

The Citrus Psylla, *Trioza erytreae* (Del Guercio) (Hemiptera: Triozidae): A Review

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ABSTRACT

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The literature on the citrus psylla, *Trioza erytreae*, published since 1897, is reviewed. The citrus psylla is an important vector of the greening disease of citrus. The stages of development and life history are discussed. Of the factors that influence population size, flushing of the host plants and high saturation deficits are the most important. Methods of population monitoring and control are summarised. The main means of reducing vector numbers and therefore the spread of greening disease, are resistance of citrus trees to greening disease, restricting citrus growing to hot, low-lying regions of the country, and strict vector control in nurseries. Requirements for further research, are discussed.

INTRODUCTION

The presence of the citrus psylla, *Trioza erytreae* (Del Guercio) was first reported in Southern Africa in 1897 (Lounsbury, 1897). Initially this insect was considered as a minor pest of citrus nursery trees and occasionally also of new flush in citrus orchards (Van der Merwe, 1923).

Leaves infested by the insect are distorted and often characterized by local chlorosis where the nymphs develop. Once the nymphs have attained maturity the leaves assume their normal colour but not their natural shape (Van der Merwe, 1923; Catling, 1973). A less frequent effect of infestations is that small flush points may sometimes be so densely packed with eggs, that they may shrivel and fall off (Catling, 1972b). The status of the citrus psylla was raised to that of a major citrus pest when McClean and Oberholzer (1965b) reported that the adult of *T. erytreae* is a vector of the greening disease of citrus in South Africa.

It has been known since 1929 that greening disease affects sweet oranges in

parts of South Africa (Oberholzer et al., 1963). Severely diseased trees are badly stunted, usually rather sparsely foliated and are at times inclined to heavy leaf drop (Oberholzer et al., 1963). Eventually severe tree decline takes place (McClellan and Oberholzer, 1965a). Diseased trees produce poor crops of predominantly greened, worthless fruit which fail to ripen and cannot be used for processing as they impart an objectionable bitter-salty flavour (Oberholzer et al., 1963).

The importance of greening in South Africa has been emphasised by the fact that approximately 100 000 sweet orange trees have been rendered commercially unprofitable (Oberholzer et al., 1963) and fruit losses of between 30 and 100% have been recorded in individual orchards (Schwarz, 1967). Consequently, farmers from certain areas have been forced to curtail citrus production (Green and Schwarz, 1970; Moll et al., 1980).

Two strains of the greening disease can be distinguished. The more destructive one, which is heat tolerant, is referred to as the "Asian" or heat-tolerant strain. The other was named the "South African" or heat-sensitive greening strain (Bové et al., 1974). In India, China and South-east Asia the vector of the heat-tolerant strain is the oriental psylla, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) (Masson et al., 1976).

The importance of *T. erythrae* has led researchers to study many aspects of the biology of this pest. Apart from a bibliography of the more than 200 published works (Van den Berg and Fletcher, 1988) two short review articles have been published (Van den Berg and Nel, 1981; Aubert, 1987). However, because so much information has been published subsequently, or has not been included in these articles, it was deemed necessary that a more complete review be undertaken.

SYSTEMATIC POSITION AND SYNONYMS

Trioza erythrae is placed in the family Triozidae within the superfamily Psylloidea of the order Hemiptera (Capener, 1970; Hollis, 1984).

In the following list of synonyms the most obvious mis-spelled species and author names are omitted. The synonyms regarded of importance are: citrus psylla (*Trioza*), (Lounsbury, 1897); psyllidengalle, (Rübsaamen, 1899); *Aleurodes erythrae* Del Guercio, (Del Guercio, 1918); *Trioza citri* Laing, (Waterston, 1922); *Trioza merwei* Pettey, (Pettey, 1923); *Spanioza merwei* (Pettey), (Enderlein, 1926); *Spanioza erythrae* (Del Guercio), (Boselli, 1930); *Spanioza erythrae* del G., (Van der Merwe, 1941); *Trioza erythrae* del Guercio, (Schwarz, 1968).

DISTRIBUTION

The citrus psylla was first described from the Eritrea region of Ethiopia by Del Guercio (1918). It was reported on citrus from the Eastern Cape and Stel-

lenbosch, South Africa during 1897 (Lounsbury, 1897). It has also been reported to occur in Kenya (Waterston, 1922), Zimbabwe and Uganda (Van der Merwe, 1923) and, according to Harris (1936) it occurs from Ethiopia down the entire length of the east coast of Africa to the Cape. It is also present on the Islands of St Helena, Mauritius, Madagascar (CIE, 1967) and Réunion (Moreira, 1967). Recently it has also been reported from North Yemen (Bové and Garnier, 1984), Saudi Arabia and the Yemen Arab Republic (Bové, 1986), Cameroun, Gabon and Rwanda-Burundi (Aubert et al., 1986).

STAGES OF DEVELOPMENT

Illustrations of the immature stages and/or the adult citrus psylla have been published by many workers. The most detailed are those of Moran and Blowers (1967) and Catling and Annecke (1968).

The egg is oval, smooth and pear-shaped. When freshly laid it is lemon yellow and corresponds to no. 4/2 in Wilson's colour chart (Moran and Blowers, 1967). Posteriorly, the egg has a short stalk which is inserted into the leaf tissue. As the embryo within it develops, the egg turns a dark yellow colour. Shortly before eclosion two red nymphal eye spots become visible towards the anterior end of the egg (Moran and Blowers, 1967). Van der Merwe (1923) and Annecke and Cilliers (1963) gave approximate measurements of 0.5 mm. Moran and Blowers (1967), gave the average length of the egg as 0.28 mm (0.22–0.31 mm) which is the same as the average length given by Catling (1967).

According to Blowers and Moran (1967) a feature of the egg is a spherical mass of short rod-like "symbiotic" organisms that form the mycetome. In adults, the symbionts are confined to specialized cells which form two large masses or mycetomes lying just anterior to the reproductive organs. Transmission of the micro-organisms takes place during the oogenesis by invasion of the egg at the posterior pole.

In its open gall, the nymph is very closely applied to the leaf surface and only the dorsal surface of the body and the waxy filaments are visible. There are five nymphal instars. They are all pale yellow in colour with red eye spots. The body is surrounded by a white waxy fringe of filaments, which are short at the beginning of each instar but which increase considerably in length during the intermoult period. The number of filaments increases with each moult. There are 50, 100, 200, 300 and 450 filaments, respectively, around the first to fifth instar nymphs. On moulting to the fourth instar, two pale brown spots appear on the abdomen. These darken in the fifth instar (Moran and Blowers, 1967).

The approximate lengths of the first to fifth instar nymphs as recorded by Van der Merwe (1923) have possibly been estimated and seem to be incorrect. The lengths given by Moran and Blowers (1967) are considered to be very accurate and are in close agreement with those given by Catling (1967). The

latter may be based on the length data of the former authors. However, this is not mentioned by Catling (1967). The lengths of the first to fifth instar are 0.345 mm (0.25–0.41), 0.50 mm (0.44–0.56), 0.72 mm (0.63–0.75), 1.025 mm (0.94–1.125) and 1.52 mm (1.38–1.66), respectively (Moran and Blowers, 1967).

At emergence the adult is pale green with black eyes. A progressive colouration to dark brown follows with maturation but the wings are always clear (Van der Merwe, 1923; Moran and Blowers, 1967; Begemann, 1984b). The sexes are easily distinguished by the shape of the abdomen which ends in a sharp point in females and bluntly in males. The external genitalia also differ in structure (Petty, 1923; Moran and Blowers, 1967). Body length information is provided by Petty (1923), Moran and Blowers (1967) and Catling (1967), the latter estimates may be derived from Moran and Blowers (1967). The lengths of adult males being 2.17 mm (1.88–2.50) and those of females 2.24 mm (1.88–2.50) (Moran and Blowers, 1967).

Begemann (1984b) lists eight characteristics which can be utilized to age-group citrus psylla. The process of sclerotization of the body is completed in about 5 days and at an age of about 10 days the malpighian tubes become visible through the dorsal abdomen.

LIFE HISTORY

Eggs may be found on the shoot tips of the youngest growth (Van der Merwe, 1923; Annecke and Cilliers, 1963; Moran and Blowers, 1967). They are sometimes laid on tender young thorns (Annecke and Cilliers, 1963) and occasionally on flower buds and on young lemon fruit (M.A. van den Berg, unpublished data, 1989).

Apart from serving to attach the egg to the leaf, the egg stalk may have a water-absorbing function (Blowers and Moran, 1967). This would explain the fact that eggs shrivel if the twig carrying egg-bearing leaves is cut off and allowed to dry (Van der Merwe, 1923). Depending on temperature, the eggs may take 5–17 days to hatch (see Table 1).

On eclosion the first instar nymph wanders about for a short time before settling down to insert its mouthparts and begin feeding (Moran and Blowers, 1967). The preferred site for settling is the youngest growth available. This includes soft stems. On young leaves the nymphs are usually restricted to the underside, and are only rarely found on the upper surface of the leaf (Van der Merwe, 1923). However, the latter may be colonized under crowded conditions (Annecke and Cilliers, 1963; Moran and Blowers, 1967). The reason for preferring the ventral leaf surface is unknown. Once the nymphs have settled they remain in the same place. They may move if they are disturbed or become overcrowded (Van der Merwe, 1923; Moran and Blowers, 1967).

There is often high mortality in the period between eclosion and settling of

TABLE 1
Incubation period, nymphal development and duration of the broods in days

Stage	Reference		Moran and Blowers (1967)	Catling (1973)				
	Van der Merwe (1923)	Annecke and Cilliers (1963)						
	Summer	Winter	Temperature plateau of 21°C, 4 h °C day ⁻¹ above and 38 h °C day ⁻¹ below 20°C	Temperature of 27°C, 24 h °C day ⁻¹ above and 33 h °C day ⁻¹ below 20°C	Mean 25°C	Mean 14°C		
Incubation period	5-7	?-11	8-10	11-17	8.06 (7-10)	6	15	
Nymphal instars								
First	3-5	3-7			7.56 (4-15)		6.83 (4-11)	
Second	2-3	3-5			4.37 (2-11)		3.91 (2-8)	
Third	2-4	5-6			4.07 (3-7)		4.21 (2-8)	
Fourth	3-5	5-9			4.39 (2-7)		3.80 (3-5)	
Fifth	4-7	6-23			7.32 (5-13)		6.32 (4-9)	
Total nymphal stage	17-?	?-45	22.6°C 18-20 Summer	17.7°C up to 34 Winter	27.41 (23-35)	23.47 (21-25)	17	43
Duration of brood		25-38	36.95 (31-48)	up to 47				Catling (1972b) June 33.8 Aug. 30.6 Sept. 30.3 Nov. 28.8 Dec. 27.8

the crawlers (M.A. van den Berg, unpublished data, 1989). Both citrus cultivar and the time of year seem to have important effects on this mortality. However, further research is required.

Feeding activity induces the formation of a pit-like depression beneath the body of the nymph. The depression later develops into an open gall (Van der Merwe, 1923; Annecke and Cilliers, 1963; Moran and Blowers, 1967).

Several authors have studied the effect of temperature on developmental rate. Nymphal development depends mainly on temperature (Table 1) and may take from 17 to 45 days. The first instar lasts the longest. The reason for this is unknown but it is probably associated with the time taken for the crawlers to settle and establish themselves. According to Catling (1973) the threshold temperature for nymphal development is between 10 and 12°C.

Nymphal development is prolonged on poorly nourished citrus leaves. In the field, young growth in poor condition also causes high rates of mortality and produces flattened nymphs of reduced size (Catling, 1971). The effect of fertilisation and irrigation of the host plant on the life span and fertility of the adults has not yet been studied.

Moran (1967) found that the final moult took place throughout the day and night with a peak of 81% that moulted during the period between 18.00 to 08.00 h. On the other hand, Catling (1973) stated that the final moult usually takes place during the early morning, beginning at first light. The adult's wings expand fully in about 2–3 h (Catling, 1967). This period seems very long as it has also been recorded to be about 20 min (M.A. van den Berg, unpublished data, 1989). More detailed studies to confirm these observations are necessary.

Field colonies consisted of 50–86% females but a few male-less colonies have been recorded (Catling, 1973). In culture, it was found that the proportion of males declined steadily until no males were produced at all and the colonies died out (Catling, 1973; Moll, 1974). As yet no explanation has been provided for this phenomenon and this merits further study. However, Begemann (1984c) has since succeeded in rearing a colony which maintained normal sex ratios.

BEHAVIOUR AND REPRODUCTIVE BIOLOGY

Almost immediately after the wings have expanded the adult usually commences feeding close to the nymphal gall (Catling, 1967). Moran (1968a) established that young leaves of lemon, *Citrus limon* (L.) Burm. f., were significantly more attractive as feeding sites for adults of the citrus psylla than four indigenous host plants.

Feeding habits that may have an effect on greening disease transmission warrant further research.

The excrement of the nymphs and adults is voided in the form of white granules. Under severely infested branches the latter are so numerous that

other parts of the tree appear to have been dusted (Van der Merwe, 1923). Detailed analysis has shown that starch, disaccharide sugars, ammonia and 15 amino acids are present in the excreta (Catling, 1971).

In an insectary, mating may take place as soon as the teneral adult hardens i.e. in about 3 days in summer and 7 days in winter. Mating occurs at any time of day, and is initiated by the male. Mating pairs align themselves in parallel with both sexes facing the same direction and remain in coitus for about 4 min (Catling, 1973). The period of 2 h mentioned by Catling (1967) seems to be erroneous. Females have been observed to mate 2–4 times a day (Catling, 1973).

Females that have developed beyond the pre-oviposition period, are capable of laying fertile eggs immediately after mating (Catling, 1978). Females remain fertile for 11–16 days, and under favourable conditions the fertility of eggs is usually greater than 95% (Catling, 1973). Details of the mating behaviour and the possible role of pheromones, which may possibly be used in a monitoring system, are lacking and further research is required.

On emergence, the female shows little ovarian development (Blowers and Moran, 1967). The development of the first mature eggs requires a period reported to be from 3 to 14 days (Van der Merwe, 1923). At temperatures of 14–15°C and 24–26°C the pre-oviposition period is 6–7 and 3–5 days, respectively. However, in the absence of young flush the pre-oviposition period is extended (Catling, 1969a) and many females probably die without laying eggs (Catling, 1972b).

Gravid females of *T. erytreae* begin ovipositional behaviour by wandering slowly about on the leaves stopping frequently to pierce and “test” the leaf surface with the paired ventral valvulae. The sawing motions of the valvulae cut a minute hole in the leaf tissue into which the egg stalk is forced as the egg is laid. Given the choice between pairs of young lemon leaves of differing hardness, the female laid more than twice the number of eggs on the softer leaves (Moran and Buchan, 1975).

Moran (1968b) established that *T. erytreae* showed a significant preference for oviposition on the young leaves of lemon over leaves of four indigenous Rutaceae plants. The prior presence or absence of eggs on leaves or feeding preference by the triozyds did not influence their choice of oviposition sites (Moran and Buchan, 1975).

Eggs are laid almost throughout the adult females lifespan. Van de Merwe (1923) mentioned that the maximum egg production occurred at the beginning of the egg-laying period. Catling (1973) reported that it occurred towards the middle of the adult lifespan. However, these observations are based on a limited number of observations and further studies are required to resolve the conflicting results.

The number of eggs produced by this triozyd has been studied by Van der Merwe (1923), Moran and Blowers (1967) and Catling (1973). The work by

Catling is the most detailed and revealed that the average number of eggs is 827 (31–2542).

Some individuals were observed to deposit more than 100 eggs day⁻¹ (Catling, 1978). Oviposition is completely suspended on dormant trees.

There are conflicting opinions over the dispersal ability of the citrus psylla. According to Catling (1973) this triozid does not appear to possess strong dispersal powers. In a later publication Catling (1978) stated that adults have weak dispersal powers. This statement is probably incorrect as, Samways and Manicom (1983) have demonstrated that the citrus psylla can readily locate and invade isolated areas of flush over several hundred metres. Dispersion patterns show that citrus psylla adults tend to accumulate in the row adjacent to the source of infestation and along edges of orchards bordered by windbreaks.

A sound knowledge of the dispersal ability of the citrus psylla and the role, if any, played by wind in this process is important. This will give an indication of minimum inter-orchard distance required to prevent cross-infestation and associated greening disease.

Preliminary results indicate that most flight activity takes place shortly before sunset and ceases with the onset of darkness (M.A. van den Berg, unpublished data, 1989). It is therefore possible that many of the dispersing psylla would spend the night on plants other than their normal hostplants (Rutaceae). This has been observed on a number of non-host plants. Thus, greening disease may possibly be transferred to other host and non-host plants from which it could be transferred back to citrus. Taking this into account it is obvious that the epidemiology of greening disease may be even more complex than originally thought.

The lifespan of adults on citrus has been studied under experimental conditions. The longest recorded lifespan for males is 73 days and for females 82 days. The absence of young flush on a host plant was found to prolong the pre-oviposition period and to extend their longevity (Catling, 1969a).

According to Catling (1973) adult citrus psylla survive for less than 55 h if suitable foliage is not available to feed on. The influence of duration of starvation on ability to transmit greening disease should be determined since this will also influence the effective disease-dispersal distance of the vector.

No stage was found to undergo diapause. Adults overwinter on semi-dormant trees and may live for 2–3 months. During this period they feed on mature leaves (Catling and Annecke, 1968). According to Catling (1972b), there were eight overlapping field generations per year at Malkerns, Swaziland. Catling (1978) reports that they will continue to breed on citrus throughout the year if flushes are available.

GREENING DISEASE: DISTRIBUTION AND TRANSMISSION IN SOUTH AFRICA

Although greening disease occurs mainly in the Transvaal some diseased trees have been found in Natal. Greening disease has also been observed in

several citrus groves in the Eastern and Western Cape where trees had originated from nurseries in the Transvaal (Schwarz, 1967). High density populations of *T. erytreae* occur periodically in certain parts of the Cape Province, such as the Stellenbosch and Swellendam areas (identifications by D. Hollis, Department of Entomology, British Museum (Natural History), London). However, greening disease has not spread from these areas. For this reason it has been suggested that *T. erytreae* found in the Cape may be incapable of transmitting greening disease, indicating that different races of *T. erytreae* may be present or that isomorphic species may exist. Both of these possibilities require further investigation.

The first report that the adult citrus psylla is a vector of greening disease was made by McClean and Oberholzer (1965b). This was later confirmed by other workers (e.g. McClean and Schwarz, 1970; Catling, 1970b).

Single individuals of the citrus psylla can transmit the greening pathogen in sufficient quantities to lead to symptom expression (Catling and Atkinson, 1974). However, the number of triozyds that are actual carriers is comparatively small (McClean, 1974; Catling and Atkinson, 1974) and fairly high vector populations are needed before appreciable disease transmission occurs (Catling, 1969b). According to Van Vuuren et al. (1986) the adult citrus psylla is able to acquire the greening organism within 24 h of commencing to feed and can transmit the disease after a further 24 h.

Generally it has been found that only adult psylla can acquire and transmit the causal agent (McClean and Oberholzer, 1965b; Catling, 1970b; Moll and Martin, 1973; Moll and Van Vuuren, 1977). However, McClean (1974) states that the nymphal stage may sometimes become infected by feeding on diseased tissue. However, there may be some delay in the adult stage, before such carriers are fully infective and capable of transmitting the disease. Since the adults are the only dispersive instar the entire question of nymphal infection and subsequent adult infectivity requires further clarification.

Only the less destructive, heat-sensitive strain of greening disease appears to be present in South Africa. However, work by Massonie et al. (1976) and Aubert et al. (1979) has shown that *T. erytreae* can also transmit the more virulent Asian strain of the disease.

FACTORS INFLUENCING POPULATION SIZE OF THE VECTOR

Plants

The citrus psylla breeds exclusively on young plant tissue which should not reach maturity (i.e. when the delicate green appearance is lost) before completion of the nymphal life-span (Van der Merwe, 1923; Moran, 1967; Catling, 1972b). Thus, the flushing rhythm of their host plants imposes a corresponding rhythm on the citrus psylla (Catling, 1969a, 1972a).

Moran and Brown (1973) studied the ultrastructure of the citrus psylla antenna. Antennal chemoreception of secondary plant substances of the host plant was demonstrated, indicating that this could play a role in host plant selection. The evidence suggested that these antennally mediated effects were olfactory, but that antennal-tip gustation of leaf surface absorbate is probably also involved.

Any factor which promotes dormancy in host-plant growth will assist in limiting populations of *T. erythrae* (Catling, 1969a). Ways of enforcing dormancy in citrus trees during certain periods of the year require investigation. Appropriate irrigation regimes and/or the use of growth regulators appear to be the most promising. The influence of this on the population size of the citrus psylla and on the trees and their crop should also be determined.

Young citrus trees flush more often and more densely than mature trees (Catling, 1969a), and bear relatively more young growth. The latter has a high nitrogen content (Catling, 1971) and young trees sometimes support larger psylla populations than adjacent mature trees (Catling, 1969a). Citrus flush 3–4 times annually, of which the spring flush is by far the biggest. The main trioqid population increase takes place on this flush (Catling, 1969a).

Limes, *Citrus aurantifolia* (Christm.), and lemons, *C. limon*, are known to flush more freely than the sweet orange, *C. sinensis* (Linn.). Within the sweet orange group, navels flush more profusely, and mid-season cultivars less profusely than Valencias (Catling, 1969a). The flush and dormant periods of different citrus cultivars seem to occur at different periods of the year. If cultivars with flush periods that do not coincide are planted in the same area, the psylla breeding period will be prolonged. Trees in such areas may be subjected to more intense citrus psylla attacks than trees in areas where growth-flush is synchronized. Synchronized growth may thus prove to be an important factor in reducing psylla population levels in certain areas and clearly warrants further investigation.

At Rustenburg, navel trees whether irrigated or dry-land, produce new growth almost throughout the year and can support psylla breeding throughout the year. Neglected or dying trees can serve as a source of inoculum for greening disease. They should either be removed or placed under the same control programme for the citrus psylla as that utilized in well-managed orchards (Van den Berg and Vercueil, 1985).

Certain citrus cultivars seem to be better suited to psylla breeding than others. This can probably be ascribed to the fact that the flush does not harden before the life cycle is completed. Selection of cultivars for utilization in areas where there is a high incidence of greening disease may reduce its prevalence.

According to Van der Merwe (1923), development from egg to adult has only been recorded on the following Rutaceae indigenous to Southern Africa: *Clausena anisata* (Wild.) Hook. f. ex Benth., *Vepris lanceolata* (Lam) G. Don. and

Zanthoxylum capense (Thumb.) Harv. Begemann (1984a) added *Oricia* sp. to this list.

The indigenous bush surrounding orchards in some of the citrus growing areas undoubtedly supports *T. erytrae* populations which may be a source of re-infestation despite repeated insecticide treatment of orchards (Moran, 1968b). However, alternative host plants appeared to be of little or no significance in the Letaba district (Catling and Annecke, 1968). In this area, as well as at Malkerns, no evidence was found of any large indigenous reservoir of *T. erytrae* (Catling, 1969a). Similar investigations in other areas are obviously required.

Development of immature stages was observed on all citrus cultivars and varieties grown in South Africa during 1923 and also later in 1978 (Van der Merwe, 1923; Catling, 1978). However, little work has been done on the preference of the citrus psylla for certain cultivars and whether some may have a resistance to psylla development. These aspects merit further study.

Weather conditions

Sensitivity of the nymphal stages to high temperatures was first reported by Van der Merwe (1923). Moran and Blowers (1967) established that high temperatures (approximately 8 h day⁻¹ at 32°C) prevented eggs from hatching, induced high mortalities in all other stages, and also inhibited ovarian development in the adult female.

Catling (1969c), Green and Schwarz (1970), Schwarz and Green (1970) and Green and Catling (1971) found that there was a polynomial relationship between the saturation deficit and the survival of psylla eggs and juvenile nymphs. It was found that population fluctuations at Nelspruit over 3 years (Van Vuuren and Moll, 1984) and the apparent absence of citrus psylla during 1982 and 1983 at Rustenburg (Human and Bedford, 1985) could be explained by this relationship.

Annual accumulated values of the saturation deficit (Schwarz and Green, 1970; Green and Catling, 1971) also throw light on past outbreaks; for example, in the Rustenburg district increases in the numbers of citrus psylla for a few years were followed by local extinction in marginal areas. This was traced to changes in the saturation deficit levels (Green and Schwarz, 1970; Green and Catling, 1971).

According to Samways (1987b), an increasingly high saturation deficit index has a negative long-term impact on adult citrus psylla numbers. However, weekly fluctuations in the size of adult psylla populations cannot be correlated with the weekly saturation deficit index. The reason for this remains unclear.

The citrus psylla favours well-shaded breeding sites in the lower section of the tree canopy. It is frequently found in large numbers near windbreaks and rarely colonizes small trees in the hot regions during summer months. There

is also a tendency for higher populations to develop in mild seasons or following spells of cool overcast weather during summer months (Catling, 1969c).

According to Catling and Annecke (1968), there was an almost linear relationship between altitude and previous citrus psylla incidence in South Africa. Groups of 50 sweet orange trees placed in orchards for a period of 17 months had a total of 39 colonies at Letaba (600 m altitude), 984 at Fairview (850 m) and 3353 at Forest Hill (1280 m). Populations were consistently highest in the cool, moist upland regions and were low and isolated in the hot, arid lowlands. The same pattern was observed in Réunion Island, where *T. erythrae* was most prevalent in cooler areas above about 500 m (Bové and Cassin, 1968; Aubert, 1985).

Minimum winter temperature does not appear to cause any significant citrus psylla mortality, and violent rainstorms have also no significant effect on the sessile stages (Catling, 1967). On the other hand, hail directly destroys the young stages and damages breeding sites. However, severe hailstorms also stimulate subsequent strong growth flushes in citrus (Catling, 1969a), and an outbreak of citrus psylla has been correlated with a destructive hail storm 4 months earlier (Human and Bedford, 1985).

Parasitoids

Two primary parasitoids and 13 secondary and tertiary hyperparasitoids are associated with the citrus psylla in Zimbabwe (McDaniel and Moran, 1972). The primary parasitoids are the external parasitoid *Tamarixia* Waterston (Eulophidae) and the internal parasitoid *Psyllaephagus pulvinatus* (Waterston) (Encyrtidae).

Tamarixia dryi was described from Kenya (Waterston, 1922). It lays its eggs singly beneath the third, fourth or fifth instar nymphs. The ectoparasitic larva sucks out the body contents of the nymph and when fully grown binds the remains of its dead host with filaments to the edges of the leaf gall. Begemann (1984a) also reared *Tamarixia dryi* from an unidentified triozid on wild fig. The latter and other triozids may possibly be important alternative hosts for *Tamarixia dryi*.

Psyllaephagus pulvinatus was described by Waterston (1922). It is an internal parasitoid and was found to be mainly active towards midsummer (Catling, 1972b).

These two primary parasitoids have considerable impact in controlling the numbers of their host, *T. erythrae* (McDaniel and Moran, 1972). According to Van der Merwe (1923) more than 75% of the nymphs may be parasitised. Catling (1969b) recorded that during periods of favourable synchrony at least 40–50% of the nymphs were parasitised and less than 10% under conditions of poor synchrony.

Catling and Annecke (1968) found that hyperparasitism was of little appar-

ent significance in the Letaba district. However, according to McDaniel and Moran (1972) and Annecke and Moran (1982) the secondary parasitoid *Aphidencyrthus cassatus* Annecke (Encyrtidae) is at least partly responsible, through its impact on the two primary parasitoids, for high population levels of the citrus psylla.

Predators

Lounsbury (1897) mentions a syrphid larva and Van der Merwe (1923) listed two syrphids and a number of unidentified spiders. Catling and Annecke (1968) added an erythraeid mite and Samways (1984a) a coccinellid to the list. In a more detailed study, Catling (1970a) found that predators are more active from midsummer to early winter. He found six lacewings, a dusty wing (hemeroboid), two syrphids, a coccinellid, two predatory mites and a large number of undetermined spiders as predators of this trioqid. Predation of the eggs of citrus psylla by spiders, as mentioned by Catling (1970a) may be erroneous.

Van der Merwe (1923) and Catling and Annecke (1968) considered that predators play a minor role in the population dynamics of the citrus psylla. However, Catling (1970b) found that predators clearly assist in suppressing populations of the citrus psylla, but that they are unable to maintain numbers at economically acceptable levels.

Predators of *T. erytrae* that have been recorded from Réunion are two coccinellids, two syrphids and a mirid species (Etienne, 1978).

Further research on predators of the citrus psylla is warranted.

Pathogenic micro-organisms

Catling (1969d) considered that there were no micro-organisms associated with *T. erytrae*. However, a fungus, *Cladosporium oxysporum* (Blerk. and Curt.), caused mortality in field populations of the nymphs (Samways and Grech, 1986), and M.A. van den Berg, unpublished data, 1989) found three unidentified species of fungi that attack the nymphs on indigenous Rutaceae. The value of microbial agents for control merits further investigation.

Competition

Overcrowding of breeding sites and consequent mortality can contribute to a midsummer population crash. However, severe competition appears to be infrequent in the field (Catling, 1972b).

When oviposition sites are scarce, small flush points may be so densely packed with eggs that they shrivel and fall off (Catling, 1972b). In overcrowded situations, females may also oviposit on more advanced leaves which can result in a decline in both egg hatch and nymphal survival (Catling, 1971). Under se-

vere nymphal competition only 10–20% attain the adult stage (Van der Merwe, 1923).

On some spring and summer flushes competition may occur between *T. erytreae* and the citrus aphid, *Toxoptera citricidus* (Kirkaldy) (Catling, 1969a). Aphids are quick to colonize developing flush points, and in spring their copious honeydew renders many flush points unattractive to *T. erytreae*.

Another form of competition that occurs on citrus and indigenous Rutaceae which leads to egg and nymphal mortality is competition with leaf feeders e.g. the larvae of *Papilio* spp. and tip wilters (M.A. van den Berg, unpublished data, 1989).

Interaction among ecological factors

Table 2 summarises the age-specificity mortality factors for the citrus psylla. Of these factors, high saturation deficits, the flushing rhythm of citrus and natural enemies are the most important (Catling and Annecke, 1968). The heaviest mortality occurs during the egg and the initial nymphal instars.

In declining order of importance the following factors seem to govern the seasonal abundance of *T. erytreae* in a favourable summer region: The availability and quality of the flush, lethal weather extremes, actions of parasitoids and predators and interspecific and intraspecific competition (Catling and Annecke, 1968; Catling, 1972b; M.A. van den Berg, unpublished data, 1989).

POPULATION MONITORING AND CONTROL

Biological

The two primary parasitoids, *Tamarixia dryi* and *P. pulvinatus* were introduced from Transvaal, South Africa to Réunion (Aubert, 1975; Etienne and Aubert, 1980). About 33 000 laboratory reared *Tamarixia dryi* and 12 500 *P. pulvinatus* were released in citrus orchards (Etienne, 1978; Etienne and Aubert, 1980). Within 5 years, *Tamarixia dryi* was well established and the citrus psylla had been drastically reduced. On the other hand, *P. pulvinatus* has not been seen again (Etienne and Aubert, 1980).

Tamarixia dryi also parasitises *Trioza eastopi* Orian which feeds and breeds on the common weed *Litsea chinensis* Jacq. The parasitisation of *T. eastopi* was partly responsible for the control achieved with *T. erytreae* (Aubert and Quilici, 1983).

After a survey with fluorescent yellow traps over a period of 2 years in 12 different sites, Aubert and Quilici (1986) stated that they had clear evidence of total elimination of *T. erytreae* from Réunion. Small numbers of *Tamarixia*

TABLE 2
Age-specificity of important mortality factors for the citrus psylla

Stage:	Nymphal instars					Adult	Reference	
	Egg	I	II	III	IV			V
Mort. factor								
Flushing of host	Essential for breeding						Essential for oviposition	Van der Merwe (1923)
High temperature combined with low humidity	Highly susceptible	Highly susc.	Increasing resistance from instars II to V			Sensitive	Catling (1969c); Green and Catling (1971)	
Parasitoids	No paras. recorded	Not susc.				No paras. recorded	McDaniel and Moran (1972)	
<i>Tamarixia dryi</i> Waterston		Not susc.	Susc. but rarely attacked	Susc. but attacked	Susc. and favoured (Not always fatal)*		McDaniel and Moran (1972) *Catling (1972b)	
<i>Psyllaephagus pulvinatus</i> (Waterston)		Not susc.	Susc. but only occas. attacked	Highly favoured	Susc. but only occas. attacked		McDaniel and Moran (1972)	
Predators	Susceptible to predators at all stages							
Competition	Severe						Slight	Catling (1970b)
Intraspecific		Very severe	Moderately severe	Moderate	Moderate to slight		Van der Merwe (1923); Catling (1972b); M.A. van den Berg (unpublished data, 1989)	
Interspecific	Not severely affected in egg or nymph stages							
Aphids							Reduce attractiveness of foliage	Catling (1972b)
Phytophagous insects and tip wilters	Very severe at egg and nymph stages						Not susc.	M.A. van den Berg (unpublished data, 1989)

dryi were also imported to Mauritius and although this parasitoid took longer to control *T. erytrae* than at Réunion, it was equally successful (Aubert, 1985).

The introduction of new natural enemies for improving the biological control of *T. erytrae* has been suggested by McDaniel and Moran (1972). During 1983, the parasitoids *Diaphorencyrtus aligharensis* (Shafee, Alam and Agarwal) and *Tamarixia radiatus* Waterston, parasitoids of *Diaphorina citri*, were introduced to South Africa (Van den Berg, 1984). These were screened in quarantine but appeared to be too specific to parasitise *T. erytrae*.

The introduction of two parasitoids, *Prionomitus mitratus* (Dalm.) (Hym: Encyrtidae) and *Tamarixia triozae* Burks (Hym: Eulophidae) and the predatory anthocorids, *Anthocoris antevolens* White, *A. melanocerus* Reuter and *A. nemoralis* (F.) has been recommended (Van den Berg, 1984) but this work has not yet received attention.

Monitoring

Population assessments have been made by a direct count of colonies on the lower 1.2 m of the citrus tree canopy (Catling, 1970b). Visual inspections have also been used to establish the presence of citrus psylla for control purposes at Zebediela Estates, Northern Transvaal (Van der Kooij et al., 1986).

Yellow sticky traps proved to be useful as monitors of citrus psylla populations (Catling, 1970b; Moll and Van Vuuren, 1977; Van Vuuren and Moll, 1984; Gilbert, 1984).

Urban (1976) showed that *T. erytrae* is positively phototaxic to light of wavelength 550 nm (yellow-green). On the basis of this work, Samways (1984b, 1987a) developed a monitoring-trap which is highly attractive to the citrus psylla.

Chemical control should be applied as soon as eggs of the citrus psylla can be seen (Pyle, 1979). When two or more citrus psylla adults or egg batches and/or nymphal colonies are seen on young flush points on one side of 10 trees per orchard, chemical control should be considered (M.A. van den Berg, unpublished data, 1989).

If the threshold of 2 psylla per 3 saturn yellow traps is exceeded, control measures should be considered (Samways et al., 1986; Samways, 1987b).

Physical and chemical

The eradication of native host plants from the vicinity of the orchard has been recommended to reduce citrus psylla outbreaks (Van der Merwe, 1923). Such measures have also included the removal of infested citrus shoots (Lounsbury, 1897; Van der Merwe, 1923), or elimination of out of season flush (M.A. van den Berg, unpublished data, 1989).

Prior to 1932, sprays containing tobacco extract, paraffin emulsion (Louns-

bury, 1897), resin (Van der Merwe, 1923) and alboleum (Andries, 1932) were used for control. From 1929 to 1950 citrus trees were fumigated with HCN to control red scale (Bedford, 1968). This would also have had an influence on psylla populations. More recently nicotine, oil emulsions, demeton, mercaptothion, parathion, azinphos-methyl, dichlorvos, dimethoate and thiometon have been recommended (Fochessati, 1961; Wyninger, 1968).

The following foliar sprays are at present registered for the control of citrus psylla in South Africa (Bot et al., 1986): chlorpyrifos, dimethoate, endosulfan, isofenphos, monocrotophos, oxydemeton methyl and triazophos. The nematocidal aldicarb suppresses this pest.

Catling (1969d) has recommended a spray programme based on three foliar applications of dimethoate and in another programme endosulfan and isofenphos or triazophos are used (Van den Berg et al., 1983).

Dimethoate can be applied as a foliar spray or to the soil of nursery trees (Milne, 1977) either by microjet or drip irrigation (Milne and De Villiers, 1977) or by applying it to seed beds or around the trees with a watering can (Milne et al., 1978). However, it should be noted that certain cultivars are sensitive to this insecticide (Milne et al., 1978). Furthermore, it has been found that there was a very severe phytotoxic interaction between the herbicide bromacil and dimethoate when applied simultaneously or even 12 weeks apart (Milne and De Villiers, 1980).

Buitendag and Bronkhorst (1984, 1986) established that monocrotophos applied to the bark of citrus will kill psylla on the foliage. An applicator was designed for the application of insecticides in this manner and, the relation between monocrotophos dosage rates and tree trunk circumference has been determined. This application was apparently not toxic to various rootstock seedlings or to Valencia trees.

Strategy

The selection and breeding of resistant citrus cultivars is one approach to controlling the greening disease problem (De Lange et al., 1984). Both sexual breeding and in vitro selection of resistant callus and protoplasts have received attention.

Psylla populations are restricted by high temperatures combined with low humidities, and the psylla problem can be largely avoided by restricting citrus growing to the hot, low-lying regions of the country where these conditions prevail (Moran, 1968b; Aubert, 1986).

Catling (1969d) suggested that preventive chemical control should be applied before the start of the major spring flush cycle to reduce psylla populations later in the season. This has been done at Zebediela since 1980 where, according to Begemann (1984a) almost complete control has been achieved

with dimethoate applied to the soil during winter and endosulfan foliar sprays later in the season whenever psylla was spotted.

Greening disease has been a problem in the Zebediela orchards for approximately 40 years. Since 1980 reduction of the greening inoculum and the psylla population has yielded positive results. Progress in preventing the spread of the disease has been reported for the first time (Begemann, 1984a).

Citrus psylla populations will probably also be reduced where the following control measures are practised. Firstly, where possible cultural practices (especially irrigation) should be utilised to encourage winter tree dormancy and well-defined flushes in the summer (Catling, 1969a). Secondly, cultivars with flushing periods that do not coincide, may be prone to higher psylla attacks and if this is so, they should not be planted in the same area (M.A. van den Berg, unpublished data, 1989).

Greening disease can only be controlled successfully if infected plant material is eradicated in the orchards (Green and Schwarz, 1970; Kotze, 1982; van den Berg and Vercueil, 1985) and replaced with greening-free nursery trees (Kotze, 1982, 1985).

Strict control of nurseries through a registered disease-free certification scheme is essential for avoiding the spread of greening disease and its vector(s) (Aubert, 1986).

New orchards should be established as far as possible from indigenous rutaceous host plants of the citrus psylla (Aubert, 1986).

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