633.61:632.753.3:591.526(88)

MEDEDELINGEN LANDBOUWHOGESCHOOL
WAGENINGEN • NEDERLAND • 82-7 (1982)

VARIABILITY IN THE OCCURRENCE OF THE SUGAR CANE FROGHOPPER, *AENEOLAMIA FLAVILATERA* (HOMOPTERA: CERCOPIDAE), ON SUGAR ESTATES IN GUYANA AND SURINAM

F. WIEDIJK

Department of Entomology, Wageningen Agricultural University, The Netherlands

(Received 6-VII-1982)

H. VEENMAN & ZONEN B.V. – WAGENINGEN – 1982

Mededelingen Landbouwhogeschool
Wageningen 82-7 (1982)
(Communications Agricultural University)
is also published as a thesis

ABSTRACT

WIEDIJK F. (1982), Variability in the occurrence of the sugar cane froghopper, *Aeneolamia flavilatera* (Homoptera: Cercopidae), on sugar estates in Guyana and Surinam. Ph. D. thesis, Wageningen. 60 p., 24 figs., 10 tabs., 32 refs., English and Dutch summaries.

Significant numbers of the sugar cane froghopper, *Aeneolamia flavilatera,* are generally not found to be present on sugar cane during the periodically occurring prolonged dry periods. This is primarily attributable to drought induced quiescence in the froghopper eggs, which delays the appearence of the next generation of active froghopper stages. It appears that the density of the post-drought populations of active froghopper stages is primarily dependent on the density of the pre-drought, quiescence sensitive egg populations. Effective froghopper control depends on the timely control of the first generation of post-drought active stages, because of the potentially rapid build-up of the froghopper infestation during prolonged rainy periods through a combination of relatively high reproduction capacity and wind accelerated adult dispersal. Control of the first generation of post-drought populations of the active stages should be based on a field by field prognosis through the interpretation of regularly updated field records of the approximate density of the active froghopper stages. The spatial distribution of froghopper infestations within one sugar estate can be influenced markedly by 'block-wise' harvesting. This in turn allows the potential effectiveness and efficiency of froghopper control measures to be greatly enhanced.

CONTENTS

1. INTRODUCTION

1.1. PROBLEM AND OBJECTIVE

Sugar cane froghoppers, i.e. insects of the superfamily Cercopoidea (Homoptera) that feed on sugar cane, are common pests of this crop in North, Central and South America and a number of Caribbean countries (FEWKES, 1969). In a review of reports on studies of the biology and control of sugar cane froghoppers that belong to the 9 genera that attack sugar cane in the New World, FEWKES (1969a and 1969b) further states that the genus *Aeneolamia* is the most widely distributed and economically the most important. Species of this genus are pests of sugar cane in Mexico, Central America, Venezuela, Guyana, Surinam, Brazil and Argentina, and the islands of Trinidad and Granada. One of the species, *Aeneolamia varia saccharina* (DIST.), a most serious pest of sugar cane in Trinidad, has received much research attention in reaction to the obviously urgent needs of the economically vital sugar industry of Trinidad (EVANS, 1971 and 1972; FEWKES, 1961, 1963, 1964 and 1966; HAGLEY, 1966 and 1967; KING, 1975; NORTON and EVANS, 1974; PICKLES, 1931 and 1933; WILLIAMS, 1919; WITHYCOMBE, 1926). Research on *A. varia saccharina* has resulted in effective control strategies which rely heavily on the correct timing of aerial sprays of insecticides against the adults on the sugar cane leaves.

Research on *Aeneolamia flavilatera* (URICH), which is closely related to *A. varia saccharina* and occurs as an economically important sugar cane pest in Guyana and Surinam, by contrast has been rather scarce. This is probably the main reason for an apparent lack of an effective and efficient control strategy for *A. flavilatera* in both Guyana and Surinam. It is clear that the chances of the improvement of *A. flavilatera* control are generally constrained by the limitations of the understanding of the apparently irregular occurrence of this froghopper (JAMES, 1946; WILLIAMS, 1918) in relation to measurable environmental factors. The objective of the work presented here was to study the population dynamics of *A. flavilatera* in relation to its environment, in an attempt to improve current control measures by way of giving adequately reliable guidelines for a correct timing of chemical control action and possibly, by way of recommending potentially effective alternative control methods based on cultivation measures. This study, which was carried out in Surinam (on the 2500 ha 'Marienburg' estate, during the period August, 1975–June, 1977) and in Guyana (on various estates of the 65,000 ha 'Guyana Sugar Corporation', during the period April, 1978–October, 1978), builds on the results of previous research on *A. flavilatera* by WILLIAMS (1918), PICKLES (1945) and JAMES (1946). The results of research on other sugar cane froghoppers, which was extensively reviewed by FEWKES (1969), proved to be highly useful as material for comparing certain characteristic similarities/dissimilarities in the environmental relations of differ-

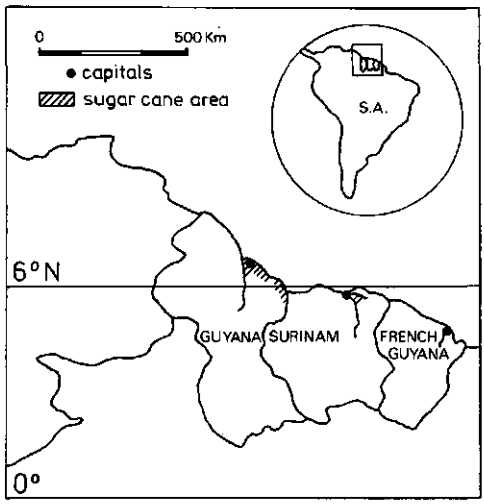

FIG. 1. Area of study.

ent froghopper species vis-à-vis distinct differences with regard to apparent periodicity patterns and the climate. A digest of the literature is given in Chapter 2 and Section 3.1.

In studying the periodicity in the occurrence of *A. flavilatera* on sugar cane, it appears necessary initially to consider the integral *A. flavilatera*/sugar cane ecosystem. This means that, within the context of the earlier defined study objective it is necessary to consider the whole of the agricultural system that produces the sugar cane. In order to be able to take account of the potential impact of cultivation measures, e.g. harvesting and irrigation, the basic unit in large scale sugar cane farming, i.e. the sugar estate, must be considered. More than 95% of the sugar is produced in this way in both Guyana and Surinam. Furthermore, the effects of the climate, which act as independent variables, need to be analysed and interpreted. The remaining part of this introductory chapter is devoted, therefore, to the description of the main characteristics of both the sugar cane cultivation as it is presently practiced in Guyana and Surinam, and the climate that affects the sugar cane cultivation areas of these two countries.

1.2. SUGAR CANE CULTIVATION

Sugar is the most important agricultural export commodity produced in Guyana, where approximately 60.000 ha are under cane cultivation. Twelve sugar estates, varying in size from 3000–8000 ha, are present. Each estate functions independently. In Surinam, sugar cane production is concentrated on one 2500 ha estate, which aims to provide all of the national requirements.

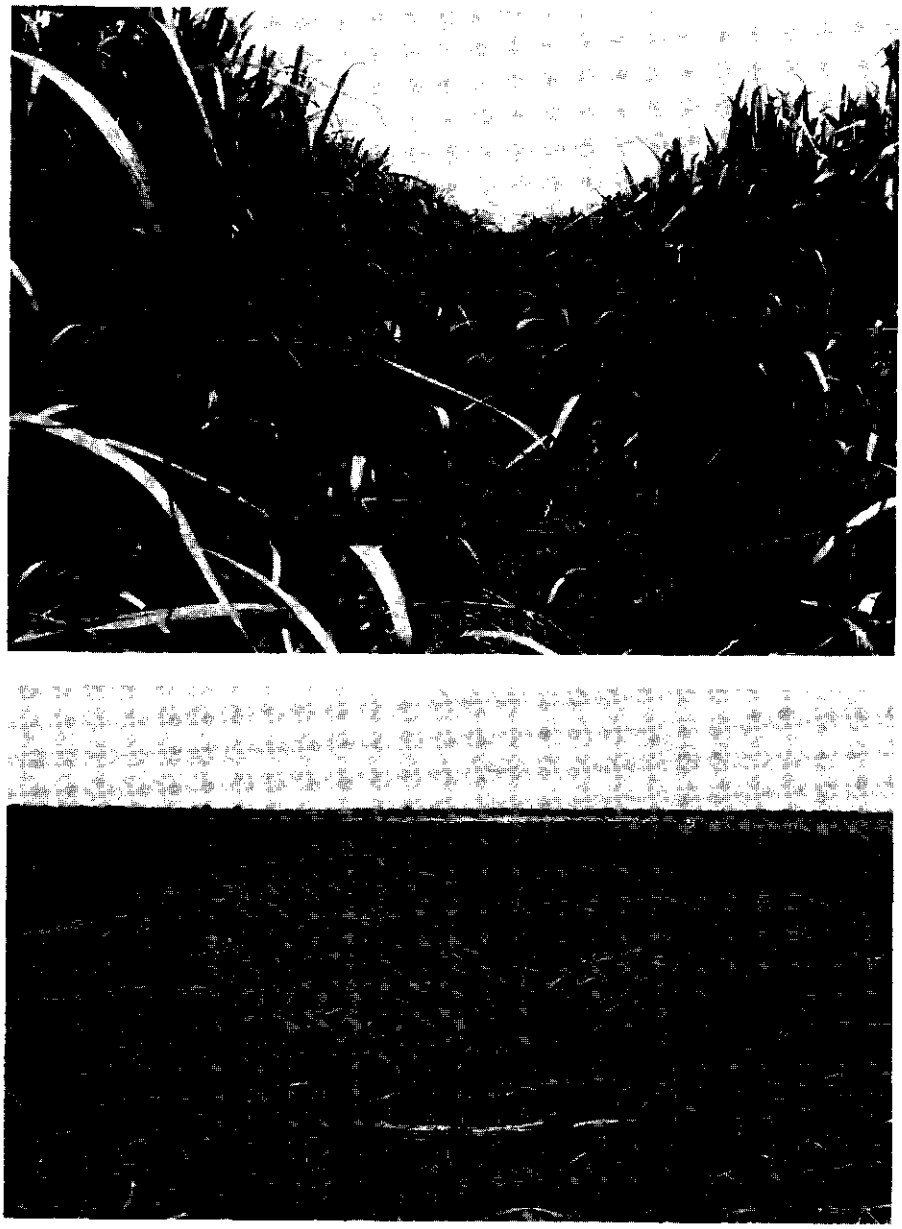

FIG. 2. Field with sugar cane coverage (above) and a recently reaped cane field, revealing cambered bed lay-out (below).

The total target area of research, i.e. the total sugar cane cultivation area of Guyana and Surinam, is shown in Fig. 1. All estates are situated in the coastal plain, which is characterized by mostly heavy clay soils that often lie below the high-water mark, which makes the successful growing of sugar cane in these areas dependent on the functioning of a complicated drainage system, based on the use of pumps and sluices. Effective drainage differs locally because of differences of surface level, the existence of scattered sandy areas and differences in the effectiveness of the local drainage system itself. Direct drainage of the cane plants is effected through surface run off of water surplus by growing the sugar cane on cambered beds (Fig. 2). The transformation of cambered beds into a 'ridge and furrow' lay-out is gradually proceeding in Guyana (approximately 20% of the total sugar cane area is at present transformed) in view of plans to mechanize harvesting in the future; all sugar cane harvesting in both Guyana and Surinam is presently done by hand. Supply of water, which is generally of much less concern than discharging surplus, is sometimes practised in Surinam before planting by way of overhead irrigation. In Guyana, planting is generally preceded by a flood fallow period of approximately 6 months. Plant crops (i.e. crops grown out of planted cane) are generally followed by at least 4 ratoon crops (i.e. crops grown out of the shoots that emerge out of the cane stools that are left after harvest) before the land is ploughed and otherwise prepared for the next planting. A range of different sugar cane clones is present within every sugar estate. It often concerns newly developed clones (mostly 'Barbados' and 'Demerara' varieties) that are judged to be the best suited for new plantings. Yield and apparent resistance potential against pests and diseases are the major selection criteria. The application of fertilizer is more or less standard procedure on all of the different estates (NPK and urea at fixed rates, at different points in the growth cycle of the cane). Under normal circumstances, sugar cane yields 50–100 tons of cane per ha, at 5–10% of sugar per ton of cane.

Sugar estates in Guyana and Surinam have their own sugar factories that process the sugar cane directly after it is harvested into sugar, molasses (generally utilized for the production of rum) and the left-over of pressed out sugar cane fibre (generally utilized as fuel in the running of the factory).

A drainage system divides the sugar cane area of each estate into 5–10 ha fields. As a rule, all available sugar cane fields are harvested once a year. In Guyana, one distinguishes between a 'spring crop' and an 'autumn crop', since harvesting is usually twice a year interrupted for a few months, when periodical technical revisions take place. In Surinam, harvest activities generally continue throughout the year, i.e. whenever the factory is not out of function as may occur during 1–3 months a year through necessary technical revisions. If one divides the total cultivated area of a sugar estate by the number of available harvesting days, one finds the average area of land that is harvested per day; i.e. on a sugar estate of e.g. 6000 ha, 20–30 ha will be harvested per day, when assuming that 200–300 harvesting days are available in a year. The consequences of the characteristic sugar cane harvesting procedure in the context of *A. flavila-*

tera population development, will be subject to discussion in Chapter 3.

Harvesting is normally preceded by the burning of the sugar cane, so that most of the leaf material (especially the dried out component) is removed in order to facilitate manual harvesting; the canes are not significantly damaged by the burning. The layer of cane debris that is left on the fields after harvesting (often referred to as 'trash') is generally also burned. The latter is done as a measure of general field hygiene (removal of ant and termite nests and other potential sources of damage for the next ratoon crop) but also as a specific measure of protection against froghopper infestation. This aspect will be discussed in more detail in Chapters 4 and 5.

The most important tool in protecting sugar cane from pests and diseases in general is the breeding of resistant cane clones, but *A. flavilatera* and a number of other sugar cane pests (FEWKES, 1969a; JAMES, 1947) continue to necessitate chemical control action, since clones having resistance to those pests have not yet been developed. In view of its potential damage and frequency of occurrence, *A. flavilatera* is clearly the most important of these pests on sugar cane in Guyana and Surinam (Section 2.1). In Surinam, chemical control is achieved primarily by applying BHC-dust (5% at 50–100 kg/ha) to the soil surface, to control the froghopper *nymphs* that reside in the top-soil layer. Chemical control of froghoppers in Guyana is generally directed at the froghopper *adults* by the aerial spraying of insecticides (Sevin, Dipterex and others) on the sugar cane foliage, as is also done in the case of *A. varia saccharina* in Trinidad. The occurrence in froghopper populations of resistance to the more frequently used insecticides, which has given rise to serious concern in the practice of controlling *A. varia saccharina* on sugar cane in Trinidad (FEWKES, 1969b), has up till the present not been reported to be a problem of significance in the control of *A. flavilatera*.

1.3. THE CLIMATE

Guyana and Surinam lie in the intertropical convergence zone at 6° N (Fig. 1). The main characteristics of the climate of these two countries are similar throughout the sugar cane cultivation area situated in the coastal plain.

Approximately 2500 mm of total annual rainfall is distributed in time in such a way, that a marked 'wet' season in the period April–August is alternated with a marked 'dry' season in the period August–November, while rainfall appears to be irregularly distributed during the rest of the year. The representation of both average monthly rainfall and the average monthly duration of sunshine in Fig. 3, indicate the factual highly negative correlation of these two climatic parameters. It is furthermore indicated in Fig. 3, that the mean daily air temperature shows limited seasonal variation, ranging from 22–31 °C with an annual average of approximately 26 °C. The air humidity is relatively high on average, which is a common feature of all humid tropics, and ranges from 60–95%. Day-length deviates little from 12 hours all the year round, as is to be expected at a latitude of 6° N. The prevailing trade-wind from the north-east blows inland

during almost all of the year; recorded maxima of wind speed rarely exceed 5 m/s, and the wind speed is generally much less during the night.

Rainfall and the highly negatively correlated duration of sunshine, are of primary importance in terms of seasonal variability of the climate. In anticipation of a detailed discussion of the micro-climatic factors that directly affect the object of study, i.e. *A. flavilatera,* in Section 3.3, a preliminary analysis of the variation of the climatic parameter rainfall is given in Fig. 4 and Fig. 5. Fig. 4, depicting the geographical variation of rainfall recordings within the boundaries of the 2500 ha 'Marienburg' estate in Surinam, shows that significantly local differences may occur to the extent that the selective utilization of local rainfall recordings, as effected in the case of the more specific rainfall recordings that are presented in Chapter 3, may be of the utmost importance. The seasonal variation of the intensity of the rainfall, as depicted in Fig. 5, appears to be characterized by a large proportion of rainy days with heavy rains (i.e. days with more than 5 mm of rainfall) during the wet season in the period April–August, in comparison with the rest of the year.

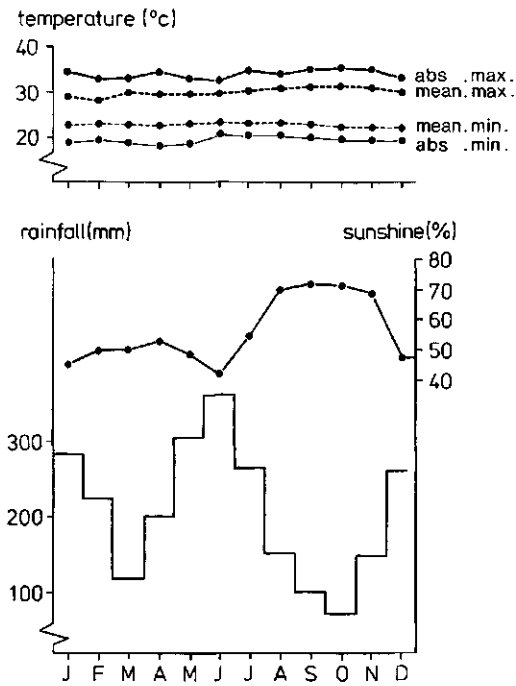

FIG. 3. Absolute and average monthly maxima and minima air temperatures over 1962–1972, and average monthly rainfall and duration of sunshine ('Campbell-Stokes' registration) over 1959–1974, from daily recordings at the main weather station of 'Marienburg' sugar estate, Surinam.

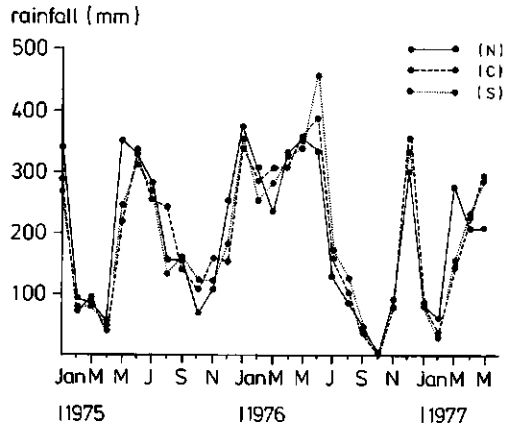

FIG. 4. Geographical variation of rainfall (monthly totals) within the 'Marienburg' estate boundaries, i.e. as recorded at the northern main weather station (N), the central auxiliary weather station (C) and the southern auxiliary weather station (S), which are situated at equal distances of approximately 5000 m from each other, over the period January, 1975–May, 1977.

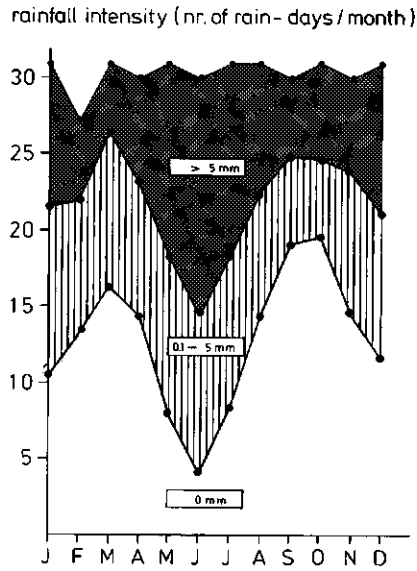

FIG. 5. Variation of the intensity of rainfall, as recorded by the average monthly fluctuations of the number of days with a rainfall of respectively 0 mm, 0.1–5 mm or more than 5 mm, at the main 'Marienburg' weather station over 1959–1974.

2. *AENEOLAMIA FLAVILATERA* ON SUGAR CANE

2.1. TAXONOMY AND PEST STATUS

Six species of the neotropical genus *Aeneolamia* are recognized to feed on sugar cane (FEWKES, 1969a), amongst which is *Aeneolamia flavilatera* (URICH). This species, first described by URICH (1914) from specimens collected in Demerara (Guyana), was initially listed as *Tomaspis flavilatera*. FEWKES (1969a) distinguishes six subspecies, noting the following geographical distribution: *A. f. caripensis* FENNAH, *A. f. funebris* FENNAH, *A. f. guarici* GUAGLIUMI, *A. f. nirguensis* GUAGLIUMI and *A. f. talmana* FENNAH, all in Venezuela, and *A. f. flavilatera* (URICH) in Guyana. *Aeneolamia flavilatera flavilatera* (URICH), the object of the present study that is recorded as *A. flavilatera* for the sake of brevity, is found not only in Guyana but also in Surinam and French Guyana (Fig. 1). Since this froghopper is of no economic importance to the marginal sugar cane cultivation in French Guyana, the present study deals with the situation in Guyana and Surinam only.

Originating from the savannahs where it may be found feeding on a variety of wild grasses (MYERS, 1935; GUAGLIUMI, 1962), *A. flavilatera* was first reported to attack sugar cane in 1914 (WILLIAMS, 1918), i.e. long after the beginning of sugar cane farming in these countries in the 17th century. This may be due to a necessary period of adaptation of *A. flavilatera* to environmental conditions within the new sugar cane habitat (FEWKES, 1969a), or it may result from the lack of records or the misjudging of froghopper damage. Since the first reports on sugar cane damage caused by *A. flavilatera* have been issued, annual overall crop loss due to froghopper infestation has been found to fluctuate from a negligible degree of damage, to a most serious destruction of the sugar cane e.g. in 1946, when heavy froghopper attack resulted in the forced close down of 'Cane Grove' estate in Guyana (JAMES, 1946). At present, *A. flavilatera* is considered to be a sugar cane pest of major importance in both Guyana and Surinam. Estate field reports indicate periodically recurring froghopper attacks that are forcing estate management to invest continuously in either prevention and detection, or technical control of this insect. The actually inflicted froghopper damage is generally considered to be high in comparison with other current sugar cane pests in these countries.

Froghopper damage is inflicted by both the adults (through sucking on the cane leaves) and the nymphs (through sucking on the cane roots), but the latter is considered to be of relatively minor importance (JAMES, 1946). Adult feeding causes the so called 'froghopper blight', which refers to the yellowing and further gradual necrosis of the leaf tissue around the feeding punctures resulting in loss of photosynthetic area of the host plant. The saliva injection that precedes the actual feeding of the adults, is likely to play an important role in inflicting host plant damage. Nymphal feeding alone, i.e. apart from adult damage, may cause

yellowing and stunting of cane plants as has been shown in the case of *A. varia saccharina* in Trinidad (KERSHAW, 1913; WITHYCOMBE, 1926). In practice, the damage that is caused by the nymphs does not clearly become manifest, through the generally occurring combination of nymphal damage with adult caused damage.

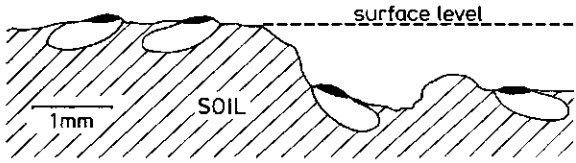

FIG. 6. Diagram of the usual post-oviposition situation of the eggs of *A. flavilatera* (lateral view).

2.2. DESCRIPTION OF DISCERNED DEVELOPMENTAL STAGES

Embryonic development takes place in the soil underneath the host plant of *A. flavilatera,* where the eggs are deposited in a characteristic position just under the soil surface (Fig. 6) by means of an approximately 2 mm long ovipositor.

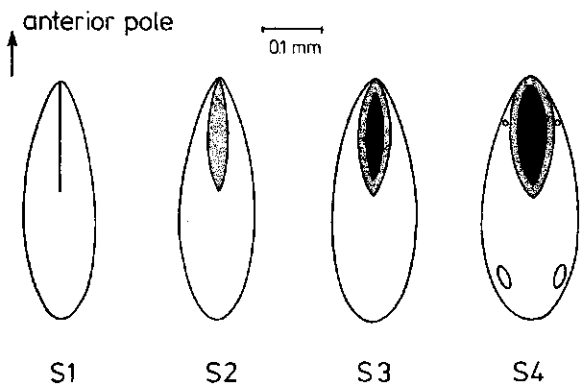

FIG. 7. Stages of *A. flavilatera* egg differentiation, as based on the description of changing features of the outer appearance of the egg (frontal view) during embryonic development:

S_1 – entirely pale yellow; the egg-shell or chorion already showing the 'hatching line', which is the suture along which the egg-shell will split later on.

S_2 – underneath the hatching line, a dark elliptical area has become visible, which will later on develop to be the 'hatching lid'; a reddish roundly shaped pigment spot is hidden underneath the dark streak, near the anterior pole of the egg.

S_3 – the egg-shell has partly split along the hatching line, thus exposing the black hatching lid; the pigment spot is now somewhere underneath the hatching lid and moving on downwards (i.e. away from the anterior pole) as blastokinesis advances.

S_4 – blastokinesis has taken place; the above mentioned pigment spot has split in two and these are visible at both sides, near the posterior pole of the egg (the abdominal pigment spots of the embryo); the two newly developed distinct red spots that are now present near the anterior pole of the egg, are the eye-spots of the embryo.

It has been reported that only a very small proportion (1–2%) of all froghopper eggs that are deposited in sugar cane fields is not found in the soil, but in moist decaying cane debris (the cane 'trash') (FEWKES, 1969a). At oviposition, the eggs are entirely pale yellow, spindle shaped and measuring 0.8 × 0.3 mm. The subsequent embryonic development is accompanied by a number of easily detectable changes of the egg's outer appearance. The detailed description of these changes during the embryonic development of *A. varia* by FEWKES (1966), has been found to also be valid for *A. flavilatera*. Within the scope of the present study, it was considered useful to distinguish 4 different sub-stages (Fig. 7), since this specific distinction is convenient in determining the existing differences of response to physical environmental factors, as will be discussed in detail in Chapter 4. For a description of the 4 egg sub-stages (S_1, S_2, S_3 and S_4 respectively) reference is made to the caption of Fig. 7.

Embryonic development is terminated when the S_4-stage of development is completed; the hatching process is initiated by the pushing away of the egg's 'hatching lid' by the first nymphal instar, which is then still enveloped in its embryonic cuticle. The latter is normally ruptured and shed when the nymph is halfway out of the egg-shell, or shortly thereafter. Immediately after the shedding of the embryonic cuticle, the nymph starts walking over the soil surface in search of a suitable root to feed on and will continue to feed on sugar cane roots until nymphal development is completed. After feeding has started, the nymph soon begins to produce the characteristic frothy spittle that apparently protects its soft body from drying out and from attacks by a number of natural enemies (Section 2.4). The nymphs constantly keep themselves surrounded by the froth, which may serve as a clear indicator of *A. flavilatera* infestation in the sugar cane fields (Fig. 8). Depending on the texture of the top-soil layer, a varying proportion of all nymphs present can be spotted as 'spittles' at the soil surface, because nymphs may descend in cracks and hide under clods of

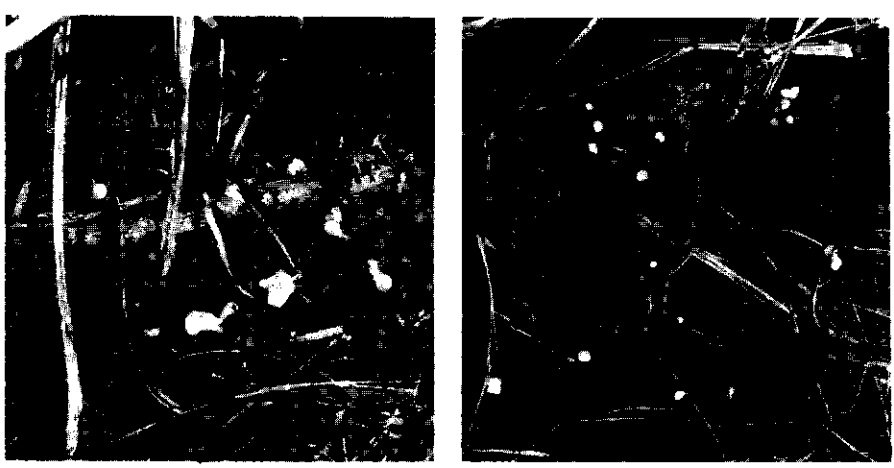

FIG. 8. Characteristic 'spittles', indicating the presence of *A. flavilatera* nymphs.

soil or cane debris. However, more than 90% of the nymphs on average, are found in a thin top-soil layer of 2 cm (Section 3.2.2). The nymphal froth production takes place through the blowing of air into a viscous fluid excreted from the anus during feeding (KERSHAW, 1914). A total of 5 nymphal instars can be discerned. Two non-overlapping ranges of head width clearly distinguish the first from the second instar, while progressive stages of wing development distinctly mark the last three instars (Table 1). JAMES (1946) and WILLIAMS (1918) described a total of 4 nymphal instars only, since they did not distinguish the first from the actual second. All nymphal instars of *A. flavilatera* are probably xylem feeders, as has been shown to be fact for the closely related *A. varia* by HAGLEY (1967). Nymphal development is completed when the fifth and final instar produces a so called 'froth chamber', i.e. a relatively big frothy covering that is made out of a more viscous kind of spittle, in which the transformation into the adult stage is to take place. It is found, that the nymphs sometimes ascend a grass stem up to 10–20 cm before they perform their final act of the production of the froth chamber (WILLIAMS, 1918) but most froth chambers are found at the soil surface level, near to the canes.

When the transformation into adults is completed and their exo-sceletons are hardened within the protective covering of the froth chambers, the adults ascend to the foliage and start feeding on the sugar cane leaves. The *A. flavilatera* adults (Fig. 9) are approximately 8 mm in length and have a light brown pigmentation, except for a yellowish margin at the anterior side of the forewings. Females and males emerge in an approximate ratio of 2:3 (JAMES, 1946); the females are slightly larger, darker brown and have less conspicuous yellow markings than the males but they can only be discerned with certainty by examining the genitalia. *A. flavilatera* adults are probably parenchyma feeders like *A. varia,* for which it was shown that the adults generally feed on the border parenchyma of the vascular bundles of the cane leaves (WITHYCOMBE, 1926; HAGLEY, 1966 and 1976). Directly after emergence, female adults are ready to mate. Oviposition may start 2–3 days after copulation. Oviposition takes place in the soil underneath the cane foliage where the adults feed; generally, oviposition takes place during the night only. During the day, *A. flavilatera* adults often hide in the cane leaf axils, or may be found feeding on the leaves of both the older canes and the cane shoots. Although adults have also been seen feeding on wild grasses in open parts of the cane fields and along the drains of the sugar estates,

TABLE 1. Discriminating features of the five nymphal instars of *A. flavilatera*

Instar	Head width range (mm) ($n = 10$)	Total length range (mm) ($n = 10$)	Wing pad development
1	0.29–0.31	0.7–0.9	none
2	0.47–0.57	1.2–1.5	none
3	0.61–0.95	1.7–2.2	on mesothorax only
4	1.04–1.30	3.7–5.1	length about equal to width
5	1.61–1.81	5.7–6.8	length about twice width

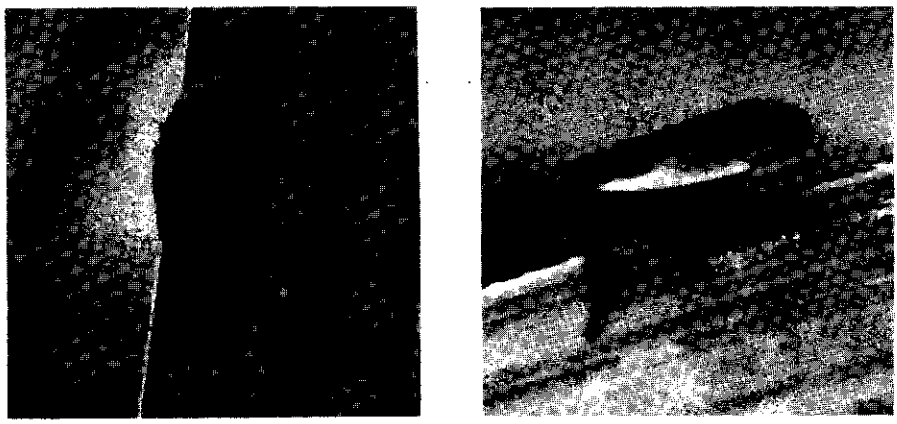

FIG. 9. *A. flavilatera* adult stage.

it cannot be confirmed that periodic occurrence at such places is characteristic for *A. flavilatera*, as was stated by PICKLES (1945).

2.3. LIFE-CYCLE

One of the main differences between *A. flavilatera* and various other species of sugar cane froghoppers, is the absence of a distinct diapausing egg stage in *A. flavilatera* (FEWKES, 1969a; JAMES, 1946). However, while *A. flavilatera* is said to be capable of breeding all the year round in continuously suitable ('damp') locations it appears that, in common with many other sugar cane froghopper species, the dry seasons and recurrent harvesting periods usually interrupt this continuous cycle in sugar cane. This would arise primarily because moisture is essential for *A. flavilatera* oviposition, which would thus be fully inhibited when air dry conditions occur in the soil. Moreover, it is stated that almost all ('well over 90%') of the *A. flavilatera* eggs die after 28 days of air dry conditions in the soil. JAMES (1946) concludes, that *A. flavilatera* is generally dependent on adult migration for the re-infestation of sugar cane fields after either harvesting or the dry season, whereas many other sugar cane froghopper species can rely on a resident diapausing egg population for re-infestation as soon as the adverse dry conditions are over.

As stated above, *A. flavilatera* does not produce diapausing eggs that contribute to any significant variability of the average generation time under suitable conditions, as in the case of e.g. *A. varia* that produces a gradually increasing proportion of diapausing eggs in subsequent generations (FEWKES, 1963b; KING, 1975a). JAMES (1946 and 1947) gives estimates of the average duration of the life-cycle of *A. flavilatera* that range from 54–62 days (i.e. 16 days for mean embryonic development, 33 days for mean nymphal development and 8 days for mean period of female maturation). Thus, 6 generations of *A. flavilatera*

may occur per year in those situations where conditions remain suitable for development. However, in sugar cane, the number of generations of *A. flavilatera* and many other sugar cane froghopper species (FEWKES, 1969a) is generally limited to 4, as there are several months per year when there is insufficient moisture for oviposition and embryonic development. A more detailed discussion of the literature with regard to the latter is given in Section 3.1.

2.4. NATURAL ENEMIES

The various predators and parasites of the different developmental stages of *A. flavilatera* in Guyana and Surinam that are known to date, have all previously been recorded by WILLIAMS (1918) and JAMES (1946 and 1947). They list 2 egg parasites, viz. *Oligosita giraulti* CRWD. (Chalcididae: Hymenoptera) and *Anagrus* sp. (Mymaridae: Hymenoptera), 1 nymphal predator, viz. *Salpingogaster nigra* SCHINER (Syrphidae: Diptera), 1 entomogenous fungus infecting the adult stage, viz. *Metarrhizium anisopliae* (METCH.) (Entomophthoraceae) or green Muscardine fungus, and a number of predators attacking the adult froghoppers, viz. ants, spiders, lizards and birds.

FEWKES (1969a) points out, that in general the climatic conditions in sugar cane plantations are much less favourable to the most important natural enemies of froghoppers than to the froghoppers themselves. In all cases, the incidence of the more or less specific natural enemies of *A. flavilatera* (i.e. *Oligosita* sp., *Anagrus* sp., *Salpingogaster* sp. and green Muscardine fungus) is reported to generally stay at a low level (WILLIAMS, 1918; JAMES, 1946 and 1947).

In the course of the present study, only three of the above listed specific natural enemies of the froghoppers were found to occur in the sugar cane fields in both Guyana and Surinam, viz. *M. anisopliae* (only relatively dense adult populations of more than 30 adults per m^2 were occasionally found to be infected, resulting in 10–15% of the adults killed by the fungus), *Anagrus* sp. (only relatively dense host egg populations have occasionally been found parasitized to the extent that some isolated foci of infestation resulted in 10–30% host egg mortality) and *S. nigra* (regular examination of the nymphal froth deposits of the froghoppers revealed the only sporadic occurrence of one or two syrphid larvae predating on a froghopper nymph inside of its 'spittle').

It appears, that significant infection by the main natural enemies of *A. flavilatera*, i.e. by *M. anisopliae* and *Anagrus* sp., occurs only rarely and highly irregularly in time. Furthermore, the incidence of a significant rate of host population infection appears to be largely irresponsive to the overall occurrence of the froghoppers. Consequently, all natural enemies are considered to be of secondary importance in regard to regulating periodicity in the occurrence of *A. flavilatera*, i.e. within the context of the present study.

3. ASSESSMENT OF THE POTENTIAL VARIABILITY IN THE NUMBERS OF *AENEOLAMIA FLAVILATERA* IN RELATION TO THE ENVIRONMENTAL CONDITIONS ON SUGAR ESTATES

3.1. INTRODUCTION: REVIEW OF THE LITERATURE AND ESTATE FIELD REPORTS

The first *A. flavilatera* attack on sugar cane of apparently alarming proportions has been reported to have taken place at 'Plantation Ogle', Guyana, in 1915 (WILLIAMS, 1918). Since then, occasional reports on *A. flavilatera* infestation have been issued through estate field reports on a quarterly or annual basis. After 1945, i.e. when JAMES (1946 and 1947) reported the results of his research on 'the bionomics and control' of this sugar cane pest, these estate field reports contain frequent notes on *A. flavilatera* in terms of roughly quantified 'seriousness' of the inflicted infestation. The basic reference material of the estate field reports with regard to *A. flavilatera* is largely made up of data collected by especially appointed teams of froghopper 'pest scouts', who form the estate froghopper inspection service which provides the basis for chemical control planning. It appears that, although reliable data on actual *A. flavilatera* population counts are missing altogether, the compilation and interpretation of all relevant data from these field reports largely confirm the findings of JAMES (1946) with regard to the following phenomena:

1) Years in which *A. flavilatera* infestation is serious and wide-spread, exist next to years in which *A. flavilatera* infestation is negligible or even apparently nil; i.e. in practice, distinct 'froghopper years' have been identified.

2) Every year, there appears to be at least one prolonged period without rain (the 'dry season', lasting 2–4 months and in general occurring during the period August–November, as previously stated in Section 1.3) which appears to coincide more or less with a period of a seemingly total absence of both adults and nymphs of *A. flavilatera* on sugar cane. With regard to the presence of eggs during this period, no conclusive data appear to be available except for the statement by JAMES (1946) (Section 2.3) that '...it is certain that air dry conditions in the soil will destroy at a conservative estimate well over 90 percent of the eggs of *A. flavilatera* within 28 days and that probably about six weeks in the same medium would suffice to destroy all of them...'. That the latter is not, in general, true will be discussed in detail in Chapter 4 in the context of a general discussion on environmental impact on all discerned developmental stages of *A. flavilatera,* but it will also emerge in Section 3.2.3 of the present chapter.

3) Whereas the dry season coincides with the interruption of all *A. flavilatera* population development within the sugar estate boundaries, harvesting may induce local interruptions of froghopper activity (i.e. only in the infested fields that are harvested) at any time, on an annual basis. In general, recently reaped fields stay free of significant numbers of froghopper nymphs (no 'spittles') and adults (no 'blight') until approximately 4 months after harvesting, when a closed

new canopy cover of sugar cane leaves has been formed (Section 3.2.1).

4) Froghopper activity is reported often to recur in the same fields. JAMES (1946) explained this phenomenon by indicating the drought resistance properties of *A. flavilatera* eggs (see also point 2 above). However, in regard to longer term aestivation (i.e. through diapause) of the eggs through the dry seasons, which plays a highly significant role in the population dynamics of *A. varia* (FEWKES, 1963), JAMES (1946) made the following statements: '...*A. flavilatera* seems to occupy an intermediate position as regards the evolution of long periodism in the Cercopidae. In *A. varia* the phenomenon is a highly specialised development which plays a vital part in enabling the species to cope successfully with the conditions of its environment. In *A. flavilatera* it is much less highly developed and cannot be considered to play a decisive role in the economy of the species...'.

5) In consequence of the apparent insignificance of diapause in *A. flavilatera*, JAMES (1946) considers this froghopper species to be dependent on adult migration for the re-infection of sugar cane after a severe dry season has occurred. The generally leeward directed spread of *A. flavilatera* is apparently caused by the accelerating effect of the wind on actual adult migration through flying.

6) The effect of submersion of *A. flavilatera* on embryonic development and mortality, has been investigated by JAMES (1946) in relation to the generally practiced cultivation measure of flood fallowing in Guyana (see Section 1.2). It is reported that '...short period floodings up to about a month would have a preservative rather than a destructive effect on froghopper eggs in the soil...' and '...the immersion of heavily infested land for a period of at least a year is necessary to ensure the reduction of eggs to unimportant numbers...'. Possible causes for this phenomenon are not indicated.

3.2. FLUCTUATIONS OF THE NUMBERS OF *AENEOLAMIA FLAVILATERA*

3.2.1. *Introduction*

In order to broaden the available base of data on the population development of *A. flavilatera* on sugar cane, population counts were performed in 3 markedly different fields of 'Marienburg' estate (Surinam), i.e. in fields with a significantly different age/height of the sugar cane cover and at widely separated sites within the estate boundaries. These population counts were carried out weekly on a continuous basis, during the period May, 1976–May, 1977.

The 3 sampled fields were situated in areas of the estate that were the main foci of *A. flavilatera* infestation at the start of the sampling period. Contrary to the froghopper populations in the sampled fields, newly developed foci of *A. flavilatera* infestation outside the sampling areas received the commonly applied technical control measures, so that the presented population counts cannot be considered representative for the froghopper population development on the entire estate, during the sampling period. However, the above mentioned differences of the 3 chosen sampling areas may be considered more or less representa-

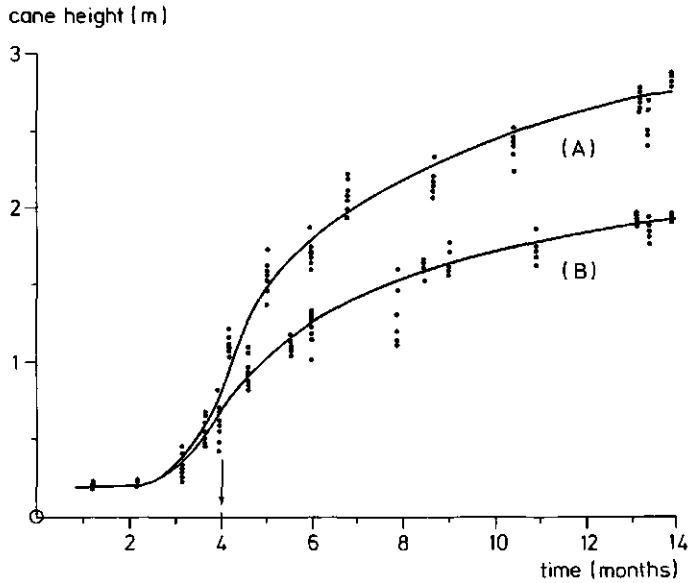

FIG. 10. Average sugar cane growth rate: (A) increase of the total cane height (i.e. including the top leaves), (B) increase of the length of the cane stalk (i.e. excluding the top leaves).

tive for the vast differences in environmental conditions that simultaneously exist in the different fields that make up any sugar estate in Guyana and Surinam. The main reason for the latter is the characteristic mode of sugar cane harvesting (Section 1.2). I.e., at the individual *field* level, harvest activities imply the annually recurring destruction of the resident adult population and an at least important reduction of the resident nymphal and egg populations, through the combined effects of pre-harvest burning of the cane, the mechanical disturbance during harvesting and the following post-harvest burning of cane debris. It appeared that recently reaped fields generally stayed free of noticeable numbers

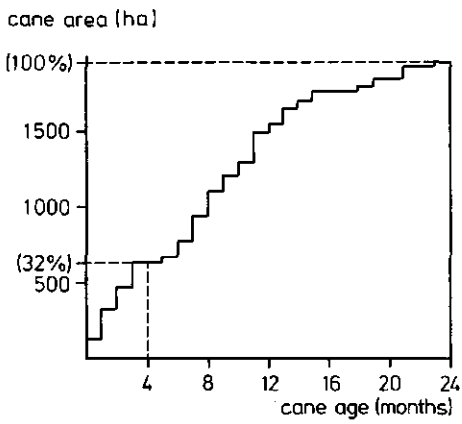

FIG. 11. Characteristic age distribution of the sugar cane of an estate (example: 'Marienburg' estate situation on 31 December, 1975).

of *A. flavilatera* until approximately 4 months after harvest, i.e. when the growth rate of the sugar cane accelerates (Fig. 10) and a new closed canopy of sugar cane leaves is being formed (see also Section 3.1). At the sugar *estate* level, the spatial distribution of fields that thus provide differential potential for *A. flavilatera* population development, i.e. as indicated by their differently aged sugar cane cover, appears to be comparable to a more or less chess-board like pattern which changes continuously with time. However, the statistical distribution of the area of fields with differently aged sugar cane cover (Fig. 11) remains more or less the same for a particular sugar estate as a whole. A total of approximately two thirds of the total cane area of an estate is constantly covered by a closed canopy of sugar cane leaves. It therefore appears that ample area with potential suitability for froghopper population development remains to be available within the sugar estate boundaries at all times, whereas extremely adverse conditions for *A. flavilatera* population development are annually induced through harvesting in each of the fields that make up the entire estate's area under sugar cane. It follows, that harvesting and also the issue of food availability are critical factors to be considered at the individual field level, as these factors periodically severely restrict froghopper population development. However, since the aver-

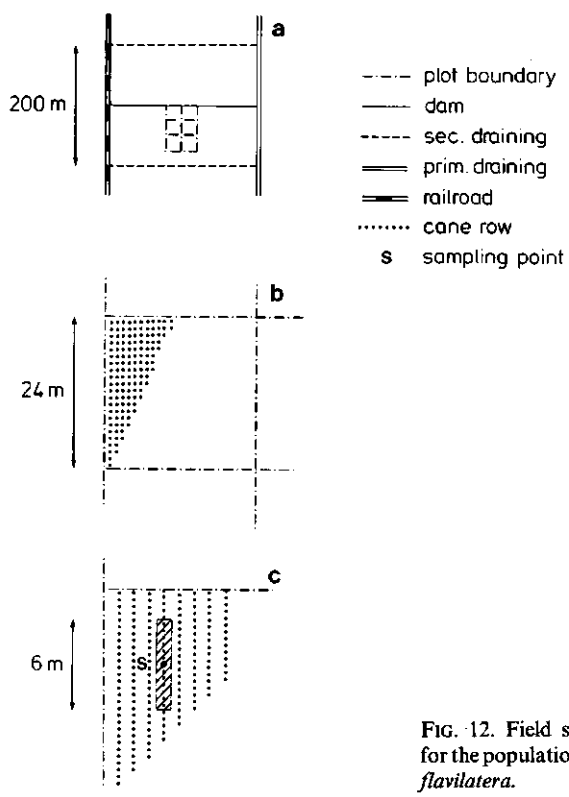

FIG. 12. Field sampling plan for the population counts of *A. flavilatera*.

age effect of these factors at the sugar estate level is in itself not significantly variable over the years, this effect is of no consequence for an explanation of the periodicity in the occurrence of froghoppers over the entire estate's area. In contrast, the weather is a variable that does affect the environmental conditions over the entire estate. The actual fluctuations of the habitat's micro-climatic factors, i.e. as a function of both the weather and the age/height of the sugar cane cover, will be subject to a detailed discussion in Section 3.3. In the next Sections 3.2.2. and 3.2.3, the population counts of *A. flavilatera* in the 3 different fields that were sampled, are presented in combination with concurrent recordings of the average weekly values of the 3 discerned main environmental parameters, viz. duration of sunshine, rainfall and percentage moist soil surface of the area under a closed canopy of sugar cane leaves.

3.2.2. *Methods*

Within each of the 3 *A. flavilatera* infested fields that were selected for the population counts (field size: 200 × 250 m; see Fig. 12a), control measures were omitted both shortly before and during the observational period. Centrally positioned rectangular areas of 0.35 ha were marked out in each field, to form the areas to be surveyed. These survey areas were subdivided into 6 plots (size: 24 × 24 m; see Fig. 12a and b), forming the 6 strata of a stratified random sampling scheme (SNEDECOR and COCHRAN, 1976). Random co-ordinates of each of 5 sampling points within each plot, were newly determined for each sample series (i.e. once per week for each of the 3 fields), by drawing 5 pairs of numbers out of 1–24, from statistical tables of at random assorted digits. In the field, these co-ordinates could be traced easily by counting the fixed number of sugar cane plant rows along one border of the plot (i.e. over a 1–24 range of rows with an interspace of 1 m, per sampling point) and by taking the fixed number of 1 m steps along the selected cane row (i.e. over a 1–24 m range, per sampling point). The population counts were performed during the mornings of fixed days, i.e. one morning per week per field on one series of 6 plots, with a total of 30 sampling points/co-ordinates.

At each sampling point, the adults were counted first in order to minimize disturbance and possibly consequent escape. Since the *A. flavilatera* adults may be present on the leaves of both the larger cane stalks and the shoots (these appear after some 4 months as a lower layer of the crop) both canes and shoots were inspected. Around each of the sampling points, 40 canes and 40 shoots (belonging to 5–6 cane stools) were selected at random and the total number of *A. flavilatera* adults present, separately recorded for both canes and shoots. These adult counts were converted to numbers per unit of area (m^2) by means of counts of both canes and shoots at all respective sampling points.

The nymphs were counted per 6 m of cane row, covering 6 m^2 when including the adjacent soil surface, with the sampling point co-ordinates at the centre of the inspected strip of soil surface (Fig. 12b and c). Nymphal counts were done indirectly, by counting the nymphal froth deposits (Fig. 8, Section 2.2). The size of the 'spittles' that surround the nymphs, is generally found to be propor-

tional to the size of the nymphal developmental stages (Table 1, Section 2.2). However, the presence of 2 or more small sized nymphs inside one larger froth mass, is not uncommon. Furthermore, a certain fraction of the total number of froth deposits per unit of sampling area, escapes detection when 'spittles' are hidden within the cane stool, or are below the soil surface. Consequently, no distinction was made as to the various nymphal stages; all directly visible 'spittles' were counted as separate units and added up. Thereupon the counts were corrected through multiplication by an experimentally determined factor, being the average value of the quotient of the number of nymphs actually present and the numbers of 'spittles' counted. The multiplication factor was determined in a series of small plots, each one consisting of 1 m of cane row and its adjacent soil surface (i.e. plots of 1 × 1 m). Different soil moisture conditions were also taken into consideration. The plots were examined accurately up to a depth of 10 cm, following the normal routine counting of the 'spittles'. It appeared, that the soil moisture condition does not have a significant effect on the multiplication factor ($P > 0.25$); the confidence interval (C.I.)[1] for 39 ($= n$) pooled data is 3.17 $\pm$ 0.19. Thus, all 'spittle' counts were multiplied by the factor 3.17, and the confidence limits appropriately adapted. It was found, that over 90% of the nymphs reside in the upper 2 cm soil layer.

The isolation of *A. flavilatera* eggs from soil samples taken in the field, was achieved by washing the soil through sieves of respectively 5.1, 0.5 and 0.25 mm mesh; the contents of the bottom sieves (0.25 mm), existing of small, largely organic debris and the froghopper eggs, was subsequently washed into petri dishes and examined under magnification. Examination of soil samples that were taken at random from the 5 mm top-soil layer of infested fields, showed a high degree of clustering in the distribution pattern of the egg populations. The latter, in combination with the fact that the extraction of eggs from the soil appeared to be highly labour intensive, made the egg population sampling costs far too high for the compilation of regular egg population counts within acceptable confidence limits, so that these were not further pursued.

3.2.3. *Results*

The data on the *A. flavilatera* population development in different fields of the 'Marienburg' estate in Surinam, referred to in Sections 3.2.1 and 3.2.2, have been summarized in Fig. 13. Both adult and nymphal population density are indicated for 3 fields which chiefly differed in regard to the age/height of the sugar cane cover. The concurrent recordings of the average weekly values of the duration of sunshine, rainfall and the percentage moist soil surface of area under a closed canopy of sugar cane leaves, are also incorporated in Fig. 13.

[1] C.I. = confidence interval; when recorded data may be assumed to be normally distributed, a confidence interval (C.I.) will be added by indicating the 90% confidence limits of the mean, using 'Student's' t-distribution, e.g.: the C.I. of X is indicated by $X \pm t_{0.1}\, S/\sqrt{n}$, when $S = \sqrt{\Sigma(X - X_i)^2/n\text{-}1}$ ($i = 1,2,3 \ldots n$) and $t_{0.1}$ is a 10% point of 'Student's' t-distribution at n-1 degrees of freedom (SNEDECOR and COCHRAN, 1976).

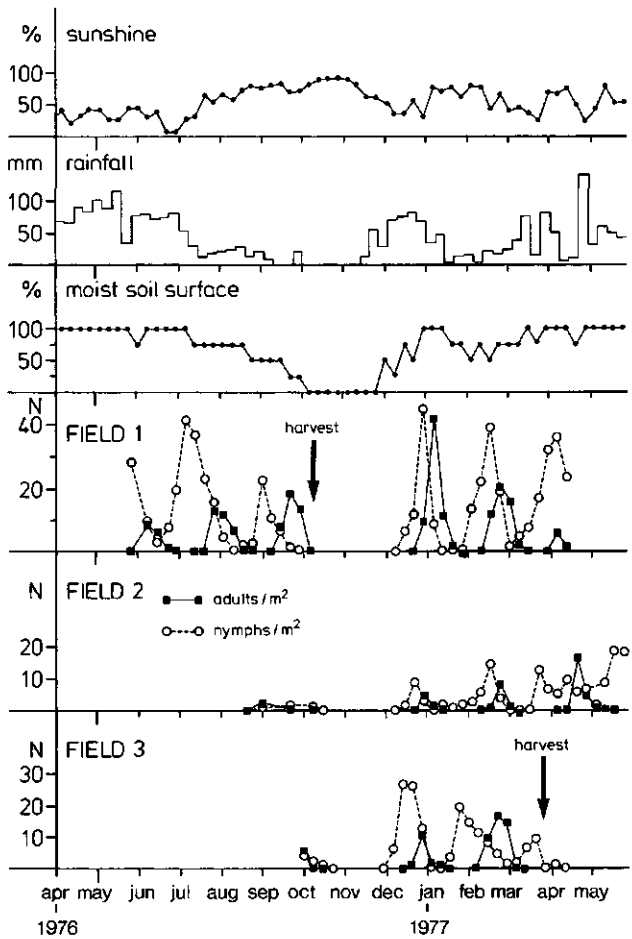

FIG. 13. Weekly population counts of *A. flavilatera* nymphs and adults in 3 different fields (i.e. *field* 1, 2 and 3 respectively) and the concurrent average weekly values of the duration of sunshine, rainfall, and mean (daily estimated) fraction of moist soil surface (see Section 3.3.3, for method of estimation) under a closed canopy of sugar cane leaves (i.e. under 6-months old cane of approximately 2 m in length) on 'Marienburg' estate: 1976–1977.

Confidence intervals of the population counts (= C.I.; see footnote 1, for the practised statistical method of computation) and progressive ages of the sugar cane covers of the fields under survey (respective values of cane height can be deduced from the sugar cane growth curve that was presented in Fig. 10, Section 3.2.1) are listed in Table 2.

Detailed analysis of the data will be discussed in Chapter 4, but the following general conclusions can be drawn and these form the basis of the rationale for the approach pursued in the subsequent sections. First of all, the data clearly show the highly significant negative impact of both harvesting and drought on

TABLE 2. Population counts of *A. flavilatera* nymphs and adults, in 3 different fields ('Marienburg' estate, Surinam: 1976–1977).

Date	Cane age (months)	C.I.[2] ($n=30$) nymphs/m^2	C.I. ($n=30$) adults/m^2
FIELD 1			
25–05–1976	7.5	28.2 ± 5.4	0
08–06	8.0	9.3 ± 1.9	8.5 ± 1.1
15–06	8.2	2.9 ± 0.9	6.8 ± 1.2
22–06	8.5	7.1 ± 1.6	0.4 ± 0.1
29–06	8.7	19.6 ± 3.2	0.1 ± 0.1
06–07	8.9	41.0 ± 6.9	0
13–07	9.2	36.3 ± 5.2	0
20–07	9.4	23.0 ± 2.1	0.7 ± 0.1
27–07	9.6	15.7 ± 1.7	12.8 ± 0.8
03–08	9.9	4.5 ± 0.8	11.6 ± 0.7
10–08	10.1	0.3 ± 0.1	7.1 ± 0.4
17–08	10.3	2.0 ± 0.3	0.4 ± 0.2
24–08	10.5	2.9 ± 0.5	0
31–08	10.8	22.3 ± 2.2	0
07–09	11.0	10.7 ± 1.8	0.1 ± 0.1
14–09	11.2	10.7 ± 0.9	6.1 ± 0.7
21–09	11.5	1.6 ± 0.3	18.6 ± 2.3
28–09	11.7	0.3 ± 0.1	13.5 ± 1.5
05–10	0	0	0
05–10/7–12–1976	0–2.0	0	0
14–12	2.2	6.1 ± 2.0	0
21–12	2.4	11.7 ± 3.8	0
28–12	2.7	44.7 ± 8.6	9.7 ± 1.1
04–01–1977	2.9	8.5 ± 2.2	41.6 ± 5.4
11–01	3.1	0.1 ± 0.2	10.9 ± 3.9
18–01	3.4	0.6 ± 0.3	1.0 ± 0.3
25–01	3.6	0.7 ± 0.5	0.3 ± 0.1
01–02	3.8	13.2 ± 4.1	0
08–02	4.1	21.9 ± 4.3	0
15–02	4.3	38.4 ± 4.9	11.9 ± 1.2
22–02	4.5	18.0 ± 3.2	20.2 ± 1.6
01–03	4.8	1.6 ± 0.8	15.1 ± 1.4
08–03	5.0	4.7 ± 1.4	1.2 ± 0.3
15–03	5.2	7.3 ± 2.0	0.1 ± 0.1
22–03	5.5	16.3 ± 5.2	0
29–03	5.7	31.8 ± 8.5	0
05–04	5.9	35.9 ± 6.2	5.2 ± 0.5
12–04	6.2	9.4 ± 3.2	1.2 ± 0.3
FIELD 2			
01–04/30–07–1976	1.6–4.6	0	0
31–08	5.7	1.3 ± 0.8	2.0 ± 0.6
20–09	6.3	0.6 ± 0.3	0.2 ± 0.2
06–10	6.8	0.1 ± 0.1	0

[2]C.I. = confidence interval; see Section 3.2.2 for method of computation.

Table 2 (continued)

Date	Cane age (months)	C.I.[2] ($n=30$) nymphs/m^2	C.I. ($n=30$) adults/m^2
13–10/08–12–1976	7.0–8.9	0	0
15–12	9.1	1.2 ± 0.6	0
22–12	9.3	8.9 ± 2.3	0
29–12	9.6	2.4 ± 0.8	4.9 ± 0.7
05–01–1977	9.8	0	0.5 ± 0.2
12–01	10.0	1.2 ± 0.4	0
19–01	10.3	0.4 ± 0.1	0
26–01	10.5	1.3 ± 0.6	0
02–02	10.7	2.4 ± 0.4	0
09–02	11.0	5.4 ± 1.5	0
16–02	11.2	14.6 ± 2.0	0.8 ± 0.4
23–02	11.4	3.3 ± 0.7	7.2 ± 0.8
02–03	11.7	0.3 ± 0.1	0.5 ± 0.1
09–03	11.9	0.2 ± 0.1	0
16–03	12.1	0.3 ± 0.1	0.3 ± 0.1
23–03	12.4	12.7 ± 3.2	0
30–03	12.6	6.4 ± 1.7	0
06–04–1977	12.8	5.0 ± 0.8	0.1 ± 0.1
13–04	13.1	9.7 ± 1.1	0.2 ± 0.1
20–04	13.3	5.7 ± 0.7	16.8 ± 0.7
27–04	13.5	6.3 ± 0.9	4.3 ± 0.5
04–05	13.8	1.9 ± 0.5	1.0 ± 0.2
11–05	14.0	8.3 ± 1.2	0.2 ± 0.1
18–05	14.2	18.0 ± 1.9	0.2 ± 0.1
FIELD 3			
01–10–1976	6.2	4.6 ± 0.6	5.1 ± 0.8
07–10	6.4	2.5 ± 0.6	0.4 ± 0.1
14–10	6.6	0.4 ± 0.1	0
21–10/30–11–1976	6.9–8.1	0	0
06–12	8.4	6.5 ± 1.3	0
13–12	8.6	26.9 ± 7.0	0.1 ± 0.1
20–12	8.8	26.0 ± 7.8	1.9 ± 0.4
27–12	9.1	12.8 ± 3.8	10.1 ± 1.4
03–01–1977	9.3	0.3 ± 0.1	1.8 ± 0.4
10–01	9.5	0	0.3 ± 0.1
17–01	9.8	3.2 ± 0.8	0
24–01	10.0	19.3 ± 2.9	0
31–01	10.2	14.4 ± 1.8	0
07–02	10.5	11.7 ± 1.5	0.1 ± 0.1
14–02	10.7	8.5 ± 1.4	9.7 ± 1.2
21–02	10.9	4.5 ± 1.0	16.4 ± 1.4
28–02	11.2	1.8 ± 0.6	14.9 ± 0.9
07–03	11.4	1.3 ± 0.6	0.5 ± 0.2
14–03	11.6	6.5 ± 1.1	0
21–03	11.9	9.7 ± 2.2	0
04–04	0.3	0.9 ± 0.3	0
18–04	0.7	0	0

the occurrence of all active froghopper stages. Specifically, harvesting inhibits further population development in every individual field that is harvested (as e.g. indicated by comparing fields no. 2 and 3 during the period April-May, 1977 in Fig. 13 and Table 2), and the period of drought that occurred towards the end of 1976 coincided with the overall absence of *A. flavilatera* nymphs and adults within the estate boundaries for more than 1 month, i.e. during the period October–November. It appears, that the periodically occurring droughts are of primary importance in regard to *A. flavilatera* population dynamics on the estate level.

Following the recorded drought in the period October–November 1976, it appeared that within 2 weeks after onset of the rains (i.e. within 1 week after a significant increase of the average percentage of moist soil surface), most of the fields that previously harboured froghopper nymphs or adults, amongst which were the 3 fields under survey, were re-infested by *A. flavilatera* in the nymphal stage. Specifically, the first active froghopper stages that were observed after the dry period were first and second nymphal instars (Table 1, Section 2.2). Consequently, it may be concluded that residual egg populations were the primary source of the estate's re-infestation by active stages of *A. flavilatera*, as adult immigration did not play any role in this case. Furthermore, the examination of soil samples taken during the period of nymphal and adult absence, generally indicated the presence of eggs, which exclusively consisted of the S_2-stage (Fig. 7, Section 2.2). The latter can be explained from the occurrence of 'quiescence' in the froghopper eggs under influence of air dry conditions (i.e. absence of free water in the top-soil layer), which will be discussed in more detail in Section 4.3.2.

Analysis of the population counts in regard to the average of adult life-span, embryonic developmental time and nymphal developmental time, indicates approximate values of 2 weeks, 2 weeks and 4 weeks, respectively. For a more detailed discussion, reference can be made to Sections 4.3.1, 4.3.2 and 4.3.3, respectively.

3.3. Fluctuations of environmental factors affecting *Aeneolamia flavilatera*

3.3.1. *Introduction*

It follows from the foregoing Sections 2.3, 2.4, 3.1 and 3.2.1 that, at the sugar *estate* level (i.e. as opposed to the individual sugar cane *field* level), the weather is the primary environmental variable to be considered in regard to the analysis of periodicity in the occurrence of *A. flavilatera* on sugar cane. The influence of the variability of the weather on froghopper population development, as effected through the direct impact of the micro-climate in *A. flavilatera's* habitat on sugar cane, is primarily determined by the variability of both rainfall and duration of sunshine (Section 1.3).

In Fig. 14, rainfall, as indicated by a stratified approximation of its monthly

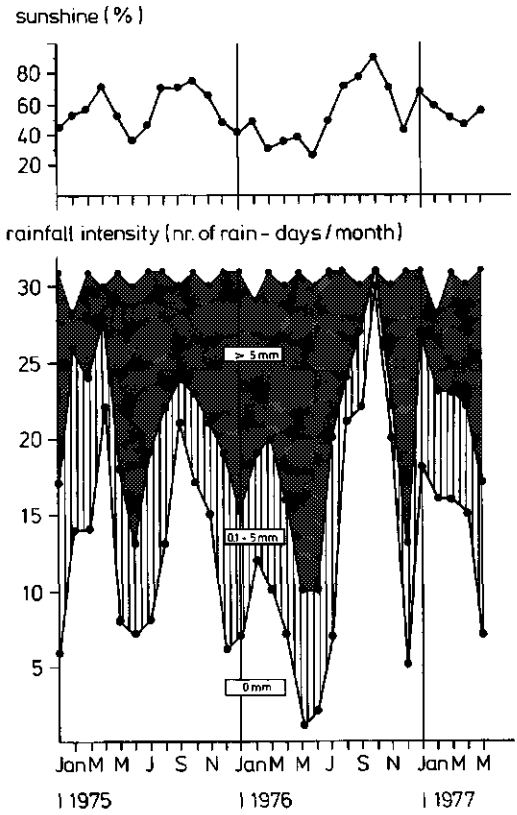

FIG. 14. Variation of the intensity of rainfall, as recorded by the average monthly fluctuations of the number of days with a rainfall of respectively 0 mm, 0.1–5 mm or more than 5 mm, and the average monthly duration of sunshine over the period: January, 1975–May, 1977 (main weather station of 'Marienburg' estate).

variability, and average monthly duration of sunshine are presented for the period January, 1975–May, 1977, which covers the period of study on 'Marienburg' estate, Surinam, where the *A. flavilatera* population counts were performed (Section 3.2). Whereas these figures may be considered to give a good indication of the actual fluctuations of the average environmental conditions on the sugar estate, it is necessary for an explanatory analysis of the concurrent froghopper population development to relate the recorded fluctuations of rainfall and sunshine to those micro-climatic factors that characterize the direct impact of the environmental conditions on the different developmental stages of *A. flavilatera*. This makes it possible to compare the established relation between weather and micro-climate with the average effect of weather fluctuations on froghopper population development, making use of the results of measurements of the effect of controlled environmental conditions on the developmental stages of *A. flavilatera* in the laboratory. The latter will be subject to discussion in Chapter 4.

A total of 5 micro-climatic parameters have been distinguished, viz. (1) moisture content and (2) temperature of the top-soil layer, both potentially affecting embryonic development, nymphal development and oviposition, and further (3) humidity, (4) temperature and (5) turbulence of the air below the canopy

of sugar cane top-leaves, which potentially affect the adults. The effect of the weather on these micro-climatic parameters differs from field to field at the individual cane field level, because of the differences in soil coverage of the fields that make up the whole of a sugar estate (Sections 1.2 and 3.2.1). In assessing the latter, the representation of all differences in soil coverage that may simultaneously exist on the different individual fields within an estate's boundaries, was approximated by a stratification into a maximum of 4 levels, viz. (1) undisturbed sugar cane coverage with a closed canopy of top-leaves, (2) sugar cane coverage with a closed canopy of top-leaves, from which all dead leaves have been removed (as is occasionally practised as a cultivation measure for the sake of prevention or control of froghopper population development), (3) coverage with the layer of cane debris as it is left after harvesting (i.e. the 'trash' which is often removed for the greater part, through burning) and (4) no soil coverage at all.

3.3.2. *Preliminary analysis*

The potential effects of the 5 micro-climatic factors, which have been discerned to represent the primary environmental parameters of the *A. flavilatera*/sugar cane ecosystem in the previous Section 3.3.1, differ markedly for the eggs, the nymphs and the adults, because of (1) the existing difference in site of occurrence (Section 2.2) and (2) because, in contrast to the eggs, both nymphs and adults can actively moderate, or escape negative effects that are imposed by the changing environmental conditions. It follows, with reference to Table 3, which presents a summary of the possible impact of the factors temperature and humidity on the various froghopper stages in their diverse habitats, that the influence of the fluctuations of both temperature and moisture on the *eggs* appear to be of primary importance in considering environmental impact on *A. flavilatera* in general. Impact of temperature and moisture on the egg stage in the field is effected in the top-soil within a depth range that generally does not deviate

TABLE 3. Summary of stage specific attributes affecting environmental impact on *Aeneolamia flavilatera*.

stage	site of occurrence	potential mobility	impact of temperature fluctuations	impact of humidity fluctuations
eggs	top-soil layer (0–5 mm)	none	continuously direct impact of top-soil temperature	continuously direct impact of top-soil moisture content
nymphs	top-soil layer (0–20 mm)	slight, confined to top-soil layer	moderated, through insulation by froth and adaptive nymphal movement	none, through the continuing protection by froth
adults	overground	unrestricted	moderated, through adaptive adult movement	moderated, through adaptive adult movement

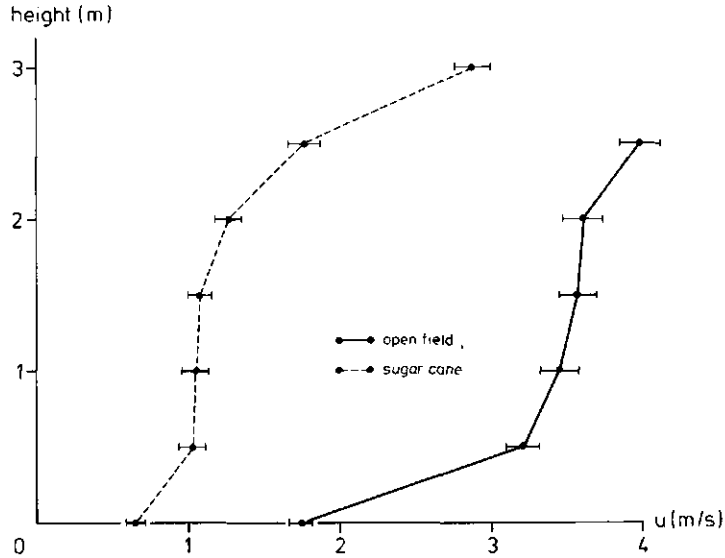

FIG. 15. The average rate of air displacement (plus indication of standard error), at different heights above the ground of both a recently reaped sugar cane field ('open field') and a field with cane of approximately 2.5 m in length (6–8 months old), as measured with a thermical anemometer (thermistor sensing) during both mornings and afternoons of 25 days (n = 50), that were selected at random over the period: May, 1978–September, 1978 ('Guyana Sugar Experiment Station', Guyana).

from 0–5 mm (because of *A. flavilatera* oviposition, specifically in this layer; see Section 2.2).

The micro-climatic conditions in the 0–5 mm top-soil layer, will generally only be subject to significant fluctuations during prolonged periods without rainfall; i.e. rainfall will stabilize the micro-climatic conditions in the top-soil, both in time and over the entire area receiving the rain, into values of maximum humidity (0 mb vapour pressure deficit) and relatively low, approximately constant temperature. Upon cessation of rainfall, both moisture content and temperature of the top-soil tend to change to an extent that is highly dependent on differences in the soil surface coverage, as simultaneously existing within the sugar estate's boundaries (Section 3.3.1); i.e. through (1) the rate of air displacement above the soil surface (Fig. 15), (2) the temperature and humidity of the air above the soil surface (Fig. 16) and (3) in the case of sun exposed soil surface, the heating effect of direct sunshine radiation. Methods and results of the assessment of actual fluctuations of the top-soil moisture condition and top-soil temperature, as resultant from both the combined effect of the above mentioned factors and rainfall, will be subject to discussion in the following Sections 3.3.3 and 3.3.4, respectively.

3.3.3. *Methods*

The methodology followed in measuring the moisture content of the 5 mm

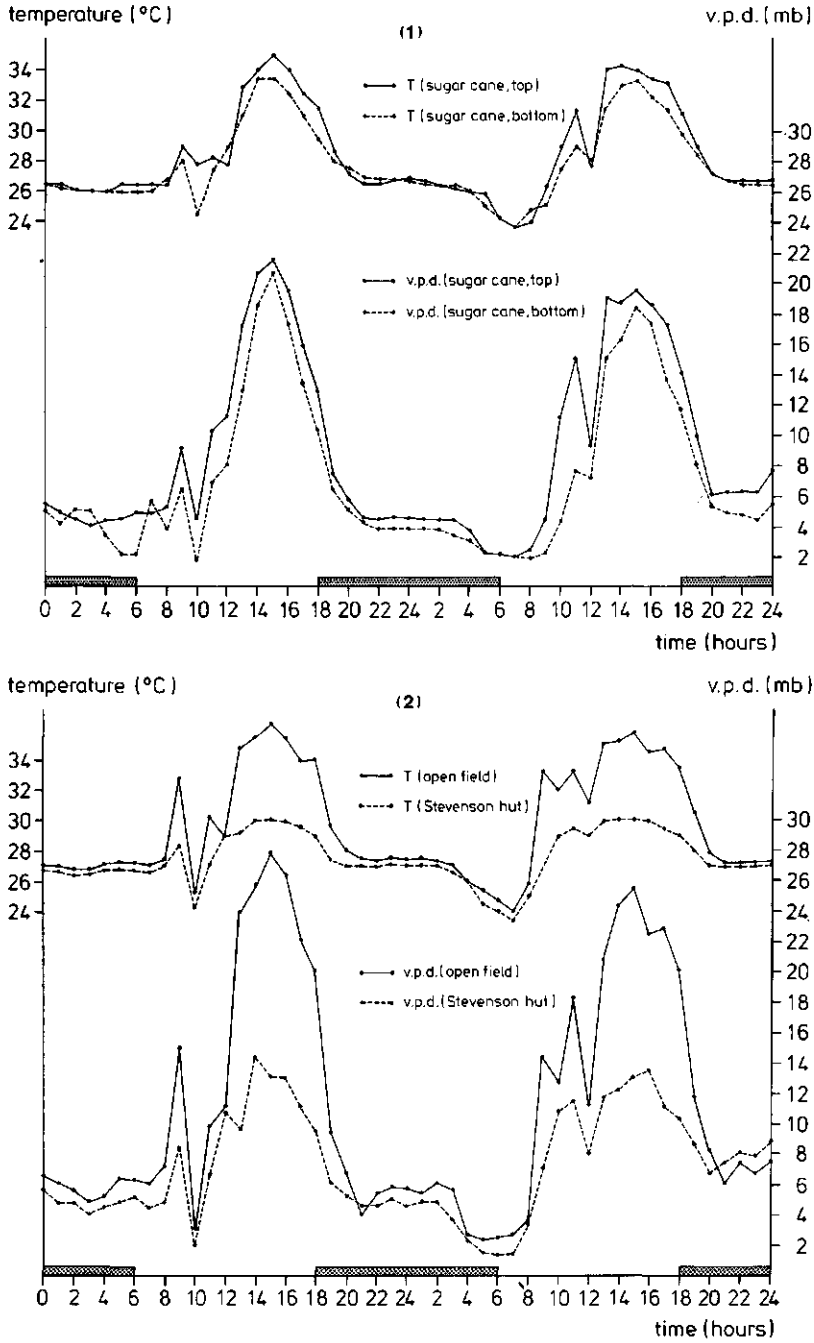

FIG. 16. Representation of the characteristic course of air temperature (mechanical registration by means of thermo-graphs; expressed in °C) and air humidity (mechanical registration of relative humidity by means of hygro-graphs; expressed in mb vapour pressure deficit = *v.p.d.*) over 2 at random selected consecutive days in June, 1976 ('Marienburg' estate) that were sunny, except for rain-showers at approximately 10 a.m. and 12 a.m. of respectively the first and second day of the recordings in: (1) 6-months old sugar cane of approximately 2 m in length, both at the top and at the bottom, and (2) at the surface of a recently reaped sugar cane field, and in the Stevenson screen of the 'Marienburg' main weather station.

deep top-soil, was determined by (1) the feasibility of recording the often violently fluctuating actual values of soil moisture in the upper 5 mm layer, and (2) the measurement accuracy that is needed for a correct interpretation of experimental results with regard to the actual impact of different degrees of soil moisture on embryonic development and mortality, and oviposition. It will appear at a later stage in Section 4.3, where oviposition is discussed in detail, that of all the potentially existing grades in soil moisture content (i.e. ranging from 'saturated' to 'air dry'), only 2 categories of soil moisture content, viz. 'air dry' and 'moist', need to be differentiated for a seemingly good approximation of the actual overall effect of environmental humidity on *A. flavilatera*. This limitation greatly enhanced the feasibility of assessing the fluctuations of relevant soil moisture values. On the basis that air dry clay (i.e. the predominant soil type in all of the area of study) has a clearly brighter appearance than even slightly moist clay, it proved practicable to perform a visual estimation of the moisture condition in the top-soil. Since the drying out of the top-soil does not come about evenly over the soil surface of any sugar cane field (it rather shows a generally patchy complexion, the soil surface around the cane stools tending to stay moist longer), it appeared necessary to introduce a rating scale of 1–5, representing estimations of the average percentage of moist (i.e. not air dry) soil surface, viz. 1 (0%), 2 (25%), 3 (50%), 4 (75%) and 5 (100%).

Measurement of the fluctuations of top-soil temperature was achieved by means of thermo-couple (Copper-Constantan) sensing. A total of 6 thermo-couples could be simultaneously operated in the field, through use of 2 battery (12 V) fed 3-line recorders. The integral weather proof temperature registration unit[3] could be left in the field for continuous measurement at any point within the sugar estate's boundaries.

3.3.4. *Results*

The recordings of the fluctuations of the average daily percentage of moist soil surface, which for a number of 4 different, representative field conditions with regard to soil surface coverage (Section 3.3.1) are presented in Fig. 17, are indicative for the following general phenomena that are apparently highly significant in regard to potential *A. flavilatera* population development:

1) The 3 discerned categories of soil surface coverage (Fig. 17: 1a, 1b and 2) have a significantly tempering effect on the fluctuations of the top-soil moisture content, i.e. as compared with the violent moisture fluctuations that uncovered top-soil (Fig. 17:3) is subject to, during periods with alternating rainfall and sunshine.

2) The post-harvesting cane debris ('trash') coverage (Fig. 17:2) is approximately as effective in tempering top-soil moisture fluctuations, as soil coverage by a closed canopy of sugar cane leaves (Fig. 17: 1a). In normally developing sugar cane, such a canopy is formed after approximately 4 months of growth following harvesting (Section 3.2.1).

[3] Developed and assembled by the Technical and Physical Engineering Research Service (TFDL) in Wageningen, Netherlands.

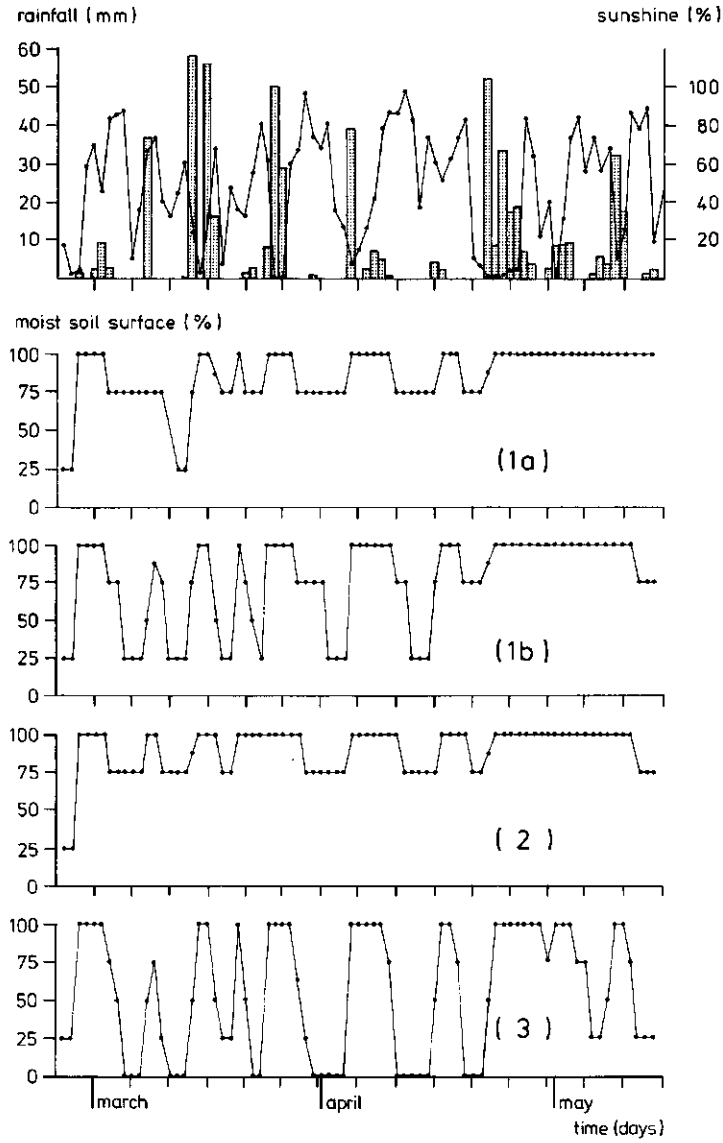

FIG. 17. Average daily fluctuations of the fraction of moist soil surface (see Section 3.3.3, for method of estimation) under different conditions with regard to soil surface coverage, viz. (1a) under a closed canopy of sugar cane leaves of initially 6-months old cane of approximately 2 m in length, (1b) same as mentioned under 1a, but all dead sugar cane leaves removed, (2) under a cover of sugar cane debris ('trash') as it is left after harvesting, and (3) no soil coverage at all; concurrent daily values of rainfall and duration of sunshine are added ('Marienburg' estate: February, 1977–May, 1977).

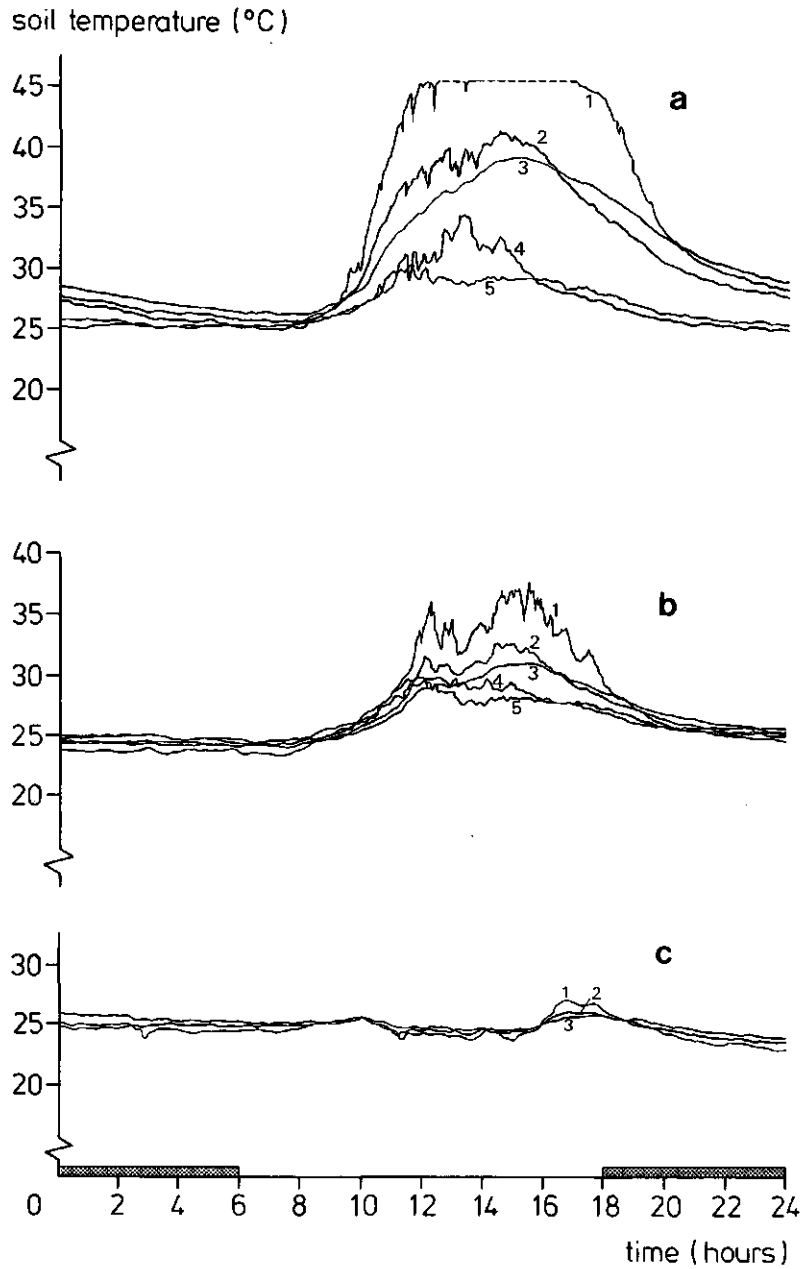

FIG. 18. Daily course of the temperature in the top-soil layer, measured by means of thermo-couples, during (a) continuously sunny conditions, (b) alternatively sunny and rainy conditions, and (c) continuously rainy conditions ('Marienburg' estate: 1976), under different conditions with regard to soil surface coverage and at different sites within the top-soil layer, viz. (1) just under the surface of fully exposed soil (i.e. over a depth range of 0–5 mm, which corresponds with the size of the thermo-couples), (2) same as mentioned under 1, but close to the base of a recently reaped cane stool, (3) same as mentioned under 1, but over a depth range of 5–10 mm, (4) under a closed canopy of sugar cane leaves of 6-months old cane of approximately 2 m in length, just under the surface of the soil near the centre line between two rows of sugar cane plants, and (5) same as mentioned under 4, but close to the base of a cane stool.

3) The component of dead cane leaves that is present within all normally developing sugar cane coverage after approximately 4 months of growth, appears to contribute to a significant extent to the overall tempering effect of a soil coverage by a closed canopy of cane leaves, as is shown by the effect of the removal of all dead sugar cane leaves (Fig. 17:1b) on top-soil moisture fluctuations (compare Fig. 17:1a).

It is important to stress, that the differential effect of top-soil coverage in regard to top-soil moisture fluctuation as discussed above, is not of relevance during the more or less regularly occurring periods that are characterized by either prolonged rainy weather or prolonged dry and sunny weather (Sections 1.3 and 3.3.1). All of an estate's area will then retain a percentage of moist soil surface of either 100 (i.e. during 'wet' periods) or nil (i.e. during 'dry' periods). A good example of the occurrence of the latter, is given in Fig. 13 (Section 3.2.3) which records the period of prolonged dry weather that occurred in the period September–November, 1976 and its effect in terms of overall dryness of the top-soil in the period October–November.

Temperature fluctuations in the top-soil layer are presented in Fig. 18, for a number of representative situations with regard to (1) the weather (Fig. 18a, b and c) and (2) both type of soil surface coverage and the site of measurement within the top-soil layer (Fig. 18a: 1, 2, 3, 4 and 5, Fig. 18b: 1, 2, 3, 4 and 5, and Fig. 18c: 1, 2 and 3; see Fig. 18 caption for a detailed description). It appears, that the temperature in the top-soil only fluctuates to a significant extent, when the impact of sunshine plays a role (as in case of the measurements that are represented in Fig. 18a and b); i.e. in the case of rainy weather, the temperature fluctuations in the top-soil appear to be negligible over all of an estate's area (Fig. 18c). The impact of sunshine on the temperature fluctuations in the top-soil, exists of the resultant of (1) the positive effect of direct sunshine radiation, (2) the positive effect of a rise in air temperature above the soil surface, and (3) the negative effect of loss of latent heat through evaporation at the soil surface (which is effective in the case of the measurements represented in Fig. 18b only, since the measurements represented in Fig. 18a were performed in air dry top-soil). Further analysis of Fig. 18a and b, reveals the following general phenomena that appear to be of importance in regard to *A. flavilatera* population development, through the effect of both soil surface coverage and difference in site within the top-soil layer of any sugar cane field, on the actual top-soil temperature fluctuations that primarily affect the embryonic development and mortality of *A. flavilatera* (Section 3.3.2):

1) The heating effect of sunshine, apparently at most in the exposed 5 mm deep top-soil layer (Fig. 18a and b:1), is significantly tempered by the effect of shading that is provided by recently reaped cane stools (Fig. 18a and b:2); i.e. the tempering effect of the minimal shading by recently reaped cane stools is approximately equal to the tempering effect of an overhead soil layer of 5 mm (Fig. 18a and b:3) in exposed top-soil.

2) A soil surface coverage of a closed canopy of cane leaves, reduces the sunshine imposed top-soil temperature fluctuations to a highly significant extent

(Fig. 18a and b: 4 and 5); i.e. the top-soil temperature fluctuations under a closed cane leave canopy, are largely independent of both the site of measurement and the duration of the impact of sunshine.

A further discussion of the above described phenomena will be pursued in Chapter 4, in view of results from experiments that were aimed at measuring the actual effect of temperature on both embryonic development and embryonic mortality, in order to determine the potential effect of the recorded temperature range in the 5 mm deep top-soil layer (i.e. in the habitat of the *A. flavilatera* eggs) as represented in the above discussed Fig. 18.

4. ASSESSMENT OF THE POTENTIAL IMPACT OF THE FLUCTUATIONS OF ENVIRONMENTAL FACTORS, ON *AENEOLAMIA FLAVILATERA* POPULATION DEVELOPMENT

4.1. INTRODUCTION: PRELIMINARY ANALYSIS

It follows from Chapter 3 (particularly, reference is made to Section 3.3) that the impact of climate on *A. flavilatera* population development in general, is primarily effective on the froghopper eggs through the fluctuations of both temperature and humidity in the 5 mm deep top-soil layer, in terms of effect on the rate of embryonic development and mortality. Evidently, the latter is only of importance when the influence of temperture/humidity fluctuations on the eggs causes significant changes in the rate of embryonic development and mortality, i.e. as compared to the existing natural (intrinsic) variability in these parameters among individual froghopper eggs. A clear example of significant intrinsic variability among eggs is found in the related froghopper species *A. varia saccharina,* in which case it was shown that subsequent generations of eggs consisted of a significantly increasing percentage of 'long-period' eggs, i.e. eggs entering into dormancy without any apparent external stimulus (FEWKES, 1963). This aspect will be taken into account in discussing the effects of fluctuations of environmental factors on embryonic development and mortality in general, in Section 4.3.2.

It appeared (Sections 2.3, 3.2.1 and 3.3.2) that in general, neither the nymphs nor the adults of *A. flavilatera* are subject to significant fluctuations of abiotic factors because of mitigation and escape possibilities, as summarized in Table 3 (Section 3.3.2). However, two exceptions in regard to potentially significant environmental impact on the froghopper adults and nymphs need to be distinguised, viz. (1) the apparently total inhibition of oviposition through air dryness of the available oviposition substrate (i.e. all of the 5 mm deep top-soil layer that lies within the potential migration range of the froghopper adults), which will be further discussed in Section 4.3.1, and (2) the nymphal mortality that may occur in the case of disturbance of the hatching process through air dry conditions in the top-soil. The latter will be considered as part of embryonic mortality in the context of the above mentioned discussion in Section 4.3.2, i.e. in regard to the impact of environmental factors on the froghopper eggs.

In addition, mention will be made of the effects of flooding, occurring occasionally through excessive rainfall or flood fallowing, on oviposition (Section 4.3.1), the eggs (Section 4.3.2) and the nymphs (Section 4.3.3). The relative importance of the latter will be subject to discussion in Chapter 5, in connection with other potentially significant environmental effects on *A. flavilatera* population development in general.

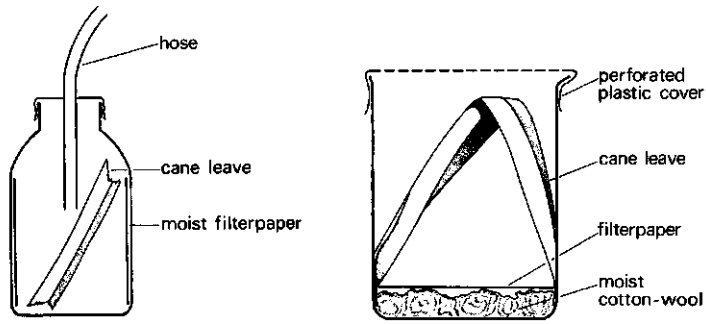

FIG. 19. Equipment employed for the collection of *A. flavilatera* eggs: simple plastic jar, used for hand-collecting of *A. flavilatera* adults in the field (left) and set-up which offers the froghopper adults ample possibility to lay eggs in the moist filterpaper that is present at the bottom of a 1 litre rearing beaker (right).

4.2. METHODS

Insect material used for laboratory experiments, originated from the field. Adults were hand trapped in simple collecting jars (Fig. 19). The adults, kept in the laboratory on daily refreshed cane leaves, accepted moist filterpaper as oviposition substrate. In the 1 litre beakers that were used as containers (Fig. 19), the *A. flavilatera* females could be kept alive for a period of 2–5 days. With 10 females and 5 males per container, an average number of approximately 10 eggs per female per day could be obtained. To prevent damaging the eggs, all experiments studying the effect of temperature and humidity on embryonic development and mortality were carried out with eggs in situ, i.e. with eggs still embedded in the filterpaper in which they had been inserted by the females. By 10–20 × enlargement of the eggs in filterpaper, the different stages of embryonic development (Section 2.2: Fig. 7) could readily be distinguished. Comparison of identical treatments of eggs deposited through oviposition in filterpaper and eggs embedded in clay (i.e. the predominant soil type in the area of study) respectively, did not reveal any significant differences in response between the two sets. By refreshing the oviposition substrate every 48 hours, eggs of a uniform age class (of an average age of 1 day) were available.

Simple, self-built thermostats and hygrostats were used in studying the impact of temperature and humidity on embryonic development and mortality. Four thermostats were put on, each made up of a well insulated aluminium foil compartment (30 × 30 × 30 cm) connected to the sensor of a contact thermometer. The latter could be set to maintain a constant, pre-fixed temperature of the air inside the foil compartment through the heating effect of ordinary electric bulbs placed on the outer side of the compartment and controlled by relays. By placing the thermostats in an airconditioned room with an average temperature of 21 °C, ranging from 20.5–21.5 °C, 5 different constant test-temperatures with a maximum deviation from the mean of 1 °C could be obtained, viz. 21, 26, 31, 36

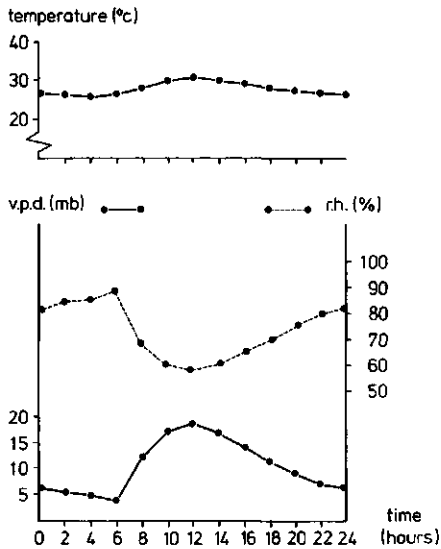

FIG. 20. Daily fluctuations of the mean values of air temperature and air humidity, in the laboratory (thermo-hygrograph registration at 'Marienburg': 1976).

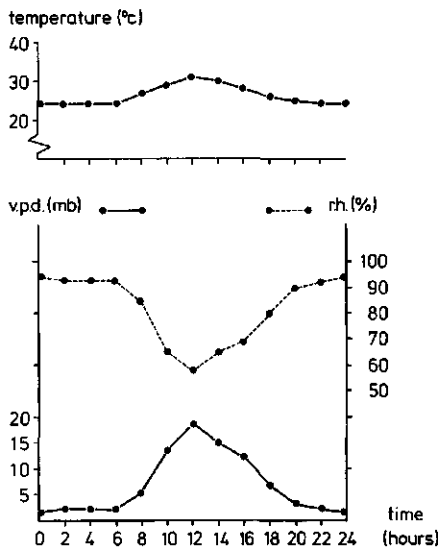

FIG. 21. Daily fluctuations of the mean values of air temperature and air humidity, in the outdoor insectary (thermo-hygrograph registration at 'Marienburg': 1976).

and 41 °C. Each temperature controlled compartment held up to 20–25 petri dishes, which were normally used as egg containers in all laboratory experiments. The petri dish also served well as a separate hygrostat when aqueous solutions of sodium hydroxide of different concentrations (MADGE, 1961) were kept in the bottom of the dishes. Filterpaper strips, containing froghopper eggs, were attached to the lids of the dishes by means of adhesive tape. In order to maintain humidity at constant levels, the dishes were sealed by means of paraffin and adhesive tape.

The effect of environmental humidity fluctuations on embryonic development and mortality was also extensively studied in simpler experiments in which eggs were exposed to either 'moist' conditions (i.e. through moistening of the filterpaper or the clay substrate with water, on a daily basis), or 'air dry' conditions (i.e. through drying of the filterpaper or the clay substrate to the air, for at least 12 hours). These experiments, as well as all other laboratory and insectary experiments that were performed without the use of thermostats or hygrostats, were subject to the fluctuations of the air temperature and air humidity in the laboratory (Fig. 20) or the outdoor insectary (Fig. 21), respectively.

4.3. Results

4.3.1. *Oviposition and egg production capacity*

The essential prerequisite for *A. flavilatera* oviposition appeared to be the availability of a substratum of adequate softness into which the eggs could be inserted just below the surface by the short ovipositor. Clay and filterpaper, both potentially serving as oviposition substrates, met this requirement only when containing sufficient moisture (i.e. unbound, or 'free' water) to alter the rigid consistency which these materials have when air dry (i.e. after the free water, that is contained by the substrates, is completely evaporated). Although inhibition of oviposition through air dryness of a substrate may be caused by more than one factor only, the substrate's rigidity appears to be a criterion that can generally be used for the practical purpose of predicting inhibition of oviposition. In the field, the extent of inhibition can be assessed by means of the method described in Section 3.3.3.; i.e. full inhibition will only occur in the case of 0% moist (i.e. not air dry) soil surface, which corresponds with condition no. 1 of the 1–5 rating scale used to assess moisture content. In intermediate conditions of moistness of the soil surface (viz. 2, 3 and 4 of the 1–5 rating scale), those areas which remain moist, and hence acceptable for oviposition, for the longest period will tend, on average, to contain more eggs than those areas which dry out more quickly. This provides an explanation for the observation that egg populations often show a high degree of clustering (Section 3.2.2); i.e. when a period of the drying out of the top-soil layer through absence of rainfall coincides with the occurrence of froghopper adults, oviposition will be concentrated on the gradually decreasing number of moist spots of the soil surface. In particular, concentrations of eggs are often found in the shielded top-soil layer in the vicinity of the cane stools (Section 3.3.4), which generally stays moist longer than other areas of the same sugar cane field (i.e. especially the area that lies in the middle of the space between the rows of cane plants).

When the minimum of moisture that is needed for egg laying is contained in the oviposition substrate (which is then defined as 'not air dry'; i.e. a minute drop of water on an air dry filterpaper or clay substratum, was sufficient supply of moisture to initiate egg laying in an area of 1–2 cm in diameter around the point contacted by the water drop), oviposition was not significantly influenced

by a further increase of the substrate's moisture content. Thus, whether completely saturated with water or only slightly moist, natural media (clay and peat) or an artificial medium (filterpaper) are all equally acceptable for egg laying by *A. flavilatera* females. However, the presence of a layer of water of 0.5 mm or more on top of the surface of a substratum, again prevented all oviposition. Thus, all soil surface that is flooded (i.e. either for shorter periods by the water pools that are occasionally formed during periods with prolonged heavy rainfall, or for longer periods during the flood fallow of cane fields as practiced in Guyana; see Sections 1.2 and 1.3), will be totally free of egg laying by *A. flavilatera*.

The maximum egg production per *A. flavilatera* female, as measured under laboratory conditions (Fig. 20) on moist filterpaper (Fig. 19), amounted to 104 eggs over 3 days. However, laboratory conditions are apparently not optimal, since adults live significantly longer in the field (Section 3.2.3): on average 3 times longer than the 2–5 days life-span of adults kept in the laboratory. Therefore, the total egg production per female in the field may be higher than the laboratory measured maximum of 104.

The maximum life-span of the froghopper adults, as measured on cane plants under outdoor insectary conditions (Fig. 21), was 12 days for the females and 7 days for the males. However, almost all of the observed caged froghopper adults lived no longer than 1 week. The adult population counts, that were previously discussed in Section 3.2, indicate an approximate life-span of 2 weeks for the females and a somewhat shorter life-span for the males (as is indicated by a shift in the sex-ratio towards more females, in hand-collected, sequentially taken samples of one adult generation), so that the above mentioned measurements of the respective maxima of 12 and 7 days may be considered realistic average values for field conditions.

4.3.2. *Embryonic development and mortality*

The intrinsic variability in embryonic developmental time among individual *A. flavilatera* eggs, was assessed by comparing the statistical mean and spread of the embryonic developmental duration in a series of 23 samples of froghopper eggs ($n = 61-100$), as indicated in Table 4. Eggs originated from field collected adults, caught at random over a period of 7 months (see Section 4.2 for methodology). All 23 samples were kept in the laboratory under apparently near optimal environmental conditions of air temperature and air humidity (Fig. 20). The resultant data in Table 4 show, that the average embryonic developmental time of the various samples of froghopper eggs does not generally deviate much from the overall average of embryonic developmental time under moist conditions in the laboratory (i.e. 15.1 days, with a confidence interval of 15.1 ± 0.1, for $n = 2128$), viz. a maximum difference of 3.0 days for all 23 samples. To give an indication of the individual variability in embryonic developmental time, the fractions of eggs that took longer than 16 days to hatch were recorded separately, together with the corresponding confidence intervals of developmental time. On average, 9.9% of the eggs took longer than 16 days (with a recorded maximum

TABLE 4. Intrinsic variability in average embryonic developmental time in days (D) of all eggs, the percentage of eggs with an individual developmental time of more than 16 days ($D > 16$), and the average duration (days) of embryonic development in the eggs that take longer than 16 days (D_{16}), under continuously moist conditions in the laboratory (i.e. under influence of the temperature fluctuations that are represented in Fig. 20: Section 4.2).

sampling date	n (= nr. of eggs/sample)	C.I.[4] of D (of all eggs)	% of eggs with $D > 16$ days	C.I. of D_{16}
20–12–76	100	15.2 ± 0.1	2	19.0 ± 0.0
27–12–76	100	15.2 ± 0.2	8	18.4 ± 2.1
03–01–77	87	14.4 ± 0.1	5	19.5 ± 1.7
10–01–77	100	15.3 ± 0.1	12	20.5 ± 0.6
18–01–77	100	14.6 ± 0.2	4	19.8 ± 1.2
24–01–77	100	14.4 ± 0.1	4	19.0 ± 1.2
27–01–77	61	13.8 ± 0.3	3	18.0 ± 0.0
14–02–77	89	16.2 ± 0.3	12	18.3 ± 0.4
21–02–77	100	14.5 ± 0.2	5	17.4 ± 0.4
28–02–77	100	14.6 ± 0.1	7	21.7 ± 1.8
04–03–77	100	15.0 ± 0.2	11	17.9 ± 0.3
10–03–77	100	14.4 ± 0.1	4	17.8 ± 0.3
17–03–77	91	16.6 ± 0.4	18	25.4 ± 2.2
05–04–77	77	15.3 ± 0.3	12	22.0 ± 1.4
11–04–77	100	14.9 ± 0.1	6	20.8 ± 1.6
18–04–77	85	15.7 ± 0.2	9	23.3 ± 3.4
25–04–77	100	14.6 ± 0.2	11	22.5 ± 1.8
03–05–77	73	13.9 ± 0.1	0	–
11–05–77	100	14.6 ± 0.2	28	17.0 ± 0.8
16–05–77	100	16.1 ± 0.3	19	22.6 ± 1.8
25–05–77	65	16.4 ± 0.2	14	29.9 ± 2.8
20–07–77	100	14.4 ± 0.1	2	17.5 ± 0.5
27–07–77	100	18.1 ± 0.3	32	23.3 ± 1.1
total:	2128	*mean:* 15.1 ± 0.1	9.9	

[4]C.I. = confidence interval; see Section 3.2.2 for method of computation.

average of 29.9 ± 2.8 and an individual maximum of embryonic developmental time of 39 days; the latter is not separately recorded in Table 4, but incorporated in the average of 29.9). Less than 5% of the eggs hatched less than 14 days after oviposition, with an individual minimum of 13 days. Thus, although the individual embryonic developmental period ranges from 13–39 days, the intrinsic variability in embryonic developmental time appears to be characterized by an on average relatively little deviation from the mean of 15 days. As a result of this it can be concluded that intrinsic variation in embryonic developmental time is of negligible consequence in regard to an explanation of the major fluctuations in *A. flavilatera* population development (see Sections 3.1 and 3.2). This means that the absence of a distinct diapausing egg stage in *A. flavilatera*, which was previously reflected upon in Section 2.3, can be confirmed; i.e., when egg diapause is assumed to be defined as embryonic developmental arrest not immediately caused by the impact of adverse environmental factors.

TABLE 5. Average embryonic developmental time (D) in days, in relation to temperature, under continuously moist conditions.

n	temperature (°C)	C.I.[5] of D	C.I. of $1/D$
60	21	23.9 ± 0.5	0.042 ± 0.001
60	26	17.1 ± 0.2	0.059 ± 0.001
60	31	14.0 ± 0.5	0.071 ± 0.003
60	36	–	–
60	41	–	–

[5]C.I. = confidence interval; see Section 3.2.2 for method of computation.

The intrinsic variability in embryonic mortality, can also be assessed from data on the same 23 samples of froghopper eggs (i.e. under identical, apparently near optimal environmental conditions). It appears, that the natural mortality, i.e. through lack of fertilization or any other defect that was not apparently caused primarily by environmental factors, ranged from 0–5.1% over all of the samples, with a total average of 2.3% ($n = 2128$). Consequently, the intrinsic variability in the rate of embryonic mortality appears to be of minor importance in the context of variability in the occurrence of *A. flavilatera*.

To determine the embryonic developmental rate in relation to temperature, the 5 different constant test-temperatures 21, 26, 31, 36 and 41 °C (see Section 4.2, for methodology) were studied with regard to their effect on embryonic development under otherwise constantly optimal, i.e. continuously moist, environmental conditions. The resultant data, which are presented in Table 5, show that the average embryonic developmental rate could only be determined for 21, 26 and 31 °C (as graphically depicted in Fig. 22), because incubation at continuous temperatures of 36 and 41 °C resulted in 100% embryonic mortality. A more detailed study of the effect of the higher temperatures on embryonic

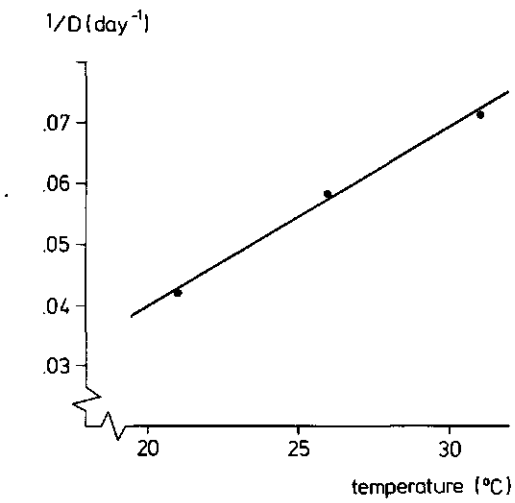

FIG. 22. Average embryonic developmental rate under moist conditions, in relation to 3 constant temperatures (viz. 21, 26 and 31 °C); $Y = -0.018 + 0.003X$ (Y: rate of embryonic development; X: temperature).

TABLE 6. The embryonic mortality (M) through impact of respectively 36 and 41 °C, under both moist and air dry conditions, over varying periods of time (otherwise: continuously moist conditions in the laboratory; i.e. under temperature fluctuations as represented in Fig. 20: Section 4.2).

n	egg stage	temperature (°C)	duration of impact (hours)	moist (+) or air dry (−)	M (%)
100	S_1	36	72	+	100
100	S_1	36	60	+	66
100	S_1	36	48	+	9
100	S_1	36	36	+	0
100	S_1	41	10	+	100
100	S_1	41	6	+	23
100	S_1	41	5	+	0
100	S_1	36	40	−	100
100	S_1	36	36	−	76
100	S_1	36	30	−	23
100	S_1	36	24	−	0
100	S_3	36	24	−	97
100	S_3	36	8	−	60
100	S_3	36	6	−	0
100	S_1	41	3	−	100*[6]
100	S_1	41	2	−	18*[6]
100	S_1	41	1	−	0

[6] *: significant rate of embryonic mortality, which may occur under actually existing environmental conditions in the field (see Section 3.3.4: Fig. 18).

mortality, was performed through measurement of the effect of 36 and 41 °C over varying shorter periods of time and under different conditions with regard to environmental moisture. The resultant data of this study, which are given in Table 6, can be interpreted in terms of the potential impact of temperature on embryonic mortality in the field, through a comparison with the data on the actual temperature fluctuations in the top-soil layer under various field conditions, as previously presented in Fig. 18 of Section 3.3.4. They show, that lethal temperature values in the top-soil do occur under specific conditions of weather and soil surface coverage, i.e. during dry and sunny weather (as represented in Fig. 18a), just under the surface of fully exposed soil (Fig. 18a: 1 and 2). However, even the minimum shading effect that is provided by a recently reaped cane stool (Fig. 18a:2) tempers the top-soil temperature fluctuations to the extent that 100% embryonic mortality (as caused by 3 or more hours of impact of 41 °C, under air dry conditions) is not likely to occur in the field as a consequence of temperature alone, i.e. even in recently reaped cane fields under continuously dry and sunny weather. Moreover, since the greater part of a sugar estate is generally not exposed to significant heating of the top-soil layer because of the tempering effect provided by the sugar cane coverage of the soil surface (see Section 3.2.1:Fig. 11), the overall effect of natural heating

of the soil surface on embryonic mortality seems to be of relatively little importance.

A further analysis of Table 6 with regard to the moisture factor, reveals the phenomenon of an increased rate of embryonic mortality in the case of air dry environmental conditions, i.e. under the impact of both 36 and 41 °C. This may be caused by (1) the absence of the cooling effect through loss of latent heat by evaporation at the egg periphery, which is operative in the case of moist environmental conditions and (2) the direct effect of the air dry conditions, that exist at 36 and 41 °C, on embryonic mortality. However, whereas the first explanation appears to be valid under field conditions, because of the noticeable rate of evaporation at the surface of moist soil through a significant rate of air turbulence at the soil surface (see Section 3.3.2: Fig. 15), it seems to be of no consequence under the applied experimental conditions which provided a stable saturated atmosphere over the wetted filterpaper containing the eggs, in closed petri dishes. Consequently, prominence must be given to the second possibility that the embryonic mortality in *A. flavilatera* eggs under influence of both 36 and 41 °C temperatures, is significantly increased through the direct effect of air dry environmental conditions.

The effect of humidity on embryonic development and mortality was studied in more detail by (1) assessment of the effect of different degrees of air dryness by means of hygrostats (Section 4.2) under apparently near optimal temperature conditions of 26 °C (i.e. a temperature which did not cause significant mortality under moist conditions), and (2) assessment of the effect of fluctuating values of air dryness that occur in the laboratory, as being comparable to the fluctuations that exist over the greater part of a sugar estate's top-soil layer (i.e. ranging from 3–20 mb vapour pressure deficit, as shown by comparing Section 4.2: Fig. 20, Section 3.3.2: Fig. 16 (1), and Section 3.2.1: Fig. 11, respectively), over varying periods of time. The data on the effect of different levels of air dryness (Table 7), show that free water contact with the egg's periphery is apparently essential for embryonic development, since prolonged absence of free water in the substrate containing the froghopper eggs caused 100% mortality in the S_1 (n = 500), S_2 (n = 500) and S_3 (n = 500) stages (see Section 2.2: Fig. 7) under otherwise apparently near optimal environmental conditions. However, the advanced S_4-stage of embryonic development was apparently insensitive to the absence of free water when the air humidity was relatively high (viz. 0–2 mb vapour pressure deficit), because all eggs (n = 100) hatched normally under those conditions. The S_4-stage was negatively affected by the enhancement of the humidity stress beyond 2 mb, through both embryonic mortality and a form of mortality which was found to occur during the hatching process, i.e. when hatching nymphs became stuck half way out of the egg or when the nymphs were unable to shed the embryonic cuticle (see Section 2.2). The data for S_4 mortality through humidity stress (Table 7) are shown separately in Fig. 23.

Although the above data are indicative for biological phenomena that appear to be highly significant for an understanding of *A. flavilatera* population development in a largely qualitative sense, it is necessary to assess the impact of (1)

TABLE 7. The effect of prolonged impact of air dry conditions, at constant levels of air dryness (i.e. by means of hygrostats), on *A. flavilatera* eggs in different stages of embryonic development, in terms of rates of embryonic mortality (*M*) and mortality during hatching (*Mh*), under a constant temperature of 26°C.

egg stage	*n*	air humidity[7]: *v.p.d.* (mb)–(%*RH*)	*M* (%)	*Mh* (%)
S_1	500	0 –(100)	100	0
S_2	500	0 –(100)	100	0
S_3	500	0 –(100)	100	0
S_4	100	0 –(100)	0	0
S_4	100	1.7– (95)	0	0
S_4	100	3.4– (90)	0	4
S_4	100	6.7– (80)	18	6
S_4	100	13.4– (60)	79	21
S_4	100	20.2– (40)	97	3
S_4	100	26.9– (20)	99	1

[7]The air humidity level is indicated by both the vapour pressure deficit in millibars (*v.p.d.* in mb) and the corresponding percentage relative humidity at 26°C (% *RH*).

actual daily fluctuations of humidity stress in the field (as previously discussed in Section 3.3.2: Fig. 16) and (2) the potential duration of air dry conditions in the field (as previously discussed in Section 3.3.4: Fig. 17), in order to be able to analyse the development of froghopper populations quantitatively, in as much as embryonic development and mortality are concerned. Since the range of the fluctuations of humidity stress applied in the laboratory was comparable to the actual field situation in that respect (viz. a range of 3–20 mb *v.p.d.* during dry, i.e. non-rainy, conditions), the effect of varying periods of air dry conditions in the laboratory (i.e. as alternated by moist conditions, through the adding

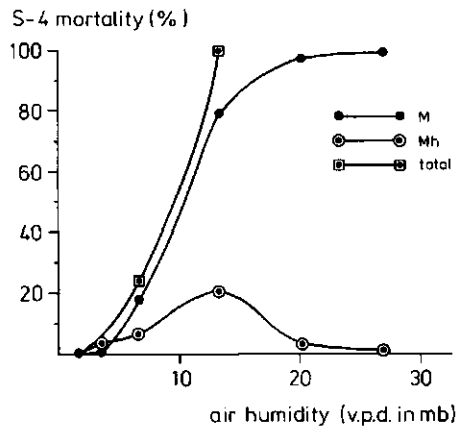

FIG. 23. Embryonic mortality (*M*) in the S_4 developmental stage, mortality during the hatching process (*Mh*) and the total of these mortalities, in relation to air humidity (expressed as: *v.p.d.* in mb = vapour pressure deficit, in millibars).

TABLE 8. The effect of varying periods of air dry conditions, i.e. under fluctuations of humidity and temperature of the air in the laboratory as indicated in Fig. 20 (Section 4.2), on *A. flavilatera* eggs in different stages of embryonic development, in terms of the rate of embryonic mortality (*M*) and the rate of mortality during hatching (*Mh*).

egg stage[8]	*n*	duration of air dry conditions (days)	*M* (%)	*Mh* (%)
S_1 (0 days old)	100	5	8	0
	100	10	9	0
	100	20	29	0
	100	30	18	0
	100	40	34	0
	100	75	96	0
	100	100	91	0
	100	110	100	0
S_1 (2 days old)	100	5	7	0
	100	10	11	0
	100	20	62	0
	100	30	83	0
	100	40	97	0
	100	50	100	0
S_1 (4 days old)	100	5	4	0
	100	10	4	0
	100	20	51	0
	100	30	80	0
	100	40	92	0
	100	50	100	0
S_2 (6 days old)	100	5	2	0
	100	10	26	0
	100	20	43	0
	100	30	91	0
	100	40	100	0
S_3 (8 days old)	100	2	18	0
	100	4	58	0
	100	6	78	0
	100	10	93	7
S_4 (12 days old)	100	2	33	12
	100	4	43	12
	100	6	40	8
	100	10	54	11

[8]The stage of embryonic development that is subjected to the air dry conditions, is indicated by both the denotation that was previously described in Section 2.2: Fig. 7 (viz. S_1, S_2, S_3 and S_4, respectively), and the denotation of the number of days of moist conditions that have passed since oviposition.

TABLE 9. The effect of varying periods of air dry conditions, under fluctuations of humidity and temperature of the air in the laboratory as indicated in Fig. 20 (Section 4.2), on *A. flavilatera* eggs in different stages of embryonic development; i.e. in terms of overall duration of embryonic development as denoted by D_1 (i.e. the average total duration of embryonic development and developmental arrest), D_2 (i.e. D_1 minus the duration of air dry conditions impact) and D_3 (i.e. D_2 minus the average duration of embryonic development under moist conditions, viz. 15.1 days, which is given in Table 4).

egg stage[9]	*n*	duration of air dry conditions (days)	C.I.[10] of D_1 (days)	D_2 (days)	D_3 (days)
S_1 (0 days old)	92	5	27.5 ± 3.1	22.5	7.4
	91	10	31.6 ± 2.2	21.6	6.5
	71	20	40.0 ± 2.7	20.0	4.9
	82	30	51.3 ± 2.2	21.3	6.2
	65	40	68.6 ± 2.6	28.6	13.5
	4	75	106.5 ± 6.6	31.5	16.4
	9	100	124.6 ± 3.4	24.6	9.5
S_1 (2 days old)	96	5	19.1 ± 0.7	14.1	−1.0
	89	10	33.1 ± 2.7	23.1	8.0
	38	20	46.2 ± 4.2	26.2	11.1
	17	30	59.1 ± 3.6	29.1	14.0
	3	40	80.3 ± 3.7	40.3	25.2
S_1 (4 days old)	96	5	19.1 ± 0.5	14.1	−1.0
	96	10	25.1 ± 0.7	15.1	0.0
	49	20	46.0 ± 4.6	26.0	10.9
	20	30	61.1 ± 3.7	31.1	16.0
	8	40	73.3 ± 8.3	33.3	18.2
S_2 (6 days old)	98	5	20.7 ± 0.5	15.7	0.6
	74	10	29.3 ± 1.2	19.3	4.2
	57	20	54.6 ± 5.1	34.6	19.5
	9	30	60.3 ± 5.1	30.3	15.2
S_3 (8 days old)	42	4	16.1 ± 0.4	12.1	−3.0
	22	6	15.9 ± 0.3	9.9	−5.2
S_4 (12 days old)	57	4	15.2 ± 0.1	11.2	−3.9
	60	6	14.9 ± 0.2	8.9	−6.2
	46	10	15.5 ± 0.4	5.5	−9.6

[9] See footnote of Table 8, for an explanation of the practised denotation.
[10] C.I. = confidence interval; see Section 3.2.2 for method of computation

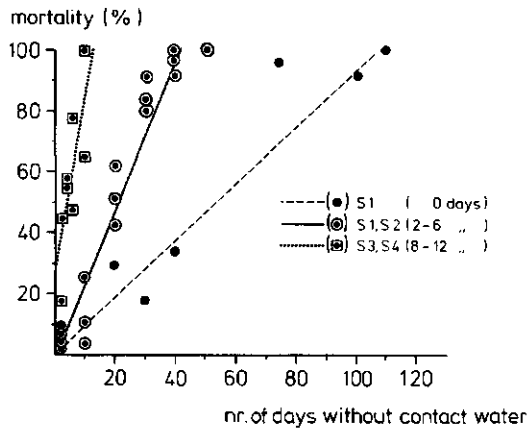

FIG. 24. Embryonic mortality in eggs of (1) 0 days old (S_1 stage), (2) 2–6 days old (S_1 and S_2 stages) and (3) 8–12 days old (S_3 and S_4 stages), in relation to the number of days without contact water impact; correlations for these 3 categories are approximated by: $Y = 1.85 + 0.95X$, $Y = -2.81 + 2.41X$ and $Y = 25.73 + 5.94X$, respectively (Y: embryonic mortality; X: duration of air dry conditions).

of sufficient water to secure contact of free water with the periphery of the eggs), may be considered representative for the actual field situation over the greater part of a sugar estate. The resultant data of a study on this are presented in Tables 8 and 9. They show, that the impact of varying periods of air dry conditions on *A. flavilatera* eggs, differed markedly for the various discerned stages of embryonic development. Of primary importance was the occurrence of developmental arrest in the early S_1 and S_2-stages of embryonic development, when free water contact was withheld[11]. The data presented in Table 8 indicate that the potential duration of quiescence in S_1 and S_2 under the influence of air dry conditions, i.e. the longest duration of impact of air dry conditions on the eggs which does not result in 100% embryonic mortality, is dependent on the stage of embryonic development at which the eggs were first subjected to the air dry conditions. A significantly longer period of impact of air dry conditions (100–110 days) was required to bring about 100% mortality in the early S_1-stage of embryonic development directly after oviposition under moist conditions (i.e. in eggs of 0 days of moist conditions after oviposition), than for eggs in later stages of development: i.e. 40–50 days in S_1-stage eggs of 2–4 days of moist conditions after oviposition, and 30–40 days in S_2-stage eggs of 6 days of moist conditions after oviposition, respectively.

When embryonic development had advanced beyond the S_2-stage, air dry conditions no longer induced developmental arrest (see Table 9) but even short periods caused severe mortality. The eggs that had entered into the S_3-stage (i.e. eggs of 8–12 days of moist conditions after oviposition) were probably much more sensitive to the impact of air dry conditions because the protective egg shell had split open in this phase of development (Section 2.2: Fig. 7). A relatively short period of 6–10 days of air dry conditions, resulted in 100% mortality in the S_3-stage eggs (Table 8). In the S_4-stage, a maximum of 65% mortality (*n*

[11]All quiescent *A. flavilatera* eggs have an S_2-stage appearance, whether quiescence is induced in the S_1-stage, or not (see Section 2.2: Fig. 7, and Section 3.2.3).

= 100) was reached after 10 days of air dry conditions, through both embryonic mortality (viz. 54%, for $n = 100$) and mortality during hatching as previously described in regard to Table 7 (viz. 11%, for $n = 100$), whereas the remainder of the eggs hatched normally (viz. 35%, for $n = 100$). The differential effects of varying periods of air dry conditions on the mortality in different developmental stages of *A. flavilatera* eggs, are shown graphically in Fig. 24.

The developmental arrest in the S_1 and S_2-stages through impact of air dry conditions was broken when free water contact with the periphery of the froghopper eggs was restored. However, embryonic development was not immediately re-activated upon the termination of the air dry conditions, as is indicated by the data presented in Table 9. The extra developmental retardation in eggs that had been quiescent during a number of days of air dry environmental conditions, i.e. apart from the duration of the air dry conditions (as found by substracting both the duration of air dry conditions and the average developmental time under moist conditions in the laboratory that is given in Table 4, viz. 15.1 days, from the total embryonic developmental time including the period of quiescence), was found to fluctuate from nil to 25.2 days and it apparently tended to increase with lengthening of the duration of the preceding quiescence.

The effect of air dry environmental conditions on embryonic development and mortality has been discussed in detail, in view of its potentially great significance in regard to *A. flavilatera* population development in general (Section 4.1).

Finally the aspect of submersion of froghopper eggs needs attention. Submersion may be caused by the locally occurring inundation of sugar estate area through flood fallowing (as practised in Guyana; see Section 1.2) or the occasional incidence of excessive rainfall. Studies showed that embryonic development in submerged eggs continued normally until just before hatching in the S_4-stage. More specifically, whether submerged in the S_1, S_2 or S_3-stage, embryonic development in *A. flavilatera* eggs was found to continue until the S_4-stage, at which point embryonic development was arrested as long as the submersion was sustained. After a submersion period of 40 days, embryos at the S_4-stage showed a high survival rate (viz. 88%, for $n = 200$); it seems likely, therefore, that the froghopper eggs would have been able to survive longer submersion periods than the longest test-period of 40 days. Embryonic development was completed in eggs that came into contact with the air for a minimal period of 1 minute or longer, i.e. all viable eggs that were taken out of the water hatched normally, whether they were immediately submerged again, or not. Hatching under water, resulted in 100% mortality through drowning of the young nymphs.

4.3.3. *Nymphal development*

The 5 nymphal instars, that were previously described in Section 2.2, may be considered to be relatively insensitive to fluctuations of environmental factors through their protective froth covering (see Section 3.3.2). Exceptions to this, emerging from the previous sections of the present Chapter 4, were the occasion-

Table 10. Average developmental time (D) in days, of the 5 nymphal stages (see Section 2.2: Table 1), under apparently near optimal conditions in regard to impact of humidity (see text of the present Section 4.3.3, for a more detailed description of the environmental conditions in this respect) and temperature (viz. influence of the temperature fluctuations in the outdoor insectary, as depicted in Fig. 21: Section 4.2).

nymphal stage(s)	n	C.I.[12] of D
1	25	3.5 ± 0.3
2	10	5.4 ± 1.3
3	15	6.0 ± 1.1
4	17	7.7 ± 1.7
5	15	10.1 ± 0.9
1–5	–	32.7 ± 5.3

[12] C.I. = confidence interval; see Section 3.2.2 for method of computation.

al occurrence of (1) the mortality of first instar nymphs during hatching under air dry conditions, i.e. when air dryness exceeded 3 millibar of vapour pressure deficit (Section 4.3.2: Table 7), and (2) the mortality of nymphs through drowning during inundation of fields, or parts of fields, through flood fallowing or excessive rains. However, the potential negative effect of flood fallowing will generally be of negligible consequence in regard to *A. flavilatera* population development at the estate's level, because its occurrence will generally be after harvesting, which itself exerts a controlling negative effect on froghopper population development (Section 3.2).

Determination of the average developmental time of the various nymphal stages (Table 10) was performed by rearing nymphs under close inspection in the outdoor insectary. This was done by breeding nymphs, taken from both the laboratory and the field, in a series of $30 \times 20 \times 10$ cm compartments containing horizontally placed, approximately 20 cm long, pieces of sugar cane stem that had been allowed to form roots for several weeks (similar to newly planted sugar cane). The values of nymphal developmental time for the various instars were provided, on an individual basis, through daily inspection of the compartments. The soil in the compartments with the rooted pieces of cane was kept slightly moist; fluctuations of humidity and temperature of the air over the compartments were as indicated in Fig. 21: Section 4.2. Since it appeared impossible in the majority of cases, to follow the entire development of an individual nymph that was taken from the laboratory egg collection as a first instar, it was necessary to take the later instars from the field and compute the duration of the whole of the nymphal development by summation of the nymphal developmental time of the separate, subsequent instars, as is indicated in Table 10. The resultant average total duration of nymphal development of 32.7 days, appears to be slightly longer than the estimate arising from nymphal population trends (Section 3.2.3).

5. DISCUSSION AND CONCLUSIONS

5.1. VARIABILITY IN THE OCCURRENCE OF *AENEOLAMIA FLAVILATERA* ON SUGAR ESTATES: LIFE-CYCLE, POPULATION DENSITY AND DISPERSAL

In an analysis of the variability in the occurrence of *A. flavilatera* on sugar estates, a clear distinction must be drawn between froghopper occurrence in the individual component fields of sugar estates, and the occurrence of froghoppers over the estate as a whole. The latter is the resultant of *A. flavilatera* population development under the markedly different environmental conditions applying to different fields, which are simultaneously operative over one sugar estate as a consequence of the sequentially harvesting of the fields throughout the year or harvest periods (Section 1.2). Thus, whereas at the individual *field* level the froghopper population development is invariably interrupted yearly through harvesting and the subsequently temporary absence of food and shelter, froghopper population development can potentially continue throughout the year at the *estate* level. Apart from overall absence of *A. flavilatera* infection or control through technical measures, the froghopper population development at the estate level is arrested only in case of prolonged drought (Sections 3.1 and 3.2). It appeared in Section 4.3, that the negative effect of prolonged dry weather on froghopper populations is primarily determined by the effect of the resultant drying out of the 5 mm deep top-soil layer, as a function of both the duration of the dry weather and the nature of the top-soil coverage (Section 3.3), on the process of oviposition and the froghopper eggs present. More specifically, air dryness (i.e. absence of unbound or free water) in the top-soil fully inhibited *A. flavilatera* oviposition and caused either quiescence (i.e. developmental arrest) in the early stages of embryonic development (viz. in S_1 and S_2), or mortality in the later stages (viz. in S_3 and S_4), as discussed in detail in Sections 4.3.1 and 4.3.2, respectively. It was also shown in Section 4.3.2, that embryonic development in eggs in which quiescence was induced through air dryness, was resumed through restoration of free water contact with the periphery of the eggs that remained viable (i.e. with a retardation in response that was found to range from nil to 25 days). The percentage viability in quiescent eggs was found to decrease with both the advancement of embryonic development at the time of induction of quiescence and the duration of the developmental arrest as sustained throughout the period of air dryness.

Thus, it may be concluded that the relative decrease in *A. flavilatera* numbers through impact of adverse environmental conditions, as a consequence of prolonged absence of rainfall, is primarily a function of (1) the stage specific composition of froghopper populations at the onset of the adverse conditions, and (2) the subsequent duration of the adverse conditions. More specifically, when a high proportion of the total number of froghopper individuals are in the quiescence sensitive S_1 and S_2-stages of embryonic development at the onset of the

drying out of the top-soil layer, this will result in a relatively high post-drought survival rate. Furthermore, if the larger part of all quiescent eggs had had their quiescence induced in the earliest stages of embryonic development, this would result in a higher survival rate in the eggs that will form the initial froghopper population after a drought (as quantified in Section 4.3.2). This may be elucidated by referring to Fig. 13 in Section 3.2.3, in which it is shown that the onset of the drying out of the top-soil layer during the September–November drought, coincided with a relatively high density of adults, and consequently a high density of eggs in the quiescence sensitive stages of embryonic development. It can be postulated, that a one month earlier onset of the drought, i.e. at the time that nymphal occurrence was predominant, would have resulted in less dense initial populations of nymphs after the drought, in December.

Next to the effect of air dryness, two other adverse environmental effects of an apparently secondary nature have been mentioned in Section 4.3.2, viz. (1) the effect of high temperatures on embryonic mortality, and (2) the effect of partial flooding of cane fields through excessive rains, on nymphal mortality. Since temperatures which cause embryonic mortality (viz. 41 °C or more, during 2 hours or more) only occur in top-soil that is fully exposed to sunshine (Section 3.3) the resultant overall effect on *A. flavilatera* mortality is limited (as it is restricted to the relatively small fraction of a total estate's area that is between the rows of cane stools of recently reaped cane fields) and it is as such operative as a locally occurring intensification of embryonic mortality through air dryness. Nymphal mortality through drowning seems occasionally to be of importance when a sugar estate's drainage system cannot immediately remove excessive rainfall, so that significant parts of fields are temporarily flooded. It appeared that embryonic mortality was not significantly influenced through flooding, because embryonic development was arrested in submerged eggs and such embryonic developmental arrest could be sustained for at least 40 days, without the occurrence of a high rate of embryonic mortality. Flooding fully inhibits oviposition (Section 4.3.1).

With regard to the natural enemies of the various stages of *A. flavilatera*, it was concluded in Section 2.4 that their importance in relation to the population development of froghoppers, is generally negligible.

The dispersal of *A. flavilatera* infestation takes place through adult migration. It was found, that wind can greatly accelerate the relatively slow rate of migration of the adults as it takes place through leaping and flying. The general direction of the spread of froghopper infestation is leeward, while the direction of migration through active movement alone, appears to be at random. It is apparent from the data on embryonic development and mortality, that the re-infestation of cane fields in which the froghopper population development has been broken through harvesting, will take place primarily through adult migration unless harvesting coincides with a prolonged period of dry weather, in which case re-infestation may take place through quiescent eggs.

It may be concluded that fluctuations in the occurrence of *A. flavilatera* are primarily determined by the course of the weather, i.e. especially by fluctuations

of rainfall. The most prominent effect is the negative influence of drought, while effects of the opposite environmental conditions of excessive rainfall, which are also found to exert negative influence on the population development of froghoppers, are much less important. When conditions are such that these population constraining effects do not occur, i.e. during prolonged periods with evenly distributed rainfall, the numbers of froghoppers that make up local populations may increase rapidly, considering the potential fecundity of *A. flavilatera,* over 1 or 2 generations, i.e. over 2–4 months. The combination of locally occurring dense adult populations and the presence of constant winds of moderate speed (Section 1.3), can produce a rapid spread of the froghopper infestation and serious damage (in the absence of technical control measures) to the sugar cane crop.

5.2. Technical control strategy

Harvesting effects an almost complete control of *A. flavilatera* at the individual *field* level. It would be sensible, therefore, to try to derive the maximum benefit from this regular operation for the *estate* as a whole. This can be done by harvesting blocks of contiguous fields and by harvesting these blocks having regard to the prevailing wind and dispersal patterns of the adult froghoppers. Prime consideration in this, is the spatial concentration of potential froghopper infestation, which will facilitate the rapid execution of overall chemical control or any other technical control measure which may need to be applied to prevent the potentially rapid spread of locally occurring froghopper infestation through adult dispersal. The adaptation of the spatial cane age distribution over an estate's area, should preferably be directed toward the harvesting of the leeward side of the estate (i.e. the side of the estate where the numbers of *A. flavilatera* are likely to build up) towards the dry season in the period August–November when all froghopper population development is generally broken through the overall drying out of the top-soil layer.

The only other cultivation measure that needs consideration, is the burning of the left-over cane debris ('trash') after harvesting (Section 1.2). It appears that, since a trash layer tends to keep the top-soil moist to a significant extent (Section 3.3), the omission of the post-harvest burning of the trash layer is likely to prevent the induction of quiescence in potentially present S_1 and S_2-stages of froghopper eggs. The resulting continuation of embryonic development in the top-soil of recently reaped fields is not likely to be harmful, in view of the absence of food and shelter for the subsequent active froghopper stages that consequently die before inflicting any significant damage. In the case of quiescence induction, *A. flavilatera* infection may potentially be sustained for at least 100 days in the form of a quiescent egg population (Section 4.3.2) which may hatch at the time that the re-grown sugar cane vegetation can once more shelter the development of froghopper populations. Although trash burning would tend to reduce the rate of oviposition in dry weather, through oviposition inhibition

in air dry soil (Section 4.3.1), this factor may be considered negligible when harvesting towards the leeward estate's side is practiced. Moreover, even if leeward fields would be harvested first, immigrating *A. flavilatera* females from upwind would on average not contribute significantly to the increase of egg population density, through the limited availability of food and shelter for the adult females in recently reaped cane fields (Sections 3.1 and 3.2.1). It seems therefore, that there are strong arguments against post-harvest trash burning as far as froghopper control is concerned; coupled with the positive effects of mulching in general (retention of organic matter and protection of the top-soil against negative effects of exposure to the impact of rainfall and sunshine) a strong case can be made to stop the current practice of post-harvest trash burning.

Chemical control of *A. flavilatera* can be directed at either the *nymphs* or the *adults*; the eggs cannot be chemically controlled, because effective and economically usable ovicides do not exist at present. The effective control of the nymphs is less dependent on an accurate timing of the application of the chemicals, i.e. in contrast with adult control, because (1) rapid nymphal control is relatively less urgent in view of the apparently lesser direct nymphal damage of the sugar cane, and the absence of nymphal capacity to disperse, and (2) the duration of the presence of nymphs in the field, and thus the period during which they can be subjected to chemical control, is approximately twice as long as in the case of the adults. However, the effectiveness of the nymphal control is highly dependent on the accessibility of the sugar cane crop (which appears to be insufficient after approximately 4 months of cane growth) in order to direct the chemicals efficiently, whereas chemical control of the adults can be undertaken at any time through aerial spraying of the foliage.

Disregarding the method of chemical control that is found to be appropriate in a practical sense, the effectiveness of the control is basically determined by the accuracy of its timing. In the case of nymphal and adult control of *A. flavilatera*, a prompt response to the timely detection of relatively low population density infection foci, in the order of magnitude of 1 adult or 1 nymph per 50 stems (or per 10 cane stools) respectively, is needed. Although the figures are rather arbitrary in the virtual absence of exact data with regard to the relationship between yield and the size of the pest population, some supportive data are provided by Norton and Evans (1974) who conclude with regard to the control of *A. varia saccharina* on Trinidad, that the appropriate density at which to spray the first generation is 5 adults per 100 stems. As a consequence, it appears to be essential to keep a field by field record of the course of the *A. flavilatera* infestation in terms of a specification of the stages that are found to be present as well as an estimation of the approximate population density. The regular updating of this record by specially assigned teams, would provide for the minimal data needed to take decisions in regard to pest management on a field by field basis.

Chemical control should preferably be directed at the first generation of nymphs or adults after a period of drought, i.e. before the froghopper-advantageous weather conditions induce population build-up and consequent adult dis-

persal. This may be effectively achieved by concentrating the attention on those fields that previously harboured froghoppers, as would be indicated in the field records compiled by 'pest scouting' teams.

6. SUMMARY

The sugar cane froghopper, *Aeneolamia flavilatera* (URICH), is one of the most serious pests of sugar cane in the area of study, which lies in the two South American countries Guyana and Surinam, at 6°N. The total, yearly inflicted froghopper damage in the economically important sugar cane cultivation of these two countries has been found to fluctuate widely. Froghopper damage is primarily caused by the feeding of the adults on the sugar cane leaves, which results in the so called 'froghopper blight' (a rapidly spreading necrosis of the leaf tissue around the punctures that are caused by the adult sucking) and a consequent reduction in sugar yield through loss of photosynthetic area of the plant. The 5 nymphal instars, which feed trough sucking on the roots of the sugar cane plants, are apparently of secondary importance in regard to the direct causation of damage.

In order to analyse the irregular occurrence of froghopper caused sugar cane damage, with a view to reducing this damage to tolerable levels, a study of the population dynamics of *A. flavilatera* was made on a number of 3000–8000 ha sugar estates in both Guyana and Surinam (1975–1978).

Oviposition takes place at the soil surface underneath the sugar cane plants, whereby the eggs are deposited in the 5 mm deep top-soil layer. It was shown that the environmental conditions in this habitat fluctuate markedly and are dependent on the weather and stage of growth of the cane. Whereas the fluctuations of temperature and humidity in the top-soil directly affect the froghopper eggs, both adults and nymphs can either escape or moderate adverse environmental conditions, the adults through adaptive movement and the nymphs because of the tempering of environmental impact by means of the insulating capacities of the characteristic froth or 'spittle', in which they keep themselves enveloped during the whole of nymphal development.

Consequently, the environmental impact on *A. flavilatera* population development in general, appeared to be dominated by the effect of temperature and humidity fluctuations in the top-soil on embryonic development and mortality. Further investigation showed, that the effect of humidity on both the rate of development and mortality in the froghopper eggs was the predominant factor, in view of the fluctuations of the environmental conditions over the whole of a sugar estate's area.

Embryonic development was found to be discontinued under influence of air dryness (i.e. in absence of unbound water contact with the periphery of the eggs), whereby the early stages of embryonic development entered into quiescence, whereas the later stages died after some days. Quiescence in *A. flavilatera* eggs can potentially be prolonged for at least 100 days, which explains the frequently observed recurrence of froghopper infestation after prolonged dry periods, during which active froghopper stages appear to be entirely absent. The latter was shown through a series of population counts which were performed over a 1

year period, on a weekly basis, in 3 different fields harbouring froghopper populations. It appeared that quiescence is broken through restoration of free water contact, with a retardation period ranging from nil to approximately 4 weeks. The size of the initial froghopper populations after prolonged dry periods can more or less be anticipated, through consideration of the density of quiescence sensitive stages in egg populations at the onset of the dry period, as indicated by the coinciding adult density.

Another apparent significantly adverse effect of drought on *A. flavilatera* population development was found to be the inhibition of oviposition in air dry soil.

In addition to the adverse effects of prolonged dry periods, excessive rainfall may also exert a negative influence on froghopper population development through the partial flooding of fields, which results in nymphal mortality and oviposition inhibition.

In the case of prolonged absence of adverse environmental effects, i.e. during prolonged periods with evenly distributed rainfall, froghopper populations may rapidly build up over 1–2 generations, in 2–4 months. The wind induced acceleration of the dispersal of adults of locally dense populations is then liable to cause a rapid spread of *A. flavilatera* infestation.

A number of concluding suggestions in regard to an apparently optimal strategy of prevention and control of froghopper infestation that are given, include the exploitation of 'block wise' harvesting schemes and the accurate field by field record keeping upon which pest management decisions can be based.

7. ACKNOWLEDGMENTS

I respectfully extend my gratitude to Professor Dr. J. de Wilde and Dr. Ir. J. B. M. van Dinther of the department of Entomology of the Agricultural University in Wageningen, for their unfailing confidence and support in all that needed to be done for the completion of this study.

The Netherlands Foundation for the Advancement of Tropical Research (WOTRO) in The Hague, is gratefully acknowledged for its continuing financial and administrative support.

Sincere gratitude is extended to the Directors of the 'Mariënburg' sugar estate in Surinam, and the Guyana Sugar Experiment Station in Guyana for their cordial co-operation in getting the research field work done.

I am furthermore indebted to Dr. F. Haworth of the International Service for National Agricultural Research (ISNAR) in The Hague, for his critical reading of the manuscript and advising me on aspects of the use of the English language.

Last but certainly not least, I extend gratitude to my friends in both Surinam and Guyana who persevered in helping me to get those basic data from laboratories and sugar cane fields through storm and shine. In particular, thanks are due to Glenn Podiwongso of 'Mariënburg' sugar estate, Surinam.

8. SAMENVATTING

De suikerrietschuimcicade, *Aeneolamia flavilatera* (URICH), is één van de belangrijkste suikerrietplagen in het bij het onderzoek betrokken gebied dat gelegen is in de twee Zuid-Amerikaanse landen Guyana en Suriname, op 6°N.B. De totale, jaarlijks door deze suikerrietschuimcicaden (ook wel 'froghoppers' genaamd) veroorzaakte schade in de economisch van groot belang zijnde suikerriet-cultuur aldaar, blijkt zeer sterk te kunnen fluctueren. Froghopper-schade wordt voornamelijk veroorzaakt doordat de adulten zich voeden op de suikerrietbladeren, hetgeen resulteert in de zogenoemde 'froghopper blight' (een zich snel verspreidende necrose van het bladweefsel rondom de plaatsen waar de adulten het blad hebben aangeprikt om te zuigen) en een daaruit voortvloeiende vermindering van de suikeropbrengst vanwege het verlies van foto-synthetiserend oppervlak van de plant. De vijf onderscheiden larvale stadia, die zich voeden middels het zuigen aan de wortels van de suikerrietplanten, blijken van secundair belang te zijn voor het direkt veroorzaken van schade.

Ten einde het onregelmatige optreden van de door froghoppers veroorzaakte schade te analyseren, met als doel het terugbrengen van de schade binnen aanvaardbare grenzen, is een onderzoek inzake de populatie-dynamiek van *A. flavilatera* uitgevoerd op een aantal 3000–8000 ha grote suikerondernemingen in zowel Guyana als Suriname (1975–1978).

Ovipositie vindt plaats aan het bodemoppervlak onder de suikerrietplanten, waarbij de eieren worden afgezet in het 5 mm dikke toplaagje van de grond. Aangetoond werd dat de milieu-omstandigheden in die habitat sterk kunnen fluctueren in afhankelijkheid van het weer en het groeistadium van het suikerriet. Terwijl de fluctuaties van temperatuur en vochtigheid in de bodemtoplaag direkt van invloed zijn op de froghopper-eieren, kunnen zowel de adulten als de larven aan ongunstige milieu-omstandigheden ontsnappen of de invloed daarvan verzwakken; de adulten middels aanpassing door verplaatsing en de larven door de isolerende eigenschappen van het karakteristieke schuim waarmee zij zich gedurende de gehele larvale ontwikkeling omhullen.

Het blijkt dan ook, dat de invloed van het milieu op de populatie-ontwikkeling van *A. flavilatera* in hoofdzaak wordt bepaald door de invloed van de fluctuaties van temperatuur en vochtigheid op de embryonale ontwikkelingssnelheid en mortaliteit. Het effect van vochtigheid op zowel de onwikkelingssnelheid als de mortaliteit van de eieren is van overheersend belang in het licht van de fluctuaties van de milieu-omstandigheden zoals die over het gehele areaal van een suikeronderneming kunnen optreden.

De embryonale ontwikkeling blijkt onder invloed van droogte (d.w.z. bij afwezigheid van kontakt van de buitenkant van de eieren met ongebonden water) te worden onderbroken, waarbij de vroege embryonale ontwikkelingsstadia een ontwikkelingsstilstand ondergaan en de latere stadia na enige dagen sterven. De stilstand in de embryonale ontwikkeling van *A. flavilatera* kan tot minstens

100 dagen geprolongeerd worden, hetgeen verklaart, wat vaak wordt waargenomen, dat een plaag van froghoppers terugkeert na langdurende droge perioden waarin aktieve froghopper-stadia volledig afwezig blijken te zijn. Dit laatste werd aangetoond door populatietellingen die over een periode van één jaar wekelijks in drie verschillende velden werden uitgevoerd.

Het is gebleken dat de embryonale ontwikkelingsstilstand wordt verbroken door het herstellen van het kontakt met ongebonden water, met een vertragingsperiode die uiteen kan lopen van nihil tot ongeveer 4 weken. De dichtheid van beginpopulaties van froghoppers na lange droge tijden kan min of meer worden voorspeld, aan de hand van de dichtheid van ontwikkelingsstilstand-gevoelige ei-stadia in de ei-populaties aan het begin van de droge periode, zoals die wordt aangegeven door de gelijktijdig optredende dichtheid van de adulten.

Een ander significant nadelig effect van droogte op de populatie-ontwikkeling van *A. flavilatera* bleek te zijn, dat ovipositie in droge grond wordt onderdrukt.

Naast de nadelige effecten van lange droge perioden kan overvloedige regen ook een nadelige invloed op froghopper-populaties uitoefenen indien overstroming van velden optreedt. Overstroming resulteert in larvale mortaliteit en onderdrukking van ovipositie.

In het geval dat nadelige milieu-effecten voor langere tijd uitblijven, d.w.z. in perioden met gelijkmatig verdeelde regenval, kunnen froghopperpopulaties, tijdens de ontwikkeling van 1–2 generaties in 2–4 maanden, snel in dichtheid toenemen. De door de wind veroorzaakte versnelling van de verspreiding van adulten van plaatselijk voorkomende populaties met hoge dichtheden kan er dan voor zorgen dat de *A. flavilatera*-infectie zich in hoog tempo uitbreidt.

Suggesties met betrekking tot een optimale strategie ter voorkoming en bestrijding van froghopper-plagen behelzen ondermeer het invoeren van 'bloksgewijze' oogstschema's en het nauwgezet bijhouden van veld-rapporten waarop het juiste tijdstip en de wijze van bestrijding gebaseerd kunnen worden.

9. REFERENCES

EVANS, D. E., 1971. The distribution and sampling of the adult froghopper *Aeneolamia varia saccharina* DIST. (Homoptera: Cercopidae) on sugar cane. Trop. Agric. Trin., Vol. **48**, no. 3: 255–262.

EVANS, D. E., 1972. The spatial distribution and sampling of *Aeneolamia varia saccharina* and *A. postica jugata* (Homoptera: Cercopidae). Ent. Exp. & Appl. **15**: 305–318.

FEWKES, D. W., 1961. Stool size as a factor in the sampling of sugarcane froghopper nymph populations. J. Econ. Ent. **54**: 771–772.

FEWKES, D. W., 1963a. The effect of exposure to dry conditions on the eggs of *Aeneolamia varia saccharina* (Homoptera: Cercopidae). Ann. Ent. Soc. Am. **56**: 719–720.

FEWKES, D. W., 1963b. Some observations on egg diapause in the Trinidad sugar-cane froghopper, *Aeneolamia varia saccharina* (Homoptera, Cercopidae). Ent. Month. Mag. **99**: 224–228.

FEWKES, D. W., 1964a. The fecundity and fertility of the Trinidad sugar-cane froghopper, *Aeneolamia varia saccharina* (Homoptera, Cercopidae). Trop. Agric. Trin., Vol. **41**, no. 2: 165–168.

FEWKES, D. W., 1964b. Rep. Tate & Lyle cent. agric. Res. Stn. Trin. 1963: 88–106.

FEWKES, D. W., 1966. Structure and development of the egg of *Aeneolamia varia saccharina*. Rep. Tate & Lyle cent. agric. Res. Stn. Trin. 1965: 429–442.

FEWKES, D. W., 1969a. The biology of sugar cane froghoppers. In: J. R. WILLIAMS, J. R. METCALFE, R. W. MUNGOMERY and R. MATHES (Eds.), Pests of sugar cane; Amsterdam, Elsevier: 283–307.

FEWKES, D. W., 1969b. The control of froghoppers in sugar cane plantations. In J. R. WILLIAMS, J. R. METCALFE, R. W. MUNGOMERY and R. MATHES (Eds.), Pests of sugar cane; Amsterdam, Elsevier: 309–324.

GUAGLIUMI, P., 1962. Las plagas de la cana de azúcar en Venezuela, **1**; Maracay, Venezuela, Minist. Agric. Cría: 322–347.

HAGLEY, E. A. C., 1966. Site of feeding of the froghopper. Rep. Tate & Lyle cent. agric. Res. Stn, Trinidad 1965: 408–413.

HAGLEY, E. A. C., 1967. Studies on the aetiology of froghopper blight of sugar cane. II. Probable role of enzymes and amino acids in the salivary secretion of the adult froghopper. Proc. Br. W. Indies Sug. Technol. 1966: 187–192.

JAMES, H. C., 1946. The bionomics and control of *T. flavilatera* UR., the Demerara sugar cane froghopper. Proc. Br. W. Indies Sug. Technol. 1946: 34–79.

JAMES, H. C., 1947. Insect pests of sugar cane. Sug. Est. Overseers Manual Instr. Brit. Guiana repr., 35 pp.

KERSHAW, J. C., 1913. Froghopper notes. Bull. Dep. Agric. Trin. Tobago **12**: 3–62.

KERSHAW, J. C., 1914. The alimentary canal of a cercopid. Psyche, Camb. **21**: 65–72.

KING, A. B. S., 1975a. Factors affecting the phenology of the first brood of the sugar-cane froghopper *Aeneolamia varia saccharina* (DIST.) (Homoptera, Cercopidae) in Trinidad. Bull. Ent. Res. **65**: 359–372.

KING, A. B. S., 1975b. The extraction, distribution and sampling of the eggs of the sugar-cane froghopper, *Aeneolamia varia saccharina* (DIST.) (Homoptera, Cercopidae). Bull. Ent. Res. **65**: 157–164.

MADGE, D. S., 1961. The control of relative humidity with aqueous solutions of sodium hydroxide. Ent. Exp. & Appl. **4**: 143–147.

MYERS, J. G., 1935. The ecological distribution of some South American froghoppers of the genus *Tomaspis* (Hom., Cercopidae). Trop. Agric. Vol. **12**, no. 5: 114–118.

NORTON, G. A. and D. E. EVANS, 1974. The economics of controlling froghopper (*Aeneolamia varia saccharina* (DIST.) (Hom., Cercopidae)) on sugar-cane in Trinidad. Bull. Ent. Res. **63**: 619–627.

PICKLES, A., 1931a. Notes on the ecology of *Tomaspis saccharina* DIST. (Homoptera, Cercopidae), in Trinidad. Trop. Agric. Vol. **8**, no. 5: 127–130.

PICKLES, A., 1931b. On the oviposition of *Tomaspis saccharina*, DIST. (Rhynch., Cercop.) an insect pest of sugar-cane in Trinidad. Bull. Ent. Res. **22**: 461–468.

PICKLES, A., 1933a. Entomological contributions to the study of the sugar cane froghopper. I. The study of biotic factors of control. Trop. Agric. Trin. **10**: 222–233.

PICKLES, A., 1933b. Entomological contributions to the study of the sugar cane froghopper. II. The influence of host relations and of cultural operations in limiting blight incidence amongst plant canes. Trop. Agric. Trin. **10**: 240–245, 286–295.

PICKLES, A., 1945. Observations on *Tomaspis flavilatera* URICH, an insect pest of sugar cane in British Guiana. Proc. Br. W. Indies Sug. Technol. 1945: 46–52.

SNEDECOR, G. W. and W. G. COCHRAN, 1976. Statistical methods. Iowa State Univ. Press, 593 pp.

URICH, F. W., 1914. Description of a new froghopper from British Guiana. Bull. Ent. Res. **5**: p. 43.

WILLIAMS, C. B., 1918. A froghopper on sugar-cane in British Guiana. Bull. Ent. Res. **9**: 163–173.

WILLIAMS, C. B., 1919. Rainfall, sugar production and froghopper blight in Trinidad. Trinidad and Tobago Bull. Vol. **18**, no. 3: 153–167.

WITHYCOMBE, C. L., 1926. Studies on the aetiology of sugar-cane froghopper blight in Trinidad. Ann. Appl. Biol. **13**: 64–108.