

SHORT COMMUNICATION

A bruchid beetle and a viable seedling from a single diaspore of *Attalea butyracea*

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Seeds of the palm *Attalea butyracea* (formerly known as *Scheelea zonensis* in Panamá and *Scheelea rostrata* in Costa Rica—Bradford & Smith 1977, Forget *et al.* 1994, Henderson 1995) are contained within stony endocarps. For the purposes of this paper, individual fruits or their seed-bearing endocarps will be referred to as diaspores; all of the seeds of a given fruit are surrounded by the stony wall of a single indehiscent endocarp. Although single-seeded diaspores are the norm for *A. butyracea*, two- and three-seeded diaspores are also produced. The frequency of multiseeded diaspore production is reported to vary within the geographic range of *A. butyracea*. Smith (1975) and Bradford & Smith (1977) found that 23% of diaspores were two-seeded and 4% were three-seeded in Guanacaste, Costa Rica, while the respective frequencies for Barro Colorado Island (BCI), Panamá were 5% and 0.2%. They proposed that the frequency of multiseeded fruits in *A. butyracea* varies geographically as a result of evolutionary responses by populations of *A. butyracea* to historical differences in the relative risks of attack by rodent vs. insect seed-predators, primarily by beetles in the family Bruchidae (Bradford & Smith 1977, Smith 1975).

Bradford & Smith (1977) showed that predation by rodents accounted for a significantly higher proportion of seed mortality for undispersed diaspores found directly beneath adult palms in their Panamanian site as compared to

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their Costa Rican site. Furthermore, seeds of multiseeded diaspores attacked only by bruchids had higher probabilities of survival than seeds of multiseeded diaspores attacked by rodents, since rodents frequently destroyed all of the seeds in multiseeded diaspores (Bradford & Smith 1977). Larval bruchids, in contrast, rarely breach the endocarp walls that separate the seeds of multiseeded diaspores, perhaps due to negative selection on exploratory digging through endocarp walls, since inadvertently creating holes to the outside environment too early in larval development may have high associated costs (e.g. increased exposure to pathogens). Smith (1975) and Bradford & Smith (1977) speculated that multiseeded diaspores are favoured in locations where rodent seed-predators are relatively rare, yet bruchid beetles remain relatively common. In such cases, multiseeded diaspores provide the opportunity for one seed to be eaten by a bruchid while at least one other seed is spared if the diaspore were infested with a single bruchid beetle. However, to date no diaspore of *A. butyracea* has been reported to have given rise to both a seed-predatory insect and to a seedling. Herein we provide the first report of such an occurrence, together with the results of experiments to determine the germination probabilities and bruchid survival probabilities of seeds buried to different depths. We also discuss the limitations of studies to date for determining the net consequences of seed-related activities by granivorous rodents for the evolution and population dynamics of *A. butyracea* and its bruchid seed-predators.

We collected 126 bruchid-attacked diaspores of *A. butyracea* from the forest floor on BCI in mid-July 1993. No more than 20 diaspores were collected from beneath any one adult. The bruchid seed-predators of *A. butyracea* on BCI do not oviposit on the diaspores until the inner stone or endocarp is exposed (Bradford & Smith 1977; Wright 1983, 1990). We therefore chose diaspores from which the husk (exocarp) and pulp (mesocarp) had been removed, presumably by vertebrate frugivores, and which had at least one bruchid egg attached to the endocarp. Although we did not quantify bruchid attack at this stage, most diaspores had at least one bruchid entrance hole in the endocarp. Forget *et al.* (1994) passed a thin needle through the entrance holes they encountered to determine which holes fully perforated the endocarp. We did not use this technique since we did not want to damage or kill any bruchids that might be in the holes or that had entered seeds, since we were interested in the survival probabilities of those bruchids.

Additionally, we collected > 200 mature and intact (and therefore not attacked by bruchids) diaspores of *A. butyracea* in early July 1993 from a population of palms along Old Gamboa Road, c. 16 km from the BCI site. No more than 30 diaspores were collected from beneath one adult. We allowed caged spiny rats (*Proechimys semispinosus*) to remove the fruit husks and pulp from these diaspores, to expose their endocarps to approximately the same extent as the bruchid-attacked diaspores we collected in mid-July (see above). We

selected 180 of the resulting diaspores whose endocarps remained intact and that had no evidence of bruchid attack (i.e. no bruchid eggs attached to the endocarp and no bruchid larval entrance holes through the endocarp).

We randomly assigned the bruchid-attacked diaspores to nine lots of 14 and diaspores without evidence of bruchid attack to nine lots of 20. In order to protect the diaspores from vertebrate seed-predators, each lot of diaspores was placed in a wire-mesh, 15-cm deep, cylindrical cage with a wire-mesh, 40-cm diameter, circular base and lid. On 24 July 1993 cages were buried, in the forest near the laboratory clearing on BCI, so that their bases were at one of three depths: 0, 2 and 5 cm below the soil surface. For cages in the 2 and 5 cm depth treatments, respectively, 2 and 5 cm of the sides of the cages were also buried, while 13 and 10 cm of the sides were exposed aboveground. All diaspores were in contact with the bases of their cages, such that the depth of burial for the seeds' most deeply buried sides corresponds to the depth of burial of the cages' bases. The cages were evenly spaced within an area of 60 m², such that all nearest-neighbour cages were at least 2 m apart and treatments were located at random with respect to the locations chosen for the cages.

The cages were periodically checked for seedling emergence. All diaspores that had produced a seedling by 6 August 1994 were removed on that date, were examined for bruchid exit holes, and were opened in a vice to determine the number of seeds per diaspore. Seeds of *A. butyracea* have been shown to germinate as much as 3 y after maturation (Harms & Dalling 1995), so the remaining diaspores were left in place for > 2.5 y more, during which time they continued to be periodically checked for seedling emergence. Upon termination of the experiment on 14 March 1997 all remaining diaspores were removed from the cages, were examined for bruchid exit holes, and were opened to determine the number of seeds which had produced a seedling or a bruchid. Seven diaspores disappeared from the cages during the course of the experiment, presumably due to complete decomposition. It is unlikely that diaspores were removed from the cages since we did not notice any holes or breaks in the wire-mesh cages.

Of the 124 bruchid-attacked diaspores that we recovered, we observed a single diaspore give rise to both a bruchid exit hole and a viable seedling (Table 1). This diaspore came from the surface treatment and had germinated one seedling sometime between 15 June 1994 and 6 August 1994 (when it was removed from its cage). Although we did not capture the emerging bruchid, we are confident that it was an adult bruchid beetle, at least two species of which are known to infest seeds of *A. butyracea* in Central America and which leave characteristic exit holes in the endocarp (Bradford & Smith 1977, Forget *et al.* 1994, Janzen 1971b, Johnson *et al.* 1995, Smith 1975, Wilson & Janzen 1972; Wright 1983, 1990). Upon dissecting the diaspore we found that the beetle and the seedling emerged from separate seeds, i.e. the diaspore was two-seeded.

Table 1. Number of germinating diaspores of *Mitella biyracea*, comparing bruchid-attacked vs. non-bruchid infested (i.e. intact) diaspores, subjected to three burial depths. All multiseeded diaspores that gave rise to a seedling and/or a bruchid are indicated with superscripts.

| Bruchid treatment | Burial depths (cm) | Number of diaspores at the beginning of the experiment | Number of diaspores that germinated at least one seedling, but produced no bruchids | Number of diaspores that produced at least one bruchid, but never germinated a seedling | Number of diaspores that germinated a seedling and produced a bruchid | Total number of diaspores recovered upon termination of the experiment |
|-------------------|--------------------|--------------------------------------------------------|-------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------|-----------------------------------------------------------------------|------------------------------------------------------------------------|
| No bruchids | 0 | 60 | 34 | 0 | 0 | 58 |
| | 2 | 60 | 26 | 0 | 0 | 60 |
| Bruchid-attacked | 5 | 60 | 22 | 0 | 0 | 57 |
| | 0 | 42 | 9 | 23 ¹ | 1 | 40 |
| | 2 | 42 | 13 ² | 23 ¹ | 0 | 42 |
| | 5 | 42 | 9 | 21 | 0 | 42 |

1. Including two two-seeded diaspores in which a bruchid emerged from both seeds of each diaspore.

2. Including two two-seeded diaspores in which both seeds of each diaspore produced a seedling.

Of the 175 initially unattacked diaspores we recovered, no diaspores gave rise to a bruchid beetle (Table 1). A significantly larger proportion of unattacked diaspores produced seedlings than bruchid-attacked diaspores (46.9 vs. 25.8%, respectively; $\chi^2 = 13.6$, $df = 1$, $P < 0.05$). However, there was no evidence that burial, at least down to 5 cm, affected germination success (44.9% of buried diaspores gave rise to > 1 seedling, while 34.8% of unburied diaspores did; $\chi^2 = 2.8$, $df = 1$, $P > 0.05$). Furthermore, there was no evidence that burial adversely affects the development of bruchid beetles, at least in terms of the probability of an exit hole appearing in a bruchid-attacked diaspore ($\chi^2 = 0.8$, $df = 2$, $P > 0.05$) (Table 1).

It should be noted that none of the single-seeded diaspores nor any of the individual seeds of multiseeded diaspores of *A. butyracea* produced both a seedling and an insect seed-predator. This is in striking contrast to several large-seeded woody dicot species that also grow on BCI and are capable of tolerating extreme levels of seed-damage inflicted by seed-predators. *Beilschmiedia pendula* (Lauraceae), *Gustavia superba* (Lecythidaceae) and *Prioria copaifera* (Fabaceae) are examples of species whose large seeds routinely produce viable seedlings even after giving rise to one or several adult insect seed-predators (Dalling *et al.* 1997, Dalling & Harms 1999). The average level of damage to a seed expected from a seed-predator depends in part on what part or parts of the seed are being consumed (e.g. cotyledons vs. embryo) and in what quantities (which is especially relevant if the embryo remains intact).

The pattern of multiseeded fruit production in *A. butyracea* is similar to that found in several wind-dispersed dicot species on BCI (Augspurger 1986, Augspurger & Hogan 1983). For example, *Lonchocarpus pentaphyllus* (Fabaceae) produces two-, three- and four-seeded fruits at low frequency and multiseeded fruits of *L. pentaphyllus* rarely suffer complete loss of all seeds to seed-predatory insects (Augspurger & Hogan 1983). Among the striking differences between *A. butyracea* and *L. pentaphyllus*, however, are their seed-dispersal strategies; *L. pentaphyllus* relies on wind to disperse its winged seeds and seed number per fruit significantly alters dispersal distances (Augspurger & Hogan 1983). Whether multiseeded diaspores of *A. butyracea* are differentially dispersed, i.e. differentially scatter-hoarded by rodents, remains among the unanswered questions regarding the natural history of this palm.

The current study also indicates that bruchid attack is not a *fait accompli* in seed death; 25% of initially bruchid-attacked single-seeded diaspores produced seedlings, presumably due to bruchid death early in development (Janzen 1971b; Wright 1983, 1990). It is also possible that some larval bruchids never fully penetrated the endocarps since we did not attempt to determine whether the entrance holes in these endocarps passed completely through the endocarp walls as did Forget *et al.* (1994).

We observed that both a pre-dispersal seed-predator (*sensu* Janzen 1971a) and a viable seedling can emerge from the same diaspore of *A. butyracea* under

natural, albeit experimental, conditions if the diaspore contains multiple seeds. However, to understand the evolutionary significance of multiseededness and its variation throughout the geographic range of this or any palm species, the relative frequencies with which single-seeded and multiseeded diaspores give rise to at least one seedling must be determined in the field. Furthermore, since diaspores of *A. butyracea* are commonly dispersed by scatter-hoarding rodents throughout the palm's range (Forget *et al.* 1994, Janzen 1971b, Wilson & Janzen 1972), the relative frequencies of germination success of both dispersed and undispersed diaspores must be accounted for (Price & Jenkins 1986), as opposed to simply scoring seed viability for those diaspores that were left unburied by rodents, as in Janzen (1971b) and Bradford & Smith (1977).

Since burial does not seem to affect the probability of bruchid beetle emergence from bruchid-attacked diaspores of *A. butyracea*, estimates are needed of the probability of seed germination after burial by a scatter-hoarding rodent, taking into account the probability of bruchid-infestation before burial. Estimates of the proportions of diaspores buried, eaten or left by rodents, as in Forget *et al.* (1994), are not sufficient to determine the net effects of rodents on a population of *A. butyracea*, since these estimates do not take into account the subsequent effects of bruchids on seeds (both buried and unburied) left uneaten by rodents. Despite speculation that some palm species require scatter-hoarding mammals to survive in the face of bruchid-attack (Smythe 1989), before we are able to ascertain whether or not scatter-hoarding by rodents has a net positive or negative effect on *A. butyracea* in any given location we need estimates of the probability of germination vs. death (by bruchids or otherwise) for diaspores that are naturally dispersed vs. not dispersed by scatter-hoarders, as has been suggested by Price & Jenkins (1986) for understanding granivorous rodent-plant interactions in general.

Finally, the magnitude of the indirect effects of rodents on bruchid populations, especially the degree to which rodents limit *Attalea*-specific bruchids (Forget *et al.* 1994), depends in part on the fate of buried bruchids. Unfortunately, we do not know the fate of the bruchids that created the exit holes in the buried diaspores. It is possible that even though bruchids are capable of completing their development within buried seeds they nevertheless are adversely affected by burial, perhaps by being unable to dig their way up to the soil surface. However, we find it unlikely that bruchids are incapable of digging up from buried seeds to the soil surface in the field, since one of us has observed several bruchid beetles dig up through 10-cm of soil in plant pots in which seeds of *A. butyracea* had been buried and placed in a growing house (K. E. Harms, *pers. obs.*). The relative proportions of bruchids emerging from buried seeds are unknown albeit important for determining the indirect consequences of rodents for the population dynamics of *A. butyracea*'s bruchids.

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