INSECT VECTORS OF PHYTOPLASMAS

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Summary

The principal means of dissemination of phytoplasmas is by insect vectors. The interactions between phytoplasmas and their insect vectors are, in some cases, very specific, as is suggested by the complex sequence of events that has to take place and the complex form of recognition that this entails between the two species. The commonest vectors, or at least those best known, are members of the order Homoptera of the families Cicadellidae, Cixiidae, Psyllidae, Cercopidae, Delphacidae, Derbidae, Menoplidae and Flatidae. The family with the most known species is, without doubt, the Cicadellidae (15,000 species described, perhaps 25,000 altogether), in which 88 species are known to be able to transmit phytoplasmas. In the majority of cases, the transmission is of a trans-stage form, and only in a few species has transovarial transmission been demonstrated. Thus, two forms of transmission by insects generally are known for phytoplasmas: trans-stage transmission occurs for most phytoplasmas in their interactions with their insect vectors, and transovarial transmission is known for only a few phytoplasmas.

1. Introduction

The phytoplasmas are non culturable parasitic prokaryotes, the mechanisms of dissemination is mainly by the vector insects. The commonest vectors, or at least those best known, are members of the order Himeptera, from the families Cicadellidae, Cixiidae, Psyllidae, Cercopidae, Delphacidae, Derbidae, Menoplidae and Flatidae. In the majority of cases, transmission only occurs between stages; transovarial transmission has only been demonstrated in a few species (Beanland *et al.*, 2000; Hanboonsong *et al.*, 2002; Kawakita *et al.*, 2000; Lee *et al.*, 1998; Marcone *et al.*, 2001; Parry, 1990).

The interactions between phytoplasmas and their insect vectors are, in some cases, very specific, as indicated by the complex sequence of events that must take place and the precise recognition events that must occur between the two organisms. In other cases, a single insect species has the ability to transmit more than one phytoplasma, *e.g.* *Hishimonus sellatus*, which can transmit six different phytoplasmas (Weintraub and Beanland, 2006), and some phytoplasmas are transmitted by more than one species of insect, with individual vectors able to be infected by two or multiple races of phytoplasmas (Weintraub and Beanland, 2006).

From a wild phytoplasma race causing onion yellowing (OY-W), a second race or line was obtained (OY-M) that caused only mild symptoms after passage over a period of 11 years through plants of *Chrysanthemun coronarium* (using the insect vector *Macrosteles striifrons*). A third line (OY-NIM) was obtained from the line causing mild symptoms (OY-M) after transmission by grafting for 2 years without the involvement of insect vectors. The phytoplasma line OY-NIM was apparently unable to pass across the intestine or survive in the haemolymph of the insect vector.

The relations between phytoplasmas and their insect vectors can be beneficial, deleterious or neutral in terms of their impact on the fitness of the insect host. The first reports suggested that infection by phytoplasmas was prejudicial to the insect hosts (Severin, 1946, cited by Weintraub and Beanland, 2006), whilst the most recent reports suggest that phytoplasmas can increase the fitness of their insect hosts (Beanland, 2000). Weintraub and Beanland (2006) determined that exposure to a race of aster yellows (AY) increased the longevity and fecundity of females of *M. quadrilineatus*; however, exposure to another race of AY increased the longevity of the insects tested but not the number of offspring produced. The effects of infection by phytoplasma on the insect host have implications for the incidence and dispersion of the disease (Weintraub and Beanland, 2006). Infection by phytoplasmas can have different effects on different vector species; for example, Madden *et al*. (1995) reported that the phytoplasma causing maize bushy stunt had a less deleterious effect on its primary vector *B. elimatus* than on its secondary vector *D. maidis*. Moreover, in the insect *Scaphoideus titanus*, which transmits the phytoplasma causing symptoms of grapevine flavescence dorée (FD), a diminution in fecundity was reported in females of this insect exposed to bean plants (*Vicia faba*) infected by the phytoplasma causing FD. The diminution in fecundity was revealed after dissection of 42-day-old adult females and determining, by counting under the microscope, that the number of eggs contained by insect adults exposed to plants infected by FD was only about 50% of the number found in adults exposed to healthy plants. In the same way, the number of nymphs emerging per infected female was only one third that of females not infected by FD (Bressan *et al*., 2005). Environmental factors, such as temperature, can also regulate the effects of infection by phytoplasmas of their insect hosts; thus Garcia *et al*. 1991, reported that infection by disease X could be deleterious for the vector *Paraphlepsius irroratus* at low temperatures but not in the range 25 to 30°C.

Those phytoplasmas that reduce the fitness of their insect hosts may have had a relatively short evolutionary relationship with these insect species, as selection would reduce the deleterious effects on the insect hosts (Weintraub and Beanland, 2006). Only those phytoplasmas that do not kill their hosts would be able to survive to be introduced to a host plant and subsequently be acquired by another vector (Weintraub and Beanland, 2006).

Recent reports have suggested that phytoplasmas were initially associated only with insects, since they generally tend to cause damage in their host plants but not in their insect hosts, rather in some cases extending the life expectancy of the insect and increasing its fecundity (Beanland *et al*., 2000). Phytoplasmas can infect many different organs and tissues in insects, including salivary glands, the intestine, haemolymph, ovaries and testes, amongst others, but in plants they only infect phloem tissue; and phytoplasmas can be transmitted transovarially to the next insect generation (although only a few cases have so far been reported), whilst seed transmission is unknown in plants (Nishigawa *et al*., 2002; Kawakita *et al*., 2000).

The transmission of phytoplasmas by insect vectors is of a persistent form (Tedeschi and Alma, 2004). Once an insect vector feeds on a diseased plant it acquires the phytoplasma via the alimentary canal; the phytoplasma can pass intracellularly across the epithelial cells of the intestine and multiplies inside a vesicle, or it can pass through both layers of cells (epithelial layer and basal membrane) and enter the haemocoel (Lefol *et al*., 1994). The phytoplasmas circulate in the haemolymph, from where they can infect and reproduce in other tissues, such as Malpighian tubules, fat bodies, brain, and reproductive organs; for example, the phytoplasma causing flavescence dorée acquired from infected beans binds strongly to tissues of the alimentary tract, haemolymph and salivary glands, but not to the muscles or genital organs of its insects hosts, *Scaphoideus titanus* and *Euscelidius variegatus (*Lefol *et al*., 1994). The molecular factors involved in the movement of phytoplasmas across the various insect tissues are still unknown; however, Oshima *et al*. (2004) produced a mutant onion yellowing (OY) phytoplasma that is not transmitted by cicadellid insects and whose genome (870 Kb) is smaller than that of the wild type OY (1,000 Kb) from which it originated, suggesting that the mechanisms of attachment to the cells of the insect had been lost. Susuki *et al*. (2006) reported that the membrane protein of the surface of phytoplasmas, referred to as antigenic membrane protein (Amp), forms a complex with three insect proteins (actin and the heavy and light chains of myosin). The complexes, Amp-microfilaments, were detected in all species of cicadellids, but not in the cicadellids that do not transmit OY, suggesting that the formation of the complex is correlated with the capacity of the cicadellids to transmit phytoplasmas. The OY phytoplasma was localized in the microfilaments of the smooth visceral muscle around the intestinal tract of the insects.

To be transmitted to plants, phytoplasmas must penetrate and accumulate at high levels in the acinar cells posterior to the salivary glands. In the salivary glands there are three barriers that the pathogens must overcome before they can be expelled with the saliva: the basal lamina, the basal plasmalemma and the apical plasmalemma. Cicadellid insects can be infected with a phytoplasma and still be incapable of transmitting it to healthy plants, perhaps due to the barrier of the salivary glands (Wayadande *et al*., 1997, cited by Weintraub and Beanland, 2006).

The retention of the infection in the insect vectors after molting is evidence that the pathogen moves towards the mid-layer of the intestine, which is not lost during molting; for this reason the infection is retained throughout the life of the insect, even though the efficiency of transmission of the adults is reduced (Tedeschi and Alma, 2004).

The cycle of transmission of phytoplasmas depends on the life cycle (monovoltine, multivoltine) and feeding habit (monophagous, polyphagous) of their insects vectors; polyphagous vectors have the potential to inoculate a wide range of plant species, depending on the resistance to infection of each host plant. Various studies have demonstrated that insects that do not normally feed on certain species of plants can acquire and transmit phytoplasmas to these plants under laboratory conditions. Thus, in many cases, the host ranges of vectors limit the dispersion of phytoplasmas by these species; the absence of specific cell membrane receptors for phytoplasmas can further limit their spread. For example, the cicadellids *Euscelidius variegatus, Macrosteles quadripunctulatus* and *Euscelis incisus* are able to acquire the Chrysanthemum yellows (CY) phytoplasma from infected chrysanthemum plants and transmit it to healthy plants of the same species; however, only *M. quadripunctulatus* and *E. variegatus* can acquire CY from *Vinca* infected with CY and transmit it to uninfected plants (Bosco *et al*., 1997). On the other hand, none of the cicadellids acquire the phytoplasma from celery plants infected by CY, for which phenomenon the term 'dead-end host' has been proposed, referring to plants that can be inoculated and subsequently show infection but from which the phytoplasmas cannot be acquired by insects when they feed on these plants (Weintraub and Beanland, 2006).

The symptoms of phytoplasma attack resemble those of hormonal imbalance (Pecho and Vizarova, 1990, cited by Weintraub and Beanland, 2006) and changes in the translocation of carbohydrates and amino acids in plants (Lepka *et al*., 1999); therefore, the infection can show systemically but the phytoplasmas may not be present in the tissues showing symptoms (Weintraub and Beanland, 2006). On the other hand, the biochemical imbalances caused by the infection may impede the acquisition of phytoplasmas (Weintraub and Beanland, 2006).

2. Factors Involved in the Transmission of Phytoplasmas by the Insect Vector

Some of the factors involved in the ability of the insect vector to transmit phytoplasmas are the genus, sex, and the age of the insect (nymphal instars, or adults either recently emerged or mature). For years, investigators have found that the genus of leafhoppers can influence the acquisition and transmission of phytoplasmas (Chiykowski and Sinha, 1989; Swenson, 1971). Females of *M. quadrilineatus* were more efficient than males at transmitting AY to lettuce, although perhaps equal percentages of males and females would have transmitted phytoplasmas if both had been analyzed as the adult (Beanland *et al*., 2000). And on the other hand, high titers of phytoplasmas have been observed in the salivary glands of young males of *E. variegatus* compared to females (Lefol *et al*., 1994). In the same way, another factor that influences the capacity for transmission of the vector is its age; recently emerged nymphs of *E. variegatus* do not acquire CY with the same efficiency as nymphs of the fifth instar (Palermo *et al*., 2001), and in some cases the transmission is greater when the phytoplasmas are acquired by nymphs rather than adults (Moya and Nault, 1998; Murral *et al*., 1996). The differences in behavior between males and females of insect vectors could be one reason to explain the differences observed between genera, and could affect the dynamics or distribution of the disease as males move around and between plants searching for the females (Hunt *et al*., 1993).

The race of the phytoplasma and the environmental conditions are also factors that can interact with the age of the vector in the ability of leafhoppers to transmit phytoplasmas (Murral *et al*., 1996).

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Additional effort is need to identified linkages between phytoplasma classification, mechanisms of pathogenicity and plant response.

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Additional References

(The three articles listed below give a good summary of the complex interactions between plants, insect vectors and phytoplasmas, and therefore represent a good guide for and introduction to this type of phytopathological problem.)

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Biographical Sketch

R. I. Rojas-Martínez: Master of Sciences, specializing in Phytopathology (1992), Doctorate in Sciences, specializing in Phytopathology (1999). Research Professor of the Colegio de Postgraduados. Since 1998 Rojas-Martínez worked with interactions between plants, phytoplasmas and their insect vectors. To date, Rojas-Martínez published 14 articles and two book chapters on this theme. Rojas-Martínez supervised through graduation 6 masters students and two doctoral students. Their investigations focused on the detection, classification and management of phytoplasmas.