Diapause termination in the millet stem borer, *Coniesta ignefusalis* (Lepidoptera: Pyralidae) in Ghana as affected by photoperiod and moisture

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Abstract

Studies were conducted in northern Ghana in 1997 and 1998 on the effects of contact moisture and photoperiod on the termination of larval diapause in the stem borer, *Coniesta ignefusalis* (Hampson). Results obtained over the two years consistently showed that on its own, photoperiod had no significant effect on diapause termination. In combination with contact moisture, however, a long day photoperiod of 13L:11D accelerated diapause termination and increased the cumulative percentage pupation. Contact with moisture was crucial for diapause termination but its influence was more pronounced in larvae collected from the field after March. Generally, access to moisture earlier than April resulted in very high larval mortality. These observations, together with the fact that some of the larvae (12%) denied access to water throughout the experimental period subsequently pupated, suggest that moisture may not be the sole factor triggering diapause termination in *C. ignefusalis*. The implications of these findings are discussed.

Introduction

Environmental factors play an important role in the survival, growth and development of insects. Although diapause responses in insects may be genetically controlled (Andrewartha, 1952; Beck, 1968), environmental conditions usually play a precise and critical role in determining whether or not, and to what degree, diapause will develop in a given population (Masaki, 1980; Tauber *et al*., 1986). However, the extent to which environmental conditions affect diapause varies considerably among species and even within the same species. This can range from almost complete reliance on environmental cues (Harris, 1962; Adkisson *et al*., 1963; Usua, 1973; Scheltes, 1978) to genetic predominance (Denlinger, 1986; Tauber *et al*., 1986). Although the ecology of insect diapause has been extensively studied in insects, most of the available data are on temperate insects. Here the insects are usually subjected to marked seasonal changes in photoperiod and temperature (Chippendale & Reddy, 1973). The situation for tropical insects is quite different since, in most cases, there are usually relatively minor changes in daylength from one location to the other. Under such conditions, factors such as temperature and rainfall may play more dominant roles in regulating the onset and termination of diapause (Denlinger, 1986). It has been shown for some tropical stem borers that the key environmental factors influencing diapause are rainfall, temperature, photoperiod and food (Harris, 1962; Adkisson *et al*., 1963; Usua, 1973; Scheltes, 1978; Kfir, 1993a,b). These factors vary greatly from one location to another and even between seasons at the same location. In the Sudan savanna zone of Ghana (11°01′N) where the current studies were undertaken, the long term average daylength varies between 11.5 and 12.7 h and the rainfall pattern is erratic, with total annual precipitation seldom exceeding 900 mm (Kasei, 1991; Kasei & Rudat, 1994). In this zone, larvae of the millet stem borer, *Coniesta ignefusalis* (Hampson) (Lepidoptera: Pyralidae) go into diapause at the end of the cropping season in November and remain in this state until May in the following year when adults emerge (Tanzubil, 1998). As a survival tactic therefore, *C. ignefusalis*

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appears to have evolved a life cycle that ensures that diapause termination and subsequent adult emergence coincide with periods when millet plants are established in the field and are in the right state to afford sites for oviposition and subsequent larval development. As with most tropical borers however, the exact factor(s) responsible for the regulation of diapause have not been clearly established. Since the maintenance of *C. ignefusalis* populations from one year to another depends on successful diapause development, it is important to determine precisely which factors regulate or influence diapause and to what extent such factors can be modified to affect its initiation, maintenance and termination. This paper discusses the effects of photoperiod and moisture on termination of diapause in *C. ignefusalis* in northern Ghana.

Materials and methods

Effect of wetting larvae (contact moisture) on diapause termination

In Ghana, late millet is planted in June and harvested in November, after which the stalks are cut down and either left in situ, or are carried home by farmers for domestic use. The insect goes through four generations in a year with some of the third, and all of the fourth generation larvae entering diapause in the millet stalks in which they remain until the beginning of the next cropping season. Each month from February to June 1997, therefore, diapausing *C. ignefusalis* larvae were taken from millet stalks collected from the field around Manga, Ghana (11°01N, 09°16W). Based on visual observation and their relative activity, healthy larvae were selected and maintained in sections of dry millet stalks kept in vials (10 mm × 5 mm). Both ends of each vial were plugged with gauze to prevent escape. Two larvae were kept in each vial and 20 vials constituted a replicate. Treatments were replicated five times, giving a total of 200 larvae per treatment. The treatments were: (i) larvae maintained in the laboratory and denied access to water (Lab, dry); (ii) larvae maintained in the laboratory with regular access to water (Lab, wet); (iii) larvae maintained in the field and denied access to water (Field, dry); and (iv) larvae maintained in the field with access to water (Field, wet). Stalks were split open weekly to monitor mortality and termination of diapause which was marked by pupation. On each of these dates, a drop of water (1 µl) was applied topically to the dorsal surface of each larva in the treatments involving wetting. Larvae were subsequently allowed a 60 s contact with the water before being returned to the stalks. In these treatments also, drops of water were applied to the gauze as often as necessary to keep conditions moist. Data on mortality and pupation were expressed as percentage of larval numbers at the start of the experiment and were subjected to one-way ANOVA. The Least Significant Difference (LSD) technique was employed to test differences between treatment means. In 1998, this experiment was repeated for the months of April and May, with some modifications to reduce larval mortality. Pieces of stalk were cut into 6 cm lengths and both ends of each piece were artificially drilled to produce cavities large enough to accommodate a single diapausing larva. Larvae were introduced into the cavities and the openings were sealed tightly with pieces of millet stalk material to simulate field conditions. It was possible, with this method, to examine larvae and to take relevant records without having to split open the stalks, an activity that presumably led to the high larval mortalities observed in the 1997 experiments. In 1998 also, the pieces of stalk were maintained in bundles with the help of elastic bands rather than kept in glass vials as was done the previous year. Data collected were again subjected to one-way ANOVA.

Effect of photoperiod on diapause termination

Diapausing larvae were collected in the field in March 1997 and maintained in dry millet stalks held in glass tubes. Both ends of each tube were plugged with cotton wool. Twenty-six larvae were subjected to each of four different photoperiods in the laboratory. Each treatment had five replicates, giving a total of 130 larvae per treatment. Dark chambers were created by means of thick black fabric nailed onto hollow boxes and tested (by a local pin-hole camera operator) to ensure that they were light-proof. Continuous lighting was provided in the room from two 1.2 m fluorescent tubes located above the cultures. A standby generator (240 W) was used to provide power anytime the central power supply failed. The photoperiods tested were: 11L:13D (short day), 13L:11D (long day), 12L:12D (neutral day) compared with an ambient laboratory photoperiod of *c.* 11.6 ± 0.4 h of daylight during the experimental period. The ambient temperature in the laboratory varied between 29.2 and 34.5°C with relative humidity values of 36–45%. Larvae were observed weekly for the first fortnight and then every other day, for mortality and/or pupation. The experimental set up was modified in 1998 to reduce mortality as described earlier in the study of the effects of wetting on diapause termination. Also this time, Gallenkamp incubators rather than the improvised dark chambers were used. Data were subjected to one-way ANOVA with treatment means separated by LSD.

Effect of photoperiod and contact moisture on diapause termination

In this experiment, larvae collected from the field in March 1997 were subjected to different photoperiods and

Table 1. Mortality in diapause *Coniesta ignefusalis* larvae as affected by access to water during the dry season (1997).

Treatment	% total mortality (February)	% total mortality (March)	% total mortality (May)
Lab, dry	45.0 ± 6.0 c	55.1 ± 6.0 c	36.5 ± 2.3 c
Lab, wet	100 a	100 a	54.5 ± 2.7 b
Field, dry	73.4 ± 7.6 b	70.0 ± 7.1 b	63.5 ± 3.2 a
Field, wet	100 a	100 a	66.5 ± 2.9 a

Within the same column, figures followed by the same letter are not significantly different at $P = 0.001$.

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Table 2. Effect topical application of water at different times of the year (in April and in May) on mortality, diapause termination and pupation in *Coniesta ignefusalis* larvae (1998).

Treatment	Days to pupation (April)	Days to pupation (May)	% total mortality (April)	% total mortality (May)	% total pupation (April)	% total pupation (May)
Lab, dry	71.8 ± 1.2 a	41.8 ± 1.4 a	31.4 ± 1.4 ab	28.5 ± 2.0 b	14.4 ± 4.3 c	12.50 ± 3.7 b
Lab, wet	38.8 ± 1.5 b	16.8 ± 1.1 d	17.5 ± 5.2 c	12.5 ± 1.8 d	82.8 ± 5.4 a	87.50 ± 5.1 a
Field, dry	66.3 ± 1.8 a	28.8 ± 1.5 b	42.4 ± 1.8 a	36.9 ± 3.4 a	15.0 ± 5.7 c	20.00 ± 2.3 b
Field, wet	42.5 ± 1.8 b	21.3 ± 1.1 c	29.4 ± 5.8 bc	25.0 ± 2.8 c	70.6 ± 5.8 b	75.00 ± 8.7 a
P	0.001	0.001	0.008	0.005	0.001	0.001

Within the same column, figures followed by the same letter are not significantly different at the given level of *P*.

maintained under dry (no access to water) or wet (regular access to water) conditions in the laboratory. Larvae were held in pieces of stalk prepared in the same way as described earlier. Test photoperiods were 11L:13D (short day) and 13L:11D (long day) and wetting was carried out as described earlier in the 1998 experimental set-up. Larval numbers and replication were the same as for the moisture experiment and similar types of observations were made.

Effect of wetting stalks (artificial rainfall) on diapause termination.

Stalks known to be heavily infested with *C. ignefusalis* diapause larvae were collected in March 1998 in the field and stored outside in a fenced area at the Manga Research Station. They were then divided into heaps of 1000 stalks, and each heap received one of the following treatments in four replications: (i) stalks watered daily; (ii) stalks watered twice a week; (iii) stalks watered three times a week; (iv) stalks watered fortnightly; and (v) stalks maintained dry. Watering was done using a Cooper Pegler (CP) 15 knapsack sprayer. From preliminary studies, it was established that about 10 l water adequately wetted 100 stalks, therefore each heap was sprayed with 100 l water at the start of the experiment. The spray volume was adjusted for all other subsequent sprays according to the number of stalks remaining in the heap. Weekly samples of 50 stalks were drawn from each stack and split open to monitor diapause termination as evidenced by appearance of pupae.

Results

Effects of contact moisture on diapause termination

None of the *C. ignefusalis* larvae collected in the field and given access to water in February and March in 1997 pupated (table 1). During these months, contact with water led to 100% larval mortality within four weeks. Larval mortality was also high during the other months, though some larvae survived to pupation. Mortality was generally higher in the larvae that were wetted than those denied access to water ($P = 0.001$, $F_{3, 19} = 29.8$ and 23.3 for February and March, respectively). Mortality was generally higher in the insects maintained in the field than those maintained in the laboratory under dry conditions (table 1).

Pupation was observed only in *C. ignefusalis* larvae subjected to wetting in April and May (figs 1 and 2). None of the larvae given access to water earlier than April pupated. The time taken from first wetting to pupation also varied between months. Whereas it took larvae given access to water in April up to six weeks to pupate (fig. 1), those

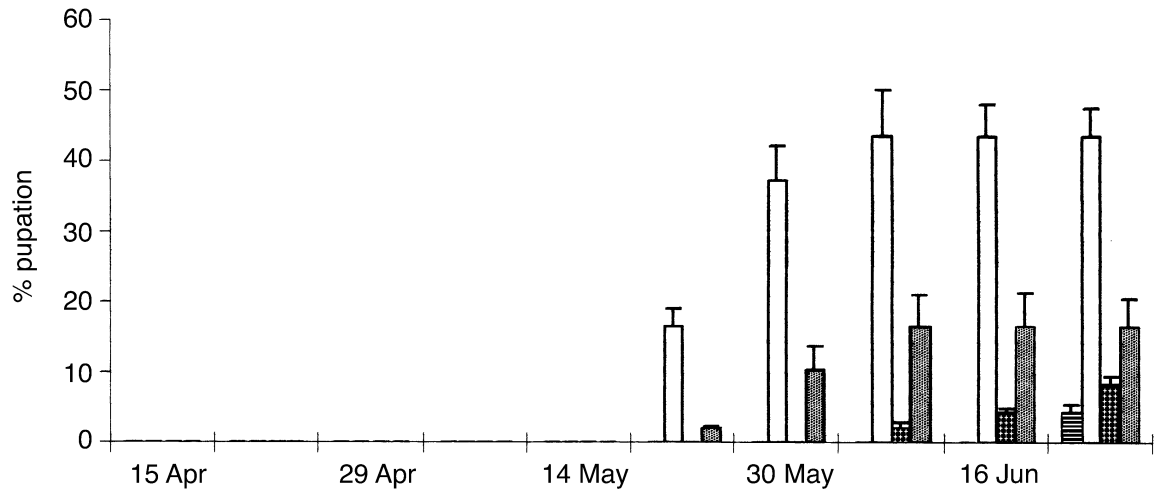

Fig. 1. Effect of topical application of water on diapause termination and pupation in *Coniesta ignefusalis* larvae. Water applied on 7 April 1997. ▤, Lab, dry; □, lab, wet; ▨, field, dry; ▦, field, wet.

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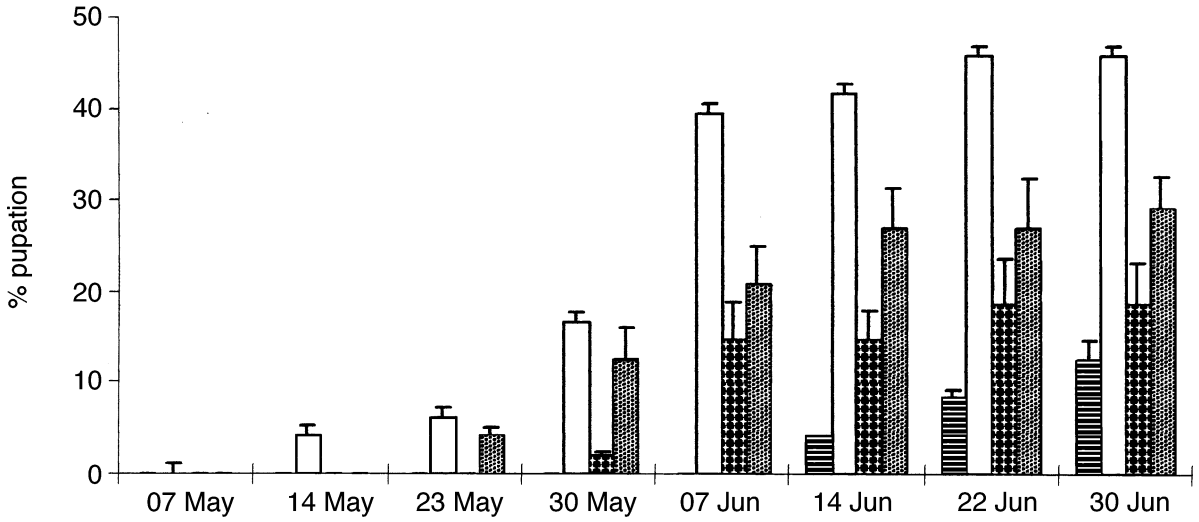

Fig. 2. Effect of topical application of water on diapause termination and pupation in larvae of *Coniesta ignefusalis*. Water first applied on 1 May, 1997. ▤, Lab, dry; □, lab, wet; ▨, field, dry; ▦, field, wet.

watered in May pupated within two weeks (fig. 2). Significantly higher numbers of pupae were obtained from larvae given regular access to water in the laboratory in both April ($P > 0.001$, $F_{3, 1} = 20.5$) and May ($P > 0.001$, $F_{3, 12} = 12.6$) than from those larvae given similar treatment but kept in the field. When larvae were denied access to water, there was a higher incidence of pupation in the field compared with the laboratory. Similarly in 1998, higher levels of pupation were recorded in larvae that received topical application of water than in those maintained dry (table 2) (P 0.001, F = 55.2 (April) and 47.7 (May)). Though some larvae denied access to water pupated as in the previous experiment, they did so after a considerably extended period ($P < 0.001$, F = 112.9 and 72.7 for April and May, respectively), and the percent cumulative pupation was lower than those that had regular access to water.

Effect of photoperiod on diapause termination

As shown in table 3, photoperiod alone did not significantly affect the termination of diapause in *C. ignefusalis*. Up to eight weeks after treatment, no pupae were recorded in any of the three treatments. Rather, most larvae died, and mortality appeared to increase with increasing daylength ($P < 0.01$, $F_{3, 12} = 5.9$).

Table 3. Effect of photoperiod on diapause termination in *Coniesta ignefusalis* larvae with no access to water.

Treatment	% cumulative mortality		% cumulative
	(after 8 weeks)	(after 10 weeks)	pupation
11:13 L:D	35.4 ± 2.7 a	69.8 ± 13.1 b	0
12:12 L:D	43.8 ± 2.7 a	79.2 ± 11.7 a	0
13:11 L:D	40.6 ± 3.6a	75.0 ± 12.9 ab	0
Ambient	43.8 ± 2.5a	70.4 ± 12.4 b	0

Within the same column, figures followed by the same letter are not significantly different at $P = 0.01$.

Combined effect of photoperiod and moisture

The combination of photoperiod and moisture availability had a positive effect on the rate of diapause termination (table 4). *Coniesta ignefusalis* larvae given access to water under long day conditions pupated within about 20 days and 68% of test insects pupated within 60 days. Under the same photoperiodic conditions, only 6% of larvae denied access to water pupated and the rate of pupation was significantly lower ($P < 0.01$, $F_{5, 19} = 4.54$), first pupation being recorded 44 days after treatment. Similarly, under short day conditions, first pupation was recorded in *C. ignefusalis* larvae maintained in wetted stalks 40 days after treatment and only 4% of larvae had pupated by the end of the experiment. None of the larvae maintained under dry and under a short day regime pupated. Results from the 1998 experiments confirmed that a long day photoperiod of 13 h alone did not significantly influence diapause termination in *C. ignefusalis* but, in combination with access to water, it had an accelerating effect. As shown in table 5, the highest levels of pupation were recorded for larvae maintained under long day conditions and given regular access to water ($P < 0.001$, $F_{5, 14} = 96.1$). Larvae maintained under such conditions were also the earliest to pupate ($P <$

Table 4. Combined effects of photoperiod and wetting on diapause termination in *Coniesta ignefusalis* larvae (1997).

Treatment	Days to pupation	% total pupation	% total mortality
11:13 Wet	39.8 ± 3.5 a	4.2 ± 2.9 bc	82.3 ± 3.5 a
11:13 Dry	–	0.0c	78.1 ± 1.9 ab
13:11 Wet	19.5 ± 1.7 c	68.8 ± 5.5 a	30.2 ± 4.6 d
13:11 Dry	44.5 ± 3.3 a	6.3 ± 5.5 bc	70.8 ± 3.8 b
Ambient wet	28.8 ± 4.2 b	62.6 ± 6.9 a	36.4 ± 3.1 d
Ambient dry	40.6 ± 2.0 a	8.0 ± 2.2 b	61.6 ± 4.5 c

Within the same column, figures followed by the same letter are not significantly different at $P = 0.01$.

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0.001, $F_{5, 14}$ = 48.9), followed by those given water under ambient conditions. The longest period taken from the start of the experiment to termination of diapause was recorded in larvae maintained under dry and under short day length conditions. Generally, larvae given access to water pupated earlier than those denied access under similar conditions.

Effect of wetting millet stalks on diapause termination

The time taken for *C. ignefusalis* larvae to terminate diapause and pupate decreased with increasing frequency of watering from 39 days in stalks watered daily to 68 days in those watered weekly, fortnightly or not at all ($P < 0.001$, $F_{5, 15}$ = 15.9) (table 6). There were no significant differences in the rate of pupation between watering stalks daily and doing so every other day. Pupation was highest in stalks watered twice weekly (86.5%) and lowest in those kept dry throughout the experimental period ($P < 0.001$, $F_{5, 15}$ = 22.2). Differences in the overall pupation levels among stalks watered daily, thrice weekly and weekly were not significant.

Discussion

It is generally acknowledged that seasonality in tropical environments is driven primarily by variations in rainfall pattern (Denlinger, 1980; Young, 1982; Jones, 1987). Diapause larvae are known to react to moisture and contact with water has been reported to induce pupation in diapause larvae of some stem borers (van Dinther, 1961; Beck, 1967; Usua, 1970; Rodriguez-del-Bosque *et al*., 1990), but the exact process remains controversial. In *C. ignefusalis*, diapause termination usually coincides with the onset of the rains (Harris, 1962) and it has been shown in the current studies that water is a key factor, essential for diapause larvae to resume growth and subsequently, pupate. Results from the work presented in this paper confirmed that in *C. ignefusalis*, contact with water significantly increases both the rate of diapause termination and the percentage of larvae that do so. In the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae), water intake is required to activate the neuro-endocrine system to produce and release the hormones required to terminate diapause (Beck, 1967). This might well be applicable to *C. ignefusalis*, hence the difference observed in diapause termination between larvae given access to water and those denied it. Breaking of diapause by rain or moisture is believed to be connected with an increase in the water content of larvae (van Dinther, 1961). This could result from absorption of water vapour from the air or absorption through the cuticle of water present in the stalks. In the current studies, both routes of absorption appear to have been involved, as the higher incidence of pupation in larvae kept dry in the field is suggestive of absorption of water vapour from the air. Significant weight gains were observed in *C. ignefusalis* larvae maintained in the field without access to water, over those kept in the laboratory under similar conditions (Tanzubil, 1998). Hydration of larvae was also probably achieved via active uptake of water applied topically or through the stalks. *Coniesta ignefusalis* larvae were often observed drinking water that was applied topically, and Kfir (1991) observed active imbibition of water by diapause larvae of the sorghum stem borers, *Busseola fusca* (Fuller) (Noctuidae) and *Chilo partellus* (Swinhoe) (Pyralidae) in South Africa. In Kenya, Okuda (1988), demonstrated the important role played by water in the termination of larval diapause in *B. fusca* but concluded that water contact rather than drinking was what accelerated diapause termination. In the current studies, emphasis was on studying the influence of water on diapause termination under field conditions within millet stalks, it was therefore not possible to accurately distinguish the contact action of water from direct uptake.

The results demonstrate clearly that contact with water accelerates diapause termination only in larvae of *Coniesta ignefusalis* that have completed diapause. This is evident from the observation that sudden contact with water early in the dry season did not result in spontaneous diapause termination as happened in May but resulted in very high larval mortality. The practical implication of this observation is that larvae exposed to off-season rains naturally suffer high mortality. In Ethiopia, Gebre-Amlak (1989) similarly obtained higher mortality in *B. fusca* larvae given access to water between December and February and concluded that access to water early in diapause did not induce pupation but rather increased natural mortality. Okuda (1988) similarly reported that *B. fusca* larvae do not respond to moisture during the first three to four months of diapause. Kfir (1993b), however, noted that though the presence of water early in diapause did not trigger spontaneous pupation it increased survival and longevity of diapausing *Chilo partellus* larvae. The present results suggest that there are at least two distinct stages in diapause development in *Coniesta ignefusalis*. In the first stage, access to water does not result in spontaneous diapause termination while in the second, it does. These periods could well represent the

Table 5. Combined effects of photoperiod and contact water on diapause termination in *Coniesta ignefusalis* larvae (1998).

Treatment	Days to pupation	% total pupation	% total mortality
11:13 Wet	33.2 ± 1.3c	11.0 ± 3.6 bc	44.0 ± 2.5 ab
11:13 Dry	78.6 ± 5.9 a	4.5 ± 2.2 c	54.5 ± 3.7 a
13:11 Wet	19.6 ± 1.2 d	78.5 ± 5.0 a	21.5 ± 5.0 d
13:11 Dry	43.0 ± 2.0 b	13.5 ± 2.5 bc	48.5 ± 4.9 ab
Ambient wet	29.8 ± 1.1 c	73.0 ± 2.7 a	27.0 ± 2.7 cd
Ambient dry	43.2 ± 2.8 b	17.0 ± 3.7 b	37.5 ± 5.3 bc

Within the same column, figures followed by the same letter are not significantly different at $P = 0.001$.

Table 6. Effect of wetting millet stalks on termination of larval diapause in *Coniesta ignefusalis*.

Watering frequency	Days to first pupation	% total pupation
Daily	38.8 ± 3.3 c	66.1 ± 8.4 bc
Thrice weekly	38.0 ± 3.5 c	73.7 ± 3.8 ab
Twice weekly	50.0 ± 3.9 b	86.5 ± 5.4a
Weekly	67.8 ± 4.0 a	64.2 ± 6.1 bc
Fortnightly	68.0 ± 2.8 a	54.9 ± 3.6 c
None	68.8 ± 4.6 a	13.1 ± 2.5 d

Within the same column, figures followed by the same letter are not significantly different at $P = 0.001$.

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diapause maintenance and post-diapause periods identified by Denlinger (1986) in his review on diapause in insects. The diapause maintenance period in *C. ignefusalis* in Ghana presumably lasts until March and during this period, contact moisture would not normally trigger termination of diapause in field populations of the insect. During the second stage, however, access to water positively influences the rate of diapause termination resulting in a high incidence of pupation. This would appear to be a useful evolutionary trait for enhanced survival. If water was the only factor terminating diapause, it would mean that out of season rains (e.g. the rains in March) would trigger diapause termination, pupation and adult emergence at a time when no host plants are present in the field for infestation. This would be catastrophic indeed for the insect.

One other important observation is that pupation occurred even in some of the larvae maintained throughout under dry conditions. This supports the earlier conclusion that water does not appear to be the only factor regulating diapause termination in *C. ignefusalis*. Reddy & Chippendale (1973) reported similar results from studies with the southwestern corn borer, *Diatraea grandiosella* Dyar (Lepidoptera: Pyralidae) and postulated that larvae that pupate under dry conditions probably had a higher percentage of tissue water. In the current experiments, however, an additional factor could be the ability of such larvae to absorb water from the atmosphere. This appears logical since atmospheric relative humidities at Manga increase towards May (Tanzubil, 1998), the only time that such pupation took place. The higher percentage pupation recorded in larvae kept under dry conditions in the field than those maintained under similar conditions in the laboratory gives further support to this assertion.

Photoperiod is known to be one of the environmental factors that has significant impact on many aspects of insect behaviour such as oviposition, hatching, larval growth, voltinism and food consumption (Beck & Hanec, 1960; Yamaoka & Hirao, 1981). Limited studies on the influence of photoperiod on diapause in tropical stem borers have suggested its involvement in diapause termination in such important crop pests as *O. nubilalis* (McLeod & Beck, 1963), pink bollworm *Pectinophora gossypiella* (Saunders) (Gelechiidae) (Bull & Adkisson, 1960), *B. fusca* (Kfir, 1993a) and *Chilo partellus* (Kfir, 1993b). Current results, however, failed to confirm a significant independent role for photoperiod in diapause termination in *Coniesta ignefusalis*. The results, however, suggest that long days of up to 13 h can have a positive effect on termination of diapause in larvae that have access to water. Field data and observations support this contention. Diapause termination in the field occurs around April/May (Tanzubil, 1998) and weather records (Kasei, 1991) show that these periods are characterized by the onset of rainfall (access to water) and lengthening photoperiods. From studies conducted in Nigeria, Harris (1962) also associated diapause termination in cereal stem borers with the onset of the rains and the concomitant higher relative humidities and lower temperatures. Kfir (1993a,b) reported that a combination of long day, water availability and high temperature were required to terminate diapause in *B. fusca* and *Chilo partellus* in the laboratory. In the current experiments conducted over two years, 13 h light in combination with moisture significantly accelerated diapause termination in *Coniesta ignefusalis*. It appears reasonable therefore to conclude that diapause termination in field populations of *C. ignefusalis* in northern Ghana is favoured by the resumption of the rains and an increasing daylength.

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