Bulletin of Insectology ***60*** *(2): 169-173, 2007*
ISSN 1721-8861

Insect vectors of phytoplasmas and their control – an update

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Abstract

Phytoplasmas are phloem-limited, insect-transmitted, plant pathogenic bacteria that are responsible for hundreds of diseases world-wide. Because transmission occurs quickly, plants become infected before insecticides can act on the vector. The single most effective means of controlling the vector is to cover plants with insect exclusion netting; however, this is not practical for most commercial crops. Because of these limitations, researchers are turning to genetic manipulation of plants to affect vector populations and pathogen transmission. These novel control schemes include symbiont control (SyBaP), plant lectins, and systemic acquired resistance (SAR).

Key words: Taxonomy, symbiont control, plant lectins, systemic acquired resistance

Introduction

Phytoplasmas are important phloem-limited, insect-transmitted pathogenic agents causing close to a thousand diseases, many of which are lethal, in hundreds of plant species. They are non-cultivable degenerate gram-positive prokaryotes in the class *Mollicutes*. A large body of research has accumulated in the past 20 years that addresses the biology, ecology, vector relationships and epidemiology of crop diseases caused by phytoplasmas, which has been recently reviewed by Christensen *et al.* (2005), Weintraub and Beanland (2006), and Bertaccini (2007). In this review, an update of recent developments, focusing primarily on insect vectors and on their control is provided.

Taxonomy

The single most successful order of insect phytoplasma vectors is the Auchenorrhyncha. They are efficient vectors of phytoplasmas because: nymphs and adults feed similarly and are in the same physical location, often, both immatures and adults can transmit phytoplasmas, they feed specifically in phloem cells, and phytoplasmas are propagative and persistent in them. Within the groups of phloem-feeding insects only a small number, primarily in three taxonomic groups, have been confirmed as vectors of phytoplasmas; Cicadellidae, Fulgoromorpha (in which four families of vector species are found), and two genera in the Psyllidae. In Weintraub and Beanland (2006), 92 confirmed vector species were listed; table 1 contains an additional five confirmed vector species, and some previously known vectors with new phytoplasma associations.

Phytoplasma specificity/acquisition

Insect vectors feed specifically in phloem cells, obtaining nutrition from free amino acids and sugars. Phytoplasmas are acquired passively during feeding in infected plants. The feeding duration necessary to acquire a sufficient titre of phytoplasma is the acquisition access period (AAP), which can be as short as a few minutes, but is generally measured in hours; the longer the AAP, the greater the chance of transmission (Purcell, 1982). However, it is unknown how phytoplasma titre in plants affects the AAP. The period of time that elapses from initial acquisition to the ability to transmit the phytoplasma is known as the latent period (LP) and is sometimes referred to as the incubation period. During the LP, the phytoplasmas move through, and replicate in, the competent vector's body. There are some specific leafhopper-phytoplasma relationships; for example: *Macrosteles striifrons* Anufriev can transmit onion yellows, but not rice yellow dwarf phytoplasmas, while *Nephotettix cincticeps* Uhler can transmit rice yellow dwarf but not onion yellows phytoplasmas.

The molecular factors related to the movement of phytoplasmas through the various insect tissues are still unclear; however progress is being made. Oshima *et al.* (2002) constructed phage libraries of onion yellows phytoplasma and determined the sequence of 153 independent clones and eventually Oshima *et al.* (2004) estimated the total phytoplasma genome size to be 860 kb, and determined the function of some genes based on comparisons with other known bacterial gene functions. Among the genes elucidated was an immunodominant membrane protein (Amp) that Suzuki *et al.* (2006) determined interacts with microfilament complexes in muscle cells surrounding the intestinal tract of the insect and seems to be responsible for vector-phytoplasma specificity.

Although grapevines are subject to phytoplasma infection on almost every continent, it has been notoriously difficult to confirm vector status. Using an old method – injection of pathogen directly into the hemocoel of potential vectors – Bressan *et al.* (2006) were able to select potential new vector candidates and eliminate others from consideration. *Scaphoideus titanus* Ball, a leafhopper imported from North America, is the natural vector of "flavescence dorée" (FD) in Europe. By injecting FD phytoplasma into a number of potential vector

Table 1. Confirmed phytoplasma vectors, taxonomy, pathogen association, host plant and distribution.

Vector Species	Reference	Disease Association/ Phytoplasma group	Host Plants	Distribution
DELTOCEPHALINAE				
Circulifer tenellus (Baker)	Munyaneza *et al.*, 2007	Columbia basin potato purple top	Beets, potatoes, weeds	Oregon, Washington USA
Fieberiella florii Stål	Tedeschi and Alma, 2006	Apple proliferation/ 16SrX-A	Apple	Italy
Macrosteles sp.	Borth *et al.*, 2006	16SrI-B group	Watercress, plantain, lettuce	Hawaii, USA
Neoaliturus fenestratus (Herrich-Schäffer)	Salehi *et al.*, 2006	Lettuce phyllody, wild lettuce phyllody (16SrIX)	Lettuce, wild lettuce, periwinkle, sowthistle	Iran
Orosius cellulosus Lindberg	Laboucheix *et al.*, 1972	Cotton phyllody/16SrII-F	Cotton	Africa
Orosius lotophagorum (Kirkaldy)	Behncken, 1984	Little leaf disease	Bellvine	Australia
"	Shinkai, 1964	Witches' broom of sweet potato	Sweet potato	Japan
Orosius orientalis (Matsumura)	Mirzaie *et al.*, 2007	Garden beet witches' broom	Beets	Iran
Yamatotettix flavovittatus (Matsumura)	Hanboonson *et al.*, 2006	Sugarcane white leaf disease	Sugarcane	Thailand
FULGORIDEA CIXIIDAE				
Reptalus panzeri (Löw)	Jovic *et al.*, 2006	Maize redness	Maize	Serbia

species, a membracid and a cercopid, they were able to demonstrate that three cicadellid species have the potential to transmit FD. Additionally, the three newly identified species were able to acquire FD from infected broad beans and transmit them to healthy plants in the laboratory, further strengthening the supposition that they could transmit the phytoplasma under field conditions. Since 13 species were not able to transmit FD even by circumventing the midgut barrier, there is little chance that they could transmit phytoplasmas in a natural setting. This technique narrows the potential list of vectors and may lead to greater success in determining vector status.

Vector-host plant interactions play an important role in limiting or expanding phytoplasma spreading. Broadly polyphagous vectors have the potential to inoculate a wider range of plant species, depending on the susceptibility of each host plant. Several studies have shown that insects that normally do not feed on certain plant species can acquire and transmit phytoplasma to those plants under laboratory conditions. Hence, in many cases, the plant host range of a vector, rather than lack of phytoplasma-specific cell membrane receptors, will limit the spread of phytoplasma by that species.

Traditional control

Traditional vector control methods are insufficient to control the disease (Weintraub and Beanland, 2006). The most reliable means of controlling vectors is by covering the crop with insect-proof screening. Papaya is subject to three different phytoplasma diseases (Guthrie *et al.*, 1998), the latter two being chronic diseases: dieback (causing 10-100% tree death per season in Australia), yellow crinkle (causing 2-27% tree death/season) and mosaic (causing 5-8% tree death/season). Management practices consisted of rouging yellow crinkle- and mosaic-infected trees and ratooning (pruning by removing symptomatic shoots and allowing lateral shoot development) dieback-infected trees to reduce the inoculum load (Guthrie *et al.*, 1998). More recently, Walsh *et al.*, (2006) demonstrated that the pathogen vectors could be 100% controlled by covering the trees with insect exclusion netting. Screening was compared to systemic insecticide (imidacloprid) treatments and non-treated control – there was no difference in disease incidence between the insecticide and control trees. However, these authors concluded that due to the cost of erecting a screen support structure and the reduced pollination within the screening, only cash-crops could justify the expense.

Screening is the only method to attain excellent vector control; however, its applicability is so severely limited due to the logistics of large scale agriculture in major crops – sugar cane, corn, rice, fruit trees, and grapes – that its use can not even be contemplated. On the other hand, conventional insecticides, even when frequently used (e.g. Wally *et al.*, 2004), will not control the appearance of disease because pathogen transmission occurs faster than insecticides can act, and there is often a constant influx of new vectors from surrounding habitats. At best, use of insecticides might help control vector populations, and thus reduce intra-crop transmission. Kaolin, a nonabrasive fine-grained aluminosilicate mineral, applied as a particle film, is a new version of a very old type of inorganic chemical control which may prove to be useful. The glassy-winged sharpshooter, *Homalodisca coagulata* (Say), is a vector of the bacterium, *Xylella fastidiosa* Wells *et al.* which causes Pierce's disease in grape, and a host of other diseases in other crops. Initial work by Puterka *et al.* (2003) demonstrated that kaolin protected grape plants from feeding and oviposition by the leafhopper, by physically coating the plant with a mineral film. Tubajika *et al.* (2007) showed that grapevines treated with kaolin were less likely to become infected with the bacteria and fewer leafhoppers were found in treated fields. While chemical control of vectors likely will continue for the foreseeable future, vector management will slowly shift to genetic manipulation of crops.

Symbiont control

A new and potentially very powerful tool for controlling pathogen transmission is through the manipulation of symbiotic bacteria. Many arthropods carry a diverse assembly of symbiotic microorganisms that are maternally inherited and which have major effects on their hosts. These bacteria can be genetically modified to prevent the transmission of pathogens; arthropods containing these transformed bacteria are called paratransgenic. To develop such symbiotic-control methods it is necessary to first identify microorganisms in the target vector whose characteristics appear promising: 1) the symbiont is present in the same organs as the pathogen, and 2) the symbiont exhibits a potential to spread rapidly into the host populations. Once identified, cultured and modified, these bacteria can compromise transmission: by reducing vector competence, by expressing a gene product that could kill the pathogen, by inducing cytoplasmic incompatibility, and causing a high offspring-mortality rate, or by creating physical competition for space that the pathogenic bacteria would normally occupy.

This symbiont-based strategy is already being applied against several insect-borne human-disease pathogens, including the Chagas' disease agent. Research with leafhoppers transmitting the xylem-limited bacterium *X. fastidiosa*, which replicates in the foregut of the sharpshooter, *H. coagulata*, is also progressing apace. A symbiont, *Alcaligenes xylosoxidans* subsp. *denitrificans*, has been identified, cultured, modified and successfully reintroduced into leafhoppers via several plants (citrus, chrysanthemum, grape, periwinkle and crepe myrtle) and is expected to be competing with the pathogen for space and resources, thus reducing the vectoring capacities of the host (Bextine *et al.*, 2005). Similarly, another bacterium, *Cardinium hertigii*, has been identified and localized in the fat bodies and salivary glands of the leafhopper *S. titanus*. Because this insect is the vector of the phytoplasma that causes FD its presence in the same locations as the FD phytoplasma may eventually be instrumental in symbiotic control efforts (Bigliardi *et al.*, 2006; Marzorati *et al.*, 2006). One of the major challenges in this field is the delivery of the transgenic bacteria to the target vectors without adversely affecting the environment or other insect populations.

Plant lectins

As stated above, phytoplasma vectors feed specifically in phloem cells, obtaining nutrition from free amino acids and sugars. As such, the activity of carbohydrate-binding plant lectins, which would directly affect vector nutrition and/or be toxic, has been examined as a means of controlling vectors. These lectins are usually inserted into the target plant by *Agrobacterium* rolC (from *A. rhizogenes*), specific for expression of the lectins and stability in the phloem (Saha *et al.*, 2006). There are two plant lectins that have shown efficacy in vectors: snowdrop lectin (*Galanthus nivalis* agglutinin, GNA) (Nagadhara *et al.*, 2004) and a 25-kDa homodimeric lectin, *Allium sativum* leaf lectin (ASAL) (Dutta *et al.*, 2005). The mechanism of GNA is complex and not fully understood: it is not degraded by midgut proteases; it binds to D-mannose in the midgut of insects and is transported across the epithelial barrier to the circulatory system (Fitches *et al.*, 2001). In bioassay, feeding on GNA rice caused 90% mortality in *Sogatella furcifera* (Nagadhara *et al.*, 2004) and 29% and 53% mortality in *Nephotettix virescens* Distant and *Nilaparvata lugens* Stål, repsectively (Foissac *et al.*, 2000). ASAL has a high degree of sequence similarity to GNA (Majumder *et al.*, 2004); however, it may decrease the permeability of the gut membrane and seems to be effective at much lower levels than GNA (Biandyopadhyay *et al.*, 2001). A major receptor of GNA in the phytoplasma vector *N. lugens* is 26 kDa ferritin, thus ASAL may also be involved in iron homeostatasis (Du *et al.*, 2000).

One of the primary functions of spider venom is to paralyze prey; often these toxins are polypeptides that target the nervous system of the host. Some of these polypeptides bind to specific receptors and can affect the neuronal ion channels, neuronal receptors or presynaptic membrane proteins. Since GNA is able to cross the intestinal epithelium, it has the potential to transmit peptides fused to it into the hemolymph. In a novel application of this idea, Down *et al.* (2006) demonstrated the insecticidal effects of spider venom (SFI1) on the planthopper, *N. lugens*. Although the SFI1/GNA fusion product and smaller levels of GNA was found in the hemolymph, the mechanism of toxicity is not known. Possibly the fusion protein was cleaved, allowing the SFI1 toxin to act.

Systemic acquired resistance

Plants can activate defence mechanisms when challenged by either an arthropod or pathogen. This response – termed systemic acquired resistance (SAR) – can also be elicited by a number of chemicals (Sticher *et al.*, 1997). *Colladonus montanus* (Van Duzee) is an efficient vector of X-disease in fruit trees, and can also efficiently transmit the phytoplasma to *Arabidopsis thaliana* Columbia under laboratory conditions. Infected *A. thaliana* is stunted and produces fewer or no siliques. Treatment with benzothiadiazole (BTH) protected plants from phytoplasma; ~ 74% of non-treated control plants became infected, as compared to only 35% of the plants protected with 4.8 mM BTH a week prior to leafhopper feeding (Bressan and Purcell, 2005). The mechanism for this effect is not clear: the plant phloem could have been morphologically modified to prevented phytoplasma from establishing or replicating, but the BTH could also have elicited production of a substance inhibiting vector feeding, hence inhibiting transmission. Fewer leafhoppers survived on BTH-treated *A. thaliana* than on non-treated plants.

Conclusions

The number of new confirmed phytoplasma vectors has not kept pace with the number of new phytoplasmas described. This is partially due to the ease of describing new phytoplasmas in lieu of the current molecular methods available to researchers.

The most effective means of insect vector control is through physical prevention – either by use of screening or by use of a mineral coating on the plant itself. New methods will, by necessity, most likely revolve around genetic modification of the plant to either prevent phytoplasma replication within the plant or to prevent/reduce vectors feeding on the plant.

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