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Biology and population dynamics of the potential sugarcane Fiji disease vector *Perkinsiella saccharicida* (Homoptera: Delphacidae) in Réunion: evidence of its loss of biotic potential

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Abstract

There is a risk that irrigation schemes that have been developed to enhance sugarcane, *Saccharum* spp, cropping on the island of Réunion could markedly broaden the distribution range in which outbreaks of the insect *Persinkiella saccharicida* Kirkaldy (Homoptera: Delphacidae), a sugarcane Fiji virus disease vector, have already occurred. This trend was confirmed by the results of laboratory studies and monthly surveys carried out in six sugarcane fields distributed throughout the island. A complex of efficient entomophagous organisms were also observed, including *Tytthus* spp. (Hemiptera: Miridae), and they were found to be capable of reducing *P. saccharicida* populations. These latter planthoppers also seemed to have lost part of their biotic potential as compared to those of the same species in its endemic area abroad. It is thus recommended that pest species be carefully monitored in cropping areas where large-scale irrigation schemes have been developed.

Keywords: *Perkinsiella saccharicida*, biology, population dynamics, sugarcane, biological control, *Tytthus* spp., Réunion.

INTRODUCTION

The sugarcane commodity channel is a major economic entity on the island of Réunion. This crop is presently grown on a total area of 25 900 ha, or 60% of the usable arable land. The current increased productivity of this sugar- and fuel-oriented subsector has led to an increase in the sugarcane cropping area. French public authorities, with EU-funding support, have thus set up a large-scale irrigation scheme that is geared towards developing dry areas on the island. This spectacular project aims to transfer excess water from the eastern side of the island, under high rainfall conditions, to the western side where water is in short supply (Payet, 1997). This water diversion project—whereby water will be tapped from sites with high rainfall (Mafate, Salazie) and transited via some 30 km of tunnels through relatively inaccessible, rugged mountain areas—is aimed at making about 9 000 additional hectares of land suitable for sugarcane cropping (Fig. 1). In 1998, 1 500 ha was already being irrigated and the project will be under way until 2010, so a further 7 500 ha will also gradually be developed.

However, in terms of crop pests, this newly irrigated area has risks, especially of promoting the spread of certain piercing-sucking insects such as *Perkinsiella saccharicida* Kirkaldy (Homoptera: Delphacidae), which belongs to the species complex that was reviewed by Fennah (1979). This potential Fiji disease (FDV) vector is present in Réunion. FDV was first identified in 1890 in Fiji but is endemic to Papua New Guinea (Kerr, 1983). The pathogen belongs to the Rheoviridae family and is ultimately capable of killing the host plant (Rott et al., 2000). FDV has been detected in a third of all countries colonised by *P. saccharicida*, including Madagascar where the insect arrived in the eastern coastal region in the early 1950s. The fact that a susceptible sugarcane variety (M134-32) was planted on over 80% of the sugarcane cropping area apparently triggered this epidemic (Sigwalt, 1962). In Australia, this also occurred after cv POJ 2878 (1930-1940) and then cv NCo 310 were sown in the Bundaberg region in 1969-1977. Although FDV symptoms have not been detected in Madagascar since 1971, the conclusions of an FAO mission report state that it is not possible to definitively conclude that the disease has been eradicated from this region (Egan, 1991).

In Réunion, in the late 1980s, professional in sugar industry stakeholders are already worried about the potential impact of this type of disease since 80% of the cropping area has been replanted with cv R 570. This variety is high yielding but, according to the findings of tests carried out by the Australian Bureau of Sugar Experiment Stations, is highly susceptible to FDV. As no sure data are available on Fiji disease patterns in Madagascar—a country that is not far from Réunion and with which there is substantial trade—professional Réunion sugar industry stakeholders asked the French Agricultural Research Centre for International Development (CIRAD; Centre de coopération Internationale en Recherche Agronomique pour le Développement, France) to conduct a study to assess the potential benefits of preventive biological control treatments. Although this piercing-sucking insect is not yet infected, there is still a risk, especially since the virus may also be transmitted via sugarcane cuttings.

Here we present the results of a study which was carried out in 1989 and 1990 on the biology and population dynamics of *P. saccharicida* under the conditions that prevail in Réunion. No previous studies have focused on this insect on the island. Despite the age of these data, they will still provide a starting point for future studies conducted to check whether large-scale irrigation development schemes could change the disease-vector status of *P. saccharicida* and to assess the risk of FDV developing on the island.

MATERIAL AND METHODS

The study was carried out at six sugarcane cropping sites in Réunion (Fig. 1). Sugarcane is grown at elevations ranging from 0 to 600 m around the entire island. The mean monthly temperatures are shown in Fig. 2. Data collected at the measuring station closest to the study site was corrected to account for the difference in elevation between this and the six other study sites ($\pm 0.75^\circ\text{C}$ per 100 m elevation, correlation coefficient > 0.90 , Chopart et al., 2002). The eastern and western sides of the island differed markedly in terms of rainfall levels, while the northern and southern sides were transitional (Fig. 1, Table 1).

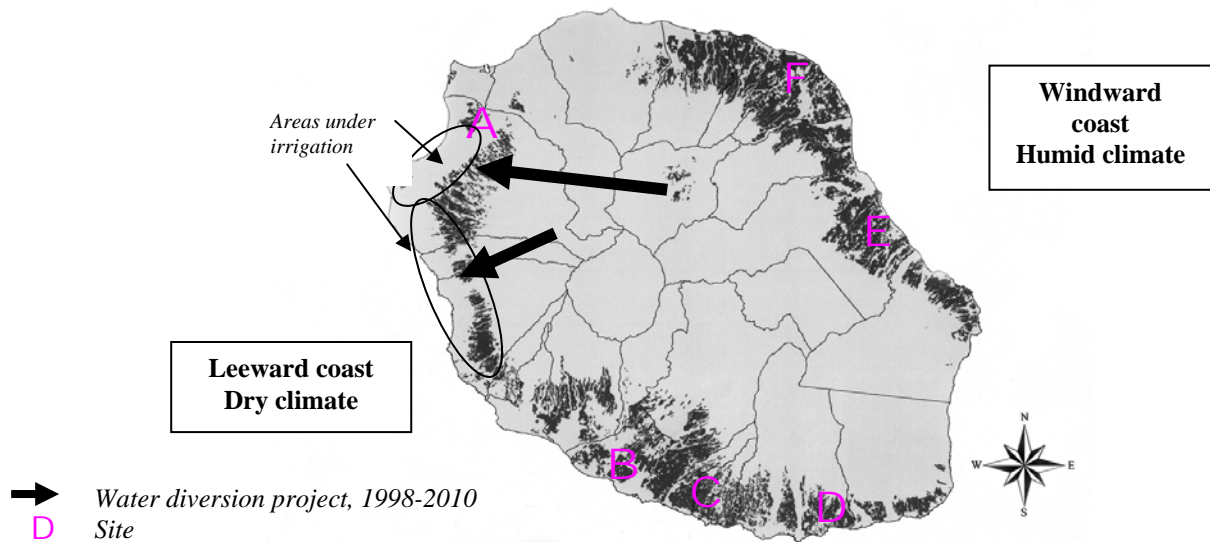


Fig. 1. The sugarcane cropping area and the six *P. saccharicida* study sites on the island of Réunion.

Table 1. Rainfall levels (mm) in the study areas recorded during the *P. saccharicida* survey (Réunion, 1989-1990).

Site	1989/1990								
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Le Port (Savanna, A)	11,4	10.4	65.4	14.2	64.5	8	41.2	3	22
Ligne Paradis (Le Gol, B)	4,5	15	45.5	5	112	109	29.5	40.5	60
No Station (Bassin Plat, C)	nd	nd	nd	nd	nd	nd	nd	nd	nd
Le Baril (Grande Anse, D)	238.4	108.4	851	211.6	391.8	284.8	412.2	203	202
Beaufonds (Beaufonds, E)	38.5	105.2	524.6	424.4	656.8	56.8	766.5	150.6	199.8
Gillot (La Vigne, F)	42	79.7	256.2	162.9	182.5	103.2	131.8	39.4	68

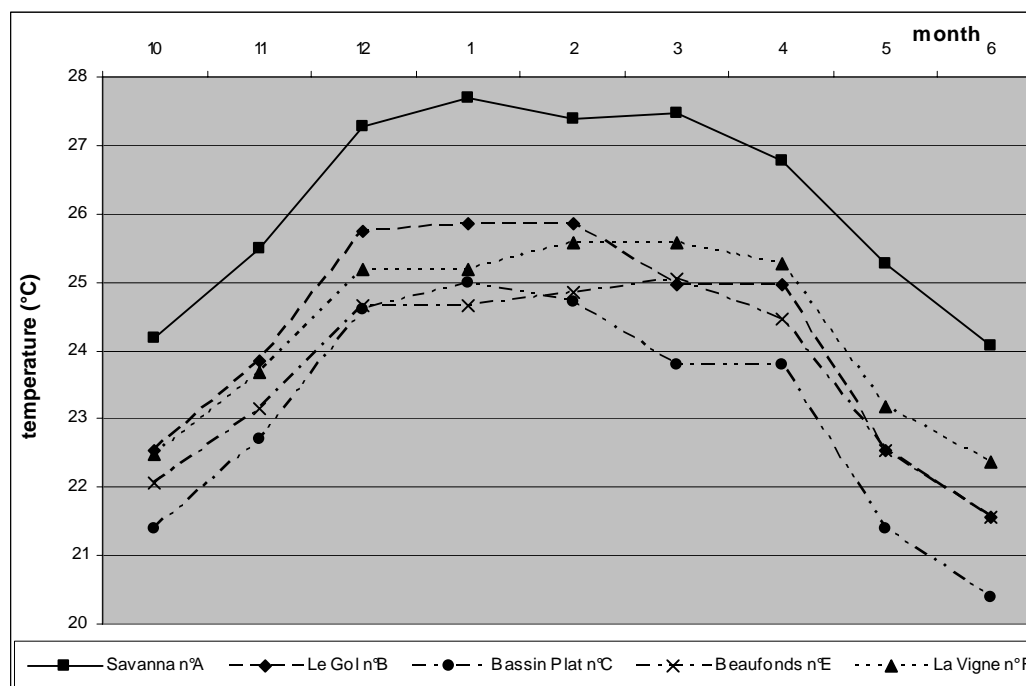


Fig. 2. Mean monthly temperature patterns recorded during the *P. saccharicida* survey at the study sites (Réunion, 1989-1990).

Experimental studies on the biology of the insect

Experimental studies were carried out on the biology of *P. saccharicida* in order to gain insight into its population patterns in the natural environment and to be able to compare the results with those obtained in other parts of the world where this pest prevails. These studies were conducted in climate-controlled rooms ($25 \pm 1^\circ\text{C}$, 60–70% r.h.; L16:D8).

Life cycle studies

Adult insects that had been reared under routine conditions (Taniguchi et al., 1980) were deposited on sugarcane leaves and left there for 2 h (Fig. 6, A.). Leaves on which eggs had been detected were placed in plexiglass boxes ($20 \times 10 \times 2 \text{ cm}^3$) with green moistened blotting paper on the bottom. This technique ensured high humidity in the boxes and facilitated the detection of nymphs after hatching. After 8 days, the eggs were monitored twice daily. Forty eggs were monitored overall. Each nymph was subsequently transferred to a cylindrical plastic box (4 cm dia., 1 cm height) with moistened blotting paper on the bottom and a screened opening to ensure air circulation. The nymphs were fed sugarcane leaves. They were monitored four times daily so as to determine exactly when moulting occurred. At each moult, exuviae were examined and removed from the boxes.

Fertility studies

After emergence, pairs of adults were placed in containers made with the bottoms of plastic water bottles (8 cm dia., 20 cm height). They were sealed with muslin and the bottoms were coated with moistened sterile sand in which a sugarcane leaf was inserted. The leaf was replaced daily throughout the adult life cycle and checked under a magnifying glass for the presence of egg clusters. After a female had laid its first egg, the length of the pre-oviposition period was noted. Then the number of clusters and eggs per cluster were recorded until the

female's death so as to determine its fertility rate. Ten pairs of insects were monitored in triplicate under the same rearing conditions.

Study on the effects of temperature on egg development

As field populations were found to decline during the cold season, a specific study was carried out to determine the egg incubation period according to temperature. Twenty egg clusters (reared eggs) were studied overall. The four treatments were as follows: i/ usual rearing conditions (25°C, L16:D8); ii/ 25°C, L11:D13); iii/ 20°C, L16:D8); and iv/ natural conditions: mean 22°C (min. 16.5°C; max. 28°C, L11:D13).

Studies on the population dynamics of *P. saccharicida* and associated organisms

The population dynamics of *P. saccharicida* and its antagonists were studied in two phases, i.e. a preliminary scouting operation and a monthly survey. The preliminary scouting involved visiting 23 sugarcane plots between 11 May and 26 June 1989, but only the overall results are reported here. This operation was supplemented by methodological trials (use of a D-Vac vacuum, model 1-A, D-Vac Company, P.O. Box 2506, Ventura California, 93002, USA; visual monitoring; trapping). The visual monitoring method of Bull (1981) was adopted to measure population patterns throughout the year. A monthly survey was carried out on sugarcane plots between October 1989 and May 1990. The monitored plots were sown with the R 570 sugarcane variety, which was 2–3 months old during the first visit and almost ripe at the end of the monitoring period.

The population dynamics criteria used in this study were the number of *P. saccharicida* adults and egg clutches. Visible adults were counted on 4 x 10 adjacent sugarcane stalks growing within a 1 ha area per plot. Eggs were counted on leaf 5 (from the top of the stem) on 10 groups of three adjacent sugarcane stems. This latter monitoring operation was facilitated by the fact that an incision made by *P. saccharicida* in a sugarcane leaf rib during oviposition provided a port of entry for the fungus *Glomerella tucumenensis* (Speg.) Arx & E. Müller and the egg clusters were often surrounded by a reddish halo (Fig. 6, B and C). Fifty egg clusters per plot were selected on leaves 7 and 8 so as to quantify the efficacy of antagonistic organisms in controlling this pest on the basis of the aspect of the destroyed eggs (Table 5). The leaf ribs were incubated in plastic bottles containing a small amount of water so that the newly laid eggs would have time to develop signs of viability or parasitism, and they were dissected 5–6 days after harvest. The focus was especially on detecting potential entomopathogens. Fifty nymphs and adults captured with a D-Vac were squashed, stained with Loeffler's methylene blue, while 50 others were fixed in Zenker-formol fixative, embedded in paraffin, cut into 7 µm thick slices and stained according to the Mann-Dominici method.

Statistical treatment

For the laboratory studies, we calculated the means and standard deviations when the population distributions were normal. Wilcoxon (adult life cycle) and Kruskal-Wallis (life cycle according to temperature) tests were used to highlight significance differences. For counts in sugarcane fields, we adopted the sequential sampling plan developed by Allsopp & Bull (1990) based on Iwao's regression indices and relationships between the variance and mean according to Taylor's power law. The accuracy levels were 10 and 25% according to the mean observed densities.

RESULTS

Experimental studies on the biology of *P. saccharicida*

Life cycle

The complete life cycle from egg to emergence was around 43.7 days at 25°C. The sex ratio was balanced. The mean egg incubation period was 15 days. Table 2 gives the lengths of the five nymphal instar periods. The high losses recorded for the first instar were due to the fact that some young, fragile and hard to detect nymphs were crushed. The 4th to 5th instar moult may have been hampered by the low humidity conditions.

Table 2. Egg incubation times and periods of the five *P. saccharicida* instars studied under laboratory conditions (25°C, Réunion, 1990).

Life stages	egg	instar 1	instar 2	instar 3	instar 4	instar 5
Mean time (in hours)	360±24	88±13	98±8	126±24	136±30	240
N° individual tested	40	22	18	14	12	4

Clutches contained one to seven eggs (mean 3.7 eggs; N = 106 clusters) (Table 3). Despite the high variability in the adult lifespan (females: 5–61 days; males: 3–24 days), the mean lifespan of females was significantly higher than that of males (23.5 vs 11.3 days; P=0.02 according to the Wilcoxon test, SAS Institute Inc., 2004. SAS On lineDoc® 9.1.1.3 Cary, NC: SAS Institute Inc., NPAR1WAY procedure). Acute mortality periods were detected for both sexes (5–6 days and then 11–12 days). Half of the female population was affected by these critical periods, whereas the other half lived for at least 30 days.

Table 3. Reared *P. saccharicida* egg number distributions (Réunion, 1989-1990).

Egg number per cluster	1	2	3	4	5	6	7	Total
Frequency	3	4	27	34	24	11	3	106
% total	2.8	3.8	25.5	32.1	22.6	10.4	2.8	100

Female fertility

The preoviposition period was determined for 27 out of the 35 females tested, considering the early mortalities recorded (5–6 days). This period ranged from 5 to 14 days (mean 9.6 ± 2 days). For isolated pairs, if the male died before 6 days old, no viable eggs were laid. The number of eggs laid per female was 14–145 (mean 74.7). The usual variation coefficients could not be used in this latter case. The graphs show a discontinuous series of peaks.

Influence of the photoperiod and temperature on eggs

The photoperiod had no impact on the incubation period. However, *P. saccharicida* was sensitive to temperature changes: the development period was 2.6-fold longer when the temperature declined by 5°C (Table 4). The low percentage of hatching at 20°C was mainly due to cold-induced leaf rib contraction which led to crushing of the eggs. Despite this problem, the differences in incubation period were significantly different at the three tested temperatures (P=0.0001 according to the Kruskal-Wallis test, SAS Institute Inc., 2004. SAS On lineDoc® 9.1.1.3 Cary, NC: SAS Institute Inc., NPAR1WAY procedure).

Table 4. Incubation times of *P. saccharicida* eggs according to temperature (Réunion, July–August 1990).

Treatment	Hatching onset (days)	Hatching end (days)	Mean Time	Hatching (%)
1. (25°C, L.D 16:D8)	13	18	15.5±1.5	100
2. (25°C, L.D 11:D13)	13	18	15,6±1.6	100
3. (20°C, L.D 16:D8)	34	-	36.5±(2.3•)	30
4. (≈22°C, L.D 11:D13)	23	31	26.3±2.1	90

• incomplete data

Survey of population variations

P. saccharicida population dynamics

The fact that the *P. saccharicida* population dynamics trends were similar at all monitoring sites on the island is interesting, as clearly noted at the Savanna site (Fig. 3). The reference scale for all sites was based on the maximum values obtained at a single site (Savanna) where *P. saccharicida* showed marked population variations (up to 300 egg clusters and 3.8 adults per stem), with a very uniform series of transitions between egg laying periods and adult emergence. At Savanna, the emergence of the main 1989-1990 generation was detected as early as November 1989, after the visible disappearance of the previous generation noted during the preliminary scouting. The population decline began in April, even though the conditions were still suitable from three standpoints: climate, insect biology and vegetative stage of the sugarcane plants. The same overall patterns were noted at the other sites but to a less marked extent. An imbalance between the number of observed egg clusters and the resulting adult populations was noted, although we found that on average an egg cluster could give rise more than three offspring.

The preliminary scouting operation revealed that *P. saccharicida* was present in sugarcane fields throughout the island, even at elevations as high as 600 m, but the following survey confirmed that the numbers were not high enough, even at Savanna, to directly cause any crop damage. Generally, two winged forms of adults were noted: macropterous individuals with normal wings, and brachypterous-type koeliopterous individuals with wings that extended to the end of the abdomen and were tipped with a tegument that was midway between macro- and brachypterous forms. As previously reported in Mauritius (Williams, 1957), koeliopterous males were found in lower numbers (1.9%) than koeliopterous females (20.9%) (N = 769), whereas only females have been reported (unknown levels) in South Africa (Harris, 1970). The mean number of eggs per cluster was 3.5. The monitored upper leaf surfaces (leaves 5–8 from the top) had been the site of 84.3% of clusters (N = 362). The sex ratio was balanced, even though we noted variations of between 40 and 60%, in favour of either sex. *P. saccharicida* was always associated with another delphacid species, i.e. *Dicranotropis muii* Kirkaldy. The biology of this latter species is close to that of the studied *P. saccharicida*, but these species may be distinguished on the basis of several differences: *D. muii* adults are smaller and yellowish in colour, they roost on the under side of leaves, contrary to *P. saccharicida*, which roosts on the upper side, egg clusters are covered with a transparent veil and there are one or two eggs per oviposition, which are also smaller (- 20 %) (Williams, 1957).

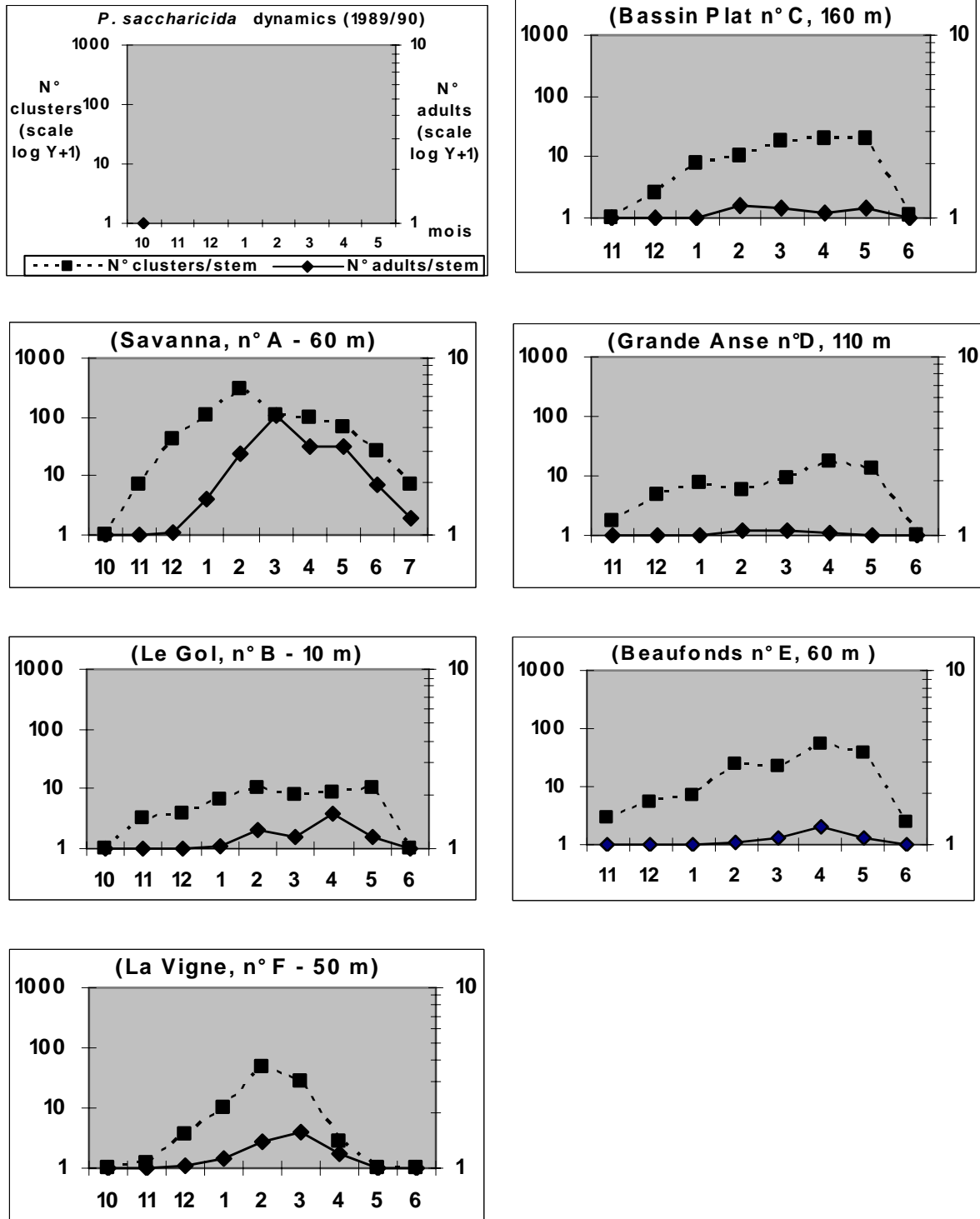


Fig. 3. Regional population dynamics of *P. saccharicida* (Réunion, 1989-1990).
 Statistics adults/stem: density >3.5, P=0,1 ; density <3.5, P=0,25 (Allsopp and Bull, 1990)

Antagonistic organisms

List of inventoried organisms

Six main entomophagous organisms that attack *P. saccharicida*, i.e. egg parasites or predators, was identified (Table 5). The nymphs were preyed upon by a Dryinidae hymenopteran species (*Pseudogonatopoides mauritianus* Williams). So-called ‘stylopisation’ may be noted, whereby a larval ‘sac’ protrudes from the abdomen between tergites 5 and 6, but this phenomenon was only observed in a few adult males (0.5%). Note that *Anagrus optabilis* (Perkins) and *Aprostocetus pallidipes* (Perkins) are common parasites of *P. saccharicida* and *D. muiri*. A scant number of dead *D. muiri* individuals were collected—this death was due to the development of a Strepsipteran *Elenchus* Curtis sp.

Table 5. The six entomophagous organisms detected on *P. saccharicida* in Réunion (1989-1990) (identifications: G. Delvare, Laboratoire de Faunistique, CIRAD, Montpellier, France).

Species	Order and family	Type of action
<i>Tytthus mundulus</i> (Breddin)	Heteroptera, Miridae	Empties eggs by sucking
<i>Tytthus parviceps</i> (Reuter)	Heteroptera, Miridae	Empties eggs by sucking
<i>Anagrus optabilis</i> (Perkins)	Hymenoptera, Mymaridae	Egg parasitisation
<i>Aprostocetus pallidipes</i> Perkins	Hymenoptera, Eulophidae	Complex parasitism behaviour: first an egg parasite, then becomes a predator when the larva hatched from a parasited egg and subsequently eats the other eggs in the cluster (Fig. 6, plate E.)
<i>Pseudogonatopoides mauritianus</i>	Hymenoptera, Dryinidae	Larva parasitisation

Several spider species were found during the D-Vac sampling, but they were not identified. The predatorial status of certain spider species that weave a web at the leaf-stem interface where *P. saccharicida* is often found was confirmed.

No fungal diseases were noted. Moreover, screenings for intracellular infectious agents such as rickettsia and viruses were negative and no cytoplasm modifications were detected. Nuclei of all monitored individuals had not been modified and seemed normal. However, a symbiotic yeast was detected in the haemolymph. Relatively few of these symbionts were detected in some individuals as compared to others.

Population dynamics of the main entomophagous organisms

The dissections regularly revealed cumulated variations in the antagonism of *P. saccharicida* due to the three entomophagous genera at the different sites (Fig. 4). *Tytthus mundulus* (Breddin) was identified throughout the island. *Tytthus parviceps* (Reuter) was only detected in the Savanna area, but at high densities. This site showed clear trends with respect to entomophagous population dynamics. A low percentage of egg infestation was noted from December to February (Fig. 5). This period occurred 1–2 months prior to the increase in adult populations noted in the field, i.e. the length of one generation. The percentage of eggs destroyed by mirids gradually increased from March to over 80% in May. *Tytthus* spp. were dominant at this time, whereas the egg parasitism rate was found to have dropped (Fig. 5).

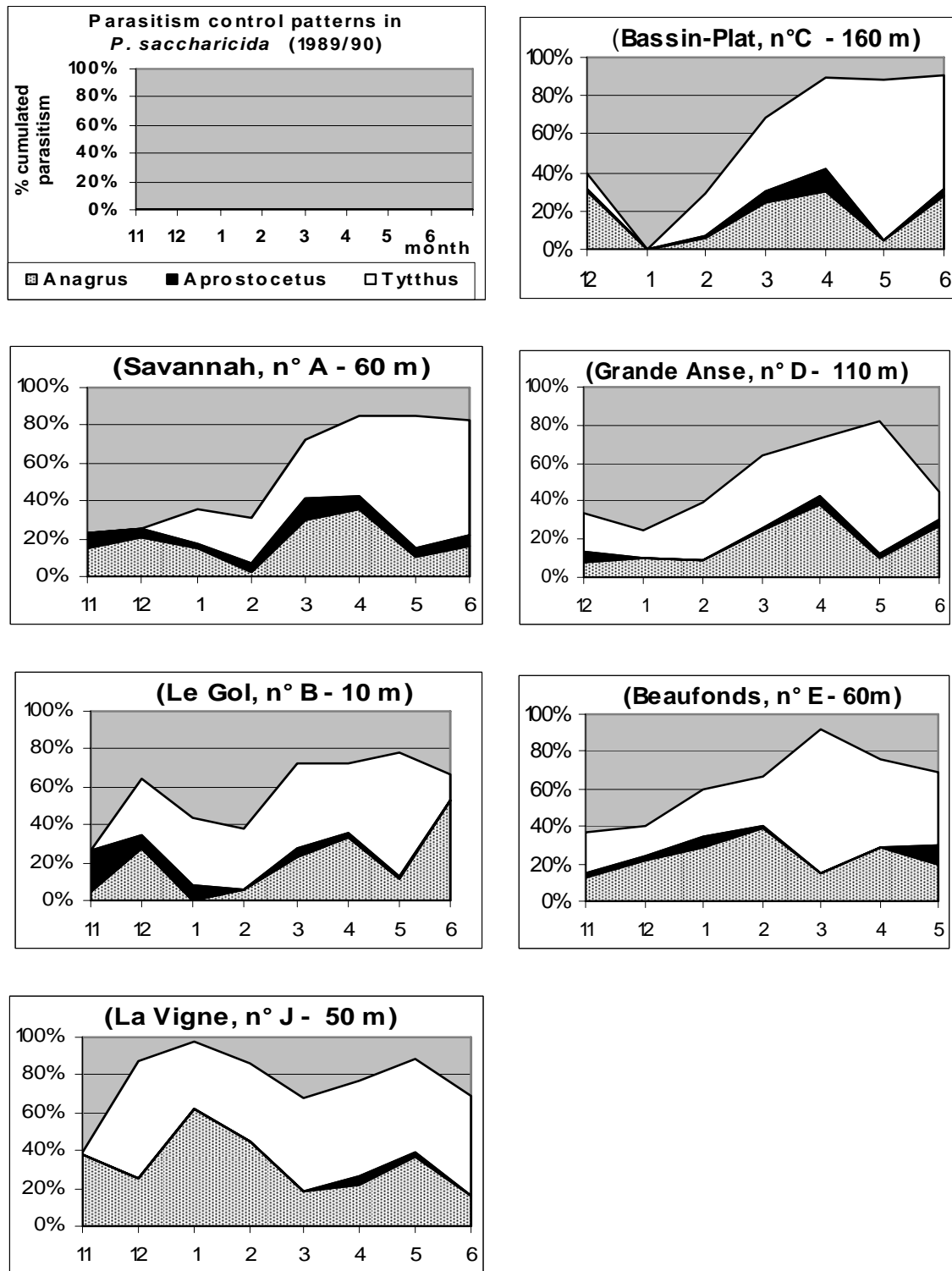


Fig. 4. Regional population dynamics of the main entomophagous organisms that attack *P. saccharicida* (Réunion, 1989-1990).

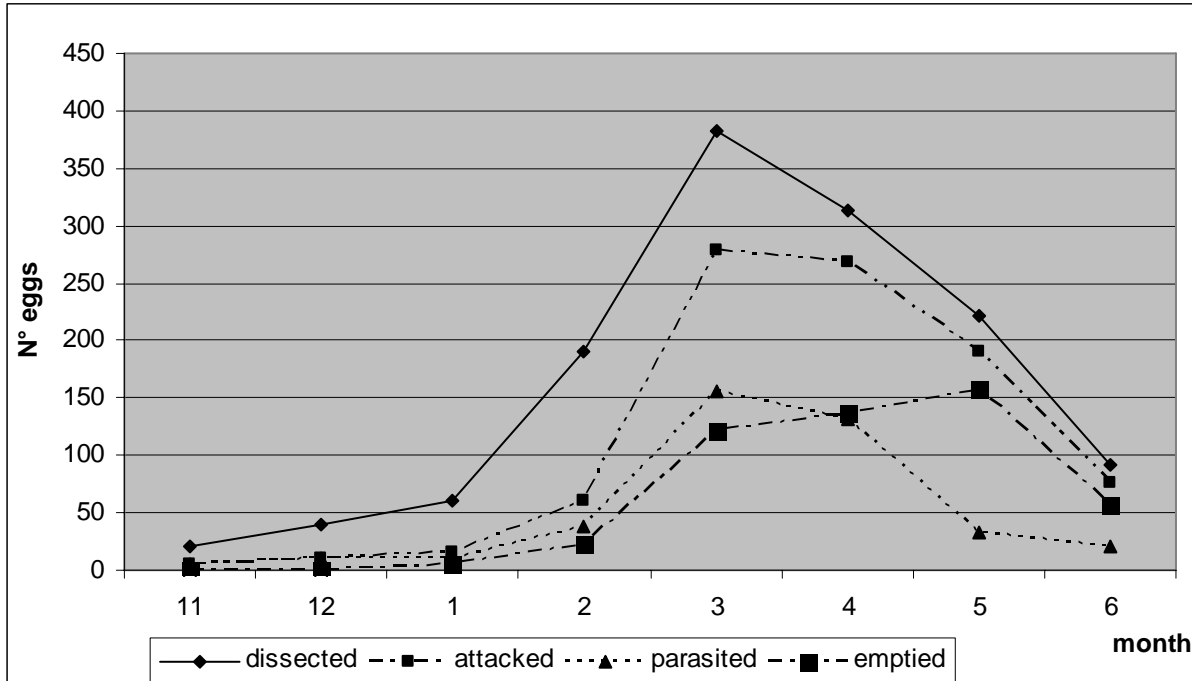


Fig. 5. Population dynamics of the main entomophagous organisms that attack *P. saccharicida* showing that the predators (*Tytthus* spp.) ultimately prevailed over the egg parasitoids (*Anagrus* sp. and *Aprostocetus* sp.) (Réunion, Savanna, 1989-1990).

At all sites, the viable egg frequency was high between November-December and February, decreasing gradually as a result of the combined action of all antagonists, which had even more of an impact than the thermal factor. The mortality rates of the different antagonists were identical, but predatorial bugs were by far the most efficient antagonist. *A. pallidipes* was found in very low numbers, as it had never parasitised more than 10% of the egg clusters as the Delphacidae population density increased (Fig. 6, E). *A. optabilis* was the most efficient, having parasitised up to 40% of the eggs. Its population numbers increased until February-April, and subsequently declined to the benefit of *Tytthus* spp.

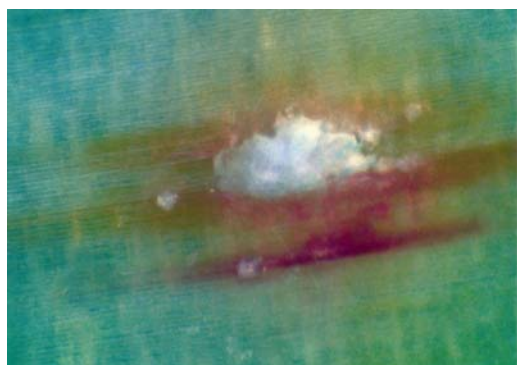
Figure 6. *P. saccharicida* plates.



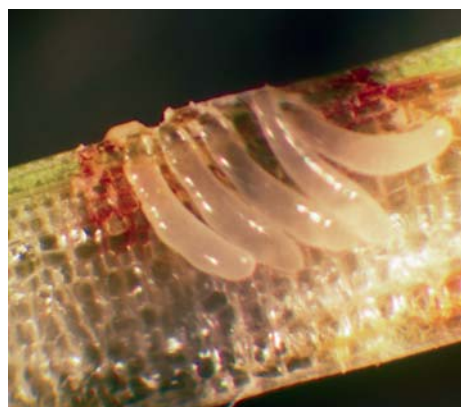
A. Position of reared *P. saccharicida* adults on a sugarcane leaf



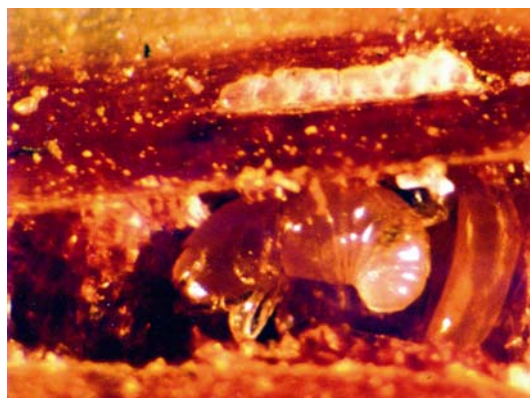
B. Appearance of egg clusters and *P. saccharicida* feeding punctures in a sugarcane leaf rib



C. White waxy substance and sign of the presence of the fungus *Glomerella tucumenensis*



D. *P. saccharicida* egg cluster in a leaf rib



E. An *Aprostocetus pallides* larva destroying a *P. saccharicida* egg cluster.

DISCUSSION

This survey clearly highlighted the densities of *P. saccharicida* populations under the diverse range of conditions that prevail in Réunion, along with its annual population dynamics and natural control mechanisms, while also generating some data on biological criteria, some of which were especially heterogeneous (adult lifespan, egg number/female). This diversity could not be solely explained by the rearing conditions, and we put forward the hypothesis that several groups of individuals were present. In sugarcane fields, the mean recorded densities were likely representative, considering the sampling intensity. It is understood that, in visual monitoring surveys, all adult insects present will not be detected and nymphs populations that are relatively hidden under the leaf sheaths will be overlooked. Moreover, some egg clusters may be partially located on the under side of leaves (Laverde & Borja, 1998).

The number of adults per stem was the most reliable criterion for comparing our results with previously published data. Only the Savanna site (Site A, maximum adults per stem = 3.8 in March 1990) was in compliance with the accuracy levels ($P = 0.10$) defined in the statistical studies of Allsopp & Bull (1990) for adult insect counts (at least 3.5 adults per stem in sequential counts comparable to those conducted in our study). This original feature showed that the insect seemed to have a preference for a mean temperature of 25°C and especially high humidity conditions maintained by steady irrigation, thus confirming the results obtained in Madagascar (Sigwalt, 1962). At the Gol site (site B) and La Vigne site (site E), the accuracy level was only $P = 0.25$ for this type of sampling. Sosa (1983) published differences ranging from 9 to 36 adults per stem in Florida, while Ayquipa & Gomez (1984) and Laverde & Borja (1998) reported similar densities in South America (7–34 according to the former author and 25 adults per stem and up to 40 for the latter). In Hawaii, according to Egan & Hall (1983), this number could reach 300, which means there would be substantial crop loss due to direct sap sucking prior to the introduction of predatorial bugs in 1920. Bull (1981) indicated 60 adults per stem in Australia in February 1974, with the *P. saccharicida* migration-triggering threshold being 20 adults.

The biological performances of *P. saccharicida* could also be compared to those recorded in other countries. The incubation time and life cycle are in agreement with previous findings (Williams, 1931; Williams, 1957; Sigwalt, 1962; Bull, 1972; Yepes et al., 1988; Laverde & Borja, 1998; Fernandez & Escobar, 2000; Mendoza, 2005). Amongst the other possible criteria, the number of eggs per cluster is the easiest and surest to monitor (Fig. 6. D). It was found to be 3.5 in Réunion, Mauritius and Madagascar, and ranged from 4.6 to 5.6 (Bull, 1972), with egg clusters consisting of 1 to 21 eggs in Australia (Bull, 1981), or a reduction of about 25–50% in Réunion. In Florida, the mean is 4.5, with egg clusters of 1–12 eggs (Sosa, 1983), whereas means of 4.1 were obtained in Colombia (Laverde & Borja, 1998) and 4.3 in South Africa (Harris, 1970). The mean lifespan of female adults and their fertility were also lower in Réunion than previously recorded in Australia: 23 days and 75 eggs per female in Réunion, for 1–2 months and 300 eggs in Australia. The rearing conditions could be partially responsible for this difference, but the Australian data were also obtained with laboratory-reared insects, so other factors must also have been involved. Our results were in line with those obtained by Frappa (1955) in Madagascar. He observed the same level of early adult mortality, the same thresholds (up to 12 days) and low egg cluster levels. His life cycle results, which were obtained at a mean temperature of 26–27°C, were comparable to ours. Frappa (1955) also noted that *P. saccharicida* was sensitive to temperature variations. The similar results obtained on the biology of *P. saccharicida* in the two islands, whose sugarcane history is partly linked, provides additional proof of the negative evolution of this insect, even

if it was not possible to pursue the research in Reunion due to the financial specifications and time limit of the project. The other previously published results come from reviews or are not accurate enough to determine the actual variability in the biological features considered, probably in association with the statistical differences noted in our study. They are correlated with the capacity of piercing-sucking insects to host many primary symbiotic organisms that are essential for their survival, along with secondary organisms that have a less fundamental but sometimes a considerable impact (Oliver et al., 2003; Weeks et al., 2003). Variability in the number of symbiotic yeasts detected per planthopper sampled in Réunion could be explained by the loss of symbionts during fixation and subsequent treatments affecting the analysed samples, or could reflect a fluctuation associated with causes intrinsic to the insects. As there is natural variability in the insect-symbiont association, it would be interesting to determine if there is a correlation between this variation and the differences in life cycle and fertility noted in the biological study.

All of these conclusions suggest that *P. saccharicida* lacks part of its biotic potential in Réunion and Madagascar. Only a few individuals of this species must therefore have been initially introduced, or this loss could have been due to genetic depletion or loss of symbionts which could not be rectified in this island environment. These are broad ranging issues for which few results have been obtained and would thus warrant further research.

Our results on the annual population dynamics of *P. saccharicida*, its growth during the hot and humid seasons, and its decline under the influence of less suitable abiotic conditions were in agreement with most previous findings (Harris, 1970; Bull, 1981; Sosa et al., 1986). Bull (1972, 1981) proposed that there are four generations per year, with the adults disappearing almost completely during the southern winter (June–August), and the nymphs being concentrated at the base of sugarcane stubble in autumn (April–May), taking shelter under dry leaves. The factors underlying this evolution are the change to cooler climatic conditions and the gradual harvesting of sugarcane crops between June and December. In addition to the temperature and humidity, a third less recognized factor is therefore the diversity of crop vegetative stages available, so when the insect arrives in a crop field it is able to quickly select the most suitable host plant for its development. Note, however, that Williams (1957) found that in Mauritius *P. saccharicida* was more readily visible during the southern winter, whereas in Hawaii this higher visibility was found to be associated with the increase in the percentage of more prolific brachypterous females and with the higher susceptibility of associated entomophagous organisms to the declining temperature and high winds (Williams, 1931).

The regional differences noted in the insect's population dynamics in Réunion should also be considered with respect to the abiotic conditions. For an insect that is so susceptible to temperature changes, the mean monthly differences of 1.5–2.5°C between Savanna (site A) and La Vigne (site E), or 2.1–3°C between Savanna and Beaufonds (site D) must have had an impact on its population density. The regularity of the humidity conditions could be a further influential factor, since the most abundant populations were located in dry areas that were regularly and abundantly irrigated (Savanna), as compared to areas that were also highly humid, but to a more variable extent because of the temporary and irregular rainy season (Beaufonds, La Vigne) (Table 1).

The direct effects of the environmental conditions were boosted by the additional impact of a complex of predators and parasitoids. It is likely that the increase in *Tytthus* spp. populations was responsible for the decreased egg parasitism noted. Indeed, bugs will attack *P. saccharicida* eggs regardless of whether they are infested with parasites or not. The high efficacy of bugs could also be partly explained by the fact that it has a faster life cycle, i.e. 26

days as compared to 40 days for the delphacid (Fernandez & Escobar, 2000). This diversity of antagonistic organisms present is surprising since no introductions had been officially recorded. The two most common parasitoids (n.b. because of its lifestyle, the impact of *Aprostocetus* was likely underestimated) could have been naturally introduced upon the arrival of living sugarcane rootstock that had been shipped from other countries during varietal exchanges, which mainly began in the late 18th century, but it is less likely that this occurred with respect to the two mirid species. This was already noted by the natural absence of bugs on the two islands located close to Réunion (Madagascar, Mauritius) (Sigwalt, 1962; Williams, 1957). It is more likely that they were introduced in Réunion during Mauritian biological control operations targeting these species in 1956-1957 (Greathead, 1971). However, few reports are available on populations inducing severe crop damage simply due to sap sucking, as occurred in Hawaii, prior to the introduction of predatorial bugs (Egan & Hall, 1983) or in Ecuador recently (Mendoza Mora, 2005). During our active research, we observed no signs of diseases in the insect, whereas studies have been carried out in South America to assess the efficacy of two entomopathogenic fungi (*Metarhizium* sp. and *Beauveria* sp.) (Rico & Victoria, 1988; Badilla et al., 2004). In Madagascar, Giannotti et al. (1973) detected microorganisms resembling mycoplasmas of relatively unknown origin and role.

The findings of this study and the situation described indicated that a complex of insects antagonistic to *P. saccharicida* is present and is efficiently fulfilling its antagonistic roles, even though we observed inevitable competition between egg parasites and egg predators. As part of the Reunion water diversion project, this uneven balance should be closely monitored to check for possible changes over time (Ameixa & Kindlmann, 2008).

The temperate tropical climatic conditions did not seem to be optimal for this stenothermal insect, which is susceptible to even minor decreases in temperature. Its biological capacities also seem to have been reduced following its introduction in this island environment, which took place long ago. As another favourable factor, Francki et al. (1986) showed that *P. saccharicida* was a poor virus vector. These authors deposited adults on Fiji disease infected sugarcane plants and noted that only 15% of the 537 planthoppers tested were infected and only 6% were able to transmit the virus to healthy plants.

The Savanna area could eventually be closely monitored for early detection of Fiji disease infestation, since three factors at this site may be conducive to the development of this disease: it has the highest temperatures on the island, humidity is constant because of the irrigation system, and the sugarcane crop is present at all of its development stages.

It would also be essential to ensure that only cuttings from quarantine glasshouses are imported, especially if they are coming from a country where the Fiji disease virus is present. Madagascar is the closest country in this respect.

Finally, the sugarcane cropping area should be managed so as to avoid situations where one variety prevails too markedly over the others, unless this is unavoidable because of one variety's overriding economic potential. For the highest yielding variety R 570, which is still grown on over 70% of the total sugarcane cropping area, the two parents have two varieties in their ancestry (cv POJ 2878 and R445) which have been ranked at level 7 on an Australian scale of Fiji disease susceptibility. Hence, the situation must be closely monitored while ensuring that all of the above mentioned precautionary measures be taken. Finally, it would be important to assess the impact of the introduction of irrigation on the western part of the island on the population dynamics of all other insects present, such as the scale insect *Aulacaspis tegalensis* Zehntner (Homoptera: Diaspididae), another piercing-sucking sugarcane pest that could have a negative impact on crop yields.

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