

Whitefly-Plant Relationships: Behavioural and Ecological Aspects

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Summary

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Introduction

Whiteflies (Homoptera, Aleyrodidae) rank among the most noxious insects attacking field and greenhouse crops around the world (Mound and Halsey, 1978). Larval instars, as well as adults, feed on the phloem sap of hundreds of species of plants and cause damage by the excretion of honeydew that falls on

leaves and fruits and serves as a suitable growth medium for fungi, that hamper photosynthesis and render fruits unmarketable. Furthermore, whiteflies can act as vectors for virus diseases.

The development or improvement of non-chemical control methods for whiteflies requires a thorough understanding of the interactions between the insects and their host plants, as well as the relations between whiteflies and their natural enemies (as discussed in Chapters 7 and 12). This chapter deals with the former, i.e. behavioural and ecological aspects of whitefly-plant relationships. This broad field of study covers several important aspects, such as the selection of species and parts of plants for feeding and oviposition, the relations between preference and performance, the development of spatial distribution patterns within and between plants, and population dynamics on various host plants. We welcome an opportunity to discuss interesting similarities in behaviour and ecology of whiteflies, but we realize that it is difficult to select representative data for each species. Moreover, we acknowledge at the outset that it is impossible to formulate a generalized picture of the Aleyrodidae as a group.

Since most studies on whiteflies deal with species of economic importance, available data are often restricted to pest species. However, even for those species, a genuine comprehension of the whitefly-plant relationship is still beyond our reach. For instance, substantial basic research has been devoted to the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood). This species is a key pest of many greenhouse vegetables and ornamentals. Commercially successful biological pest control programs have been developed (Vet, van Lenteren and Woets, 1980; Eggenkamp *et al.*, 1982; Hussey and Scopes, 1985; van Lenteren and Woets, 1988 (Onillon, Chapter 12)). However, the greenhouse whitefly cannot be controlled effectively on all important crops. Further basic research is therefore essential, to improve biological control or to develop other control methods, e.g. host-plant resistance. Another whitefly species, *Bemisia tabaci* (Genn.), has been a pest in field crops world-wide since the mid seventies (Butler, Henneberry and Hutchison, 1986; Gerling and Ohnesorge, 1986). Although this pest creates problems on a much larger scale than *T. vaporariorum*, its ecology is still poorly known. The need for chemical control of *B. tabaci* is presently strongly debated. Chemical control is difficult and expensive, may lead to decimation of natural enemies, and may create other pest problems (Eveleens, 1983 (see Chapter 13)). The lack of basic behavioural and ecological data seriously hampers the development of new, non-chemical pest management strategies.

In this chapter we discuss a number of topics relevant to a fundamental understanding of whitefly behaviour and ecology, which is essential for development of new control strategies or improvement of existing methods. The following questions will be addressed:

1. How do whiteflies select their feeding and oviposition substrate?

2. Is there a relationship between host-plant preference and performance, in particular for polyphagous whitefly species?
3. Can we explain the development of spatial distribution patterns and population dynamics of whiteflies based on host-plant preference and performance?

Selection of Feeding and Oviposition Sites

The relationship between selection of oviposition sites and growth, survival and reproduction of offspring is a central element in the evolution of host associations between herbivorous insects and plants (Singer, 1986; Thompson, 1988). For many insect species, the selection of an oviposition substrate is a critical phase in their life. This is certainly true for whiteflies, since in most species the larval stages are completely sessile, except for the early first crawler stages which have very limited dispersal capacities on the leaf where they have been deposited as eggs. Oviposition site selection by female whiteflies thus has a profound effect on their fitness. As most whiteflies feed and oviposit on the same leaves, feeding and oviposition site selection go hand in hand.

In a variable environment, whiteflies may encounter several plant species that differ substantially in suitability for the phytophage. However, host suitability may also vary significantly among individuals of a given plant species, as well as among parts of a given plant. Thus, whiteflies should select those plant parts that are most suitable for feeding and oviposition. The selection process can be regarded as consisting of different phases (Hassell and Southwood, 1978), mediated by visual (Prokopy and Owens, 1983), olfactory (Visser, 1986, 1988) and gustatory stimuli (Städler, 1986). Host plants may be recognized from a distance or only after landing. In the following discussion we trace the whitefly through distinct phases of its foraging behaviour: host-plant selection before landing, host-plant selection after landing, and selection of feeding and oviposition sites within the plant.

SELECTION OF HOST-PLANT SPECIES BEFORE LANDING

Colour is the most important factor in host-plant selection by whiteflies from a distance. For *B. tabaci*, colour is the only factor mentioned in the literature. It is attracted most strongly to yellow/green, followed in decreasing order by yellow, red, orange/red, dark green, and purple (Husain and Trehan, 1940). Mound (1962), who studied olfaction and colour sensitivity, found no reaction to odour of the host plant or to conspecific individuals. *Bemisia tabaci* did, however, react to two ranges of wavelengths: blue-ultraviolet and yellow. He suggested that short wavelengths (blue-UV) might play a role in migration behaviour, while attraction to longer wavelengths might facilitate host-plant location. *Bemisia tabaci* seems to be attracted to either yellow or blue/UV, but not to both at the same time. El-Helaly, Rawashi and Ibrahim (1981a,b)

provide data supporting Mound's conclusions. *Bemisia tabaci* is positively phototactic, and a positive correlation between light intensity and attraction was found irrespective of the sex of adults. This correlation held for all colours tested, although only females showed a definite colour preference. Attraction to yellow has also been reported by Ahmad and Harwood (1973), Berlinger (1980, 1986) and Sharaf (1982).

Extensive study has been made of colour vision in *T. vaporariorum*. Lloyd (1921) first reported a 'colour tropism' when he found it trapped on yellow sticky traps in greater numbers than on other colours. Moericke, Schneiders and Vogt (1966) observed that placing a yellow card below a tethered, flying whitefly evoked cessation of wing movement and a 'fall reflex'. This response did not occur when the yellow card was placed above or in front of the whitefly, or if the card was of any of a series of twenty greys, ranging from white to black. MacDowall (1972) established a 'phototactic action pattern' for *T. vaporariorum* which peaked at 550 nm and closely followed the transmission spectrum of a tobacco leaf. He found no evidence for colour vision, but studied only the range from 475 to 625 nm. Vaishampayan *et al.* (1975) measured the response of *T. vaporariorum* to reflected and transmitted light of various colours and found, like Lloyd (1921), that most whiteflies were trapped on a yellow surface. Smaller numbers were trapped on an unsaturated than on a saturated yellow surface, even though more light was reflected from the unsaturated surface across the spectrum (400–700 nm). Coombe (1982) studied the behaviour of *T. vaporariorum* under violet (400 nm) and green (550 nm) light. Under 400 nm the whiteflies took off more readily and walked faster than under 550 nm. When simultaneously illuminated with equal quanta of 550 and 400 nm light in flight, they oriented towards 400 nm. He concluded that in nature flying adults would orient towards the sky (i.e. circa 400 nm) but would tend to land on a green plant because plants reflect maximally at 500 nm. This is supported by results of Affeldt *et al.* (1983), who recorded a maximum capture of *T. vaporariorum* on traps reflecting 500–600 nm light, and inhibition of landings under 400–490 nm light. Woets and van Lenteren (1976) and van Lenteren and Woets (1977) studied selection behaviour with four different host-plant species and coloured substrates in wind tunnel and olfactometer experiments. They concluded that leaf shape, leaf structure and leaf odours did not play a role in selection. The only factor which influenced the number of landings on a plant or a non-plant substrate appeared to be colour. The more yellow the substrate, the more landings occurred. The response to colour in these experiments was not correlated with host-plant suitability; this initial landing response should be regarded merely as selection of a potential feeding and/or oviposition substrate. According to most authors, the first steps in host-plant selection in *T. vaporariorum* – orientation and landing – are mediated largely, if not exclusively, by a response to colour.

These conclusions are corroborated by studies of another whitefly species, *Aleurocanthus woglumi* Ashby, whose adults are attracted to objects that

strongly reflect light in the 500–600 nm range (Dowell, 1979). Attraction is independent of both shape and size of the object. It appears that visual cues draw *A. woglumi* adults to any green plant in the environment. In this species no olfactory orientation has been observed (Dowell, 1979).

The only species for which a reaction to host-plant odour has been found is *Aleyrodes proletella* (L.) (= *A. brassicae*). Like *B. tabaci* and *T. vaporariorum*, *A. proletella* displays a preference for yellow-green colours (Trehan, 1941). It also reacts to UV-radiation (Moericke, 1954) and to the odour of crushed cabbage leaves (Butler, 1938). Mound (1962) relates this response to host-plant odour to the much stronger host specificity of this species compared to *B. tabaci* and *T. vaporariorum*.

SELECTION OF HOST-PLANT SPECIES AFTER LANDING

We know of no studies explicitly addressing selection behaviour of *B. tabaci* on the plant or in choice situations with plants of different species. The behaviour that follows after a host plant has been selected for feeding was described in detail by Pollard (1955), who made a morphological study of the penetration behaviour of *B. tabaci* on cotton. He recorded that stomata can be used to enter the leaf, that the stylets usually follow an intercellular path through the parenchyma, and that plasmolysis of parenchyma cells adjacent to the stylets rarely occurs. Stylets often end in phloem tissue, which is not blocked, unlike in jassids, and there is no wound response.

Flight experiments with *T. vaporariorum* and observation of its behaviour on plants showed that this species can detect whether it is on a suitable host plant only after landing and internal probing (van Lenteren and Woets, 1977; van Sas, Woets and van Lenteren, 1978; Verschoor–van der Poel and van Lenteren, 1978). Rejection of a host plant occurs after probing for a few minutes (Noldus, Xu and van Lenteren, 1986b; van Vianen, Xu and van Lenteren, 1988a), a time span during which the stylets have penetrated just beyond the leaf surface (Janssen, Tjallingii and van Lenteren, 1989). Thus, host-plant discrimination seems to be based on internal chemical or physical plant properties. Once on a plant, visual stimuli probably determine the place where a whitefly will start probing, since whiteflies walk to the shaded side of a leaf regardless of whether that is the adaxial or abaxial surface. Whiteflies often land on the upper surface, start walking until they reach the edge of the leaf, then walk to the underside, where they usually start probing immediately. This is not simply a response to gravity but apparently also to light intensity because, when the leaf underside is exposed to strong light, whiteflies stop feeding, walk to the unlighted upper side and resume feeding there (Coombe, 1982).

The behaviour of greenhouse whiteflies is strongly influenced by host-plant species. After landing and walking to the shaded side of the leaf, whiteflies probe the plant with their stylets (van der Kamp and van Lenteren, 1981; Noldus, Xu and van Lenteren, 1986b). On some host plants (eggplant, cucumber and gherkin) they do not move about on the plant after their initial probes,

and stay on the same leaf for several days. However, on other plants (gerbera, melon, tomato and especially sweet pepper) they frequently change position between probes and often leave the plant within a few hours (van Sas, Woets and van Lenteren, 1978; Verschoor-van der Poel and van Lenteren, 1978). In experiments where whiteflies were released into a cage with four different host-plants (eggplant, cucumber, tomato and sweet pepper), a consistent change was observed within 24 hours after the first landings: the number of individuals on eggplant and cucumber always increased, and on tomato and sweet pepper always decreased. After 24 h, whiteflies were most abundant on eggplant, followed by cucumber, tomato and sweet pepper (Verschoor-van der Poel, 1978).

The penetration process in *T. vaporariorum* is similar to that described above for *B. tabaci*. Stylet penetration activities of this species have recently been investigated in detail through behavioural observations, electrical penetration graph (EPG) recordings (Figure 3.1) and transmission electron microscopy (Janssen, Tjallingii and van Lenteren, 1989). Electrical penetration graphs showed seven distinct patterns, five of which could be correlated with components of the stylet-penetration process: leaf surface penetration, intercellular penetration and salivary sheath secretion, phloem sieve element penetration, xylem penetration and short penetrations in cells. The pathway is almost completely intercellular before the phloem is reached, which occurs no sooner than half an hour after the start of a penetration. Therefore, rejection of a host plant, which occurs within a few minutes, cannot be based on probing of the phloem. Apparently, *T. vaporariorum* is able to select a suitable feeding site during probing of the apoplast in the mesophyll layer, shortly after the onset of penetration.



Figure 3.1. Electrical penetration graph (EPG) of *Trialeurodes vaporariorum* probing in a cucumber leaf (after Janssen, Tjallingii and van Lenteren, 1989). A whitefly is included in an electrical circuit via a gold wire attached to its thorax. Changes in electrical properties as a result of penetration activity lead to a characteristic pattern. During this penetration two short penetrations of cells occurred (pd), and, finally, a phloem sieve element was penetrated intracellularly (E(pd)). Pattern A reflects leaf surface penetration and pattern C represents intercellular penetration and salivary-sheath secretion. See Tjallingii (1988) for details about the methodology.

For *A. woglumi* it has been found that, once on a plant, females are able to discriminate between good, poor and non-host plants (Dowell, 1979). Ovipositional preference observed in the laboratory exactly followed the order found in field studies, i.e. from high to low: orange, surinam cherry, gardenia and fern. The movement of *A. woglumi* adults away from poor or non-host plants, together with their tendency to remain on good host plants, causes adults to aggregate on good hosts, as found for *T. vaporariorum*.

Scanning electron microscopy of the apex of the labium of six species of whiteflies, including *B. tabaci* and *T. vaporariorum*, revealed that all possess seven pairs of sensilla symmetrically positioned on either side of the labial groove (Walker and Gordh, 1989). In *Parabemisia myricae* (Kuwana), a transmission electron microscopical study showed several sensillae with multiple innervation. The sensillae have a dendritic canal with an apical pore, suggesting a chemosensory function. Similar transmission electron microscopical studies for other whiteflies, combined with sensory physiological and behavioural experiments, will be necessary before it can be determined whether these labial sensillae are used in host-plant selection.

SELECTION OF FEEDING AND OVIPOSITION SITES WITHIN A PLANT

Female whiteflies use the same leaf for oviposition and feeding. The circular egg patterns which are often found on relatively smooth leaves are the result of concurrent feeding and oviposition, whereby the female rotates around the point where her stylets are inserted into the leaf.

Leaf age is a major factor influencing *B. tabaci* densities within a plant. *B. tabaci* females prefer young leaves for oviposition (Khalifa and El-Khidir, 1964; Avidov and Harpaz, 1969; Gameel, 1977; Ohnesorge, Sharaf and Allawi, 1980). Vertical distribution patterns have been described for *B. tabaci* on tomato, eggplant and cotton (Ohnesorge, Sharaf and Allawi, 1980; von Arx, Baumgärtner and Delucchi, 1984). Eggs are laid predominantly on the under-sides of leaves and, on hairy plant species, *B. tabaci* refrains from ovipositing on very young leaves (Mound, 1965).

More is known about selection of feeding and oviposition sites by *T. vaporariorum*. Flight cage experiments demonstrated that greenhouse whiteflies do not select a leaf of a certain age from a distance; *T. vaporariorum* landed randomly on tomato leaves of different ages (Noldus, Xu and van Lenteren, 1986b). Nonetheless, *T. vaporariorum* prefers young leaves, as demonstrated by behavioural observations on leaves of different ages (Figure 3.2). Naive females stay longer on young than on old leaves. On old leaves they move and probe more frequently, spend less time probing and feeding, and depart sooner. Residence times on old leaves are further decreased after prior experience on young leaves. Female *T. vaporariorum* transferred from old to young leaves spend significantly more time probing and feeding and stay longer on young leaves. Prior experience thus clearly affects selection behaviour, which is a

well-established phenomenon in phytophagous insects (Papaj and Prokopy, 1989). Oviposition occurs only on young leaves and the first egg is usually laid before phloem feeding, i.e. during probing. Because development to adulthood takes three to four weeks, adult whiteflies emerge from the middle part of the plant. Newly emerged whiteflies move upward and reach the top of the plant within about three days (Noldus, Xu and van Lenteren, 1985, 1986a). It has been suggested that whiteflies might be attracted to the top of the plant because of the higher intensity of light reflection or transmittance there (MacDowall, 1972; Vaishampayan, Waldbauer and Kogan, 1975). However, the process of leaf probing after landing and arrestment on preferred leaves might also lead to the observed aggregation in upper layers. Our studies with *T. vaporariorum* on tomato indicate that genuine feeding site selection takes place, via indirect assessment of leaf suitability. Within-plant leaf selection is probably effected by chemical differences between the leaves (Noldus, Xu and van Lenteren, 1986b) measured during probing of the apoplast in the mesophyll layer

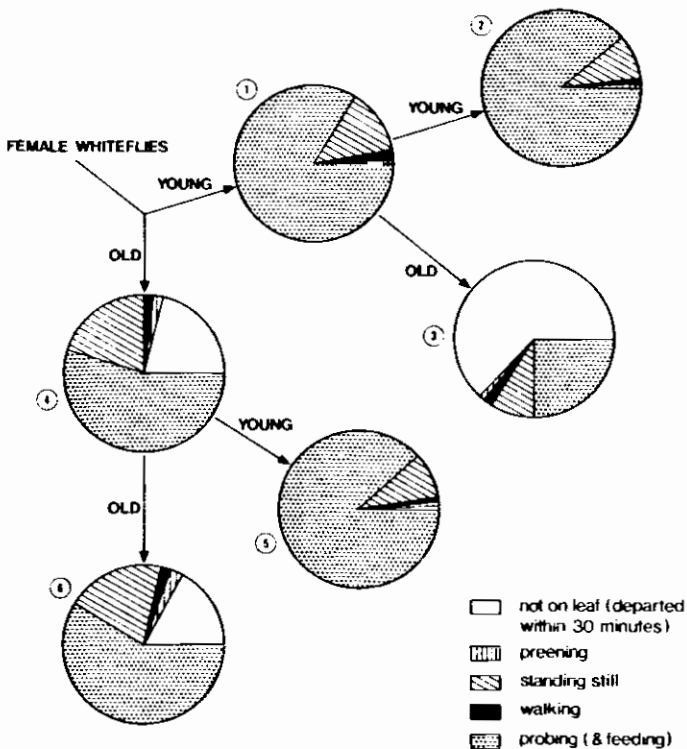


Figure 3.2. Time allocation by female adults of *Trialeurodes vaporariorum* on young and old tomato leaves. Whiteflies originated from medium-aged leaves. 1 = young leaf, 2 = young leaf after young leaf, 3 = old leaf after young leaf, 4 = old leaf, 5 = young leaf after old leaf, 6 = old leaf after old leaf (Noldus, Xu and van Lenteren, 1986b).

(Janssen, Tjallingii and van Lenteren, 1989). The distribution pattern and density of leaf hairs or other morphological properties, such as the length of epidermal cell boundaries at which penetration takes place and the density of the phloem veins, do not appear to influence host selection behaviour of *T. vaporariorum* (van der Kamp and van Lenteren, 1981; van Vianen, Xu and van Lenteren, 1988a).

Different species of whiteflies may have different leaf age preferences within the same plant species. *Parabemisia myricae* strongly prefers to oviposit on incompletely expanded, growing citrus leaves, while *Dialeurodes citri* (Ashmead) and *Aleurothrixus floccosus* (Maskell) prefer completely expanded young leaves for oviposition (Walker and Zareh, 1989).

Like *B. tabaci* and *T. vaporariorum*, *P. myricae* also penetrates plant tissue mainly intercellularly, and the objective appears to be the phloem (Walker, 1985). *Parabemisia myricae* penetrates mature leaves less frequently than young leaves. Walker (1987, 1988) suggests that mature citrus leaves possess a probing deterrent on the cuticle, and that maturity renders the cuticle of citrus leaves less penetrable. Impenetrability cannot be the only explanation for selection. A role in leaf-age selection by the labial chemoreceptors of *P. myricae* has been suggested (Walker and Gordh, 1989), but remains disputable, since evidence for selection prior to probing in leaves (Walker, 1987) and isolated cuticles (Walker, 1988) is ambiguous.

LEAF HAIRS AND HOST-PLANT SELECTION

Leaf hairiness clearly influences host-plant selection by whiteflies. Direct effects can be twofold: hairs can provide a physical barrier (Duffey, 1986) as well as a favourable microclimate (Willmer, 1986) for phytophages. As mentioned above, *B. tabaci* does not oviposit on the very hairy top leaves of hairy cotton varieties (Mound, 1965). However, moderate hairiness seems to be preferable. Pollard and Saunders (1956) studied cotton pests on two very closely related 'Sakel' varieties differing only in hair density. They compared a glabrous strain with one having hairs of moderate length and density on the lower leaf surface. The hairy variety contained more *B. tabaci*, aphids, mites, and thrips, but was resistant to *Empoasca* leafhoppers. Hairy-leaved, jassid-resistant cottons carry larger populations of whiteflies than similar glabrous-leaved varieties (Mound, 1965). This difference in population density was not attributable to fecundity of adults, predators, parasitoids, or competition from jassids. Mound suggested that the higher suitability of the hairy variety was due to microclimatic effects. Several other authors (e.g. Khalifa and El-Khidir, 1964; Evans, 1965; Omran and El-Khidir, 1978; Ozgur and Sekeroglu, 1986) found the same relationship between *B. tabaci* density and hairiness. Butler and Wilson (1984) and Butler, Rimon and Henneberry (1988) studied the relationship between two whitefly species, *B. tabaci* and *Trialeurodes abutilonea* (Haldeman), and hairiness in cotton, and also found many more whiteflies on hairy than on smooth cotton. On okra and super-okra

(near glabrous), low *T. abutilonea* and *B. tabaci* numbers were recorded. They suggested that the lower whitefly numbers on smooth and okra-type leaves could be explained by the openness of the plant canopy, resulting in more light and wind, a higher temperature and lower humidity. In general, lowest whitefly populations are found on okra and super-okra leaves, on glabrous leaves and on plants with a high gossypol content (Butler, Rimon and Henneberry, 1988). However, cotton lines resistant to whiteflies and aphids are susceptible to jassids and to *Pectinophora gossypiella* (Sanders) (Butler, Rimon and Henneberry, 1988), which illustrates again that selection for resistance to one pest organism may create problems with others. Although all empirical observations of densities of *B. tabaci* in relation to leaf hairiness support the hypothesis of a preference for (moderately) hairy leaves, the process leading to higher whitefly densities on hairy leaves has yet to be elucidated.

For *T. vaporariorum* no significant relationships between the degree of leaf hairiness and host acceptability or suitability have been found. Development time and oviposition rate do not differ between hairless and hairy cucumber lines (van Lenteren, unpubl.), but we must add that *T. vaporariorum* has been studied only at relatively high humidities under glasshouse conditions. Hairiness of the host plant does, however, have a great effect on the searching capacity of *Encarsia formosa* Gahan, a parasitoid of *T. vaporariorum* (see also Chapter 12). For two species of host plants, cucumber and gerbera, we have established that an increase in hair density leads to a proportional decrease in walking speed of the parasitoid (Hulspas-Jordaan and van Lenteren, 1978; Li *et al.*, 1987; van Lenteren, unpubl.). Thus, changes in trichome density directly influence the third trophic level and indirectly influence the pest insect. Such effects illustrate that plant breeding programmes must address effects of changes in the host plant on both the pest insect and its natural enemies (see Chapter 11). Relationships between host-plant characteristics and suitability for whiteflies are discussed in more detail later in this chapter.

SELECTION OF FEEDING AND OVIPOSITION SITES:

CONCLUDING REMARKS

1. Whiteflies exhibit colour preferences: they are attracted to substrates with a yellow-green colour. Attraction to ultraviolet is illustrated for some whitefly species and may relate to migration behaviour.
2. Whiteflies do not appear to use olfactory cues in host-plant selection. Reaction to host-plant odour has only been found for *A. proletella*, a relatively host-plant specific species.
3. No long-distance reaction to other host-plant characteristics has been found.
4. Whiteflies seem to distinguish between species of host plants primarily by probing the apoplast of the mesophyll just below the epidermis, rather than by probing the phloem. Stylets usually end in the phloem vessels. For *T. vaporariorum* and *B. tabaci*, hierarchies of host-plant preference have been established.

5. Within a plant, whiteflies prefer young leaves for feeding and oviposition. Selection occurs by short probes in the mesophyll. High leaf-hair density, a thick cuticle, and a probing deterrent on the cuticle may affect the selection process.
6. Both immature and adult whiteflies occur in specific distribution patterns, which appear to be at least partly due to reactions to differences in host plant and leaf characteristics. Understanding the within- and between-plant distribution of whiteflies is of fundamental importance for the design of whitefly sampling programmes (Ekbom and Xu, Chapter 5).

Host-Plant Suitability and its Relationship with Host-Plant Preference

Whiteflies, like all insects with sessile immature stages, are subject to strong selective pressures for choosing those species or parts of plants that are most suitable for feeding and oviposition. In the previous section we have outlined patterns of preference between and within plants. Here we examine to what extent observed hierarchies in host preference reflect hierarchies in host suitability. Host suitability is defined here as the various aspects of a host plant that affect the performance of immature or adult insects utilizing that plant as food (Singer, 1986). Since most whitefly species have overlapping generations, the growth rate of populations can be used as a parameter for host suitability (Caswell and Hastings, 1980). This rate can be measured directly or estimated through autecological experiments. For *T. vaporariorum*, development time, pre-adult mortality, fecundity and longevity have been determined on a range of host plants. However, for other whitefly species the available information is very limited. In the following sections various performance components are reviewed, and correlations with preference are sought. We concentrate on the two most extensively studied species, *T. vaporariorum* and *B. tabaci*.

One should be cautious with the interpretation of autecological data. In many reports, host-plant varieties are not mentioned, nutrient conditions of plants are not specified, and the existence of different whitefly strains is ignored. For instance, fertilizers can affect the nitrogen content of plants and thus their suitability for whiteflies (Onillon *et al.*, 1986). Differences in growing season may also lead to different growth of plants and thus to differences in host-plant suitability. Still, we are convinced that the large differences observed in host-plant preference and population development of whiteflies at least partly reflect differences in suitability among host-plant species.

HOST-PLANT SUITABILITY: VARIATION BETWEEN PLANT SPECIES AND CULTIVARS

Development time

Temperature and host plant exert the greatest influence on development time of *T. vaporariorum*. Most development times of pre-adult stages have been measured at constant temperatures around 22°C. Development times deter-

mined at fluctuating temperatures between 15 and 25°C do not differ from those measured at the average constant temperature: development rate (the reciprocal of development time) is a linear function of temperature within this range. The lower threshold for development is ca. 8°C and the upper threshold is almost 35°C (Hulspas-Jordaan and van Lenteren, 1989). Lower and upper threshold temperatures differ among developmental stages. Second-order polynomials best describe whitefly development over the total temperature range (Hulspas-Jordaan and van Lenteren, 1989). We have compiled information on 118 development times for nine different host-plant species and for temperatures between 7 and 40°C. Substantial variability exists, even among experiments on the same host plant at similar temperatures. Nevertheless, host-plant species can generally be ranked from short to long development times as follows: eggplant < cucumber = gherkin = melon < tobacco < bean = tomato < gerbera < sweet pepper. In Figure 3.3 results are presented from one experiment in which four species of host plants were compared (van Bruggen, 1975).

Development time of *B. tabaci* varies greatly between different host-plant species. Development rate of *B. tabaci* reared on sweet potato (*Ipomoea batatas*) was high on cucumber and sweet potato, intermediate on nine other host plants, including eggplant and several Cucurbitaceae, low on six host plants, including tomato, and zero on beet (Coudriet *et al.*, 1985). Rate of development is positively correlated with temperature (Azab, Megahed and El-Mirsawi, 1971; Butler, Henneberry and Clayton, 1983). The lower and upper developmental thresholds are 11 and 33°C, respectively. Rate of development is maximal at 28°C. On cotton, development from egg to adult takes 20 days at that temperature (Gerling, Horowitz and Baumgärtner, 1986).

Mortality of immatures

Like development time, total pre-adult mortality of *T. vaporariorum* is highly variable, even within one plant species. On tomato the average pre-adult mortality is 17.5% at temperatures between circa 12 and 30°C. On several other host plants (cucumber, bean, tobacco) immature mortality is also independent of temperature within this range. Most mortality occurs in the egg and first larval stages. We examined almost 70 mortality measurements for ten host-plant species, at temperatures from 12 to 37°C. The host-plant sequence for mortality from low to high is: eggplant < cucumber = gherkin = melon < bean < tomato < gerbera < tobacco < poinsettia = sweet pepper. Figure 3.4 shows results of an experiment with four plant species (van de Merendonk and van Lenteren, 1978).

The only comprehensive life table for *B. tabaci* is the one on cotton published by Horowitz, Podoler and Gerling (1984), who conclude that mortality of *B. tabaci* is highest during the crawler and young nymphal stages, which is mainly due to climatic factors. Host-plant suitability, measured as pre-adult mortality, shows the same trend as that for *T. vaporariorum*: cucumber (and other Cucurbitaceae) and eggplant are far more suitable hosts than tomato, which in turn is a better host than pepper (Coudriet *et al.*, 1985).

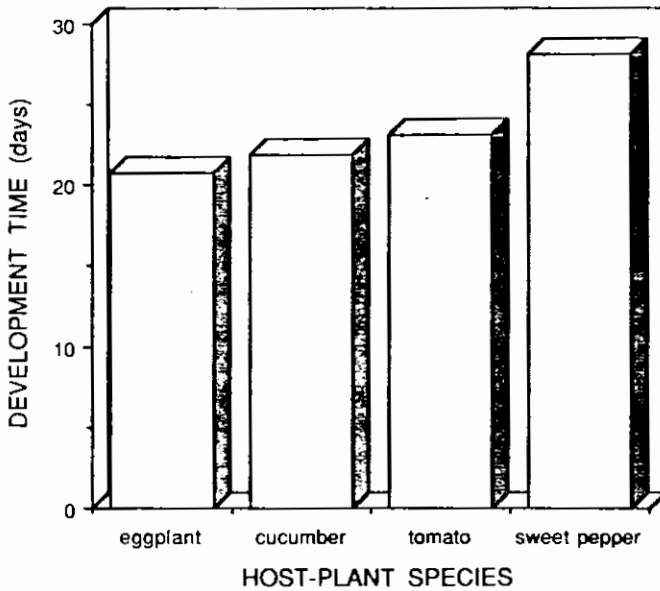


Figure 3.3. Development time from egg to adult of *Trialeurodes vaporariorum* on four host-plant species at 22.5°C.

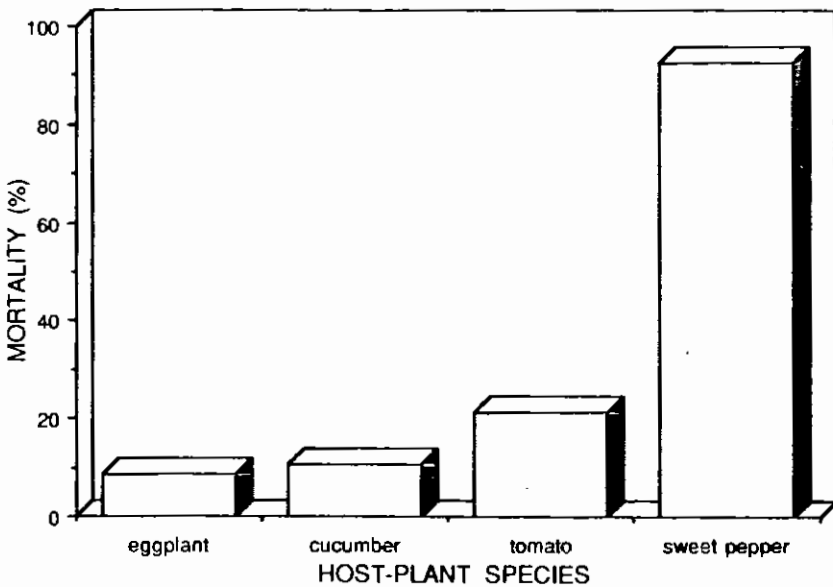


Figure 3.4. Pre-adult mortality of *Trialeurodes vaporariorum* on four host-plant species at 25°C (after van de Merendonk and van Lenteren, 1978).

Fecundity

On tomato the pre-oviposition period of *T. vaporariorum* averages 1.3 days at the usual temperature regime. The pre-oviposition period of *B. tabaci* in the field ranges from 1 to 8 days at temperatures above 20°C (Butler, Henneberry and Hutchison, 1986) and at lower temperatures can be much longer. Most mating occurs during the first day after emergence (Khalifa and El-Khidir, 1964; Azab, Megahed and El-Mirsawi, 1971).

Fecundity of *T. vaporariorum* is highly variable, and is influenced by species, cultivar and physiological state of the host plant, greenhouse temperature range and experimental set-up (type of cage, frequency of whitefly transfer). Fecundity is constant from 18 to 27°C but decreases at lower and higher temperatures. Fifty-two values of fecundity measured on nine host-plant species yield the following ranking: eggplant > cucumber = gherkin = melon = gerbera = tobacco > bean = tomato > sweet pepper. In Figure 3.5 the results of an experiment by van Boxtel (1980) on four plant species are presented. Most information on fecundity of *B. tabaci* applies to cotton. On this crop, fecundity varies between 20 and 350 eggs, depending on cultivar, prior experience to pesticides, and experimental conditions.

The oviposition rate of *T. vaporariorum* is age-dependent, gradually increasing during the first days, and reaching a plateau that is maintained until shortly before the female dies. We distinguish a pre-oviposition period, a maturation period during which the oviposition rate increases, and the remaining period with a rather constant oviposition rate, which is termed the *daily oviposition capacity*. Although most experiments have been done at 22°C, large variation exists. The average oviposition rate on tomato at 22°C is 5.5 eggs/female/day. Under glasshouse temperature regimes averaging 20–25°C, the oviposition rate ranges from less than 1 to 10 eggs/female/day and depends on the host-plant species. Oviposition rate is constant from 20–35°C, but decreases below 20°C. Seventy-six values for the daily oviposition rate, observed for nine host-plant species at temperatures between 12 and 35°C yield the following ranking: eggplant > cucumber = gherkin = melon = gerbera = tobacco > bean = tomato > sweet pepper. Maximum oviposition of *B. tabaci* occurs within the first week of adult life (Gameel, 1974). Oviposition rates for *B. tabaci* on cotton average approximately 10 eggs/day/female at temperatures between 25 and 30°C (Gerling, Horowitz and Baumgärtner, 1986).

Sex ratio

The sex ratio of *T. vaporariorum* is normally 1:1, and is independent of temperature and host-plant species. Mated females can lay both haploid (male) or diploid (female) eggs, while unmated females lay only haploid eggs.

The sex ratio of *B. tabaci* is usually 1:1 on cotton (Gameel, 1978). However, other studies indicate that the sex ratio is sufficiently variable to preclude

generalization (Butler, Henneberry and Hutchison, 1986; Gerling, Horowitz and Baumgärtner, 1986).

Longevity

Adult longevity of *T. vaporariorum* varies greatly, even when determined on the same plant cultivar at similar temperatures. The same factors play a role, as mentioned for fecundity. Average maximum longevity on tomato is approximately 75 days, which is reached at 15°C. At temperatures between 5 and 15°C there is a positive correlation between temperature and longevity. Above 15°C there is a strong negative correlation. Average longevity of *T. vaporariorum* on tomato cv. Moneydor at 22°C is 50 days. Females live much longer than males (van Boxtel, 1980). Sixty-eight values of longevity from nine different host-plant species yield the following ranking: eggplant > cucumber = gherkin = melon = gerbera = tobacco > bean = tomato > sweet pepper.

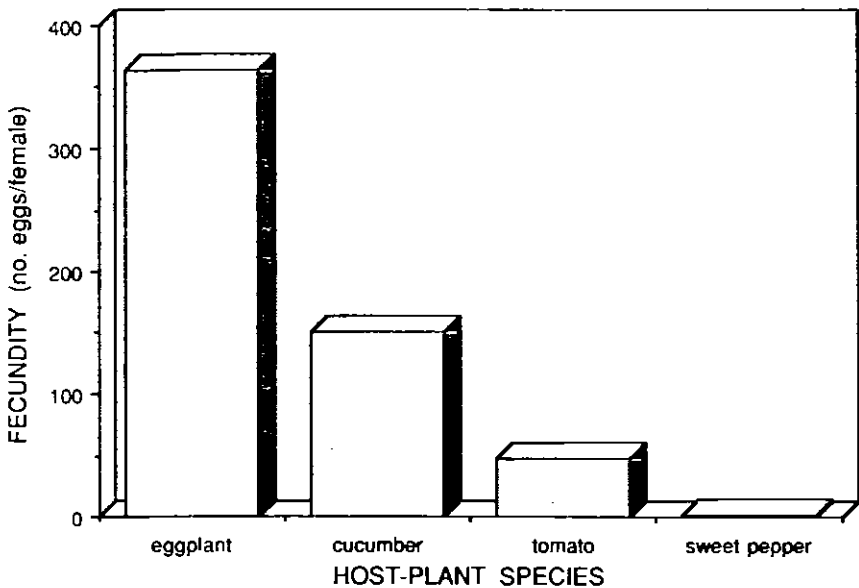


Figure 3.5. Fecundity of *Trialeurodes vaporariorum* on four host-plant species at 22°C (after van Boxtel, 1980).

Longevity of *B. tabaci* adults is 10–15 days in the field during summer (temperatures in the high twenties), and 30–60 days in winter (temperature around 15°C) (Gerling, Horowitz and Baumgärtner, 1986). In the laboratory, longevity of females is ca. 10 days, both at 26.7 and 32.2°C (Butler, Henneberry and Hutchison, 1986), and exceeds that of males.

Preference-performance relationships between plant species and cultivars

The variability in experimental procedures, plant cultivars and whitefly strains makes it difficult to generalize about host-plant suitability. Therefore we choose to discuss one series of experiments, carried out over a time span of three years with the same whitefly strains and host-plant cultivars, in order to illustrate general trends. Other results do not contradict these trends.

Expressing host-plant preference by *T. vaporariorum* as the number of whiteflies present on a plant in a choice situation, yielded the following ranking of species: eggplant > gherkin > cucumber > [gerbera] > melon > tomato > sweet pepper. We found the following relationships between preference and performance of *T. vaporariorum*: the more a plant species is preferred, the greater the total number of eggs laid per female, the higher the oviposition rate, the higher the longevity of females, the shorter the development time from egg to adult, and the lower the mortality of individuals of all stages (van Boxtel, Woets and van Lenteren, 1978; van de Merendonk and van Lenteren, 1978; van Sas, Woets and van Lenteren, 1978; Verschoor-van der Poel and van Lenteren, 1978). Clearly, the preference of *T. vaporariorum* for a host plant reflects its suitability for the whitefly. However, host-plant preference alone cannot be used to determine host-plant suitability. For example, on gerbera longevity and fecundity are high, whereas oviposition rate, developmental rate and larval survivorship are low.

Variation in host-plant suitability has obvious consequences for biological control by the parasitoid *E. formosa*. Information from commercial greenhouses suggests that the better a host plant is for the whitefly, the more difficult control may be. For example, biological control via seasonal inoculative releases with *E. formosa* is easy on sweet pepper and tomato and difficult or impossible on plants classified as good host plants for *T. vaporariorum* (van Lenteren and Woets, 1988). The rate of population growth of *T. vaporariorum* on sweet pepper and tomato is lower than the potential rate of population growth of *E. formosa* (van Lenteren and Hulspas-Jordaan, 1983; Yano *et al.*, 1989a,b). However, on several other host plants these rates are either similar or that of *E. formosa* is lower. In such cases biological control is only possible with periodic inundative releases. The efficacy of biological control using *E. formosa* is also influenced by the degree of hairiness of leaves. As leaf-hair density increases, the probability for the parasitoid of finding whitefly larvae decreases (e.g. Hulspas-Jordaan and van Lenteren, 1978; Li *et al.*, 1987) (see also Chapter 12).

Intraspecific variability in whiteflies and host plants

In the previous sections we have frequently mentioned the difficulties in comparing experimental results due to great variability in experimental conditions, host-plant cultivars and origin of *T. vaporariorum*. This variability also seriously hampers construction of models that simulate the population dynamics of whiteflies on different host plants, and complicates predictions on the feasibility of biological control with *E. formosa*. Hulsbas-Jordaan and van Lenteren (1989) thoroughly illustrate these difficulties vis-à-vis selecting data for parameters of their whitefly model (see page 75). Often authors do not mention the plant cultivar they have used, although sometimes part of the variability in performance can be attributed to variation in host-plant cultivar (Figure 3.6).

Studies concerning host-plant resistance illustrate the differences in suitability of host-plant cultivars for whiteflies (e.g. de Ponti, 1984 and Chapter 4). Confusion about the pest status of an insect may arise if cultivars are not specified. For example, *T. vaporariorum* is often a pest on sweet pepper in central European countries, but not in western Europe. Cultivars originating from central Europe are more suitable for whitefly development than those from western Europe or North America (Laska, Betlach and Havrankova, 1986). This is confirmed by recent work of van Lenteren and van Vianen (unpubl.) with sweet pepper (see below). Genotypic variation within a host-plant species in suitability for the whitefly is also known for *B. tabaci*. Berlinger (1986), Butler, Henneberry and Hutchison (1986) and De Ponti, Romanov and Berlinger (Chapter 4) review this information in the context of selecting *B. tabaci*-resistant host plants, especially for cotton. We would like to stress that host-plant resistance has thus far been only marginally exploited and deserves more attention.

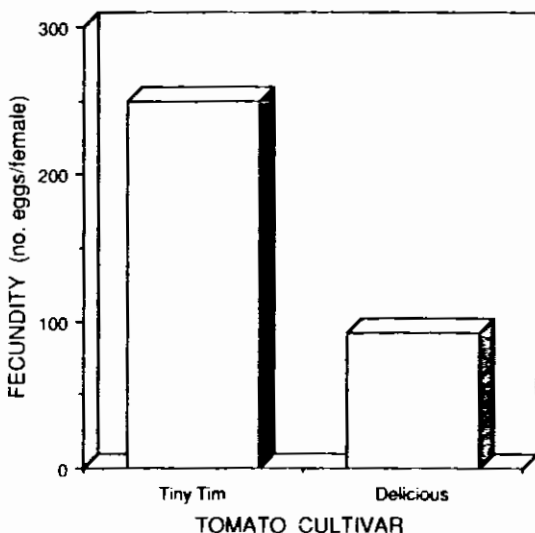


Figure 3.6. Fecundity of *Trialeurodes vaporariorum* on two host plant cultivars (after Curry and Pimentel, 1971).

Not only do plant cultivars differ in their suitability for whiteflies, but whiteflies from different localities also show variation in performance on the same cultivar. In an experiment carried out simultaneously in the Netherlands and Hungary (van Lenteren and van Vianen, unpubl.), performance of Dutch and Hungarian *T. vaporariorum* strains was compared on commonly used Dutch and Hungarian sweet pepper cultivars. Dutch and Hungarian whiteflies differed considerably in developmental characteristics on the same host-plant cultivar (Figure 3.7).

Hungarian whiteflies develop best on Hungarian sweet pepper, which might reflect a long relationship between host plant and pest insect. In contrast, Dutch whiteflies do not perform best on local cultivars, possibly because of the shorter evolutionary history of the plant-herbivore relationship. However, Dutch whiteflies respond rapidly to selection, displaying improved performance on sweet pepper within a few generations (van Boxtel, 1980). Figure 3.8 shows that a whitefly strain originating from tomato and reared for three generations on sweet pepper has a higher fecundity on sweet pepper than does the original tomato strain. Dorsman and van de Vrie (1987) found the same effect; whiteflies reared for a number of generations on gerbera develop faster, have far lower mortality and greater longevity on gerbera than do whiteflies originating from a culture on tomato and reared for the first generation on gerbera.

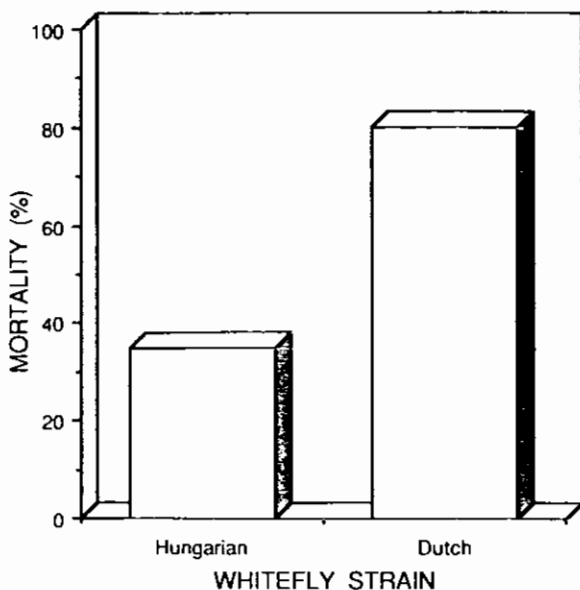


Figure 3.7. Pre-adult mortality of Hungarian and Dutch *Trialeurodes vaporariorum* strains on the same sweet pepper cultivar (van Lenteren and van Vianen, unpubl.).

These examples indicate local selection for adaptation to relatively poor host plants, i.e. sweet pepper and gerbera. According to Gerling, Horowitz and Baumgärtner (1986) "... it is expected that such a widely spread pest as *B. tabaci* may develop local strains and the variation in the developmental durations, longevities and fecundities obtained by various authors may hint at such developments." To date, there is no published information to substantiate this expectation. However, changes in reproductive capacity after transfer between host-plant species have been found (Gerling and Or, unpubl.) (Figure 3.9). A significant increase in fecundity on cotton occurred when *B. tabaci* originating from *Lantana camara* was reared for three generations on cotton. The same was found when *B. tabaci* was transferred from cotton to lantana. Such transfers between host plants occur annually in Israel, and the results suggest that, after transfer from lantana to cotton, selection occurs for individuals that develop and reproduce well on cotton. This conclusion is corroborated by the observation that *B. tabaci* numbers are low during the first part of the cotton season (May until July) in Israel, despite temperatures and condition of cotton plants that could allow much larger populations.

The results outlined above further stress that inspection and quarantine measures should not only be directed at pest species as such, but should also consider differences among strains.

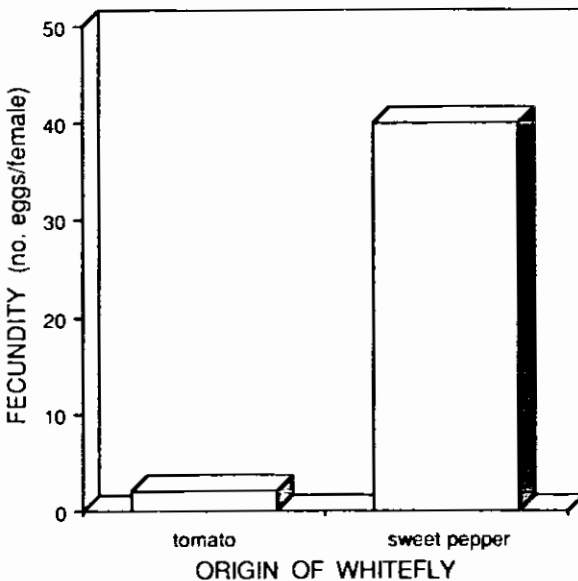


Figure 3.8. Fecundity on sweet pepper of *Trialeurodes vaporariorum* strains with a different rearing history (after van Boxtel, 1980).

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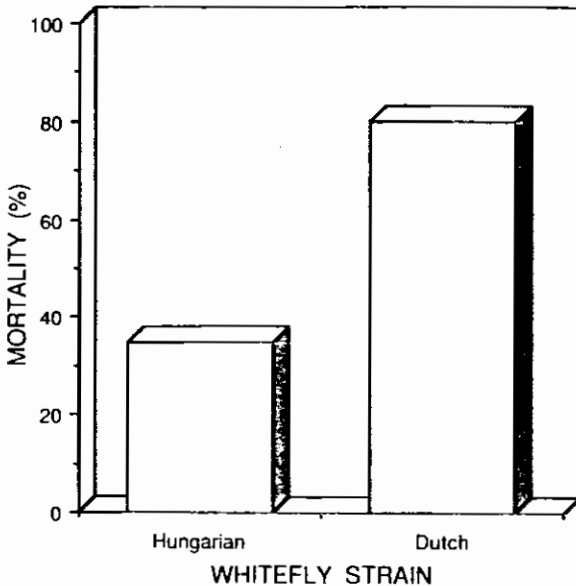


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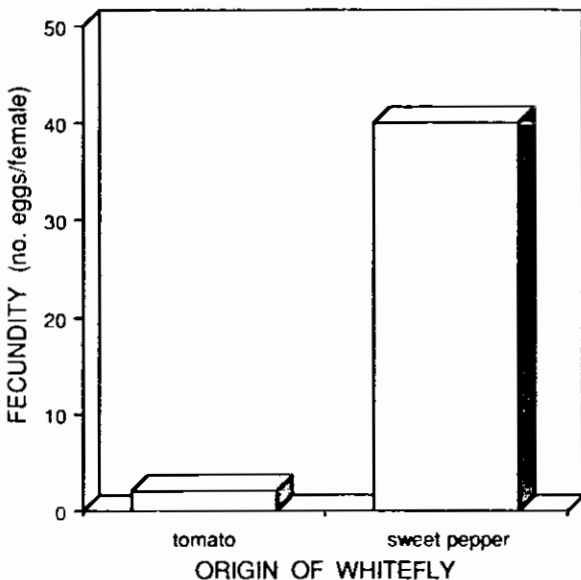


Figure 3.8. Fecundity on sweet pepper of *Trialeurodes vaporariorum* strains with a different rearing history (after van Bostel, 1980).

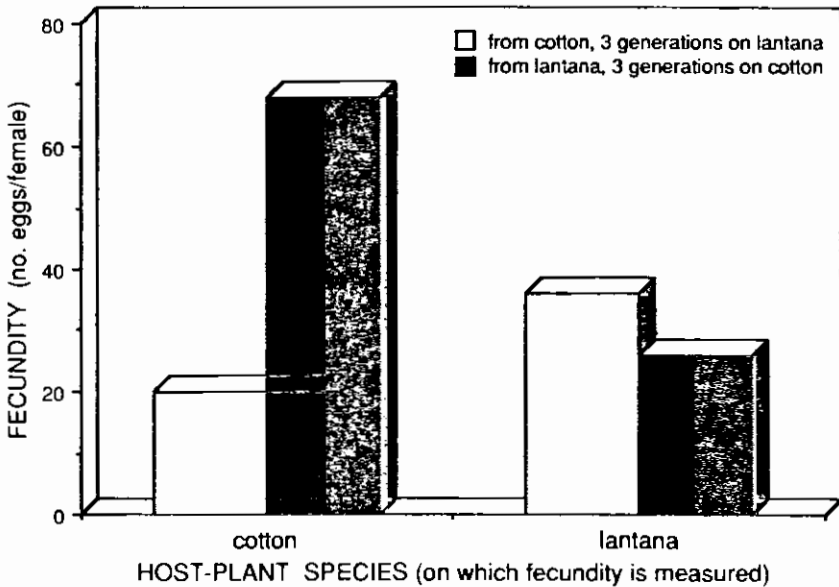


Figure 3.9. Fecundity on cotton and lantana of *Bemisia tabaci* reared for three generations either on cotton or lantana (after Gerling and Or, unpubl.).

PREFERENCE - PERFORMANCE RELATIONSHIPS WITHIN HOST PLANTS

In the whitefly literature several functional explanations for feeding- and oviposition-site selection by whiteflies have been proposed. Many studies only address feeding site selection or oviposition. For the whitefly species discussed in this article, the processes of feeding- and oviposition-site selection are strongly linked. Substrate selection may be mediated by different, or even conflicting, criteria. Zones of the plant may differ in their value for various fitness components of the herbivore. For example, young leaves may provide the best compromise between optimal development of immatures and nutritional quality for adults.

Why do whiteflies prefer young leaves?

Physical factors. Trichomes on the leaf surface can hamper feeding and oviposition by insects, by serving as a barrier that prevents access to the surface or by releasing sticky exudates that trap herbivores (Duffey, 1986). For instance, young apical cotton leaves cannot be used by *B. tabaci* for oviposition and

feeding because of the high hair density (Mound, 1965). The presence of glandular hairs makes *Lycopersicon hirsutum* and *Solanum pennellii* unsuitable hosts for *T. vaporariorum* (Gentile, Webb and Stoner, 1968), a trait that is utilized in plant-resistance programmes (see also Chapter 4). Alternatively, leaf hairs may also increase the suitability of certain plant parts, by creating a more favourable microclimate (Willmer, 1986) (see pages 55-6).

Various mechanical barriers can prevent successful penetration. The thickness of the cuticle may be a decisive factor. The cuticle of mature citrus leaves is much thicker than that of both young citrus leaves and leaves of many other host plants (Walker, 1985, 1987). The impenetrability of old leaves may be the reason for the 100% mortality of first instars of *P. myricae* on old leaves (Walker and Aitken, 1985). Further, the distance between the leaf cuticle and vascular tissue determines whether the insect can reach its food source with its stylets. However, in *T. vaporariorum*, none of these factors seem to be underlying causes for leaf-age preference (van der Kamp and van Lenteren, 1981).

Finally, zones of the plant may differ in the extent to which they offer protection against adverse climatic conditions, such as precipitation or high temperatures (Willmer, 1986). Whiteflies usually do not occur on the youngest leaves of host plants. High temperatures might prevent whiteflies from feeding and ovipositing on these uppermost leaves.

Chemical factors. Chemical barriers may prevent penetration by whiteflies. For example, the cuticle of old citrus leaves appears to contain a probing deterrent for *P. myricae* (Walker, 1987, 1988).

Leaves of different ages can vary widely in nutritional quality. Young tomato leaves have a lower water content, and a higher sugar and nitrogen content, than old leaves (Noldus, Xu and van Lenteren, 1986b). For *B. tabaci* the chemical content is a measure of host-plant suitability: the numbers of *B. tabaci* are positively correlated with leaf nitrogen (Joyce, 1958), and peak numbers of whiteflies on leaves with a pH of 6.0-7.5 and a sucrose content of 15% have been recorded (Husain, Puri and Trehan, 1936; Berlinger, Magal and Benzioni, 1983). Whether this is the result of a distinct preference has not been determined. Feeding on old leaves can have a detrimental effect on fecundity (Abbassi, 1980).

Biotic factors. Due to the limited dispersal capacities of immature whiteflies, only a limited zone within the plant is eligible for oviposition, i.e. those leaves that stay on the plant sufficiently long (5-7 weeks) to allow total development from egg to adult.

Finally, leaves of different ages may vary in their quality as a refuge against natural enemies. This factor is often linked with the degree of hairiness (see below).

Why do whiteflies feed and oviposit on the underside of leaves?

Several explanations for the occurrence of nymphs and adults on the lower leaf surface have been advanced, and they are summarized in Table 3.1. Due to limited experimental evidence, it is not yet possible to distinguish between proximate and ultimate factors.

Thinness of the cuticle plays a role in success of penetration for *B. tabaci* in cotton plants (Hargreaves, 1915; Pollard, 1955). Based on stylet measurements, Pollard (1955) concluded that the phloem is well within reach of *B. tabaci* nymphs on the lower, but not on the upper surface of cotton leaves, and he therefore suggested that the main reason for the occurrence of this whitefly on the underside of leaves is the limited stylet length. We have observed successful penetration of both upper and lower cuticle by *T. vaporariorum* adults in eggplant, cucumber, tomato and sweet pepper (van Lenteren and van der Kamp, unpubl.). *T. vaporariorum* adults and nymphs have sufficiently long stylets to reach the phloem either from the upper or lower leaf surface, and the host plants mentioned above have no tissues like sclerenchyma or xylem preventing the whiteflies from reaching the phloem (van der Kamp and van Lenteren, 1981). For this species it is not the distance from phloem to cuticle which determines where the individuals are found.

Stomata can be used to enter the leaf by *B. tabaci* and *T. vaporariorum*, but they do not play an important quantitative role. Individuals of both species usually penetrate the leaf at epidermal cell boundaries, but intracellular penetrations have been found as well (Pollard, 1955; van der Kamp and van Lenteren, 1981).

Protection from rain seems to be an important explanation: a rather effective way to reduce whitefly numbers is intensive spraying of the undersides of leaves with water only (van Lenteren, personal observation).

Light seems to play a role as well. Whiteflies apparently do not simply exhibit positive geotaxis after landing on a leaf, but move to the shaded side, whether this is the adaxial or abaxial side (Coombe, 1982).

The last explanation listed in Table 3.1, the dorsal position of the anus and the method of ejecting excreta, is difficult to judge. Did the position of the anus and the excretion method evolve as a result of whiteflies developing at the leaf underside, or was it a premise for successful development at this position? In any case, if leaves with developing whitefly larvae on the underside are turned 180 degrees, the insects become covered with honeydew and suffer high mortality (van Lenteren, personal observation).

HOST-PLANT PREFERENCE AND HOST-PLANT SUITABILITY: CONCLUDING REMARKS

1. Two polyphagous whitefly species, *T. vaporariorum* and *B. tabaci*, show strong and consistent preferences among plant species on which development has been established. Characteristics such as development time, immature mortality and fecundity also differ greatly among host-plant species, and, for

- T. vaporariorum*, host-plant suitability correlates well with host-plant preference. Differences in host-plant suitability, both within and between plant species, provide opportunities for selecting for resistance against whiteflies.
2. Differences in host-plant suitability are accompanied by different rates of population growth of whiteflies. Data on suitability of the plant cultivars in terms of whitefly population growth rate are necessary to estimate the success of biological control.
 3. Variability in performance of different whitefly strains on the same host-plant cultivar has recently been found for *T. vaporariorum* and may occur in *B. tabaci*. This observation necessitates characterization of whitefly populations. It should also result in extreme care with international transport of potentially infected plant material.

Spatial Distribution Patterns and Population Dynamics

The capacity of whiteflies to select specific feeding and oviposition sites, in combination with variation in host-plant suitability, leads to characteristic distributions of whiteflies over plants. Differences in host-plant suitability are accompanied by different rates of population growth. Understanding the development of spatial distribution patterns and population dynamics is a prerequisite for the construction of population models and the development of sampling methods for whiteflies.

Based on the information presented under the previous headings, it can be predicted that, in a mixture of host-plant species, whiteflies will be abundant on some and rare on others. However, in recognition of present-day agricultural practices, this section is largely devoted to a description of processes that occur within monocultures.

Table 3.1. Suggested explanations for the occurrence of whiteflies on the underside of leaves.

Explanation	Suggested by	Important for	
		<i>Bemisia tabaci</i>	<i>Trialeurodes vaporariorum</i>
Thinness of lower cuticle	1	+ (1,2)	- (3)
Proximity of phloem to lower surface	1	+ (2)	- (3)
Presence of stomata	1	- (2)	- (3)
Protection from rain	1	+ (1)	+ (4)
Negative phototaxis	1,5		+ (5)
Positive geotaxis	5		- (5)
Dorsal position of anus and method of ejecting excreta	1	+ (1)	+ (4)

References: 1. Hargreaves (1915). 2. Pollard (1955). 3. van der Kamp and van Lenteren (1981). 4. van Lenteren (pers. obs.). 5. Coombe (1982).

Trialeurodes vaporariorum

Spatial distribution of whiteflies can be divided into vertical distribution within plants and horizontal distribution between plants. Most published vertical distributions of the greenhouse whitefly are "snapshots" and thereby do not elucidate how distributions have developed (Hargreaves, 1915; Weber, 1931; Xu, Zhu and Zhang, 1984; Xu, 1985). We have recently studied how the vertical distribution of *T. vaporariorum* adults within tomato plants develops in time, by recording the position of individual whiteflies on tomato plants once every hour during the first five days after emergence (Noldus, Xu and van Lenteren, 1985)(Figure 3.10). As observed by Lloyd (1922), no emergence and hardly any movement occurred during the dark period. Light seems to trigger

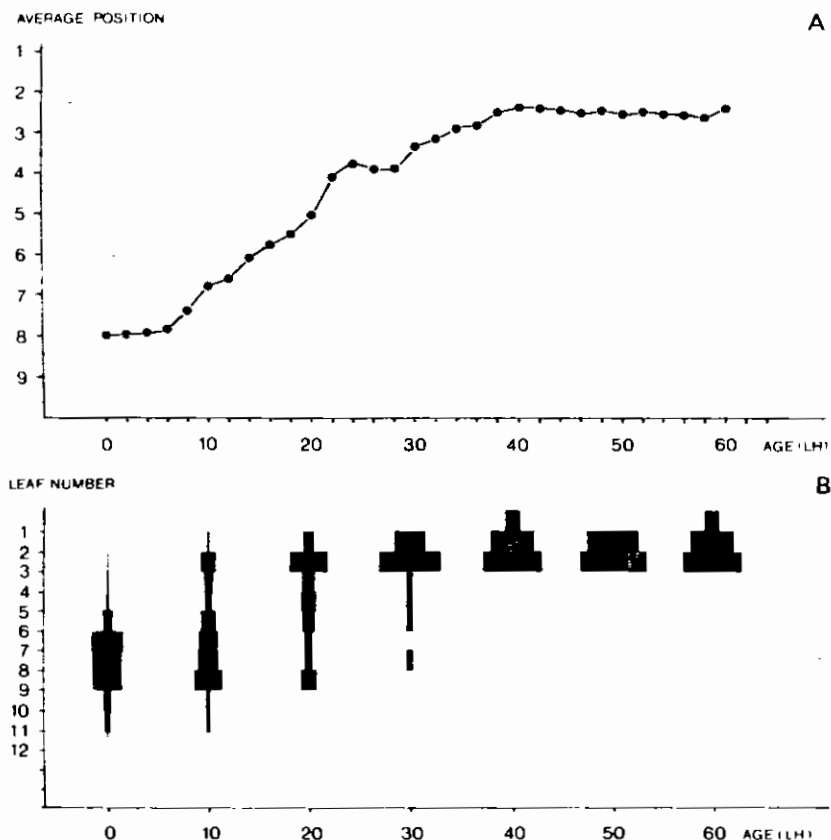


Figure 3.10. Distribution of adults of *Trialeurodes vaporariorum* within a tomato plant at various intervals (light hours = LH) after emergence. Positions are expressed as leaf numbers, counted from the top of the plant. a: average position of a group of adults, b: proportion of adults on different leaves (Noldus, Xu and van Lenteren, 1985).

the onset of emergence and movement. Most emergence of *T. vaporariorum* occurred 1–4 hours after sunrise. During the first four hours dispersal movement was minimal; newly emerged *T. vaporariorum* use much of this time for unfolding and drying their wings (Hargreaves, 1915; Weber, 1931). Subsequently, the insects gradually started moving around on the leaflet of emergence. Approximately nine hours after emergence, actual upward movement commenced as whiteflies departed from the leaf of emergence. After ca. three days, they reached the upper layer of leaves and their positions stabilized at, on the average, 2.5 leaves from the top of the plant. During the light period, the rate of movement was positively correlated with temperature.

Upward migration is accomplished primarily by flight from one leaf level to a higher level, within the plant of emergence or in a neighbouring plant. In this way, *T. vaporariorum* aggregate on the upper leaves, where most feeding and oviposition occur. Because the larvae are largely sessile, a typical vertical distribution of developmental stages of *T. vaporariorum* within the plant arises (Hargreaves, 1915; Weber, 1931; Xu, Zhu and Zhang, 1984; Noldus, Xu and van Lenteren, 1985; Xu, 1985). In our experiment (Noldus, Xu and van Lenteren, 1985) only 10% of the whiteflies remained on the plant of emergence. The average rate of movement of animals whose positions could be traced for several days was 2–5 cm per 2 hours, with a gradual increase in activity during the day and a distinct peak between 15.00 and 17.00 h.

Horizontal distribution patterns of *T. vaporariorum* have been published by several authors (Yamada, Koshihara and Tanaka, 1979; Ekbom, 1980; Xu *et al.*, 1980; Eggenkamp *et al.*, 1982; Yano, 1983; Noldus *et al.*, 1986). Little information is available on actual dispersal behaviour. Noldus, Xu and van Lenteren (1986a) and van Vianen, Xu and van Lenteren (1988b) conducted experiments in small greenhouses with tomato plants where whiteflies, released from a point source, were sampled once every two hours (Figure 3.11). During the first six hours almost all *T. vaporariorum* remained on the plant of emergence (Noldus, Xu and van Lenteren, 1986a). From 6 to 10 h after emergence horizontal movement gradually increased to a relatively stable average dispersal speed of 3.5 cm/h. The population continued to disperse at this speed until the end of the third day, when the insects were, on average, 1.25 m from the plant of emergence. Subsequently, the distribution remained stable and little movement was observed. The degree of aggregation at the start of the experiment was very high (all *T. vaporariorum* on the central plant of emergence) and decreased during three days, after which time it stabilized at a low level, with a distribution pattern fitting to a negative binomial distribution (Noldus, Xu and van Lenteren, 1986a). Experiments done at different whitefly densities and temperatures revealed similar results (van Vianen, Xu and van Lenteren, 1988b). At higher temperatures, dispersal started earlier and larger distances were covered. Whitefly aggregation remained strong and only part of the distributions fitted the negative binomial model.

AV. DISTANCE FROM PLANT OF EMERGENCE (cm).

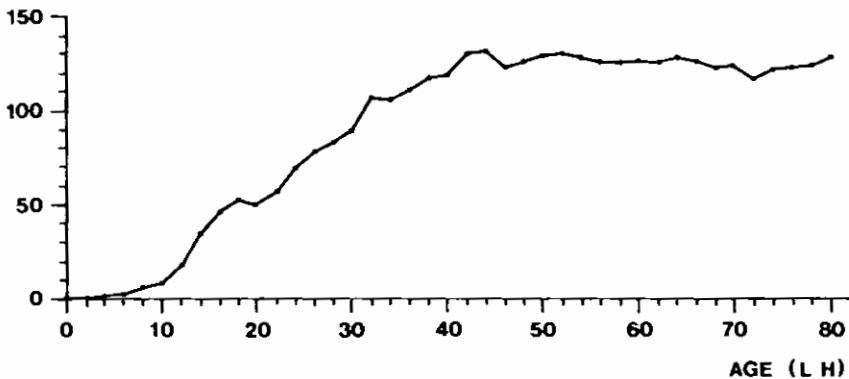


Figure 3.11. Average net horizontal distance moved by adults of *Trialeurodes vaporariorum* at various intervals (light hours) after emergence on a central tomato plant (Noldus, Xu and van Lenteren, 1986a).

The experiments on vertical and horizontal movement both indicate that movement is mainly restricted to the first few days after emergence. If a group of *T. vaporariorum* emerges at the same place and the same time under given environmental conditions in a greenhouse, then the vertical distribution within the plant, as well as the size of the area it occupies will be determined within a few days, after which time dispersal of that generation ceases. This suggests the existence of a dispersal period in the early adult life of *T. vaporariorum*, coinciding with the pre-oviposition period. Such a dispersal phase is known for many other insect species (e.g. Southwood, 1962). Speed and degree of dispersal are influenced by abiotic factors (e.g. temperature, light intensity and direction, photoperiod, wind speed), as well as by biotic factors (e.g. population density, quality and quantity of food, structure and density of plants). Higher temperatures and longer photoperiods may result in earlier stabilization of horizontal and vertical distribution patterns.

The distribution of *T. vaporariorum* is aggregated at several spatial levels: within a leaf, within a plant and between plants. On a leaf or leaflet, all developmental instars are aggregated (Yano, 1983). With high host density on the leaf, a decrease from strong aggregation in adults and eggs to near-randomness in pupae may be observed (Xu, 1985). Within a plant, the vertical distribution is distinctly stratified with respect to different developmental stages (Xu, Zhu and Zhang, 1984; Noldus, Xu and van Lenteren, 1985, 1986a). Between plants, *T. vaporariorum* also exhibits a considerable degree of aggregation. A distinction should be made between the distribution of individuals among

plants and the distribution of infested plants in a greenhouse. The observed degree of aggregation depends on the size of the area of study. In small experimental glasshouses (10–100 m²), distribution of individuals between plants may fit a negative binomial distribution (Ekbom, 1980; Xu *et al.*, 1980), while in a large commercial glasshouse (6,480 m², 18,000 plants) this distribution was so highly aggregated throughout the season that it could not be described by either the Poisson, negative binomial or Neyman type A distribution model (Eggenkamp *et al.*, 1982; Noldus *et al.*, 1986). In small greenhouses a random distribution of infested plants may occur (Yano, 1983), while in a large greenhouse we find distinct aggregation of infested plants in infested zones (Eggenkamp *et al.*, 1982; Noldus and van Lenteren, 1989). A whitefly population in a small greenhouse appears to correspond with an infested zone in a large greenhouse (Noldus *et al.*, 1986).

When these different levels of spatial aggregation are considered, it becomes easier to compare results of different studies of spatial distribution of *T. vaporariorum*. It is not surprising that distributions of greenhouse whiteflies between plants do not fit the Poisson distribution, as true randomness is very rare among insect populations (Taylor, Woiwod and Perry, 1978). However, the lack of fit to any theoretical distribution complicates the development of sampling methods. Sampling methods derived from studies in small greenhouses (Xu *et al.*, 1981; Yano, 1983) cannot be extrapolated to large greenhouses, because of the differences in spatial distribution of *T. vaporariorum* in the two scales of study. The absence of easy and reliable sampling methods prevents growers from monitoring the population density of the pest and determining the timing and size of parasitoid releases (Eggenkamp *et al.*, 1978; Ekbom, 1980; Noldus *et al.*, 1986; see also Chapter 5). The extreme aggregation of the insects renders simple sampling of *T. vaporariorum* an illusion.

Bemisia tabaci

Emergence of adult *B. tabaci* takes 5–15 min and is followed by wing expansion, which occurs on or near the pupal case and takes 40–50 min (Azab, Megahed and El-Mirsawi, 1971). Emergence generally occurs during the day. Rate of emergence is highest during the first four hours after sunrise (Husain and Trehan, 1933; Azab, Megahed and El-Mirsawi, 1971; Butler, Henneberry and Clayton, 1983; Musuna, 1986). Males emerge on average a little earlier than females (Gerling, Horowitz and Baumgärtner, 1986). Data of Musuna (1986) suggest that *B. tabaci* adults migrate from the place of emergence to young leaves during the morning hours.

Vertical distribution patterns of *B. tabaci* resemble those described for *T. vaporariorum*, but may be less pronounced due to the architecture of the plant, like cotton (Trehan, 1944; Khalifa and Khidir, 1964; Ohnesorge, Sharaf and Allawi, 1980; von Arx, 1982; von Arx, Baumgärtner and Delucchi, 1984; Ohnesorge and Rapp, 1986).

Bemisia tabaci adults demonstrate two distinct flight patterns: short- and long-distance flight (Berlinger, 1986). Short-distance flights occur under the plant canopy (Avidov, 1956; Ohnesorge, Sharaf and Allawi, 1980). Newly emerged adults leave the lower leaves on which they emerged and move to upper leaves to feed and oviposit (Avidov, 1956). Long-distance flights occur when adults take off from their host plant, get caught in an air current and drift passively (Varma, 1963). *Bemisia tabaci* have been captured at heights up to 305 m (Glick and Noble, 1961) and displacement occurs over distances of several kilometres (Costa, 1975). In fallow fields near a cotton crop, peak catches were obtained between 6.00 and 9.00 h in the morning (Gerling and Horowitz, 1984). In a cotton field, maximum catches occurred later in the morning and at noon. These individuals presumably were in a searching mode for feeding and oviposition sites, rather than in a dispersal phase (Gerling and Horowitz, 1984). In traps 100 m away from cotton fields whiteflies were caught from 11.00 h until sunset (Joyce, 1983). Most whiteflies were found in the trap at 5 m and numbers decreased with trap height. Sampling with aircraft above cotton fields also yielded highest catches at the lowest elevation (8 m), but whiteflies were still caught at 60 m. Trapping of airborne *B. tabaci* was consistent with a model of passive transport: during the morning, convection evidently carries *B. tabaci* aloft (to at least 1,600 m), while late in the afternoon, collapse of convection is accompanied by increased densities at lower levels (Joyce, 1983). Bellows *et al.* (1988) studied flight activity of *B. tabaci* in different crops and found that the number of *B. tabaci* caught during daylight hours was strongly positively correlated with temperature, but not with humidity. At night, few whiteflies were caught and no relationship with temperature was found. Temperature and light thresholds are suggested to affect the number of *B. tabaci* taking flight. Gerling and Horowitz (1984) and Berlinger (1986) interpret whitefly flights as follows: whiteflies take off in a dispersal phase when they are receptive to UV, they fly upward to the sky, and settle on yellow-green objects after a long-distance flight. Take-off is thought to occur if flies are in a dispersal phase, or if leaves are in an unsuitable physiological condition (e.g. leaf senescence [Avidov and Harpaz, 1969], leaves of a non-host plant). According to Gerling and Horowitz (1984), the bulk of the airborne population caught over fallow fields are flies in a dispersal phase. Recent information (Byrne, unpublished) indicates the presence of two types of adults in a population of *B. tabaci*, with a low or high propensity to disperse. Whether the ratio between the two types changes, for example as a result of a change in plant suitability, is not known. *B. tabaci* populations are considered to be continuously mobile in areas where a variety of host plants is consistently available. Intensification of agriculture and growing of new suitable host plants for *B. tabaci* provide bridges between cotton seasons and may have led to increased pest status (Joyce, 1983; Coudriet *et al.*, 1985).

POPULATION DYNAMICS AND MODELLING

Overall theory and practice of population dynamics and modelling of whitefly populations are discussed in Chapter 6. In the following sections we wish to summarize the state of knowledge as far as it relates to host-plant relationships.

Trialeurodes vaporariorum

Most information on population dynamics of *T. vaporariorum* is derived from experiments carried out in small experimental greenhouses. *T. vaporariorum* populations initially develop exponentially as long as no natural enemies or other limiting factors are present (Hulspas-Jordaan and van Lenteren, 1989). Growth of whitefly populations stops only when plants are so heavily infested that they begin to deteriorate and die. In such situations, hundreds of whiteflies can be present per leaf. Few studies deal with whitefly populations under practical conditions (Eggenkamp *et al.*, 1982). Experience over the past 20 years in commercial greenhouses has taught us that whitefly populations indeed develop exponentially if no biological or chemical control is applied. However, predicting population growth for specific situations is complicated by many interrelated factors. Hulspas-Jordaan and van Lenteren (1989) and Yano *et al.* (1989a,b) have recently developed a simulation model, based primarily on autecological data such as described earlier that can be used to predict the reaction of the whitefly-host-plant system to changes in the agroecosystem, e.g. a change in the temperature regime, or use of new host-plant cultivars. This (state-variable, temperature-driven, explanatory, dynamic, deterministic) model can be used to simulate population growth of *T. vaporariorum* on a variety of crops (Figure 3.12) and to predict the development time of *T. vaporariorum* under different temperature conditions. At present, the model can only be validated for *T. vaporariorum* on tomato, which yields a good fit (Hulspas-Jordaan and van Lenteren, 1989). No data are available for validation on other crops. Manipulation of development time, pre-adult mortality, fecundity and adult longevity revealed that, on most host plants, changes in development time had by far the greatest effect on population growth, followed by changes in fecundity (Hulspas-Jordaan and van Lenteren, 1989; Yano *et al.*, 1989a,b). This finding is consistent with theoretical expectations of the effect of changes in life-history components on population growth rate (Lewontin, 1965; Snell, 1978; Caswell and Hastings, 1980). Additionally, Yano *et al.* (1988b) showed that, on relatively poor host plants, such as sweet pepper, where pre-adult mortality is high, changes in survivorship of immatures influence population growth as strongly as development time and fecundity.

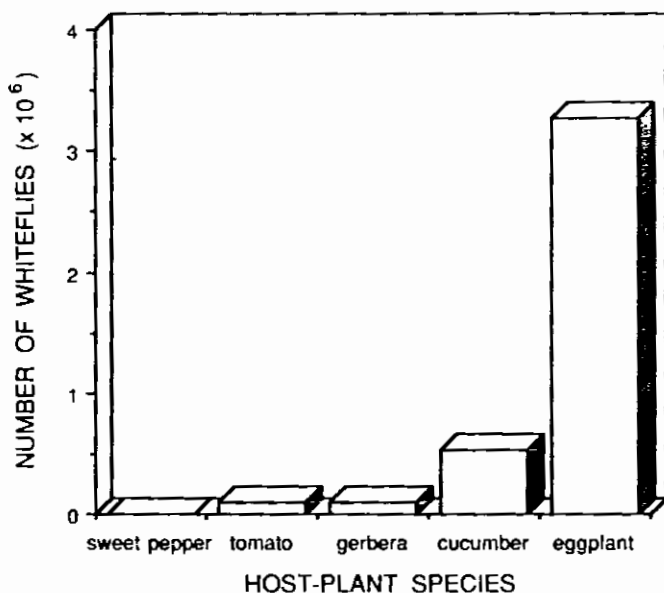


Figure 3.12. Simulated number of *Trialeurodes vaporariorum* (all stages) on different host plants after 80 days. Initial density: 100 eggs, temperature: 22°C (after Yano et al., 1989b).

Bemisia tabaci

A fair amount of scattered information exists on the population dynamics of *B. tabaci*, but the use of inadequate sampling methods (i.e. inadequate for a reliable description of population fluctuations) precludes any but the very general conclusion that, on many plant species, populations increase exponentially as long as basic environmental and host-plant conditions are met. In cotton, "... population dynamics... is typically characterized by exponential growth..." (Butler, Henneberry and Hutchison, 1986). The only studies providing insight into the population-dynamical relationship between *B. tabaci* and host plants are those for cotton by von Arx (1982) and von Arx, Baumgärtner and Delucchi (1983). Their model, based on autecological data of *B. tabaci*, and coupled with a detailed growth model of the cotton plant, accurately simulates population dynamics, particularly during the initial period of plant growth.

SPATIAL DISTRIBUTION PATTERNS AND POPULATION DYNAMICS: CONCLUDING REMARKS

1. The occurrence of highly clustered whitefly populations, both in *T. vaporariorum* and *B. tabaci*, necessitates very large numbers of samples for reliable population estimates. This makes sampling time-consuming and expensive. Population numbers are often estimated on the basis of insufficient sample sizes or inadequate sampling methods, which leads to considerable errors (Eggenkamp, Ellenbroek and van Lenteren, 1980). For *B. tabaci*, the situation is more complex than for *T. vaporariorum*, due to the enormous size of the (cotton) fields to be sampled and the less pronounced vertical distribution patterns of *B. tabaci* in cotton (Horowitz, 1986; Ohnesorge, 1986). As stated by Butler, Henneberry and Hutchison (1986), "... there are about as many techniques used to provide relative estimates of whitefly populations as there are researchers" and often "... the number of samples taken was decided on feasibility rather than on a calculation of the number of samples which should be taken based on distribution patterns of whitefly to ensure biologically clear and valid results."
2. A start has been made on experimental analysis of factors that cause population fluctuations in whiteflies. For simple situations, such as monocultures in glasshouses, population growth can now be estimated through model simulations.
3. For some crops, horizontal and vertical distribution patterns over time are now known. In *T. vaporariorum* the development of distribution patterns is in line with our knowledge of the host-plant selection behaviour of the insects. *T. vaporariorum* shows a dispersal phase of a few days, after which distribution patterns stabilize. Aggregation of *T. vaporariorum* is very strong, even on a relatively unsuitable host plant such as tomato.
4. For *B. tabaci* it is more difficult to relate behavioural data to distribution patterns. Within-plant distribution arises through a similar process of leaf selection via stylet probing, as in *T. vaporariorum*. Horizontal distribution patterns, for which very few reliable data are available, are more difficult to interpret. There is empirical evidence for the existence of a dispersal phase, but this has not yet been tested thoroughly.

Conclusions

The questions posed in the introduction can be only partially answered. Basic behavioural and ecological information, a prerequisite for a comprehensive picture of host-plant selection and population dynamics, is presently available for only a few whitefly species.

How do Whiteflies Select their Feeding and Oviposition Substrate?

In flight, polyphagous whitefly species seem to react only to certain colours. No long-distance responses to other host-plant characteristics have been found for any polyphagous species. Attraction to ultraviolet light has been established for several species and is thought to indicate a dispersal phase. Attraction to yellow-green causes whiteflies to land on potential host plants, but actual selection of a host plant or plant parts occurs after landing. Whiteflies scan the cuticle with their stylets, or make short probes in the plant tissue just below the epidermis. Contact with phloem vessels – the primary feeding site for whiteflies – is not necessary to select a suitable host plant. Through a process of probing and horizontal and vertical movement, whiteflies are able to select host plants in a mixture of plant species, and to select certain leaves for feeding and oviposition within a plant. Feeding and oviposition occur simultaneously. Too few data on host-plant selection are available to generalize about relatively host-specific species.

One of the most intriguing questions is what specific factors determine whether whiteflies remain on or leave a host plant? The proximate factors mediating host-plant selection are still unknown. Such knowledge would facilitate selection or manipulation of host plants in such a way that they become less acceptable to whiteflies.

Is there a Relationship between Host-plant Preference and Host-plant Suitability?

For *T. vaporariorum*, the answer is yes. Whitefly population growth is much faster on plants selected for feeding and oviposition than on unpreferred plants. However, host-plant preference may evolve rapidly. Information for both *T. vaporariorum* and *B. tabaci* indicates that local whitefly populations may adapt to host plants on which they initially developed poorly.

Within whitefly species, do populations differ in host-plant preference and, as a result of that, do rates of population development vary on the same host plant? How fast do such differences evolve? How do we characterize different populations? Recent information on *T. vaporariorum* and *B. tabaci* suggests that among-population variation may be extensive. However, most studies report only the species name of the host plant and whitefly. We encourage authors to provide specific information on the host plant (cultivar, rearing method) and whitefly (origin, rearing plant species) with which they work. Biotaxonomic studies are needed to estimate the amount of intraspecific variation and to provide simple methods for identifying biotypes. Some experiments have already indicated that adaptation (through selection) of whiteflies to an initially poor host plant can occur within a few generations. Detailed information on rates of adaptation is important, both for judging the durability of host-plant resistance, and for predicting the risks of importing certain whitefly biotypes.

Can we Explain the Development of Distribution Patterns and Population Dynamics Based on Host-plant Preference and Host-plant Suitability?

At present, we can partly explain the development of distribution patterns for *T. vaporariorum*, but less so for *B. tabaci*. Insight into host-plant selection behaviour on plants of different suitability helps to explain the development of distribution patterns. Adult emergence and movement patterns for *T. vaporariorum* show that, after a few days, the horizontal and vertical distribution patterns become stable and that whitefly distribution is highly aggregated. *T. vaporariorum* dispersal has been studied in greenhouses only, where dispersal capacity is clearly limited. However, *B. tabaci* can be transported over very large distances (kilometres).

There is evidence for a dispersal phase in *T. vaporariorum*, and there are indications for one in *B. tabaci*. Does a dispersal phase exist in all whiteflies? If a dispersal phase exists which is limited to the first days of adult life, then the development of distribution patterns can be predicted, particularly in combination with knowledge about the main factors causing dispersal. Information on development of distribution patterns is necessary for insight into the epidemiology of viruses transmitted by whiteflies, for the development of methods for introduction of natural enemies into a crop, and for a final evaluation of the feasibility of sampling.

Population dynamical information for whiteflies is limited. Growth is exponential as long as the physiological condition of the host plant remains good and temperature conditions are favourable. Population growth rate can be estimated for *T. vaporariorum* on a number of host plants, and for *B. tabaci* on cotton by simulation models based on autecological information. Additional autecological data are essential to obtain a better picture of population dynamics.

What factors determine population fluctuations in whiteflies? This is a general question which requires long-term studies. Research in this field has, however, already taught us that the results of biological control are largely determined by the rate of population development of whiteflies on a certain host-plant species and cultivar. The important role of natural enemies in reduction of population numbers of *T. vaporariorum* has been well established and is illustrated by successful biological control programmes (van Lenteren and Woets, 1988). For *B. tabaci*, the role of natural enemies is more difficult to interpret, but is presently under intensive study (see also Chapter 7).

In this chapter, different factors influencing whitefly population dynamics have been treated separately for the sake of simplicity, but this can be misleading. For the development of new control strategies, direct and indirect relationships between host plant, whitefly and natural enemies should be studied. In studies of such tritrophic systems, one rapidly becomes aware of potential interference between demands for host-plant resistance and biological control. On the other hand, one may discover possibilities for harmonious integration of these two control methods. We envision a great future for studies of tritrophic systems in whiteflies.

Summary

Understanding host-plant selection and population dynamics by whiteflies requires basic behavioural and ecological information. Such information is presently available for a few species. When searching for feeding and oviposition sites in flight, whiteflies react only to a limited range of colours. In polyphagous species no long-distance responses to any other plant characteristics have been found. Attraction to ultraviolet light has been recorded in several species and is supposed to indicate a dispersal phase. Attracted by yellow-green, whiteflies alight on potential host plants, but actual selection of a host plant, or part of a plant, occurs after landing. Whiteflies scan the cuticle with their stylets, or make short probes in the leaf tissue just below the epidermis. Contact with phloem vessels – the primary feeding source – is not necessary for the selection of a suitable host plant or feeding site within a plant. The host-plant preference pattern of *Trialeurodes vaporariorum* correlates well with host-plant suitability. Whitefly population growth is much faster on plants preferred for feeding and oviposition, than on unpreferred plants. However, host-plant preference may evolve rapidly. There is evidence for both *T. vaporariorum* and *Bemisia tabaci* that local populations may adapt to host plants – on which they initially develop poorly – within 3–5 generations.

We are beginning to understand how spatial distribution patterns of whiteflies arise. Movement of *T. vaporariorum* occurs mainly during the first few days after emergence and, within zones of infestation, distances covered are limited to a few metres. The resulting distributions are highly aggregated. In *B. tabaci* the situation is more complicated, partly since, in contrast to *T. vaporariorum* in greenhouses, *B. tabaci* can be transported over large distances. There is evidence for a dispersal phase in the early adult life of *T. vaporariorum*. Data suggest that such a phase also exists in *B. tabaci*.

Information on population dynamics of whiteflies is limited. Population growth is exponential as long as host plants remain in good physiological condition and temperatures are favourable. Population growth rate of *T. vaporariorum* can now be estimated on a number of host plants by means of simulation models based on autecological data. The same applies to *B. tabaci* on cotton. Data on host-plant suitability – in terms of whitefly population growth rate – are definitely needed to estimate the success of biological control and to evaluate host-plant resistance.

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References

- ABASSI, M. (1980). Recherche sur deux homoptères fixes des citrus, *Aonidiella aurantii* Mask. (Homoptera, Diaspididae) et *Aleurothrixus floccosus* Mask. (Homoptera, Aleyrodidae). *Cahiers des Recherches agronomiques* 35, 1-168.
- AFFELDT, H. A., THIMJAN, R. W., SMITH, F. F., and WEBB, R. E. (1983). Response of the greenhouse whitefly (Homoptera: Aleyrodidae) and the vegetable leafminer (Diptera: Agromyzidae) to photospectra. *Journal of Economic Entomology* 76, 1405-1409.
- AHMAD, M. and HARWOOD, R. F. (1973). Colour preference as a population indexing technique in the whitefly, *Bemisia tabaci* (Genn.) (Aleyrodidae: Homoptera). *Pakistan Journal of Agricultural Science* 10, 19-24.
- ARX, R. E. VON (1982). *Analysis of the subsystem cotton - Bemisia tabaci (Genn.) (Sternorrhyncha: Aleyrodidae) in the Sudan Gezira*. Ph.D. Thesis, Swiss Federal Institute of Technology, Zürich, 113 pp.
- ARX, R. E. VON, BAUMGÄRTNER, J. and DELUCCHI, V. (1983). A model to simulate the population dynamics of *Bemisia tabaci* Genn. (Stern., Aleyrodidae) on cotton in the Sudan Gezira. *Zeitschrift für Angewandte Entomologie* 96, 341-363.
- ARX, R. E. VON, BAUMGÄRTNER, J. and DELUCCHI, V. (1984). Sampling of *Bemisia tabaci* (Genn.) (Sternorrhyncha: Aleyrodidae) in Sudanese cotton fields. *Journal of Economic Entomology* 77, 1130-1136.
- AVIDOV, Z. (1956). Bionomics of the tobacco whitefly (*Bemisia tabaci* Gennad.) in Israel. *Ktavim* 7, 25-41.
- AVIDOV, Z. and HARPAZ, I. (1969). *Plant pests of Israel*. Israel University Press, Jerusalem, 549 pp.
- AZAB, A. K., MEGAHED, M. M. and EL-MIRSAWI, D. H. (1971). On the biology of *Bemisia tabaci* (Genn.). *Bulletin de la Société entomologique d'Égypte* 55, 305-315.
- BELLOWS, T. S., PERRING, T. M., ARAKAWA, K. and FARRAR, C. A. (1988). Patterns in diel flight activity of *Bemisia tabaci* (Homoptera: Aleyrodidae) in cropping systems in southern California. *Environmental Entomology* 17, 225-228.
- BERLINGER, M. J. (1980). A yellow sticky trap for whiteflies: *Trialeurodes vaporariorum* and *Bemisia tabaci* (Aleyrodidae). *Entomologia experimentalis et applicata* 27, 98-102.
- BERLINGER, M. J. (1986). Host plant resistance to *Bemisia tabaci*. *Agriculture, Ecosystems and Environment* 17, 69-82.
- BERLINGER, M. J., MAGAL, Z. and BENZONI, A. (1983). The importance of pH in food selection by the tobacco whitefly, *Bemisia tabaci*. *Phytoparasitica* 11, 151-160.
- BOXTEL, W. VAN (1980). *Determination of host-plant quality of eggplant, cucumber, tomato and sweet pepper for Trialeurodes vaporariorum* (in Dutch). M.Sc. Thesis, University of Leiden, 146 pp.
- BOXTEL, W. VAN, WOETS, J. and LENTEREN, J. C. VAN (1978). Determination of host-plant quality of eggplant (*Solanum melongena* L.), cucumber (*Cucumis sativus* L.), tomato (*Lycopersicon esculentum* L.) and paprika (*Capsicum annum* L.) for the greenhouse whitefly (*Trialeurodes vaporariorum* (Westwood)) (Homoptera: Aleyrodidae). *Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* 43, 397-408.
- BRUGGEN, A. H. C. VAN (1975). *Influence of the host plant on developmental time and mortality of the greenhouse whitefly, Trialeurodes vaporariorum (Westwood), and its parasite Encarsia formosa Gahan* (in Dutch). M.Sc. Thesis, University of

Leiden, 80 pp.

- BUTLER, C. G. (1938). On the ecology of *Aleyrodes brassicae* Walk. (Homoptera). *Transactions of the Royal Entomological Society, London* 87, 291–311.
- BUTLER, G. D. and WILSON, F. D. (1984). Activity of adult whiteflies (Homoptera: Aleyrodidae) within plantings of different cotton strains and cultivars as determined by sticky-trap catches. *Journal of Economic Entomology* 77, 1137–1140.
- BUTLER, G. D., HENNEBERRY, T. J. and CLAYTON, T. E. (1983). *Bemisia tabaci* (Homoptera: Aleyrodidae): development, oviposition, and longevity in relation to temperature. *Annals of the Entomological Society of America* 76, 310–313.
- BUTLER, G. D., HENNEBERRY, T. J. and HUTCHISON, W. D. (1986). Biology, sampling and population dynamics of *Bemisia tabaci*. *Agricultural Zoology Reviews* 1, 167–195.
- BUTLER, G. D., RIMON, D. and HENNEBERRY, T. J. (1988). *Bemisia tabaci* (Homoptera: Aleyrodidae): populations on different cotton varieties and cotton stickiness in Israel. *Crop Protection* 7, 43–47.
- CASWELL, H. and HASTINGS, A. (1980). Fecundity, developmental time and population growth rate: an analytical solution. *Theoretical Population Biology* 17, 71–79.
- COOMBE, P. E. (1982). Visual behaviour of the greenhouse whitefly, *Trialeurodes vaporariorum*. *Physiological Entomology* 7, 243–251.
- COSTA, A. S. (1975). Increase in the population density of *Bemisia tabaci*, a threat of wide-spread virus infection of legume crops in Brazil. In *Tropical diseases of legumes* (J. Bied and K. Maramorosch, Eds.), pp. 27–49. Academic Press, New York.
- COUDRIET, D. L., PRABHAKER, N., KISHABA, A. N. and MEYERDIRK, D. E. (1985). Variation in developmental rate on different hosts and overwintering of the sweet-potato whitefly, *Bemisia tabaci* (Homoptera: Aleyrodidae). *Environmental Entomology* 14, 516–519.
- CURRY, J. P. and PIMENTEL, D. (1971). Life cycle of the greenhouse whitefly, *Trialeurodes vaporariorum*, and population trends of the whitefly and its parasite, *Encarsia formosa*, on two tomato varieties. *Annals of the Entomological Society of America* 64, 1188–1190.
- DORSMAN, R. and VRIE, M. VAN DE (1987). Population dynamics of the greenhouse whitefly *Trialeurodes vaporariorum* on different gerbera varieties. *IOB/WPRS Bulletin* 10 (2), 46–51.
- DOWELL, R. V. (1979). Host selection by the citrus blackfly *Aleurocanthus woglumi* (Homoptera: Aleyrodidae). *Entomologia experimentalis et applicata* 25, 289–296.
- DUFFEY, S. S. (1986). Plant glandular trichomes: their partial role in defence against insects. In *Insects and the plant surface* (B. E. Juniper and T. R. E. Southwood, Eds.), pp. 173–183. Edward Arnold, London.
- EGGENKAMP – ROTTEVEEL MANSVELD, M. H., ELLENBROEK, F. J. M., LENTEREN, J. C. VAN and WOETS, J. (1978). The parasite-host relationship between *Encarsia formosa* Gahan (Hym., Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Hom., Aleyrodidae). VIII. Comparison and evaluation of an absolute count and a stratified random sampling programme. *Zeitschrift für Angewandte Entomologie* 85, 133–140.
- EGGENKAMP – ROTTEVEEL MANSVELD, M. H., ELLENBROEK, F. J. M. and LENTEREN, J. C. VAN (1980). The greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) and its parasite *Encarsia formosa* Gahan: population dynamics and sampling problems. *Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* 45, 545–553.

- EGGENKAMP - ROTTEVEEL MANSVELD, M. H., LENTEREN, J. C. VAN, ELLENBROEK, J. M. and WOETS, J. (1982). The parasite-host relationship between *Encarsia formosa* Gahan (Hym., Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Hom., Aleyrodidae). XII. Population dynamics of parasite and host in a large, commercial glasshouse and test of the parasite-introduction method used in the Netherlands. *Zeitschrift für Angewandte Entomologie* 93, 113-130 (first part), 258-279 (second part).
- EKBOM, B. S. (1980). Some aspects of the population dynamics of *Trialeurodes vaporariorum* and *Encarsia formosa* and their importance for biological control. *IOBC/WPRS Bulletin* 3 (3), 25-34.
- EL-HELALY, M. S., RAWASHI, I. A. and IBRAHIM, E. G. (1981a). Phototaxis of the adult whitefly, *Bemisia tabaci* (Gennadius) to the visible light. I. Effect of the exposure period on the insect's response to different wavelengths of the visible light-spectrum using a devised simple technique. *Acta Phytopathologica Academiae Scientiarum Hungaricae* 16, 181-188.
- EL-HELALY, M. S., RAWASHI, I. A. and IBRAHIM, E. G. (1981b). Phototaxis of the adult whitefly, *Bemisia tabaci* (Gennadius) to the visible light. II. Effects of both light intensity and sex of the whitefly adults on the insect's response to different wavelengths of light spectrum. *Acta Phytopathologica Academiae Scientiarum Hungaricae* 16, 389-398.
- EVANS, D. E. (1965). Jassid populations on three hairy varieties of Sakel cotton. *Empire Cotton Growing Review* 42, 211-217.
- EVELENS, K. G. (1983). Cotton-insect control in the Sudan Gezira: analysis of a crisis. *Crop Protection* 2, 273-287.
- GAMEEL, O. I. (1974). Some aspects of the mating and oviposition behaviour of the cotton whitefly *Bemisia tabaci* (Genn.). *Revue de Zoologie et Botanique Africaine* 88, 784-788.
- GAMEEL, O. I. (1977). *Bemisia tabaci*. In *Diseases, pests and weeds in tropical crops* (J. Kranz, H. Schmutterer and W. Koch, Eds.), pp. 320-322. Paul Parey, Berlin.
- GAMEEL, O. I. (1978). The cotton whitefly *Bemisia tabaci* (Genn.) in the Sudan Gezira. *Third Ciba-Geigy seminar on the strategy for cotton pest control in the Sudan (Basel, 8-10 May 1978)*, 111-131.
- GENTILE, A. G., WEBB, R. E. and STONER, A. K. (1968). Resistance in *Lycopersicon* and *Solanum* to greenhouse whiteflies. *Journal of Economic Entomology* 61, 1355-1357.
- GERLING, D., HOROWITZ, A. R. and BAUMGÄRTNER, J. (1986). Autecology of *Bemisia tabaci*. *Agriculture, Ecosystems and Environment* 17, 5-19.
- GERLING, D. and HOROWITZ, A. R. (1984). Yellow traps for evaluating the population levels and dispersal patterns of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). *Annals of the Entomological Society of America* 77, 753-759.
- GERLING, D. and OHNESORGE, B. (Eds.) (1986). *Bemisia tabaci* - ecology and control. *Agriculture, Ecosystems and Environment* 17, 1-152.
- GLICK, P. A. and NOBLE, L. W. (1961). Airborne movement of the pink bollworm and other arthropods. *USDA Bulletin* 1255, 1-20.
- HARGREAVES, E. (1915). The life-history and habits of the greenhouse whitefly (*Aleyrodes vaporariorum* Westd.). *Annals of Applied Biology* 1, 303-334.
- HASSELL, M. P. and SOUTHWOOD, T. R. E. (1978). Foraging strategies of insects. *Annual Review of Ecology and Systematics* 9, 75-98.
- HOROWITZ, A. R. (1986). Population dynamics of *Bemisia tabaci* (Gennadius):

- with special emphasis on cotton fields. *Agriculture, Ecosystems and Environment* 17, 37-47.
- HOROWITZ, A. R., PODOLER, H. and GERLING, D. (1984). Life table analysis of the tobacco whitefly *Bemisia tabaci* (Gennadius) in cotton fields in Israel. *Acta Oecologica/Oecologia Applicata* 5, 221-233.
- HULSPAS-JORDAAN, P. M. and LENTEREN, J. C. VAN (1978). The relationship between host-plant leaf structure and parasitization efficiency of the parasitic wasp *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae). *Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* 43, 431-440.
- HULSPAS-JORDAAN, P. M. and LENTEREN, J. C. VAN (1989). The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). XXX. Modelling population growth of greenhouse whitefly on tomato. *Agricultural University Wageningen Papers*, 89, 1-54.
- HUSAIN, M. A. and TREHAN, K. N. (1933). Observations on the life-history, bionomics and control of the whitefly on cotton (*Bemisia gossypiperda* M. & L.). *Indian Journal of Agricultural Science* 3, 701-753.
- HUSAIN, M. A. and TREHAN, K. N. (1940). Final report on the scheme of investigations on the whitefly on cotton in the Punjab. *Indian Journal of Agricultural Science* 10, 101-109.
- HUSAIN, M. A., PURI, A. N. and TREHAN, K. N. (1936). Cell sap acidity and the incidence of whitefly (*Bemisia gossypiperda*) on cottons. *Current Science* 4, 486-487.
- HUSSEY, N. W. and SCOPES, N. (1985). *Biological control: the glasshouse experience*. Blandford Press, Poole, Dorset, 240 pp.
- JANSSEN, J. A. M., TJALLINGII, W. F. and LENTEREN, J. C. VAN (1989). Electrical recording and ultrastructure of stylet penetration by the greenhouse whitefly. *Entomologia experimentalis et applicata*, in press.
- JOYCE, R. J. V. (1958). Effect of the cotton plant in the Sudan Gezira on certain leaf-feeding insect pests. *Nature* 182, 1463-1464.
- JOYCE, R. J. V. (1983). Aerial transport of pests and pest outbreaks. *EPPO Bulletin* 13, 111-119.
- KAMP, R. J. VAN DER and LENTEREN, J. C. VAN (1981). The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). XI. Do mechanical barriers of the host plant prevent successful penetration of the phloem by whitefly larvae and adults? *Zeitschrift für Angewandte Entomologie* 92, 149-159.
- KHALIFA, A. and EL-KHIDIR, E. (1964). Biological study on *Trialeurodes lubia* and *Bemisia tabaci*. *Bulletin de la Société Entomologique d'Égypte* 48, 115-129.
- LASKA, P., BETLACH, J. and HAVRANKOVA, M. (1986). Variable resistance in sweet pepper, *Capsicum annuum*, to glasshouse whitefly, *Trialeurodes vaporariorum* (Homoptera, Aleyrodidae). *Acta entomologica bohemoslovaca* 83, 347-353.
- LENTEREN, J. C. VAN and WOETS, J. (1977). Development and establishment of biological control of some glasshouse pests in the Netherlands. In *Pest management in protected culture crops* (F. F. Smith and R. E. Webb, Eds.), pp. 81-87. USDA, ARS-NE-85, Washington.
- LENTEREN, J. C. VAN and HULSPAS-JORDAAN, P. M. (1983). Biological control of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) at low greenhouse temperatures: a summary. *Proceedings International Conference on Integrated Plant Protection Budapest (3-7 July 1983)* 3, 1-7.
- LENTEREN, J. C. VAN and WOETS, J. (1988). Biological and integrated control in greenhouses. *Annual Review of Entomology* 33, 239-269.

- LEWONTIN, R. C. (1965). Selection for colonizing ability. In *The genetics of colonizing species* (H. G. Baker and G. L. Stebbins, Eds.), pp. 77-94. Academic Press, New York.
- LI, Z. H., LAMMES, F., LENTEREN, J. C. VAN, HUISMAN, P. W. T., VIANEN, A. VAN, and PONTI, O. M. B. DE (1987). The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera, Aleyrodidae). XXV. Influence of leaf structure on the searching activity of *Encarsia formosa*. *Journal of Applied Entomology* **104**, 297-304.
- LLOYD, L. (1921). Notes on a colour tropism of *Asterochiton* (*Aleurodes*) *vaporariorum*, Westwood. *Bulletin of entomological Research* **12**, 355-359.
- LLOYD, L. (1922). The control of the greenhouse whitefly (*Asterochiton vaporariorum*) with notes on its biology. *Annals of applied Biology* **9**, 1-32.
- MACDOWALL, F. D. H. (1972). Phototactic action spectrum for whitefly and the question of colour vision. *Canadian Entomologist* **104**, 299-307.
- MERENDONK, S. VAN DE and LENTEREN, J. C. VAN (1978). Determination of mortality of greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) eggs, larvae and pupae on four host-plant species: eggplant (*Solanum melongena* L.), cucumber (*Cucumis sativus* L.), tomato (*Lycopersicon esculentum* L.) and paprika (*Capsicum annum* L.). *Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* **43**, 421-429.
- MOERICKE, V. (1955). Neue Untersuchungen über das Farbsehen der Homopteren. *Proceedings Conference on Potato Virus Diseases, 2nd meeting (Lisse-Wageningen, 1954)*, 55-69.
- MOERICKE, V., SCHNEIDERS, H. and VOGT, B. (1966). Flughemmung und Fallreflexhaltung als Reaktion auf Gelbreiz bei *Trialeurodes vaporariorum* (Westwood). *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz* **73**, 6-14.
- MOUND, L. A. (1962). Studies on the olfaction and colour sensitivity of *Bemisia tabaci* (Genn.) (Homoptera, Aleyrodidae). *Entomologia experimentalis et applicata* **5**, 99-104.
- MOUND, L. A. (1965). Effect of leaf hair on cotton whitefly populations in the Sudan Gezira. *Empire Cotton Growing Review* **42**, 33-40.
- MOUND, L. A. and HALSEY, S. H. (1978). *Whitefly of the world. A systematic catalogue of the Aleyrodidae (Homoptera) with host plant and natural enemy data*. British museum (Natural History), 340 pp.
- MUSUNA, A. C. Z. (1986). A method for monitoring whitefly, *Bemisia tabaci* (Genn.), in cotton in Zimbabwe. *Agriculture, Ecosystems and Environment* **17**, 29-36.
- NOLDUS, L. P. J. J. and LENTEREN, J. C. VAN (1989). Host aggregation and parasitoid behaviour: biological control in a closed system. In *Critical Issues in Biological Control* (M. Mackauer, L. E. Ehler and J. Roland, Eds.). Intercept, Andover.
- NOLDUS, L. P. J. J., XU, R. M. and LENTEREN, J. C. VAN (1985). The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). XVII. Within-plant movement of adult greenhouse whiteflies. *Zeitschrift für angewandte Entomologie* **100**, 494-503.
- NOLDUS, L. P. J. J., XU, R. M. and LENTEREN, J. C. VAN (1986a). The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). XVIII. Between-plant movement of adult greenhouse whiteflies. *Zeitschrift für Angewandte Entomologie* **101**, 159-176.

- NOLDUS, L. P. J. J., XU, R. M. and LENTEREN, J. C. VAN (1986b). The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). XIX. Feeding-site selection by the greenhouse whitefly. *Journal of Applied Entomology* **101**, 492-507.
- NOLDUS, L. P. J. J., XU, R. M., EGGINKAMP-ROTTEVEEL MANSVELD, M. H. and LENTEREN, J. C. VAN (1986). The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). XX. Analysis of the spatial distribution of greenhouse whiteflies in a large glasshouse. *Journal of Applied Entomology* **102**, 484-498.
- OHNESORGE, B. (1986). *Bemisia tabaci* - ecology and control: Introduction. *Agriculture, Ecosystems and Environment* **17**, 1-3.
- OHNESORGE, B. and RAPP, G. (1986). Monitoring *Bemisia tabaci*: a review. *Agriculture, Ecosystems and Environment* **17**, 21-27.
- OHNESORGE, B., SHARAF, N. and ALLAWI, T. (1980). Population studies on the tobacco whitefly *Bemisia tabaci* Genn. (Homoptera: Aleyrodidae) during the winter season. I. Spatial distribution on some host plants. *Zeitschrift für Angewandte Entomologie* **90**, 226-232.
- OMRAN, H. H. and EL-KHIDIR, E. (1978). Über die Bevorzugung von Blatthaaren zur Eiablage bei *Bemisia tabaci* (Genn.) (Hom., Aleyrodidae). *Anzeiger für Schadlingskunde, Pflanzenschutz und Umweltschutz* **51**, 175.
- ONILLON, J. C., ONILLON, J., BRUN, P., FRANCO, E. and DECOUX, G. (1986). Effect of fertilizer on the population level of the citrus whitefly *Dialeurodes citri* (Homoptera, Aleyrodidae). *Proceedings of the Experts' Meeting Integrated Pest Control in Citrus Groves (Acireale, 26-29 March 1985)*, 109-120. Balkema, Rotterdam.
- OZGUR, A. F. and SEKEROGU, E. (1986). Population development of *Bemisia tabaci* (Homoptera: Aleyrodidae) on various cotton cultivars in Cukurova, Turkey. *Agriculture, Ecosystems, and Environment* **17**, 83-88.
- PAPAJ, D. R. and PROKOPY, R. J. (1989). Ecological and evolutionary aspects of learning in phytophagous insects. *Annual Review of Entomology* **34**, 315-350.
- POLLARD, D. G. (1955). Feeding habits of the cotton whitefly, *Bemisia tabaci* Genn. (Homoptera, Aleyrodidae). *Annals of Applied Biology* **43**, 664-671.
- POLLARD, D. G. and SAUNDERS, J. H. (1956). Relations of some cotton pests to jassid resistant sakel. *Empire Cotton Growing Review* **33**, 197-202.
- PONTI, O. M. B. DE (1984). Recent developments of resistance to glasshouse whitefly in tomato and to twospotted spider mite in cucumber. *IOBC/WPRS Bulletin* **7** (4), 43-44.
- PROKOPY, R. J. and OWENS, E. D. (1983). Visual detection of plants by herbivorous insects. *Annual Review of Entomology* **28**, 337-364.
- SAS, J. VAN, WOETS, J. and LENTEREN, J. C. VAN (1978). Determination of host-plant quality of gherkin (*Cucumis sativus* L.), melon (*Cucumis melo* L.) and gerbera (*Gerbera jamesonii* Hook) for the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). *Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* **43**, 409-420.
- SHARAF, N. S. (1982). Determination of the proper height, direction, position and distance of a yellow sticky trap for monitoring adult sweetpotato whitefly populations (*Bemisia tabaci* Genn., Homoptera: Aleyrodidae). *Dirasat* **9**, 169-182.
- SINGER, M. C. (1986). The definition and measurement of oviposition preference in plant-feeding insects. In *Insect-plant relations* (J. Miller and T. A. Miller, Eds.), pp. 65-94. Springer, New York.

- SNELL, T. W. (1978). Fecundity, developmental time, and population growth rate. *Oecologia* 32, 119-125.
- SOUTHWOOD, T. R. E. (1962). Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* 37, 171-214.
- STÄDLER, E. (1986). Oviposition and feeding stimuli in leaf surface waxes. In *Insects and the plant surface* (B. E. Juniper and T. R. E. Southwood, Eds.), pp. 105-121. Edward Arnold, London.
- TAYLOR, L. R., WOJWOD, I. P. and PERRY, J. N. (1978). The density-dependence of spatial behaviour and the rarity of randomness. *Journal of Animal Ecology* 47, 383-406.
- THOMPSON, J. N. (1988). Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia experimentalis et applicata* 47, 3-14.
- TJALLINGII, W. F. (1988). Electrical recording of stylet penetration activities. In *Aphids, their biology, natural enemies and control* (A. K. Minks and P. Harrewijn, Eds.), pp. 95-108. Elsevier, Amsterdam.
- TREHAN, K. N. (1941). Effect of coloured screens on oviposition and development of some British whiteflies. *Indian Journal of Entomology* 3, 121-138.
- TREHAN, K. N. (1944). Further notes on the bionomics of *Bemisia gossypiperda* M. & L., the whitefly of cotton in the Punjab. *Indian Journal of Agricultural Science* 14, 53-63.
- VAISHAMPAYAN, S. M., WALDBAUER, G. P. and KOGAN, M. (1975). Visual and olfactory responses in orientation to plants by the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). *Entomologia experimentalis et applicata* 18, 412-422.
- VAISHAMPAYAN, S. M., KOGAN, M., WALDBAUER, G. P. and WOOLLEY, J. T. (1975). Spectral specific responses in the visual behaviour of the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). *Entomologia experimentalis et applicata* 18, 344-356.
- VARMA, P. M. (1963). Transmission of plant viruses by whiteflies. *Bulletin of the National Institute of Sciences of India* 24, 11-33.
- VERSCHOOR - VAN DER POEL, P. J. G. (1978). *Host-plant selection by the greenhouse whitefly, Trialeurodes vaporariorum* (Westwood) (in Dutch). M.Sc. Thesis, University of Leiden, 39 pp.
- VERSCHOOR - VAN DER POEL, P. J. G. and LENTEREN, J. C. VAN (1978). Host-plant selection by the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). *Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* 43, 387-396.
- VET, L. E. M., LENTEREN, J. C. VAN and WOETS, J. (1980). The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). IX. A review of the biological control of the greenhouse whitefly with suggestions for future research. *Zeitschrift für Angewandte Entomologie* 90, 26-51.
- VIANEN, A. VAN, XU, R. M. and LENTEREN, J. C. VAN (1988a). The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). XXVII. Feeding-site selection by the greenhouse whitefly on different host-plant species. *Journal of Applied Entomology* 105, 149-153.
- VIANEN, A. VAN, XU, R. M. and LENTEREN, J. C. VAN (1988b). The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). XXVIII. The influence of

- whitefly densities and temperature on the horizontal dispersal of whiteflies. *Journal of Applied Entomology* **105**, 436-449.
- VISSER, J. H. (1986). Host odor perception in phytophagous insects. *Annual Review of Entomology* **31**, 121-144.
- VISSER, J. H. (1988). Host-plant finding by insects: orientation, sensory input and search patterns. *Journal of Insect Physiology* **34**, 259-268.
- WALKER, G. P. (1985). Stylet penetration by the bayberry whitefly, as affected by leaf age in lemon, *Citrus lemon*. *Entomologia experimentalis et applicata* **39**, 115-121.
- WALKER, G. P. (1987). Probing and oviposition behaviour of the bayberry whitefly (Homoptera: Aleyrodidae) on young and mature lemon leaves. *Annals of the Entomological Society of America* **80**, 524-529.
- WALKER, G. P. (1988). The role of leaf cuticle in leaf age preference by bayberry whitefly (Homoptera: Aleyrodidae) on lemon. *Annals of the Entomological Society of America* **81**, 365-369.
- WALKER, G. P. and AITKEN, D. C. G. (1985). Oviposition and survival of bayberry whitefly, *Parabemisia myricae* (Homoptera: Aleyrodidae) on lemons as a function of leaf age. *Environmental Entomology* **14**, 254-257.
- WALKER, G. P. and GORDH, G. (1989). The occurrence of apical labial sensilla in the Aleyrodidae and evidence for a contact chemosensory function. *Entomologia experimentalis et applicata*, **51**, 215-222.
- WALKER, G. P. and ZAREH, N. (1989). Leaf age preference for oviposition by three species of whitefly (Homoptera: Aleyrodida) on *Citrus limon*. Submitted.
- WEBER, H. (1931). Lebensweise und Umweltbeziehungen von *Trialeurodes vaporariorum* (Westwood) (Homoptera - Aleurodina). Erster Beitrag zu einer Monographie dieser Art. *Zeitschrift für Morphologie und Ökologie der Tiere* **23**, 575-753.
- WILLMER, P. (1986). Microclimatic effects on insects at the plant surface. In *Insects and the plant surface* (B. E. Juniper and T. R. E. Southwood, Eds.), pp. 65-80. Edward Arnold, London.
- WOETS, J. and LENTEREN, J. C. VAN (1976). The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). VI. The influence of the host plant on the greenhouse whitefly and its parasite *Encarsia formosa*. *IOBC/WPRS Bulletin* **1976** (4), 151-154.
- XU, R. M. (1985). Dynamics of within-leaf spatial distribution patterns of greenhouse whiteflies and its biological interpretations. *Journal of Applied Ecology* **22**, 63-72.
- XU, R. M., ZHU, Q. R. and ZHANG, Z. L. (1984). Systems approach to greenhouse whitefly population dynamics and strategy for greenhouse whitefly control. *Zeitschrift für Angewandte Entomologie* **97**, 305-313.
- XU, R. M., LI, Z. H., LI, T. Y. and LIU, L. F. (1980). Spatial patterns of adults of greenhouse whiteflies *Trialeurodes vaporariorum* Westw. in greenhouses. *Acta entomologica sinica* **23**, 265-275.
- XU, R. M., LI, Z. H., LI, T. Y. and LIU, L. F. (1981). Research on sampling techniques of adults of greenhouse whiteflies (*Trialeurodes vaporariorum* Westw.). *Journal of Beijing Normal University* **1981** (4), 95-102.
- YAMADA, H., KOSHIHARA, T. and TANAKA, K. (1979). Population growth of the greenhouse whitefly *Trialeurodes vaporariorum* on greenhouse cucumber. *Bulletin of the Vegetable and Ornamental Crops Research Station* **A5**, 191-199.
- YANO, E. (1983). Spatial distribution of greenhouse whitefly (*Trialeurodes vaporariorum* Westwood) and a suggested sampling plan for estimating its density in greenhouses. *Researches in Population Ecology* **25**, 309-320.
- YANO, E., LENTEREN, J. C. VAN, RABBINGE, R. and HULSPAS-JORDAAN, P. M. (1989a).

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- YANO, E., LENTEREN, J. C. VAN, RABBINGE, R. VIANEN, A. VAN and DORSMAN, R. (1989b). The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). XXXII. Simulation studies of population growth of greenhouse whitefly on eggplant, cucumber, sweet pepper and gerbera. *Agricultural University Wageningen Papers*, 89, 75-100.