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INFLUENCE OF TEMPERATURE AND HOST PLANT CONDITION ON PREIMAGINAL DEVELOPMENT AND SURVIVAL IN THE SORGHUM SHOOTFLY *ATHERIGONA SOCCATA*

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Abstract—Temperature–time and temperature–velocity equations are given for egg, larval and pupal stages of the sorghum shootfly, *Atherigona soccata*. Preimaginal development (from egg deposition to adult emergence) on sorghum CSH-1 seedlings lasted 19.5, 26.3, 33.8 and 76.8 days at 30, 25, 20 and 15°C, respectively. The sorghum shootfly showed optimal development and survival at 30°C. Lower threshold temperatures were 13.8, 10.2 and 11.8°C for the egg, larva and pupa, respectively. Host plant condition affected larval development and survival; pupal weight was higher and larval mortality lower in insects reared on fertilized and normally watered seedlings than on unfertilized and water stressed seedlings.

Key Words: Atherigona soccata, sorghum shootfly, temperature, host condition, preimaginal development

INTRODUCTION

ALTHOUGH the sorghum shootfly, *atherigona soccata* Rondani, is most serious as a pest in the Old World Tropics, it has also been recorded at latitudes as northern as 26°N in China (Shie Shiang-Lin *et al.*, 1981) and 43°N in Europe (Rondani, 1871). At these latitudes, sorghum is grown only as a summer crop, and mean winter temperatures often do not exceed 5°C. The first data on the effect of temperature on *A. soccata* preimaginal development were given by Swaine and Wyatt (1954); they reported a mean duration of 2, 8 and 6.8 days for egg, larval and pupal stages, respectively, at a mean temperature of 27.2°C Nye (1960), Barry (1972) and Taksdal and Baliddawa (1975) made similar observations; adult emergence was found to take place 16.8 to 29.5 days after egg deposition at room or field temperature. The first precise data on shootfly development at three constant temperatures were given by Doharey *et al.* (1977). Raina (1981) reported mean developmental periods of 2, 10 and 6–7 days for egg, larva and pupa, respectively, at 30°C.

With the recent development of research on various aspects of sorghum shootfly biology and in particular on its population dynamics, the acquisition of reliable data on the effect of temperature on egg hatch, pupation, adult emergence and other events in the life cycle of the pest has become necessary. Laboratory and mass-rearing of the insect also requires a detailed knowledge of time–temperature relationships. Studies were, therefore, undertaken to determine the effects of temperature on development and survival of sorghum shootfly preimaginal stages. It is generally accepted that, with the exception of widely fluctuating temperatures, values recorded in the laboratory at different constant temperatures remain applicable to wild populations of different origins (Howe, 1967). It is expected that information presented here will be useful in explaining population dynamics of the pest in Asia as well as in Africa.

Host plant physiology and plant chemical composition are known to affect host plant selection and larval physiology in a number of insects; Rahier (1978) reported that high protein contents favoured the development of aphid (*Myzus persicae*) colonies and the selection of plants by alates; low water and protein content of the maize stalk have been shown to induce diapause in the stem-borers, *Chilo partellus* and *Chilo orichalcociliella* (Scheltes, 1978). Although no attempt is made here to associate larval physiology with the chemistry of the host plant, an experiment was designed to bring to light the effects of a poor growing condition of the sorghum seedling on development and survival of the sorghum shootfly larva.

MATERIALS AND METHODS

Shootflies were obtained from third instar larvae collected from a sorghum field in Nairobi and maintained under greenhouse conditions at 27.5 ± 2.5°C, 60 ± 15% r.h. Rearing procedures were those described by Unnithan (1981). Eggs were laid on sorghum seedlings between 08.00 and 09.00 hr in order to avoid the effect of diurnal rhythm which would have distorted the distribution of hatchings; within minutes after the end of the egg-laying period, leaf pieces bearing eggs were transferred onto moist filter paper in Petri dishes. Egg hatch experiments were performed in an environmental chamber set at different constant temperatures under a 12-hr photophase, with lights on at 06.30 and off at 18.30 hr.

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Each experiment comprised of at least 50 synchronized eggs and was repeated five times. Observations were taken every hour under binocular microscope after the first hatched eggs were noted.

In another experiment, 2-week old sorghum seedlings (susceptible hybrid CSH-1 from India, grown in plastic pots containing black cotton soil) were artificially infested by introducing freshly hatched larvae (one per seedling) into the whorl using a camel hair brush. Seedlings were transferred to environmental chambers set at 15 ± 2, 20 ± 1 and 30 ± 1°C and at alternating temperatures of 20 ± 1°C (scotophase) and 30 ± 1°C (photophase), which is here considered as equivalent to constant 25°C (Laudien, 1973). Four hundred and fifty seedlings were used for each temperature regimen. Daily observations were made on 30 randomly selected seedlings; 15 to 30 living insects were recovered on each occasion. Larvae were washed in distilled water and weighed. Pupae were recovered at the base of the plant or in the lower half of the stem, never in the soil; they were washed in a 1% solution of sodium hypochlorite, rinsed in distilled water, weighed and then kept individually in glass vials (7.5×2.5 cm) containing 15 g of sterilized sand moistened with five drops of distilled water. The number of dead larvae in each instar was also recorded. Observations were discontinued when all insects recovered from the seedlings reached the pupal stage.

The effect of host plant nutrition on larval development was studied with insects of the same origin as above; five CSH-1 seedlings each were planted in 10.5×10-cm plastic pots containing a mixture of sand, black cotton soil and red soil in equal proportions. Prior to their infestation, plants were maintained in an outdoor screen cage ($2 \times 2 \times 2$ m), where temperature ranged from 11 to 35°C (mean daily temperature: 22.1°C). Young seedlings were normally watered until 13 days after germination. After this period, they were divided in two groups: half of the plants (control) received twice 75 ml per pot of a 15 g/l solution of Welgro® containing 15% nitrogen, 30% soluble phosphoric acid, 15% potash and the following trace elements: magnesium, manganese, iron, copper, boron and molybdenum. Pots with these plants received 75 ml water each every two days, that is a total of 525 ml before plants were infested, 32 days after germination. The seedlings, which had reached the sixth stage, were infested as described earlier. The other half of the plants (experimental) did not receive fertilizer and were subjected to water stress: pots with these plants received 50 ml water each every 3 or 4 days; they reached the sixth leaf stage only 60 days after germination. The total amount received by the experimental plants was 600 ml. After this period, they were infested and transferred to the greenhouse. Twenty-five plants were dissected every 2 days, starting 8 days after infestation. Pupation sometimes took place in the soil, when the host plant was too weak and had completely wilted before the larva could complete its development; the larva then left its host to pupate in the soil. Consequently, the soil was sifted and pupae were searched for after the plants had been pulled out and dissected. The following parameters were recorded: height of the shoot (measured from stem base to ligule of last expanded leaf); shoot diameter (measured 4 cm above stem base); developmental stage of the insect; weight of the larva at 8 days after infestation; and weight of the pupa.

The effect of temperature on the duration of preimaginal stages was assessed using three different methods of analysis. The time taken by 50% of individuals to reach a given stage was estimated graphically by plotting the cumulative percentage of insects reaching that particular stage against the duration of exposure at a given temperature. This method was used for egg (Fig. 1) and larval stages (Fig. 2). Mean (and median) development time was calculated for the egg stage only; it could not be assessed for the other stages because successive observations on the same individuals were impossible without disturbing the insects. Several methods have been devised for the assessment of development rate in insects which cannot be observed individually at given intervals. Data are usually obtained from ran-

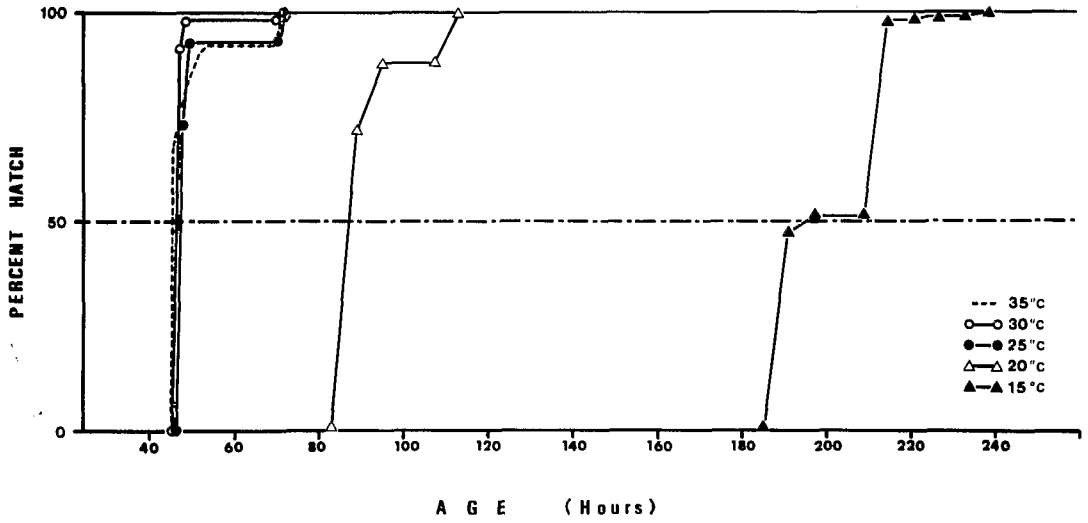

Fig. 1. Graphical estimation of time taken by 50% of the eggs to complete their development at five constant temperatures.

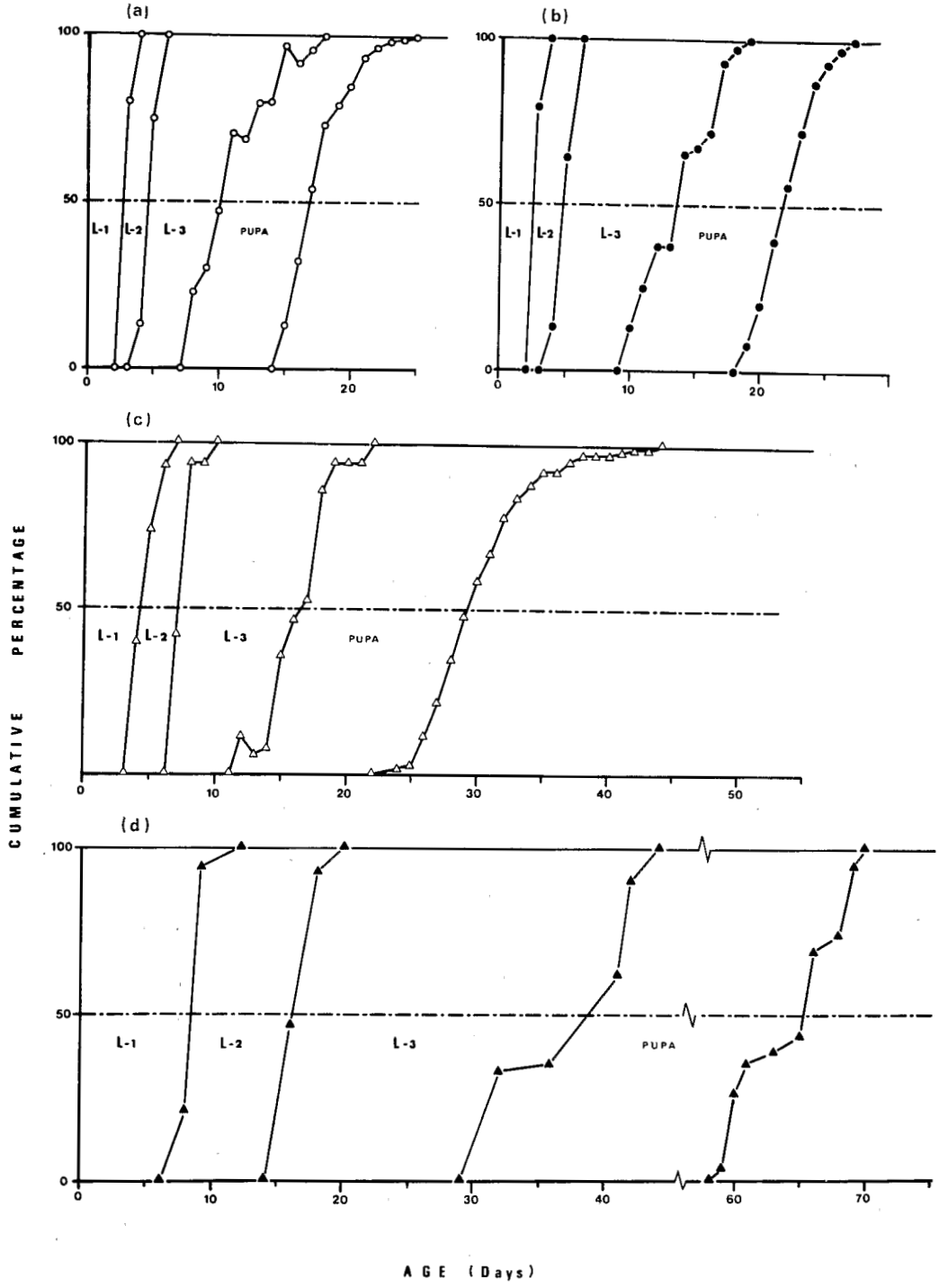

Fig. 2. Graphical estimation of time taken by 50% of the individuals to reach a given larval stage and the pupal stage at (a) 30; (b) 25; (c) 20; and (d) 15°C.

dom samples taken at regular intervals from a cohort of insects; after examination, the sampled insects are not returned to the cohort. Data are then treated by probit (Finney, 1971) or logit analysis (Mertz and Robertson, 1970; Chatterjee and Price, 1977) procedures, which provide an estimation of the duration between the 50% points of successive stages (ED_{50}). The applicability of both methods to the study of insect development was discussed by Yamada (1973) and Howe (1975). In the present case, a comparison of the two methods revealed that, although slightly more cumbersome, the probit procedure consistently gave a better fit than the logit; chi-square analysis between observed and expected data showed no heterogeneity at the 5% probability level for all stages at all temperatures. It was therefore decided that the probit procedure was adequate for the study. $TL2_{50}$, $TL3_{50}$, TP_{50} and TE_{50} were defined as the times when

50% of the insects moulted into the second instar, 50% moulted into the third instar, 50% pupated and 50% emerged to adults, respectively. The duration of the first instar was, therefore, defined as $TL2_{50}$ minus hatching time; that of the second instar, $TL3_{50}$ minus $TL2_{50}$; that of the third instar, TP_{50} minus TL_{50}; pupal stage duration was TE_{50} minus TP_{50}.

The method described by Davidson (1944) was used to determine the equations for the effect of temperature on developmental time (generating the temperature–time curve) and of temperature on the percentage of development per unit of time; the latter, which is of the form

$$\frac{100}{D} = \frac{K}{1 + e^{a-bt}}, \quad (1)$$

generates a sigmoid or logistic curve, the temperature–velocity curve, which is the reciprocal of the temperature–time curve. The determination of the theoretical zero temperature for development is usually based on the assumption that the reciprocal is not a sigmoid, but a straight line; the equation of this line is determined by the least squares method, and the zero temperature is the x-intercept of the extrapolated regression line. Another method, in which the equation of the straight line is obtained by expanding equation (1) around its point of inflexion ($t = a/b$; $100/D = K/2$) was preferred because too few values lied on the linear part of the sigmoid curve:

$$\frac{100}{D} = \frac{1}{2} - \frac{a}{4} + \frac{b}{4}t. \quad (2)$$

The x- intercept of this line gives the zero temperature:

$$t_0 = \frac{2-a}{b}. \quad (3)$$

RESULTS

Egg stage

Time taken for completion of embryonic development in 50% of the eggs, mean and median development times at various constant temperatures are given in Table 1. Hatching started after 46 hr incubation at 25, 30 and 35°C, after 83 hr at 20°C and after 185 hr at 15°C. The hatching period was also extended at low temperatures: it lasted 54 hr at 15°C, 29 hr at 20°C and 26 hr at 25 and 30°C. The equation of the temperature–time curve, which expressed the duration (D) in days of the egg stage as a function of temperature (t), was

$$D = \frac{1 + e^{7.38 - 0.39t}}{0.53},$$

the equation of its reciprocal, the temperature–velocity curve, was

$$\frac{100}{D} = \frac{53.25}{1 + e^{7.38 - 0.39t}}.$$

Table 1. Effect of temperature on embryonic development duration

Temperature (°C)	Graphical estimation (days)	Median duration (days)	Mean duration (days + SD)
15	8.15	8.21	8.47 ± 0.51
20	3.63	3.71	3.86 ± 0.43
25	1.97	1.94	1.98 ± 0.21
30	1.94	1.88	1.90 ± 0.12
35	1.93	1.94	2.05 ± 0.27

The optimal temperature is defined by Laudien (1973) as the temperature at which developmental time is shortest; as development did not take significantly longer at 25 and 30°C than at 35°C, the optimal temperature range for embryonic development occurred between 25 and 35°C. The theoretical minimum development time, which is the ordinate of the horizontal asymptote of the temperature–time curve, was $D_m = 1.88$ days, very close to the observed minimum of 1.90 days at 30°C. Davidson (1944) defined the optimum temperature as the temperature (or range of temperatures) at which the maximum number of insects are able to complete their development; egg mortality was significantly

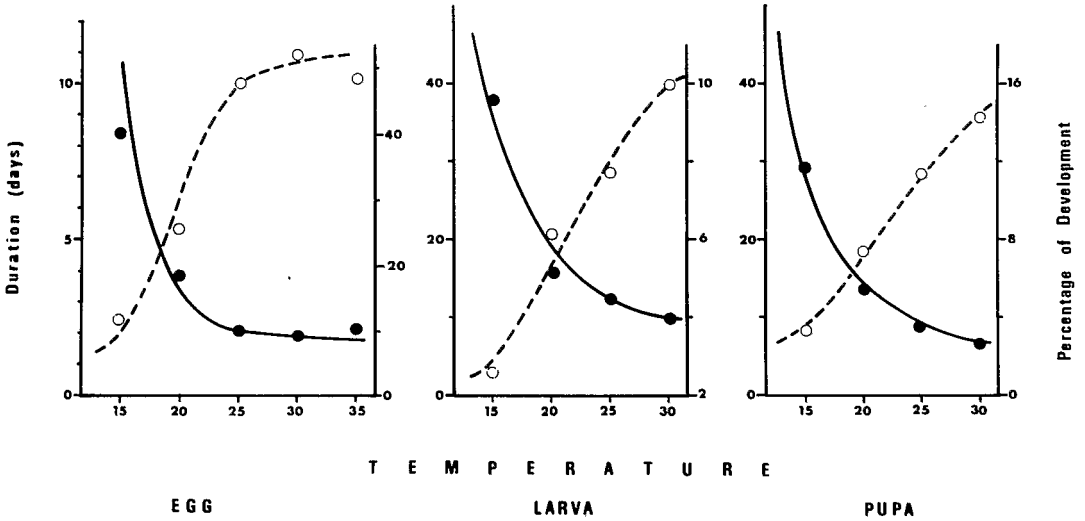

Fig. 3. Temperature–time (full circles) and temperature–velocity (open circles) for *A. soccata* egg, larval and pupal stages.

Table 2. Effect of temperature on egg, larval and pupal mortality in *A. soccata* reared on CSH-1

Temperature (°C)	Mortality (%) Egg	First instar	Second instar	Third instar	Pupa
15	10.81	17.04	0.74	0.00	22.30
20	3.46	2.22	0.32	0.63	25.39
25	6.82	11.76	0.78	1.57	13.41
30	1.73	13.78	1.78	1.33	13.84
35	21.77	—	—	—	—

higher at 15 and 35°C than at other temperatures (Table 2), indicating that the optimal temperature (*sensu* Davidson) lies between 20 and 30°C.

Based on equation (3), the lower threshold temperature was 13.8°C and the equation of the temperature–velocity line was

$$\frac{100}{D} = 5.15t - 71.35,$$

although the zero temperature was not experimentally determined, it was noted that no hatching occurred at 10°C. At 37.5°C, embryonic development was inhibited, and eggs dried up within a few days; the upper hatching threshold therefore occurred between 35 and 37.5°C.

Larval stage

The duration of each of the three larval instars was assessed at 15, 20, 25 and 30°C using graphical estimation and probit analysis methods; corresponding data are given in Table 3. The optimum temperature (*sensu* Laudien) for larval development was 30°C. At 35°C, plants wilted and dried up; all insects died before pupation. It was not known whether this mortality was due to the deterioration of the host plant or to the lethal effect of high temperature. The equation of the temperature–time curve (based on probit data) for the whole larval stage (Fig. 3b) was

$$D = \frac{1 + e^{3.88 - 0.18t}}{0.12},$$

its reciprocal, the temperature–velocity equation, was

$$\frac{100}{D} = \frac{11.88}{1 + e^{3.88 - 0.18t}}.$$

The theoretical minimum larval development duration was $D_m = 8.41$ days, less than the observed minimum of 10.1 days necessary for the larva to complete its development at 30°C. Duration of the second instar was the shortest at all temperatures, representing 12% (at 30°C) to 19% (at 15°C) of the total larval period. First instar duration represented 21–27% of the larval period, and third instar duration was the longest (56–64% of the larval period). The minimum threshold temperature was 10.2°C and the equation of the temperature–velocity line

$$\frac{100}{D} = 0.55t - 5.57.$$

Mortality in the first instar was high at all temperatures, but was negligible in the second and third instars. A chi-square test indicated that mortality was independent of temperature, except in the first instar (Table 2). Mortality in the first instar was minimum at 20°C and increased at both lower and higher temperatures. Data on increase in larval weight from the time of hatching to pupation are presented in Fig. 4; growth was exponential until the eighth, tenth, thirteenth day at 20, 25 and 30°C, respectively; at 15°C, prepupal weight was higher than at any other temperature, although growth was slower.

Pupal stage

The pupal period for insects reared at the same temperature since the first larval instar was 7.46 ± 0.14 days at 30°C, 8.77 ± 0.16 days at 25°C, 13.41 ± 0.29 days at 20°C and 29.51 ± 0.70 days at 15°C. The optimum temperature (*sensu* Laudien) was 30°C. The equation of the temperature–time curve was

$$D = \frac{1 + e^{4.30 - 0.19t}}{0.18},$$

and that of the temperature–velocity curve was

$$\frac{100}{D} = \frac{17.71}{1 + e^{4.30 - 0.19t}}.$$

The minimum pupal period, computed from the first equation, was $D_m = 5.64$ days. A chi-square test failed to show any significant effect of temperature on pupal mortality. The lower limiting temperature was 11.8°C; the equation of the temperature–velocity line was

$$\frac{100}{D} = 0.86t - 10.18.$$

Table 3. Effect of temperature on larval development duration (in days)

Temperature (°C)		First instar	Second instar	Third instar	Total
15	Graphical	8.44	7.76	22.60	38.80
	ED_{50}*	9.04 ± 0.04	7.33	21.89	38.22 ± 1.55
20	Graphical	4.30	2.90	9.30	16.50
	ED_{50}	4.35 ± 0.17	2.83	9.01	16.19 ± 0.31
25	Graphical	2.65	2.10	8.75	13.50
	ED_{50}	2.68 ± 0.30	2.02	8.21	12.90 ± 0.39
30	Graphical	2.65	1.15	6.35	10.15
	ED_{50}	2.64 ± 0.10	1.21	6.23	10.08 ± 0.39

*$ED_{50} \pm$ SD for first instar and total larval stage.

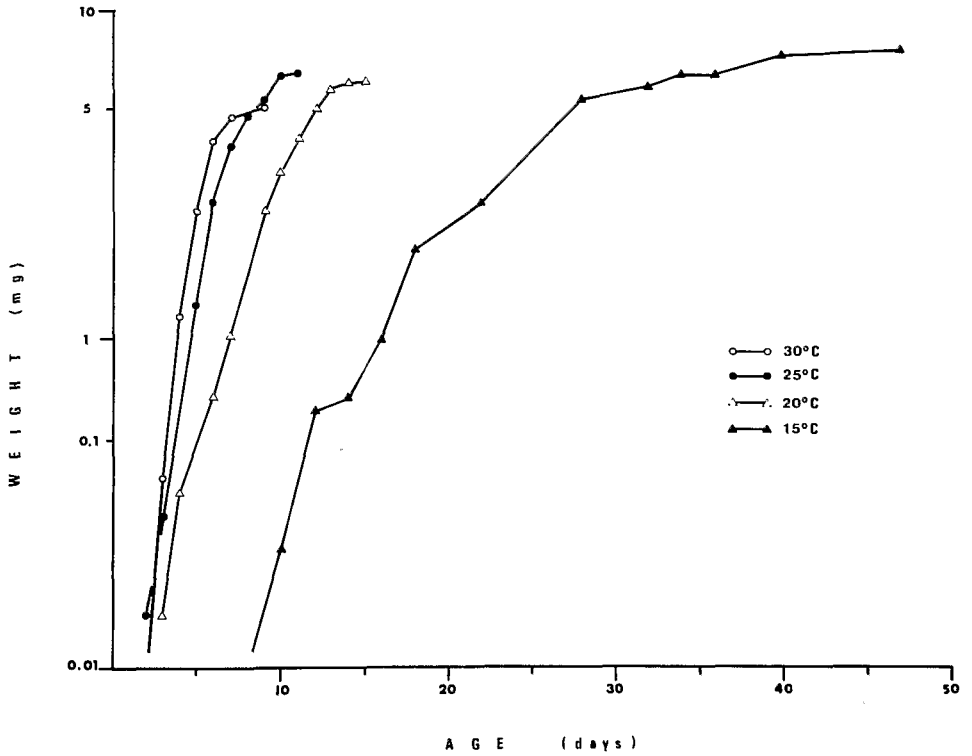

Fig. 4. Effect of temperature on growth of *A. soccata* larvae reared on CSH-1 sorghum seedlings.

The fresh weight of less than 48-hr old pupae was affected by the temperature at which larvae had been reared; there was a strong correlation between temperature and pupal weight in females ($r = -0.580$; $P < 0.001$) as well as in males ($r = -0.485$; $P < 0.001$). In both sexes, pupal weight decreased with increasing temperature (Fig. 4). The slopes of the two regression lines differed significantly, indicating that females were heavier than males at all temperatures, and that temperature had a stronger effect on females than on males (Fig. 5).

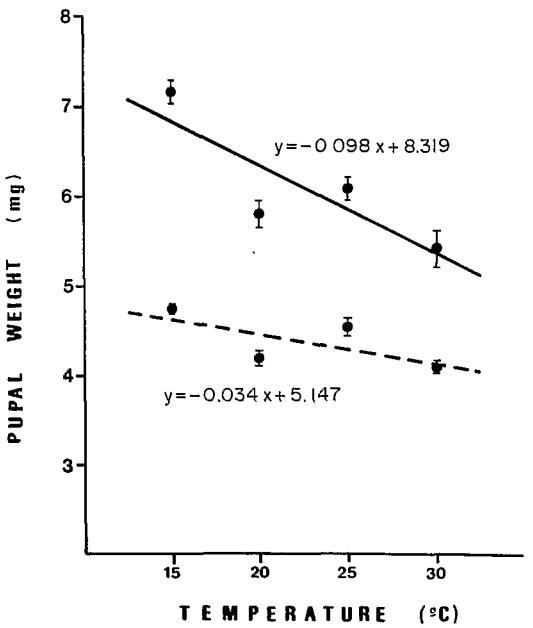

Fig. 5. Pupal weight of *A. soccata* males (broken line) and females (solid line) reared at different temperatures. Each dot represents the arithmetic mean (±SD) of 30 individual measurements.

Influence of plant nutrition

Experimentally stressed seedlings were significantly shorter (82.4 mm) than control plants (108.3 mm); stem diameter was also less in stressed plants (2.6 mm) than in control plants (3.0 mm). Larval mortality was higher in stressed than in control plants (Table 4). In stressed plants, 31.2% of the first instar larvae failed to enter the shoots, probably because of the tightness of the whorl leaves, which prevented the downward movement of newly hatched larvae. Mortality was also high among larvae which had managed to enter the shoots: 20.4% of them died before cutting the growing point of the seedling, which is a prerequisite for successful establishment of larvae (Raina, 1981). These figures were significantly higher than those obtained in control plants; total larval mortality amounted to 55.9% in stressed plants, against 17.4% in control plants.

The weight of larvae 8 days after hatching (third instar) was significantly lower in stressed than in control plants. The mean larval period was extended by about 4 days in stressed plants; the first pupae appeared earlier (after only 8 days) in stressed plants, because tissues tended to dry up faster, thus inducing premature pupation. These pupae were smaller and less dark than normal pupae. Mean pupal weight was significantly lower for pupae in stressed plants.

Table 4. Effect of host plant nutrition on preimaginal development in *A. soccata*

	Per cent larval mortality				Larval weight at 8 days (mg)†	Larval stage duration (days)†	Pupal weight (mg)†
	Failure to enter shoot	Failure to cut growing point	2nd, 3rd instar mortality	Total			
Control	7.6 ± 1.4	3.3 ± 3.5	6.5 ± 5.0	17.4 ± 7.7	8.97 ± 1.96	10.52 ± 0.59	6.53 ± 1.70
Stressed plants	31.2 ± 9.4***	20.4 ± 8.1**	4.2 ± 4.0 (NS)	55.9 ± 10.1***	5.39 ± 2.26**	14.83 ± 2.33*	5.20 ± 1.42*

†Mean ± standard deviation.
***Significant at $P < 0.0001$.
**Significant at $P < 0.001$.
*Significant at $P < 0.01$.
NS = Not significant.

DISCUSSION

Several factors prohibit a precise assessment of the goodness of fit (by a chi-square test; see Howe, 1975) of the two curves expressing the relationship between temperature and rate of development, the sigmoid and the straight line: the small number of temperatures tested; the difficulties arising from the necessity of maintaining the host plant under unfavourable conditions; the difficulty of keeping the experimental temperatures (specially the lowest ones) constant for extended periods; and the fact that the genetic homogeneity of populations in successive experiments could not be verified. Visual examination of Fig. 3 however, suggests that this relationship has a sigmoidal form over the range 15–30 or 35°C. The logistic model fits experimental data reasonably well and provides a good estimation of the minimum developmental time.

The comparison with previous reports of the duration of preimaginal stages is delicate, because of the lack of adequate information on the temperature at which rearing took place, on the varieties which the larvae were fed, or on the methods used to assess mean development periods, specially in the larval stage. When compared with seven other cultivars, CSH-1 produced the biggest larvae (Raina *et al.*, 1981), which indicates that antibiosis is one of the mechanisms involved in the resistance of certain sorghum cultivars to the shootfly. Duration of larval development is therefore likely to be affected by the variety on which the larva is reared. Raina (1981), who used the hybrid CSH-1 at a constant temperature of 30°C, reports durations of the preimaginal stages which are in very close agreement with our own observations. Doharey *et al.* (1977), using the same variety at three constant temperatures found incubation periods longer and larval periods much shorter than ours; there is no indication, however, of the number of larvae used in each experiment, nor of the method used in the computation of average larval periods. Earlier reports are usually based on very limited numbers of insects; Swaine and Wyatt (1954), for example, report a duration of 2 days for the first instar and 3 days for the second and third instars; this is based on the observation of 1, 3 and 4 insects, respectively. The duration of 8 days for the whole larval stage is obviously and underestimation: at the average temperature of 81°F, the temperature-time equation for the larval period yields a duration of 11.4 days. On the other hand, Taksdal and Baliddawa (1975) record a duration of 21 days for the larval stage; the rearing temperature is not indicated, but the duration of 6.0 days for the pupal stage suggests a temperature of about 27°C; at this temperature, the larval period should not last more than 12 days.

The assumption of linearity of the relationship between developmental rate and temperature, although not entirely satisfactory (Davidson, 1944; Phelps and Burrows, 1969), does provide an estimation of the lower threshold temperature, which is widely used in the determination of the thermal constant or thermal unit accumulation (Wigglesworth, 1974; Chmiel and Wilson, 1979; Weinberg and Lange, 1980; Havelka, 1980; Steven-

son, 1981). Most of the sorghum produced in Kenya is grown in areas where temperature is well above the zero temperature for egg development (13.8°C) all the year round; in the main sorghum growing region, Mbita has a mean monthly temperature ranging between 24.3°C in July and 25.5°C in October. Similar figures are to be found in the Coast Province, where sorghum is also widely grown. Sorghum is however grown in areas of higher altitude (Meru and Embu districts), where temperatures, specially at night, are only slightly above, or even below 13.8°C during part of the year. At Embakasi, where a population of *A. soccata* established on the wild sorghum *S. arundinaceum*, was studied in 1979–1980 (Delobel and Unnithan, 1981), mean temperatures in July are only 3°C above the lower threshold for egg development. Shootfly development in those areas is likely to be slackened or even stopped during the coldest months. A similar situation prevails in the tropical highlands of Ethiopia, Uganda and Sudan, where high altitude cultivars, with a high degree of cold tolerance, have been developed (Doggett, 1965). In parts of the world where sorghum is grown as a summer crop, winter temperatures are certainly the limiting factor which causes the extension of the post-harvest generation over several months (Shie Shiang-Lin *et al.*, 1981).

The temperature found to be most suitable for a rapid development of shootfly preimaginal stages was 30°C, which is also the optimum temperature for sorghum growth (Purseglove, 1975); at this temperature, mortality was low, except in the first instar. These results are in accordance with data by Doharey *et al.* (1977). There have been many publications in recent years in which the concept of optimum temperature has been discussed. In addition to the simple concepts of Davidson (1944) and Laudien (1973), other criteria have been proposed, such as oxygen uptake, fat consumption, proteolytic and esterase activities (Wigglesworth, 1974). Each criterion leads to a different definition of the optimum temperature which is likely to give a different result. It must also be stressed that the relationship between temperature and rate of development varies with factors which may be difficult to control, such as age and health of parents, air humidity or nutritional status of the host plant. This last factor is closely dependent on plant growing condition, as shown in the present experiment on the effect of host plant nutrition on larval development. Taking host plant condition into consideration is all the more important as it also affects host plant selection by shootfly females (Delobel, 1982). In this respect, the use of adequate experimental designs, such as blocks or latin squares, in order to eliminate the effect of soil heterogeneity in field studies, is strongly advocated.

The present study has demonstrated that lower temperatures produce heavier individuals in *A. soccata*. This observation is consistent with the idea that rapid development occurring at higher temperatures results in small body size (Laudien, 1973); examples of this are found in the Diptera *Aedes aegypti*, *Drosophila spp.* (Laudien, 1973) and *Glossina morsitans* (Bursell, 1960). The relationship between body size and temperature is however less clear in other insects, particularly in Lepidoptera (Oldiges, 1959).

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