeed <i>et al.</i> , 1994; Schneider <i>et al.</i> , 1995a Schneider <i>et al.</i> , 1997b; C. Marcone, unpublished result

(continued)



<b>PIGEON PEA WITCHES' -BROOM (PPWB) GROUP</b>			Pathogen	Country	Reference
Host	PPWB	FS, rRFLP, DB			
Pigeon pea witches'-broom	PPWB	FS, rRFLP, DB	<i>Cajanus cajan</i> (pigeon pea) <i>Cajanus cajan</i> (pigeon pea) <i>Echium vulgare</i> (blueweed, viper's bugloss) <i>Crepis setosa</i> (hawksbeard) <i>Picris echioides</i> (bristly ox-tongue) <i>Knautia arvensis</i> (field scabious)	Florida	Lee et al., 1993c; Gundersen et al., 1994; N.A. Harrison et al., unpublished Marcone et al., 1997a Marcone et al., 1997a Schneider et al., 1997b Marcone et al., 1997a
Caribbean pigeon pea witches'-broom	CPPWB	FS		Italy	
<i>Echium vulgare</i> yellows	EVY	FS, rRFLP		Italy	
= <i>Crepis setosa</i> phyllody	CrSP	rRFLP		Italy	
= <i>Picris echioides</i> phyllody	PiEP	rRFLP		Italy	
<i>Knautia arvensis</i> phyllody	KAP	rRFLP	Italy		
<b>CIRSIMUM PHYLLODY (CirP) GROUP</b>					
Cirsium phyllody	CirP	FS, rRFLP	<i>Cirsium arvense</i> (Canada thistle)	Germany	Schneider et al., 1997b
<b>SUGARCANE WHITE LEAF (SCWL) GROUP</b>					
Sugarcane white leaf	SCWL	FS, rRFLP, DB, S	<i>Saccharacum officinarum</i> (sugarcane)	Thailand	Seemüller et al., 1994; Marcone et al., 1997d; Viswanathan, 1997
Sugarcane grassy shoot	SCGS	SS, rRFLP	<i>Saccharacum officinarum</i> (sugarcane)	Thailand	Wongkaew et al., 1997
Rice yellow dwarf	RYD	FS, SS, rRFLP, DB	<i>Oryza sativa</i> (rice)	Japan	Namba et al., 1993; Gundersen et al., 1994; Kirkpatrick et al., 1994
Leafhopper-borne	BVK	FS, rRFLP	<i>Psammotettix cephalotes</i> (leafhopper)	Germany	Seemüller et al., 1994; Marcone et al., 1997d
<b>BERMUDA GRASS WHITE LEAF (BGWL) GROUP</b>					
Bermuda grass white leaf	BGWL	FS, SS, rRFLP, S	<i>Cynodon dactylon</i> (Bermuda grass)	Italy, Thailand, India	Sarindu and Clark, 1993; Marcone et al., 1997d; Wongkaew et al., 1997
= Annual blue grass white leaf	ABGWL	rRFLP	<i>Poa annua</i> (annual blue grass)	Italy	Lee et al., 1997b
Brachiaria white leaf	BRAWL	SS, rRFLP, S	<i>Brachiaria distachya</i> (brachiaria grass)	Thailand	Sarindu and Clark, 1993; Wongkaew et al., 1997
? Dactyloctenium white leaf	DACWL	SS, rRFLP	<i>Dactyloctenium aegyptium</i> (crowfoot grass)	Thailand	Nakashima et al., 1996; Wongkaew et al., 1997
<b>TANZANIAN LETHAL DECLINE (TLD) GROUP</b>					
Tanzanian lethal decline	TLD	FS, rRFLP	<i>Cocos nucifera</i> (coconut palm) <i>Cocos nucifera</i> (coconut palm) <i>Cocos nucifera</i> (coconut palm)	Tanzania, Kenya	Harrison et al., 1994a; Tymon et al., 1997
Cape St. Paul wilt	CPSW	rRFLP		Ghana	
= Awka disease	AWAT	rRFLP		Nigeria	
<b>LETHAL YELLOWING (LY) GROUP</b>					
Coconut lethal yellowing	LY	FS, PS, SS, rRFLP, DB	<i>Cocos nucifera</i> (Coconut palm)	Florida	Gundersen et al., 1994; Harrison et al., 1994b; Kirkpatrick et al., 1994
= Lethal yellowing of other palms		rRFLP	Various palms	USA, Mexico	Harrison et al., 1994a
Yucatan lethal decline	YLD	FS, rRFLP	<i>Cocos nucifera</i> (coconut palm)	USA, Mexico	Harrison et al., 1994a

(continued)

Table 2 (continued)

Phytoplasma group and group members associated with the diseases listed <sup>1</sup>	Acronym(s) of phytoplasma	Evidence of identity or similarity <sup>2</sup>	Plant or insect host	Geographic area	Selected references
<b>LOOFAH WITCHES'-BROOM (LFWB) GROUP</b>					
Loofah witches'-broom	LFWB	FS, rRFLP	<i>Luffa cylindrica</i> (loofah)	Taiwan	Lee <i>et al.</i> , 1993c; Gundersen <i>et al.</i> , 1994
<b>ASH YELLOWS (AshY) GROUP</b>					
Ash yellows	AshY	FS, SS, RFLP, cRFLP	<i>Fraxinus</i> spp. (ash)	USA	Mäurer <i>et al.</i> , 1993; Seemüller <i>et al.</i> , 1994; Griffiths <i>et al.</i> , 1994a
= Lilac witches'-broom	LWB	rRFLP	<i>Syringa</i> spp. (lilac)	USA	Griffiths <i>et al.</i> , 1994a
<b>CLOVER PROLIFERATION (CP) GROUP</b>					
Clover proliferation	CP	FS, rRFLP, cRFLP	<i>Trifolium hybridum</i> (alsike clover)	Canada	Lee <i>et al.</i> , 1991, 1993c; Gundersen <i>et al.</i> , 1994
= Potato witches'-broom	PWB	PS, rRFLP, cRFLP	<i>Solanum tuberosum</i> (potato)	Canada	Lee <i>et al.</i> , 1991, 1993c; Gundersen <i>et al.</i> , 1994
= Alfalfa witches'-broom	AWB	cRFLP	<i>Medicago sativa</i> (alfalfa)	Canada	Khadhair and Hiruki, 1995
= Beet leafhopper transmitted virescence	BLTVA	PS, rRFLP	<i>Catharanthus roseus</i> (petiwinkle)	California	Lee <i>et al.</i> , 1991; Gundersen <i>et al.</i> , 1994; Kirkpatrick <i>et al.</i> , 1994
= California tomato big bud	WWP	rRFLP	<i>Lycopersicon esculentum</i> (tomato)	California	Shaw <i>et al.</i> , 1993
Willow witches'-broom	BLL	cRFLP	<i>Salix</i> spp. (willow)	Canada	Khadhair and Hiruki, 1995
Brinjal little leaf	BLL	FS, rRFLP	<i>Solanum melongena</i> (eggplant)	India	Schneider <i>et al.</i> , 1995a
<b>ELM YELLOWS (EY) GROUP</b>					
Elm yellows	EY, ULW	FS, SS, RFLP, cRFLP	<i>Ulmus</i> spp. (elm)	USA, Europe	Lee <i>et al.</i> , 1993b; Mäurer <i>et al.</i> , 1993; Marcone <i>et al.</i> , 1997e
Flavescence dorée	FD	FS, rRFLP, cRFLP, S	<i>Vitis vinifera</i> (grapevine)	France	Seemüller <i>et al.</i> , 1994; Daire <i>et al.</i> , 1997; Marcone <i>et al.</i> , 1997e
German flavescence dorée	GFD	cRFLP	<i>Vitis vinifera</i> (grapevine)	Germany	Daire <i>et al.</i> , 1997
Alder yellows	ALD	FS, rRFLP	<i>Alnus glutinosa</i> (European alder)	Europe	Marcone <i>et al.</i> , 1997e
= Eucalyptus little leaf	ELL	rRFLP	<i>Eucalyptus</i> spp. (eucalypt)	Italy	Marcone <i>et al.</i> , 1996d
= Spartium witches'-broom	SpaWB	rRFLP	<i>Spartium junceum</i> (Spanish broom)	Italy	Marcone <i>et al.</i> , 1997e
Rubus stunt	RuS	FS, cRFLP, rRFLP	<i>Rubus</i> spp. (brambles)	Europe	Mäurer and Seemüller, 1994; Marcone <i>et al.</i> , 1997e
Cherry lethal yellows	CLY	rRFLP, cRFLP	<i>Prunus avium</i> (sweet cherry)	China	Zhu <i>et al.</i> , 1996
Hemp dogbane yellows	HDI	rRFLP	<i>Apocynum cannabinum</i> (hemp dogbane)	New York State	Griffiths <i>et al.</i> , 1994b
Jujube witches'-broom	JWB	rRFLP, cRFLP	<i>Ziziphus jujuba</i> (jujube)	China	Zhu <i>et al.</i> , 1996
? Olive yellows		rRFLP	<i>Olea europaea</i> (olive)	Italy	Poggi Pollini <i>et al.</i> , 1996

<sup>1</sup> Phytoplasmas are named according to the disease they are associated with (e.g. phormium yellow leaf phytoplasma). All phytoplasmas listed in the various groups appear to be distinct except those marked with '=' or '?'. = indicates that the phytoplasma is identical or very similar to that preceding it in the Table.

<sup>2</sup> See Table 1 for type of experimental data.

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