Rodent resistance in cacao, Theobroma cacao L.

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Received May 1992; revised December 1992

The neotropical red squirrel (Sciurius granatensis Humbolt) was identified as the rodent damaging cacao pods in field studies in three locations in Trinidad. The rodent was observed to express a significant preference for ripe rather than unripe pods of cacao. Clonal variation in attractiveness of unripe cacao pods to the rodent was found to be consistent over sites. However, in pods that were attacked, the extent of damage caused was found to be independent of both ripeness and accession. An evolutionary argument is proposed which suggests that grazing deterrents may be present in unripe cacao pods, but not ripe ones. It is further argued that such grazing deterrents may be exploited by cacao breeders in developing rodent-resistant clones.

Keywords: Theobroma cacao; Cacao; Rodent resistance; Grazing deterrent; Pod damage

Natural seed dissemination in *Theobroma cacao* depends upon monkeys, rats, or squirrels (Toxopeus, 1985). Such vertebrates inflict massive losses on cacao yield worldwide. Thorold (1975) conservatively estimated that more than 60 species of vertebrates attack cacao globally. This list is highly diverse and includes elephants, monkeys, bats, civets, woodpeckers, and parrots. However, rodents, such as squirrels and rats, are responsible for most attacks (Bhat et al. 1981; Cruz, 1983).

The extent of pod loss in different countries varies greatly. Estimates range from a few per cent in Ghana (Wharton, 1962) to more than 90% in Peninsular Malaysia (Juan and Bose, 1979). Globally the annual loss due to vertebrate damage is estimated to be about 5 to 10% (Entwistle, 1985). This is similar in magnitude to black pod disease, the major fungal disease of cacao.

The problem is of considerable importance since most pods which are even slightly nibbled are rapidly lost to fungal pod rot (Coulibaly, 1982). Furthermore, damaged pods which are harvested can result in slimy fermentations and off flavours in the beans (Quesnel and Lopez, 1975).

Rodents have been controlled by the use of poison baits and firearms. However, the former which has been used indiscriminately has been criticized for its high costs and resistance problems (Everard, 1964; Lawrence, 1991). The latter has never been effective and can result in serious damage to the cacao trees themselves. Biological control by means of the introduction of mongoose species into various West Indian islands and Fiji have not been successful (Entwistle, ibid.).

Casual field observations indicated that certain

cacao clones were more prone to rodent attack than others. The present study was performed to investigate the potential for identifying cacao clones which are unattractive to rodents.

Materials and methods

Experiment 1

Five cacao accessions were selected at random from the International Cocoa Germplasm Trinidad (ICGT): IMC14, IMC55, ICS40, ICS84, 2210, during March 1992. Ten intact ripe and 10 intact mature unripe pods were collected from each accession. Gloved hands were used at all times when handling pods to prevent contamination by human scent. The pods were weighed and labelled. String was tied to their cut peduncles to enable them to be attached to cacao trees at the field site.

The 20 pods from each of the five accessions were then taken to an abandoned cacao estate on the southern slopes of Trinidad's northern range at Mount St. Benedict (10°40' N, 61°24' W). In this estate large numbers of the neotropical red squirrel Sciurius granatensis (Humbolt) had been observed, and most of the cacao pods had been attacked by rodents.

For each of the five accessions, the 10 ripe and 10 unripe pods were tied throughout a single tree selected at random. The number of pods damaged was monitored daily for a period of six days after which the pods were harvested and final weights were recorded.

Experiment 2

Since virtually all ripe pods were damaged in the first experiment, only unripe pods were used in Experiment 2.

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Ten cacao accessions were selected during March 1992 to represent a wide spread of genetic diversity from the ICGT, (ICS1, ICS68, ICS95, IMC6, IMC27, IMC67, PA46, PA169, AMAZ12, SCA6). For each accession 30 mature unripe pods were collected. As before, gloves were used when handling pods. Again, all pods were weighed and labelled, and string was attached to their peduncles.

In this experiment three field sites were used (Mount St. Benedict, Maracas Valley, and El Tucuche). These sites were located in abandoned cacao estates in Trinidad's northern range, and each was approximately 2.5 km from the other.

For each of the 10 accessions at each of the three sites, 10 unripe pods accession⁻¹ were firmly attached throughout a single tree chosen at random. After a period of one week the pods were collected and the number of damaged pods recorded. Final weights of all pods were again recorded.

Results

The damage to all pods observed throughout the experiments was consistent with that caused by the neotropical red squirrel, rather than rats, in that the damage was directed at the sweet pulp around the beans and not at the pod itself (Urich, 1911). Furthermore, the damage was observed to occur during the day, and rats are considered to be nocturnal feeders.

Experiment 1

The cumulative number of both damaged ripe and damaged unripe pods pooled over the five accessions was plotted against time (Figure 1). The chi-square (χ^2) value of the final number of damaged and undamaged pods, both ripe and unripe, again pooled over accessions was 16.23 (P < 0.01; 1 df). Clearly, rodents prefer ripe pods to unripe pods.

A one-way analysis of variance with unequal replication was performed on the arc sine transformation of the proportions of weight lost from ripe versus unripe damaged pods. No significant difference was observed in the damage to ripe or unripe pods. The amount of tissue removed from a pod which

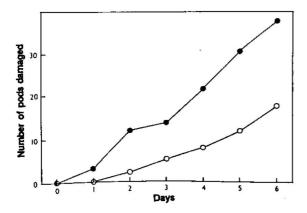


Figure 1 Cumulative number of damaged ripe (•) and unripe (O) pods.

was attacked by rodents was independent of ripeness. The pod usually was emptied of its beans and associated mucilage.

Experiment 2

The number of pods damaged for each of the 10 accessions at all three sites is presented in Table 1. Data were pooled over sites to obtain a χ^2 value for varieties (59.4; df 9; P = 0.001) and pooled over accessions to obtain the χ^2 value for sites (72.6; df 18; P = 0.001). The χ^2 for site × varieties interaction (15.3; df 18) was calculated using Mather's (1966) method, but it was not significant.

The significant effect of sites results from differing levels of rodent damage at the three sites. Most damage was observed at the Maracas Valley site and least damage was found at El Tucuche. This may have resulted from different rodent population densities between the sites. The significant effect of varieties was striking; SCA6 was observed to be consistently damaged at all sites, while IMC6 was never touched. The ranking of rodent preference for the different accessions was similar at the different sites. This is reflected in the non-significant χ^2 for site \times varieties interaction. The same accessions are favoured by the rodents irrespective of site and individual animals involved. Following this observation, in July 1992, 30 unripe pods of IMC6 were placed in the field in monoculture at the Mount St. Benedict location. Again this accession was observed to be untouched after a period of one week.

A one-way analysis of variance with unequal replicates was again performed on the arc sine transformation of the proportions of weight lost from damaged pods, over all the accessions. Again no significant difference was found in the extent of damage inflicted on attacked pods from different accessions. The amount of tissue removed from a pod attacked by the rodent was independent of variety.

Discussion

The high percentage of ripe pods damaged during the first experiment (Figure 1) clearly demonstrates

Table 1 Number of pods damaged at the three field sites

| Accession | Mount St. Benedict | Maracas | El Tucuche | Total |
|-----------|-----------------------|---------|---------------|-------|
| ICS1 | 1 | 3 | 0 | 4 |
| ICS68 | 3 | 6 | 5 | 14 |
| ICS95 | 4 | 3 | 1 | 8 |
| IMC6 | 0 | 0 | 0 | 0 |
| IMC27 | 2 | 5 | 2 | 9 |
| IMC67 | 4 | 9 | 2 | 15 |
| PA46 | 2 | 7 | 1 | 10 |
| PA169 | 7 | 8 | 0 | 15 |
| AMAZ12 | 3 | 9 | 4 | 16 |
| SCA6 | 10 | 10 | 3 | 23 |
| Total | 36 | 60 | 18 | 114 |

that squirrels are a serious pest of ripe cacao pods. The χ^2 test reveals a highly significant preference for ripe pods rather than unripe ones. This is, of course, not unexpected in a species whose seed dispersal mechanism depends upon vertebrates such as monkeys and rodents. Any genotype whose ripe pods were unattractive to rodents is unlikely to disperse its seeds and would be rapidly selected against. This observed preference for ripe pods is likely to be related to the many changes associated with fruit ripening. In cacao, these include colour changes, an increase in free sugars, softening of the mucilage component, and a tendency for hardening of the pod wall.

It was surprising that once unripe and ripe pods were damaged, they were eaten to the same extent. This suggests that the squirrels' preference for ripe pods is related to colour and smell rather than its taste. Thus, once a squirrel has engaged upon eating a pod, its stage of ripeness and hence taste and hardness do not appear to deter the squirrel from consuming the entire pod contents. During the experiment a few pods were observed to be only slightly attacked; the following day such pods were usually totally eaten. The occurrence of slightly damaged pods was not frequent enough to make any significant observations.

Experiment 2 demonstrated that at the three sites with differing levels of squirrel attack, the preference of squirrels for specific accessions was consistent (Tables 1 and 2). This suggests that the clone SCA6 which is consistently attacked may possess some property that is attractive to squirrels. This is supported by anecdotal evidence which reports that SCA6 is consistently favoured wherever it is grown. On the other hand IMC6 (which was observed to be undamaged by rodents in this experiment) may contain a grazing deterrent in its unripe pods. In this experiment, accessions did not fall into discrete eaten and non-eaten classes (with the exception on IMC6) but showed a range of attractiveness to squirrels. This may indicate a polygenic nature to any grazing deterrent in unripe pods rather than a major gene effect.

The findings that the level of damage to pods which were attacked by squirrels was independent of variety suggest that squirrel preference is related to the appearance and scent of the pod rather than its taste. The favoured SCA6 pods when ripe contain pulp which is very sweet to the taste, but this does not explain their attractiveness when unripe.

Although it is expected that all ripe pods should be attractive to rodents because of the seed dispersal mechanism, this is not the case for unripe pods. Genotypes whose pods are attractive before their seeds are fully developed will be selected against. Thus, it may be predicted that unripe pods may contain grazing deterrents to discourage animal damage until the seeds are mature. The identification of accessions whose unripe pods are unattractive to rodents may reduce the length of time that pods are attractive, and this may allow most pods to be harvested before damage. However, given the large natural geographic range of cacao (Cheesman, 1944), it is likely that there are many different species of rodents which attack cacao and that cacao may therefore have evolved several grazing deterrents in its unripe pods. Such grazing deterrents could be exploited by plant breeders in developing cacao clones that are resistant to rodent damage.

Varietal variation in attractiveness to the neotropical red squirrel has been demonstrated in this study. However, it is unclear what property of the unripe pods is responsible for this or whether the same preference is expressed by other rodents. These preliminary experiments indicate that clone IMC6 is immune to damage at three locations, and independently in monoculture. Clearly further work is required to assess the potential identified in this study for developing rodent-resistant cacao clones.

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