Why Are Seeds of the Central American Guanacaste Tree, *Enterolobium cyclocarpum*,[1] Not Attacked by Bruchids[2] Except in Panama?[3]

CLARENCE DAN JOHNSON[4] AND DANIEL H. JANZEN[5]

ABSTRACT

Environ. Entomol. 11: 373–377 (1982)

The ranges of most other bruchids are usually contiguous with their hosts, but *Stator generalis* (Coleoptera: Bruchidae) is known to feed only in exposed seeds of guanacaste, *Enterolobium cyclocarpum* (Leguminosae: Mimosoideae),in a restricted area of central Panama. Because this tree is widespread in the neotropics and yet is not preyed upon by seed beetles throughout the rest of its range, we fed seeds from Mexico, Guatemala, El Salvador, Honduras, and Costa Rica, and from other areas of Panama, to *S. generalis*. They were able to develop normally in all these seeds; thus, we rejected the hypothesis that seeds from central Panama were chemically unique. We hypothesize that *S. generalis* has not spread northward, because guanacaste seeds are not available in amounts or a pattern appropriate for *S. generalis* to survive. This is because cattle and horses eat nearly all the fruits, thereby widely scattering the cleaned seeds. Small rodents which have access to horse and cattle dung remove the seeds even farther from a state accessible to bruchids. Further, variability in the number of seeds set and available in a specific locality may also reduce the pool of bruchids available for emigration and raise the chance for local extinction. Probably a pool of fruit-free seeds exposed on the surface of the ground only accumulates in sufficient quantity to maintain a population of *S. generalis* in localities such as city parks, gardens, corrals, and other areas where there is considerable human traffic. The possible effects of Pleistocene large mammals on this system are also discussed.

That the distribution of bruchid beetles is usually contiguous with that of their hosts has been demonstrated in recent papers on *Acanthoscelides* (Johnson 1981a), *Sennius* (Johnson and Kingsolver 1973, Johnson and Slobodchikoff 1979), *Stator* (Johnson 1981b, Johnson and Kingsolver 1976), and *Mimosestes* (Kingsolver and Johnson 1978). When it was discovered that the widespread guanacaste tree *Enterolobium cyclocarpum* (Jacq.) Griseb. (Mimosoideae) seeds were fed upon by a bruchid beetle only in a restricted area in central Panama, it was of interest to us as to why this unusual situation exists.

The guancaste tree has a natural distribution from the lowlands of central Mexico (the states of Sinaloa and Tamaulipas) to southern central South America. From Costa Rica north, its large, hard seeds (Janzen and Higgins 1979, Janzen 1981a,b,c) are not attacked by any species of seed-eating bruchid or curculionid beetle. This absence of a bruchid seed predator is substantiated by large collections of guanacaste seeds by both of us from Mexico to Costa Rica, by the absence of bruchids reared from Central American guanacaste seeds in the very large collections of Neotropical bruchids in the U.S. National Museum, and by explicit search for such bruchids in Guanacaste Province, Costa Rica (see below). However, in central Panama its seeds are preyed on by the larvae of the bruchid *Stator generalis* Johnson and Kingsolver. Why has this beetle not spread northward on the abdundant food resource that appears to be available? Here we test the hypothesis that the Mexican and northern Central American guanacaste seeds are chemically unavailable to *S. generalis*, and we reject this hypothesis.

Materials and Methods

All *S. generalis* used in this study were reared from seeds collected at the following sites in Panama: Panama Viejo, Panama City, 26 March 1979 (C. D. Johnson no. 1010–79); near Gatun Locks, Canal Zone, 25 March 1979 (C.D.J. no. 1005–79); Panama Viejo, 25 March 1980 (C.D.J. no. 2105–80); Balboa, C.Z., 28 March 1980 (C.D.J. no. 2167–80); 28 km SE La Chorrera and San Carlos, Panama Province, 29 March 1980 (C.D.J. no. 2196–80 and no. 2197–80); and Aguadulce, Coclé Province, 31 March 1980 (C.D.J. no. 2234–80). The seeds were placed in paper bags in the field, and then in the laboratory they were placed in large glass jars. The tops of the jars were covered with paper towels which had been treated with a 1% Kelthane in acetone solution to protect against pyemotid mites. The shelves on which the jars were placed were also covered with Kelthane-treated towels. Kelthane does not affect bruchids. In all experimental cultures but five, 20 seeds collected in 1978, 1979, or 1980 were placed in a covered petri dish and then about 20 *S. generalis* were introduced into the dish along with the seeds. A few drops of honey and a moist sponge were also placed in each dish to provide food and water for the adults. The adults were removed after 6 or 7 days. When second-generation adults emerged from seeds they were removed immediately so that additional oviposition did not occur. All adults had emerged about 2 months after initial oviposition. The seeds used in these experiments were then transferred to jars with

[1] Leguminosae: Mimosoideae.
[2] Coleoptera: Bruchidae.
[3] Received for publication 9 March 1981.
[4] Dept. of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011.
[5] Dept. of Biology, University of Pennsylvania, Philadelphia, PA 19104.

0046-225X/82/02003-7305$02.00/0

an additional 20 *S. generalis* to see if the bruchids would continue to oviposit on and develop in these seeds until the food had been used up. The seed source localities reported in Table 1 were determined by seed availability.

Table 1.—Experimental use of *E. cyclocarpum* seeds by *S. generalis*[a]

Locality where seeds collected	Culture no.[b]
Mexico	
19 km NW Tepic	602–79
2 km NW Cuajinicuilapa	743–79 and 1302–80
4 km NE Tehuantepec	559–79
35 km W Zanatepec	342–78
69 km SW Cintalapa	1082–79
2 km S Atoyac	1267–80
9 km N Puerto Escondido	1321–80
22 km N Pochutla	1348–80
41 km N Pinotepa Nacional	1410–80
29 km N Acapulco	1455–80
Chichen Itza	1689–80
16 km N Champotón	1652–80
Guatemala	
22 km W Coatepeque	784–79
5 km N Escuintla	1028–79
El Salvador	
24 km NW Acajutla	820–79
16 km NW Santa Tecla	1019–79
Honduras	
20 km SE Comayagua	1998–80
2 km W Comayagua	2084–80
Costa Rica	
Santa Rosa National Park	
Finca La Pacifica, Cañas	
Panama	
25 km SE Santiago	962–79
41 km E Santiago	2203–80
9 km E Santiago	2212–80
25 km SW La Chorrera	896–79
28 km SE La Chorrera	2196–80
3 km N Balboa	975–79
Balboa	2163, 2164, 2166, 2168–80
Panama Viejo, Panama	2104–80, 2105–80, 2306–80
10 km NE Summit Gardens	2253–80, 2254–80
Summit Gardens	2107–80
10 km SE Penonomé	2200–80
Nata	2202–80
6 km & 18 km N Ocú	2230 and 2232–80
14 km SW Aguadulce	2233–80
1 km N El Llano	2294–80
Barro Colorado Island	2334–80

[a] *S. generalis* was able to complete its development in seeds from all localities.
[b] Culture numbers of C.D.J.

Stock cultures of *S. generalis* were maintained on the seeds collected at Panama Viejo and San Carlos.

In Santa Rosa National Park, northwestern Guanacaste Province, Costa Rica, an area containing a substantial reproducing population of guanacaste trees, an explicit attempt was made to locate *S. generalis*, despite the fact that none had been observed in 4 years of study of the seed crops of this tree. In March 1980, at the time of first guanacaste fruit fall, 10 metal screen bags (mesh 8 by 8 mm),each containing 20 dormant guanacaste seeds, were placed in the litter below each of three large, fruit-bearing guanacaste trees. The seeds were examined closely for *S. generalis* eggs and exit holes in April, May, July, October, and December 1980, and in March 1981. No sign of *S. generalis* was encountered.

The Prey

Guanacaste trees are rare as adults, but they are extremely large (up to 40 m in height and 2 m dbh) and conspicuous (Fig. 1). They are often left standing when forest is cleared. These two traits make them a familiar part of the landscape in the Central American Pacific coastal lowlands. They are widely planted or encouraged as garden, shade, and park trees, again adding to their persistence in regions extensively denuded of forest. In addition, they have been widely and deliberately introduced around the world, so that contemporary major geographic distributions are not pre-Columbian. Finally, the fruits are readily eaten by horses and cattle, and therefore the seeds move about through livestock shipments. This means that the omnipresence of guanacaste trees in ranching areas throughout Central America could have been in great part generated by the ranching industry.

In areas originally clothed in deciduous forest, guanacaste trees are leafless for most of the dry season and produce a new crop of leaves 1 to 5 weeks before the rains begin. During March and April, slightly before leafing, the tree produces a large crop of white inflorescences, which in turn generates a crop of minute, dormant fruits. These fruits remain small until the following January, when they rapidly swell to somewhat curved discs that are 6 to 10 cm in diameter and bear 5 to 20 large seeds 1.5 to 2 cm long (Fig. 2). These fruits eventually turn brown and fall from the tree in March and April, about the time the first flower buds are appearing.

The mature fruits are indehiscent, and their fall from the tree is a behavioral presentation to a now extinct megafauna of seed dispersers (Janzen and Martin, unpublished data).In Costa Rica, if the tree under consideration is growing in a forest relatively undisturbed by humans and their animals, the fallen fruits lie unopened for 1 to 3 months. A few are eaten by tapirs and peccaries (seed dispersers and seed predators [Janzen 1981a]).

However, the bulk are eventually gone through by forest mice, *Liomys salvini*, and the seeds are removed and eaten in underground burrows. In removal experiments in Santa Rosa National Park, the mice got better than 98% of the seeds from fallen guanacaste fruits within 3 months after they fell (Janzen, unpublished data). Fruits may also open by rotting if there are no animals to open them. On Barro Colorado Island, Panama, a wildlife preserve, fruits were removed almost immediately from beneath two forest trees, presumably by pacas and agoutis, animals that do not eat the hard seeds.

However, if range cattle or horses have free access to the area below the parent guanacaste tree, the

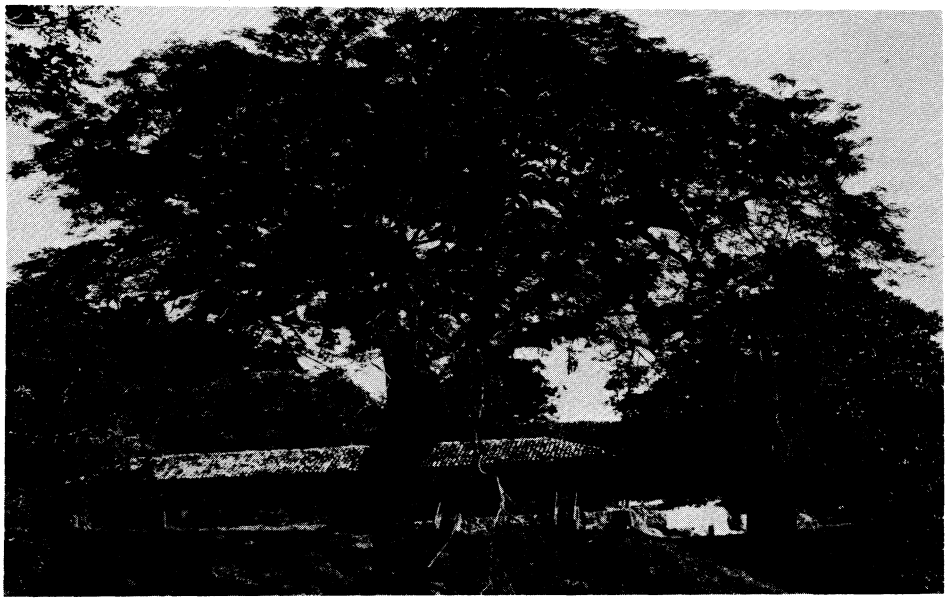

FIG. 1.—Adult guanacaste tree, *E. cyclocarpum*, growing near the Casona, Santa Rosa National Park, Guanacaste Province, Costa Rica.

FIG. 2.—Portion of a newly fallen crop of guanacaste fruits below the tree in Fig. 1 (ruler is 15 cm long). Inset: mature guanacaste fruit next to mature dormant guanacaste seeds (the white seed is split in half).

fruits are eaten almost the day they fall. Cattle digest few if any of the seeds, and defecate them a few days later. Horses digest most of the seeds, but defecate some (Janzen 1981c). The dung is degraded by rain, mice searching for seeds, and dung beetles, and the seeds disappear shortly into the soil or are eaten by mice. This means that in the bulk of the natural habitats occupied by Central American

guanacaste trees, the seeds and indehiscent fruits are not available in quantity or large concentrations. However, in city parks, cattle pens, and some roadside sites, the seeds accumulate in quantity on a hard ground surface. All are areas frequented by humans. One such area was a railroad yard in Balboa which had a large number of seeds and a thriving *S. generalis* population.

The Seed Predator

S. generalis is a representative small bruchid and is known only from central Panama, in the area from Aguadulce, Coclé Province, to Panama City, a distance of about 150 km. We believe this statement of a restricted range to be accurate for Central America, owing to the extensive bruchid collecting both of us have been doing for the past 15 years in Mexico and Central America, with both of us frequently focused on its sole host. It may, however, attack guanacaste seeds in South America, but this has not been investigated. *S. generalis* locates clean seeds of guanacaste trees on the soil surface, on the surface of cow dung, or exposed within decomposing fruits. The beetle glues single eggs to the seed surface, as do most other *Stator* species on their seed hosts. The larva mines through the seed coat and into the seed contents, where it develops feeding on the cotyledonary tissues. The adults emerge about 6 weeks after oviposition. Despite extensive collecting and rearing from seeds throughout the Pacific coastal plain of Panama and Costa Rica (Janzen 1980), *S. generalis* has not been reared from any other species of plant, and we have no reason to believe it has other Central American hosts than guanacaste.

The Question

Why does *S. generalis* not spread throughout much or all of the guanacaste distribution in Central America and Mexico? The easiest and least interesting answer is that there is something unique about the climate and other physical conditions of central Panama that meets the physical needs of *S. generalis*. We find this hypothesis to be particularly unappealing because there is simply no evidence to support it and it is impossible to test. However, laboratory studies of R. Kistler (unpublished data) have shown that larvae of *S. generalis* have slower rates of development than two other species of *Stator* but do develop normally between 25 and 35° C, as do more widespread species of *Stator*. The fecundity of adult *S. generalis* increases linearly between 25 and 35° C and is actually higher than that of two other species of *Stator*. Thus, *S. generalis* larvae and adults differ somewhat from other, much more widespread *Stator* species under the same temperature regimes but not enough for temperature differences to restrict their distribution.

It is possible, though unlikely, that some defensive trait of a guanacaste seed is relaxed in central Panama. To test this hypothesis, we offered seeds from 43 Mexican and Central American guanacaste cultures to the laboratory population of *S. generalis* (Table 1). The bruchids oviposited on all of them and developed successfully in all of them. Later generations continued to develop in them until the food supply was exhausted. This result was expected and rejects the hypothesis that Panamanian guanacaste seeds are chemically unique. There is no reason to believe the Panamanian guanacaste trees represent a distinct population. The central Panamanian trees may even be derived from Costa Rican or western Panamanian seed brought into central Panama by livestock or humans.

We suggest the following working hypothesis for the absence of *S. generalis* north of central Panama. *S. generalis* does not spread northward because the guanacaste seeds are not available in amounts or a pattern appropriate for the life cycle of *S. generalis*. For example, cattle and horses range thoroughly through the habitat of guanacaste in western Panama and areas to the north. They eat nearly all the fruits, thereby widely scattering the cleaned seeds. Furthermore, small rodents have access to horse and cattle dung in many of the partly forested and brushy pastures. These rodents remove the seeds even further from a state accessible to the bruchid. We doubt that a pool of fruit-free seeds exposed on the ground surface accumulates in sufficient quantity to maintain a population of *S. generalis*, except in exceptional localities such as city parks, gardens, corrals, and other areas where there is considerable human traffic. Movement of *S. generalis* from central Panama to more northern areas is thereby reduced to a process of island hopping, coupled with frequent extinction of local populations. We predict that if *S. generalis* were introduced to the right sites in Costa Rica, Guatemala, etc., it would establish and persist.

Variability in the number of seeds set and available in a specific locality may also reduce the pool of bruchids available for emigration and raise the chance for local extinction. At the Panama Viejo site there were about 10 times the number of seeds on the ground in 1979 as there were in 1980. In 1979, almost every seed had an egg glued to it, but in 1980 ca. 1 seed in 200 did.

Discussion

At least five species of *Stator* have distributions from the United States (*S. limbatus, S. pruininus, S. sordidus, S. vachelliae*) or southern Mexico (*S. vittatithorax*) well into South America (Johnson and Kingsolver 1976). However, each of these species has many hosts, and the bare seeds of their hosts are generally common in natural habitats.

Janzen and Martin (unpublished data) have postulated that guanacaste was one of the plants dispersed by Pleistocene large mammals. At the time when there was an active and large Central American herbivorous megafauna, *S. generalis* would have had an extremely difficult time finding concentrations of seeds and might well have existed on the seeds in some peculiar local circumstance, such as seeds in dung dropped around a waterhole in open grassland very far from seed-eating, small rodents

(which tend to be most abundant in the vicinity of woody vegetation). With the removal or loss of the megafauna, life for *S. generalis* should have become next to impossible because almost all seeds would have been left below the guanacaste tree crowns (and thus in woody vegetation) and therefore harvested by rodents before the beetles could produce a generation. If guanacaste grew as an Indian village tree, however, life would have begun to look up for the beetle perhaps 1,000 to 5,000 years ago as agricultural systems developed in Central America.

With the introduction of livestock, the system may be now back to a rough approximation of the Pleistocene case, except that the adult guanacastes are being harvested without replacement, for timber and the livestock tend to generate diffuse rectangular seed shadows in wind-blown pastures.

There is a conspicuous, unapproached question in this system. Could *S. generalis* have a different usual host and the records on guanacaste in central Panama be simply due to variation in host specificity? We think not, owing to the thoroughness of our collections.

Acknowledgment

R. Johnson and M. Johnson provided valuable help in the field, and R. Conway, D. Kirkbride and R. Kistler conducted the laboratory experiments and helped with seed collections in the field. NSF grant DEB 78–05962 (CDJ)and DEB 80–11558 (DHJ) provided funds for this research.

REFERENCES CITED

Janzen, D. H. 1980. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. J. Ecol. 68: 929–952.

1981a. Digestive seed predation by a Costa Rican Baird's tapir. Biotropica (in press)

1981b. Guanacoste tree seed-swallowing by Costa Rican range horses. Ecology 62: 587–592.

1981c. *Enterlobium cyclocarpum* seed passage rate and survival in horses, Costa Rican Pleistocene seed dispersal agents. Ibid. 62: 593–601.

Janzen, D. H., and M. L. Higgins. 1979. How hard are *Enterolobium cyclocarpum* (Leguminosae) seeds? Brenesia 16: 61–67.

Johnson, C. D. 1981a. Relations of *Acanthoseclides* with their plant-hosts, pp. 73–81. *In* V. Labeyrie [ed.], The ecology of bruchids attacking legumes (pulses). Series Entomologica, Vol. 19. W. Junk. 233 pp.

1981b. Interactions between bruchid (Coleoptera) feeding guilds and behavioral patterns of pods of the Leguminosae. Environ. Entomol. 10: 249–253.

Johnson, C. D., and J. M. Kingsolver. 1973. A revison of the genus *Sennius* of North and Central America (Coleoptera: Bruchidae). U.S. Dep. Agric. Tech. Bull. 1462. 135 pp.

1976. Systematics of *Stator* of North and Central America (Coleoptera: Bruchidae). Ibid. 1537. 101 pp.

Johnson, C. D., and C. N. Slobodchikoff. 1979. Coevolution of *Cassia* (Leguminosae) and its seed beetle predators (Bruchidae). Environ. Entomol. 8: 1059–1064.

Kingsolver, J. M., and C. D. Johnson. 1978. Systematics of the genus *Mimosestes* (Coleoptera: Bruchidae). U.S. Dep. Agric. Tech. Bull. 1590. 106 pp.