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**INTERSPECIFIC COMPETITIVE INTERACTIONS
BETWEEN THE LARGER GRAIN BORER
PROSTEPHANUS TRUNCATUS (HORN)
(COLEOPTERA: BOSTRICHIDAE) AND THE MAIZE
WEEVIL *SITOPHILUS ZEAMAI* MOTSCHULSKY
(COLEOPTERA: CURCULIONIDAE) IN MAIZE STORES**

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Interspecific competitive interactions between the larger grain borer *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) and the maize weevil *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae) in maize stores

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Abstract: Interspecific interactions between the larger grain borer *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) and the maize weevil *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae) were studied during two storage seasons: 1994-95 (a short-term) and 1995-96 storage (long-term) in maize stores, in Benin. Maize cobs were randomly sampled from stores in order to examine (1) colonisation patterns of *P. truncatus* and *S. zeamais*; (2) how each species influences distribution of the other; (3) other factors which may influence *P. truncatus* and *S. zeamais*. For both storage seasons, *P. truncatus* and *S. zeamais* populations were initially aggregated on few cobs, but not associated with each other. The degree and strength of association increased with each sampling occasion with respect to the Ochiai, Jaccard and Dice indices of association. *P. truncatus* was found on most cobs and on some cobs in very high numbers (>300 insects). Almost all cobs with *P. truncatus* contained at least a few *S. zeamais* individuals, but many cobs with *S. zeamais* contained no *P. truncatus*. By regressing Taylor's *b* coefficients of one species on the mean adult and reared-out densities of the other, aggregation of *S. zeamais* was found to have no significant correlation with mean density of adult *P. truncatus* and a weakly positive one with reared-out densities of *P. truncatus*. Aggregation of *P. truncatus* showed a negative relationship with mean and reared-out densities of *S. zeamais*. The same procedure with Lloyd's mean crowding index (m^*), the aggregation of *S. zeamais* also showed a similar relationship with mean and reared-out densities of *P. truncatus* as observed with Taylor's *b* coefficient. *P. truncatus* aggregation, however, was not found related to mean and reared-out *S. zeamais* density, contrary to results using Taylor's *b* coefficient. Preliminary analysis of each species' rate of reproduction, as measured by the ratio of F_1 adults with parent adults, showed a mutual negative relationship. Husk number and extension past ear, number of visible holes on the husk, density of earworms and other insect species within cobs were found to play a significant role in initial colonisation of cobs.

Key words: Colonisation, interspecific competition, maize, population dynamics, *Prostephanus truncatus*, *Sitophilus zeamais*, spatial distribution.

Introduction

Scientists over the years have held strongly different views about the importance and role of interspecific competition as a significant and consistent process in structuring communities, population dynamics and evolution among herbivores. Recently, Denno *et al.*, (1995) examined 193 pair-wise species interactions representing all major feeding guilds and provided information on the occurrence, frequency, symmetry, consequences, and mechanisms of competition. Interspecific competition occurred in 76% of the interactions, was often asymmetric, and was frequent in most guilds (sap feeders, wood and stem borers, seed and fruit feeders) except free-living mandibulate folivores. Phytophagous insects were more likely to compete if they were, for example, closely related, introduced, aggregative, or fed on discrete resources. Such characteristics appear to apply to the larger grain borer *Prostephanus truncatus* (Horn) (Col.: Bostrichidae), a highly destructive pest of farm-stored maize recently introduced into West Africa from Central America and Mexico, and the maize weevil *Sitophilus*

zeamais Motschulsky (Col.: Curculionidae), a cosmopolitan pest of stored maize. Competition between *P. truncatus* and *S. zeamais* in maize stores involves exploitation of a transient food supply (i.e. grains on the cob), transient in the sense that the store is emptied or the grain becomes unsuitable. There is evidence that both insect species congregate in response to aggregation pheromones produced by their colonising males (Hodges *et al.*, 1984, for *P. truncatus*; Walgenbach *et al.*, 1983, for *S. zeamais*).

Previous work examining competition between the two insects (Howard, 1983; Haubruge and Verstraeten, 1987; Giga and Canhão, 1993), have examined the interaction at the laboratory using shelled grains. A mechanism demonstrated in laboratory experiments does not necessarily play an important role in the field, even if it can be demonstrated in theory and in experiments excluding other variables (Sevenster and van Alphen, 1993). Schoener (1983), reviewing the topic of competition, and Kozar (1987) emphasized the importance of using field data gathered from wide geographical area when considering an analysis of competition. Crawley and Patrasudhi (1988) stated that the real role of competition cannot be properly judged because of its fortuitous occurrence in time and space unless sufficiently large samples are considered. This paper examines the role of competition in influencing abundance and distribution of the two insects in stores under field conditions. Specific aims are to examine: (1) colonisation patterns of *P. truncatus* and *S. zeamais*; (2) how each species influences distribution of the other; and (3) other factors which may influence the distribution of *P. truncatus* and *S. zeamais*.

Materials and Methods

Two field experiments: 1993-94 short-season and 1994-95 long season were carried out, each corresponding with the maize growing and storage pattern in the southern part of Benin.

1994-95 short season experiment

A short-storage season on-farm trial, was conducted at Dogbo in the Mono Province. The location for the study was chosen because of the importance of maize production and storage and also because of the high incidence of *P. truncatus* and *S. zeamais*. A popular short cycle downy mildew resistant variety, popularly known as DMR, was planted on 7 September, 1994 at the onset of rains on three plots. Each plot consisted of ten 11-metre long rows and spaced at 0.75m. Three seeds per hill were planted at 50cm spacing and plants thinned to two per hill after planting. An NPK (15-15-15) fertilizer treatment was applied 3 weeks after sowing, and no other chemical or insecticide were applied to the crop. The plants were harvested on December 19, 1994 when the crop was physiological mature. At harvest, 100 cobs were randomly selected in order to collect baseline data on the following: husk extension past ear, number of visible holes on the husk, number of husk leaves, number of earworm damage sites on dehusked cobs, grain moisture content, densities of *P. truncatus* and *S. zeamais* as well as other associated insect species. Each cob was placed separately in a 1-litre Kilner jar. The tops of the jars were covered with a fine wire mesh for ventilation. Each jar was examined every week for four weeks ('rearing-out') and the number of insects that emerged was recorded.

Six stores were built in two rows of three and stocked with the remaining harvested maize in December 1994. The stores used in the experiment were the circular 'awa' type, about 1.8 m in diameter and about 0.8m in height, consisting of a 2m x 2m split 'bamboo' platform supported by eight wooden legs on the exterior and one post in the centre. The structural wood was from *Tectona grandis* (Verbenaceae), and the roof was thatched with leaves of *Imperata cylindrica* (Gramineae). Galvanised wire mesh ('chicken wire') was attached from each leg to the central post, dividing the store into four equal vertical sections. Maize cobs were placed on the structure, with the husk on, to mimic the traditional stacking process, where 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, thoroughly sampled without affecting the rest of the store. One randomly selected section was sampled per store per monthly sampling occasion, and each section was only sampled once. After each sampling occasion, the section was 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, 16 cobs were randomly selected from each of the five subsections per store: top, bottom, 'surface', 'middle', and 'inner' zones to obtain data as in the baseline sampling procedure. These latter three zones were vertical zones, each of about 30 cm depth, as one moved from the exterior of the store to the interior. Ninety-six cobs were sampled per store from six stores for a total of 480 cobs per sampling occasion. Sampled cobs were placed immediately into paper bags and taken to the laboratory for analysis.

1995 - 96 long-season experiment

This experiment was carried out at the International Institute of Tropical Agriculture (IITA) substation, Cotonou, in the Atlantique Province. Four maize varieties were used: Benin Local Floury (BLF), DMR and Gbogbe (all 90-day varieties), and TZSR-W, a 120-day variety. BLF and Gbogbe (both local varieties) were obtained from farmers in the Mono Province, while DMR and TZSR-W (both improved varieties) were obtained from the germplasm collection of IITA. The varieties were selected to combine basic contrasting characteristics normally grown by farmers in Bénin. The varieties were planted on April 28, 1995, in a randomised complete block design with four replications. NPK (14-13-13) fertilizer treatment was applied 3 weeks after sowing. Agronomic practices such as inter- and intra-row spacing were same as those in the short-season experiment. Because of the differences in the maturity of the varieties and the storage structures used for this experiment, i.e. 'cribs' and awa for early and late harvest, respectively, two sets of harvests were carried out for the four varieties. For storage in cribs, the early-maturing varieties BLF, DMR and Gbogbe were harvested on September 4, 1996, and TZSR-W on October 2. For storage in awa, BLF, DMR and Gbogbe were harvested on October 2, and TZSR-W on October 30.

Sixteen stores, eight of the 'awa' type and eight 'cribs' were constructed and arranged in a four by four matrix with awa alternating with cribs. Distance between adjacent stores was 10 metres. For each store type, each variety was replicated two times. The structural design for the awa stores in this experiment was same as in the short-season experiment, except for the vertical sections which were divided into eight sections. Cribs (3 m high, 1 m dia.) were constructed according to specifications recommended by FAO (1985), where mean daily relative humidity ranged between 75 and 80%. The wood for the structural components was from *Fagara xanthonyloides* (Rutaceae), the walls were woven using stems of from *Mallous oppositifolius* (Euphorbiaceae), the floor and roof were formed from *Elaeis guineensis* (Palmae), and the roof was thatched with leaves of *Imperata cylindrica* (Gramineae). Cribs were divided into 8 equal vertical sections with chicken wire. In order to prevent rodent entry, all stores were fitted with rat guards. Sampling was carried out on each store from each random section and rebuilt with cobs from replacement stores as in the short-season experiment. Twenty cobs were obtained for baseline data collection. Data were obtained as described in the short-season experiment except that only five cobs were randomly selected from each of the three subsections per store: top, 'middle' and bottom zones, i.e. 15 cobs per store, giving a total of 240 cobs per sampling occasion.

Data analysis

Since the long-season experiment involved more sampling occasions than did the short-season experiment, analyses of long-term data were carried out only for the long-season. In order to observe trends in insect density and distribution so as to explain colonization patterns and competitive interactions between the two insects, the total numbers of *P. truncatus* and *S. zeamais* emerging from each jar (= cob) during each sampling occasion were recorded and graphed.

Presence-absence data of reared-out insect densities of the long season experiment was used to measure interspecific association since this method evaluates the extent to which requirements of the two species are similar (Southwood, 1984). This author notes that interspecific competition (and other factors) may lead to a 'misleading' lack of association if the measure is based on abundance. The Ochiai, Dice, and Jaccard indices (Ludwig and Reynolds, 1988) were used to measure the strength of the association. For these indices, +1 = complete positive association, -1 = complete negative association and 0 = no association.

In order to determine how each species influences distribution of the other, two aggregation indices, Taylor's b coefficient and the Lloyd's mean crowding index m^* of one species (pooled across subsections per store per sampling occasion) was regressed on the mean and reared-out adult densities of the other for the long season experiment. Examining only one index may not be reliable since m^* may provide biased estimates if the range in means is very large (Davis, 1994).

Taylor's power law states that the variance (s^2) of a population is proportional to a fractional power of the arithmetic mean m in the form:

$$s^2 = am^b$$

and therefore:

$$\log s^2 = \log a + b \log m$$

where the parameter a is a scaling factor related to sample size (Taylor, 1984) and the parameter b is a constant, an index of aggregation, dependent on the behaviour of the species or the environment. The slope b can be used to classify dispersion patterns as random ($b = 1$), aggregated ($b > 1$), or uniform ($b < 1$). Lloyd's mean crowding index (m^*) where $m^* = m + \{(s^2/m) - 1\}$ (Lloyd, 1967), is the mean number of other individuals per individual in the same quadrat (= cob). As an index, mean crowding is highly dependent upon both the degree of clumping and the population density.

In order to determine other factors which may be correlated with *P. truncatus* density within sampling occasion, density of adults obtained from the 'rearing out' was regressed on cob length, husk extension past the cob, number of holes in the husk, number of husk leaves, number of earworm damage sites on dehusked cobs, grain moisture content, and per cob densities of *S. zeamais* before rearing-out using the SYSTAT 5.0 (Wilkinson, 1992) stepwise multiple regression. The same procedure was used for *S. zeamais* rearing-out densities. A forward and backward stepwise multiple regression procedure was used and the predictors in the final models were cross-checked interactively. Since some of the predictors were highly correlated with one another, and there was the likelihood of constructing a highly multi-collinear final model which tend to have unstable regression coefficient estimates, 'tolerance' was set to a of 0.1 and a to enter and remove were both set to 0.05.

Results and Discussion

In phytophagous insects, host plant-related factors, natural enemies, physical factors, and intraspecific competition are thought to maintain herbivore densities at low levels where interspecific competition is rare (Denno *et al.*, 1995). A rural grain store, however, may be an exceptional case, because of its small size and isolation. Data on insect density from the rearing-out of single cobs provides information on competition for oviposition sites, or facilitation of cob attack by one species with respect to another. Densities of *P. truncatus* and *S. zeamais* for individual cobs were plotted on the same graph to observe how the association of the insects on the same cob changed over time (Fig. 1). Generally, *S. zeamais* and *P. truncatus* populations are aggregated on cobs, but not necessarily associated with each other, nor do they occur at uniform densities. At harvest, few *P. truncatus* were reared from the cobs. For the short season-experiment, *P. truncatus* remained aggregated onto few cobs, on sampling occasion 1, but as of sampling occasion 2, *P. truncatus* density increased more than *S. zeamais* density. By sampling occasion 4, *P. truncatus* was found on most cobs and on some cobs in very high numbers (>300 insects). Almost all cobs with *P. truncatus* contained at least a few *S. zeamais* individuals, but many cobs with *S. zeamais* contained no *P. truncatus*. Substrate degradation may contribute to the dynamics of the two insects.

Insect distribution for the long-season was similar to that observed for the short-season experiment (Figs 2 and 3). Irrespective of store type or maize variety used, sampling occasions 1 and 2 suggests that initial colonisation of *P. truncatus* is aggregated onto few cobs. From sampling occasion 3 to 5, densities of both insects increased with that of *P. truncatus* occasionally attaining densities above 150 insects. These densities were however, relatively

lower than those found during the short season experiment. The differences in density of *P. truncatus* at the two experimental sites could be due to the higher incidence of *P. truncatus* in this particular part of Benin, i.e. Mono Province, which borders Togo, the country where the insect was first reported in West Africa. A possible explanation for the higher *S. zeamais* densities is the use of cribs and awa for the long season experiment as opposed to only awa for the short season experiment. Cobs are harvested much earlier for awa stores, thus lowering the level of field infestation. The increasing density of *P. truncatus* in the middle of the storage season suggests that substrate degradation played at best a minor role in the reproductive success of *P. truncatus*, compared to *S. zeamais*, since larval *P. truncatus* is able to develop in the frass produced by tunneling adults (see Ayertey *et al.*, this volume). Densities of both insects decreased after sampling occasion 6, with that of *S. zeamais* decreasing relatively more than that of *P. truncatus*.

Using rearing-out data, *P. truncatus* and *S. zeamais* were found to be associated with each other, and the degree of association increased with the duration of storage (Fig. 3). The trend in association of the two insects as measured by the three indices for both store types was similar. Among the three indices, a closer relationship was found between the Ochiai and Dice indices. Generally, association increased sharply after sampling occasion 1, to its maximum value at sampling occasion 5 and leveled off by the end of the experiment. From these results it is not clear whether both species simply have similar environmental requirements, or one or both of the species has an affinity for the other.

By regressing Taylor's *b* coefficients of one species on the mean adult and reared-out densities of the other, aggregation of *S. zeamais* was found to have no significant correlation with mean density of *P. truncatus* ($r^2 = 0.04$, $P > 0.05$). However, with reared-out densities of *P. truncatus*, the relationship was weakly positive ($r^2 = 0.25$, $P < 0.05$) (Fig. 5). Aggregation of *P. truncatus* showed a strong negative relationship with mean and reared-out densities of *S. zeamais* ($r^2 = 0.42$ and 0.35 , $P < 0.05$, respectively) (Fig. 6). The rearing out of larvae is considered a better measure of distribution than adult density on the day of sampling, since not all insects recorded on cobs may not have been residents on that particular cob but rather were migrating to it during the process of sampling. In addition, the action of sieving grain and removing adults may disrupt the development of eggs and larvae in the grain.

Using Lloyd's mean crowding index (m^*), the aggregation of *S. zeamais* also showed a similar relationship with mean and reared-out densities of *P. truncatus* ($r^2 = 0.10$, $P > 0.05$; and 0.80 , $P < 0.05$, respectively) as observed with Taylor's *b* coefficient (Fig. 7). *P. truncatus* aggregation did not change with mean and reared-out *S. zeamais* density ($r^2 = 0.07$ and 0.11 , $P > 0.05$, respectively) (Fig. 8), contrary to what was observed using Taylor's *b* coefficient (Fig. 6). Although Taylor's Power law has been shown to fit data very well, it is an empirical model which lacks definite theoretical background. Lloyd's mean index (m^*) is considered easier to interpret ecologically since it is based on the assumption of mutual interference or competition among individuals (Davis, 1994).

Preliminary analysis of each species' rate of reproduction, as measured by the ratio of F_1 adults with parent adults, suggests that densities of one insect is negatively related with the other. Being a voracious borer on cobs, the tunneling activity of *P. truncatus* may degrade the substrate by adversely influencing oviposition sites, thus survival and development of *S. zeamais* within grains may be reduced. Larvae of *S. zeamais* are known to exhibit aggressive behaviour with conspecifics and other larvae developing within the grain. However, this would be limited to individual grains and for stores stacked with cobs having numerous grains, this internecine activity may not play an important role in the reduction of the rate of reproduction of *P. truncatus*. A possible reason for the reduction of the rate of reproduction of *P. truncatus* observed in the field trials may have been due to predation by the histerid, *Teretriosoma nigrescens* (Lewis) which is associated with *P. truncatus* and *S. zeamais* on damaged cobs. In laboratory trials at different moisture contents of 8.5 to 14%, 10 adult *T. nigrescens* were able to prevent populations of up to 100 adult *P. truncatus* from increasing (Rees, 1985). Recent work by Ayertey *et al.* (this volume) has shown the ability of *T. nigrescens* to suppress *P. truncatus* on maize cobs in the presence of *S. zeamais*.

A number of factors such as adult densities at the time of sampling, extension of the husk past the ear, husk leaf number, number of visible holes on the husk, density of earworms and other insect species within cobs were found to play a significant role in initial colonisation

of cobs. Densities of adult *P. truncatus* or *S. zeamais* at the time of sampling were the most important predictors in the model in explaining densities for reared-out adults of each insect species. For this experiment, *P. truncatus* densities before rearing-out explained 70.3, 9.9, 6.4 and 40.6% of the variance in reared-out densities during the first, second, third and fourth sampling occasions, respectively, (Table 1) while *S. zeamais* densities before rearing-out accounted for 54.9, 41.0, 25.8, 32.6 and 34.7% of the variance in reared-out densities during the baseline, first, second, third and fourth sampling occasions, respectively (Table 2). Initial attraction to maize over short distances by *P. truncatus* is thought to be due to volatiles emanating from the grains. However, field studies both in Mexico (Tigar *et al.*, 1994) and Togo (Wright *et al.*, 1993) suggest that there is no long-range attraction of adult *P. truncatus* and host selection may occur largely by chance. Honda and Ohsawa (1990) found that emission of volatile chemicals from maize attract *S. zeamais*. The importance of the level of field infestation of cobs by for the progress of infestation during storage has been demonstrated by Borgemeister *et al.*, (1994) for *P. truncatus* and Markham (1981) for *S. zeamais*.

Husk extension past ear was often found to be negatively correlated with infestation by *P. truncatus* and *S. zeamais* during both storage seasons, and this study confirms previous work have shown the importance of good husk cover to prevention of attack by *S. zeamais* (Kossou *et al.*, 1993). Schulten (1976) also noted the importance of inter-varietal differences in extension of the husk over the tip of the cob, the tightness of the husk and the number of sheaths forming the husk as some of the factors protecting the cob in the field from infestation by storage pests, and that damage to the sheaths by Lepidoptera larvae, birds and rodents may allow storage insects to enter otherwise well-protected cobs. The number of husk leaves was found to be negatively correlated with densities of *P. truncatus* early in the long season (Table 3), although this was not observed in the short season, and was only once observed for *S. zeamais*. Earworm density as well as number of visible holes on husk leaves were also factors that significantly ($P < 0.05$) explained the densities of reared-out adults of *P. truncatus* and *S. zeamais* early in the season for both experiments. Densities of other storage pests, e.g., *Carpophilus* spp., *Cathartus* spp., *Cryptolestes* spp., *Palorus* spp. and *Tribolium* spp., most of which are associated with damaged grains, were correlated with reared-out densities of *P. truncatus* and *S. zeamais* during various sampling occasions for each experiment although no general trend was observed. *Tribolium* spp. has also been observed preying on *P. truncatus* and *S. zeamais* in laboratory colonies. The different patterns of correlation of these secondary insect species on sampling occasions for the two experiments demonstrates the complexity of the ecology of individual species and their interactions with the two primary insects in stores, and suggests that other, undetermined factors could have played a role.

The method of presentation of grains may affect its susceptibility to *P. truncatus* and *S. zeamais*. In Tanzania, Golob *et al.*, (1985) showed that maize stored on the cob suffered considerably more damage by *P. truncatus* than shelled grain. Once into the grain, the pest establishes itself by extension of its tunnels along the rows of tightly packed seed. This would be more difficult to achieve in a discontinuous medium like loose grain. *S. zeamais* on the other hand, prefers shelled grain to grain on the cob since during oviposition, females lay their eggs near the germ where both germ and endosperm tissues are easily accessible to the newly hatched larvae (Kossou *et al.*, 1992).

Contrary to the view that repulsed distributions of herbivores in the field indicate interspecific competition, this study showed that *P. truncatus* and *S. zeamais* were positively associated although there was evidence of interspecific competition. The strong positive associations observed may result from both species responding similarly to host plant variability (e.g. nutrition) for feeding, oviposition or development. There is evidence that larvae of both insects show preference for germ feeding during development within the grain (Vowotor *et al.*, in press). For either insect species, it is likely that feeding and oviposition sites are not chosen on the basis of competitor presence or absence. These observations may further emphasise the weakness inherent in inferring interspecific competition from insect distributional data (Hastings, 1987).

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Table 8.1a-d: Summary statistics of regression analysis of factors influencing reared-out densities of *P. truncatus* from maize cobs for 1995-96 long-season field storage experiments conducted at Dogbo, Mono Province, Bénin¹.

a) Sampling occasion 1

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	28.93	0.860	0.839	33.64	0.000	70.3

b) Sampling occasion 2

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	3.262	0.463	0.305	7.038	0.000	9.9
Husk extension past ear	-0.077	0.030	-0.111	-2.567	0.011	1.1

c) Sampling occasion 3

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	1.118	0.252	0.199	19.63	0.000	6.4
Husk extension past ear	-0.742	0.208	-0.159	-12.78	0.000	3.0
<i>S. zeamais</i> (before rearing-out)	0.069	0.027	0.116	6.645	0.010	1.3

d) Sampling occasion 4

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	1.395	0.093	0.561	15.03	0.000	40.6
<i>Carthatus</i> spp.	0.264	0.069	0.142	3.827	0.000	1.8
Moisture content	-3.267	1.091	-0.104	-2.996	0.003	1.0
Husk extension past ear	-1.259	0.500	-0.090	-2.520	0.012	0.7

¹No insects were reared-out from the 100 cobs randomly sampled during the baseline sampling occasion. A total of 480 cobs were sampled during sampling occasions 1, 2, 3 and 4.

Table 8.2a-e: Summary statistics of regression analysis of factors influencing reared-out densities of *S. zeamais* from maize cobs for 1994-95 short-season field storage experiment conducted at Dogbo, Mono Province, Bénin¹.**a) Baseline sampling**

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>S. zeamais</i> (before rearing-out)	3.010	0.314	0.679	9.596	0.000	54.9
<i>Cathartus</i> spp.	0.010	0.105	0.174	2.451	0.016	2.6

b) Sampling occasion 1

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>S. zeamais</i> (before rearing-out)	2.153	0.109	0.662	387.2	0.000	41.0
Number of earworm infested sites on dehusked cob	3.089	0.500	0.153	38.23	0.000	26.2
Husk extension past ear	-1.995	0.363	-0.138	30.19	0.000	2.6
<i>Cathartus</i> spp.	0.211	0.045	0.155	21.74	0.000	1.8

c) Sampling occasion 2

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>Cathartus</i> spp.	0.264	0.047	0.180	5.567	0.000	48.0
<i>S. zeamais</i> (before rearing-out)	1.289	0.059	0.703	21.89	0.000	25.8
Earworms	0.328	0.090	0.083	3.626	0.000	0.8
Husk extension past ear	-0.869	0.243	-0.082	-3.578	0.000	0.7
<i>Cryptolestes</i> spp.	9.216	2.855	0.073	3.227	0.001	0.5
Visible holes on husk leaves	0.778	0.380	0.047	2.046	0.041	0.2

d) Sampling occasion 3

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	Δr^2 change
<i>Cathartus</i> spp.	0.141	0.072	0.057	1.977	0.049	48.5
<i>S. zeamais</i> (before rearing-out)	1.969	0.071	0.811	27.75	0.000	32.6
<i>Carpophilus</i> spp.	2.807	0.576	0.093	4.876	0.000	0.8
Husk extension past ear	-1.067	0.371	-0.056	-2.872	0.004	0.4
<i>Palorus</i> spp.	2.465	0.875	0.062	2.816	0.005	0.3
Number of earworm infested sites on dehusked cob	0.854	0.353	0.046	2.422	0.016	0.2

e) Sampling occasion 4

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	Δr^2 change
<i>Cathartus</i> spp.	0.459	0.077	0.166	5.928	0.000	42.3
<i>S. zeamais</i> (before rearing-out)	1.539	0.055	0.773	28.01	0.000	34.7
Husk extension past ear	-2.650	0.451	-0.128	-5.878	0.000	1.5
Visible holes on husk leaves	-0.751	0.303	-0.056	-2.872	0.004	0.5
<i>P. truncatus</i> (before rearing-out)	2.465	0.875	0.062	2.816	0.005	0.2

¹One hundred cobs were randomly sampled during the baseline sampling occasion. A total of 480 cobs were sampled during sampling occasions 1, 2, 3 and 4.

Table 8.3a-h: Summary statistics of regression analysis of factors influencing reared-out densities of *P. truncatus* from cobs of four maize varieties in two types of stores during the 1995-96 long-season field storage experiments conducted at the IITA substation, Cotonou, Bénin¹.

Early season

a) Sampling occasion 1

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	1.557	0.171	0.494	9.082	0.000	24.7
Earworms	0.146	0.039	0.202	3.082	0.000	4.1
Husk extension past ear	-0.056	0.023	-0.130	-2.389	0.018	1.8

b) Sampling occasion 2

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	2.133	0.160	0.668	13.30	0.000	40.3
<i>Palorus</i> spp.	-0.500	0.122	-0.209	-4.091	0.000	3.0
<i>S. zeamais</i> (before rearing-out)	0.091	0.026	0.174	3.526	0.001	2.1

c) Sampling occasion 3

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	0.597	0.081	0.455	7.366	0.000	31.5
Number of husk leaves	-1.135	0.495	-0.126	-2.294	0.023	1.8
<i>Cryptolestes</i> spp.	0.556	0.267	0.128	2.284	0.038	1.2

d) Sampling occasion 4

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	0.848	0.121	0.415	6.989	0.000	31.5
<i>Tribolium</i> spp.	-0.666	0.264	-0.150	-2.526	0.012	1.2

Late season

e) Sampling occasion 5

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	0.259	0.044	0.398	5.840	0.000	10.2
Husk extension past ear	-1.124	0.354	-0.190	-1.375	0.002	5.5
<i>Tribolium</i> spp.	-0.473	0.149	-0.222	-3.171	0.002	2.6
<i>Cathartus</i> spp.	0.160	0.070	0.138	2.282	0.023	1.8

f) Sampling occasion 6

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	0.173	0.027	0.412	6.430	0.000	16.8
<i>Cryptolestes</i> spp.	0.065	0.023	0.174	2.831	0.005	2.1
<i>Tribolium</i> spp.	-0.173	0.077	-0.142	-2.233	0.027	1.6

g) Sampling occasion 7

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	0.127	0.023	0.338	5.559	0.000	10.6
<i>S. zeamais</i> (before rearing-out)	-0.084	0.029	-0.179	-2.886	0.004	2.3
Number of earworm infested sites on dehusked cob	-1.275	0.590	-0.131	-2.160	0.032	2.1
Husk extension past ear	-0.746	0.371	-0.124	-2.012	0.045	1.5

h) Sampling occasion 8

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>P. truncatus</i> (before rearing-out)	0.208	0.025	0.458	8.159	0.000	17.4
<i>S. zeamais</i> (before rearing-out)	0.295	0.062	0.262	4.723	0.000	7.6
<i>Cathartus</i> spp.	-0.142	0.046	-0.176	-3.118	0.002	2.9

¹No insects were reared-out from cobs randomly sampled during the baseline sampling occasion. A total of 80 and 240 cobs were sampled during the baseline and subsequent sampling occasions, respectively.

Table 8.4a-h: Summary statistics of regression analysis of factors influencing reared-out densities of *S. zeamais* from cobs of four maize varieties in two types of stores during the 1995-96 long-season field storage experiments conducted at the IITA substation, Cotonou, Bénin¹.

Early season

a) Sampling occasion 1

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>Cathartus</i> spp.	0.107	0.019	0.323	5.512	0.000	23.0
<i>Crytolestes</i> spp.	6.663	1.507	0.229	4.422	0.000	4.8
<i>S. zeamais</i> (before rearing-out)	0.546	0.163	0.194	3.357	0.001	4.6
Visible holes on husk leaves	0.606	0.202	0.158	2.995	0.003	3.0
Husk extension past ear	-0.33	0.100	-0.17	-3.30	0.001	2.8
Earworms	0.344	0.171	0.105	2.012	0.045	1.1

b) Sampling occasion 2

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>S. zeamais</i> (before rearing-out)	0.492	0.115	0.257	4.269	0.000	21.6
<i>Cathartus</i> spp.	0.256	0.052	0.289	4.880	0.000	7.9
Husk extension past ear	-1.575	0.412	-0.208	-3.819	0.000	4.8
<i>P. truncatus</i> (before rearing-out)	1.737	0.625	0.148	2.781	0.006	2.1

c) Sampling occasion 3

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>S. zeamais</i> (before rearing-out)	0.484	0.056	0.519	8.657	0.000	40.8
<i>Carpophilus</i> spp.	3.284	1.006	0.175	2.790	0.001	1.9
<i>Cathartus</i> spp.	0.219	0.079	0.158	2.790	0.006	1.4
<i>Tribolium</i> spp.	-3.125	1.522	-0.11	-2.05	0.041	1.0

d) Sampling occasion 4

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r ² change
<i>S. zeamais</i> (before rearing-out)	0.798	0.083	0.610	9.665	0.000	38.3
Husk extension past ear	-1.707	0.554	-0.151	-3.085	0.002	2.5
<i>Palorus</i> spp.	-1.070	0.305	-0.197	-3.507	0.001	2.6
<i>Cathartus</i> spp.	0.244	0.084	0.167	2.896	0.004	1.9

Late season

e) Sampling occasion 5

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r^2 change
<i>Cathartus</i> spp.	0.173	0.084	0.280	4.490	0.000	15.5
Husk extension past ear	-1.177	0.393	-1.171	-2.992	0.003	4.5
<i>S. zeamais</i> (before rearing-out)	0.251	0.053	0.316	4.781	0.000	4.4
<i>Tribolium</i> spp.	-0.458	0.153	-0.173	-2.790	0.006	3.2
Number of husk leaves	-1.153	0.494	-0.135	-2.790	0.020	1.6

f) Sampling occasion 6

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r^2 change
<i>S. zeamais</i> (before rearing-out)	0.077	0.017	0.290	4.564	0.000	8.7
<i>Tribolium</i> spp.	-0.221	0.062	-0.242	-3.589	0.000	5.5
<i>Palorus</i> spp.	0.051	0.024	0.132	2.091	0.038	4.7
<i>P. truncatus</i> (before rearing-out)	-0.066	0.020	-0.211	-3.293	0.001	2.4
<i>Cryptolestes</i> spp.	0.053	0.019	0.190	2.875	0.004	2.8

g) Sampling occasion 7

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r^2 change
<i>S. zeamais</i> (before rearing-out)	0.137	0.020	0.436	6.865	0.000	18.8
<i>Tribolium</i> spp.	-0.222	0.074	-0.195	-2.987	0.003	1.9
<i>Cryptolestes</i> spp.	0.020	0.010	0.137	2.013	0.045	1.4

h) Sampling occasion 8

Variable	Coeff.	Stand. error	Stand. coeff.	T	P	% r^2 change
<i>S. zeamais</i> (before rearing-out)	0.080	0.015	0.335	5.148	0.000	6.6
<i>Cathartus</i> spp.	-0.150	0.047	-0.207	-3.193	0.002	3.5
Moisture content	1.314	0.555	0.145	2.369	0.019	2.1

¹No insects were reared-out from cobs randomly sampled during the baseline sampling occasion. A total of 80 and 240 cobs were sampled during the baseline and subsequent sampling occasions, respectively.

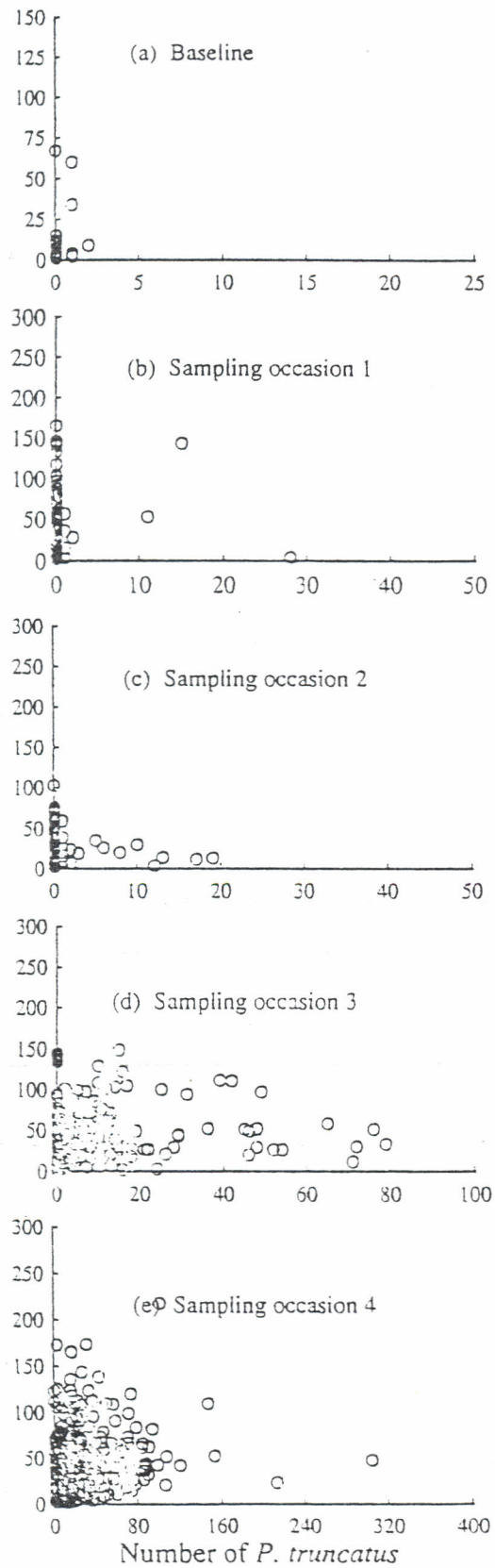


Fig. 8.1: Distribution of *S. zeamais* and *P. truncatus* on cobs of the maize variety DMR after rearing-out. (a) One hundred cobs were randomly sampled. (b) to (e) Sixteen cobs were randomly sampled from each of 5 sections (top, surface, middle, inner and bottom) of a 'crib' on each sampling occasion after harvest. A total of six cribs were sampled.

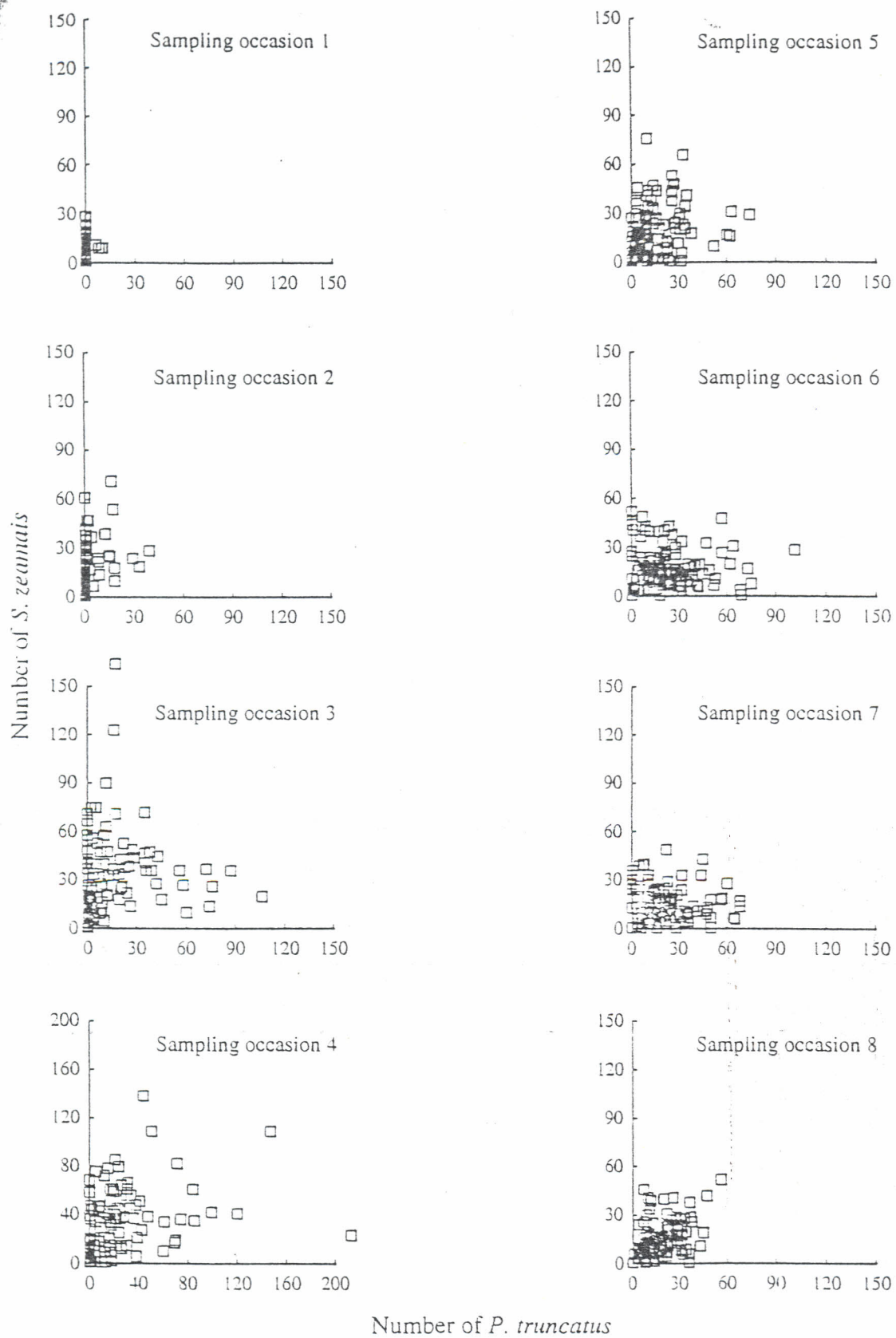


Fig. 8.2: Number of *S. zeamais* and *P. truncatus* obtained from cobs of four maize varieties (BLF, DMR, Gbogbe and TZSR-W) after rearing-out at the IITA substation, Cotonou, Bénin. A total of 120 cobs were randomly sampled from awa stores on each sampling occasion.

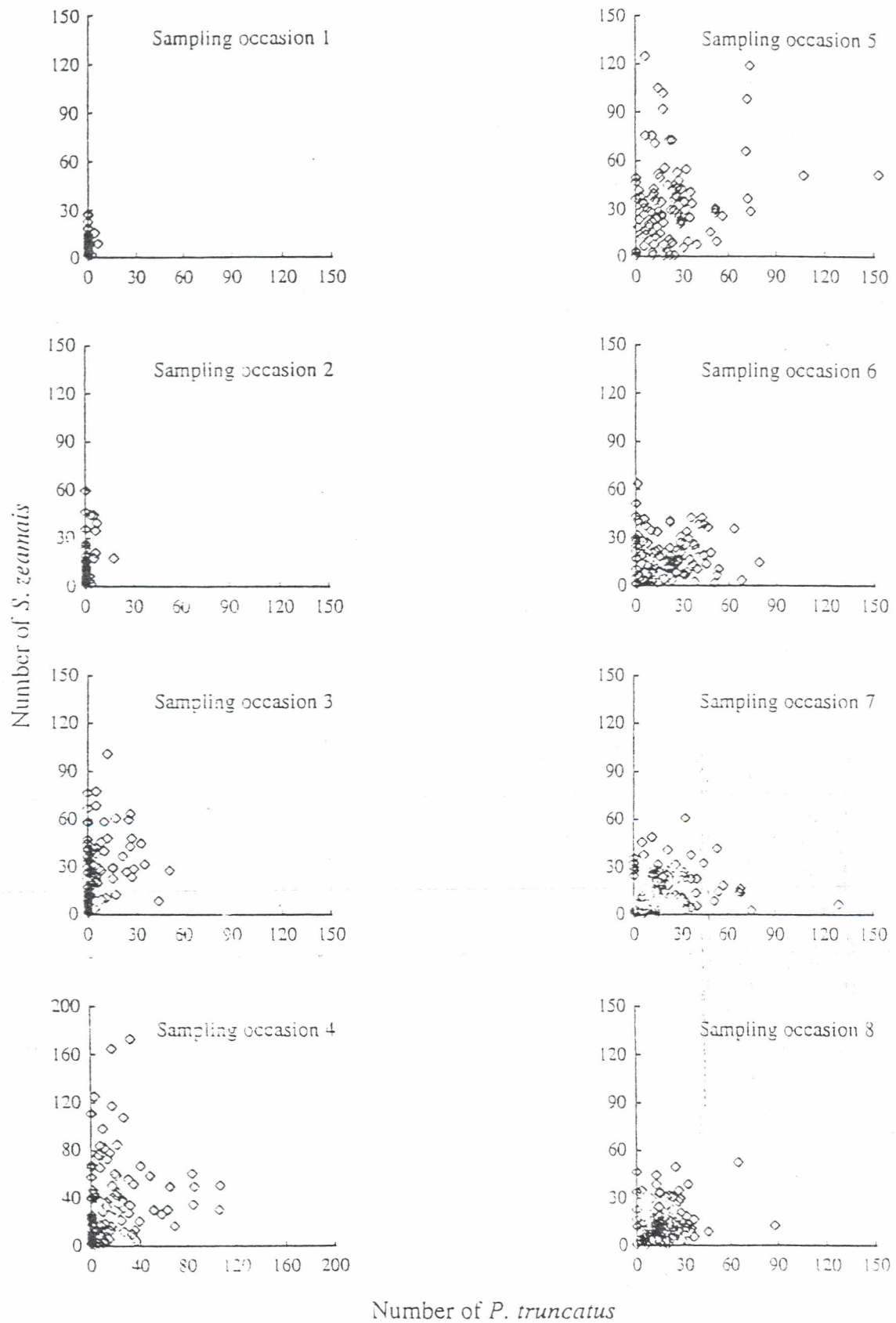


Fig. 8.3: Number of *S. zeamais* and *P. truncatus* obtained from cobs of four maize varieties (BLF, DMR, Gbogbe and TZSR-W) after rearing-out, at the IITA substation, Cotonou, Bénin. A total of 120 cobs were randomly sampled from cribs on each sampling occasion.

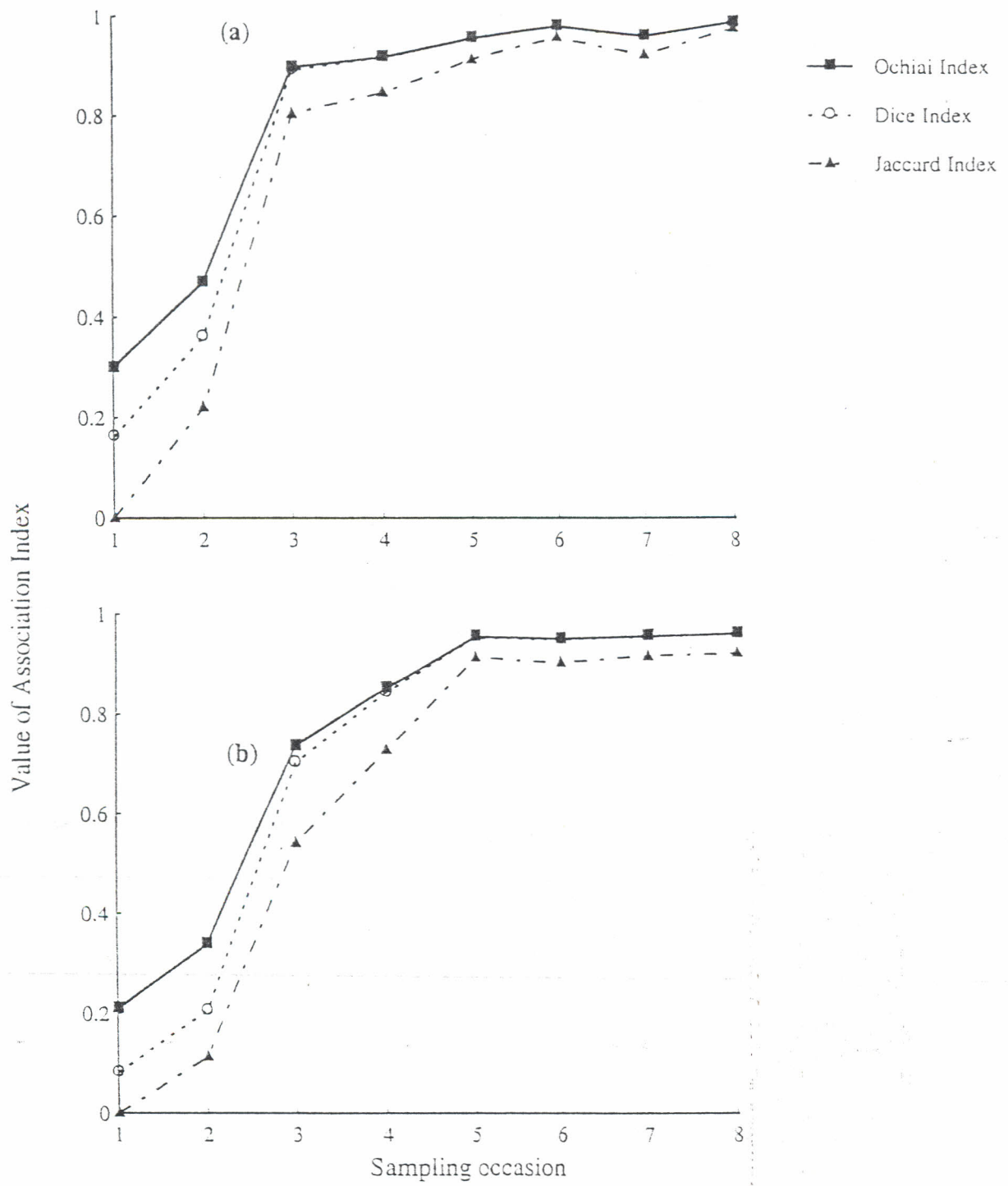


Fig. 8.4: Association between *P. truncatus* and *S. zeamais* reared-out from maize cobs during an eight month sampling period in (a) ava and (b) cribs using 3 association indices.

Taylor's *b* coefficient for *P. truncatus*

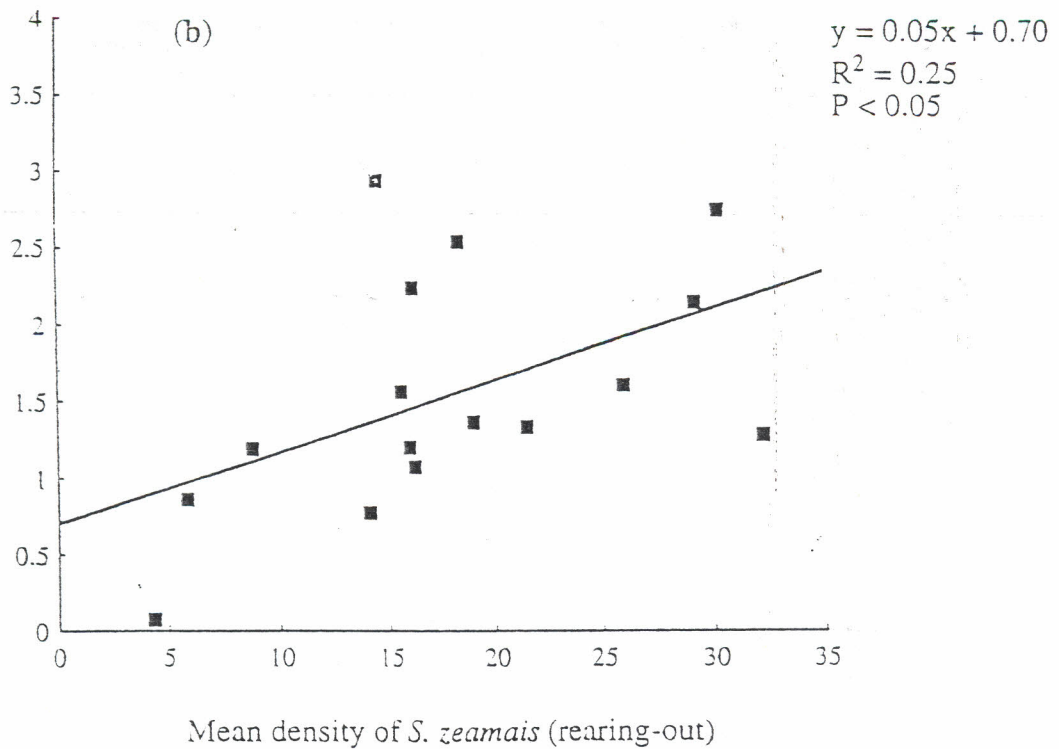
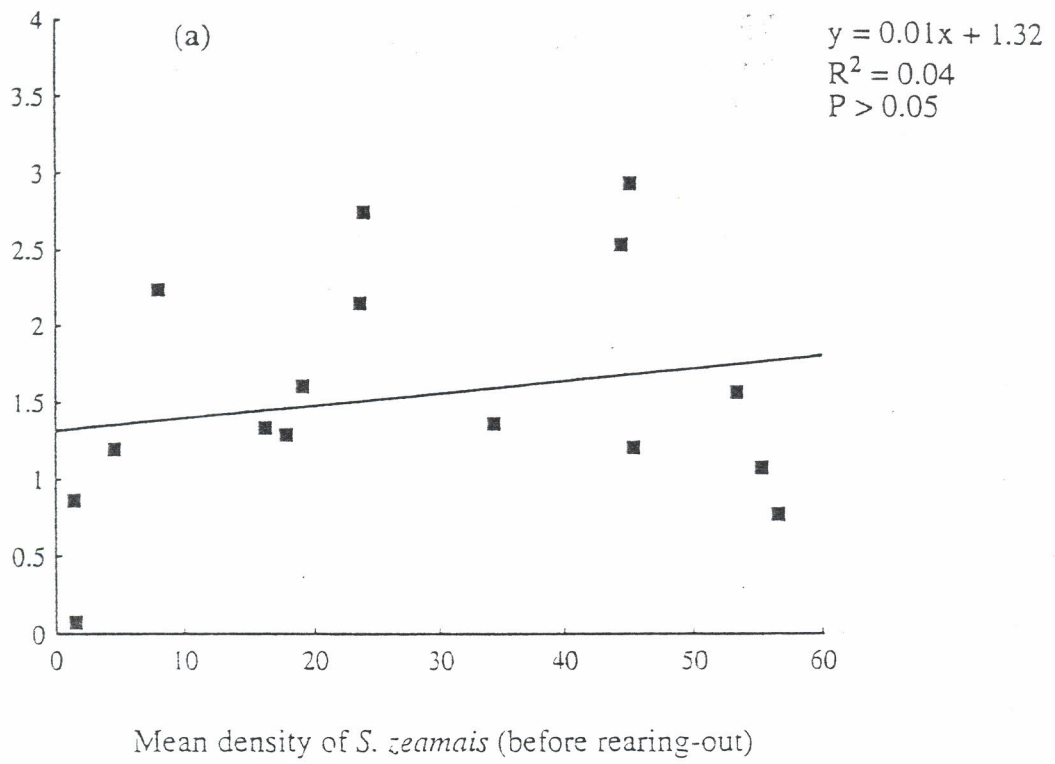


Fig. 8.5: Relationship between mean density of *S. zeamais* with *P. truncatus* (a) before rearing-out and (b) after rearing-out using Taylor's *b* coefficient.

Taylor's *b* coefficient for *S. zeamais*

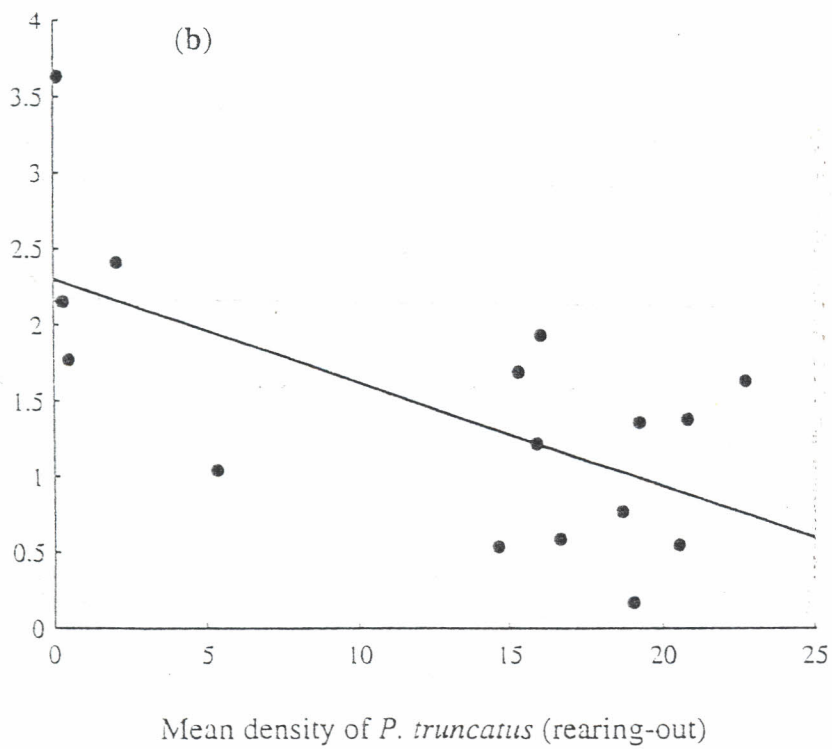
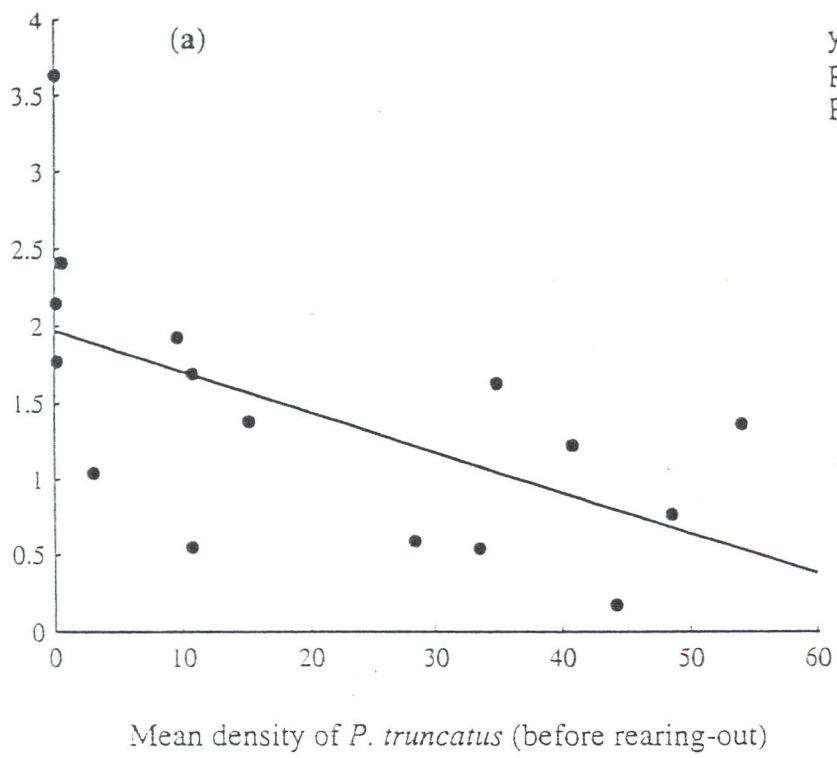


Fig. 8.6: Relationship between mean density of *P. truncatus* with *S. zeamais* (a) before rearing-out and (b) after rearing-out using Taylor's *b* coefficient.

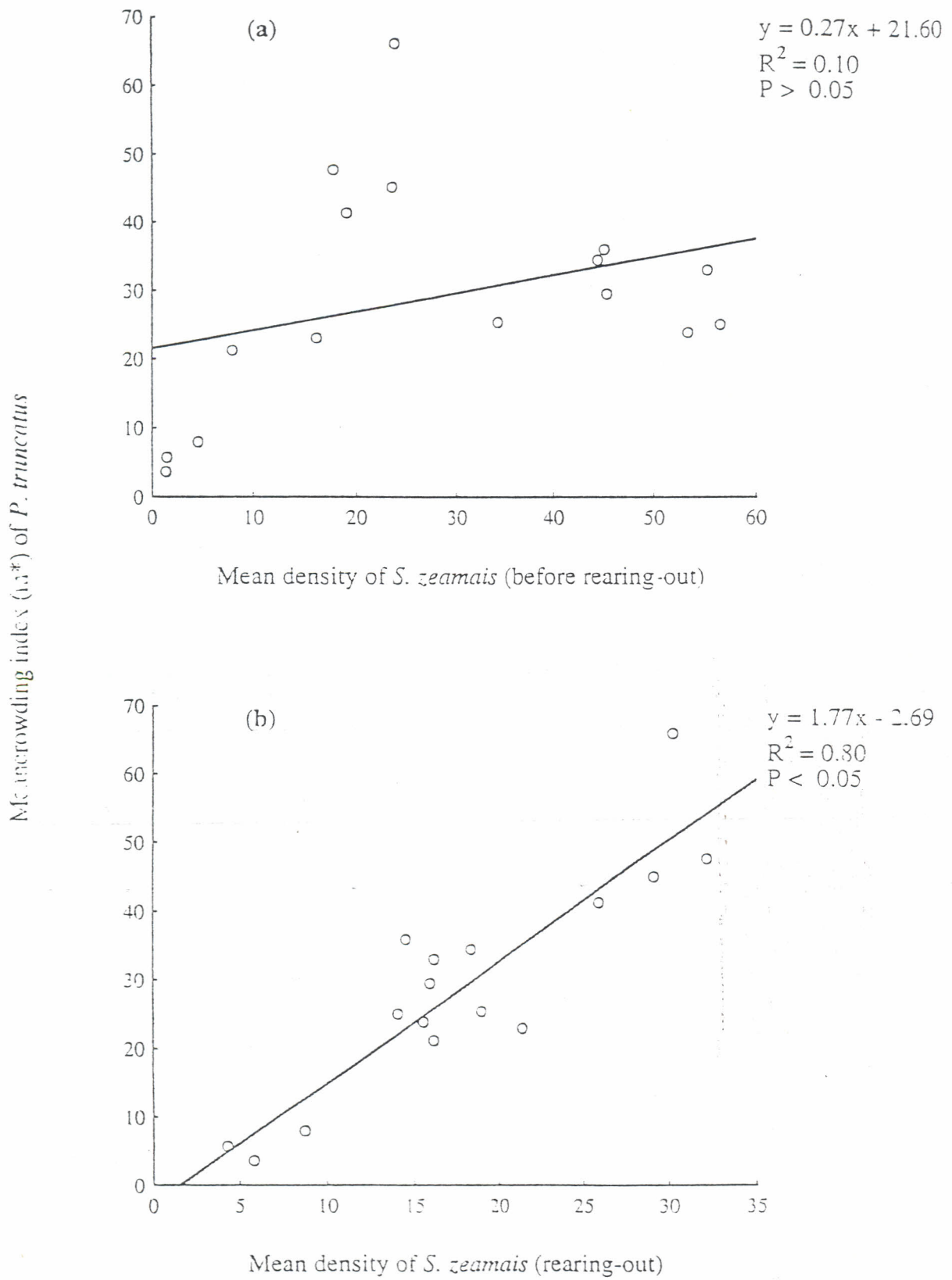


Fig. 8.7: Relationship between mean density of *S. zeamais* with *P. truncatus* (a) before rearing-out and (b) after rearing-out using Lloyd's mean crowding index (m^*).

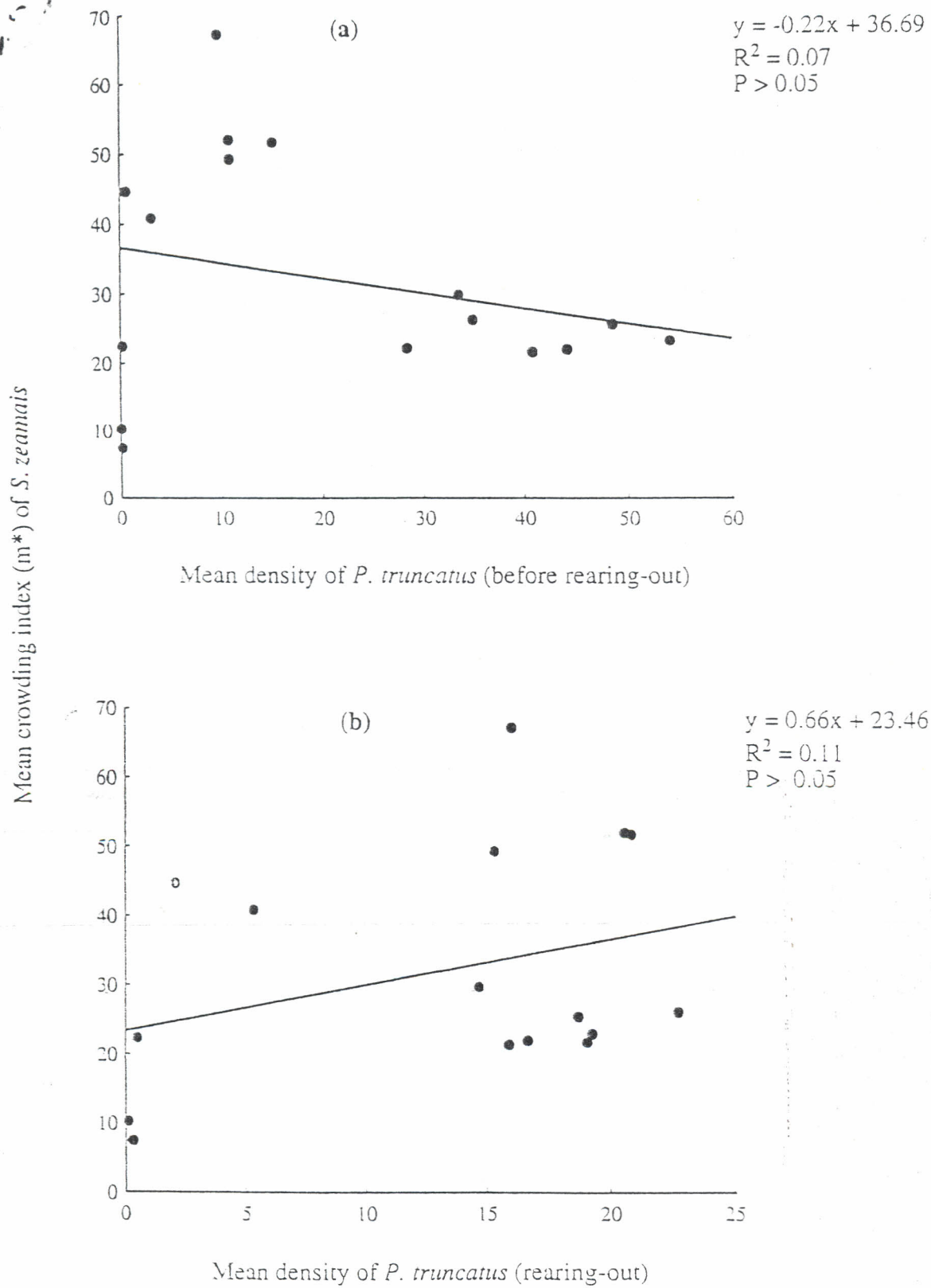
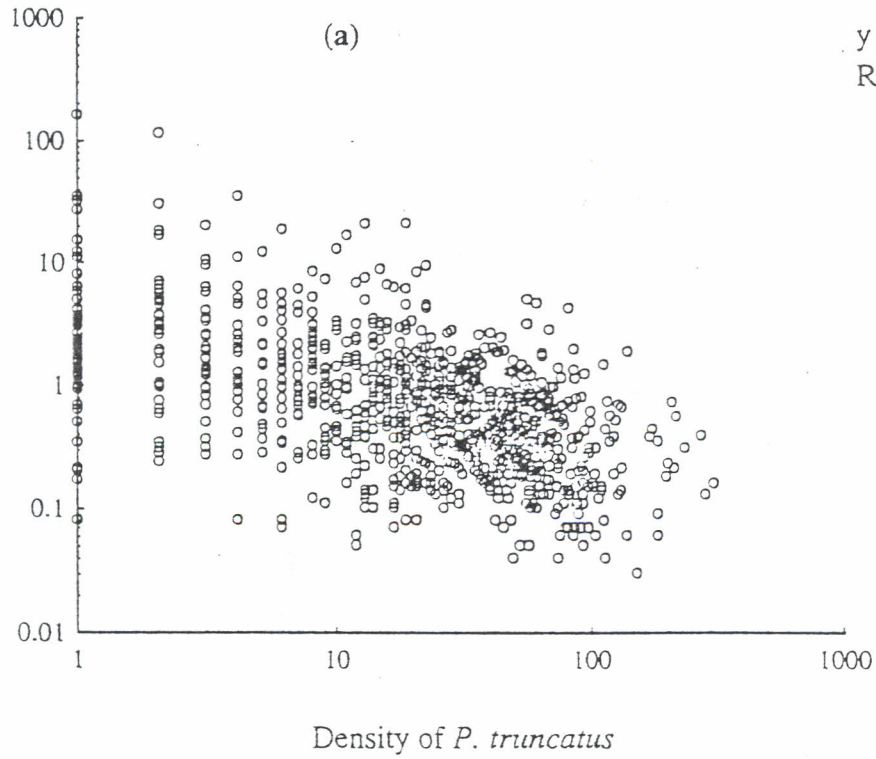


Fig. 8.8: Relationship between mean density of *P. truncatus* with *S. zeamais* (a) before rearing-out and (b) after rearing-out using Lloyd's mean crowding index (m^*).

Ratio of density of F_1 *S. zeamais* (rearing-out) to density of adults at sampling (before rearing-out)



Ratio of density of F_1 *P. truncatus* (rearing-out) to density of adults at sampling (before rearing-out)



Fig 8.9: Effect of (a) density of *P. truncatus* on the rate of increase of *S. zeamais* and (b) density of *S. zeamais* on the rate of increase of *P. truncatus* in cobs of four maize varieties (BLF, DMR, Gbogbe and TZSR-W) in stores. (Scales of axes are in logs).