

Arthropod communities and succession in baobab, *Adansonia rubrostipa*, fruits in a dry deciduous forest in Kirindy Forest Reserve, Madagascar

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From an insect's perspective, fruits of many plant species are an ephemeral resource such as carrion (Payne 1965; Tabor *et al.* 2004), dung (Koskela 1972; Koskela & Hanski 1977) or rotting wood (Fager 1968): all these systems are relatively small and distinct, consist of organic matter and undergo a clear decomposition process, with several stages of decay (Schoenly & Reid 1987), characterized by specific fauna. Frugivorous insects, particularly Diptera, Coleoptera, Hemiptera and Lepidoptera, frequently invade fruits/seeds during development on maternal plants (*e.g.* Janzen 1969, 1971; Lachaise 1977; Lachaise *et al.* 1982; Fukumoto & Kajimura 2001); fruit invasion and post-dispersal seed predation continues after fruit falls (Winston 1956; Janzen 1969; Lachaise *et al.* 1982; van Klinken & Walter 1996). The sequence of invasions leading to their disintegration might be complex, especially in large fruits. In the only comprehensive study on succession in fruits, Winston (1956) found a wide range of organisms, including fungi, crustaceans, molluscs, arachnids and insects, in decomposing acorns of *Quercus rubra*. He traced several pathways of acorn decomposition, covering the entire sequence from intact nuts to assimilation of shell remains into soil humus. Other studies on invertebrate fruit invasion generally focused on Diptera breeding in fleshy fruits (Lachaise 1977; Lachaise *et al.* 1982; Nunney 1990; Hodge & Arthur 1996; Klinken & Walter 1996), but not on fruits as microcosms, undergoing heterotrophic succession by various organisms with concurrent decomposition, in a manner analogous to carrion or dung.

Not all fruits can support a wide variety of arthropod fruit predators, and vertebrate frugivory often interrupts insect succession (Sallabanks & Courtney 1992; van Klinken & Walter 1996). However, fruits of the Malagasy baobab, *Adansonia rubrostipa* (Jum. & H. Perrier 1909), are capable of hosting diverse invertebrate communities, which may develop largely without disturbance. The

large, globose, dry berries develop during the dry season. They are shed towards the beginning of the rainy season, in October–December (Baum 1995, 1996). A firm, woody pericarp up to 5 mm thick protects numerous large (up to 16 × 12 × 8 mm – Baum 1995) seeds in hard seed coats, enveloped in dry, spongy matrix. Both pulp and seeds are of high nutritive value (Osman 2004), which attracts several animal species. Human exploitation of baobab fruits is intensive and relatively well assessed, especially in African *Adansonia digitata* (*e.g.* Baum 1996; Du Puy 1996; Gebauer *et al.* 2002). Less is known about faunal frugivory, and existing observations are limited to vertebrates, with invertebrate fruit invaders only briefly mentioned (Baum 1996; Du Puy 1996). However, in the dry deciduous forest of Kirindy we found a much larger proportion of *A. rubrostipa* fruits damaged by insects than destroyed by vertebrates. Many of these fruits hosted large and diverse arthropod communities, responsible for rapid decomposition of pulp and seeds. Therefore we attempted to survey multi-species invertebrate assemblages in the fruits of *Adansonia rubrostipa* in Kirindy, and describe arthropod succession inside the fruits and their role in fruit decomposition.

The study was carried out in November 2004 at the beginning of the rainy season, in a dry deciduous forest in Reserve Forestière de Kirindy, on the western coast of Madagascar. Data were collected in a PS1 grid system (area: approximately 20 ha), established in unlogged forest west of Deutsch Primate Zentrum field station. The weather was sunny and no precipitation was recorded during the study.

Adansonia rubrostipa fruits, dropped in that season, were collected from the ground under the trees throughout the grid system. They were collected over five days from under 42 trees, randomly selected from 72 fruiting baobabs in the PS1 system. If there were fewer than 10 fruits under a particular tree, excluding fragments of fruits destroyed prematurely, or those destroyed

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by mammals on the ground, with only pericarp remaining, they were all sampled. In 11 cases where there were more than 10 fruits under a single tree, a sample of 10 was taken, consisting of the smallest and largest fruits and a random sample of medium-sized fruits. Size was the only criterion used.

Fruits were analysed on the same day. They were weighed and fruit surface and presence and types of openings, namely insect or mammal hole or crack, were described. The fruit was then crushed to reveal the contents, and manually inspected for invertebrates present. Animals were identified to morphospecies (Cranston & Hillman 1992; Oliver & Beattie 1993) and counted where feasible. Sample specimens were retained in 70 % ethanol for further identification purposes. Finally, the condition of both pulp and seeds was graded from 0 (completely destroyed) to 4 (intact), roughly reflecting the proportion of pulp/seeds in good condition. Total fruit condition was calculated as the sum of 'pulp condition' and 'seed condition' grades, thereby ranging from 0 to 8.

Data were analysed with Statistica v. 6.0. (Statsoft 2001)

In total, 269 *Adansonia rubrostipa* fruits were inspected. Fruit weights ranged from 2 to 185 g. 40 % of fruits did not have external openings, which would allow opportunistic invertebrates to invade the fruit; 52 % had holes drilled by insect through the pericarp, 2 % had mammal-made holes (but content largely intact), while in 6 % the pericarp was crushed as a result of hitting the ground.

Fruits collected during the study represented a wide range of decomposition stages, from intact to highly degraded. Although seeds tended to degenerate slightly more rapidly, pulp and seed condition were highly correlated (Spearman's correlation test, $n = 256$, $\rho = 0.708$, $P < 0.001$). Fruit condition grading suggested more or less equal distribution of fruits between stages of decay 1–7 ($\chi^2 = 12.5$, d.f. = 6, $P = 0.051$), and a fifth of fruits were awarded each of extreme grades (0 or 8). However, there was a large variance between trees (two-way ANOVA, with tree as a random factor and fruit weight as a continuous variable: the effect of tree $F_{41,226} = 3.68$, $P < 0.001$). No effect of fruit size on its condition was detected. Opened fruits were generally in worse condition than unopened ones ($t = 9.458$, d.f. = 268, $P < 0.001$). However, in most of the fruits without external

openings there was some damage – only 42 % showed no traces of insect feeding inside; by contrast, only 7 % of opened fruits (mostly crush-opened) showed no traces of feeding.

Thirty-four invertebrate morphospecies, belonging to 13 orders, were found inside baobab fruits. They are listed and briefly described in Table 1. Unfortunately, we were unable to identify the phytophages to species level. Inside one fruit, up to six arthropod morphospecies, belonging to up to five orders, were found. Fruit size influenced species number, *i.e.* larger fruits hosted more morphospecies (two-way ANOVA, with tree as a random factor and fruit weight as a continuous variable: the effect of fruit weight $F_{1,226} = 44.01$, $P < 0.001$) and orders ($F_{1,226} = 28.31$, $P < 0.001$); however, there was a considerable variation between trees (ANOVA for the number of species, as above: $F_{41,226} = 2.36$, $P < 0.001$). Several fruit invaders were more often found in larger fruits, including the most abundant: curculionids (logistic regression, $n = 269$, Wald = 100.9, $P < 0.001$), pyralids ($n = 269$, Wald = 93.5, $P < 0.001$) and tenebrionids ($n = 269$, Wald = 103.7, $P < 0.001$).

Damaged fruits hosted more diverse arthropod communities. The number of species increased with the progress of fruit decay ($r^2 = 0.038$, d.f. = 267, $P = 0.001$). A comparison of fruit condition with the frequency of invaders (Fig. 1) suggests taxa preferences to particular stages of fruit decomposition.

Baobab fruits were found to host a variety of invertebrate species (Table 1). In fruits collected in a small, uniform fragment of forest we found 34 invertebrate morphospecies, belonging to 13 orders, despite the fact that microinvertebrates such as mites were likely to avoid detection. Furthermore, problems with specimen identification (mostly in the field) made distinguishing between related species in collected samples difficult – particularly as some of the insects were collected at larval stages, and there was no chance of raising them to adults. Nevertheless, *Adansonia rubrostipa* fruits from Kirindy Forest host one of the highest arthropod species numbers recorded for fruits of a single plant species (Nakagawa *et al.* 2003; van Klinken & Walter 1996). These insects belong to distinct ecological groups, generally similar to those distinguished among carrion or dung decomposers (Payne 1965; Koskela & Hanski 1977; Tabor *et al.* 2004). Weevils and pyralid moths are probably obligatory baobab fruit-feeders, entirely

Table 1. Arthropod morphospecies found in *Adansonia rubrostipa* fruits in Kirindy Reserve, Western Madagascar.

Taxon	Freq. ¹ (%)	Comments
Coleoptera		
Curculionidae:	13.8	Young adults, pupae and larvae found; up to 9 individuals in one fruit. Feed both on pulp and seeds.
<i>Cryptorhynchini</i> sp.	(+1.8)	
Tenebrionidae sp.	14.0 (+0.8)	Main secondary fruit invaders, sometimes abundant – >100 in one fruit. Feed on pulp, often destroying it completely.
Nitidulidae, 2 spp.	1.9	In damaged fruits, a few individuals per fruit.
Cucujoidae, 2 spp.	1.5	In damaged fruits, a few individuals per fruit.
Scolytidae spp.	1.9	Feed on pulp of fruits in good condition, several individuals per fruit.
Dermestidae, 2 spp.	0.8	Single larva found twice, in highly damaged fruits.
Lepidoptera		
Pyralidae sp.	6.3 (+11.1)	Feed on pulp and seeds. Drill large holes in fruit shell; only larvae and pupae found inside the fruit, up to 11 per fruit.
Unknown family, 1 sp.	5.9	Larvae and pupae found in highly decomposed fruits.
Hymenoptera		
Formicidae		
<i>Crematogaster</i> , 2 spp.	2.2	Isolated individuals or large nests.
<i>Monomorium</i> sp.	4.1	2 to 15 individuals per fruit.
<i>Tetraponera</i> sp.	0.4	A few individuals per fruit.
<i>Leptothorax</i> sp.	1.1	Single individuals.
Sphecidae, 2 spp.	0.8	Build few-celled nests filled with paralysed spiders or caterpillars in highly decomposed fruits.
Ichneumonidae sp.	1.1	Probably the parasitoids of curculionids.
Isoptera		
Termitidae	5.6	Completely destroy pulp, then seeds, then pericarp; form temporary nests or foraging colonies. Sometimes a few individuals per fruit, usually a few hundred.
<i>Trinervitermes</i> sp.		
<i>Cryptotermes</i> sp.		
Hemiptera		
Lygaeidae sp.	5.5	Secondary fruit invader, locally abundant. Generally not more than 20 individuals per fruit.
Pyrrhocoridae	0.4	Abundant in the forest, commonly feeds on pulp of smashed fruits. Found inside the fruit once.
<i>Dysdercus</i> sp.		
Psocoptera		
Liposcelidae spp.	4.4	Mycetophages; found in decomposed fruits, usually few individuals, but sometimes very numerous.
Orthoptera		
Gryllidae, 3 spp.	1.5	Nymphs found in highly decomposed fruits.
Diptera		
Tipulidae sp.	0.4	Found once, in totally decomposed fruits.
Blattaria , 2 spp.		
	0.8	Single nymphs, in highly damaged fruits.
Chilopoda , 2 spp.	1.5	} Found in the fruits singly. Predators from the second trophic level; might be using baobab fruits as hideouts, and/or as supplementary hunting grounds.
Arachnida: Araneae , 3 spp.	3.0	
Arachnida: Pseudoscorpionida , 1 sp.	0.8	

1: proportion of fruits in which a taxon was found; in brackets, the proportion of fruits in which traces of feeding and remains (droppings, pupa shells) of the given morphospecies were found.

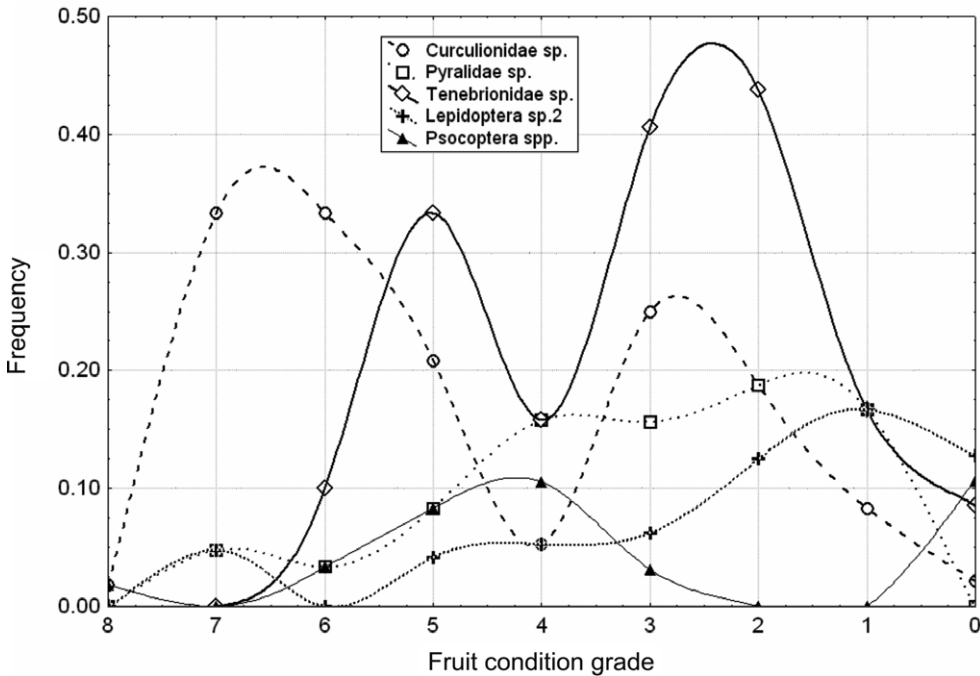


Fig. 1. Condition of *Adansonia rubrostipa* fruit versus frequency of common fruit invaders. Curves were fitted to data points using a bicubic spline smoothing procedure.

dependent on these fruits for reproduction. Tenebrionid beetles commonly feed and breed inside the fruits, it is not known whether they use other resources. One species, a parasitoid ichneumon wasp, feeds on obligatory fruit predators. Other fruit-associated insects are likely to be more generalistic: e.g. lygaeid bugs are known to feed on seeds, and booklice generally feed on fungus growing in decomposing matter. Predatory species, such as spiders, book scorpions and some ants, might use the fruits as hunting grounds, as they are densely populated and safe from larger predators. Many of the invertebrates found were probably adventive species – using highly damaged fruits as a habitat, or just shelter. This group could include centipedes, crickets, tipulid flies and sphecid mud wasps. Termites and *Crematogaster* ants are a distinct category: they monopolize some fruits and transform them into nests or feeding colonies, lasting until all the resources they use are gone. Participation of generally saprophagous or adventive species in the invertebrate community seem to increase with decreasing fruit condition, when baobab fruit content loses its distinctiveness and becomes accessible to non-specialists.

Results obtained, together with small assays not described here, enabled us to suggest a general pattern of baobab fruit invasion by invertebrates (Fig. 2). The first animals invading fruits are weevils (Curculionidae: Cryptorhynchini) and moths (Pyralidae), infesting fruits whilst still on the tree, probably during development. In each case the insect, or their obvious traces or remains, was found in a sixth of the fruits; the two rarely coexisted. They feed on both pulp and seeds, but are rarely responsible for serious damage to the seed population. It is likely that the weevils have no means of leaving the fruit on their own, without external factors opening it, as many fruits contained young adult beetles, eager to escape when the fruit was open. By contrast, pyralid moths are almost certainly able to leave the fruits: no adult moth was ever found inside, and in all the fruits with moth remains (droppings, pupa shells) there were large holes drilled through the pericarp, possibly made by larvae just before pupation. The holes provide ideal gateways to pulp and seeds for secondary invaders. The most abundant of them, tenebrionid beetles (found in 15 % of fruits), enter fruits while still on the tree, and are often present in large numbers, destroying fruit pulp completely.

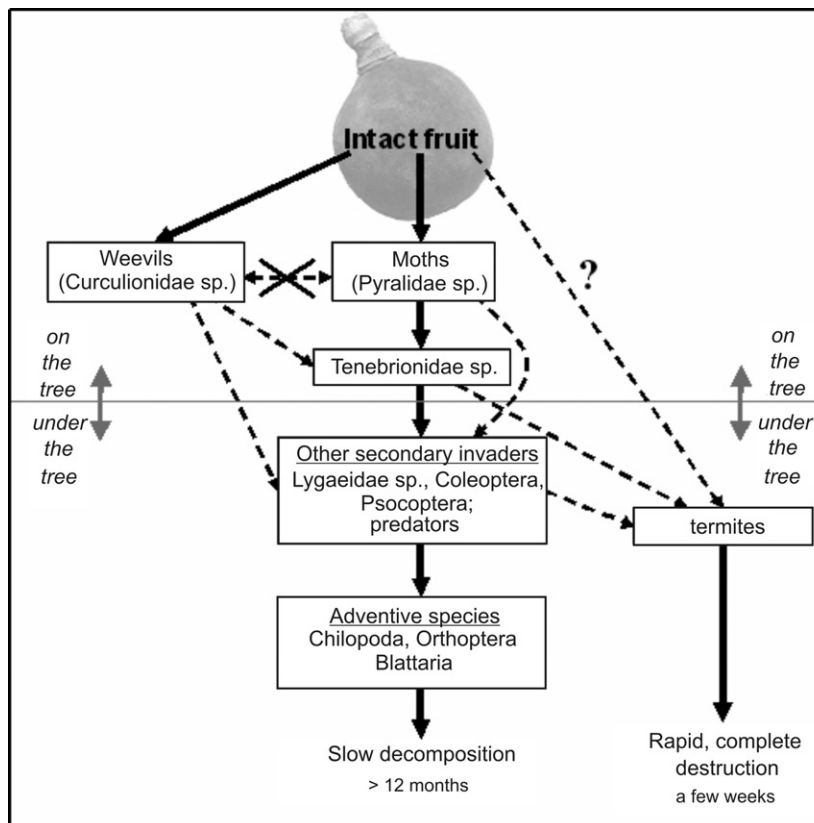


Fig. 2. General pattern of invertebrate succession in *Adansonia rubrostipa* fruits in Kirindy Forest Reserve.

On the ground, while the former taxa are still present, several other groups invade the fruit and destroy seeds and pulp rapidly: bugs (Lygaeidae), nitidulid and cucujoid beetles, later booklice (Psocoptera) and moths (Lepidoptera sp. 2). In 15 % of fruits graded 1 to 6 there was some fungal growth. Predatory species also visit large fruits: book scorpions, spiders and ants were occasionally found. This mid-successional stage, fruit condition grades 2–5, is characterized by the highest species diversity, with up to 6 species detected in one fruit. At that time, several smaller holes appear in the fruit shell; it is not clear which species are responsible for drilling them, it is also not known which insects destroy seeds left by curculionids and pyralids. Some fruits are monopolized by ants or termites and transformed into nests or foraging colonies; this might also happen at the stage when the fruit becomes accessible, but still has high nutritional value. Highly damaged fruits (grade 0–1) become home to a different set of animals, consisting of potentially adventive species: centi-

pedes, crickets, mud wasps, cockroaches and others, using them as hideouts and maybe, to some extent, feeding on decomposed pulp and seeds or on decomposers. In Kirindy Forest it takes over a year for the fruit shell to decompose completely (Du Puy 1996; this study), unless termites accelerate the process. Termite-invaded fruits are destroyed rapidly: pulp, seeds, then pericarp might be gone within few weeks. We encountered several baobab fruits eaten to a certain extent; although the actual importance of termite predation was not quantified, it is high locally.

It is difficult to extrapolate the results from this study to other habitats. Samples from other parts of Kirindy Forest did not differ in species composition or fruit condition, while in a sample taken from a clustered group of *A. rubrostipa* trees growing in an unprotected area 30 km north of Kirindy the same insect species as in Kirindy occurred in different configurations, e.g. weevils frequently coexisted with pyralid moths. The same pyralid,

curculionid, tenebrionid and lygaeid species were found in a few *Adansonia rubrostipa* fruits analysed in mid-December in the dry spiny forest of Ifaty, around 370 km south from Kirindy. However, without a systematic study nothing can be said about large-scale geographic or temporal variation in fruit arthropod communities. Such a study could add to our knowledge on utilization of the same patchy resource in three spatial scales: between ecosystems, between trees within a habitat, and between fruits under a particular tree.

Invertebrate communities inside other Malagasy baobab species' fruits, with differing fruit shell, pulp and seed characteristics, as well as to environmental factors in the trees' habitats (Baum 1995, 1996) might be very different. More interesting would be the comparison of arthropod succession patterns inside the fruits of Malagasy baobabs and their African (*Adansonia digitata*) and Australian (*A. gibbosa*) relatives, as the fruit predator communities must have developed and evolved independently, since the speciation of the baobabs through long-distance dispersal which occurred not less than seven millions years ago (Baum *et al.* 1998). For example, fruits of *A. gibbosa* have a fragile pericarp, which often cracks when still on the tree (Baum 1995): has the protective shell become useless in the absence of specialized seed predators? If this was the case, it would suggest that fruit characteristics, along with fruit insect communities, might lead to conclusions about the

evolutionary history of plants in their present habitats. Furthermore, the comparison of *Adansonia digitata* fruit communities in mainland Africa and in areas where the species was introduced tens or hundreds years ago, including Madagascar and several areas throughout the tropics (Baum 1995), would provide an important insight into local invertebrates' response to a new, abundant resource. Learning about the succession patterns in the absence of specialized fruit predators initiating the invasion could add to our knowledge on arthropod utilisation of new ecological niches, as well as improving the understanding of biology of introduced plant species.

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