3-1. Geographical distribution

Just before *Trioza erytreae* was confirmed to be a vector of greening disease, OBERHOLZER et al. [369] revealed that in the Transvaal, South Africa, the triozid was abundant in somewhat cooler areas at altitudes of more than 3,000 ft (about 900 m) and was seldom found in great numbers in hot, dry regions at low altitudes. The former areas coincided with the main areas of greening outburst and in the latter ones the disease was either absent or of no commercial significance.

CATLING [102] pointed out that high temperature combined with low relative humidity brought about high mortality of *T. erytreae* at the egg and first-instar nymphal stages, showing significant correlation between percent survival of eggs and first-instar nymphs and maximum saturation deficit calculated from daily maximum temperature and minimum relative humidity (the calculation was based on the mean of the three severest days during the study period). The value of maximum saturation deficit against 70% mortality of eggs and first-instar nymphs on the regression line was 34.6 mb, and CATLING and GREEN [112] regarded it as a threshold of weather extreme.

SCHWARZ and GREEN [452] have summarized the influence of weather extremes upon *T. erytreae* populations as follows: The longer the period in which saturation deficit index (SDI) values over 35 mb are recorded for an area, the less suitable it is for the build-up of population. GREEN and CATLING [190] emphasizes the importance of considering the seasonal distribution of near lethal SDI values as well as the duration of those values. If the period of near lethal SDI values takes place at the time of high population vitality accompanied with vigorous flushing of host plants, loss of the immature stages will be compensated by an abundant supply of eggs from female adults which do not suffer so much owing to their relatively high tolerance to weather extremes. In contrast, if the period mentioned above comes at the time of population stagnation with low flush density, the influence of weather extremes will occasionally be so serious as to reduce the population to a near zero level.

The results of the above-mentioned analytical studies show that altitude alone cannot be a reliable indicator for the distribution of *T. erytreae*. For example, in Ethiopia the main area with heavy infestation of this triozid is located at altitudes of more than about 1,500 m [10], much higher than the altitude that indicates the lower limit of the *T. erytreae* prevalent area in the Transvaal, South Africa [369]. This would probably be a reflection of the much harsher climate for *T. erytreae* in Ethiopia than in South Africa.

As for ABATE [10], it is also noted that he observed *Ficus sycomorus* (cf. section 2-2) harboring heavy populations of *T. erytreae* in many areas along the rift valley lying between altitudes of 950 and 1,600 m. Provided that the taxonomical identification of his psylloid collections was correct, the phenomenon he observed is of keen interest.

Quite different from *T. erytreae*, *Diaphorina citri* is prosperous under a hot and dry climate. In his survey conducted in Reunion, where both species were distributed, CATLING [109] did not find *T. erytreae* on the western coastal plain, the hottest and driest part of the island. In the island *T. erytreae* was predominant above an elevation of 500 m, while *D. citri* was predominant below 400 m. However, this does not mean that the areas of the distribution of both species were distinctly separated from each other. In fact, there were two sites where the two species were observed to coexist.

D. citri is more tolerant to weather extremes and higher in climate adaptability than *T. erytreae*. It is usually abundant in low lands but even at considerably high altitudes its populations occasionally attain an epidemic level. For instance, in Sichuan, China, of three citrus orchards observed between elevations of 1,090 and 1,210 m, two were so severely infested with *D. citri* that nearly 100% infection of greening disease had been realized there, and in the other one greening infection rate was 40% with the presence of psyllids [554]. At the same survey no psyllid was recorded in any of the orchards observed at altitudes of more than 1,400 m.

Through their laboratory and outdoor experiments, XIE et al. [546] found that *D. citri* is able to survive low temperatures that are lethal for citrus. According to them, however, a long spell of low temperatures (such as more than 100 hours between -2 and -5℃) affected seriously the survival of adult insects. In some other articles it is pointed out that a severe winter with a continuance of temperatures lower than usual tends to suppress more or less notably the upsurge of psyllid population in the following spring

[25r, 555].

Judging from the findings mentioned above, it is believed that extremes of low temperatures often exert decisive influence on the distribution of *D. citri* in areas of high altitudes or high latitudes. In contrast, extremely high temperatures do not seem to restrict the distribution of the psyllid so often, though their impact on psyllid populations is not negligible. In Haryana, India, the nymphal population declined sharply during May and June, when rises in daily maximum temperature above 40℃ were often accompanied with low evening relative humidity of 10 to 30% [270]. Nevertheless, extinction of the psyllid has not taken place there.

In the world there still exist regions free from both *T. erytreae* and *D. citri* in spite of their possession of climatic conditions suitable for the species. The Mediterranean basin and South America but Brazil can be mentioned as examples. BOVÉ [67], who has analyzed the infestation of both species in the Arabian peninsula, warns of the possible danger of invasion of these vector insects into the Mediterranean region and emphasizes the necessity of strengthening plant quarantine against it.

3-2. Complex of factors governing seasonal prevalence

3-2-1. Host plant conditions, especially flushing rhythms of citrus

According to CATLING [106], the fundamental factors governing *Trioza erytreae* populations on citrus plants in southern Africa are flushing rhythm and occurrence and sequence of lethal weather extremes, and natural enemies and flush quality are ecological factors of lesser importance. VAN DEN BERG and NEL [508] has given a diagram showing seasonal transitions in combination and interaction of prevalent ecological factors as summarized in the following : In spring, the phase of population increase, there exist plentiful and nutritious flushes and extremes of climate are critical for short periods. In midsummer, when high population sooner or later decline rapidly, high parasitism and a rapid decrease in flush volume are characteristic. In autumn, when triozids are low to moderate in number, all factors operate but seasonal weather conditions and flushing rhythm are relatively important. And in winter, the phase of population stagnation, small or negligible flush volume restrains the production of offspring.

In spring and early summer, the nitrogen content of young citrus flush is highest [105], and the proportion of egg to adult survivals in *T. erytreae* tends to be high [106]. Since phloem sap psylloids ingest is not always considered to be highly nutritious [203], the presence of abundant young flushes with high nitrogen content is significant for rapid multiplication of a *T. erytreae* population.

Field studies conducted by CATLING [100] in the Transvaal and Swaziland revealed that the prolonged flushing of citrus trees in the cooler, moister upland areas was more favorable to *T. erytreae* than the shorter, well-defined flush cycles prevalent in the arid, lowland areas. It can therefore be said that the climate in upland areas is not only directly but also indirectly advantageous to the triozid for building up large populations. CATLING [100] has also observed that winter nuclei of *T. erytreae* which were formed on small but significant winter flushes frequently developed into heavy populations in the following spring.

Flushing rhythms of citrus are primarily important for the *D. citri* population, too. The highest population peak usually takes place during the period of flush outburst after the dormant or semi-dormant season of citrus (for instance, HUSAIN and NATH [221], REGMI and LAMA [406]). In Indonesia NURHADI [367] has described some differences in seasonal fluctuation of psyllid populations between East Java, where the dry season is very distinct and, accordingly, flushing is usually well defined, and West Java, where a wet type of climate is prevalent and flushing is almost continuous.

Flushing on individual citrus trees is influenced by such factors as age and variety. It is well known that young trees are highly attractive to both *T. erytreae* and *D. citri*, because they grow vigorously, bearing plentiful flushes. In southern Africa, CATLING [100] frequently observed quite large populations of *T. erytreae* on immature trees even at the time when mature trees were semi-dormant. In the Philippines the rapid spread of greening disease in replanted groves is believed to be attributable to high attractiveness to the vector, *D. citri*, of abundant flushes on the young trees constituting those groves [99]. Trees affected with greening disease tend to have out-of-season flushing and this sometimes exerts an influence on the local vector populations [100].

At present there is no citrus cultivar resistant to the psylloids. The size of sustainable psylloid population, however, differs among cultivars. Lemon (*Citrus limon*) and lime (*C. aurantifolia*) are regarded as preferential plants for *T. erytreae*, because they offer frequently good quality flushes for oviposition [45, 46]. VAN DEN BERG [499] has demonstrated that when irrigated regularly, navel oranges (*Citrus sinensis*) bear flushes for most of the year and can support triozid populations best throughout the year, while in lemon continuous, vigorous flushing is restricted to a part of the year, but as far as this restricted period is concerned, lemons can support the highest triozid populations.

Lime is also mentioned as one of the preferred host plants for *D. citri* [34, 36]. In an area where *Murraya paniculata* hedge is common, this plant plays an important role as a reservoir of *D. citri* population. XIA and XU [543] have observed that *M. paniculata* bore fresh shoots more abundantly and harbored a significantly heavier psyllid population than citrus did.

3-2-2. Weather extremes

Since this subject was already discussed in section 3-1, some additional comments are given here.

It should be noticed that the occurrence and duration of weather extremes are considerably variable even in the same locality. For instance, Rustenburg, South Africa, was judged as quite unsuitable for *T. erytreae* from the result of the calculation of so-called 'band of probable saturation deficit index (SDI) values' based on meteorological data for six years from 1962/63 to 1967/68 (Fig. 3 in GREEN and CATLING [190]) *. However, when the authors analyzed meteorological data over longer periods and calculated a trend in 'annual accumulated lethal-range SDI values', they found some years most

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* This conclusion is contradictory to OBERHOLZER et al. [369] who mentioned Rustenburg as one of the areas with high infestation of *T. erytreae*.

favorable for the triozid in the 1940s and 1950s for Rustenburg.

CATLING [106] attached importance to frequency and timing of lethal weather extremes during the period of population rise following the winter stagnation, because they largely determine the rate of the population increase and the population peak to be attained (cf. Fig. 4 in his article).

In the case of *D. citri*, adverse effect of rainfall has been pointed out by many authors (for instance, LAKRA et al. [270]). Heavy rains are reported to wash eggs and nymphs off the young shoots where they were present [406, 544]. It is guessed that rainfall would also cause significant depression or sometimes interruption of the egg-laying activity of female adults.

3-2-3. Natural enemies and competitors

Prior to discussing the controlling effect of natural enemies, comments are presented on the scientific names of some of the parasitoids concerned.

a) PRINSLOO [379] has pointed out that the eulophid parasitic on *Trioza erytreae* in southern Africa is not *Tetrastichus radiatus* Waterston but *T. dryi* Waterston. Therefore, *T. radiatus* mentioned in such articles as ANNECKE and CILLIERS [20], CATLING [101, 106, 107] and MCDANIEL and MORAN [318] should be read *T. dryi*.

b) Both *T. dryi* and *T. radiatus* have been transferred to the genus *Tamarixia* by M. W. R. de Graham in 1987*. Therefore, *Tetrastichus radiatus* = *Tamarixia radiata*.

c) HAYAT [196] has established a new genus, *Diaphorencyrtus* (Encyrtidae) and transferred *Aphidencyrtus aligarhensis* Shafee, Alam et Agarwal, a parasitoid of *Diaphorina citri*, to the new genus. PRINSLOO [383] has suggested that *Aphidencyrtus diaphorinae* Myartseva et Tryaptzyn is most likely a synonym of *D. aligarhensis*. Independent of this, LIN and TAO [281] have described a new species, *Psyllaephagus diaphorinae*, from Taiwan. SHUI-CHEN-CHIU et al. [468] have presented their opinion that the Taiwanese encyrtid species described under the name of *Psyllaephagus diaphorinae* Lin et Tao is *D. aligarhensis*.

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* *Bull. Br. Mus. Nat. Hist. (Ent.)*, 55 (1), 392p. (Citation from QUILICI [393])

d) AUBERT and QUILICI [46] commented that the encyrtid parasitic on *D. citiri* might not have been *Psyllaephagus harrisoni Robinson* as described by ÉTIENNE [145] and ÉTIENNE and AUBERT [146]. They considered the correct name to be *D. aligarhensis*.

All the species mentioned above attack the nymphal stages of hosts. Neither *T. erytreae* nor *D. citri* has any reliable record on egg parasitoid (GHESQUIÈRE [174] described the encyrtid, *Psyllechthrus oophagus*, as an egg parasitoid of *T. erytreae*, but he himself has since offered a doubt about the taxonomic identification of the host species [175]).

As mentioned by MCDANIEL and MORAN [318], the ectoparasitic eulophid, *Tamarixia dryi* (the authors tentatively used the name *Tetrastichus ?radiatus*), and the endoparasitic encyrtid, *Psyllaephagus pulvinatus* Waterston, are the principal primary parasitoids of *T. erytreae* in southern Africa. CATLING [101] has emphasized the importance of the synchrony between these parasitoids and the host. He found that during periods of favorable synchrony at least 40-50% of the susceptible stages were parasitized but under conditions of poor synchrony parasitism frequently dropped below 10%. According to Fig. 2 in his article, a summary of the results of his field work conducted at one of his observation sites, considerably high parasitic activity took place from the early season when the host still remained at a low level of density, nevertheless later the host population showed a steep rise until attaining the first, highest peak. This fact suggests that the parasitoids are not so powerful as to overcome the host population vigorously multiplying in a favorable season. The same figure in CATLING [101] also indicates high activity of the secondary parasitoid, *Aphidencyrtus cassatus* (Encyrtidae) (= *Aphidencyrtus* sp. in his article), in later season. CATLING, however, does not think that this species was likely to seriously influence the parasitism of *T. erytreae*.

T. dryi and *P. pulvinatus* were found to attack another triozid, *Trioza* sp., feeding on two common species of creepers [101]. The author has pointed out the role of the alternate host as a natural, unsprayed reservoir of the parasitoids.

A. cassatus attacks both *T. dryi* and *P. pulvinatus*. Other than this secondary parasitoid there are a variety of minor secondary parasitoid species, some of which are also tertiary, as shown in a diagram presented by McDaniel and Moran [318] (according to Prinsloo [382], *Marietta exitiosa* and *Euxanthellus* sp. in the diagram should be *M. javensis* (Howard) and *E. philippiae* Silvestri, respectively). In Africa, with the exception of southern Africa, *T. erytreae*-parasitoid relationships have not yet been clarified to any great extent.

T. radiata is the most important of the parasitoids of *D. citri*. In India, according to Husain and Nath [221], the percentage of the parasitism was often so high that as many as 95% of the nymphs might occasionally be parasitized. Their opinion is that in localities where *D. citri* is present but does not increase greatly in numbers, this parasitoid is functioning as a factor regulating the psyllid population. *T. radiata* has been reported not to be naturally distributed in Taiwan [468] and the Philippines [99].

In West Java no parasitoid attacking *D. citri* has been reported, while in East Java *D. aligarhensis*, on one hand, is widely distributed in almost all citrus growing areas and *T. radiata*, on the other hand, is only sporadic for unknown reasons [367]. As pointed out by Prinsloo [383], it is likely that *D. aligarhensis* is widely distributed in the Oriental region. In fact, records of this parasitoid have come from the Philippines [172] and mainland China [392], and probably from Taiwan as mentioned above [468]. There is a report that the number of *D. citri* killed in host feeding by *Psyllaephagus diaphorinae* (? = *D. aligarhensis*) was larger than that in parasitism by the same parasitoid [281].

Both *T. radiata* and *D. aligarhensis* have complicated relationships with hyperparasitoids [220[r], 392, 468]. In Taiwan, a comparison in species composition of hyperparasitoid fauna has been made between *D. aligarhensis* and *T. radiata*, the latter of which is an alien introduced into Taiwan as a biological control agent, and revealed that some of the main species parasitic to *D. aligarhensis* were also attacking *T. radiata* [127, 128, 128-1]. This fact should be noticed because the introduced parasitoid suffered from indigenous hyperparasitoids within a few years of its introduction.

Outstanding success in biological control of *T. erytreae* and *D. citri* has been accomplished by using the eulophids, *T. dryi* and *T. radiata* in Reunion. This topic is dealt with in section 4-1.

As predators, lacewings, syrphids, coccinellids, mites and spiders are common to many species of Psylloidea [203]. Some of them, however, have been reported to show a marked preference for aphids that are sympatric with psylloids on the citrus tree [103, 508].

In case of the pear psylla, *Psylla pyri* (L.), the anthocorid, *Anthocoris nemoralis* (F.), which is known as most commonly preying on psylloids, is included in the biocomplex of the psyllid [17c, 199c]. Among the predators of *T. erytreae* and *D. citri*, however, there seems to exist no species with such a high degree of dependence on psylloids as *A. nemoralis.*

Furthermore, CATLING [103] found that predators were poorly synchronized with *T. erytreae* during early summer, when the triozid were undergoing a rapid population build-up, although in midsummer they were observed to assist in suppressing triozid populations together with several other factors such as weather extremes and parasitoids.

In Reunion predators were unable to reduce the population level in either *T. erytreae* or *D. citri* due to a conspicuous time lag in the build-up of their populations during the spring flush of host plant growth [146]. Concerning *D. citri*, the same phenomenon was observed in Nepal [272]. On the other hand, CHEN [126] has reported to detect highly effective predacious activities in his life-table study of *D. citri*.

In their research work carried out at citrus groves under an integrated control program in South Africa, VAN DEN BERG et al. [506] are likely to rate the role of the predators somewhat higher than CATLING [103] or ÉTIENNE and AUBERT [146] did. They attach importance to spiders in particular and also evaluate the predatory effect of ants on indigenous rutaceous plants and in orchards where ants are not controlled. SADANA and KAUR [418r] suggest usefulness of the salticid spider, *Marpissa tigrina* Tikader, as a naturally occurring biological control agent, because the salticid was found to be a voracious feeder on *D. citri* through their laboratory experiments.

In *T. erytreae* and *D. citri*, since oviposition and nymphal growth take place only on flush points of host plants, it is natural to consider that intraspecies competition due to overcrowding is apt to happen around a population peak with extremely high density. In fact, CATLING [100] attributed the cause of a crash of *T. erytreae* population observed in the midsummer of a certain year to mortality heightened due to overcrowding.

Interspecies competition with sympatric aphid species, especially *Toxoptera citricidus*, has also been reported [100, 543].

3-3. Dispersal and its relationship with the disease dissemination

HODKINSON [203] gives a sketch on dispersal behavior of Psylloidea. In brief, the ability of adults to fly any distance under their own power is restricted, but it is also true that there are certain species that disperse long distances on air currents. In addition, he has presented many examples of psylloid species of economic importance which are spreading their influential area over wide ranges by means of artificial transportation with plant materials [202c].

As Psylloidea are commonly called 'jumping plant lice', adults of this group of insects easily jump and fly off from the host plant when disturbed. After leaving the plant, however, they usually show no tendency to continue flying any distance by themselves as mentioned above.

H. D. Catling observed the flight habit of both *Trioza erytreae* and *Diaphorina citri* as follows. In *T. erytreae* adults circled several times in the air and then resettled near the taking-off point [108]. The behavior of *D. citri* adults appears to be fundamentally the same. They flew strongly for a few seconds before alighting near their taking-off point [99].

It should be noticed that the flight habit of *T. erytreae* adult has another aspect which was not described above. In this connection, CATLING [108] was aware that *T. erytreae* adults were potentially 'powerful fliers'. SAMWAYS and MANICOM [430] observed the process of adult invasion in spring from the adjacent citrus orchard to their experimental plot where all foliage of citrus was removed during the preceding winter to stimulate the spring growth of new shoots. As a result of strong attraction to new flushes, adults invaded the plot in exponentially increasing numbers exhibiting unexpectedly high flight activity. Nevertheless, SAMWAYS [426] later obtained poor results in his mass-trapping experiments using yellow sticky surfaces and pesticide-treated trap trees ; the *T. erytreae* population in the experimental block remained unchanged contrary to his expectation of success in trapping so many adults as to bring about a significant reduction of the population. According to him, the failure of the experiments appears to have been associated with host plant and climatic conditions. As these conditions were apparently suitable for the adults at the time of experiment, they probably did not take off from their breeding sites in spite of the presence of the yellow surfaces as a stimulant.

Thus, SAMWAYS [426] explains the two contradictory aspects of the flight habit of *T. erytreae* as follows : when conditions are favorable, the adult is relatively immobile and disperses only weakly, but when conditions become adverse, it exhibits a considerable power of dispersal to locate a new flush point.

In *D. citri*, too, it is well known that adults are strongly attracted to plentiful new flushes on young citrus plants and in the area infested with the psyllid, greening disease tends to spread rapidly in plantings with such young trees. Therefore, the species is believed to display its great ability to locate new flush points under certain conditions. At the same time, B. Aubert (personal communication) is aware that the flight behavior of *D. citri* contains something different from that of *T. erytreae*. He has been conducting a study to detect it.

As mentioned above by citing HODKINSON [203], dispersal of such tiny insects as psylloids is largely assisted by prevailing winds. According to field trials carried out by VAN DEN BERG and DEACON [505], *T. erytreae* adults released in a ploughed open land were able to disperse with the aid of prevailing winds to a distance of at least 1.5 km. It should be noticed, at the same time, that a tendency toward even distribution has been reported by SAMWAYS [428] ; he observed that the mean density of adult *T. erytreae* at a certain locality of the eastern Transvaal was not significantly different for managed citrus, neglected citrus and natural rutaceous bush, which were all distributed there. In this case there may have existed such a condition to enable the triozid to diffuse all sides as an absence of the prevailing winds toward a definite direction.

In Reunion a field plot consisting of 220 disease-free Valencia sweet orange (*Citrus sinensis*) was established in 1970, and after a latent period of five years values of an index showing the severity of greening disease continued rising exponentially until 1979, the disease being always severer in the western half of the plot than in the other half [189]. Statistical analyses by the authors indicate that the disease moved from west to east in spite of the prevailing winds from the eastern direction. Therefore, the vector migration from nearby infected groves would have been against the prevailing winds, suggesting disease dissemination as the result of active migration of the vectors rather than passive transport due to wind (according to GOTTWALD and AUBERT [187], the vector species concerned was *D. citri*).

AUBERT [38] points out a fairly great possibility of long transportation of *D. citri* due to strong winds in the regions with frequent attacks of typhoons.

In their insectary experiment using single *T. erytreae* adults, CATLING and ATKINSON [110] revealed that only 1.6% of the insects tested were able to transmit greening disease. As suggested by McCLEAN [313], such low transmission efficiency would be compensated by the large numbers of adults that emerge during some flush periods.

In *D. citri* very low transmission efficiency has been reported by HUANG et al. [214]. However, XU et al. [550] have obtained a high rate of infection with the psyllid in their experiments with serial exposure of test plants to single adults.

In the Philippines close relationship was found between size of the vector population and spread of the disease [16]. In Java large farms situated some distance from villages were mostly free from the disease even when in the villages there existed a lot of diseased backyard citrus trees [531]. In Thailand, as illustrated by SCHWARZ et al. [455], main citrus growing areas are distributed being more or less distinctly separated from one another, and there is a wide variation in the incidence of greening disease among these areas, this probably suggesting independence to a considerable extent of the respective areas concerning the infestation with the psyllid vector. SCHWARZ et al. [455] also found that in two of the severely affected areas there were a number of orchards which were completely free from the disease, probably because they were protected from *D. citri* by being surrounded with rubber plantings and bamboo hedges, respectively.