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HUMIDITY EFFECTS ON *ATHERIGONA SOCCATA*: EGG DEVELOPMENT AND HATCH

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Low humidity affects the duration of egg development in the sorghum shootfly *Atherigona soccata*. The relationship between incubation period and saturation deficit is hyperbolic; at 25°, the incubation period increases from 2 days in water-saturated air to more than 8 days in air with 7 mm saturation deficit. Egg survival is adversely affected by low humidity, and the relationship between egg survival and saturation deficit is affected by temperature: mortality increases more rapidly with increasing saturation deficit at 15° than at higher temperatures. Observations made in the laboratory and in the field indicate that egg mortality is proportional to the evaporative power of the air in which eggs are incubated (the evaporative power being the product of saturation deficit by duration of embryonic development). The protection against desiccation achieved by *A. soccata* eggs through both active and passive mechanisms is an indication of the adaptation of the pest to semi-arid and arid environments.

KEY WORDS: *Atherigona soccata* — Diptera — Sorghum shootfly — *Sorghum bicolor* — Saturation deficit — Evaporative power — Embryonic development — Hatching.

The sorghum shootfly, *Atherigona soccata* Rondani (Diptera, Muscidae), is a major pest of sorghum in the semi-arid tropics of Africa and Asia (Young, 1981). In Kenya, sorghum is the typical cereal crop in the Lowlands, where precipitation is meagre (less than 900 mm per year) and erratic; it is replaced by maize in zones with more abundant precipitations (Cobley & Steele, 1976). As shootfly populations remain active throughout the year (Delobel & Unnithan, 1981), successive generations undergo a succession of marked dry and rainy seasons, and eggs are subjected to widely variable temperature and humidity conditions. Shootfly egg survival is not affected by the heavy rains which occur during rainy seasons (Delobel & Lubega, 1983); predators and parasites reduce egg survival, but their effectiveness is usually limited (Taley & Thakare, 1979).

Temperature and humidity remain the critical factors in the ecology of sorghum shootfly eggs; the evaluation of the effect of constant temperatures associated with saturated air humidity on embryonic development has been reported earlier (Delobel, 1983). The primary aim of the present work is to examine the relations between incubation in different unsaturated air humidities and shootfly egg development and hatchability, and to investigate the mechanisms which enable the egg to overcome the effect of excessively low atmospheric humidities.

MATERIALS AND METHODS

Rearing procedures for shootfly were those described by Unnithan (1981); adults were obtained from 3rd-instar larvae collected from a sorghum CSH-1 field in Nairobi and fed on an artificial diet (Singh *et al.*, 1983). Since egg-laying and hatching occur mostly at the beginning of the photophase (Raina, 1982), conditions were synchronized throughout the experiment by introducing sorghum seedlings for oviposition between 8.00 and 9.00 a.m. Pieces of sorghum leaves bearing eggs were clipped from the plants and placed in plastic petri dishes with pinholes under various temperature and humidity regimes, and with 12 hr light/day. 60—120 eggs were used in each experiment.

Constant saturation deficiencies were maintained in 1 dm^3 desiccators filled with 150 cl saturated salt solutions; the following salts were used (in parentheses is the saturation deficiency obtained at 20°): $CaCl_2.6H_2O$ (12.01 mm); $K_2CO_3 + NaHCO_3$ (10.45 mm); $NaNO_3$

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+ NH_4NO_3 (8.36 mm); NH_4NO_3 (6.96 mm); KCl + NaCL (5.75 mm); $(NH_4)_2SO_4$ (5.05 mm); K_2SO_4 (1.74 mm). Data corresponding to eggs incubated on moist filter paper have been reported earlier (Delobel, 1983).

Embryogenesis was monitored by examining the eggs under binocular microscope every 6 hr after they had reached the black spot stage; this stage is defined as the time when, under transmitted light, melanization of the larval mandibles could first be observed; this stage was reached in 24 hr at 30°. Duration of the embryonic development is defined here as the period between egg deposition and the time 50% of the eggs hatched; it was determined graphically (Delobel, 1983). Eggs with perfectly translucent contents were considered as unfertilized.

Data for the assessment of temperature and humidity effect on hatching were obtained by incubating the eggs 24 hr at 30° in water-saturated air (wet filter paper), then transferring them to various temperature and humidity regimes. Details of the different regimes are given under the corresponding sections of the results. Field experiments were conducted in Nairobi. Gravid ♀♀ were allowed to oviposit on 100 potted CSH-1 seedlings for 2 hr. Plants were transferred to the field, and embryonic development was monitored daily until all fertile eggs had hatched. Air temperature and rh were recorded on a thermohygrograph placed 75 cm above the soil in a screened shed. The same experiment was repeated 11 times at 1 month intervals.

Atmospheric humidities were expressed in terms of saturation deficit (SD); SD is the difference between the maximum water vapour pressure at a given temperature and the actual vapour pressure at the same temperature; its values are expressed in mm of mercury. Since the pioneering work of Buxton (1931) and Johnson (1940, 1942), many authors (Ferro & Chapman, 1979; Montgomery & Nielsen, 1979) have stressed that SD was superior to rh as a humidity index in situations where different temperatures were involved, since the drying power of air at a given rh varies with temperature. The saturation deficit causing death by desiccation in 50% of the eggs was used as a measure of the noxiousness of low humidities; it was determined by probit analysis (Finney, 1971) after the normality of the distribution of egg mortalities had been tested using Lilliefors test. The evaporative power of air (EP, in mm Hg × hr) is the product of saturation deficit by embryonic development duration; this parameter, unlike saturation deficit, takes into account the effect of time of exposure on egg mortality (Wigglesworth, 1974). The relationships between saturation deficiency (or evaporative power) and embryonic development at different temperatures were determined by regression analysis; the following models were tested: $y = ax + b$ (linear); $y = a + \frac{b}{x}$ (hyperbolic); $y = ae^{bx}$ (exponential); $y = ax^b$ (power); $y = a + b \operatorname{Log} x$ (logarithmic); $y = a + bx + cx^2$ (quadratic). Coefficients a, b and c were calculated for the equations which gave the best fit to the curves and the best correlation coefficients.

RESULTS

Durations of embryonic development. The duration of egg development increased with increasing humidities; at 25°, the relationship between incubation period and saturation deficit was hyperbolic (Fig. 1):

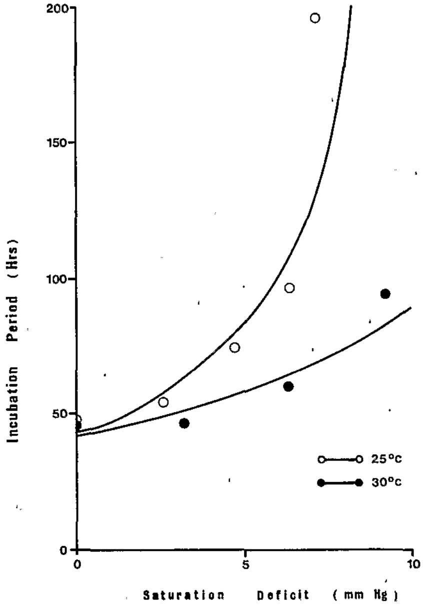

Fig. 1. Effect of humidity at 25 and 30° on embryonic development time.

$$y = \frac{1}{0.0225 - 0.0021x} \quad (r = 0.954; P < 0.05),$$

where y is the incubation period and x the SD; at 30°, a similar relationship was found:

$$y = \frac{1}{0.0274 - 0.0018x} \quad (r = 0.930; P < 0.10).$$

At these two temperatures, the % development per hour (the reciprocal of incubation period) was a linear function of SD. Low survival prevented similar analysis of data at other temperatures. The longest recorded incubation period was 196 hr at 25° and a humidity with a SD of 7.07 mm; at this humidity, only 8.4% of the eggs hatched. At suboptimal humidities, a small proportion of larvae often died in the process of hatching.

Egg mortality. Mortality increased with increasing saturation deficit. The effect on mortality of increasing SD at different constant temperatures during the first part of egg development (up to black spot stage) was best described by a series of quadratic equations $y = a_0 + a_1x + a_2x^2$, where y is the % of eggs dying before they reached the black spot stage, x the SD, and a_0, a_1 and a_2 are constants (Fig. 2A). Similar relationships existed between SD and overall egg mortality (Fig. 2B). The values of constants a_0, a_1 and a_2 for eggs incubated at 15, 20, 25 and 30° are given in Table I.

The thermohygrogram of egg mortality (Fig. 3) illustrating the effect of various humidity and temperature regimens on shootfly egg survival confirmed that the relationship between egg mortality and SD was dependent on temperature: survival was higher at or near the optimum temperature of 30° (Delobel, 1983) than at lower temperatures. Above 35° and below 15°, mortality was high, even at high humidity, which is attributable to the harmful effect of temperature.

Correlation between EP and egg mortality at 15, 20, 25, 30 and 35° was poor or not significant; however, when pooled, data for the different temperatures yielded a significant correlation at $P < 0.001$; this indicated an almost directly proportional relationship between egg mortality and EP of the air in which eggs were incubated, irrespective of temperature (Fig. 4).

Eggs laid on sorghum seedlings and incubated in the field were subjected to daily SD

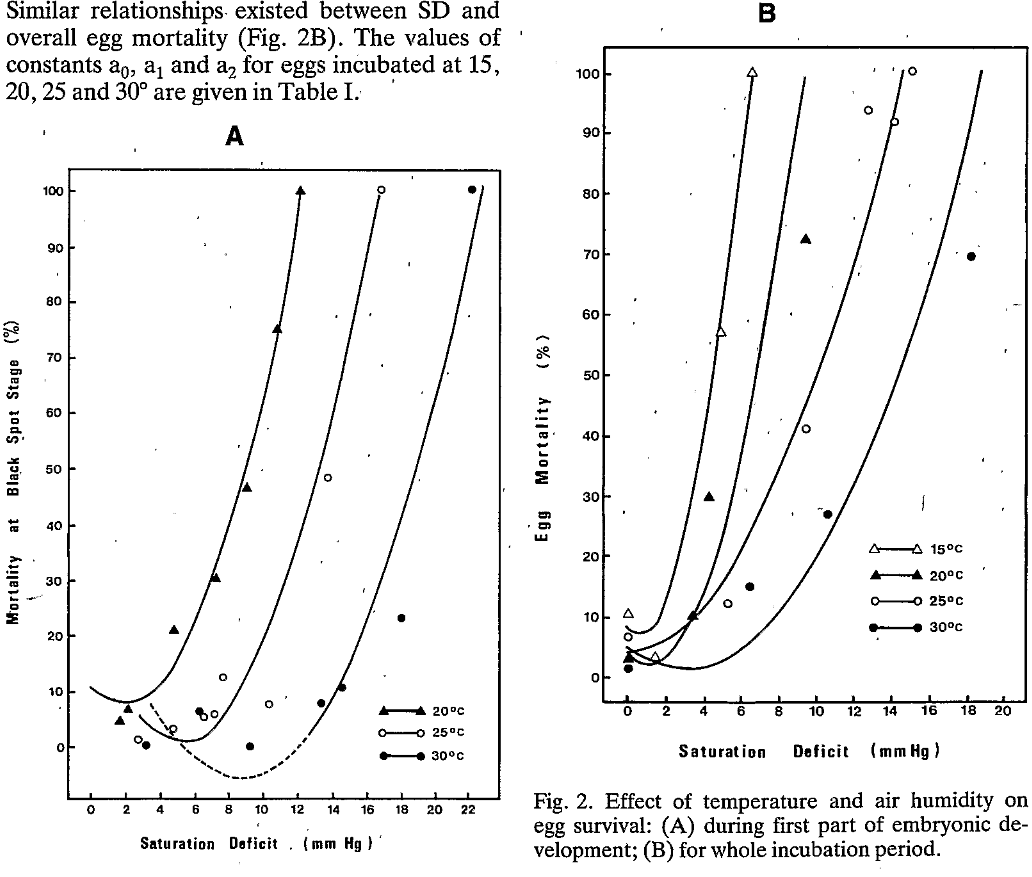

Fig. 2. Effect of temperature and air humidity on egg survival: (A) during first part of embryonic development; (B) for whole incubation period.

TABLE I

Parameters of mortality/saturation deficit equations: A — Mortality at black spot stage; B — Overall egg-mortality

A	a_0	a_1	a_2	R^2	Probabilities
20°	11.9378	−3.9342	0.9152	0.9853	$P < 0.001$
25°	22.6332	−8.2793	0.7800	0.9592	$P < 0.001$
30°	33.2941	−9.2119	0.5339	0.9171	$P < 0.001$
B					
15°	77.9385	−7.0259	10.6956	0.9919	$P < 0.01$
20°	3.5140	−5.8195	5.4428	0.9999	$P < 0.001$
25°	4.5779	0.1708	1.7789	0.9587	$P < 0.001$
30°	4.8506	−4.5167	1.5203	0.9568	$P < 0.05$

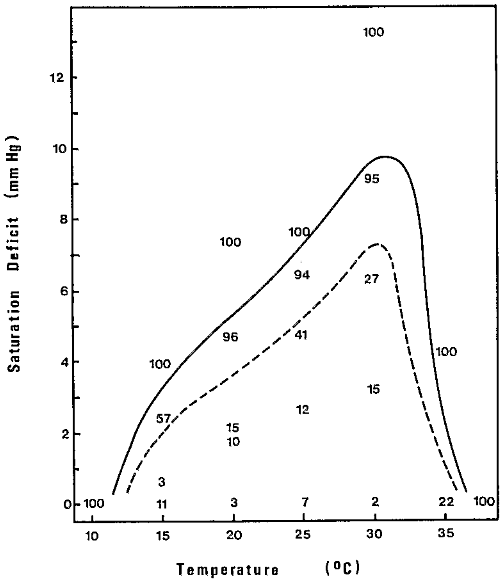

Fig. 3. Thermohygrograph of mortality for *A. soccata* eggs under controlled temperature and humidity conditions. Solid line: 100%, dotted line: 50% mortality level.

varying from 5 mm during the rainy season to 10 mm during the dry season. Mortality due to desiccation did not exceed 5.7% during the rainy season, increasing to 17% during the dry season. Egg mortality recorded on each occasion was plotted against the EP of the air, calculated on the basis of the theoretical incubation period at the daily mean temperature recorded during egg exposure; see Delobel (1983) for the equation giving egg development time as a function of temperature. A significant correlation at $P < 0.001$ existed between field egg mortality and ambient EP; the regression line, however, had a strongly negative x-intercept and a less steep slope than the line derived from laboratory data (Fig. 4).

The first part of embryogenesis (up to black spot stage) was less sensitive to low humidities than the later part. When eggs were incubated in saturated air at 30° till black spot stage be-

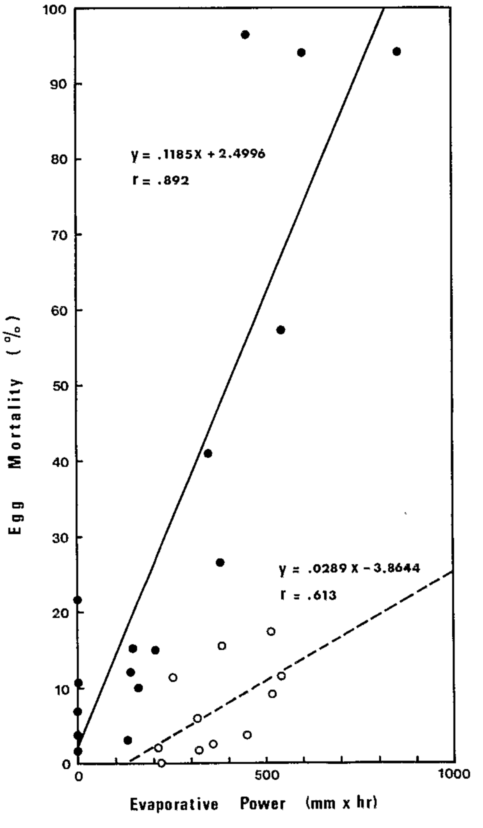

Fig. 4. Effect of air evaporative power (EP) on egg mortality in laboratory (●) and field (○) situations.

fore their transfer to various humidities and 20 or 30°, no mortality was observed at black spot stage; saturation deficits necessary to prevent 50% of the eggs from reaching the black spot stage were 23.64 and 9.54 mm, whereas saturation deficits necessary to prevent 50% of the eggs from hatching (after incubation in saturated air till black spot stage) were only 8.06 and 3.20 mm at 30 and 20°, respectively. As expected, continuous incubation in air with a saturation deficit increased hatching failure; the saturation deficits necessary to induce 50% mortality in eggs left at the same humidity throughout their development were 6.18 and 2.76 mm at 30 and 20°, respectively.

DISCUSSION

The extension of embryonic development duration at lower humidities (and constant temperature) results from the depression of egg metabolism due to water loss; low humidities induce in some insect eggs (collembolans, grasshoppers) a dormancy which may last several months (Wigglesworth, 1974). Most insect eggs, however, fail to hatch when exposed to low humidities for shorter or longer periods. The form of the relationship between duration of embryonic development and saturation deficit has been found hyperbolic or quadratic in the few insects for which it has been studied in detail (Ferro & Chapman, 1979; Montgomery & Nielsen, 1979). The hyperbolic relationship found in the present study at 25 and 30° indicates a similar effect of SD in *A. soccata*. The extension of embryonic development duration with an increase in SD is greater at 25° than at 30°, which matches observations made by Ferro & Chapman (1979) on *Tetranychus urticae*; the authors suggested that the difference was due to an accelerated rate of development at high temperatures. Our own results, however, suggest that the phenomena are similar at various temperatures (hence the same hyperbolic relationship), but that this reality is masked by high mortality levels occurring at suboptimal temperatures (Delobel, 1983).

Our findings on the effect of humidity on shootfly egg viability are in accordance with the general conclusion drawn by Doharey *et al.* (1977) that shootfly egg survival is reduced by low humidity; they found, however, that egg viability at 25° was greater at 30% than at 60 or 90% rh; this observation was not confirmed by the present experiments.

Low humidity increases water loss through the chorion, and resistance to desiccation depends on the ability of the egg to retain water through physical and physiological processes against Dalton's law (which states that water evaporates from a water surface at a rate which is directly proportional to the saturation deficit of the air above the water surface) (Wigglesworth, 1974). Resistance to desiccation varies greatly among insect eggs; in the crane flies *Tipula oleracea* and *T. paludosa*, normal egg development requires a saturation deficit not higher than 0.4 mm (Meats, 1968). In the black vine weevil *Otiorrhynchus sulcatus*, saturation deficits higher than 8 mm result in 100% mortality (Montgomery & Nielsen, 1979). Eggs of the blowfly *Lucilia sericata* can survive saturation deficits of up to 16 mm (Evans, 1934). Those differences are most consistent with the idea that intrinsic resistance to desiccation is closely related to the environment in which the egg is usually laid, eggs of insects associated with humid environments having stricter requirements than others: *Tipula* eggs are laid in damp soil, eggs of *O. sulcatus* in shady places protected from direct sunshine by dense foliage canopy, whereas *L. sericata* ♀♀ lay their eggs on bare, unprotected soil. In this respect, *A. soccata* eggs are fairly well protected from desiccation by their position on the undersurface of the lower leaves of sorghum seedlings.

Sensitivity to air humidity also varies during embryonic development. Tsitsipis & Abatzis (1980) found that the early embryonic stages of *Dacus oleae* were more sensitive to low relative humidities than were the later stages. Ferro & Chapman (1979) obtained similar results with eggs of *T. urticae*. Evidence from the present experiments indicates that shootfly eggs are most sensitive to low humidity during the later stages of their development (from black spot stage to hatching) than during the earlier ones. Clark (1935) in *Rhodnius* and Jones & Heming (1979) in *Mamestra configurata* found that low hatchability of eggs incubated in dry air was partly due to the desiccation of the chorion, which became too hard to be broken by the young larva. Although hardening of the chorion was not observed in *A. soccata*, there is some evidence that larvae weakened after an incubation in high SD may remain trapped in the dry chorion as they emerge from it.

The necessity of integrating the effect of temperature on the duration of embryogenesis with that of humidity on egg survival has been recognized as early as 1935, when Mellanby, commenting work by Märks (1933) on eggs of *Habrobracon juglandis*, showed that mortality varied proportionally with the product of developmental period by saturation deficit, in accordance with Dalton's law. The linearity of the relationship has also been demonstrated in the flea *Xenopsylla cheopis* (Gunn, 1935); Andrewartha & Birch (1954) have suggested that it is sigmoid rather than linear. Our results demonstrate that, at least within the range of EP observed, egg mortality in *A. soccata* is proportional with the product of saturation deficit by time of exposure. However, as Gunn (1935) pointed out, mortality is no longer proportional to saturation deficit when eggs are incubated at suboptimal temperatures; in the sorghum shootfly, Dalton's law remains valid only in the temperature range 15—25°. The discrepancy observed between laboratory and field data probably stems from the inaccuracy of field humidity measurements, which were largely underestimated; also, fluctuating temperatures and humidities may have effects on egg survival different from consant ones.

In conclusion, *A. soccata* eggs exhibit a quite remarkable adaptation to arid and semi-arid environments. Their intrinsic resistance to desiccation, as far as one may judge from the comparison with other insect eggs, is relatively high. Moreover, certain features enable shootfly eggs to avoid confrontation with the hostile environment: laid on the lower leaves of sorghum seedlings measuring less than 20 cm, they benefit from high humidity levels existing just above the ground (Delobel, 1981); the form of growth of the sorghum plant, characterized by an intense production of tillers (especially in the wild species) provides as well a good protection against excessive sunlight and evaporation. The synchronization of hatchings with the onset of photophase (Raina, 1982), again places the hatching larva in most favourable conditions: as saturation deficit is at its lowest in the morning, humidity is usually sufficient to ensure normal hatching. Also, high morning humidity results in the deposition of dew on the leaves and the accumulation of water in the leaf whorl; the presence of liquid water enables the emerged larva, which is extremely sensitive to desiccation, to crawl on the leaf surface towards the whorl, where it enters the stem. The presence of hydrophobic hairs around the posterior spiracles of the 1st-instar larva (Shie Shiang-Lin *et al.*, 1981) obviously reflects an adaptation to life in a liquid environment, which is remarkable in this pest of semi-arid zones.

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RÉSUMÉ

Effets de l'humidité sur le développement embryonnaire et l'éclosion de la mouche du sorgho, Atherigona soccata *Rondani (Diptères: Muscidae)*

L'humidité a une influence directe sur la durée du développement embryonnaire chez la mouche du sorgho. La relation entre la durée de développement et le déficit de saturation de l'air dans lequel l'œuf est incubé est de forme hyperbolique; à une température constante de 25°, l'incubation dure seulement 2 jours dans un air saturé de vapeur d'eau, mais plus de 8 jours dans un air ayant un déficit de saturation de 7 mm, ce qui correspond à une humidité relative d'environ 70%. La survie de l'œuf est également affectée par les faibles humidités; la relation entre taux de survie de l'œuf et déficit de saturation dépend de la température. Des expériences de laboratoire montrent que la mortalité de l'œuf n'est pas proportionelle au déficit de saturation de l'air, mais plutôt à son pouvoir évaporant; le pouvoir évaporant est une grandeur qui tient compte non seulement du déficit de saturation, mais aussi à la durée pendant laquelle l'œuf est soumis à ce même déficit de saturation. Ceci est par ailleurs confirmé chez des œufs soumis à des conditions naturelles en champ de sorgho. Les œufs de mouche de sorgho présentent des adaptations à la fois passives (choix de la plante hôte par la ♀, position de l'œuf sur la plante) et actives (résistance intrinsèque à la dessiccation, éclosions se produisant au moment où la rosée se dépose sur les feuilles) à la vie dans des environnements semi-arides ou même arides.

REFERENCES

Andrewartha, H. G. & Birch, L. C. (1954). *The distribution and abundance of animals*. Univ. Chicago Press, U.S.A.

Buxton, P. A. (1931). The law governing the loss of water from an insect. *Proc. ent. Soc. London* **6**: 27—31.

Clark, N. (1935). The effect of temperature and humidity upon the eggs of the bug *Rhodnius prolixus* (Heteroptera Reduviidae). *J. anim. Ecol.* **4**: 82—87.

Cobley, L. S. & Steele, W. M. (1976). *An introduc-*

tion to the botany of tropical crops, 2nd ed., Longman, London, U.K.

Delobel, A. G. L. (1981). Oviposition and larval survival of the sorghum shootfly, *Atherigona soccata* Rond., as influenced by the size of its host-plant. *Z. angew. Entomol.* **93**: 31—38.

—— (1983). Influence of temperature and host-plant condition on preimaginal development and survival in the sorghum shootfly *Atherigona soccata*. *Ins. Sci. Application* (in press).

Delobel, A. G. L. & Lubega, M. (1983). Rainfall as a major mortality factor in the sorghum shootfly. *Trop. Pest Management* (in press).

Delobel, A. G. L. & Unnithan, G. C. (1981). The status of *Sorghum arundinaceum* as a host of *Atherigona soccata* in Kenya. *Ins. Sci. Application* **2**: 67—71.

Doharey, K. L., Srivastava, B. G., Jotwani, M. G. & Dang, K. (1977). Effect of temperature and humidity on the development of *Atherigona soccata* Rondani. *Indian J. Entomol.* **3**: 211—215.

Evans, A. C. (1934). Studies on the influence of the environment on the sheep blow-fly, *Lucilia sericata* Meig. 1. The influence of humidity and temperature on the egg. *Parasitology* **26**: 366—377.

Ferro, D. N. & Chapman, R. B. (1979). Effects of different constant humidities and temperatures on two-spotted spider mite egg hatch. *Environ. Entomol.* **8**: 701—705.

Finney, D. J. (1971). *Probit analysis*. University Press, Cambridge, U.K.

Gunn, D. L. (1935). Bemerkung zum Aufsatz von H. Märks: "Wird der Wasseraushalt der Insekten durch das daltonsche Gesetz bestimmt?" *Anz. Schädlingsk.* **11**: 6—8.

Johnson, C. G. (1940). The longevity of the fasting bed-bug (*C. lectularius* L.) under experimental conditions and particularly in relation to the saturation deficiency law of water loss. *Parasitology* **32**: 239—270.

—— (1942). Insect survival in relation to the rate of water loss. *Biol. Rev.* **17**: 151—177.

Jones, M. P. & Heming, B. S. (1979). Effects of temperature and relative humidity on embryogenesis in eggs of *Mamestra configurata* (Walker) (Lepidoptera: Noctuidae). *Quaestiones Entomologicae* **15**: 257—294.

Märks, H. (1933). Wird der Wasserauhalt der Insekten durch das daltonsche Gesetz bestimmt? *Anz. Schädlingsk.* **9**: 66—68.

Meats, A. (1968). The effect of exposure to unsaturated air on the survival and development and eggs of *Tipula oleracea* L. and *T. paludosa* Meigen. *Proc. R. ent. Soc. London* (A) **43**: 85—88.

Mellanby, K. (1935). The evaporation of water from insects. *Biol. Rev.* **10**: 317—333.

Montgomery, M. E. & Nielsen, D. G. (1979). Embryonic development of *Othiorhynchus sulcatus*: effect of temperature and humidity. *Ent. exp. & appl.* **26**: 24—32.

Raina, A. K. (1982). Daily rhythms in the sorghum shootfly, *Atherigona soccata*: oviposition, egg-hatch and adult eclosion. *Physiol. Entomol.* **7**: 65—70.

Shie Shiang-Lin, Fan Zi-De & Su Zhou-Hua (1981). Studies on the sorghum shootfly in China. *Ins. Sci. Application* **2**: 39—47.

Singh, P., Unnithan, G. C. & Delobel, A. G. L. (1983). An artificial diet for sorghum shootfly larvae. *Ent. exp. & appl.* **33**: 122—124.

Taley, Y. M. & Thakare, K. R. (1979). Biology of seven new hymenopterous parasitoids of *Atherigona soccata* Rondani. *Indian J. agric. Sci.* **49**: 344—354.

Tsitsipis, J. A. & Abatzis, C. (1980). Relative humidity effects, at 20°, on the eggs of the olive fruit fly, *Dacus oleae* (Diptera: Tephritidae), reared on artificial diet. *Ent. exp. & appl.* **28**: 92—99.

Unnithan, G. C. (1981). Aspects of sorghum shootfly reproduction. *Ins. Sci. Application* **2**: 87—92.

Wigglesworth, V. B. (1974). *The principles of insect physiology*. Seventh Edition, Chapman & Hall, London, U.K.

Young, W. R. (1981). Fifty-five years of research on the sorghum shootfly. *Ins. Sci. Application* **2**: 3—9.

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