Controlling the larger grain borer, *Prostephanus Truncatus* in maize using host plant resistance and biological control techniques

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Abstract

In East and West Africa, the accidental introduction of *Prostephanus truncatus* Horn (Coleopteras: Bostrichidae) in the early 1980s resulted in destructive outbreaks in small farm maize stores. Initial attempts to control the pest in Africa through the use of insecticides have had limited success. The use of host plant resistance and biological control as management strategies in the context of integrated pest management (IPM) are being evaluated in West Africa. Here we report on field and laboratory experiments to evaluate maize varietal effects on storage pest dynamics and grain damage and on some research studies investigating the underlying processes. Bionomics and predation behaviour of *Teretriosoma nigrescens* Lewis (Coleoptera: Histeridae), a biological control agent, currently being released in West Africa against *P. truncatus* are being evaluated as are the effects of competition between *P. truncatus* and *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae). The effects of abiotic factors (temperature and relative humidity) are also investigated under controlled conditions and by validation studies, observing population dynamics under a range of natural temperature/humidity regimes in different agro-ecological zones. A systems model, presently being developed, provides a unifying framework for considering the influence of these diverse biotic and abiotic factors. The potential use of this information in developing an IPM strategy is discussed.

Introduction

Maize is the most important cereal crop in West Africa, providing a source of income to small- and large-scale farmers alike. Small-scale farmers traditionally store maize on the cob with the husks intact in open ventilated stores or cribs. While two important pests, the maize weevil, *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae) and the Angoumois grain moth, *Sitotroga cerealella* Oliveier (Lepidaptera: Gelechiidae) are cosmopolitan in distribution, a third pest, the larger grain borer (LGB), *Prostephanus truncatus* Horn (Coleoptera: Bostrichidae), native to Mexico and Central America, became established in East and West Africa during the 1980s. To date, the insect has been confirmed to be present in Tanzania, Kenya, Burundi, Rwanda, Malawi and Zambia within the eastern and southern African outbreak areas and in Togo, Benin, Guinea, Burkina Faso, Nigeria and Ghana in West Africa (Hodges 1994). In Ghana, the pest status of *P.truncatus* has greatly increased, becoming most sever in the Volta Region, which shares a common border with Togo, the country where the pest was first reported in West Africa (Krall 1984).

Chemical control methods, based on direct application to cobs of binary insecticide dusts, consisting of a synthetic pyrethroid to control the larger grain border and an organophosphate to control other storage pests, have not been widely accepted by small-scale farmers in West Africa.

Farmers apparently perceive the treatment as ineffective (possibly because of the rapid breakdown of the active ingredient under the humid ambient conditions. They may also be unwilling to invest in a prophylactic treatment, especially when the incidence of the pest is erratic and unpredictable. Other reasons cited for the lack of adoption are the high cost of the insecticide itself or the unacceptability of other improved storage practices proposed along with the insecticide application. In addition, it should be noted that chemical control in stores, like any insecticide application, implies a danger to human health and the environment through possible misuse of the product. Furthermore reliance on synthetic pyrethroids for control of *P. truncatus* brings with it the possibility of inducing resistance, as has already been observed in laboratory populations of this insect (Golob et al. 1990).

At the International Institute of Tropical Agriculture (IITA) in Benin, efforts are under way to better develop a understanding of the basic ecology and biology of the larger grain borer and the conditions that lead to its damaging outbreaks, thus providing a basis for targeting control efforts. No maize variety has been reported as yet to be truly resistant to storage pests. However, experiments carried out at IITA, using different varieties stored as cobs with and without the husks under small-scale traditional methods, have demonstrated the protective role of husk cover in reducing grain losses to *P. truncatus* (unpublished data).

In Ghana, the predator *Teretriosoma nigrescens* Lewis (Coleoptera: Histeridae), identified as a biological control of *P. truncatus* (Boeye et al. 1988), has been released at various sites in the Volta Region and studies of establishment, dispersal and impact are in progress (Compton and Ofosu 1994). However, evidence from Mexico and Central America, the pests area of origin, suggests that adequate control is unlikely by this predator alone (Markham et al. 1991).

In view of the strong tradition of on-farm maize storage in this part of West Africa, there is a continuing need for improving small-scale on-farm storage systems in this region. Improvements should be based, as far as possible, on traditional methods and combined with the potential of host plant resistance and biological control among others, to provide a solution through the development of an integrated control strategy. As a first step towards developing a sound strategy, quantitative data are being collected on the potential contribution of each component and this will be followed by an assessment of the relative costs of various possible control strategies. This information is vital since there is an interdependent relationship among crop, pest and natural enemy such that no control strategy is self-evidently superior to, or more cost-effective, than others. As part of the exercise to determine the role of each component, a series of experiments are begin conducted in Ghana in collaboration with the large Grain Borer Project at the Plant Health Management Division (PHMD) of IITA, Benin.

In this paper, we investigate: the role of maize variety in pest population dynamics in traditional West African maize stores; the interaction of *P. truncatus* with *S. zeamais*, at the cob and grain level, in field and laboratory studies and factors affecting *T. nigrescens* dynamics and their ecological implications. Particular attention was given in these studies to assessing the effects of relative humidity and the associated variable grain moisture content on pest and natural enemy dynamics.

Controlling grain moisture content is often cited as a means of pest and pathogen control in large grain stores but the effects of lower grain moisture content on the ecology of small-scale rural stores is unclear. Previous laboratory studies (Howard 1983; Giga and Canhao 1993), suggest that *P. truncatus* is a weaker competitor at optimum conditions (usually considered to be 300°C and 70% r/h) but more tolerant of low humidity, thereby suggesting that the insect is better adapted to hot dry conditions than other pests, such as *S. zeamais*. However, West Africa where *P. truncatus* problems have been noted, the insect is doing serious economic damage in areas that are regarded as humid with rather moderate temperatures.

Results from these studies might help in interpreting factors affecting pest population dynamics in the field, and in developing and validating a multi-pest computer simulation model of these dynamics. With this approach, it will be relatively simple to answer quantitatively questions concerning the influence of the climate (through grain temperature and moisture content) and different maize varieties on the pest status of *P. truncatus.*

Materials and methods

Population dynamics studies of *P. truncatus* and *S. zeamais* in maize stores

A field trial was undertaken at the Kpeve Research Station (Long. 0.32, Lat. 6.67, Alt. 800 m), a tropical humid forest zone, from September 1994 to June 1995 in the Volta Region of Ghana where maize production follows the bimodal rainfall pattern, i.e. the long season lasting from March to July and the short one between September and November. Storage of the long season crop lasts for about 8 months (September to May) and that of the short about 5 months (January to June).

This study was divided into long and short season components. Two popular local varieties (Abutia and Dzolokpuita) and an improved variety (Abeleehi) were used. Altogether, sixteen grain stores were constructed. Twelve of the stores (four replicates for each of the three varieties) were stocked in September (for the long season experiments) and the four remaining stores were stocked in January with a new crop of the single variety Abutia. Treatments (varietal and seasonal) were arranged in a 4 x 4 Latin square design.

The stores used in the experiment were the circular 'Ewe-barn' type, about 1.8 m in diameter and about 0.8 m in height, consisting of a 2 m x 2 m split bamboo platform supported by eight wooden legs on the exterior and one post in the centre. Galvanised wire mesh (chicken wire) was attached from each leg to the central post, thus dividing the store into eight equal vertical sections. Maize cobs were placed on the structure with the husk on to mimic traditional stacking whereby large cobs are carefully stacked on the exterior and the remaining cobs thrown in at random to fill the inside of the column. Because the chicken wire provides support, a section could be completely removed and thoroughly sampled without affecting the rest of the store. One randomly selected section was sampled per store on each monthly sampling occasion. The section was then rebuilt using the remaining cobs from the sampled section plus replacement cobs taken from a nearby replacement store having similar experimental conditions.

For each sampling occasion, 26 cobs were randomly selected from each of the three subsections (surface, middle and inner layers) per store. Sampled cobs were rapidly placed into plastic bags, taken to the laboratory, weighed, the cobs shelled and the cores discarded. The shelled maize was then sieved through two sieves (mesh sizes 0.4 mm and 0.425 mm) and all adult insects were collected for identification and counting. Five moisture content determinations per section per store were made using the Dole Moisture meter. Grain weight loss was measured using the count and weigh method (Boxall 1986) insect densities per kg of whole cobs were then calculated.

Data on numbers of *P. truncatus* and *S. zeamais* were transformed by log (x + 1) and those on percentage grain weight loss were arc-sine transformed before analyses using a factorial ANOVA (a = 0.05)

Distribution of *P. truncatus* and *S. zeamais* among maize cobs

In September 1994, four grain stores were constructed at the IITA station in Cotonou, Benin, similar to those described above and using *P. truncatus* susceptible maize variety, YZSR-W with the objective of observing any association between *P. truncatus* and *S. zeamais* on the cob level. The experiment started in October 1994 and ended in May 1994. Four cobs per vertical layer (surface, middle and inner) were collected once every four weeks for eight sampling occasions. Cobs were shelled and sieved to remove adult insects, while the grain from each cob was placed separately in one litre Kilner jars covered with a fine wire mesh for adequate ventilation. Each jar was sieved every seven days for four weeks. The total numbers of *P. truncatus* and *S. zeamais* from each jar (= cob) found over four weeks were graphed to observe trends in insect population distribution and density

Interactions between *P. truncatus* and *S. zeamais* larvae in maize grains under different relative humidities

Experiments were conducted in small plastic boxes (24.5 cm long, 24.5 cm wide and 24.5 cm high) placed in a CTH chamber under a 12:12 h photo period, at 30 ± 10°C. Different relative humidities, 40 ± 5%, 70 ± 5%, and 90 ± 5% were established using saturated solutions of $MgCl_2$, NaCl and KCL, respectively (Winston and Bates 1960). Holes 5 mm deep were drilled into grains of the white maize variety TZSR-W which had been disinfested at -20°C for two weeks and moisture equilibrated at 30°C and 75% r/h for another two weeks. For each r/h regime, grains were artificially infested with a single one-day-old first instar larvae of *S. zeamais* (Urrelo and Wright 1989). After two days, varying densities (0, 1, 2, 4 and 8 individuals) of three-day-old *P. truncatus* first instar larvae (obtained following oviposition in artificial 'biscuits' of maize flour and water (Adda, C., personal communication) were placed in the kernels. An additional treatment consisted of *P. truncatus* larvae raised singly. *P. truncatus* and *S. zeamais* laevae were placed in separate holes in each kernel and the holes of *P. truncatus* were then filled with fine maize flour and plugged with a thin flour paste to prevent larvae from escaping. Kernels were placed individually in plastic cups measuring 2.5 x 2.5 x 1 cm and covered to prevent the adults from escaping. One hundred and twenty kernels were assemble for each of the five *P. truncatus* clutch-size treatments in each of the three r/h regime treatmentts.

Beginnning from Day 2 after artificial infestation of kernels with *P. truncatus* larvae, six kernels from each treatment were dissected at 2-day intervals and insect numbers, weights, sex, feeding site and stage of development (determined using head capsule widths (Subramanyan et al. 1985; Sharifi and Mills 1971) were recorded. The experiment was terminated after 40 days or when an adults of either *P. truncatus* or *S. zeamais* had emerged. The sex of *P. truncatus* adults was determined using the method of Shires and McCarthy (1976) and for *S. zeamais* using the method of Halstead (1963).

In another set of experiments similar to the above, larvae of *S. zeamais* were introduced into kernels one or two weeks before *P. truncatus*, or *S. zeamais* larvae introduced one week before those of *P. trunncatus*. Larval developmental rate and survival were recorded. Results of mean number of individuals in a kernel were plotted against days of kernel dissections.

Development of *T. nigrescens* under different humidity regimes

Thirty newly hatched *Y. nigrescens* larvae were placed individually in small glass vials (2 cm side and 6 cm high) containing 3 g of maize flour (variety TZB-SR-SE) and kept in CTH chambers at 30°C and at 40%, 70% and 90% r/h (maintained using saturated salt solutions as above). Larvae were provided an excess of *P. truncatus* first instar larvae and observed daily until emergence from the pupal chamber. *T. nigrescens* larvae were weighed every four days after hatching until the construction of the pupal chamber. Emerging larvae and adults were weighed on a high precision Mettler UM3 balance.

The effects of relative humidity on larval developmental and growth rates were evaluated using a factorial ANOVA, and pair wise comparisons of treatment means were evaluated using Scheff's post-hoc test (a = 0.05).

Results and discussion

Population dynamics studies of *P. truncatus* and *S. zeamais* in maize stores

Four pests commonly found during the storage periods were: *S. zeamais*, *P. truncatus*, Cathartus quadricollis (Cololeopetra: Silvanidae) and Carpophilus spp. (Coleoptera: Nitidulidae). The latter two were less prevalent and believed to contribute little to losses, and hence will not be discussed further here. *P. truncatus* numbers were very low in all treatments compared to *S. zeamais.* for the first half of the storage season (Figures 1a, b). *P. truncatus* densities increased greatly after the fifth sampling occasion and grain stores stocked with the local variety, Abutia, produced the greatest density. *P. truncatus* densities were found to be significantly higher in Abutia from the third sampling occasion onward (Table 1). Across all varieties, initial numbers of *S. zeamais* were higher than those recorded for *P. truncatus.* (Figure 1b). *S. zeamais* density recorded in the first three sampling occasions increased sharply, then remained stable at 200 to 400 insects per kg for the rest of the experiment. No significant differences in *S. zeamais* numbers were found with respect to variety (Table 2). The rapid increase in *S. zeamais* density at the beginning of the season may have been partly due to a high field infestation whereas the levelling-off period beginning on sampling occasion 4 could be due to substrate degradation or to some interaction with the increasing density of *P. truncatus. S. zeamais* might also have been emigrating from stores in response to environmental cues (yet to be identified). *S. zeamais* density was less variable within and among stores than *P. truncatus* throughout the storage period. In stores stocked during the short season, *S. zeamais* density increased throughout the period during which the density in those filled during the long season had levelled off.

Table 1 Numbers of *P. truncatus* recorded on cobs of 3 maize varieties stored in 'cribs' during the long season (October 1994 to May 1995) at Kpeve, Volta Region, Ghana

Sampling occasion	Mean number of *P. truncatus*[1]			F-ratio
	Abuita	Abeleehi	Dzolokpuita	
Oct. 1994	0.57	0.17	-	2.8
Nov. 1994	1.05	0.46	-	2.45
Dec. 1994	0.93 a	-	-	7.23
Jan. 1995	3.93 a	0.12	0.04	11.43
Feb. 1995	28.98 a	4.64	0.16	7.11
Mar. 1995	24.62 a	5.13	1.74	7.3
Apr. 1995	109.33 a	15.38	6.48	5.89
May. 1995	131.14 a	3.73	16.92	10.84

1; Means followed by a letter within a row are significantly different ($p<0.05$) (Scheff test).
After analysis of variance. Insect numbers determined from 3 pooled 26-cob samples per crib. Each value is a mean of 4 cribs.

Figure 1 Counts (+ S.E.) of major primary pests and percentage weight loss (+ S.E.) on one improved and two local maize varieties (stored from September 1994 to May 1995) (LS) and on one local variety (stored from January 1995 to June 1995) (SS) at Kpeve, Volta Region, Ghana. (A) Average density of *P. truncatus* per variety (B) Average density of *S. zeamais* per variety (C) Percentage grain weight loss calculated using the count and weigh method on six 1000-grain samples taken from 3 pooled 26-cob samples per crib. Each data point is a mean of 4 'cribs' + 1 S.E.

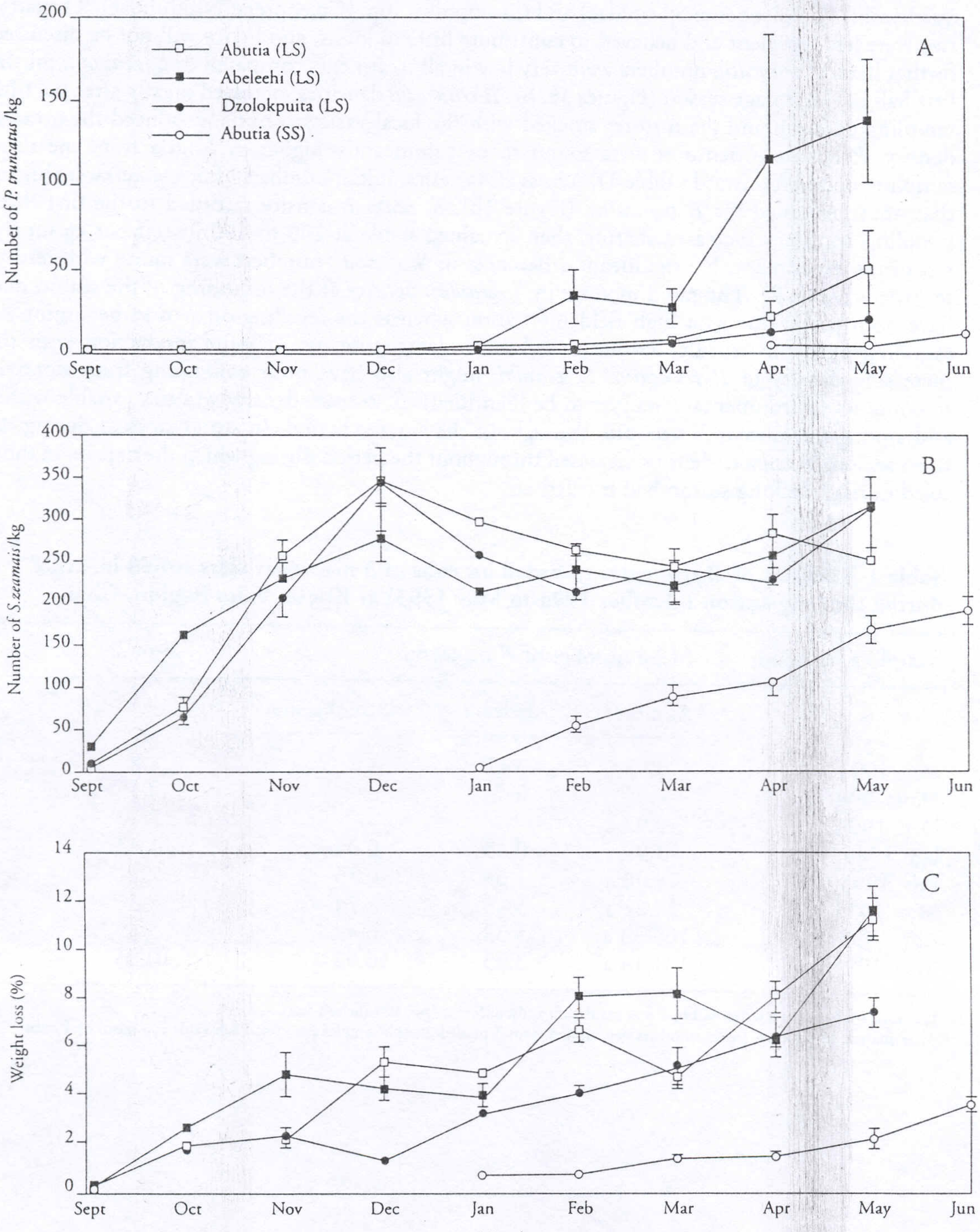


Table 2 Numbers of *S. zeamais* recorded on cobs of 3 maize varieties stored in 'cribs' during the long season (October 1994 to May 1995) at Kpeve, Volta Region, Ghana

Sampling occasion	Mean number of *S. zeamais*[1]			F-ratio
	Abutia	Abeleehi	Dzolokpuita	
Oct. 1994	169.30a	81.79	69.01	17.86
Nov. 1994	232.50	259.74	212.23	0.78
Dec. 1994	281.69	349.03	348.47	1.61
Jan. 1995	217.24	297.38	251.68	1.63
Feb. 1995	242.32	263.28	213.32	0.76
Mar. 1995	226.19	243.45	242.52	0.12
Apr. 1995	255.21	277.80	231.43	0.81
May. 1995	303.99	250.84	313.49	1.41

1; Means followed by a letter within a row are significantly different ($P<0.05$) (Scheff test) after analysis of variance. Insect numbers determined from 3 pooled 26-cob samples per crib. Each value is a mean of 4 cribs.

Differences in grain weight loss observed among varieties (Figure 1c and Table 3) were not consistent and this inconsistency was probably due, at least in part, to sampling technique. Because only one section of a store was sampled at each occasion, any spatial heterogeneity (e.g. one side experiencing higher losses than another) in grain loss within a given store would be reflected in the treatment means. At the end of the season, Dzolokpuita was found to have a significantly lower grain loss score than the other two varieties and it had the lowest score in seven of the eight sampling occasions. Comparisons of losses in Abutia between long and short season storage were made using t-tests within a sampling occasion (rather than within date) and revealed significant differences in four out of five sampling occasions (Table 4).

Distribution of *P. truncatus* and *S. zeamais* among maize cobs

Sampling on a cob-by-cob basis may provide more insight into the nature of inter-species (and intra-species) density-dependent interaction than data on average densities over pooled samples of cobs. Rearing-out data, in which cobs incubated for about four weeks, to all insects developing within the grain to emerge, provide information on competition for oviposition sites, or facilitation of cob attack by one species with respect to another. Rearing-out data plotting numbers of *S. zeamais* against numbers of *P. truncatus* on a cob-by-cob basis for a highly susceptible improved variety show differences in insect density and distribution over time (Figure 2).

Generally, both *S. zeamais* and *P. truncatus* populations aggregate on cobs, but are not necessarily consistently associated, nor occurring at uniform average densities. Sampling Occasion 1 suggests that initial colonisation of *P. truncatus* is scattered. But from Sampling Occasion 2 onward, this trend is clearer: *P. truncatus* appears at a much lower overall density earlier in the season. This density is, however, restricted to a few cobs. After Sampling Occasion 5, *S. zeamais* density decreases and that of *P. truncatus* increases. By Sampling Occasion 7, *P. truncatus* is found on most cobs and on some cobs in very high numbers (>200 insects). These results conform with findings described above in which *S. zeamais* density was found to be often higher than *P. truncatus* early in the season. The increasing density of *P. truncatus* observed suggests a superior competitive ability of this insect with increasing duration of storage. Substrate degradation is also believed to contribute to the greater reproductive success of *P. truncatus* since under this condition the insect is able to out compete *S. zeamais* by developing in the frass produced by tunnelling adults. It is thought that *P. truncatus* communities may be structured by semiochemicals (pheromones, kairomones and allomones) in host selection and colonisation, perhaps more so than *S. zeamais*.

Figure 2 Distribution of *P. truncatus* and *S. zeamais* on cobs of the maize variety TZSR-W after storage for eight months

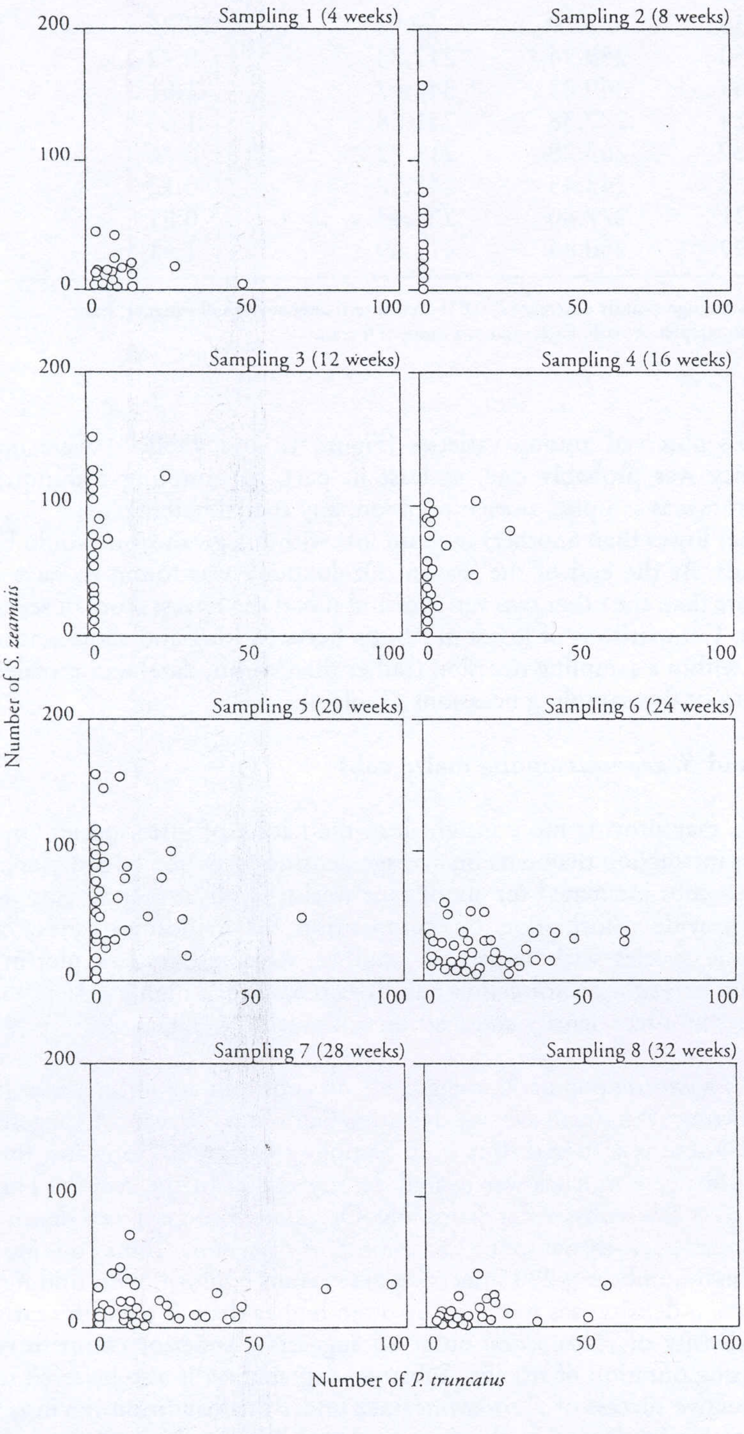


Table 3 Percentage weight loss suffered by 3 maize varieties stored in 'cribs' during the long season (October 1994 to May 1995) at Kpeve, Volta Region, Ghana

Sampling occasion	Mean of percentage grain weight loss[1]			F-ratio
	Abutia	Abeleehi	Dzolokpuita	
Oct. 1994	2.61b	1.87ab	1.56a	4.25
Nov. 1994	4.82a	2.31a	2.21a	3.19
Dec. 1994	4.24b	5.29b	1.76a	11.36
Jan. 1995	3.92a	4.62a	3.27a	2.47
Feb. 1995	8.18b	6.33ab	4.12a	9.63
Mar. 1995	8.16b	4.47a	5.23ab	3.80
Apr. 1995	6.26a	7.97a	6.13a	1.99
May. 1995	11.25b	11.19b	7.43a	5.03

1; Means followed by the same letter within a row are not significantly different from each other (P>0.05) (Scheff test) after analysis of variance. Percentage grain weight loss calculated using the count and weigh method on six 1000-grain replicates, taken from 3 pooled 26-cob samples per crib.

Table 4 Comparison of losses suffered by the local maize variety Abutial for two seasons at Kpeve, Volta Region, Ghana

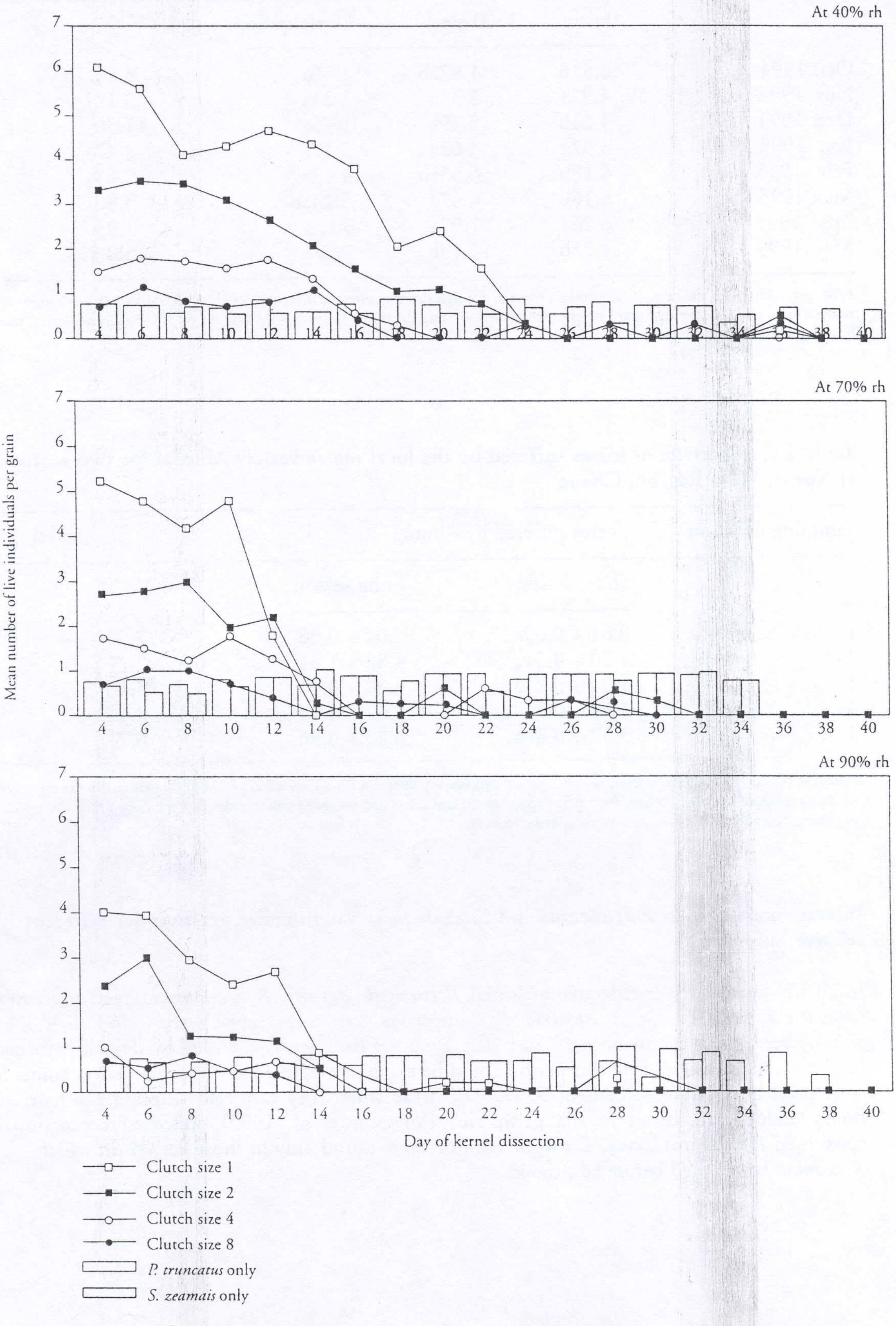
Sampling occasion	Losses suffered by Abutia[1]		t-Test
	Short season	Long season	
1	0.61 + 0.09a	2.62 + 0.06	17.91
2	1.20 + 0.24a	4.82 + 1.31	2.71
3	1.24 + 0.21a	4.24 + 0.51	5.46
4	1.97 + 0.61	3.92 + 0.52	2.44
5	3.37 + 0.45a	8.09 + 0.88	4.77

1; Means (+ S.E.) followed by a letter within row are significantly different from each other (P<0.05) (Scheff test) by t- test. Each value is a mean of 4 'cribs' + 1 S.E. Percentage grain weight loss calculated using the count and weigh method on six 1000-grain replicates, taken from 3 pooled 26-cob samples per crib.

Interactions between *P. truncatus* and *S. zeamais* larvae in maize grain under different relative humidities

In all r/h treatments, irrespective of initial *P. truncatus* density, *S. zeamais* emerged most often from the kernels (Figure 3). At 40% r/h, almost no *P. truncatus* larvae were found alive in any clutch sizes by day 26. At both 70 and 90% r/h all *P. truncatus* larvae died by day 16. Mortality in *P. truncatus* larvae during this period could be explained by the fact that this period coincided with third instar development of *S. zeamais* larvae when they tunneled through the hard and floury endosperm tissues to the germ area (Vowotor et al. 1995), killed and occasionally consumed *P. truncatus* larvae. *P. truncatus* adults were found only in those kernels in which *S. zeamais* larvae died before adulthood.

Figure 3 Inter-specific competition between *P. truncatus* and *S. zeamais* larvae at three relative humidities



The aggressive behaviour of *S. zeamais* larvae has been well documented (Sharifi and Mills 1971), and helps explain these results as well as those from experiments on the timing of infestation, in which *S. zeamais* almost always killed any *P. truncatus* larvae in the kernel, regardless of the treatment. The relatively low survival of *P. truncatus* larvae 90% r/h, compared to 40 and 70% r/h, could be explained by the fact that kernels maintained at this r/h became mouldy. At 40% r/h, *P. truncatus* apparently experienced faster development (34 days) and lower mortality as did *S. zeamais* at 90% r/h (32 days), suggesting that grain with a lower moisture content may be a niche for which *P. truncatus* is better suited.

Development of *T. nigrescens* under different humidity regimes

Relative humidity significantly affected developmental rates of *T. nigrescens* at all developmental stages, and overall developmental time was significantly shorter at 70% (23.5 days) compared to the other two humidity regimes (27 days for 40% and 28 days for 90%). The larval instars developed significantly faster at 70% than at 40% r/h. Mean larval and adult weights were also higher at 70% (2.11 mg) than at 40% (1.41 mg) or 90% r/h (1.98 mg). Its more rapid development and growth at 70% r/h compared to either 40% or 90% supports the idea that *T. nigrescens* and its prey, *P. truncatus*, share similar humidity optima.

This information can help identify conditions conducive to biological control and provide insight into the effects of different pest management strategies on insect population dynamics. Work on prey acceptability (unpublished data) has also shown that *T. nigrescens* can grow and develop with *S. zeamais* as a food source as rapidly as with *P. truncatus*. However, further studies are needed to determine the effect of the presence of *T. nigrescens* on the interaction between *S. zeamais* and *P. truncatus* and on grain store ecology as a whole.

Our work has been directed towards understanding the primary biotic and abiotic effects on insect population dynamics in West African maize stores. An understanding of the population dynamics of *P. truncatus* is especially important in developing strategies for managing this insect combining host plant resistance and biological control for use by small-scale farmers. The use of host plant resistance can have a drastic impact on *P. truncatus* populations. This technique could maintain constant and uniform suppressive pressure on each pest generation, leading to an accumulative impact which could markedly reduce the pest population during a season and over several years.

Sustained suppression without incurring abnormal environmental hazards, even when suppression is at a low level for each generation, may in a few years relegate the pest status of *P. truncatus* to one of less economic importance. Biological control techniques may also have an important role to play in the control of *P. truncatus*. There is evidence that *P. truncatus* is mainly a highly mobile forest pest coming that is only secondary, to maize stores (Nang'ayo et al. 1993) so that *T. nigrescens* may be expected to seek out the pest in its primary habitats thereby reducing the pressure of infestation on maize stores and complementing the role of host plant resistance. Host plant resistance and biological control, acting in concert, may provide density-independent mortality in times of low pest density and dynamic density-dependent mortality in times of pest increase (Bergman and Tingey 1979). The pest population development trajectory can be diminished even with low levels of plant resistance, providing a relative advantage to biological control agents (Starks and Berry 1976; van Emden 1966).

Once the effects of host plant resistance and biological control on the population dynamics of *P. truncatus* can be identified and quantified, they are incorporated in a systems model. Using the model, it could be possible to determine how the pest interacts with the abiotic environment (climate, weather, soil type, etc) and the biotic environment (the host, natural enemies, competing species, etc.) and then assess the relative importance of these factors in a wide range of climatic regimes. For example, the relationship between *P. truncatus* and *T. nigrescens* which may be affected by humidity may also be influenced by differences in susceptibility of maize varieties to *P. truncatus* attack.

It should also be possible to examine the combined effects of rate-dependent processes and make predictions (using climatic data) with regards to particular maize varieties and by realistically reflecting biological processes affecting pest population build-up, it should be possible to estimate losses expected in particular situations. These projections can then be used to guide and optimise management decisions such as when to harvest, whether to dehusk the maize and when to shell and/or sell and under what circumstances. With this information, it should be possible to avoid the use of insecticides during the initial drying and storage phase thereby taking advantage of any natural enemy activity that may be present. There is, therefore, a continuing need for work on the basic ecology and life history of the insect in order to develop an environmentally and economically sound pest management strategy.

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