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Behavioural aspects influencing plant virus transmission by homopteran insects

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ABSTRACT

Homopterans including aphids, whiteflies and leafhoppers are the major vectors of viruses comprising more than 80% of insect-transmitted viruses which represents close to 400 virus species within 39 different genera. Host plant recognition by homopterans requires a series of steps that are linked to plant virus transmission, including host searching or pre-alighting behaviour, probing on superficial tissues, settlement and stylet penetration to the target feeding tissues and salivation and continuous sap ingestion from the preferred feeding site. This review considers how vector behaviour influences the transmission and spread of plant viruses depending on the type of virus-vector relationship. Most studies have concentrated on aphid-transmitted viruses and particular probing and feeding behavioural processes and activities leading to the transmission of cuticula-borne and circulative viruses have been identified. The review also focuses on which are the most likely retention sites within the insect's body of cuticula-borne viruses. Finally, the influences of virus infection on vector behaviour such as changes in the attractiveness, settlement or feeding preference together with changes on vector performance (development, fecundity, rate of population increase and survival) are discussed.

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1. Introduction

Most of the known plant viruses are transmitted by insect vectors and are entirely dependent on the behaviour and dispersal capacity of their vectors to spread from plant to plant. Insect vectors of plant viruses belong to several orders (Hemiptera, Coleoptera, Thysanoptera, Orthoptera, Dermaptera, Lepidoptera, Diptera), but Hemiptera is by far the most important group of vectors of plant viruses. The order is divided into three suborders: Heteroptera (or true bugs), Auchenorrhyncha (hoppers) and Sternorrhyncha (aphids, whiteflies, mealybugs, psyllids). Most of the vectors of plant viruses are included in the latter two suborders, and are referred to here as homopterans which include both Auchenorrhyncha and Sternorrhyncha (Richards and Davies, 1977). One of the differences between homopterans and heteropterans is in the way in which they insert their mouthparts into plant tissue. Homopterans are less injurious to plant cells when they introduce their stylets to feed on the plant and therefore, are best suited to transmit plant viruses (Nault, 1997; Mitchell, 2004). All homopterans have piercing-sucking mouthparts comprising four tubular structures named stylets. The two maxillary stylets interlock to form two main ducts, the food and salivary canals. The two mandibular stylets are involved in mechanical activity and move independently of each other to penetrate through the intercellular spaces (Forbes, 1969).

Homopterans are vectors of about 55% of all known plant viruses (Nault, 1997), and the main vectors according to the number of virus species transmitted, belong to the families: Aphididae (aphids) and Aleyrodidae (whiteflies). Aphids transmit more than 50% of the plant viruses vectored by insects (approx. 275 virus species within 19 virus genera) (Nault, 1997), while whiteflies transmit 114 virus species within five different virus genera (Jones, 2003). Both groups of vectors are very well adapted for virus transmission because their stylets frequently pass between cells to reach the target tissue – the phloem – and can penetrate cells without causing damage. The larger stylet bundles of Heteroptera and Auchenorryhncha are more likely to take an intracellular path, and cause significant damage to plant tissues en route, which reduces the chances of virus infection (Mitchell, 2004). Furthermore, the high rates of population increase, the short life cycle and high dispersal potential make aphids and whiteflies the main group of vectors of plant viruses. Many of these cause severe yield losses and have a great impact on agriculture throughout the world.

Aphids are a very large group of about 4700 species (Remaudiere and Remaudiere, 1997), but only 450 species are known to col-

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onize food and fibre crops (Blackman and Eastop, 2007). A total of 227 aphid species of the 288 tested have been found to transmit plant viruses. Most (200) of these vector species belong to the subfamily *Aphidinae*, which includes the genera *Aphis*, *Myzus* and *Macrosiphum* (Eastop, 1983). In the case of whiteflies, 1300 species have been described, but only four species (*Bemisia tabaci*, *Trialeurodes vaporariorum*, *T. abutilonea* and *T. ricini*) have been found to transmit plant viruses (Jones, 2003). Other homopterans, such as *Cicadellidae* (leafhoppers), *Fulgoroidea* (planthoppers) and *Pseudococcidae* (mealybugs) also transmit a significant number of virus species (Nault, 1997). Below, we consider the behaviour of homopterans – with special reference to aphids and whiteflies – as it influences the transmission and spread of plant viruses.

Viruses transmitted by arthropods have been classified based on the differences in the length of time vectors retain the ability to transmit them. This classification differentiates between nonpersistent when the ability to transmit is lost within minutes or a few hours, semipersistent, when the transmission is lost after many hours, and persistent when the vector's ability to transmit remains for several days or throughout the entire life-cycle (Watson and Robers, 1939; Sylvester, 1956). Another classification used in the past refers to the retention site of the virus within the vector, and in this sense viruses retained at the tips of the stylets were called "stylet-borne" (Kennedy et al., 1962), whereas those retained at the foregut were called "foregut-borne" (Nault and Ammar, 1989). Others prefer to include both stylet and foregut-borne under the term "cuticula-borne" (Harris et al., 1996), to refer to viruses that are carried on the cuticula lining of the vector feeding apparatus. It is generally assumed that nonpersistent viruses are "stylet-borne" and that semipersistent are "foregut-borne", but as discussed below, such generalizations are inappropriate. Also, another term commonly used refers to cuticula-borne viruses as "noncirculative" to differentiate them from the "circulative" viruses which are not lost after moulting and invade the haemolymph and salivary glands of their vectors (Kennedy et al., 1962). However, as discussed later, noncirculative viruses are ingested and found throughout the gut and can be found associated to the cuticle lining of the food canal, cibarium and foregut. Therefore, this review mainly uses the classification based on the retention site of the virus within the vector (stylet, foregut or salivary glands). The term "salivary gland-borne" by analogy to the term "cuticula-borne" could be proposed to refer to viruses that are ultimately transmitted from the salivary tissues following a circulative pathway. One important difference is that circulative viruses can be found accumulating in several different tissues as they move toward the endpoint, which is the accessory or principal salivary gland. In contrast, cuticula-borne viruses do not cross the gut membranes and virions involved in transmission remain attached to the stylet tips or foregut.

2. Host plant recognition

Homopteran vectors of plant viruses follow a series of steps to search and find their host plants and identify feeding sites. These steps are a series of successive events that culminate in sustained sap ingestion once the host plant is recognized as an acceptable source for feeding. These behavioural events have been defined for aphids (Powell et al., 2006), but can be extended to other homopterans in the following way:

- Pre-alighting (before landing) behaviour.
- Plant contact and assessment of surface cues after landing.
- Probing on superficial tissues.
- Location and insertion of stylets at the appropriate feeding site.
- Salivation followed by committed sap ingestion.

2.1. Pre-alighting behaviour

Pre-alighting behaviour of insects involves phototactic response to visual cues from different sources. It is known that insects have ocular photoreceptors responding in a bandwidth of ultraviolet (200–400 nm), visible or photosynthetically active radiation (PAR) (400–700 nm) and the far red (700–800 nm) part of the electromagnetic energy spectrum. Using the electroretinogram technique Kirchner et al. (2005) determined that alate female summer migrants of *Myzus persicae* have three types of photoreceptors in the compound eye. The first was most sensitive to the green region (c. 530 nm), the second peak was in the blue-green region (490 nm) and the third peak was in the near UV (330–340 nm). Wavelengths in the UV region influence insect behaviour, such as orientation, navigation, host finding and feeding (Antignus and Ben-Yakir, 2004). For example, during flight, aphids respond strongly to visual stimuli (Kring, 1972) and locate host plants from the contrast between the soil background and the green colour of plant foliage (Kennedy et al., 1961; Döring et al., 2004). Once aphids terminate aerial transport after migration or appetitive dispersal, they lose their attraction to UV light and respond to cues coming from potential host plants (Klingauf, 1987). When leaving the air stream, aphids use visual cues and land on yellow-green objects, but are particularly attractive to intensely (highly saturated) yellow targets (Kennedy et al., 1961; Robert, 1987; Fereres et al., 1999). Visual cues, however, are unlikely to provide host-specific information (Kennedy et al., 1959; Compton, 2002).

For whiteflies, green reflected light is also a very attractive stimulus for orientation during flight. Take-off and flight behaviour of *B. tabaci* were oriented towards a green visual stimulus of 550 nm and adults preferred to land more often on a section of screen when it reflected green rather than white light (Isaacs et al., 1999). This same work showed that *B. tabaci* was able to actively control ground speed during flight at c. 20 cm/s whether the insects were flying upwind or downwind. In the case of *T. vaporariorum*, the primary photoreceptor is sensitive to light at a wavelength of 520 nm, but there is a second photoreceptor that reacts to a different extent to UV light depending on the region of the compound eye – dorsal or ventral part – (Mellor et al., 1997). Flight of whiteflies in the field is not entirely wind-oriented and they can sustain flight for more than 2 h.

Leafhoppers such as *Nephotettix virescens*, vector of rice tungro viruses (RTV), are strong flyers. In experiments using tethered-flying techniques Cooter et al. (2000) observed that a small proportion of *N. virescens* females flew continuously for periods of up to 7 h. This same work also showed that leafhoppers reared through one generation on tungro-diseased rice plants were less willing to fly than individuals maintained on healthy plants. The sharpshooter, *Homoladisca coagulata*, tends to make short hopping flights at a maximum height of 5 m instead of long-distance flights (Blua et al., 2005). Yellow colour also seems to be very attractive for leafhoppers. For example, host-oriented flights of *Dalbulus maidis* tend to peak at a narrow wavelength band close to 560 nm (Todd et al., 1990).

Phototactic response to plant-reflected wavelengths may be modified by plant volatiles detected by antennal olfactory sensilla. It is known that aphids respond to volatiles coming from their host plant (Pettersson, 1973; Nottingham et al., 1991), but the presence of host-plant odours did not affect the targeted (host-response) flight in flight chamber bioassays (Nottingham and Hardie, 1993). However, there is one example of odour-oriented flights for aphids. The carrot aphid, *Cavariella aegopodii* was caught more often in water traps baited with carvone – one component of host odour – than on unbaited traps. Furthermore, *C. aegopodii* appeared to be flying upwind towards the odour source from more than 1 m away (Chapman et al., 1981). Nevertheless, most of the literature on the

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