Factors Regulating Populations of Psyllid Vectors of Greening

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TWO PSYLLIDS, *Trioza erytreae* (Del Guercio), which is mainly confined to Africa south of the Sahara, and *Diaphorina citri* Kuw., which occurs in the Orient and Brazil, are the vectors of greening disease of citrus (3, 8). They are the only two psyllids known to breed on citrus.

This paper briefly reviews our knowledge of the ecological factors that regulate populations of these psyllids. One of the main factors, extremes of weather, is dealt with in more detail in the following paper. A general account of *T. erytreae* appeared in 1941 (14); an important contribution to its biology was the work of Moran and Blowers (13). Studies on the ecology of *T. erytreae* have been carried out since 1965, first in the northern Transvaal (South Africa) and later in Swaziland (4, 5, 6, 7, 9); similar studies were initiated on *D. citri* in the Philippines towards the end of 1968 (3).

Trioza erytreae *(Del Guercio)*

The life history of *T. erytreae* consists of an egg stage, 5 nymphal stages (instars), and a winged adult. The psyllid breeds exclusively and feeds preferentially on young foliage (flushes) of all species and varieties of citrus, and thus the sedentary, immature stages become aggregated into distinct colonies. The tropical citrus aphid *Toxoptera citricidus* (Kirk.), which also colonizes young flushes, frequently competes for breeding sites. Although there is some overlap, 8 distinct annual "field generations" or "broods" occur from June to May when the bulk of the population is in a similar stage (Fig. 1). *Trioza erytreae* disperses weakly, and in most areas, if not all, the influence of alternate, noncitrus, host plants is slight. On dormant trees when little or no flush is available for breeding sites adults feed for long periods on mature leaves. Egg laying is stimulated by the presence of flush, and the reproductive potential is extremely high. The total mean egg production for batches of 3–6 females on citrus seedlings varied from 342 to 1304 eggs per female with a maximum of more than 2,500 eggs for 1 individual.

WEATHER.—Extremes of weather, which play a dominant role in regulating the numbers of this psyllid, are treated in the following paper.

FLUSHING RHYTHM.—Population fluctuations are closely correlated with the flushing rhythm of citrus, peaks of egg colonies succeeding peaks of young flushes in regions where the insect is abundant (Fig. 1). Flushing imposes a rhythm on both the numbers and age distribution of the psyllid, field generations being more distinct on well-defined growth cycles.

In the eastern Transvaal and Swaziland there are 3 main annual flushes or growth cycles. The first, which is usually the heaviest and always bears blossom, occurs in August–September; the second appears towards midsummer in November; and the third in January–February. The timing of the second and third flushes may be varied by the rainfall pattern. The main abiotic factors regulating growth, namely temperature and moisture, have been discussed (4), but of greater relevance to the present discussion are the following 3 biotic factors causing differences in flushing rhythm, which in turn affect the numbers and oscillations of the vector.

Host species and variety.—Lemon and lime are known to flush more freely than sweet orange. Of the sweet orange varieties, Navel was found to flush more heavily than Valencia, particularly during the second flush of the season; many midseason varieties bore very low densities of flush after the spring cycle.

Age.—Young trees were found to flush more often and more densely than mature trees. Young trees sometimes supported larger vector populations than adjacent mature trees.

Greening and tree condition.—Stress and premature dropping of mature leaves may bring on compensatory, out-of-season growth. Green-

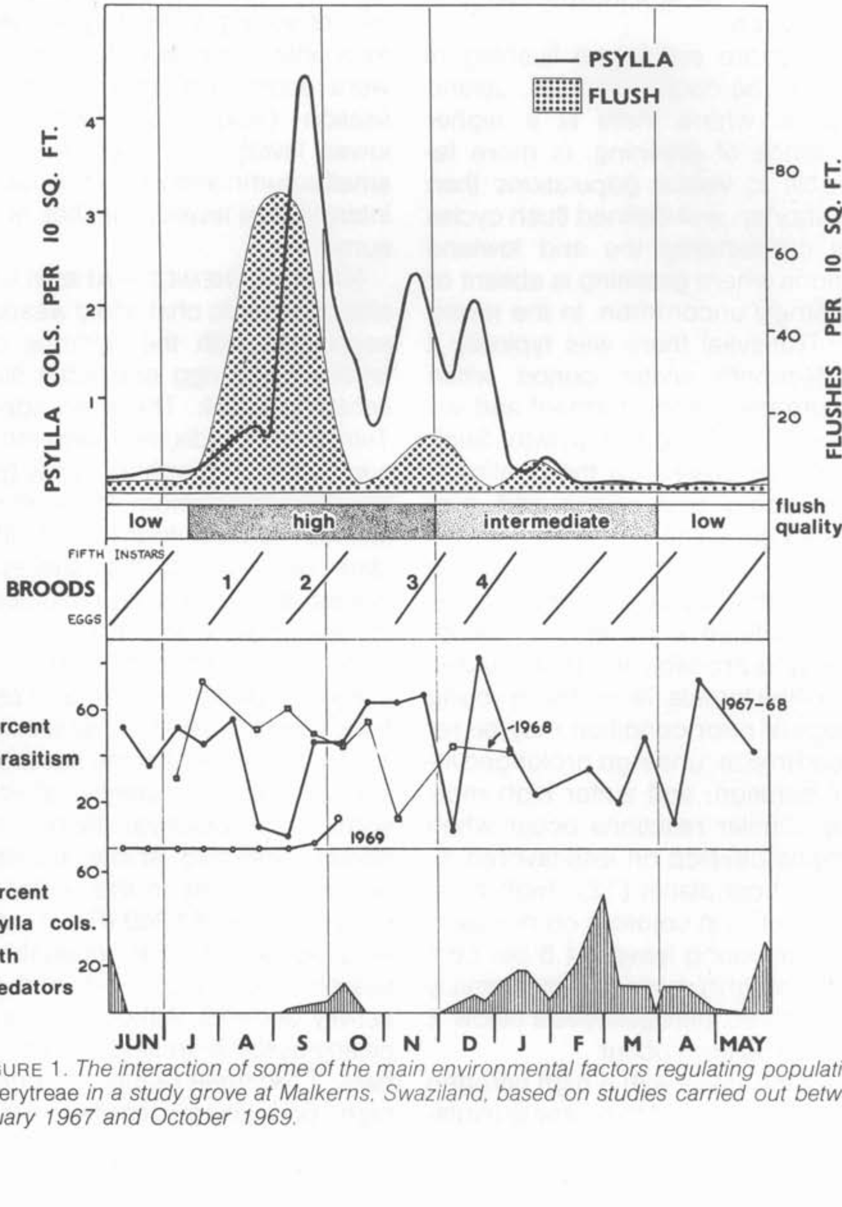

FIGURE 1. *The interaction of some of the main environmental factors regulating populations of* T. erytreae *in a study grove at Malkerns, Swaziland, based on studies carried out between February 1967 and October 1969.*

ing influences the flushing rhythm of citrus, the natural rhythm in severely affected trees being modified to one of heavier winter flushes and overlapping cycles in the growing season. Infected trees therefore tend to encourage breeding of the vector for longer periods, and dormant periods are bridged.

The more prolonged flushing of trees in the cooler, moister, upland regions, where there is a higher incidence of greening, is more favorable to vector populations than the shorter, well-defined flush cycles that characterize the arid lowland regions where greening is absent or extremely uncommon. In the northern Transvaal there was typically a 3–3½-month winter period when mature trees were dormant and virtually devoid of young growth. Such dormancy breaks up the continuity of breeding populations and suspends egg-laying.

FLUSH QUALITY.—The condition and nutritional status of young citrus leaves influence nymphal development and probably the reproductive rate of the female. Nymphs on young foliage of poor condition may be reduced in size, undergo prolonged instar duration, and suffer high mortality. Similar reactions occur when nymphs develop on less-favored alternate host plants (12). High mortality occurs in colonies on nitrogen-deficient young leaves (1.5 per cent by dry weight); however, in normally grown trees, nitrogen levels below 2 per cent seldom occur.

Healthy tissue with a high nitrogen content is believed to promote ovulation and egg laying. Sequential analyses for nitrogen content over 2 seasons revealed first a trend for higher levels of nitrogen in flush from young trees and seedlings; second that nitrogen content declines with age; and third that a definite seasonal fluctuation exists in the nitrogen content of young flush. Highest levels, frequently in excess of 4.0 per cent N, were recorded in the first flush of the season (August–September); the lowest levels, < 2.5 per cent, in the small autumn and winter flushes; and intermediate levels in flushes of midsummer.

NATURAL ENEMIES.—At least 8 species of parasitic chalcidoid wasps are associated with the nymphs of *T. erytreae,* the egg and adult stages escaping attack. The main species, *Tetrastichus radiatus* Waterston, occurs widely throughout citrus-growing areas of southern Africa where it attacks the third, fourth, and fifth instars only—called the susceptible stages. It is relatively unaffected by routine applications of insecticides.

Under conditions of favorable synchrony between parasite and psyllid host, as in the 1968–69 season (Fig. 1), 40–50 per cent of the susceptible stages are consistently attacked, some host colonies being completely decimated. At low host densities, however, as in the winter and early summer of 1969 (Fig. 1), parasites appear to be incapable of searching out their host, and their activity declines. Although parasites clearly assist in limiting vector numbers, *T. erytreae* regularly surges to high population densities on the growth cycles of early summer when, typically at the start of each field generation, 70–80 per cent of the population is present in the nonsusceptible egg and young nymphal stage.

A fairly large complex of predators, including lacewings, syrphid flies, a coccinellid beetle, and spiders, attack *T. erytreae*. The precise significance of this group of natural enemies has still to be determined; life table studies, field counts, and experiments have indicated that they may assume some importance as limiting factors from midsummer to midwinter. Peak activity occurs in February–March (Fig. 1), but there is usually a considerable time lag in host-predator relationship in early summer.

POPULATION DYNAMICS.—Populations of *T. erytreae* fluctuate violently between extremely low densities on the semidormant trees of winter to the typical outbreaks on the first flushes of early summer. Figure 1 depicts the operation of the main limiting factors believed to regulate the numbers of *T. erytreae* in a study grove at Malkerns, Swaziland, during a typical season.

During winter, April–June, lethal weather extremes are extremely rare. Predators and parasites are active—with the exception of 1969 in the case of parasites—but the density and nutritional status of young growth is at its lowest. Vector populations usually remain at low densities; fewer than 4–10 per cent of available breeding sites are colonized during this period. Scarcity of young growth and the low percentage of infested flushes suggest that either the fecundity of the vector females is drastically reduced, due perhaps to the low nutritional status of the host tissue, or that females are incapable of seeking out such widely scattered breeding sites, or both. Trees forced to flush vigorously at this time will support high vector populations. The size of this winter nucleus population, which to a great extent determines the potential for the spring population increase, is largely dependent on the flush densities of the winter months.

With the appearance of the dense and highly nutritious spring flush in July, a steady population rise begins. A threefold increase in the population occurs in the first field generation. Plentiful flush is still present in September, and the second generation of the vector frequently reaches a peak density for the season. Predator activity is low in August and September, but the influence of parasites is variable; in some seasons (1968–69) fairly high levels of parasitism are maintained. The main single factor regulating numbers in early spring is the incidence of lethal weather.

Populations decline sharply until the onset of a smaller second flush in October–November when a fresh surge of egg laying marks the start of the third brood. Flush quality is good and parasitism remains at fairly high levels. Predators are still of relatively minor importance. The rise of brood 3 and the height of its peak are again largely dependent on prevailing weather, hot, dry weather frequently occurring during this period.

Typically, the fourth brood causes a small population rise on the diminishing supply of breeding sites. In some seasons the flush may become overpopulated, resulting in considerable mortality. Towards the end of December or early January, the combined effect of lethal weather, declining flush density and quality, persistent parasite attack, and an upsurge in predator activity bring about a severe population crash. Low populations then persist throughout the autumn and winter.

Diaphorina citri *Kuw.*

The Oriental psyllid closely resembles *T. erytreae* in its life history and biology (3, 11). In the Batangas Province of the Philippines, populations are at their lowest on the semidormant trees during the dry season from December to April. The main upsurge takes place on the major flush cycle in May–June and is stimulated by the start of the rainy season; moderate populations persist during July and August. According to Husain and Nath (11), populations are similarly related to flushing rhythm in India.

Seven species of internal parasites were reared from *D. citri* in the Philippines. During July and August 1968, the most abundant of these, which was widely distributed, was an encyrtid, *Psyllaephagus* sp. This species has also been recorded from Taiwan. *Tetrastichus radiatus* has been reported as an effective parasite of *D. citri* in India (10) and West Pakistan (1), but there is no record of this species in the Philippines. Syrphid, lacewing, and coccinellid predators feed on the nymphal stages in the Philippines.

There is evidence that *D. citri* may be more resistant to extremes of weather than *T. erytreae*. Bové and Cassin (2) found large numbers of *D. citri* in the hot coastal zone of Réunion, whereas *T. erytreae* was confined mainly to the areas above 500–600 m. Lethal extremes rarely occur in the equatorial climate of the Philippines. In Batangas Province the mean maximum daily saturation deficit for the 6 severest days at Lipa City during the 1968 dry season averaged 22.1 mbars. This is considerably lower than the critical level of 34.6 mbars used to predict population densities of *T. erytreae*.

Conclusions

Populations of the 2 psyllid vectors of citrus greening are apparently regulated by 4 main environmental factors. They are the flushing rhythm of the citrus host, weather extremes, the condition and nutritional status of young growth, and natural enemies. Of these, weather extremes play a dominant role in determining the numbers of *T. erytreae*, but their significance in the regulation of *D. citri* has not been determined.

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