The Influence of Weather on the Survival and Population Fluctuations of *Trioza erytreae* (Del Guercio)—A Vector of Greening

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THIS PAPER, which summarizes recent work on the influence of weather on populations of *T. erytreae,* draws heavily on the results of field studies carried out in the northern Transvaal (South Africa) and in Swaziland from 1965 to the present (1, 2, 4, 5). It should be read in conjunction with a companion paper in this book (3) which discusses other factors that regulate populations of *T. erytreae.*

Many species of Psyllidae are known to be intolerant of high temperatures. Van der Merwe (6) first reported the sensitivity of the nymphal stages of *T. erytreae* to summer temperatures, but it was only comparatively recently that the effect of temperature was studied in detail. Under controlled, fluctuating conditions in the laboratory, Moran and Blowers (7) found that all stages flourished when the daily maximum temperature did not exceed 25°C. But with several hours per day at 32°C there was a high mortality, particularly of the egg and young nymphal stages. Catling (1, 2) and Catling and Annecke (4) showed that in the field the simultaneous occurrence of high temperatures and low humidities produce lethal conditions. The moderating effect of shade was indicated by the occurrence of high populations near windbreaks, by the choice of breeding sites on the lower section of the tree canopy, and by small trees at low altitudes being infested only in the cool months (2).

Survival of Eggs and First Instar Nymphs

The influence of weather on the survival of the immature stages of *T. erytreae* was studied by making a large number of in situ counts in 4 major study groves, 3 at varying altitudes in the Letaba district of the northern Transvaal and 1 at Malkerns in Swaziland. By marking colonies in the egg stage and following up with detailed counts at regular intervals until the emergence of adults, complete life tables were constructed showing the influence of prevailing weather. Meteorological data were recorded by means of thermohygrographs housed in standard Stevenson screens at each site.

Preliminary results indicated that the advanced nymphal stages are much more tolerant of severe weather extremes than are the eggs and first instar nymphs. This was confirmed by the laboratory exposures of Moran and Blowers (7), who showed this heat tolerance to increase with successive moults, the fully mature adult being the most resistant. Due to the occurrence of distinct field generations or "broods" when at regular intervals the bulk of the population is present as eggs and first instar nymphs, it was decided to investigate and define the precise temperature-humidity tolerance for these critical and highly vulnerable stages.

In the northern Transvaal, survivals from 32 in situ counts, involving more than 10,000 insects, were related to prevailing weather. Preliminary analysis indicated a definite trend for a decrease in survival with a rise in temperature or a decline in relative humidity (RH). Within the range studied, however, these conditions became lethal only when applied simultaneously. Additional data were obtained from a similar series of 23 counts following the fate of another 21,000 insects in Swaziland. A correlation analysis was then made between the percentage survival over the 8–13 days (mean of 10 days) of this stage and 19 aspects, or elements, of temperature and humidity. Those aspects of weather involving both temperature and humidity were shown to be the most significantly correlated with survival. The two most acceptable predictors of survival were mean daily maximum temperature with mean vapor pressure as a simple combination ($r=0.802$, $P<0.001$), and mean daily maximum saturation deficit (SD) as a single aspect ($r=-0.755$, $P<0.001$).

A scatter diagram and regression curves for survival against SD are shown in Figure 1. The variation is believed to be due to the operation of additional factors such as differences in the density of leaf canopy, foliage condition, and the differential effects of lethal weather on different stages in the development of eggs and nymphs. The closeness of the 2 survival curves indicates very similar temperature-humidity tolerances for local populations 270 km apart.

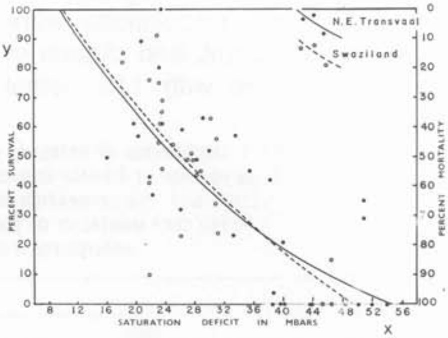

FIGURE 1. *Scatter diagrams and regression curves for egg to first instar nymph survival of* T. erytreae *(Y) against mean saturation deficit (X) for the 3 severest days of count. Northern Transvaal:* $Y=0.03\ X^2-4.18\ X+137.77$*; SE of estimate = 19.99 percentage units. Swaziland:* $Y=0.02\ X^2-3.70\ X+154.80$*; S.E. of estimate = 17.76 percentage units. After Green and Catling (5).*

Because lethal extremes are often masked by monthly means, the frequency and timing of daily SD values exceeding 34.6 mbars ("lethal days") are used in estimating survivals of *T. erytreae*.

Influence of Lethal Weather on Vector Populations

Population fluctuations of all stages of the vector were recorded at weekly to fortnightly intervals at 4 major study groves. In addition, several observation groves were selected in each region. In both study districts, moderate to high vector populations were recorded only in the upland, cool, moist regions.

In the Letaba district, *T. erytreae* was constantly active at the Forest Hill grove (Table 1) with a total of only 7 "lethal days," there being a similar cycle of seasonal abundance to that shown for Malkerns in Figure 2. On the other hand, populations were negligible in the hot, arid climate of the Letaba grove with 115 "lethal days," and, apart from small scattered infestations on the spring flush and in some years on the midsummer flush, low populations characterized the surrounding groves at this altitude. The Fairview grove with 65 "lethal days" was intermediate for altitude, weather extremes, and vector populations. At the outset of the study, the numbers of former vector colonies, as indicated by leaves pitted by nymphal feeding, revealed an identical, and linear, relationship with altitude. The higher populations recorded during the 1966–67 season were largely explained by differences in prevailing weather.

TABLE 1. OCCURRENCE OF EXTREMES OF WEATHER LETHAL TO POPULATIONS OF *T. erytreae* AT 3 STUDY GROVES IN THE NORTHERN TRANSVAAL; ON A "LETHAL DAY" THE SATURATION DEFICIT EXCEEDS 34.6 MBARS, CAUSING A 70 PER CENT MORTALITY OF EGGS AND FIRST INSTAR NYMPHS WHEN APPLIED FOR 3 DAYS (SEE FIGURE 1)

		Number of "lethal days"														
		1965						1966							1967	
Study grove	Altitude	D	J	F	M	A	M	J	J	A	S	O	N	D	J	Total
Letaba	640 m	17	20	1	5	9	6	2	5	6	8	11	9	11	5	115
Fairview	920 m	7	14	1	1	6	2	0	0	6	8	9	6	3	2	65
Forest Hill	1380 m	1	0	0	0	1	0	0	0	0	2	2	0	0	1	7

Weather is believed to be the main factor which regulated the size of vector populations at the Malkerns study grove from February 1967 to October 1969. Figure 2 shows that in the first season the population surged to a high peak in September and persisted at high densities until the crash in the first week of January. From July to January there were 13 "lethal days," only 1 occurring prior to the September peak population. Five "lethal days" occurred between September 27 and October 7 when the bulk of brood 5 was in the more tolerant third to fifth instar stage, but a slight hesitation in the rise of brood 6 was evident, many young colonies being decimated by these extremes. With the continual laying of new batches of eggs by tolerant adults, the advent of favorable weather at the end of October permitted the rise of brood 6.

In the following season populations were considerably lower, and there were 31 "lethal days" between July and January. Five "lethal days" occurred between July 11 and 28 when the bulk of brood 5 was present as eggs and young instars. There were 3 "lethal days" at the start of the following brood and, as in the previous season, a severe spell of hot, dry weather postponed the rise of the October brood. Due to the 8 "lethal days" between September 27 and October 19, no definite rise of egg colonies was evident for 4 weeks, and populations were at very low densities until early December. Very favorable weather in November and the first 2 weeks of December resulted in brood 8 momentarily approaching the densities recorded in 1967, but another hot, dry spell in the third week of December contributed to an early population crash for the season.

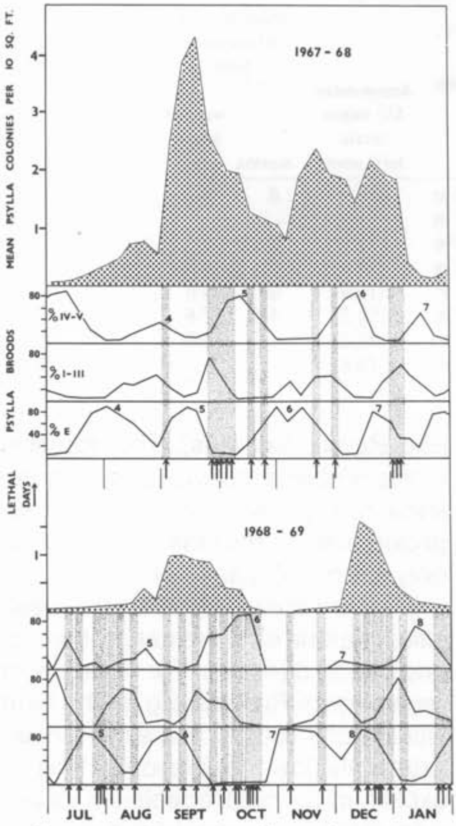

FIGURE 2. *Population fluctuations, broods of* T. erytreae, *and the occurrence of "lethal days" in a grove at Malkerns, Swaziland, for the 1967–68 and 1968–69 seasons. On each "lethal day" the saturation deficit exceeded 34.6 mbar. After Catling (2).*

Extreme conditions continued into February when the mean monthly maximum temperature was 3.4°C above, and mean RH at 1400 hours 11 per cent below the 10-year average. There were 5 "lethal days" in this month in contrast to 1 the previous season. Probably as a direct result of these severe conditions vector populations reached their lowest levels for the entire study period during late summer and winter of 1969. At the end of July, population densities were approximately one-fifth of those registered in the 2 previous seasons. As a result of this smaller residual population, there was a slow buildup on the spring flush cycle in August and September of 1969.

A Weather Index in Relation to Vector Outbreaks

A saturation deficit index (SDI) was derived from the survival regressions shown in Figure 1 by computing the mean of the 3 maximum daily SD values for successive 10-day periods, each period overlapping its predecessor by 5 days. The 73 SDI values obtained for a given year represent a near-continuous graph of the estimated egg to first instar mortality caused by extremes of weather. Series of SDI values were then computed for periods of 3–12 years for the 8 weather stations situated in certain of the main citrus areas of southern Africa (Table 2). The 34.6 mbar SDI level, which corresponds to a level of 70 per cent mortality (Fig. 1), was defined as the lethal threshold, higher values lying in the lethal range. Comparisons of weather-induced mortality near different stations in a given year were made mainly in terms of a summation of SDI units in the lethal range and termed the annual accumulated SDI. Where mean conditions were considered for several years, as in 6 of the 8 stations in Table 2, a band of probable SDI values, based on standard deviations, was described to show the seasonal trend of lethal weather. The citrus areas were then compared on the basis of the seasonal duration of the band in the lethal range and on the relative area of this band projecting into the lethal range.

TABLE 2. ACCUMULATED SDI VALUES AND CHARACTERISTICS OF THE SEASONAL BAND OF PROBABLE SDI VALUES IN EXCESS OF THE 34.6 MBAR BASELINE FOR 8 STATIONS IN CERTAIN MAJOR CITRUS AREAS OF SOUTHERN AFRICA

Station	Area	Altitude	Accumulated SDI values totals for 3 years	Characteristics of seasonal band	
				months	width in relative area
Big Bend	Swaziland	150 m	424.7	8	7.2
Malelane	E. Transvaal	360 m	411.3		
Rustenburg	W. Transvaal	1160 m	472.9	7	7.1
Addo	E. Cape Prov.	85 m	271.4	7	4.3
Nelspruit	E. Transvaal	660 m	310.0	5	4.0
Elsenburg	W. Cape Prov.	180 m	155.2	4.5	2.6
Malkerns	Swaziland	730 m	82.8	2.5	1.0
White River	E. Transvaal	900 m	75.8		

SUMMER RAINFALL AREAS.—The increase in vector activity with rise in altitude was shown to occur along the eastern escarpment areas of the Transvaal and Swaziland, and is also known to occur in Natal, Rhodesia, and even in Réunion and Madagascar. The effect is clearly explained in Table 2, which compares the annual accumulated SDI values for neighboring escarpment stations in the eastern Transvaal (Malelane, Nelspruit, White River) and in Swaziland (Big Bend, Malkerns). The duration of the probable SDI values within the lethal range is seen to vary from approximately 8 months at 150 m to only 2.5 months at 730 m.

In inland areas further to the west, altitude alone is no indicator of vector population densities. For instance, in recent years Rustenburg, at the high altitude of 1160 m, has experienced extremely low populations. This is explained by the probable SDI values calculated for these years that enter the lethal range for up to 7 months of the year (Table 2).

CAPE PROVINCE CITRUS AREAS.—The negligible vector populations characterizing these areas cannot be fully explained by the magnitude of the accumulated SDI values. It is necessary here to consider the timing of the peak SDI values in relation to the seasonal abundance of the vector. In the summer rainfall areas discussed above, peak SDI values occur in spring and early summer when populations tend to be well established on vigorously flushing trees. Under these conditions the more resistant stages are capable of producing a substantial population recovery following short periods of lethal conditions. In the Cape areas, however, the peaks fall in mid- to late summer when the trees are reported to be relatively devoid of flush and when the other limiting factors are more severe. Thus, there is a low potential for population growth, lethal weather at this time being especially crippling to vector populations.

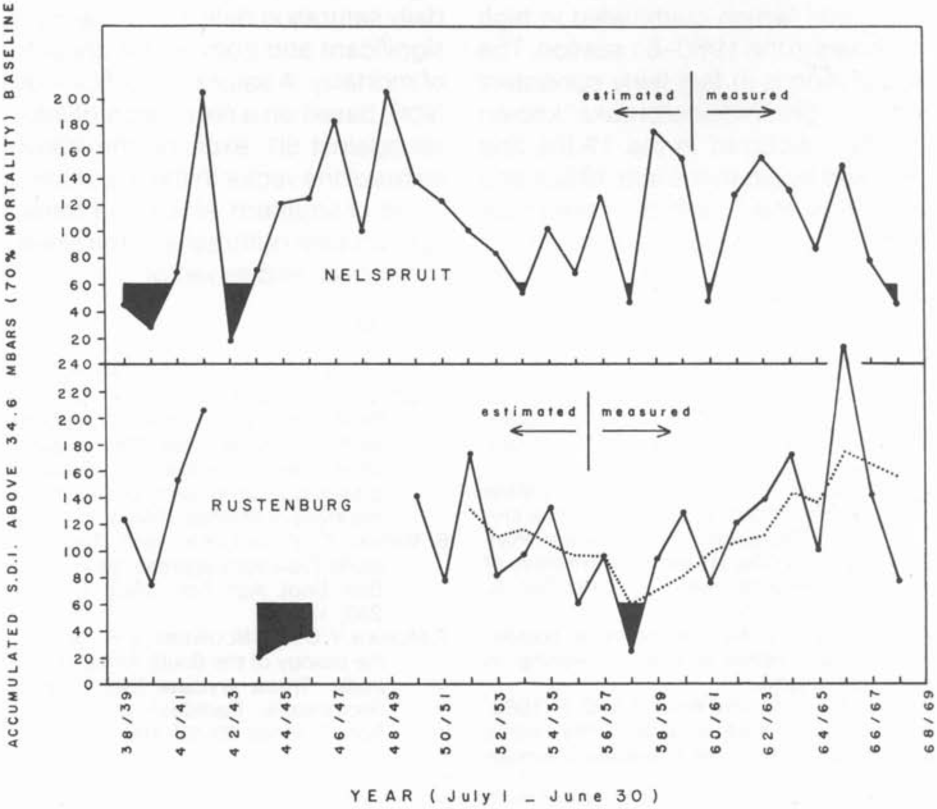

FIGURE 3. *Long-term trends in the annual accumulated lethal range saturation deficit index (SDI) values of* T. erytreae *for Nelspruit and Rustenburg, Transvaal. The shaded areas indicate values typical of those where the vector is more abundant. The broken line represents a running mean SDI value calculated from the year in question plus the 2 preceding years. After Green and Catling (5).*

PREVIOUS OUTBREAKS OF GREENING AND ITS VECTOR.—The SDI was also found to throw light on past outbreaks of *T. erytreae* and greening in the Nelspruit and Rustenburg districts. Accumulated SDI values estimated for a 30-year period for these 2 districts are shown in Figure 3. It is suggested that vector outbreaks occurred at Nelspruit in the years 1938–39 to 1942–43, that there followed a 10–12 year period when populations were at low levels, and that a gradual buildup began in the early '50s, which culminated in high numbers in the 1960–61 season. The suggestion is in fact fairly consistent with the "greening outbreaks" known to have occurred in the 1930s and '40s and again in the late 1950s and early '60s, the 2 "cycles" being separated by relatively low levels of the disease. In Rustenburg, low SDI values in the late 1950s would have favored vector populations and could account for the similar outbreak of greening.

Conclusions

Extremes of weather appear to play a dominant role in regulating the numbers of *T. erytreae.* All stages of the vector are sensitive to high temperatures combined with low humidity, eggs and first instar nymphs being particularly vulnerable. Maximum daily saturation deficit (SD) is a highly significant and convenient predictor of mortality. A saturation deficit index (SDI), based on a regression of survival against SD, explains the known status of the vector in the major citrus areas of southern Africa and throws light on past outbreaks of the greening disease and its vector.

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