Biological control in the context of an integrated management strategy for the larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) and associated storage pests

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Abstract

In Africa, the introduced larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) has received much attention as a potential target for classical biological control. The predator *Teretriosoma nigrescens* Lewis (Col.: Histeridae) is established and spreading in Bénin, following its release in neighbouring Togo. However, results of population dynamics studies at two contrasting sites in the larger grain borer's area of origin suggest that this predator is not capable of preventing destructive population increase of the target pest in maize stores. On the other hand, the results did indicate that various inter-specific and intra-specific interactions are important in determining the prevalence and destructiveness of the primary pest species. For instance, *Sitotroga cerealella* Olivier (Lep.: Gelechiidae) and *Sitophilus zeamais* Motschulsky (Col.: Curculionidae) were attacked by the pteromalid parasitoids *Pteromalus cerealellae* (Walker) and *Anisopteromalus calandrae*, (Howard) at the study sites in Mexico and Honduras, respectively. In Mexico, the impact of these and other cosmopolitan generalist parasitoids such as *Choetospila elegans* Westwood and *Lariophagus distinguendus* (Forster) (all Hymenoptera: Pteromalidae) on larger grain borer is being investigated in relation to the composition of the pest complex at different sites and the preference behaviour of the parasitoids. An intensive effort is now under way to quantify and understand the relative importance of population regulation processes within stores as compared with migration and colonisation behaviour in determining pest status. Such an understanding will provide the basis for a sound integrated control strategy.

Introduction

The accidental introduction of the larger grain borer, *Prostephanus truncatus* (Horn) (Col.: Bostrichidae), from its area of origin in Mexico and Central America (Wright 1984), has resulted in destructive outbreaks of the pest in rural maize stores in Africa (Hodges 1986). In Tanzania, dry weight losses of more than 30% over a short storage season have been recorded locally (Hodges et al. 1983; Keil 1988), although extensive surveys estimated losses at a more modest 9% overall (Hodges et al. 1983). Losses in Togo, following a second introduction of *P. truncatus*, were estimated to have risen from 7% to 30% (Pantenius 1987, 1988).

As a recently introduced outbreak pest, ostensibly causing few problems in its area of origin, larger grain borer appeared to be a prime candidate for classical biological control, by introduction of co-adapted natural enemies. Comparative studies carried out in Costa Rica (Böye 1988), indicating weight losses of 5 to 13% and some natural enemy activity, seemed to lend credence to this possibility (Boeye et al. 1988; Laborius et al. 1989). However, a reassessment of the literature (Markham et al. 1991) especially from Mexico, suggests that larger grain borer can also be highly destructive in its area of origin and that the impression that the pest is not important there is misleading, perhaps resulting from previous neglect of 'campesino' farming systems by researchers in Latin America and inaccessibility of the Spanish-language literature to researchers outside the region. Even the internationally-distributed literature details instances of severe larger grain borer damage in the Neotropics, in particular in Honduras (Hoppe 1986) and Nicaragua (Giles 1984). Indeed, observations reported in the latter publication provided the stimulus for an earlier international research effort, prior to the outbreaks in Africa, intended to evaluate the potential range and status of what was even then recognised as a highly destructive pest (Bell and Watters 1982; Shires 1977; Howard 1983).

These provisos notwithstanding, a major international effort was launched to develop biological control methods for the larger grain borer. These efforts, which centred on the predator *Teretriosoma nigrescens* Lewis (Coleoptera, Histeridae) and recently culminated in the release of this species in three African countries, are reviewed elsewhere (Markham et al., these proceedings). Attempts to monitor the impact of the releases in Togo have been severely impeded by political events in that country. However, with the natural spread of the predator into the neighbouring country of Bénin, its progress can now be monitored there. Preliminary results of this study are reported.

Previously, however, concerns about the possible inadequacies of the predator *T. nigrescens* provided the stimulus for a number of studies directed towards achieving a better understanding of the ecology, population regulation mechanisms and pest status of the larger grain borer in its area of origin. The studies were carried out with the objectives of identifying complementary strategies to improve any control achieved by *T. nigrescens* in Africa, and of suggesting integrated control strategies to limit continuing destructive pest outbreaks in Mexico and Central America. Some aspects of these studies are reported and discussed in terms of their potential for incorporation with the use of *T. nigrescens*.

Materials and Methods

Monitoring the establishment of *T. nigrescens* in West Africa

First releases of *T. nigrescens* were made at sites in southern Togo during 1991 and 1992 by staff of the national Service de Protection des Végétaux (SPV) and the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) (J. Richter and P. Mutlu, pers. comm.). Additional large releases were then made along a north-south axis of the entire country in 1993

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(A. Biliwa, pers. comm.). A small release of approximately 750 individuals was also made at a site in neighbouring Bénin in 1992, by the SPV of that country.

A program of regular trapping, established by our research group in Bénin initially to monitor the seasonal incidence and geographical spread of *P. truncatus*, was intensified, with particular emphasis on surveys in Mono Province bordering southern Togo, to monitor the spread of the predator. The surveys used sticky flight traps (Pherocon II ®, Trécé Inc., Salinas, California, USA) baited with a two-component synthetic aggregation pheromone of *P. truncatus* (AgriSense-BCS, Pontypridd, U.K.), previously developed by the Natural Resources Institute (NRI) (Dendy et al. 1989) and successfully used to trap this species and its predator in a variety of habitats in Yucatan, Mexico (Rees et al. 1990).

Traps were hung in trees along roads and in villages, spread north–south along nine zones, each approximately 5–8 km wide, parallel to the Togo–Bénin border. For logistical reasons, the number of traps and trap locations varied slightly between three surveys: a total of 37 traps were placed on the first occasion, 38 on the second and 39 on the third. Traps were changed weekly and the captured insects (*P. truncatus* and *T. nigrescens*) counted separately for a 9-week period in October to December 1992, for a 4-week period in May 1993 and another 4-week period in November 1993.

Population dynamics studies in Mexico and Honduras

Adult insect numbers, emergences and losses were monitored for a single storage season in three experimental stores at Chilcuautla, Hidalgo State, Mexico, and for two successive seasons in three bins in a store at El Zamorano, Honduras. Chilcuautla is on the central plateau of Mexico at an altitude of 1880 m. El Zamorano is at 800 m in an inland valley. Stores followed common local designs, using readily available materials. Those at Chilcuautla were open ‘cribs’ with a timber frame and walls of ‘bamboo’ (*carrizo*) in which cobs were stored without husks. The store at El Zamorano was a ‘troja’, with wooden floor and walls, divided internally by timber and wire sections into separate bins; the cobs were stored with husks intact. The stores were further subdivided with ‘bamboo’ (Chilcuautla) or light wood and wire partitions (El Zamorano) to enable stratified random sampling from the entire grain bulk throughout the storage season. Subdivisons were allocated randomly to sampling occasions and on each occasion one section from each of the three stores was sampled. At Chilcuautla, 20 cobs were taken from the top, middle and bottom of each subdivision (total 60, from each of three stores); at El Zamorano, 10 cobs were selected individually at random from three levels (total 30, from each of three bins). Maize (a local ‘criollo’ variety in Mexico, the improved variety H-27 in Honduras) was grown on nearby fields and field-dried following local practice. The maize at Chilcuautla was harvested and stored in October 1989 at a moisture content of 16%. That at El Zamorano was harvested during the first week of March 1990 at a moisture content of 13% and for the second season during the last week of January 1991 at a moisture content of 14%. The sampling interval was two weeks at Chilcuautla and three weeks at El Zamorano; sampling was continued for 40 weeks at the former site and 42 weeks and 36 weeks in successive years at the latter.

Sampling was carried out in the early morning. Cobs were placed rapidly into plastic bags and carried back to the laboratory for immediate processing. For each sample this consisted of careful sieving to remove all adult insects for subsequent identification and counting; a pooled subsample of 500 g of grain was retained for rearing out of primary pests and parasitoids, collections and counts being made after 7, 14, 21 and 28 days; a 10 g subsample was taken for moisture content determination; and an estimate of dry weight loss was made by a count-and-weigh method on a 1000 grain subsample. Methodology is given in more detail in Rios (1991) and Novillo (1991).

Parasitoid studies

Studies at Chilcuautla, Mexico, were resumed during the 1992–93 storage season with the specific objective of assessing the impact of parasitism on primary pest populations. A second study site, at Zacatepec, Morelos State, was also added. At each, three experimental cribs were set up, with a fourth store of identical maize to act as a reserve to provide cobs for assessing parasitism. Untreated maize of local varieties was purchased from farmers at or near each study site, dehusked and loaded into the cribs in December 1992; samples were taken at 2-month intervals until October 1993. A single vertical wire mesh cylinder, built into the centre of each crib at loading, provided a site where cobs, previously infested in the laboratory with known densities of the preferred stage of hosts, could be exposed in the crib at intervals during the storage season, and subsequently reared out, so as to provide estimates of the rate of parasitism. In addition, on each sampling occasion, 10 cobs per store were taken from points spread out over the remaining surface of the store (six from the surface, four from a depth of approximately 40 cm). In the laboratory, adult insects were removed, identified and counted; the shelled grain from each cob was then incubated separately in a controlled temperature room and scored daily for emergence of primary pests and parasitoids.

Results and Discussion

Establishment and spread of *T. nigrescens* in West Africa

During the first survey, in October–December 1992, early in the dry season, only a single *T. nigrescens* was captured, in the zone nearest the Togolese border. Six months later, during the rainy season, *T. nigrescens* was captured in all nine zones, representing a nominal spread of approximately 60–70 km, although the highest mean rate of capture (34.9 individuals/trap/week) was still in the zone nearest the border. After a further six months, once more in the early dry season, captures were distributed across all zones, with no major differences between average captures in each zone.

The distribution of *P. truncatus* captures also seemed to change over the three surveys. In the first survey the highest mean captures were in zone six (approximately 40 km from the Togo border), with lower numbers in the three zones nearest the border and zones seven and nine. In both the second and third surveys, mean captures tended to increase from the first to ninth zones. It is not clear to what extent these differences may reflect genuine changes in insect distribution, or a combination of seasonal effects and location effects, or even an artefact due to the smaller numbers of traps in the zones further from the border. Continuing analysis of insect abundance in samples taken from stores in the course of these surveys should shed further light on this issue.

Regular trapping carried out on a weekly basis throughout the year at a smaller number of sites (11) in Mono Province indicated a strong seasonal pattern to captures of both pest and predator. Captures were in general higher during the wet season and lower during the dry, but a close correlation with rainfall within a particular trapping interval, as reported from Honduras (Novillo 1991), was not observed here. In general, weekly captures of *P. truncatus* and *T. nigrescens* were correlated with one another. This provides further circumstantial evidence of the close adaptation of this predator to the target pest, but is perhaps surprising in view of the different roles (sexual attraction/aggregation and prey location) which the attractant plays in the two species.

Pest population dynamics and losses in Mexico and Central America

At Chilcuautla, the high altitude site in Mexico, all three major primary pests, *P. truncatus*, *S. zeamais* and *Sitotroga cerealella* Olivier (Lep.: Gelechiidae), occurred together in significant numbers in the experimental stores, both in the 1989–90 and 1992–93 storage seasons. Adult insect counts for the earlier study, are given in Figure 1a (for full details see Rios 1991). Pest population build-up was scarcely detectable during the cold winter months, corresponding to the first 18 weeks of storage. Thereafter *P. truncatus* increased sharply, becoming by far the most abundant species and, from the close correlation with weight loss data (Fig. 1b), apparently also the most destructive. *P. truncatus* also became the most abundant species in the stores at Zacatepec, the mid-altitude site in Mexico, during the 1992–93 season. After 10 months in store, the larger grain borer population had reached a density of approximately 2400 insect per kg of shelled grain, which is comparable with levels recorded in some trials in Africa.

Estimates of recruitment, based on emergences, give a somewhat different view of population dynamics than adult counts, especially in relation to *S. cerealella*. This species flies much more readily than the Coleoptera pests and therefore tends to be under-represented in the adult counts. Emergence figures for the 1992–93 season at Chilcuautla (when no attempt was made to assess adult *S. cerealella* numbers), show that *S. cerealella* was reproducing more rapidly than *P. truncatus* for the first six months in store. Similarly at Zacatepec, *S. cerealella* was more abundant in emergence samples than *P. truncatus* for the first two samples (i.e. after 2 and 4 months in store) and was more abundant than *S. zeamais* from the 2nd through 8th months, only being less abundant than the weevil in the last (October) sample.

Emergences of *S. zeamais* were less consistent than those of either of the other two primary pests. For instance, at Zacatepec in the sample corresponding to 6 months of storage, no recruitment of *S. zeamais* was detectable, though it increased sharply again in the last two samples. At Chilcuautla, emergences of this species declined over the first three sampling intervals, before increasing again at the end (see Figure 1). Further study is needed to investigate the extent to which these changes reflect sensitivity to unfavourable environmental conditions or responses to interspecific competition.

Results from the study in Honduras, which covered two successive storage seasons in the same structure, are presented in Figure 2. At this site *S. zeamais* increased ahead of *P. truncatus* in the first storage period, although the larger grain borer population was increasing rapidly in the final weeks of storage. In the 2nd year of the study, *S. zeamais* was the more common species only in the first two storage samples, corresponding to periods of 3 and 6 weeks in store. Thereafter, *P. truncatus* infestation increased rapidly, and, as at Chilcuautla, was closely correlated with the increase in grain weight loss (Fig. 2b), confirming the destructive potential of this pest. It

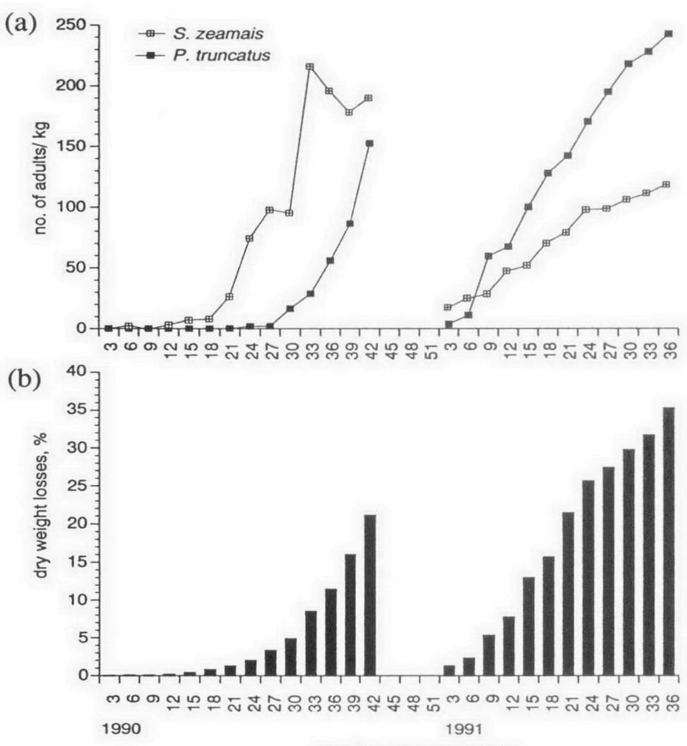

Fig. 1. Population dynamics of major primary pests and losses at Chilcuautla, Hidalgo State, Mexico. (a) Adult insect counts/kg of grain, dry weight basis (each based on three samples of 20 cobs from each of three stores, corrected for sample weight and grain moisture content). (b) Grain weight losses, dry weight (%), based on count and weigh method on 1000 grain samples from each of the 20 cob samples.

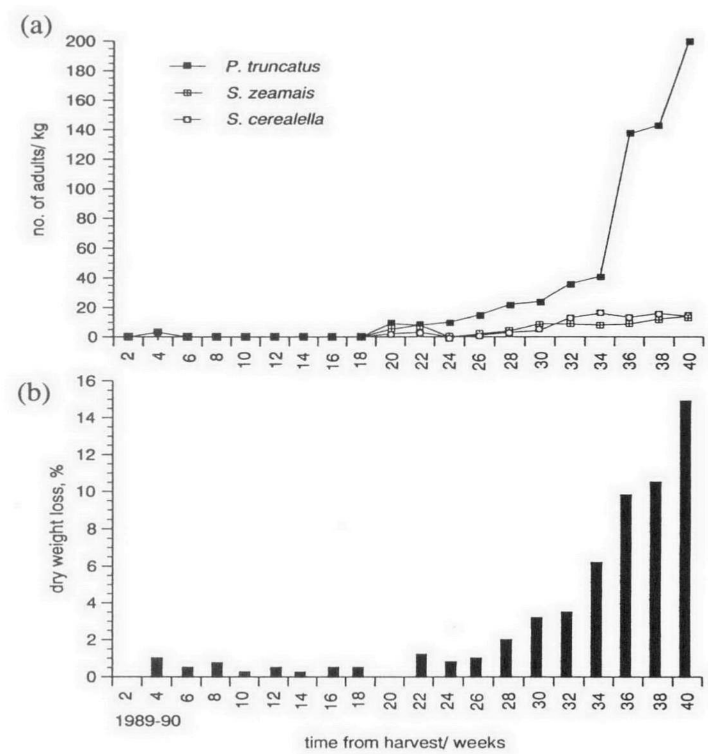

Fig. 2. Population dynamics of major primary pests and losses at El Zamorano, Honduras. (a) Adult insect counts/kg of grain, dry weight basis (each based on three samples of 10 cobs from each of three bins within a store, corrected for sample weight and grain moisture content). (b) Grain weight losses, dry weight (%), based on count and weigh method on 1000 grain samples from each of the 10 cob samples.

seems most likely that the rapid build-up of larger grain borer in the 2nd year resulted from colonisation of the newly-stored maize by individuals which had survived in the wooden structure of the store from the previous season. *S. cerealella* was not encountered in the maize stores at this study site (though it was recorded on other commodities stored nearby).

Parasitoid studies

The incidence of parasitoids at the three study sites appears to be quite different, although it should be noted that the different species of pteromalids were not routinely identified in the earlier (1989–91) studies. At both sites in Mexico, *Pteromalus cerealellae* (Walker) was the most abundant and consistently occurring parasitoid. *Anisopteromalus calandrae* (Ashmead), *Choetospila elegans* Westwood and *Lariophagus distinguendus* (Forster) were also recorded, though not in sufficient numbers to provide a clear picture of their incidence. *A. calandrae* appears to have been (on the basis of 'spot checks' of samples) the most abundant parasitoid at the Honduras study site.

The pattern of incidence of *P. cerealellae* at Chilcuautla provides very strong circumstantial evidence of this species' close association with *S. cerealella,* as reported in the earlier literature (Brower 1991). In the earlier Chilcuautla studies, the number of adult pteromalids sampled (at this site mainly *P. cerealellae*), increased in parallel with the *S. cerealella* population and then declined as the pest passed its maximum (Fig. 3a). A similar relationship is evident in the 1992–93 emergence samples from Zacatepec, though the pattern was less clear in this season at Chilcuautla (J. Hirabayashi, unpublished data). The same close association between *P. cerealellae* and *S. cerealella* is evident in the emergence data from these latter studies where the two species tended to be reared in large numbers from the same cobs. The form of the curves of adult counts from the earlier study at Chilcuautla seems to suggest that the parasitoid may be playing a role in the control of this pest, but this possibility needs to be investigated further in terms of other mortality factors, especially the impact of competition with *P. truncatus* and *S. zeamais*, and the influence of seasonal changes in climate and the state of the maize substrate. The more recent data from Mexico provides the opportunity (with daily counts of emergences from single cobs) to investigate the nature of this parasitoid's functional response and impact, but larger samples and more information on development times and preferred stages are needed before quantitative conclusions can be drawn.

At the site in Honduras, the pattern of incidence of pteromalids, here mostly *A. calandrae*, (Fig. 3b) suggests a close association with *S. zeamais*, although the correlation in their incidence was closer in the first 30 weeks of storage than thereafter. This is in line with previous accounts of the biology of *A. calandrae* (Cotton 1923; Ghani and Sweetman 1955) and consistent with the pattern of emergences from individual cobs (Novillo, unpublished data). In Figure 3b, emergences of *S. zeamais* and *P. truncatus* for the 1st week post-sampling are graphed with emergences of the parasite for the 2nd week. This is intended to give a closer estimation of the rate of parasitism, based on the known stage preference and development times of the parasitoid and host. On this basis, and assuming that the parasitoid attacked mainly *S. zeamais* (see below), the approximate rate of parasitism seems to have varied between 15 and 30% for much of the storage period. Further studies of mortality factors will be required to show whether this parasitoid contributes significantly to control of the maize weevil as has been previously suggested in the literature (Cline et al. 1985).

A principal objective of the ongoing studies in Mexico, namely the evaluation of the impact of parasitoid activity on *P. truncatus,* has not yet been realised. The methodology so far developed involves artificial infestation of cobs in the laboratory with *P. truncatus* eggs, rearing in the laboratory under optimum conditions, 'planting out' of the infested cobs into stores during the most susceptible larval stage of the pest, followed by rearing out once more in the laboratory. Three species of hymenopteran parasitoid have been reared from *P. truncatus* by this method, but only in very small numbers. Further refinement of the methodology is required, especially to check whether populations of host larvae established in cobs by artificial infestation with eggs are fully attractive to parasitoids and so provide a good estimate of the rate of parasitism that would be achieved on naturally infested cobs. If further study confirms that generalist pteromalids achieve only a low rate of parasitism on *P. truncatus*, this will run counter to previous optimistic evaluations of the potential of these natural enemies for biological control of the larger grain borer (Brower 1991). The preference behaviour of the most commonly occurring pteromalids in Mexico with respect to the three primary pests will be further investigated with a view to interpreting the incidence of parasitism observed.

Conclusion

The prospects for the predator *T. nigrescens* providing adequate control of *P. truncatus* in Africa are discussed elsewhere (Markham et al. these proceedings). At this stage the evidence for the likely effectiveness of this predator is equivocal and it will be difficult, for various reasons, to quantify its impact. With respect to evaluating the contribu-

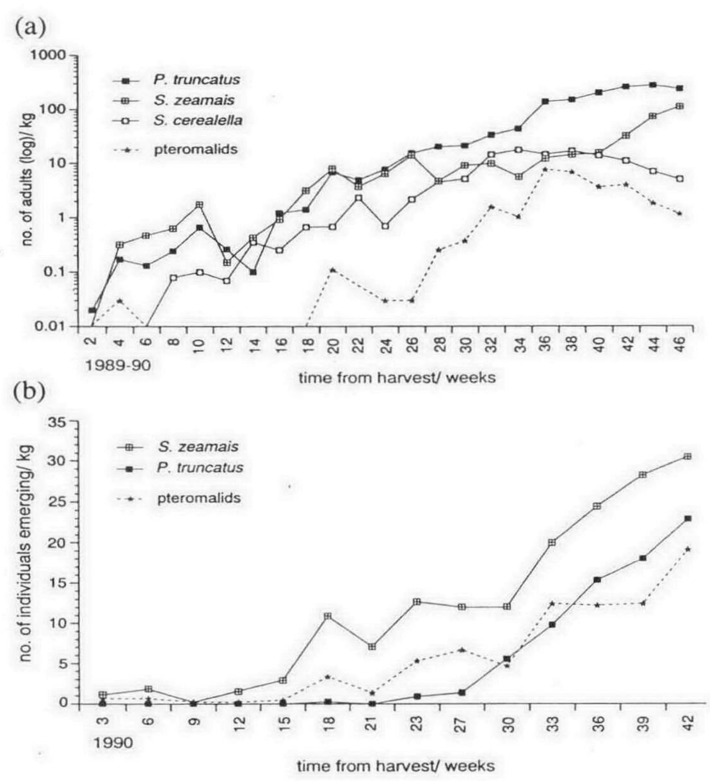

Fig. 3. Major primary pests and their pteromalid parasitoids. (a) Chilcuautla, Mexico. Data are adult insect counts/kg of grain (sampling as for Figure 1). (b) El Zamorano, Honduras. Data are insects emerging/kg grain for the period 1–7 days after sampling for pests and 8–14 days after sampling for parasitoids (based on 500 g samples derived from the pooled grain of 10 cobs, samples as for Figure 2).

tion to control which can be expected from pteromalid parasitoids in rural maize stores, further methodological work is clearly needed before definite answers can be provided. The limited evidence so far available suggests that the impact of parasitoids on *P. truncatus* may be less than that on the other major primary pests. The specific issue that must be addressed here is whether, and under what circumstances, natural enemies can provide enough control of storage pests during a limited period of crib drying to avoid the use of pesticides, given that these products are not in general very effective in crib stores (Hindmarsh et al. 1978).

One possible response to the dearth of clearly effective natural enemies of larger grain borer, is to intensify the search for additional species in the pest's area of origin. This approach is actively being pursued in our program. In one sense the prospects for finding new species are not good, given that the fauna of grain stores is already relatively well known. However, this avenue begins to look more promising in the light of recently-gained insights into the natural host plant associations of larger grain borer which appear to be with woody species, rather than cereals (Ramírez Martínez et al. 1991; Nang'ayo et al. 1993). Natural enemies are often attracted first by chemical cues from the host plant of a pest and therefore may well not readily find the pest on a 'new' host plant (such as maize in the present case). Host-plant- or environment-specific natural enemies would not make a direct contribution to control in stores but should help to reduce the pressure of infestation from natural habitats.

Whether or not additional natural enemies are eventually found, it seems evident that complementary, environmentally-sound strategies will be needed to provide adequate control of storage pests. We are looking at basic processes which affect the rates of pest build-up (and accumulated losses), such as the role of plant resistance mechanisms in reducing the susceptibility of the maize substrate and the importance of inter and intraspecies competition in determining pest dynamics in various situations. We are also investigating the basic host-finding behaviour of the insect, in terms of semiochemical responses to maize and other potential food sources, and how these may affect, qualitatively and quantitatively the incidence of larger grain borer in maize fields pre-harvest and the arrival of the pest in stores. Finally, we are investigating in larger-scale field studies, how farmer practices and environmental variables affect the process of colonisation of stored maize, and subsequent pest dynamics and losses in stores (see Borgemeister et al., these proceedings).

The overall objective is to move rapidly from investigations of biological processes to providing practical recommendations for the optimum use of ventilated stores to provide adequate, cost-effective drying and storage, while minimising losses to insects. In this context, basic studies of natural enemy activity are seen as part of the process of putting together a sound integrated control strategy, for these destructive pests of rural storage.

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