Title
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 produces 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 molts, the fully mature adult being the most resistant. Due to the occurrence of distinct field gen-
erations 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 anal-
ysis indicated a definite trend for a
decrease in survival with a rise in tem-
perature or a decline in relative hu-
midity (RH). Within the range studied,
however, these conditions became
lethal only when applied simultaneously.
Additional data were ob-
tained from a similar series of 23
counts following the fate of another
21,000 insects in Swaziland. A cor-
relation analysis was then made be-
tween the percentage survival over
the 8–13 days (mean of 10 days) of
this stage and 19 aspects, or ele-
ments, 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 tempera-
ture 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 differ-
ences 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.

Because lethal extremes are often
masked by monthly means, the fre-
cency and timing of daily SD values
exceeding 34.6 mbars (“lethal days”) are
used in estimating survivals of T.
eritreae.

**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 mid-summer 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.

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 pre-

### 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)

<table>
<thead>
<tr>
<th>Study grove</th>
<th>Altitude</th>
<th>1965</th>
<th>1966</th>
<th>1967</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>J</td>
<td>F</td>
<td>M</td>
</tr>
<tr>
<td>Letaba</td>
<td>640 m</td>
<td>17</td>
<td>20</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Fairview</td>
<td>920 m</td>
<td>7</td>
<td>14</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Forest Hill</td>
<td>1380 m</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
vious 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.

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 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.

**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**

<table>
<thead>
<tr>
<th>Station</th>
<th>Area</th>
<th>Altitude</th>
<th>Accumulated SDI values totals for 3 years</th>
<th>width in months</th>
<th>width in relative area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Bend</td>
<td>Swaziland</td>
<td>150 m</td>
<td>424.7</td>
<td>8</td>
<td>7.2</td>
</tr>
<tr>
<td>Malelane</td>
<td>E. Transvaal</td>
<td>360 m</td>
<td>411.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rustenburg</td>
<td>W. Transvaal</td>
<td>1160 m</td>
<td>472.9</td>
<td>7</td>
<td>7.1</td>
</tr>
<tr>
<td>Addo</td>
<td>E. Cape Prov.</td>
<td>85 m</td>
<td>271.4</td>
<td>7</td>
<td>4.3</td>
</tr>
<tr>
<td>Nelspruit</td>
<td>E. Transvaal</td>
<td>660 m</td>
<td>310.0</td>
<td>5</td>
<td>4.0</td>
</tr>
<tr>
<td>Elnsburg</td>
<td>W. Cape Prov.</td>
<td>180 m</td>
<td>155.2</td>
<td>4.5</td>
<td>2.6</td>
</tr>
<tr>
<td>Malkerns</td>
<td>Swaziland</td>
<td>730 m</td>
<td>82.8</td>
<td>2.5</td>
<td>1.0</td>
</tr>
<tr>
<td>White River</td>
<td>E. Transvaal</td>
<td>900 m</td>
<td>75.8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**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 (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.

![Graph](image)

**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.

Literature Cited

3. Catling, H. D. Factors regulating populations of psyllid vectors of greening. In this volume.