

Diseases of Important Crops, a Review of the Causal Fastidious Prokaryotes and Their Insect Vectors

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ABSTRACT

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Phytopathogenic fastidious prokaryotes are plant pathogens that either resist to grow in any available bacterial culture media or require specific or enriched media to grow. They include *Xylella fastidiosa*, *Leifsonia xyli* subsp. *xyli*, *L. xyli* subsp. *cynodontis* and *Clavibacter michiganensis* subsp. *sepedonicus* and *C. michiganensis* subsp. *michiganensis* that reside in xylem and spiroplasmas, phytoplasmas and *Candidatus Liberibacter* spp. that reside in phloem. *X. fastidiosa* is the causal agent of more than 19 diseases; among them Pierce's disease of grape and citrus variegated chlorosis are two major maladies that cause serious economic loss on wine and citrus juice industry. *L. xyli* subsp. *xyli*, and *L. xyli* subsp. *cynodontis* are associated with ratoon stunting disease of sugarcane and Bermuda grass stunting respectively and *C. michiganensis* subsp. *sepedonicus* with bacterial ring rot in potato and *C. michiganensis* subsp. *michiganensis* with bacterial tomato canker. Spiroplasmas are the causal agents of citrus stubborn, corn stunt and periwinkle diseases. Phytoplasmas are associated with more than 500 diseases worldwide. *Ca. Liberibacter* spp., are the causal agents of citrus Huanglongbing or citrus greening, zebra chip disease of potato and others. General characteristics of *X. fastidiosa* including (i) its scientific classification, host ranges and diseases incited, and cell shape and size, (ii) specific and enriched media for *X. fastidiosa*, (iii) symptoms induced by *X. fastidiosa*, (iv) geographic distribution of *X. fastidiosa*, and (v) the insect vectors that transmit the diseases will be discussed. Pierce's disease is the limiting factor for the establishment of wine industry for the entire southeastern United States from Texas to the Carolinas along the gulf coast of Mexico. Recent introduction of the glassy-winged sharpshooter leafhoppers in California has threatened the winery industry of California. The successful isolation of *X. fastidiosa* from the tissues with citrus variegated chlorosis (CVC) symptoms followed by the identification of the major insect vectors provided crucial information for citrus growers and citrus juice

industry to deal with the CVC crisis in Brazil. The biological characteristics of the three phloem-limited prokaryotes, namely Spiroplasma, Phytoplasma and *Candidatus Liberibacter* spp., and the diseases they induce and their vectors will be discussed. Most plant pathogenic prokaryotes do not require an active insect vector to spread them from plants to plants, while *X. fastidiosa*, *Ralstonia solanaceae*, *Candidatus Liberibacter* spp., phytoplasmas, and Spiroplasma do. To date among all known vectors, the single most successful insects vectoring the diseases belong to the Order of Hemiptera. In the past three decades, researches have emphatically addressed the biology, ecology, vector relationships and epidemiology of crop diseases caused by plant pathogenic prokaryotes which were well documented in numerous review articles. Herein a review of the significance of the insect vectors of fastidious prokaryotes that cause diseases of important crops is to be addressed.

Keywords: fastidious prokaryotes, *Xylella fastidiosa*, *Candidatus Liberibacter* spp., Spiroplasma, Phytoplasma, Huanglongbing, Hemiptera, glassy-winged sharpshooter, Pierce's disease of grape, citrus variegated chlorosis, bacterial leaf scorch of blueberry

INTRODUCTION

In the Kingdom Prokaryotae, there are two domains, *Archaea* and *Bacteria* ⁽³⁹⁾. *Bacteria* have cell membrane and cell wall, but in *Bacteria* domain under the Phylum Firmicutes, there is a Class named Mollicutes that possess only cell membrane and lack cell wall. Mollicutes, including Spiroplasma, Phytoplasma, Mycoplasma, Ureaplasma, Entomoplasma, Mesoplasma, Anaeroplasma, Asteroplasma, and Acholeplasma, are the smallest and simplest known free-living and self-replicating forms of life. They are bacteria of Gram-positive origin, as indicated by their 16S rRNA ⁽³⁴⁾. Most bacteria do not require insect vectors for their dissemination except a few; e.g., *Erwinia tracheiphila* transmitted by cucumber beetles ⁽¹⁾ and *Ralstonia solanaceae* by *Hindola striata* ⁽³⁾. However, in the fastidious prokaryote group which includes *Xylella fastidiosa*, *Candidatus Liberibacter* spp., and Spiroplasma and Phytoplasma, insect vectors are essentially required for their dissemination ^(21, 26, 37). In the case of *E. tracheiphila*-induced bacterial wilt of cucumber, the bacterium survives by overwintering in the intestines of striped cucumber beetles (*Acalymma vittata*) and spotted cucumber beetles (*Diabrotica undecimpunctata*), in which it hibernates ⁽¹⁾. In this article, the vectors that associated with the above-mentioned fastidious prokaryotes will be emphasized.

To date among all known vectors, the single most successful insects vectoring the diseases belong to the Order of Hemiptera. In the past three decades, researches have emphatically addressed the biology, ecology, vector relationships and epidemiology of crop diseases caused by plant pathogenic prokaryotes which were well documented in the following review articles: Almeida et al. ⁽²⁾, Gottwald ⁽¹³⁾, Janse and Obradovic ⁽²⁰⁾, Markham ⁽²¹⁾, Purcell ⁽²³⁾, Purcell and Hopkins ⁽²⁴⁾, Redak et al. ⁽²⁶⁾, Weintraub ⁽³⁶⁾, and Weintraub and Beanland ⁽³⁷⁾.

Fastidious prokaryotes are those that either resist to grow in any available media, such as Phytoplasma, *Candidatus Liberibacter* spp., and *Candidatus Phlomobacter fragariae* or those that require specific and enriched media, such as Spiroplasma, *X. fastidiosa*, *Leifsonia xyli* subsp. *xyli*, *L. xyli* subsp. *cynodontis* and *Clavibacter michiganensis* subsp. *sepedonicus*. Based on the inhabitant, *X. fastidiosa*, *Leifsonia* spp., and *C. michiganensis* subsp. *sepedonicus* are xylem-inhabiting while Spiroplasma, Phytoplasma, *Candidatus Liberibacter* spp., and *Candidatus Phlomobacter fragariae* are phloem-inhabiting prokaryotes.

Herein a review of insect vectors of plant pathogenic fastidious prokaryotes is provided by the authors. The information of insect vectors of phytopathogenic fastidious prokaryotes by taxonomic groups and their geographic distribution is shown in Table 1.

Xylem-limited bacterial plant pathogens and their insect vectors

According to Wells et al. ⁽³⁸⁾, *X. fastidiosa* possesses the following characteristics: predominately single, straight rods with a cell size ranges from 0.25-0.35 µm in width and 0.9-3.5 µm in length; two types of colonies: convex to pulvinate smooth opalescent with entire margins or umbonate rough with finely undulated margins; Gram-negative, nonmotile, aflagellate, oxidase negative, catalase positive, and strict aerobic; nonfermentative, nonhalophilic, nonpigmented; and require a specific and enriched medium such as CS20, PD2, PW, or BCYE for growth. The optimal temperature for growth is 26-28 °C, whereas the optimal pH is 6.5-6.9. The habitat is the xylem of plant tissue. The G+C content of the DNA is 51.0 to 52.5 mol% determined by thermal denaturation or 52.0 to 53.1

mol% determined by bouyant density.

Ever since Wells et al. ⁽³⁸⁾ named then xylem-limited bacterium as *X. fastidiosa* in 1987, *X. fastidiosa* has been reclassified into five subspecies according to their differences in genetic makeup, host range, physiology, and biochemistry. They are *X. fastidiosa* subsp. *fastidiosa* for strains of grape, almond, alfalfa, and maple, *X. fastidiosa* subsp. *multiplex* for strains of peach, plum, almond, elm, sycamore, and pigeon grape, *X. fastidiosa* subsp. *pauca* for strains of citrus ⁽²⁸⁾, *X. fastidiosa* subsp. *sandyi* for strains of oleander, daylily, jacaranda, and magnolia ⁽²⁹⁾, and *X. fastidiosa* subsp. *tashke* for strains of *Chitalpa tashkentensis*, a common ornamental landscape plant ⁽²⁵⁾. However, the last two subspecies have not been officially recognized by the researchers in the community of systematic bacteriology.

Table 1. Reported insect vectors of phytopathogenic fastidious prokaryotes by taxonomic groups and their geographic distribution

Vectors	Pathogen					Distribution	Reference
	Xylem-inhabiting		Phloem-inhabiting				
	<i>Xylella fastidiosa</i>	<i>Ralstonia syzygii</i>	<i>Candidatus Liberibacter</i> spp.	Phytoplasmas	Spiroplasmas		
Cicadomorpha							
Cercopoidea							
Aphrophoridae	+	-	-	-	-	North America	30
Clastopteridae	+	-	-	-	-	North America	30
Machaerotidae	-	+	-	-	-	Indonesia	3
Membracoidea							
Cicadellidae							
Cicadellinae	+	-	-	+	-	America; North America	26, 37
Agalliinae	-	-	-	+	-	Australia; Austria	14, 27
Aphrodinae	-	-	-	+	-	Europe	37
Coelidiinae	-	-	-	+	-	India	37
Deltocephalinae	-	-	-	+	+	Worldwide	21, 37
Iassininae	-	-	-	+	-	Australia	37
Idiocerinae	-	-	-	+	-	Europe	37
Macropsinae	-	-	-	+	-	Europe; North America	37
Scarinae	-	-	-	+	-	North America	37
Typhlocybinae	-	-	-	+	-	Southeast Asia; Caribbean region	37

Table 1. cont.

Vectors	Pathogen					Distribution	Reference
	Xylem-inhabiting		Phloem-inhabiting				
	<i>Xylella fastidiosa</i>	<i>Ralstonia syzygii</i>	<i>Candidatus Liberibacter spp.</i>	Phytoplasmas	Spiroplasmas		
Fulgoromorpha							
Fulgoroidea							
Cixiidae	-	-	-	+	-	Europe; Subtropical America; New Zealand	37
Delphacidae	-	-	-	+	-	Papua New Guinea; Europe; Asia; Cuba	37
Derbidae	-	-	-	+	-	Southeast Asia	37
Flatidae	-	-	-	+	-	Europe	37
Sternorrhyncha							
Psylloidea							
Psyllidae	-	-	+	+	-	Asia; Africa; America; Europe	13, 18, 37
Heteroptera							
Pentatomidae	-	-	-	+	-	East Asia	37
Tingidae	-	-	-	+	-	Southeast Asia	37

X. fastidiosa requires specific and enriched media to grow as compared to other bacteria ⁽⁶⁾. There are seven complex components that are used in the listed four media: soy peptone, tryptone, phytone peptone, trypticase peptone, soytone or phytone, and yeast extract; either one or two complex components for each medium; two iron sources for the medium either hemin chloride or soluble ferric pyrophosphate; four inorganic salts: ammonium phosphate, potassium phosphate (monobasic or dibasic) or magnesium sulfate; three amino acids and two Krebs cycle intermediates: citrate or succinate; and three detoxifying components: potato starch, activated charcoal, or bovine serum albumin. Rippled cell walls seemed to be unique for all *X. fastidiosa* cells regardless of the origin of its host plants. That was one of the reasons why they were first described as “rickettsia-like bacteria”. However, a thorough study of Pierce’s disease (PD) strain by Huang et al. ⁽⁵⁾ disclosed that in addition to the predominated rippled cell walls there are intermediate cell walls and smooth cell walls.

Based on the diseases reported around the world, *X. fastidiosa* causes diseases in the America Continents including North and South America. In the US, they occur

The specific symptoms vary among different hosts. Symptoms of Pierce’s disease of grapes usually start with

in the whole southeastern States along the Gulf coast of Mexico, and California. In the southern hemisphere, the diseases occur in Brazil, Argentina, and Paraguay. In Asia, the pear leaf scorch was reported in Taiwan. In Europe there was a report describing PD of grapes in Kosovo, former Yugoslavia which sits in southern Europe. The *X. fastidiosa*-induced diseases seemed to occur in the region between 15-45 degrees latitude of both north and south of Equator. It is interesting to note that Taiwan sits at the Tropic of Cancer where the pear leaf scorch disease occurs and that Sao Paulo in Brazil sits at the Tropic of Capricorn where the severe citrus variegated chlorosis (CVC) ^(8,15) and coffee leaf scorch occur. Kosovo sits at about 45 degree North of Equator.

There are 19 diseases that were confirmed to be caused by *X. fastidiosa*. They are Pierce’s disease of grape, alfalfa dwarf, phony peach (PP), plum leaf scald, CVC, periwinkle wilt, ragweed stunt, and leaf scorch of almond, elm, mulberry, oak, sycamore, pecan, maple, oleander, blueberry, coffee, pear, and *Chitalpa*. ^(6,8,15,16, 25,28,29,31) The common symptoms induced by *X. fastidiosa* include marginal leaf necrosis, scorching or scalding of leaves, early leaf fall, dieback of branches, and wilting to death. marginal leaf necrosis to chlorosis; normally a yellow band would form between the green and necrotic tissues for

white wine grapes and a purple band for red wine grapes. The following unique symptoms will follow: petioles remain attached to the canes, green island formation due to irregular maturing process of barks, dried up raisins, and eventual dying and dead vines occurs in 2-4 years after initial infection in GA (Fig. 1). In the Order Hemiptera, four main sharpshooters in the Family Cicadellidae, e. g., glassy-winged sharpshooter, blue-green sharpshooter, red-headed sharpshooter, and green sharpshooter were the important vectors for PD *X. fastidiosa*.

CVC causes severe leaf chlorosis between veins when young trees are infected. Symptomatic leaves exhibit brown gummy lesions on the lower side in corresponding to the chlorotic yellow areas on the upper leaf surface. Reduced growth vigor and abnormal flowering and fruit set occur in infected trees. Fruits from affected trees are often small and hard with high acidity which is not fitting for juice making and no fresh market value^(8,15). The major vectors for citrus variegated chlorosis in Brazil are *Acrogonia terminalis*, *Dilobopterus costalimai*, *Oncometopia fascialis*, and *Oncometopia nigricans*.

Symptoms of bacterial leaf scorch of blueberry exhibit

marginal leaf necrosis or burn which is very distinct and is surrounded by a dark line of demarcation between green and dead tissue (Fig. 2A). Prior to complete plant death, all leaves fall off, and the remaining stems display a yellow “skeletal” appearance (Fig. 2B) which was why “yellow stem” or “yellow twig” was often used to describe the disorder before “bacterial leaf scorch” was formally designated for the *X. fastidiosa*-caused disease⁽⁹⁾. Insect vectors for the blueberry bacterial leaf scorch disease are under investigation in Georgia and the glassy-winged sharpshooter leafhopper, *Homalodisca vitripennis* (formerly *H. coagulata*), is likely an important suspect.

Two xylem-limited bacteria (XLB), *Xylella fastidiosa* and *Ralstonia syzygii*, are transmitted by xylem sap-feeding insects^(2,3,24,26). In general, the sucking insects that feed predominantly on xylem sap are potential vectors of XLB⁽²⁴⁾. Among them, the confirmed vectors that transmit *X. fastidiosa* possess the transmission characteristics including the lack of a latent period, no transstadial or transovarial transmission of the bacterium, the pathogens remain persistently in adults, and the bacterium can multiply in the foregut⁽²⁰⁾.

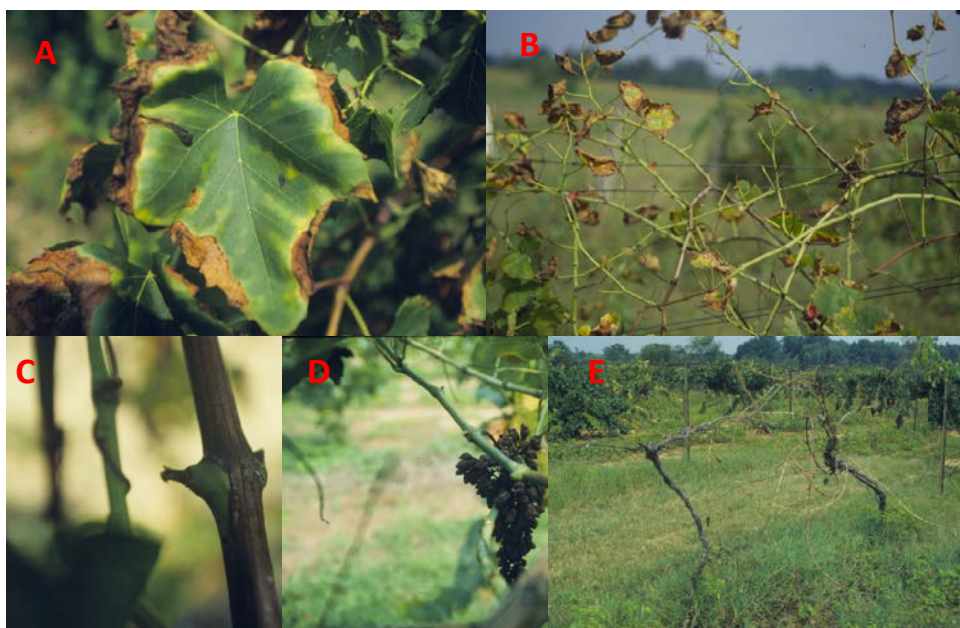


Fig. 1. Symptoms of Pierce's disease of grapes: A close-up view of marginal leaf necrosis (A), petioles remained attached to the canes after leaves fall (B), green island (C) formed due to irregular maturing process of barks, dried up raisins (D), and eventual dying and dead vines (E) in 2-4 years after initial infection in GA, USA. (Photo by Chung-Jan Chang)

Redak et al. ⁽²⁶⁾ pointed out that 39 species of Cicadellinae and 5 species of Cercopoidea have been confirmed as vectors of different strains of *X. fastidiosa* in controlled experiments from the United States to Brazil. In the United States, the glassy-winged sharpshooter leafhopper, *Homalodisca vitripennis* (Germar) [synonym of *Homalodisca coagulata* (Say) ⁽³²⁾], is the most economically important species among vectors of *X. fastidiosa*, because it provides more efficient transmission than other vectors in primitive or new distribution (e.g. in California). Furthermore, the machaerotid species *Hindola striata* is the only known vector of *Rolstonia syzygii* (formerly *Pseudomonas syzygii*) from Indonesia ⁽³⁾. In fact, the number of vector species for different strains of *X. fastidiosa* will increase considerably in the future as a result of agricultural diversification in Latin America and additional research on *X. fastidiosa*-induced diseases and

vectors in that region ⁽²⁶⁾ and in Asia. Recently, DNA fragments of pear leaf scorch (PLS) strains of *X. fastidiosa* were identified in *Kolla paulula* (Walker) (Cicadellidae: Cicadellinae) captured in fields near central Taiwan (Su and Shih, unpublished data) via polymerase chain reaction (PCR) using *X. fastidiosa*-specific primers. The mechanism of PLS transmission and fulfillment of Koch's postulates using *K. paulula* are currently under investigation in the authors' laboratories.

In summary, the majority of xylem-feeding insect vectors belong to the members of Cicadellinae, and the remainder species are from Aphrophoridae, Clastopteridae and Machaerotidae (Table 1) ^(3,26). Moreover, some taxa (Evacanthinae, Mileewaninae, and Cicadide) are predicted to be the potential vectors based on the phylogenetic hypothesis ⁽²⁶⁾.



Fig. 2. Symptoms of bacterial leaf scorch of blueberry. Marginal leaf necrosis or burn (A) which is very distinct and is surrounded by a dark line of demarcation between green and dead tissue. Prior to complete plant death, all leaves fall off, and the remaining stems display a yellow "skeletal" appearance (B) which was why "yellow stem" or "yellow twig" was often used to describe the disorder before "bacterial leaf scorch" was designated for this disease. (Photo by P. M. Brennen, University of Georgia)

Phloem-limited plant pathogenic prokaryotes and their insect vectors

In Mollicutes, the cell wall-less and phloem-limited prokaryotes, there are two major plant pathogens: Spiroplasma and phytoplasmas. Spiroplasma are cells

with helical forms during logarithmic growth. Most Spiroplasma are cultivable in enriched media that contain supplemented sterols and other ingredients ⁽⁷⁾. They are facultative anaerobic or microaerophilic. They are associated with three plant diseases: citrus stubborn and horseradish brittle root disease by *Spiroplasma citri*, corn

stunt disease by *S. kunkelii*, and periwinkle disease by *S. phoeniceum*. Phytoplasmas have been associated with more than 500 plant diseases worldwide ⁽²²⁾ ever since the historical discovery by Doi et al. ⁽¹²⁾ of then referred as mycoplasma-like organisms (MLO) found in the phloem elements of plants infected with mulberry dwarf, potato witches'-broom, aster yellows, or paulownia witches'-broom ^(22,37). Phytoplasmas are still noncultivable even though they have been classified into 30 group-subgroups and four undetermined entities based on the 16S rDNA RFLP grouping (http://plantpathology.ba.ars.usda.gov/pclass/pclass_taxonomy.html).

Spiroplasma kunkelii causes characteristic small chlorotic stripes at the leaf bases of new leaves 25-30 days after initial inoculation. The chlorotic stripes fused together and extended toward the leaf tips with green spots and stripes exhibited on a chlorotic background. The infected plants are stunted due to much shorter internodes and a proliferation of secondary shoots in leaf axils; thus it is named corn stunt disease. Corn stunt disease is transmitted by *Dalbulus maidis* (DeLong and Wolcott) and *D. elimatus* (Ball) in nature whereas it can be transmitted experimentally by *Graminella nigrifrons* (Forbes), *G. sonora* (Ball), *Stirellus bicolor* (Van Duzee), *Exitianus exitiosus* (Uhler), and *Euscelidius variegatus* (Kirsch.) ⁽³⁵⁾.

Walnut witches'-broom disease was reported by Chang et al. ⁽⁵⁾ after the MLO particles were observed in the sieve cells of the symptomatic tissues collected from Griffin, GA. Abnormal proliferation of numerous small shoots with lighter green color which resembled the shape of a broom became evident in mid-July. The insect vector for this disease is still unknown even though DNA fragments were isolated and cloned from diseased walnut and later DNA probes were developed to monitor the seasonal occurrence of walnut witches'-broom MLO ^(10,11). There are other economically important phytoplasma diseases, such as lethal yellowing of coconuts in Jamaica and lime witches'-broom in Oman and many others in Taiwan.

The other phloem-limited bacteria are the causal agent of Huanglongbing (HLB) and other diseases, *Ca. Liberibacter* spp. Striking symptoms of "yellow shoots"

were often seen in sweet orange of young and high density orchard (1,000 trees per hectare). Two most characteristic symptoms of HLB are leaves with blotchy mottle and fruits with small size and color inversion ⁽⁴⁾. HLB are transmitted by psyllid vectors. In Asia, Southeast Asia, and Oceania, *Diaphorina citri* is the vector, *Ca. L. asiaticus* is the HLB agent, and both are heat tolerant (Asian form of HLB). In Africa and Madagascar island, *Trioza erytrae* is the vector, *Ca. L. africanus* is the HLB agent, and both are heat-sensitive (African form of HLB) ⁽⁴⁾. Another HLB agent, *Ca. L. americanus*, was found in 2004 in Sao Paulo State, Brazil ⁽³³⁾ and 2005 in Florida, USA ⁽¹⁹⁾ and its vector is *D. citri*.

The phloem-limited plant pathogenic prokaryotes, phytoplasmas, spiroplasmas, and the pathogens (*Candidatus Liberibacter* spp.) of Huanglongbing (HLB), are transmitted to plants by phloem-feeding insects belonging to the Order of Hemiptera.

According to the taxonomic groups for the above-mentioned 3 pathogens, the interaction between insect vectors and spiroplasmas or *Ca. Liberibacter* spp. is more specific than the vector-phytoplasmas relationship. For example, the known vectors for HLB pathogen belong to the family Psyllidae only ^(13,18) and the vectors *Circulifer tenellus* and *Dalbulus maidis* belonging entirely to the subfamily Deltocephalinae of Cicadellidae disseminate 2 plant pathogenic spiroplasmas, *S. citri* and *S. kunkelii* respectively ⁽²¹⁾.

On the contrary, there are 92 known species belonging to 8 families in Hemiptera that are confirmed vectors of phytoplasmas. They respectively belong to each of the following family Cicadellidae (71 species), Cixiidae (6 species), Delphacidae (4 species), Derbidae (1 species), Flatidae (1 species), Psyllidae (7 species), Pentatomidae (1 species), and Tingidae (1 species) ⁽³⁷⁾. Furthermore, the above-mentioned 71 species in Cicadellidae that vector phytoplasmas could be categorized according to the following 10 subfamilies, Cicadellinae (1 species: *Graphocephala confluens* (Uhler)), Typhlocybinae (3 species: *Alebroides nigroscutellatus* (Distant), *Amrasca devastans* (Distant), and *Empoasca papayae* Oman), Agalliinae (1 species), Aphrodinae (2 species), Coelidiinae

(1 species), Iassininae (1 species), Idiocerinae (2 species), Macropsinae (5 species), Scarinae (1 species), and Deltocephalinae (54 species) [see Table 1 by Weintraub and Beanland⁽³⁷⁾]. In general, members of the first two subfamilies, Cicadellinae and Typhlocybininae, are known xylem feeders and mesophyll feeders, respectively; that means members of the two taxa can not transmit the phloem-limited pathogens. As to why they were reportedly able to transmit phytoplasmas which are strictly phloem inhabitants raises an intriguing but controversial issue that warrants further investigation.

LITERATURE CITED

1. Agrios, G. N. 2005. Plant Pathology, Fifth Edi. Elsevier Academic Press. Pages 639-642.
2. Almeida, R. P. P., Blua, M. J., Lopes, J. R. S., and Purcell, A. H. 2005. Vector transmission of *Xylella fastidiosa*: Applying fundamental knowledge to generate disease management strategies. Annu. Entomol. Soc. Am. 98:775-786.
3. Balfas, R., Lomer, C. J., Mardiningsih, T. L., and Adhi, E. M. 1991. Acquisition of *Pseudomonas syzygii* by *Hindola striata* (Homoptera: Machaerotidae). Indones. J. Crop Sci. 6:65-72.
4. Bove, J. M. 2006. Huanglongbing: a destructive, newly-emerging century-old disease of citrus. J. Plant Pathol. 88:7-37.
5. Chang, C. J., Impson, L., and Cunfer, B. 1986. Walnut witches'-broom disease in Georgia. Phytopathology 76:1139 (abstr).
6. Chang, C. J., and Walker, J. T. 1988. Bacterial leaf scorch of northern red oak: isolation, cultivation, and pathogenicity of a xylem-limited bacterium. Plant Dis. 72:730-733.
7. Chang, C. J. 1989. Nutrition and cultivation of spiroplasmas. In "The Mycoplasmas, Vol. 5" (R. F. Whitcomb and J. G. Tully, eds.), pp. 201-241. Academic Press, New York.
8. Chang, C. J., Garnier, M., Zreik, L., Rossetti, V., and Bove, J. M. 1993. Culture and serological detection of the xylem-limited bacterium causing citrus variegated chlorosis and its identification as a strain of *Xylella fastidiosa*. Curr. Microbiol. 27:137-142.
9. Chang, C. J., Donaldson, R., Brennen, P. M., Krewer, G., and Boland, B. 2009. Bacterial leaf scorch, a new blueberry disease caused by *Xylella fastidiosa*. HortScience 44:413-417.
10. Chen, J., Chang, C. J., Jarret, R. L., and Gawel, N. 1992. Isolation and cloning of DNA fragments from a mycoplasma-like organism associated with walnut witches'-broom disease. Phytopathology 82:306-309.
11. Chen, J., Chang, C. J., and Jarret, R. L. 1992. DNA probes as molecular markers to monitor the seasonal occurrence of walnut witches'-broom mycoplasma-like organism. Plant Dis. 76:1116-1119.
12. Doi, Y., Teranaka, M., Yora, K., and Asuyama, H. 1967. Mycoplasma- or PLT group-like microorganisms found in the phloem elements of plants infected with mulberry dwarf, potato witches'-broom, aster yellows, or paulownia witches'-broom. Ann. Phytopathol. Soc. Jpn. 33:259-266.
13. Gottwald, T. R. 2010. Current epidemiological understanding of citrus huanglongbing. Annu. Rev. Phytopathol. 48:119-139.
14. Grylls, N. E., Waterford, C. J., Filshie, B. K., and Beaton, C. D. 1974. Electron microscopy of rugose leaf curl virus in red clover, *Trifolium pretense* and in the leafhopper vector *Austroagallia torrida*. J. Gen. Virol. 23:179-183.
15. Hartung, J. S., Beretta, J., Brlansky, R. H., Spisso, J., and Lee, R. F. 1994. Citrus variegated chlorosis bacterium: axenic culture, pathogenicity, and serological relationships with other strains of *Xylella fastidiosa*. Phytopathology 84:591-597.
16. Hernandez-Martinez, R., de la Cerda, K. A., Costa, H. S., Cooksey, D. A., and Wong, F. P. 2007. Phylogenetic relationships of *Xylella fastidiosa* strains isolated from ornamentals in southern California. Phytopathology 97:857-864.
17. Huang, P.-Y., Milholland, R. D., and Daykin, M. E. 1986. Structural and morphological changes associated with the Pierce's disease bacterium in

- bunch and muscadine grape tissues. *Phytopathology* 76:1232-1238.
18. Hung, T. H., Hung, S. C., Chen, C. N., Hsu, M. H., and Su, H. J. 2004. Detection by PCR of *Candidatus Liberibacter asiaticus*, the bacterium causing citrus huanglongbing in vector psyllids: application to the study of vector-pathogen relationships. *Plant Pathol.* 53:96-102.
 19. Irey, M. S., Gast, T., and Gottwald, T. R. 2006. Comparison of visual assessment and polymerase chain reaction assay testing to estimate the incidence of the huanglongbing pathogen in commercial Florida citrus. *Proc. Fla. State Hort. Soc.* 119:89-93.
 20. Janse, J. D., and Obradovic, A. 2010. *Xylella fastidiosa*: its biology, diagnosis, control and risks. *J. Plant Pathol.* 92 (Supplement 1): S1. 35-48.
 21. Markham, P. G. 1983. Spiroplasmas in leafhoppers: a review. *Yale J. Biol. Med.* 56:745-751.
 22. Mc Coy, R. E., Caudwell, A., Chang, C. J., Chen, T. A., Chiykowski, L. N., Cousin, M. T., Dale, J. L., de Leeuw, G. T. N., Golino, D. A., Hackett, K. J., Kirkpatrick, B. C., Marwitz, R., Petzold, H., Sinha, R. C., Suguirra, M., Whitcomb, R. F., Yang, I. L., Zhu, B. M., and Seemuller, E. 1989. Plant diseases associated with mycoplasma-like organisms. In "The Mycoplasmas, Vol. 5" (R. F. Whitcomb and J. G. Tully, eds.), pp. 545-640. Academic Press, New York.
 23. Purcell, A. H. 1982. Insect vectors relationships with prokaryotic plant pathogens. *Annu. Rev. Phytopathol.* 20:397-417.
 24. Purcell, A. H., and Hopkins, D. L. 1996. Fastidious xylem-limited bacterial plant pathogens. *Annu. Rev. Phytopathol.* 34:131-151.
 25. Randall, J. J., Goldberg, N. P., Kemp, J. D., Radionenko, M., French, J. M., Olsen, M. W., and Hanson, S. F. 2009. Genetic analysis of a novel *Xylella fastidiosa* subspecies found in the Southwestern United States. *Appl. Environ. Microbiol.* 75:5631-5638.
 26. Redak, R. A., Purcell, A. H., Lopes, J. R. S., Blua, M. J., Mizell III, R. F., and Anderson, P. C. 2004. The biology of xylem fluid-feeding insect vectors of *Xylella fastidiosa* and their relation to disease epidemiology. *Annu. Rev. Entomol.* 49:243-70.
 27. Riedle-Bauer, M., Sára, A., and Regner, F. 2008. Transmission of a stolbur phytoplasma by the Agalliinae leafhopper *Anaceratagallia ribauti* (Hemiptera, Auchenorrhyncha, Cicadellidae). *J. Phytopathol.* 156:687-690.
 28. Schaad, N. W., Postnikova, E., Lacy, G., Fatmi, M., and Chang, C. J. 2004. *Xylella fastidiosa* subspecies: *X. fastidiosa* subsp. *piercei*, subsp. nov., *X. fastidiosa* subsp. *multiplex* subsp. nov., and *X. fastidiosa* subsp. *pauca* subsp. nov. *Syst. Appl. Microbiol.* 27:290-300.
 29. Schuenzel, E. L., Scally, M., Southammer, R., and Nunney, L. 2005. A multigene phylogenetic study of clonal diversity and divergence in North American strains of the plant pathogen *Xylella fastidiosa*. *Appl. Environ. Microbiol.* 71:3832-3839.
 30. Severin, H. H. P. 1950. Spittle-insect vectors of Pierce's disease virus. II. Life history and virus transmission. *Hilgardia* 19:357-382.
 31. Sherald, J. L. 2001. *Xylella fastidiosa*, a bacterial pathogen of landscape trees. Pages 191-202 in *Shade Tree Wilt Diseases*, edited by C. L. Ash. American Phytopathological Society, St. Paul, MN.
 32. Takiya, D. M., McKamey, S. H., and Cavichioli, R. R. 2006. Validity of *Homalodisca* and of *H. vitripennis* as the name for glassy-winged sharpshooter (Hemiptera: Cicadellidae: Cicadellinae). *Ann. Entomol. Soc. Am.* 99:648-655.
 33. Teixeira, D. C., Saillard, C., Eveillard, S., Danet, J. L., da Costa, P. I., Ayres, A. J., and Bove, J. M. 2005. '*Candidatus Liberibacter americanus*', associated with citrus huanglongbing (greening disease) in São Paulo State, Brazil. *Int. J. Syst. Bacteriol.* 55:1857-1862.
 34. Trachtenberg, S. 2005. Mollicutes. *Curr. Biol.* 15:R483-484.
 35. Tsai, J. H., and Falk, B. W. 2009. Insect vectors and their pathogens of maize in the tropics. In: E. B. Radcliffe, W. D. Hutchison & R. E. Cancelado [eds.], *Radcliffe's IPM World Textbook*, URL: <http://ipmworld.umn.edu>, University of Minnesota, St. Paul, MN.

36. Weintraub, P. G. 2007. Insect vectors of phytoplasmas and their control - an update. *Bull. Insectol.* 60:169-173.
37. Weintraub, P. G., and Beanland, L. 2006. Insect vectors of phytoplasmas. *Annu. Rev. Entomol.* 51:91-111.
38. Wells, J. M., Raju, B. C., Hung, H.-Y., Weisburg, W. G., Mandelco-Paul, L., and Brenner, D. J. 1987. *Xylella fastidiosa* gen. nov., sp. nov.: Gram-negative, xylem-limited, fastidious plant bacteria related to *Xanthomonas* spp. *Int. J. Syst. Bacteriol.* 37:136-143.
39. Woese, C., Kandler, O., and Wheelis, M. 1990. Towards a natural system of organisms: proposal for the domains *Archaea*, *Bacteria*, and *Eucarya*. *Proc. Natl. Acad. Sci. USA* 87: 4576-4579.

摘要

張宗仁^{1,2}、石憲宗³、蘇秋竹⁴、詹富智^{2,5}. 2012. 國際重要作物原核生物性病害及其媒介昆蟲之研究回顧. *植病會刊* 21: 1-10. (¹美國喬治亞大學植物病理學系; ²台中市國立中興大學植物病理學系; ³台中市霧峰區農業試驗所應用動物組; ⁴台中市霧峰區農業藥物毒物試驗所農藥應用組; ⁵聯絡作者, 電子郵件: fjjan@nchu.edu.tw; 傳真: +886-4-22854145)

植物病原微生物中有一群營養苛求原核生物，此群病原細菌無法在一般細菌性培養基生長或者須在含特殊成份或豐富複合配方之培養基才能生長。有些專一棲息於植物導管組織內如 *Xylella fastidiosa*、*Leifsonia xyli* subsp. *xyli*、*L. xyli* subsp. *cynodontis*、*Clavibacter michiganensis* subsp. *sepedonicus* 及 *C. michiganensis* subsp. *michiganensis*，而有些專一棲息於植物篩管組織內細菌如螺旋菌質體、植物菌質體及 *Candidatus Liberibacter* spp.。 *X. fastidiosa* 引起超過 19 個重要病害，其中葡萄皮爾斯病及柑橘斑駁黃化病為二個主要典型病例，曾經造成葡萄釀酒及柑橘果汁加工產業重大損失。*L. xyli* subsp. *xyli* 與 *L. xyli* subsp. *cynodontis* 分別為引起甘蔗宿根矮化病及百慕達草矮化症之病原，*C. michiganensis* subsp. *sepedonicus* 會引起馬鈴薯細菌性輪腐病及 *C. michiganensis* subsp. *michiganensis* 會引起番茄細菌性潰瘍病。螺旋菌質體為引起柑橘停滯生長、玉米矮化及日日春等病害之病原。植物菌質體在全世界被認為是引起超過 500 個病害之相關病原。*Ca. Liberibacter* spp. 被認為會引起柑橘黃龍病（別名柑橘綠化症）、馬鈴薯薯片斑紋病及其他病害。本文將論述 *X. fastidiosa* 一般特性，包括科學化分類屬性、寄主範圍、引起之病害種類、細菌型態及大小、特殊培養基需求性、病徵學、世界地理分佈及媒介昆蟲傳播病害等。美國東南地區墨西哥灣沿岸地區從德克薩斯到卡羅萊納等州建立龐大葡萄釀酒產業體系，導致葡萄皮爾斯病普遍發生，近年來加州地區人為引入媒介昆蟲褐透翅尖頭葉蟬，已對該地區葡萄釀酒產業造成極大衝擊。本文也將會討論從罹病柑橘斑駁黃化病病原組織分離 *X. fastidiosa* 病原之生物學意義及進一步鑑定主要媒介昆蟲。包括螺旋菌質體、植物菌質體及 *Ca. Liberibacter* spp. 等三種侷限篩管原核生物之生物學特性、引起之病害種類及媒介昆蟲將一併討論。大部份植物病原原核生物並不需要藉由媒介昆蟲從事植物間病原擴散，但是 *X. fastidiosa*、*Ralstonia syzygii*、*Ca. Liberibacter* spp.、螺旋菌質體及植物菌質體等則需要藉由媒介昆蟲傳播病原至健康植物。目前所有已知媒介昆蟲中能成功傳播病者大部份隸屬於半翅目昆蟲，過去 30 年許多研究學者已在不少回顧專題完整記錄植物病原原核生物引起作物病害並詳細論述其生物學、生態學、媒介昆蟲相關性與流行病學，本文僅就營養苛求原核生物之媒介昆蟲引起重要植物病害之意義作回顧論述。

關鍵詞: 營養苛求原核生物、半翅目昆蟲、柑橘黃龍病、藍莓細菌性葉緣焦枯病、螺旋菌質體、植物菌質體、褐透翅尖頭葉蟬、葡萄皮爾斯病、柑橘斑駁黃化病、及 *Candidatus Liberibacter* spp.