

STEMBORER LARVAL GROWTH AND TUNNELLING AND ITS INFLUENCE ON MAIZE VEGETATIVE GROWTH IN CÔTE D'IVOIRE

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(Accepted 19 June 1997⁺)

Abstract—Larval growth of the two main maize stemborers, *Busseola fusca* (Fuller) (Lepidoptera, Noctuidae) and *Eldana saccharina* Walker (Lepidoptera, Pyralidae), in Côte d'Ivoire was studied as a function of temperature sums. Tunnelling by unit weight was similar for both species. Early attacks by *B. fusca* (infestation until 17 days after maize emergence) resulted in deadhearts or in growth reduction. A relation combining the date of infestation, the level of attack and the development stage of maize explains the observed damage. Later attacks by both borers result in differences in damage, which are related to the larval distribution in the stem, the compensation between maize yield components, and also to the presence of a more or less active larva in the cavity.

Key Words: stemborer growth, maize growth, *Busseola fusca*, *Eldana saccharina*, Côte d'Ivoire

Résumé—La croissance larvaire des deux principaux foreurs de tige du maïs en Côte d'Ivoire, *Busseola fusca* (Fuller) (Lepidoptera, Noctuidae) et *Eldana saccharina* Walker (Lepidoptera: Pyralidae), a été étudiée en fonction de l'évolution des sommes de températures. Le volume des galeries par unité de poids a été identique pour les deux espèces. Les attaques précoces (infestation jusqu'à 17 jours après la levée) par *B. fusca* ont abouti à la production de coeurs-morts ou à la réduction de croissance des plants de maïs. Une relation combinant la date d'infestation, le niveau des attaques et le stade de développement du maïs explique les dégâts observés. Les attaques plus tardives par les deux foreurs aboutissent à des différences de dégâts, qui peuvent être expliquées par la distribution des larves dans la tige, les phénomènes de compensation entre les composantes du rendement du maïs et aussi par la présence d'une larve plus ou moins active dans la galerie.

Mots Clés: foreurs de tige, croissance larvaire, croissance du maïs, *Busseola fusca*, *Eldana saccharina*, Côte d'Ivoire

INTRODUCTION

During recent years, five maize stemborers, all Lepidoptera, have been identified in Côte d'Ivoire (Pollet et al., 1978; Dabiré, 1980; Moyal and Tran, 1992). Two of these, namely *Busseola fusca* (Fuller) (Noctuidae) and *Eldana saccharina* Walker (Pyralidae) regularly cause severe crop losses (Moyal, 1993). *Busseola fusca*, which is a species mainly restricted to the southern regions of the country (the mesophil and ombrophil sectors of the Guinean

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⁺See Editor's Note at the end of this issue.

zone) (Moyal, 1995b), lays its eggs during the first part of the maize cultivation cycle. *Eldana saccharina* is found in all parts of the country (Dabiré, 1980; Moyal, 1988) and generally attacks maize in the second part of the cultivation cycle.

A study of the effect of these two pests on yield components (Moyal, 1995a and 1996) showed the complexity of the borer influence and of the crop's response through various compensatory phenomena. In this paper, the effects of larval growth and tunnelling on maize growth are reported. At a later stage, the results of this investigation will be coupled to a maize crop model that aims to simulate the borer



effect and the crop response, in order to gain a better insight into the borer's influence on plant physiology.

MATERIALS AND METHODS

The study of *B. fusca* larval growth and tunnelling was conducted in Bouaké (7.5°N.Lat., 5.0°W.Long.), in the preforest savanna of the Guinean zone, in central Côte d'Ivoire. In this region, attacks by *B. fusca* are rare, very low and occur late in the year, in maize planted at the end of August and at the beginning of September (Moyal, 1995b). A maize crop planted on 12 July 1989 was divided into three fields. Each field was divided into plots arranged in randomised blocks. Each plot was 5 m long and 4 m wide, and was planted with five maize rows (80 cm between rows, 20 cm between plants in a row). The maize stand density was then 62,500 plants per hectare. Three treatments were applied: control with no artificial infestation by *B. fusca* larvae (T1); artificial infestation of the central row of a plot with three first-instar larvae per plant (T2); artificial infestation of the central row with five first-instar larvae per plant (T3). In each field three different infestation dates were chosen: date 1 = 10 days after maize emergence (DAE); date 2 = 17 DAE and date 3 = 24 DAE. Three replications were used for date 1 and five replications for dates 2 and 3. The maize variety was 'Composite Jaune de Bouaké', the most widely distributed variety in Côte d'Ivoire (CIDT, 1984). It has a growing season of about 100 days from sowing to harvest and a maximum yield of 6200 kg/ha (IDESSA, 1982). Fertiliser was applied at planting (300 kg/ha N-P-K 10-18-18) and 75 kg/ha urea was applied at tasselling.

After infestation, one plant was randomly sampled in each plot every 7 days, except once for dates 1 and 2, where a sampling had to be slightly delayed at the beginning of the study (interval of 10 days instead of 7, and then 4 days between this sample and the next one). Samplings of two consecutive plants were avoided to escape compensatory phenomena. The status of each sampled plant was recorded, particularly the presence of deadheart (growing point killed) and the number of leaves. The plant stems were then dissected for the presence of borers. The borers were weighed and the length and width of their cavities measured. The plant was then oven-dried at 60°C for seven days, and the dry weights of all the plant organs were recorded. The development threshold temperature for the larvae of *B. fusca* was estimated from Usua's (1968) work. This author showed that 48% of larvae stopped developing at 23.1°C, and considered this to be the temperature below which no larval development would occur. However, using the results

of the larval developmental periods at different temperatures, and given that the development temperature sum should be constant, it can be calculated that the threshold temperature is 12.8°C. Therefore, a temperature of 15°C, intermediate between these two values, was chosen for our study.

Eldana saccharina larval growth and tunnelling was studied from a similar experiment as above, and also from another trial conducted in Bouaké at the end of 1987 (maize emergence on 28/10/1987). In the latter experiment, which aimed to study the effect of the maize streak virus on maize growth and yield, twelve 20-metre-long plots were planted with ten rows of maize. Two plants showing no streak symptoms were randomly sampled per plot weekly. Both experiments however, were done under natural infestation, which is usually high in the second part of the year in Bouaké (Dabiré, 1980; Moyal, 1988). Stemborer attack began in both cases at about 50 DAE. In the first experiment, only those plants which did not suffer *B. fusca* damage were considered for the analysis (no attack by *B. fusca* occurred in the Bouaké trial). Only larval growth and tunnelling were studied since maize vegetative growth was complete by the time infestation commenced.

Under natural infestation, successive egg-layings resulted in overlapping larval cohorts. The study of larval growth was therefore carried out as follows: the average weight of each larval instar (determined using head-capsule widths according to Dabiré, 1980) was estimated and plotted versus the temperature sum needed for each instar development as estimated by Dabiré (1980). The threshold temperature was chosen at 10.6°C according to Shanower et al. (1993). This temperature was calculated by these authors for larvae grown on artificial diet whereas it was estimated at 5.5°C for larvae reared on maize stem pieces. However, the development rate was similar in both cases for all the tested temperatures, except at 25°C. It was much lower in maize stem at this temperature, which resulted in a worse regression of the development rate versus temperature for this diet, and finally in a much lower threshold temperature. Since frequent manipulations and diet changes disturb larval growth of *E. saccharina* (Girling, 1978), the growth difference observed only at 25°C might be artificial. That was the reason we chose 10.6°C as the threshold temperature.

Statistical analyses, mainly regressions, were done using Statitcf software (ITCF, 1987). Graphical studies of residuals were used to check the assumptions of normality and homoscedasticity (Chatterjee and Price, 1977; Draper and Smith, 1981).

RESULTS

*Busseola fusca**Larval weight growth*

The first two larval instars of *B. fusca* feed on the whorl leaves. In the experiment, cavities in the stems were observed for the first time 15 days after infestation. At this time (i.e. on an average at 123 day-degrees, with a threshold temperature of 15°C), about 50% of plants carrying larvae showed cavities. The average weight of the larvae in the stem (53 mg) was then similar to that of the larvae still in the whorl (62 mg). Four days later (at 164 day-degrees) all the stems showed larval infestation.

The study of the larval weight increase was preceded by an analysis which showed that larval growth did not vary with the number of larvae per stem. All data were therefore pooled to study larval growth. Figure 1a presents a plot of mean larval weight versus temperature sums. For infestations of dates 1 and 2, larval weight increased up to a maximum value and then decreased during pupation. Larval growth was very homogeneous in both cases: on date 1, only larvae were observed in the sampling-before-last and only pupae were observed in the last sampling; on date 2, only prepupal instars and young pupae were observed in the sampling-before-last and only pupae were observed in the final sampling. It can be estimated that all larvae pupated within a time interval of 32 day-degrees. Pupation for date 1

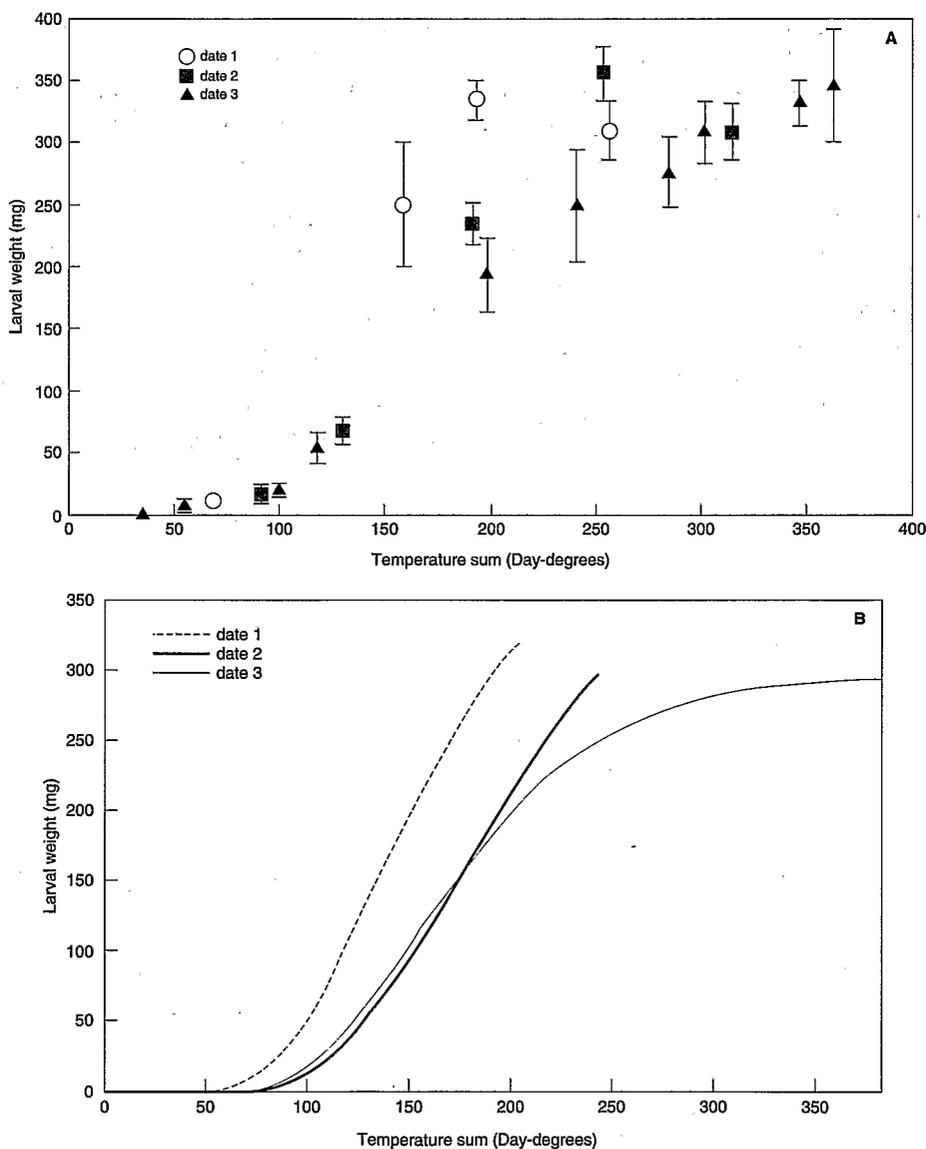


Fig. 1. (a) *Busseola fusca* larval mean weight (\pm standard error) as a function of temperature sums (base temperature = 15°C). (b) Gompertz models fitted to larval growth data. Date 1: infestation at 10 days after maize emergence (DAE). Date 2: infestation at 17 DAE. Date 3: infestation at 24 DAE

Table 1. Gompertz models [$y = a \cdot \exp(-(b/c) \cdot \exp(-c \cdot x))$] fitted to the larval weight growth of *B. fusca* and *E. saccharina*

• Species	Date of infestation	a	b	c	R ²	df	Residual variance
<i>B. fusca</i>	1	408.05	0.377	0.022	0.99	1	0.014
	2	413.5	0.291	0.017	0.99	2	1.440
	3	305.67	0.371	0.0198	0.99	10	32.10
<i>E. saccharina</i>	—	155.42	0.2738	0.0131	0.99	3	52.74

began just after the sampling-before-last, at 195 day-degrees, and for date 2 about 32 day-degrees before the sampling-before-last where only young pupae and prepupal instars were observed, i.e. at 234 day-degrees. For date 3, the increase in larval weight was more heterogeneous in the second part of larval life and pupation began at between 250 and 370 day-degrees. The temperature sum needed to complete the larval cycle increased with the date of infestation.

The larval weight data were fitted using Gompertz models, which are known to be well suited to weight-increase phenomena (Lebreton and Millier, 1982). Marquardt's method (Jolivet, 1982) gave good fits (Table 1). The fitted curves are presented in Figure 1b: larval growth was similar on dates 2 and 3 until about 180 day-degrees (i.e. a rather short period after stem infestation) and then larval growth reduced and was less homogeneous for date 3 larvae. The difference in larval growth between dates 1 and 2 occurred because, whereas larval growth in the stem

was similar for both dates, young larvae for date 2 recorded slower growth during the leaf-eating period.

Influence on plant growth

Deadhearts. The most obvious effect of *B. fusca* attack on plant growth is the appearance of deadhearts, which result from the destruction of the growing point. The percentage of deadhearts 37 DAE was 100% in the plots infested on date 1, 50% in the plots infested on date 2 and 0% in the plots infested on date 3. Infestations on date 1 all resulted in deadhearts even when only one borer survived per stem and tillers were observed from about 37 DAE. For later infestations, the percentage of deadhearts varied, depending on the density of borer population and on the maize development stage. The relation between the volume of the cavity (V) and the number of leaves (L) in plants showing deadhearts (Fig. 2) can be expressed by the following equation:

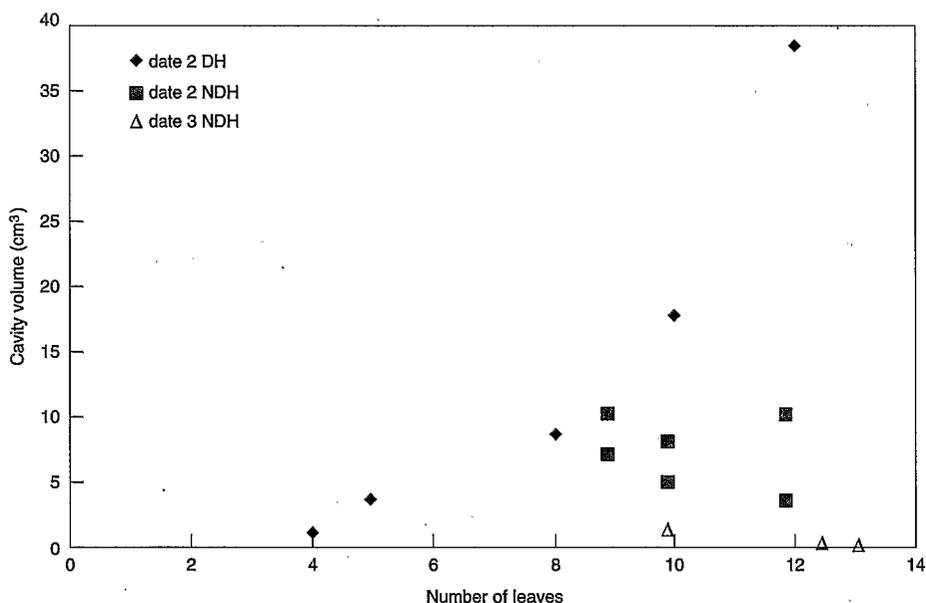


Fig. 2. Relation between the cavity volume and the maize development stage in plants showing or not showing deadhearts at 37 days after maize emergence. Date 2 DH: plants infested at 17 days after maize emergence showing deadheart; Date 2 NDH: plants infested at 17 days after maize emergence showing no deadheart; Date 3 NDH: plants infested at 24 days after maize emergence showing no deadheart

Table 2. Linear regressions for maize infested with stemborers *B. fusca* and *E. saccharina* of: (1) cavity volume (cm³) versus larval weight (mg) of *B. fusca* larvae; (2) number of leaves versus cavity volume (cm³) in plants infested with *B. fusca* larvae 17 days after maize emergence (DAE) (date 2 infestation) and showing no deadhearts; (3a) leaf dry weight versus number of leaves and (3b) leaf dry weight versus temperature sums (day-degrees) for date 2 infestation; (4) leaf dry weight versus number of leaves for plants infested with *B. fusca* larvae 24 DAE (date 3 infestation); (5a) stem dry weight versus leaf dry weight and (5b) stem dry weight versus temperature sums (day-degrees) for date 2 infestation; (6) stem dry weight versus leaf dry weight for date 3 infestation; (7) cavity volume (cm³) versus larval weight (mg) of *E. saccharina*; and (8) cavity volume (cm³) versus larval weight (mg) for both *B. fusca* and *E. saccharina*

	Explained variable	Regressor	Intercept	Regression coefficient	p (> t)	R ²	Residual standard error
1.	Cavity volume (cm ³)	<i>B. fusca</i> larval weight (mg)	0.7722	0.0163	0.0000	0.70	3.336
2.	Number of leaves	Cavity volume (cm ³)	11.44	-0.3174	0.0103	0.21	2.359
3a.	Leaf dry weight (date 2)	Number of leaves	-75.09	5.218	0.0000	0.77	8.605
3b.	Leaf dry weight (date 2)	Temperature sums		0.0734	0.0000		
4.	Leaf dry weight (date 3)	Number of leaves	-46.21	6.343	0.0000	0.71	11.09
5a.	Stem dry weight (date 2)	Leaf dry weight	-20.99	0.5926	0.0000	0.92	3.51
5b.	Stem dry weight (date 2)	Temperature sums		0.0310	0.0000		
6.	Stem dry weight (date 3)	Leaf dry weight	-5.08	0.6392	0.0000	0.91	3.20
7.	Cavity volume (cm ³)	<i>E. saccharina</i> larval weight (mg)	0.1030	0.0192	0.0000	0.68	3.59
8.	Cavity volume (cm ³)	Larval weight (both species) (mg)	0.2747	0.0182	0.0000	0.69	3.52

$$\log(V) = -0.4632 + 0.1725(L) \quad \text{Eq. 1}$$

(R² = 0.96; P = 0.0031).

All plants whose equations fall below this line did not show deadhearts. This was, for instance, the case for the sampled plants of date 3. However, a complete examination of the central rows at 37 DAE showed that the percentage of deadhearts was actually higher in the plots infested on date 3 than in the control plots (4.6% in control, 11.7% in T2 and 29.6% in T3; F(2,7) = 6.47, P = 0.026). This shows that some plants in the fields were probably less developed (i.e. had fewer leaves) or suffered more severe attack, or both, and would have been above the line of equation 1 if they had been sampled.

Tunnelling. The relation between borer growth and tunnelling was analysed from the data of dates 2 and 3 since all plants in the plots infested on date 1 had been earlier destroyed. A linear regression model was developed from both sets of data, one for each date: A model where both subsets were distinguished using an indicator variable (Tomassone et al., 1983) was compared to a model where all the data were pooled. The difference between the two models was not significant [F(2,41) = 2.23; P = 0.1024]. The stem volume eaten by borers of the same weight was then not different in either infestation date. The pooled-data model is presented in Table 2.

The relation between tunnelling and plant growth was evaluated: The number of leaves in plants

showing no deadhearts was significantly reduced in date 2, but not in date 3 infestations (Table 2) (data from the plants of the three sampling dates, i.e. 37, 44 and 51 DAE). The determination coefficient R^2 was, however, low because of the high variability of plants in maize composite varieties.

The leaf (including sheath) dry weight was highly correlated to the number of leaves per plant for both infestation dates (Table 2.3a and 2.4). The borer effect was neither significant on this variable nor on the stem dry weight, which was correlated to the leaf dry weight (Table 2.5a and 2.6). For both these variables, the significance of temperature sums varied, depending on the presence of more or less developed plants in the samples (Table 2.3b, 2.5b).

Eldana saccharina

Larval weight increase

Attack by *E. saccharina* began around 50 days after maize emergence (first- and second-instar larvae observed on this sampling). The first pupae were found 70 DAE. The Gompertz model fitted to the data is presented in Table 1.

Tunnelling

The cavity volume varied as a linear function of borer larval weight (Table 2.7). The maximum number of borers per stem was 30, for a total weight of 1519 mg. As for *B. fusca*, a model where the data from each trial were distinguished using an indicator variable did not differ significantly from a model where all data were pooled: $F(2,113) = 0.815$; $P = 0.445$. The pooled-data model is presented in Table 2.7.

Comparison of tunnelling of both species

Comparison of the cavity volumes of *B. fusca* and *E. saccharina* using an indicator variable shows that both models are not significantly different: $F(2,158) = 0.945$; $P = 0.391$. The model suitable for both borers is presented in Table 2.8.

DISCUSSION

Larval growth and tunnelling

The growth rate of *B. fusca* larvae became slower and less homogeneous as the maize crop got older. This borer species, which is well adapted to sorghum-type plants (its original host plants) (Van Rensburg et al., 1987), appears to be less adapted to infest

maize, a host plant introduced fairly recently into Africa, particularly when maize plants are mature. As a consequence, some larvae from an infestation at 24 DAE are still found 70–80 DAE. In fact, even in early infestations, changes in plant physiology, for instance when a water stress occurs, greatly affect larval growth and result in an increase in larval mortality (Moyal, 1995a), probably due to nutritional causes. These results indicate that *B. fusca* has succeeded in infesting the new host plant, maize, but the features of its growth and survival on the plant indicate the limits of its adaptation.

Although borers from later infestations stay longer in the stem, their cavities are not different in size from those due to earlier attacks. It can thus be concluded that feeding by unit time is reduced in older maize stems.

Moreover, up to 30 *E. saccharina* larvae may be found in a stem without any sign of intraspecific competition, which would have resulted in a decrease in tunnelling per unit weight.

Plant growth

Deadhearts represent the most serious damage due to early attacks by *B. fusca*. The fitted relation between the cavity volume and deadheart occurrence describes the limits of deadheart appearance for infestations from 17 DAE. Attacks by *B. fusca* begin in the whorl and then continue into the stem. The more developed the stem is, the larger the cavity has to be to result in deadheart. This explains why low density crops, where plants are more vigorous, show much fewer deadhearts than high density crops for a given population of *B. fusca* (Moyal, 1995b).

Early attacks by *E. saccharina* are rare and do not result in deadhearts (Moyal, 1996). This may be due to the larval distribution in the stem. *Busseola fusca* larvae are not found in the stem's lower internodes but only from the seventh internode upwards (Van Rensburg et al., 1987). The distribution of *E. saccharina* larvae is quite different: In our 1987 experiment for example, 60% of the sampled *E. saccharina* larvae were found in the bottom six internodes (Fig. 3). The larvae enter the stem's base, which may explain the low rate of destruction of the growing point.

The plants infested 17 DAE which did not develop deadhearts were less vigorous than their pest-free counterparts. The effect of borers is significant only on the number of leaves. These smaller plants with fewer leaves will receive less light and have a reduced photosynthetic activity. This results in inhibited ear production (Barloy, 1985; Gay and Bloc, 1985). Moyal (1996) showed that attacks at

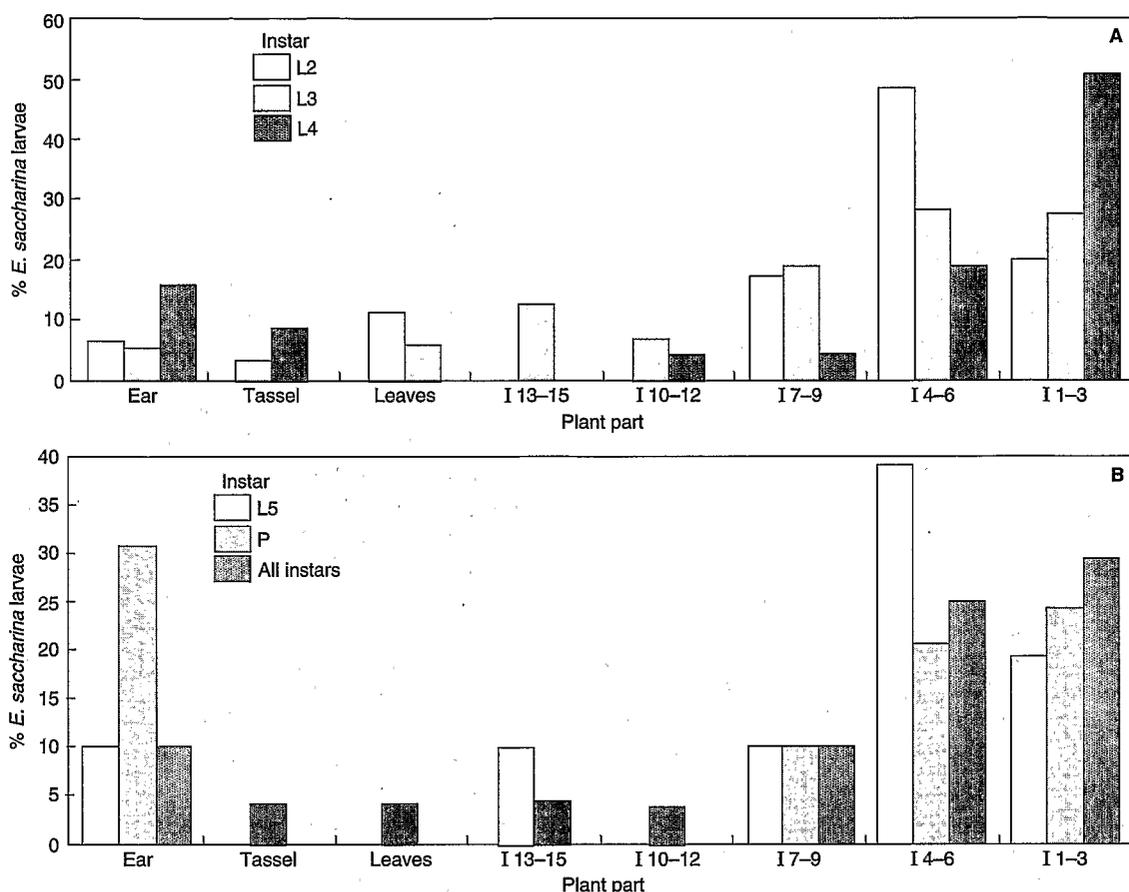


Fig. 3. Percentages of larvae of *E. saccharina* in the different parts of maize plants (I= Internode). A: larval instars L2 to L4; B: L5, pupae and total of all instars

similar dates resulted in plant sterility. Although the present trial did not aim to study crop loss, it could be noticed that plant sterility increased highly with infestation level: 98% of the harvested plants in the control plots carried cobs compared to 66.7% and 38.7% in the plots infested with 3 and 5 larvae per stem respectively.

Infestation at 24 DAE did not result in reduced plant growth. The borer effect was then restricted to the direct influence of tunnelling on ear production, kernel fertilisation and grain filling (Moyal, 1995a and 1996). Late attacks by *B. fusca* (resulting in large larvae and pupae at 80 DAE) have a major influence on plant sterility and a much less effect on grain filling (Moyal, 1996). In contrast, attack by *E. saccharina* results in much lower plant sterility (linear regression coefficient three times less than for *B. fusca*) but highly reduces grain filling (twice as much as *B. fusca*) (Moyal, 1996).

The larval distribution in the stem may also explain the minor influence of *E. saccharina* on plant sterility, since the ear is inserted between internodes 8 and 10, where few larvae of *E. saccharina* are found, particularly when borer density

is not very high. Calvin et al. (1988) showed that the position of the borer cavity in the stem influenced the effect of the larvae of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae) on yield. It seems that this factor is also important in tropical borers since the occurrence of deadhearts and sterile plants appears to depend on the site of infestation in the stem.

Late attacks by *E. saccharina*, which result in a reduction of grain filling, are often high. Due to competition, more borers are found in the upper part of the stem, although it is not rare to find up to 3 *E. saccharina* in one internode in the lower part of the stem. However, the cavities due to *B. fusca* are more important since the weight of a mature larva of this species is about twice that of *E. saccharina*. Moreover, they are located in the upper and middle parts of the plant, which provide the most photosynthetic assimilates (Gardner et al., 1985) and remobilised reserves (Cliquet et al., 1991) used for grain filling. Thus, infestation by *B. fusca* should result in a greater decrease in grain weight than infestation by *E. saccharina*. Why the inverse was observed in our study may be due to two reasons:

First, late attacks by *B. fusca* result initially in a reduction of the percentage of cob-carrying plants. It was shown by Prioul et al. (1991) that maize plants with cobs excised had a photosynthetic activity which decreased more quickly than that of undamaged plants. Additionally, Ruget (1991) showed that grain filling in high-density crops was less linked to plant reserves, than to photosynthetic activity. It can then be concluded that, in fields with few cob-carrying plants, the low photosynthetic activity of sterile plants decreases competition for sunlight which enables a better grain filling in the remaining cob-carrying plants. Such observations were already made in the case of the combined influence of borer and drought stress on plant sterility (Moyal, 1995a). Second, larvae of *B. fusca* are active mainly during the first part of grain filling, whereas larvae of *E. saccharina* are present until completion of grain filling. It is therefore possible that the presence of an active larva in the cavity causes higher stress on the plant than the presence of an older, less active larva or pupa, or when the cavity is empty. Godfrey et al. (1991) observed such a phenomenon in the case of *O. nubilalis*: this borer seemed to reduce the plant production only when an active larva was present in the stem.

As a result of this investigation it is then possible to simulate the larval growth and tunnelling as a function of temperature sums. It is also possible to predict plant killing or growth reduction due to early attacks by *B. fusca* through a relation combining the infestation date, the borer density and the maize development stage. The study also shows that the decrease in yield components due to late infestations is influenced by the distribution of borers in the stem. Finally, the results suggest that the reduction in yield due to tunnelling may vary depending on the presence or absence of an active larva in the cavity.

REFERENCES

- Barloy J. (1985) Biologie de l'élaboration du rendement, pp. 163–180. In *Physiologie du maïs* (Edited by A. Gallais). Editions de l'INRA, Paris.
- Calvin D. D., Knapp M. C., Kuang X., Poston F. L. and Welch S. M. (1988) Influence of European corn borer (Lepidoptera: Pyralidae) feeding on various stages of field corn in Kansas. *J. Econ. Entomol.* 81, 1203–1208.
- Chatterjee S. and Price B. (1977) *Regression Analysis by Example*. John Wiley & Sons, New York. 374 pp.
- CIDT (1984) *Rapport annuel d'activité*. Compagnie Ivoirienne pour le Développement du Textile, Bouaké. 178 pp.
- Cliquet J. B., Deléens E., Prioul J. L., Mariotti A. and Morot-Gaudry J. F. (1991) Etude, par utilisation des isotopes lourds, de la capacité de stockage de la tige de maïs pendant la montaison puis de la remobilisation de ces réserves vers l'épi, pp. 245–251. In *Physiologie et production du maïs* (Edited by D. Picard). Editions de l'INRA, Paris.
- Dabiré L. (1980) Biologie et écologie d'*Eldana saccharina* Walker (Lepidoptera, Pyralidae, Galleriinae) foreur du maïs en Côte d'Ivoire et inventaire des autres lépidoptères foreurs du maïs. Thèse de doctorat de troisième cycle, Université Pierre et Marie Curie, Paris. 196 pp.
- Draper N. R. and Smith H. (1981) *Applied Regression Analysis*. John Wiley & Sons, New York. 709 pp.
- Gardner F. P., Pearce R. B. and Mitchell R. L. (1985) *Physiology of Crop Plants*. Iowa State University Press, Ames. 327 pp.
- Gay J. P. and Bloc D. (1985) Détermination des composantes du rendement en grain, pp. 181–192. In *Physiologie du maïs* (Edited by A. Gallais). Editions de l'INRA, Paris.
- Girling D. J. (1978) The distribution and biology of *Eldana saccharina* Walker (Lepidoptera: Pyralidae) and its relationship to other stem-borers in Uganda. *Bull. Entomol. Res.* 68, 471–488.
- Godfrey L. D., Holtzer T. O. and Norman J. M. (1991) Effects of European corn borer (Lepidoptera: Pyralidae) tunneling and drought stress on field corn gas exchange parameters. *J. Econ. Entomol.* 84, 1370–1380.
- IDESSA (1982) *Variétés de maïs recommandées en Côte d'Ivoire*. Institut des Savanes, Ministère de la Recherche Scientifique de Côte d'Ivoire, Bouaké. 11 pp.
- ITCF (1987) *Statistf. Manuel d'utilisation*. Institut Technique des Céréales et des Fourrages, Paris. 210 pp.
- Jolivet R. (1982) *Introduction aux modèles mathématiques en biologie*. Masson, Paris. 151 pp.
- Lebreton J. D. and Millier C. (1982) *Modèles dynamiques déterministes en biologie*. Masson, Paris. 207 pp.
- Moyal P. (1988) *Les foreurs du maïs en zone des savanes en Côte d'Ivoire. Données morphologiques, biologiques, écologiques. Essais de lutte et relation plante-insecte*. Editions de l'ORSTOM, Collection Etudes et Thèses, Paris. 367 pp.
- Moyal P. (1995a) Borer infestation and damage in relation to maize stand density and water stress in Côte d'Ivoire. *Int. J. Pest Manage.* 41, 114–121.
- Moyal P. (1995b) *Ecology of the Maize Stalk Borer*,

- Busseola fusca* (Fuller) in Côte d'Ivoire. ORSTOM, Paris. 23 pp.
- Moyal P. (1996) Statistical model of crop losses caused by maize stem borers (Lepidoptera: Noctuidae, Pyralidae) in Côte d'Ivoire. *Environ. Entomol.* 25, 227–236.
- Moyal P. and Tran M. (1992) *Chilo aleniellus* (Lepidoptera: Pyralidae), a stem borer of maize in Côte d'Ivoire. *Bull. Entomol. Res.* 82, 67–72.
- Pollet A., Van Roon N. and Mauritz R. (1978) Les ravageurs du maïs en Côte d'Ivoire. Données qualitatives et quantitatives pour la Basse Côte. *Cah. ORSTOM, Sér. Biol.* 13, 71–85.
- Prioul J.L., Reyss A. and Schwebel-Dugué N. (1991) Métabolisme carboné dans les feuilles sources lors de la phase de remplissage des grains: Recherche de critères de remobilisation et de sénescence, pp. 239–244. In *Physiologie et production du maïs* (Edited by D. Picard). Editions de l'INRA, Paris.
- Ruget F. (1991) Origine des assimilats pour le remplissage des grains: Importance des remobilisations, pp. 233–238. In *Physiologie et production du maïs* (Edited by D. Picard). Editions de l'INRA, Paris.
- Shanower T. G., Schulthess F. and Bosque-Perez N. (1993) Development and fecundity of *Sesamia calamistis* (Lepidoptera: Noctuidae) and *Eldana saccharina* (Lepidoptera: Pyralidae). *Bull. Entomol. Res.* 83, 237–243.
- Tomassone R., Lesquoy E. and Millier C. (1983) *La régression. Nouveaux regards sur une ancienne méthode statistique*. Masson, Paris. 180 pp.
- Usua E. J. (1968) Temperature and relative humidity effects on the development of the immature stages of the maize stemborers *Busseola fusca* and *Sesamia calamistis*. *J. Econ. Entomol.* 61, 1091–1093.
- Van Rensburg J. B. J., Walters M. C. and Giliomee J. H. (1987) Ecology of the maize stalk borer, *Busseola fusca* (Fuller) (Lepidoptera, Noctuidae). *Bull. Entomol. Res.* 77, 255–269.

