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NATURAL HISTORY OF A WIND-POLLINATED CENTRAL AMERICAN DRY FOREST LEGUME TREE (*ATELEIA HERBERT-SMITHII* PITTIER)

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ABSTRACT

Ateleia herbert-smithii Pittier (Papilionoideae) is a moderate-sized dioecious tree endemic to about 80 km^2 of Santa Rosa National Park (250–350 m elevation) within the widespread dry forest of northwestern Costa Rica, and to an equally small area of severely perturbed dry forest in central western Nicaragua. This paper summarizes 11 years of close observation of this tree in Santa Rosa. *A. herbert-smithii* is unambiguously wind-pollinated (although the male trees are heavily visited by pollen-collecting social bees), and is the only known wind-pollinated legume in the world (however, other members of the genus are probably also wind-pollinated). Males produce pollen in pulses, and the females are continuously receptive for several weeks. Flowering and fruiting was synchronized within the population at two-year intervals from 1974 to 1984, but this perfect synchrony was disrupted by an odd-year and population-wide flowering in 1985. A large adult *A. herbert-smithii* may produce as many as a million one-seeded fruits in a crop, but more than 90% of the seeds in most crops are killed by the larvae of a single species of a monophagous weevil (Curculionidae: *Apion johnschmitti*) while the fruits are green and the seeds are just developing. In most cases, it appears that the weevils are sufficiently efficient that seed predator satiation does not occur even in the largest seed crops; instead most seed escape appears to be due to various kinds of "errors," such as when there are two seeds in a fruit and the weevil larva eats only one. The mature dormant seeds are rejected as food by the common generalist seed predator in Santa Rosa, the spiny pocket mouse (Heteromyidae: *Liomys salvini*). The foliage of *A. herbert-smithii* is eaten by very few species of insects and not browsed by vertebrates; it is relatively free of phenolics but very rich in aromatic compounds. The wind-dispersed fruits move the seeds up to several hundred meters into open pastures. If the pasture is fire-free, *A. herbert-smithii* is an aggressive colonizer and shades out the grass. While the large adults persist in secondary succession for up to 100–200 years, recruitment does not occur in forest shade and the species gradually disappears except in oak forest and a few adjacent deciduous forest types. The very small geographic distribution of this tree appears to be due to a combination of its dioecious behavior, its wind-pollination, its wind-dispersal, and its slow rate, for a tree of early successional stages, of reaching an age of abundant seed production.

I. INTRODUCTION

Most species of lowland Mesoamerican trees have (had) broad geographic distributions, are pollinated by animals, and suffer zero to moderate predispersal seed predation. *Ateleia herbert-smithii* Pittier, a moderate-sized papilionoid legume tree (Figs. 1, 2), is a strong exception to all three generalizations. Here I describe the natural history of this tree in Santa Rosa National Park in northwestern lowland Costa Rica (35 km north of Liberia in Guanacaste Province, 0–350 m elevation, 10°50′N, 85°40′W); the park is occupied by one of the two known surviving *A. herbert-smithii* micropopulations. The natural history of this tree is of more than esoteric interest. It has the potential of becoming a widely introduced tropical fuelwood tree (Hughes & Styles, 1984, and this volume) and may also be introduced as a woody rapid colonizer in severely deforested habitats; its natural history deserves scrutiny as background for management and weed potential.

Its common name in Nicaragua is "palo prieto" (C. Hughes, B. T. Styles, R. Lopez, L. D. Gomez, pers. comm.), but in the Santa Rosa area it has no vulgar epithet. It is, however, sometimes

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C. H. STIRTON & J. L. ZARUCCHI (EDS.)—ADVANCES IN LEGUME BIOLOGY
MONOGR. SYST. BOT. MISSOURI BOT. GARD. 29:293–376. 1989.

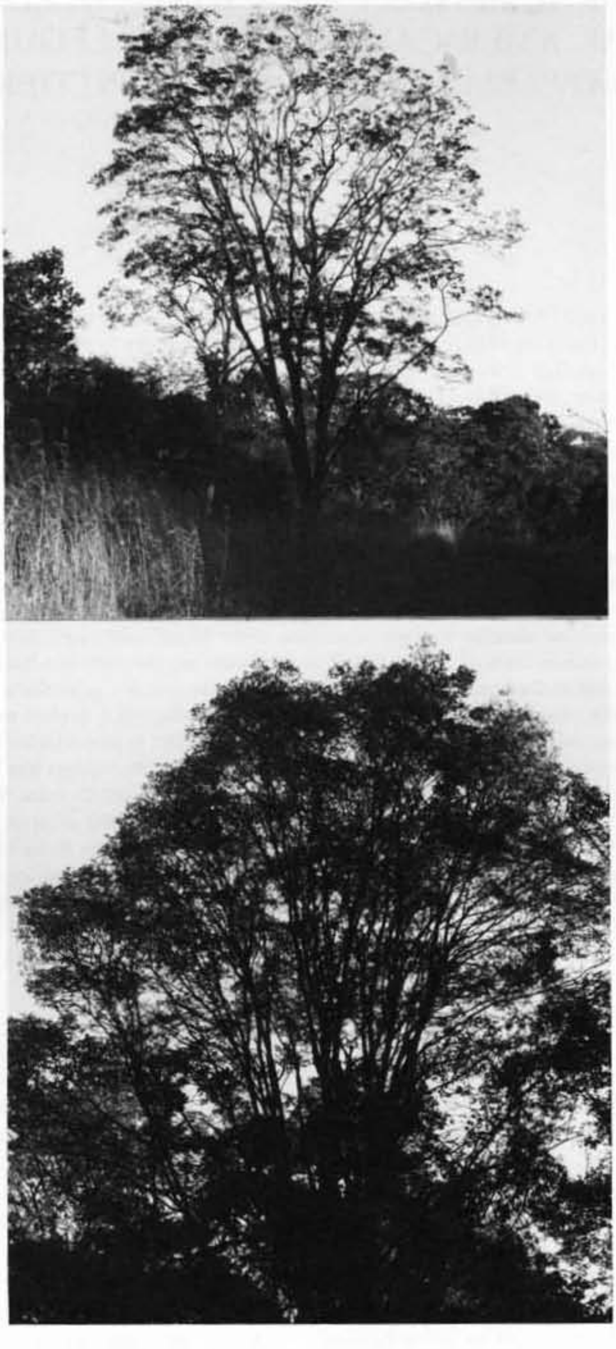

FIGURE 1. Crowns of two adult male *Ateleia herbert-smithii*. The upper tree is 15 m tall and the lower is 20 m tall. Both trees are in full leaf (August). They have more major and minor branches, and the branches are longer and thinner than is the case with females of the same age and exposure to sun. Santa Rosa National Park, Guanacaste Province, Costa Rica.

FIGURE 2. Crowns of two adult female *Ateleia herbert-smithii*. The upper tree is 10 m tall and the lower is 21 m tall (note 1.5 m tall person in crown for scale). Both trees are bearing heavy fruit crops in January; the upper tree is leafless and the lower tree has shed most of its leaves. Same locale as Figure 1.

given the name of "chaperno," a general term for *Lonchocarpus* species (Papilionoideae) in the Santa Rosa area. As it becomes the focus of biological interest, it is becoming known in the park as "ateleia" in both English and Spanish.

II. GEOGRAPHIC AND ECOLOGICAL DISTRIBUTION

Ateleia herbert-smithii was described in 1918 from an 18–m tall tree growing "5 miles south of Mamatoco, Magdalena Province, Colombia" (also recorded in flower "3 miles north of Bonda"), and Velva Rudd commented in 1968 (1968: 405) that "this distinctive species has never been re-collected. Two Colombian botanists, Dr. Armando Dugand and Dr. R. Romero-Castañeda, have unsuccessfully searched for living specimens. It may be another rare endemic that has succumbed to human activity." While it may be subsequently relocated as a small population or population fragment in Colombia, it is clearly not a widespread or common tree in that country. In 1975, Rudd identified specimens from the population of *Ateleia* growing in Santa Rosa National Park as *A. herbert-smithii* (pers. comm.), and herbarium specimens from that population have been deposited in the U.S. National Herbarium and the Missouri Botanical Garden (and then distributed from there as well). In 1982, Colin Hughes and Brian Styles discovered a small and highly disturbed population of *A. herbert-smithii* growing in the neighborhood of the village of El Bordo las Tinajas, about 2 km southeast of La Cruz de la India, on the road from Sebaco to Telica and Leon, Leon Department, Nicaragua (350–450 m elevation)(pers. comm.). In 1976, a specimen of *A. herbert-smithii* was collected 10 km north of Ciudad Dario (500 m; *D. Neill 1249*); Colin Hughes and Douglas Stevens are of the opinion that this collection is from the same population as grows at the El Bordo site (pers. comm.). Finally, the Missouri Botanical Garden has a 1983 collection of what appears to be *A. herbert-smithii* from north of Puerto Cabezas, Tuapi, Zelaya Department, Nicaragua (15 m; *J. C. Sandino 4039*; Flora of Nicaragua project). However, this site is much wetter and bears a very different vegetation from that occupying the other sites where *A. herbert-smithii* occurs; this suggests that the specimen may be misidentified.

The very patchy and local distribution of *Ateleia herbert-smithii* implied by the above records is probably an accurate statement about the pre- and post-Spanish distribution of the tree for the following reasons: 1) Plant collecting has been intensive in Mesoamerica, especially during the past 20 years for a variety of local and regional floras. The absence of *A. herbert-smithii* in collections probably means that it is absent in the field, although of course there still remains the possibility that some tiny population has been overlooked. 2) *Ateleia herbert-smithii* is a moderately large and conspicuous tree, and therefore it is unlikely to be missed by collectors. 3) *Ateleia herbert-smithii* is a tree of dry and intermediate elevation sites, and such sites have maximal accessibility to collectors. 4) Most of the Mesoamerican dry forest has been thoroughly agriculturalized. However, this habitat is still overlain with a filmy net of secondary successional fragments (fencerows, woodlots, secondary succession following pasturing and lumbering) that would harbor old adults and some juveniles of *A. herbert-smithii* as remnants of widespread populations if such widespread populations had been present when the European agriculturization of Mesoamerica began in the late 1500s. The ruderal behavior of this species (see below) reinforces this conclusion. However, its reliance on wind-pollination and its high seed mortality suggest a species that is easily extinguished if its density declines. If it originally occurred only as micropopulations on particular sites, many of these could have been obliterated by agriculturization (as Rudd suggested for the Colombian population). The latter two aspects of its biology mean that its overall rareness may be a human-generated artifact.

There are about 17 known species of *Ateleia* (all neotropical and most Mesoamerican [Rudd, 1968; Dillon, 1980]) and "all species are known from limited ranges with the exception of *A. gummifera*, which ranges throughout the West Indies and eastern coast of Central America"

(Dillon, 1980: 551). They all have similar flowers and fruits, and I suspect that all have (had) biologies quite similar to the one described below for *A. herbert-smithii* at Santa Rosa. *Ateleia herbert-smithii* is the only member of the genus that has been examined in detail in the field, in the greenhouse (C. Stirton, C. Hughes, and B. Styles), and in the laboratory (S. Tucker, this volume). I suspect that the ecological and geographic traits described here for *A. herbert-smithii* are (were) representative of most species of the genus except for *A. gummifera*.

The trees of Costa Rica have been very thoroughly collected over the past 100 years, many field biologists have worked throughout the country at least as long, and I have conducted field work for 25 years on the dry side of Costa Rica (e.g., Janzen, 1980). All of this collecting and observing has located one specimen of *Ateleia gummifera* (where the Río Higueron crosses the Interamerican Highway about 10 km south of Cañas in Guanacaste Province; S. Salas, pers. comm.) and the Santa Rosa population of *A. herbert-smithii* (which I first sampled in 1965 but could not identify at that time). I have been unable to locate any living plants of *A. gummifera* in the heavily agriculturized area where it was once collected (or elsewhere) and conclude that it has probably been recently extinguished in Costa Rica.

The detailed distribution of *Ateleia herbert-smithii* at Santa Rosa was determined by careful exploration on foot and in off-the-road vehicles, beginning within the obvious population lying along the 6 km of asphalt highway between the entrance of Santa Rosa National Park on the Interamerican Highway (35 km north of Liberia) and the park administration area, and then exploring outward until no more plants could be found. This method does not, however, census dormant seeds in the soil, seeds that may still be present in the 1–8-year-old newly cleared fields of Hacienda Ahogados (Finca Guapote) and Hacienda Rosa Maria along the southern boundary of Santa Rosa. The *A. herbert-smithii* population occupies approximately 80 km^2. It occurs in the area that is roughly bounded by the following locally well-known landmarks: the northern boundary of Hacienda Rosa Maria at its airstrip, to the Interamerican Highway, to about 1 km south of the entrance of Hacienda Poco Sol, to the Laguna Escondida in Santa Rosa, to 1 km west of the intersection of Quebrada Cebollines with the road to Playa Narango, to Quebrada Las Dantas, and thence back to the Rosa Maria airstrip. All of this area is about 250–350 m elevation.

Needless to say, if Santa Rosa National Park had been established only 20 km away along any compass direction, the population would either be as badly altered as is the El Bordo population in Nicaragua, or extinct, depending on the agricultural practices on the site. Santa Rosa has been a low-grade cattle ranch for over 400 years; that the population survived long enough to be incorporated into a national park is mostly due to the relatively low quality of the site for ranching and agriculture (Janzen, 1988); the long distance of the site from the population and political centers of Managua, Nicaragua, and San José, Costa Rica; and the ability of the plant to colonize and persist in dry forest successional microhabitats that are not burned annually.

Except for some *A. gummifera* records, virtually all *Ateleia* collection sites (Rudd, 1968; Dillon, 1980) are from Mesoamerican sites with a 5–7 month relatively rain-free dry season and a well-developed rainy season (1–2 m rainfall). South of the Isthmus of Tehuantepec in southern Mexico, these sites are often occupied by lowland oaks (e.g., *Quercus oleoides*) and edges of brushy or abandoned pastures. However, the microdistribution of *A. herbert-smithii* within Santa Rosa shows clearly that at least *A. herbert-smithii* does not require *Quercus* as an associate; only about half of its distribution in Santa Rosa presently co-occurs with *Q. oleoides* (but see the discussion for the possibility that the original ecological distribution of *A. herbert-smithii* was much narrower than at present). The forested habitats that *A. herbert-smithii* occupies tend to be at the dry end of the Mesoamerican climatic spectrum. Like most other Mesoamerican dry forest habitats, these areas are exceptionally prone to pasturization by partial forest cutting followed by cattle and annual fires (e.g., see Uhl & Buschbacher, 1985). *A. herbert-smithii* juveniles are exceptionally fire-sensitive and therefore they do not recruit well in Costa Rican dry forest pasture habitats, even though they are not browsed by cattle.

At Santa Rosa, *Ateleia herbert-smithii* is restricted to an elevation of about 250–350 m, but it does not occupy all terrain of this elevation even when this terrain extends for many kilometers away from the park.

Where there are adult seed trees at Santa Rosa, *Ateleia herbert-smithii* individuals of various ages are obvious and common members of unburned woody primary and secondary succession along roadsides, in abandoned and unburned pastures, in tree falls, in fencerows, in very deciduous forest understory (although the flimsy seedlings and saplings do not survive unless a gap occurs over them), and on landslides and cliff edges. The species grows on soils ranging from nearly bare rock on the tops of welded ash flows to pockets of deep volcanic alluvium of high quality for agriculture. Adult *A. herbert-smithii* occur from water-logged and swampy black clay soils to well-drained rock outcrops; over this distribution, however, the tree is much more common on the dry than the wet end of the gradient. It gives the impression of a very robust tree, successful in meeting the challenges of a highly seasonal tropical climate, poor soils, multi-species competition, and high herbivore loads. Although *A. herbert-smithii* is not eaten by horses and cattle, a fire hot enough to kill the aboveground parts kills the entire tree, sapling, or seedling. It is not shade tolerant. Given these traits, it is not at all obvious why *A. herbert-smithii* is not a widespread member of secondary succession throughout Pacific Central America. Its only obvious detrimental traits are its sensitivity to fire, the need for insolation for the seedlings and saplings, and its slowness to reach maturity. It does not begin to produce large fruit crops until it is at least 20–30 years old.

III. REPRODUCTION

OVERVIEW

Ateleia herbert-smithii seedlings appear immediately after the first heavy rains in late April or May and sprout from dormant hard seeds that may range in age from that year's fruit crop to three or more years old. Dormancy ends by the seed coat being broken (scarified) by drying, fungal or microbial etching, soil abrasion, etc. However, many seeds require no treatment other than placement on moist soil in order to germinate. Saplings of both sexes, growing in full sun, produce their first flowers at about 5–6 years of age and 3–4 m height. A large fruit crop may appear on a 15-year-old tree that is 4–6 m in height, but 20–30 years is a more normal age for *A. herbert-smithii* to begin to bear large fruit crops. The tree continues to flower at approximately biennial intervals for at least 100 years. Adults are dioecious (Figs. 1–5) and retain their sexual category throughout life. A sample of 50–100 adults chosen randomly always has a 50:50 sex ratio. Most flowering occurs in mid October through mid November, but some individuals flower as much as one month later or longer. The tiny white to greenish flowers (Figs. 3–5) are borne in multi-flowered elongate inflorescences, and the opening progression is from base to tip. Females continually open new flowers on an inflorescence over a period of 2–3 weeks, and an individual plant's flowers may open over a 2–5 week period. Most of the male flowers on a tree open 1–3 pulses of one morning's duration each, and individual male plants are synchronized to flower within a 3–5 week period. Pollen is heavily harvested by social bees, but pollen flow to female trees is entirely by wind. The size of fruit crops is determined in part by the favorableness of the weather for wind-mediated pollen flow. Crops range from a few tens or no fruits to two million per year (Table 1; Appendix I). The 1- or 2-seeded fruits (Figs. 6, 7) begin to expand within a few days of pollination, and seemingly full-sized immature seeds are on the tree within 1–2 months after pollination. The fruits begin to dry in the second month of the dry season (January). In February–April they are dry enough to be blown from the tree, although there is day-to-day variation due to the strength of the wind and heat of the day. The seeds in about 90% of the fruits are killed by the developing larvae of *Apion johnschmitti* Whitehead (Whitehead, 1985), a curculionid weevil, before fruit dispersal occurs (Fig. 6; Appendices I, V–VII; Tables 2–4, 6, 7).

The tree flowers near the end of one year and disperses its mature fruits in the early part of the

FIGURE 3. Inflorescences of male (upper) and female (lower) *Ateleia herbert-smithii* in full flower. The male flowers opened the morning of the photograph, while the female inflorescences bear full-sized green fruits at their bases and unopened buds at their tips. Same locale as Figure 1.

Figure 4. Male inflorescence (upper), flowers (middle), and pollen thief (bottom: *Trigona fulviventris*) of *Ateleia herbert-smithii* on the morning of opening. Same locale as Figure 1.

FIGURE 5. Female inflorescences of *Ateleia herbert-smithii*. On the right, the uppermost flower has just opened on the day of the photograph. Same locale as Figure 1.

TABLE 1. Estimated size of fruit crops per tree for *Ateleia herbert-smithii* in Santa Rosa National Park, 1974–1985.

	1974	1976	1978	1980	1982	1984	1985
Average	89,750	42,882	141,298	114,196	177,797	37,420	48,421
s.d.	51,796	63,354	218,373	133,278	278,798	82,851	140,641
n	20	33	18	25	101	37	60
Maximum	200,000	270,079	646,700	426,136	1,944,000	444,814	922,208
Minimum	20,000	944	10	1,100	124	38	762
Range	180,000	269,135	646,690	426,125	1,943,876	444,776	921,446
Median	75,000	18,672	23,106	53,952	66,302	9,300	11,927
Skewness	0.79	1.96	1.37	1.15	3.55	3.51	4.9
Kurtosis	−0.38	3.25	0.33	0.09	16.47	13.35	25.03
Probability distribution normal	0.221	0.034	0.067	0.164	0.004	0.019	0.002

next year; I have adopted the convention of using the flowering year as the label for a flowering-fruiting event (the alternative convention of using the fruiting year was unfortunately followed in Janzen, 1978).

SEEDS

The mature and living seeds of *Ateleia herbert-smithii* are flattened ovoids, very hard, smooth, red-brown, and 5–6 mm long by 3–4 mm wide. The seed coat is 0.08–0.15 mm thick and

FIGURE 6. Infructescences and individual fruits of *Ateleia herbert-smithii*. The infructescences at top are about as fruit-rich as occur, with as many as 700 fruits on the largest ones. In the lower figure, the ruler is in mm, the exit hole was made by an adult *Apion johnschmitti* weevil, and several dead weevils have been placed next to a seed (exposed by dissection), the contents of which were eaten by a weevil larva. The intact seed exposed by dissection is full-sized but not mature. Same locale as Figure 1.

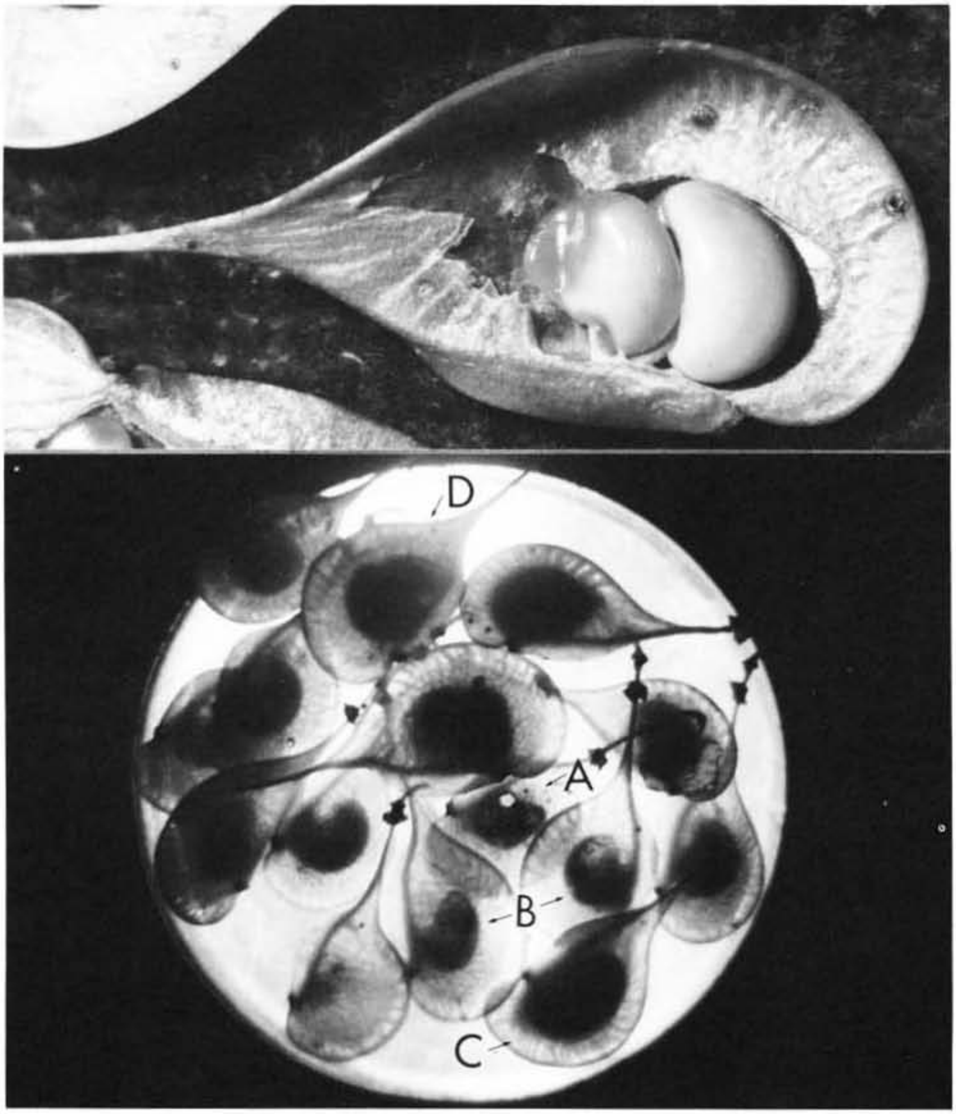

FIGURE 7. Dissected 2-seeded fruit of *Ateleia herbert-smithii* (upper). "Candled" fruits viewed by transmitted light (lower). The fruit labeled A has a weevil exit hole, and those labeled B are two other fruits with weevil-killed seeds. Fruit C has an intact seed. Fruit D has two seeds, one of which has been killed by the weevil. Same locale as Figure 1.

surrounds a layer of translucent hard and polysaccharide-rich endosperm, which in turn surrounds the cream-white and hard embryo. In the green developing fruit, the embryo is dark green and packaged in a clear endosperm and a white translucent seed coat (Fig. 6). (I assume that the green embryo is photosynthetic, cf. Janzen, 1982a.) Living, dormant, and dry *A. herbert-smithii* seeds are about 40% seed coat by live mass; and when the seed is oven-dried, the seed coat is 43% of the dry mass of the dead seed (Janzen, 1978). This approximate ratio of 3:2 seed contents to inert packaging

TABLE 2. Number of *Ateleia herbert-smithii* seeds that escaped from *Apion johnschmitti*, per tree, from 1974 to 1985 in Santa Rosa National Park.

	1974	1976	1978	1980	1982	1984	1985
Average	44,915	5,856	50,486	10,391	5,769	2,344	1,551
s.d.	34,134	12,271	110,228	17,245	8,442	6,337	4,228
n	20	33	18	25	101	37	60
Maximum	142,675	68,293	397,080	76,418	47,368	34,443	26,565
Minimum	4,365	28	10	0	20	8	12
Range	138,310	68,265	397,070	76,418	47,348	34,435	26,553
Median	42,730	1,460	4,433	2,864	2,590	183	234
Skewness	1.16	4.01	2.2	2.43	2.45	3.9	4.5
Kurtosis	1.13	17.39	3.56	6.08	6.48	15.8	21.38
Probability distribution normal	0.167	0.034	0.047	0.086	0.006	0.015	0.003
% total in largest crop	16	35	44	29	8	40	29
Tree with largest crop	18	177	UM	177	285	294	UM
% total in 2 largest crops	27	45	75	45	14	60	48

TABLE 3. Percent *Ateleia herbert-smithii* fruits containing seeds attacked by *Apion johnschmitti*, per tree, 1974–1985 in Santa Rosa National Park.

	1974	1976	1978	1980	1982	1984	1985
Average	61.55	84.68	68.23	85.54	95.1	92.04	97.99
s.d.	19.2	14.08	27.99	26.42	10.22	12.14	1.01
n	20	33	18	25	101	37	60
Maximum	89.63	99.38	96.95	97.7	99.47	99.6	99.35
Minimum	23.64	49.76	0	0	25.17	41.73	92.92
Range	65.99	49.62	96.95	97.7	74.73	57.87	6.43
Median	64.17	87.41	76.09	91.43	97.36	95.99	98.19
Skewness	−0.25	−0.84	−0.93	−2.5	−5.69	−2.66	−2.59
Kurtosis	−1.2	−0.34	−0.18	5.05	34.09	6.95	9.54
Probability distribution normal	0.264	0.197	0.21	0.038	0.5	0.025	0.117

TABLE 4. Percent seeds attacked by *Apion johnschmitti*, per tree, 1974–1985 in Santa Rosa National Park.

	1974	1976	1978	1980	1982	1984	1985
Average	56.15	82.59	68.23	82.82	94.16	91.55	97.03
s.d.	19.08	14.6	27.99	26.35	10.42	12.49	1.81
n	20	33	18	25	101	37	60
Maximum	89.63	99.38	96.95	97.56	99.47	99.6	99.35
Minimum	23.64	49.76	0	0	24.96	41.73	89.97
Range	65.99	49.62	96.95	97.56	74.51	57.87	9.38
Median	52.95	86.05	76.09	90.96	96.91	95.74	97.5
Skewness	0.22	−0.49	−0.93	−2.45	−5.22	−2.48	−1.65
Kurtosis	−1.16	−0.95	−0.18	4.86	29.92	5.82	2.93
Probability distribution normal	0.287	0.182	0.21	0.055	0.001	0.028	0.086

material was maintained over a 1.9-fold range of seed masses. After they have been scarified, healthy-appearing seeds display 100% germination within a few days when placed in moist soil, and a large number of seeds germinate directly without being explicitly scarified. Seeds that have been kept dry for six years will germinate when scarified and placed in moist soil; however, I doubt that

TABLE 5. Percent *Ateleia herbert-smithii* fruits with two seeds in them, per tree, 1974–1985 in Santa Rosa National Park.

	1974	1976	1978	1980	1982	1984	1985
Average	11.35	2.45	not available	1.44	1.26	0.8	2.23
s.d.	18.98	5.3		3.69	3.15	2.86	4.21
n	20	33		25	101	37	60
Maximum	50	19		14	20	17	21
Minimum	0	0		0	0	0	0
Range	50	14		14	20	17	21
Median	0	0		0	0	0.1	1
Skewness	1.11	2.05		2.78	3.95	5.3	3.06
Kurtosis	−0.66	2.9		6.27	17.27	27.87	9.12
Probability distribution normal	0.047	0.01		0.026	0.5	0.009	0.006

A. herbert-smithii seeds retain their dormancy through more than 2–3 rainy seasons in the field, and the bulk of the seeds probably germinate in the first rainy season following seedfall.

The mean seed mass of dry living seeds from single-seeded fruits on 18 trees in the 1974 fruit crop ranged from 32 to 60 mg, and viable seeds (from 2-seeded as well as 1-seeded fruits) ranged from 20 to 76 mg in mass (Janzen, 1978; note that the numbers assigned to seed crops in Janzen, 1978, do not correspond to the actual tree identification numbers used in Appendix I in the present paper). Different trees had significantly different mean seed masses (1.89-fold range in means), and trees ranged from having almost all of their seeds with a mass less than that of the grand mean (48 mg) to almost all seeds being heavier than the grand mean (fig. 2 in Janzen, 1978). Within a seed crop there was a 1.6- to 2.6-fold range in individual seed masses, and this broad distribution was maintained in the presence of a 4-fold variation in possible seed masses over all seed crops. In other words, as a tree's average seed mass increases, all the seeds increase about the same amount in mass.

Seeds from 1-seeded fruits had significantly more mass than did seeds from 2-seeded fruits (Janzen, 1978). However, the combined weight of an average pair of seeds in a 2-seeded fruit had more mass than did the average seed from a 1-seeded fruit. In a large sample of viable seeds pooled from 13 Nicaraguan trees at the El Bordo Las Tinajas site, there were 17,000 viable seeds/kg (C. Hughes, pers. comm.).

The percent of 2-seeded fruits (Fig. 7) varied from none to as high as 50% of the seed crop, but was most commonly from about 0–20% of the fruit crop (Fig. 8e, f; Table 5; Appendices I, V–VII). I have found only two fruits with three seeds in them and none with a greater number in the tens of thousands of fruits examined in this study.

Whole ground seeds (and leaves) of *Ateleia herbert-smithii* from Santa Rosa contained 1–3% dry mass of three uncommon amino acids (Bell et al., 1980). The El Bordo las Tinajas *A. herbert-smithii* population in Nicaragua had the same chemicals in its seeds (C. Stirton and R. Nash, pers. comm.). These same compounds were also found in the seeds and leaves of five other species of *Ateleia*, in the leaves and seeds of *Cyanthostegia matthewsii* (Benth.) Schery, and in the leaves of *C. weberbaueri* (Harms) Schery (R. Nash, pers. comm.). This allogeneric similarity reinforces the suggestion (Rudd, 1968) that *Cyanthostegia* and *Ateleia* are closely related (see Discussion). The functions of these compounds are unknown, but they are at least a part of the defensive repertoire of the seeds and leaves, both of which are eaten only by monophagic insects (see below). These chemicals are not, however, the cause of rejection of *A. herbert-smithii* seeds by *Liomys salvini*, a native rodent and seed predator at Santa Rosa (see below). However, since this rodent eats many species of dry forest seeds that are known to contain chemicals toxic to other animals, there remains the possibility that the uncommon amino acids in *A. herbert-smithii* seeds are effective defenses against other vertebrates.

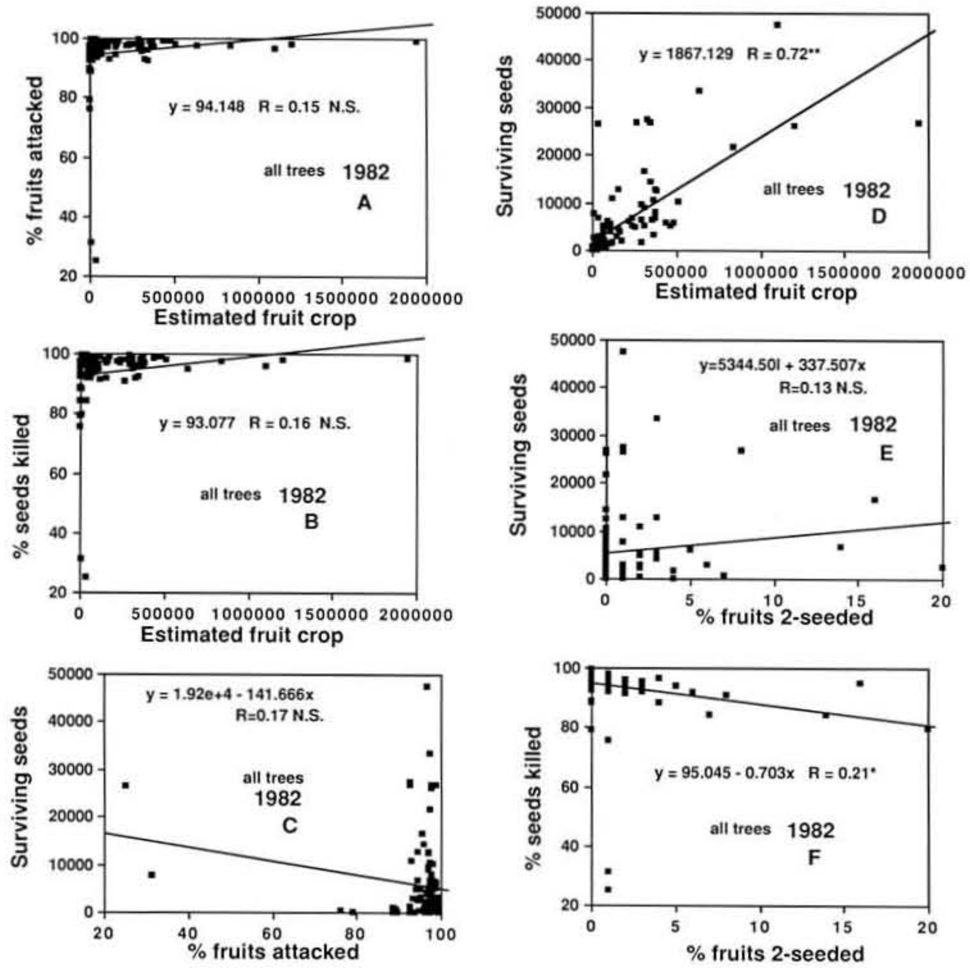

FIGURE 8. Relationships of fruit, seed, and seed predation (by *Apion johnschmitti*) parameters for all *Ateleia herbert-smithii* trees sampled in 1982. Same locale as Figure 1.

DISPERSAL

The indehiscent flat and dry mature fruits (autogyros, terminology of Augspurger, 1986a) of *Ateleia herbert-smithii* (Figs. 6, 7) are dispersed by the strong winds during the first half of the dry season at Santa Rosa (the Nicaraguan *A. herbert-smithii* population also experiences these early dry season winds; C. Hughes, pers. comm.). There is no suggestion that there is secondary dispersal (or postdispersal seed predation) by animals after wind generates the seed shadow. At Santa Rosa, no animals, including livestock, show interest in consuming the small and papery fruits while they are on the tree or after they have been dispersed. However, C. Hughes reported that cattle in Nicaragua avidly consume the fallen dry fruits; they must be very hungry cattle.

Fruits containing intact seeds are carried from zero to at least 100 m downwind from the crowns of 20-m-tall trees. When the parent tree is standing in open pasture, wind carries the fruits much farther than when the parent tree is in forest; the forest acts as a filter that literally rakes the fruits out of the air and also creates turbulence that shortens the distance that a falling fruit moves. The fruit is released into the wind when the base of the fruit snaps off at about the point of contact with the dried flower calyx. This occurs on hot and dry days and when winds are strong (gusts at Santa Rosa may reach 80 km/hr.); at night the humidity rises, making the dry fruit tissue flexible and unbreakable by wind or breeze. If the day is cloudy, the fruits are commonly moist enough that even a strong wind does not detach them. If a particular dry season has an occasional sprinkle, much cloudy weather, and only sporadic winds (as occurred in 1983), there will still be large numbers of dried fruits hanging on the trees in the last half of the dry season. These fruits turn soggy and rot with the first rains, and finally fall from the tree as they decompose.

Seed shadows at Santa Rosa are impossible to map by merely recording the location of the indehiscent dispersed fruits. This is because nearly all fruits contain dead (beetle-attacked) seeds; the few fruits with viable seeds are heavier and therefore not evenly distributed among the dead fruits. The *Ateleia herbert-smithii* fruit shadow that was described by Gladstone (1979) was irrelevant to the seed shadow, since greater than 90% of the fruits whose locations he mapped had had their seeds eaten by weevil larvae several months before the fruits fell from the tree. I assume that as the variation in seed weight increases in the crop, a wind-generated seed shadow will be more homogeneously distributed over the surface (Janzen, 1978), but this has not been empirically examined for *A. herbert-smithii* (but see Augspurger, 1986b, for an example with the rainforest legume *Platypodium*).

SIZE OF FRUIT CROP

The fruit crops produced by an individual *Ateleia herbert-smithii* varied widely in size among years (Fig. 9, Appendix I). This variation had a number of causes: 1) No female flowers (or male flowers) were produced by the population in odd-numbered years from 1973 through 1983, and therefore seed crop sizes were zero in successive even-numbered years (1974 to 1984, inclusive). 2) Even in the years of population-wide flowering (even-numbered years from 1974 through 1984, and 1985), some adult individuals bore no flowers and therefore bore no fruits. For example, tree 177 bore fruit crops of approximately the following sizes in population-wide flowering years: 153,761 (1976); 0 (1978); 188,416 (1980); 468,545 (1982); 0 (1984); 5,756 (1985) (Appendix I) (it bore no flowers in any other years from 1975 to 1985). In 1974 and 1978 it did not flower, but in each of the other even-numbered years it had approximately equal-sized, very large flower crops. 3) A given tree produced different-sized flower crops, and therefore different-sized fruit crops, among years. Tree 11 flowered in all population-wide flowering years, but in 1984 the flower crop was at best 10% of the usual size and all the flowers were shed even in the few cases where they set fruit. 4) Equally large flower crops in successive flowering years on the same tree (as well as on different trees) produced fruit crops of very unequal sizes, For example, tree UM produced the following successive fruit crops from approximately equal-sized flower crops: 646,700 (1978); 426,136 (1980); 1,204,000 (1982); 5,642 (1984); and 565,200 (1985) (Fig. 9). The severe reduction in fruit production in 1984 was due to about two weeks of cool rainy weather during UM's flowering period. However, the above kinds of variation did not obscure the obvious pattern that really large fruit crops were always on fully insolated crowns (and that small crops could occur on a crown in the full sun as well as a shaded crown).

In addition to variation among trees, there also was patterned variation within a crown. Although neither stressed nor documented here, it was obvious that certain major and minor branching systems within a tree crown characteristically bore large or small numbers of fruits per infructescence. For example, the infructescences that had more than 500 fruits on tree 11 in 1982 (Fig. 14; Appendices VI, VII) were usually on a large horizontal branch projecting out of the northern part of the crown. Sometimes this variation was related to the physical environment; north sides of crowns bore fewer fruits (and flowers) than did southern sides, branches on the outer surface of the

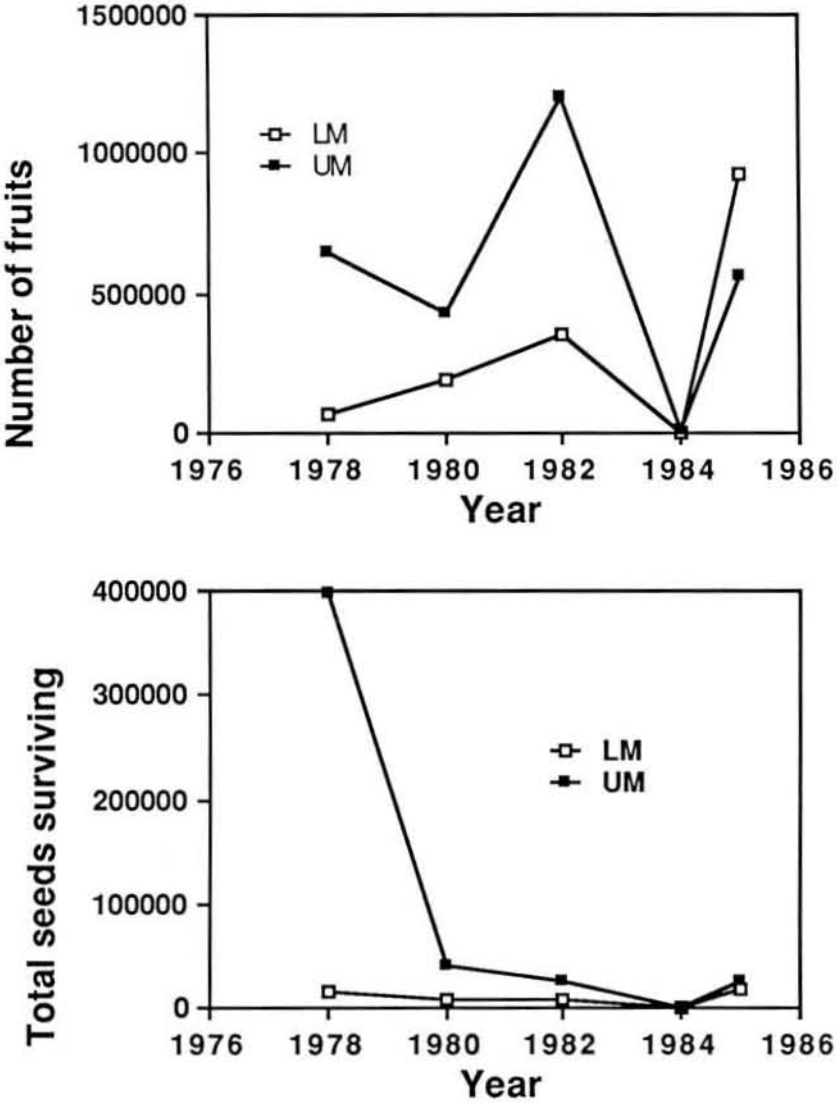

FIGURE 9. Relationship of fruit crop sizes (upper graph) to total numbers of surviving seeds (lower graph) for *Ateleia herbert-smithii* tree LM and UM throughout the census period. Same locale as Figure 1.

crown bore more fruits than did those within the crown, and branches shaded by other tree crowns bore few or no fruits. However, it also occurred that major adjacent branches in seemingly identical physical circumstances characteristically bore very different numbers of fruits.

Female crowns usually bore ten to many more flowers for each fruit that developed. There were some clear cases of fruit set limitation by lack of pollination. For example, when female flowers opened during cool and rainy days (cool and rainy spells are usually intermingled with sunny and breezy days in late October and early November), they were usually shed a few days later. There was no suggestion that these shed flowers were pollinated. The cause is obvious in the field. Not only are cool and rainy days at Santa Rosa relatively free of wind, but the rain probably sweeps the air and foliage clean of the pollen reservoir that had accumulated from previous sunny and breezy days. Furthermore, the male trees do not mass-flower except on warm, sunny, and dry days (see below for details). Such days are breezy to almost windy and herald the beginning of the dry season. In years when the dry season begins early, much of the *Ateleia herbert-smithii* flowering period is warm, dry, and breezy. In other years, such as 1984, weeks of cloudy and lightly rainy weather occur during the *A. herbert-smithii* flowering season and many open flowers were shed by females, apparently because of lack of pollination. At Santa Rosa, a rainy spell in late October or early November usually lasts 3–10 days. Once it has passed, the weather turns clear, warm, and breezy. Males begin to flower again, and many of the female flowers are once again retained as developing fruit.

While *A. herbert-smithii* do abort open female flowers and some young fruits (of various ages) before there is a conspicuous increase in seed size, nothing about the timing of fruit abortion suggests that it is a response to oviposition in the young fruit by the seed predator weevil (see below).

Ordinary adult *A. herbert-smithii* bore 5–100 thousand fruits during ordinary fruiting years (Fig. 8a; Table 1; Appendix I). However, a tree that usually bore crops of this size also bore as many as 0.3–2 million fruits in a year in which it has an exceptionally high fruit set (some of the trees with large crops in Fig. 8a had fruit crops of quite ordinary size in other years). Furthermore, there were certain trees that regularly had fruit crops of this very great size. It is presently impossible to evaluate the actual cost of such a large fruit crop, since usually more than 80–90% of the seeds were destroyed by weevils (Table 4) as they began to fill. Furthermore, there is no way to know at present what fraction of the resources of a mature seed are moved into the growing seed's tissue as it is being eaten by the weevil larva (see below). I suspect, however, that the cost to the mother of a crop in which 90% of the seeds are killed by the weevil is well less than 20% of the cost of maturing that entire crop of seeds, because the weevil is so small that it uses only a small fraction of the material needed to fill a seed. The trees that have escaped intense seed predation by the weevil in a given year and set large crops (e.g., various trees in 1974, 1976, and 1978; tree 296 in 1982; Appendix I) demonstrated that a tree can have sufficient reserves to mature a very large crop of seeds. This is also suggested by the fact that, owing to the absence of the weevil, *A. herbert-smithii* in Nicaragua matures very large seed crops (C. Hughes and B. Styles, pers. comm.).

It is tempting to suggest that the 1985 crop was generally small (Table 1) because it immediately followed the 1984 crop (without an intervening year of accumulation of reserves). Likewise, it is tempting to suggest that the small 1984 crop (in great part due to rainy weather in the 1984 flowering season) resulted in the trees having enough reserves to fruit again in 1985 but not enough to make really large crops.

FRUIT CROP SYNCHRONY

All adult female *Ateleia herbert-smithii* in Santa Rosa produced no flowers in 1973, 1975, 1977, 1979, 1981, and 1983, and flowered (and fruited) in 1974, 1976, 1978, 1980, 1982, and 1984 (Table 1, Appendix I); however, in 1985 they also flowered, thereby destroying what had appeared to be the trait of perfect population-wide fruiting synchrony. (In the 1986 flowering season, about 1% of the male trees had a very few small inflorescences on them in Santa Rosa, but no female trees bore flowers, and there were no seeds.) This flowering also destroyed the temptation to postulate a pheromonal control or magical internal calendar for the entry of newly reproductive teenage trees into perfectly biennial flowering synchrony of a dioecious tree population. The male *A. herbert-smithii* adhered perfectly to the same flowering schedule as that of the female *A. herbert-smithii*, except that a single large adult male in full heavy flower was found in 1979, and a single different male had a weak flower crop in 1983. In addition to the males growing next to the individually numbered female trees that were under intense scrutiny during the 1974–1984 flowering seasons, at least 200 other male adult *A. herbert-smithii* live in the study sites that I frequent and are sufficiently conspicuous that I would have noticed them had they flowered in the odd-numbered years other than 1985. In other words, approximately 300 adult male trees under close observation made only two flowering "errors" in 10 years.

The environmental cueing system used by *Ateleia herbert-smithii* is not obvious, and it must occur during the several rainy season months before the buds appear, unless the plant has something that functions as a memory. The 2–8 mm undeveloped inflorescences are obvious on the trees as early as the August before the October–November flowering; however, in August these buds cannot be more than a few months old. The inflorescences originate in the leaf axils of the leafy branches produced at the beginning of the rainy season (April–May) of the flowering year.

In the Nicaraguan population, the *A. herbert-smithii* flowered in 1981 (mature fruit collected in the 1982 dry season) and did not flower in 1982 (C. Hughes, pers. comm.). In 1984, this population flowered again (it bore mature fruit in 1985; D. Stevens, pers. comm.). It also bore mature fruit in 1986. This means that it flowered in both 1984 and 1985, just as did the Santa Rosa population.

VEGETATIVE SEXUAL DIMORPHISM

Most adult male and female *Ateleia herbert-smithii* can be distinguished by their crown profile; males tend toward multiple trunks and many long, thin, and semivertical branches, while females tend toward single trunks with stouter and more horizontal branches (Figs. 1, 2). The developmental cause is at least partly because female infructescence-bearing branch ends (Fig. 6) die back farther and the next year's new female branches do not elongate as much as do next year's male branches. Adult female *A. herbert-smithii* are usually 2–5 m shorter than are adjacent male trees of the same dbh and approximate age. On a fruiting year, male trees retain a dense crop of green leaves longer into the end of the rainy season than do the females, which begin to yellow and drop their leaves about the time that the fruits are beginning to contain full-sized seeds (late November or December, which is the last month of the rainy season or the first month of the dry season). There is also more biomass of wood in the crown of a male than in the crown of a female tree of the same dbh.

FLOWERING

Female flowers

Female *Ateleia herbert-smithii* flowers are borne on linear branchlets in terminal multibranched inflorescences (Figs. 3, 5); there are fewer flowers and flowering branchlets per female than per male inflorescence. The (green) branch axis immediately proximal to the inflorescence bears a shaggy and subtending rosette of that year's leaves (Fig. 3). The next year's branch will appear from one of the axils of these leaves. While I am not certain whether the *A. herbert-smithii* inflorescence should be termed literally "terminal," for all practical purposes it is terminal and dies back to the area of the axils of the subtending rosette of leaves.

Flowering branch ends occur over the entire surface of the crown, but branches that have their leaves fully exposed to the sun often make larger inflorescences (just as crowns that are fully insolated make the largest fruit crops). Maximal branch elongation (and therefore maximal leafing) appears to require full insolation; shaded portions of the crown die away or bear very sparse foliage and may entirely lack flowers. The flowering branches inside the crown are in those areas of the crown where it is not very thorough in casting shade. On the other hand, *Ateleia herbert-smithii* crowns are conspicuously diffuse (Figs. 1, 2), and enough light penetrates to allow some leafy and flowering development well within the crown.

The flowers open progressively from the base to the tip of the inflorescence. A few new ones open each day. The entire inflorescence uses 1–2 weeks to open all its flowers (and seems to slow down in cool weather). The female flower has a comparatively huge and discoid stigmatic surface (1–2 mm wide) that is directed upward and fully exposed to the air (Fig. 5). The style is shorter than the stigma is broad (this statement is, however, somewhat subjective because the style merges with the ovary). The twisted and dwarfed anthers on their short filaments do not project above the stigmatic surface (Fig. 5). The anthers do not generally open; they also contain what appears to be collapsed pollen and often fall off within a few hours of when the flower opens.

The calyces are pale green with slightly reddish hairs, and the single petal is white. The petal is reflexed backward (but not as severely as in the male flowers, Fig. 4) so that it approximates a shallow hood behind the stigma (Fig. 5). I suspect that its scooped shape and position creates local air turbulence, which results in more pollen being deposited than would be the case with more laminar air flow over the flower or inflorescence surface. The inner surface of the petal is impressed with the shape of the stigma and other floral parts that were pressed tightly against it in the bud (as can be seen in the male flowers in Fig. 4).

During the 1976 and 1978 flower crops, I enclosed ten inflorescences in window screen boxes, after having first removed all the open (distal) flowers and (proximal) developing fruits from the inflorescences. In a parallel set of equal-sized experiments, only the newly opened flowers were removed. The flower buds on all the screened inflorescences continued to open and set seed just as did those on adjacent altered and unaltered unscreened control branches. A second set of inflorescences was treated in the same way, but the experimental inflorescences were enclosed in light paper bags instead of screen. The flowers in the bags opened normally but did not set fruit and were shed a few days after opening. When these experiments are coupled with the observations below, the conclusion that *Ateleia herbert-smithii* is wind-pollinated is inescapable.

Bees visit only the male flowers (see below). During many hours of observation of female *Ateleia herbert-smithii* inflorescences, I have never seen an insect visit a female flower (except for the weevils that occasionally walk over the flowers in search of young green fruits and the occasional hunting wasp that lands on a flower while searching for caterpillars on the foliage). No nectar or other potential reward is produced by the female flowers. The female flowers are odorless to me.

Linear female flowering branchlets bear as few as 20–40 flowers and as many as 200–1,000; a terminal inflorescence usually bears 1–50 times this amount. A representative terminal inflorescence usually bears about 1,000–4,000 flowers but can bear as many as 20,000. Two thousand flowers commonly produce 25 to 300 fruits, but there may be as few as one and as many as 2,000 fruits on a branch end. The detailed observations have never been made, but a ratio of about 20 flowers to each fruit that is set in an ordinary year appears to be close to the average for an ordinary year. A medium-sized adult tree with 50,000 fruits on it would have had about 1,000,000 flowers in an ordinary year. In normal years, the very high variation in numbers of fruits per branchlet and per terminal inflorescence appears to be due in great part to variation in the amount of pollination and fertilization below the limit imposed by the size of the flower crop.

As described above, it is clear that weather conditions can influence the degree of pollination of female flowers. The amount of resources also limits fruit set. There is a suggestion that if a flower-bearing branchlet has set several hundred fruits at the base of the inflorescence (because of good weather when the first set of flower buds opened), it may shed the terminal buds without opening them; alternatively, I have observed that if the basal flowers do not set fruit, the female flower buds continue to open all the way to the end of the branchlet (and the terminal flowers can set fruit; Fig. 5).

A tree's fruit crop may be sired by any number from one to hundreds of male trees. Two large female *Ateleia herbert-smithii* at Santa Rosa grow in a pasture 400 m from the nearest adult males, which are downwind, and 600–700 m from the nearest upwind males. Nevertheless there must be sufficient pollen in the air, since they produce crops of over 100,000 fruits. In relatively intact secondary successional forest at Santa Rosa, a circle of 500 m radius around a female tree may contain as many as 50 male trees, most of which will produce 1–3 pulses of flower openings sometime during the female's flowering period. However, the leafy forest is also a giant pollen filter, and pollen flow may not be able to move as far as the distances suggested above. Despite this caveat, the usual density of the population is such that a single fruit crop is very likely to be sired by substantially more than one male.

Male flowers

Male inflorescences are longer, more branched, and more upright (Figs. 3, 4) than are female inflorescences (the latter give the impression of being stubby and more splayed out, presumably for the same reason that the stigma is enlarged). More of the leafy branchlets in a male tree bear inflorescences at their ends than is the case in female trees, but the differences are not great.

Male flower buds are very similar to those of female flowers. The greenish calyx forms an open-topped globe, with the top plugged by the curved blade of the single petal. When the flower opens, the calyx spreads out into more of a cup, the petal pops out and arches back to where the concave side points upward, and the stamens extend separately well above the calyx margin (Fig. 4). Open male flowers look superficially like female flowers, but the rudimentary ovary and style is hardly more than a shrunken nub hidden between the bases of the thick and clustered anther filaments. There are 8–14 white anther filaments per flower (10 being a very common number) and each appears to bear a fully developed and normal-appearing yellow anther. About half of the filaments are about 1–2 mm shorter than the others. The longest anthers are about 4–5 mm long, giving the impression of two tiers of anthers.

The anthers open along one side and evert the pollen, which is loose and dry. The single petal arches back from the open flower as a tiny reflexed hood converted to a scoop, and the mouth of the scoop usually opens upward and tends to fill the spaces between the flowers. I suspect that it serves as a pollen basket (pollen accumulates in the standard) until a gust of wind occurs that has sufficient strength to launch the pollen (rather than let it sift gradually to the ground as the flowers open and anthers dehisce). The curved surface of the petal may also generate air turbulence around the inflorescence, as suggested for the female flowers. (The hood on the male *Ateleia gummifera* flower drawn in fig. 5 in Dillon, 1980, is probably only partly extended and flexed) *Ateleia herbert-smithii* pollen is tricolporate, with distinctive reticulate ornamentation (Fig. 21), very similar to other *Ateleia* pollen, and resembles typical generalized papilionaceous legume pollen (K. Ferguson, pers. comm., based on male flowers from Santa Rosa *A. herbert-smithii* raised in the greenhouses at Kew Gardens by C. Stirton, 1982–1986).

When a mass of male flowers is open, the air is filled with a strong fragrant odor similar to the odor of sphingid flowers (e.g., *Alibertia, Randia, Exostemma*) but more musky. While this odor suggests that *Ateleia herbert-smithii* was once pollinated by moths, it might be a simple by-product of some other process. No nectar was visible or detectable by taste in any flowers (male or female), and the multitude of bees (Fig. 4) visiting the male flowers did not push their mouthparts down into the central interior of the flowers; instead, they very rapidly collected pollen.

Male flowers open according to a different pattern than do female flowers. For many days many buds on a given tree remain full-sized and apparently ready to open, and then on a warm, dry, and breezy morning, they open synchronously shortly before dawn. As many as half of the flower buds may open on this one morning. If this warm day follows a series of cloudy and cool days, numerous males may flower on the same morning. For example, 24–30 October 1985 was rainy, darkly cloudy, and calm. October 31 cleared up and by sunset was breezy and warm. On 1 November at least 11 large adult male trees out of 18 in one study area had huge crops of open flowers, all being heavily visited by pollen-collecting bees. However, the rain started again about 3 hours after dawn and washed masses of flowers and pollen onto the ground below the trees. November 2–4 remained cloudy and cold with afternoon rain (such a weather event is locally termed a "temporal"); there was no sign of flowers and no bee activity at the trees. November 5 dawned clear, and again numerous males had moderate crops of open flowers that were being visited by bees. Throughout this period, new flowers opened daily on the female trees, although I was left with the impression that not as many opened during the gray and cool weather as on warm days. The weather-generated synchrony among the males is not conspicuous if the weather is continuously warm and breezy; however, a detailed study of hundreds of plants over a large area might well disclose subtle synchrony. In warm breezy weather, a given tree retains its within-crown synchrony and behavior of flowering at intervals. I suspect that the within-crown synchrony is functional in satiation of pollen-collecting bees.

Copious amounts of pollen are released into the air when a pulse of opening male flowers occurs. If a flowering branch is lightly shaken, the air is filled with conspicuous clouds of golden pollen that float away in the air column, just as is the case when a pine tree branch laden with opening male cones is shaken. It is obvious that not only are cloudy and cool (and therefore wind-free in this part of Costa Rica) conditions bad for pollen flow, but morning rain washes a tree's pollen pulse to the ground from the upward directed and open flowers, converts the inflorescences into a soggy quagmire, and converts the entire forest into a monstrous tanglefoot trap for pollen by wetting the vegetation.

Ateleia herbert-smithii male flowers are very heavily visited by female social bees and largely ignored by solitary bees except for the occasional *Xylocopa* and halictid bee (no male bees visited the flowers, since they did not produce nectar and social bees do not mate at flowers). However, it is also possible that at this time of year, when only *Lonchocarpus minimiflorus* and very few other bee-pollinated woody plants are in flower at Santa Rosa, there are relatively few adult solitary bees active in the habitat. The social bees collect enormous amounts of pollen. From dawn to mid morning, an *A. herbert-smithii* male tree with a newly opened flower pulse has a greater biomass of bees in it than I have observed in the flowering crown of any other species of tree in Santa Rosa. The bee biomass is species-rich. For example, five minutes of sweeping an insect net through the air immediately over the newly opened male flowers on lower branches (3–4 m from the ground) of tree 141 on 30 October 1982 yielded the following social bee species (all were females that were collecting pollen from the flowers): *Melipona beechei* and *Trigona pectoralis, silvestriana, jatiformis,* aff. *cupira, testaceicornis perilampoides, fulviventris, angustula, capitata zexmeniae, fuscipennis, dorsalis, mellicolor, buchwaldi, frontalis,* and *buyssoni* (determinations by D. Roubik). This is the entire known native social bee fauna of Santa Rosa National Park, plus one new addition. This bee sample was taken prior to the arrival of the feral African honey bee *(Apis melifera)* in the 1984 dry season, and I have since observed this species to collect *A. herbert-smithii* pollen as well.

The male flowers are shed in the afternoon, night, and day following a flowering pulse. The ground beneath the tree may be as much as 5 mm deep in fallen flowers. As many as half of the flowers on a tree may have opened in such a pulse. However, the synchrony is not perfect within a crown, and a dribble of newly opening flowers continues for many days after. A week or more later there may be a second, but less intense flowering pulse. Following this, flowering continues to dribble on for weeks. It usually takes about 3–5 weeks for a male tree to exhaust its flower crop, but it goes faster if the weather stays continually warm, sunny, and breezy.

The bulk of the male trees flower in the late October–November period during which the bulk of the female trees open their flowers. However, there is a long tail on the distribution. A few individuals are still producing both male and female flowers in small numbers as late as mid January, and there are a few males that have their flowering pulses as late as mid December. Once the flowers have dropped, a late-flowering male is not easily recognized; however, late-flowering individual females are easily recognizable at a later date by the comparatively less mature state of their fruits (see also below with reference to escape from seed predation).

A large emergent male *Ateleia herbert-smithii* produces an enormous number of flowers. For example, on the morning of 30 October 1982, *A. herbert-smithii* 141 opened an estimated 11,800,000 flowers (37.52 kg of wet mass of flowers after most of the pollen had been shed) on 4,000 terminal inflorescences. This was its second mass flowering episode; on 21 October 1982 the first flowering episode of tree 141 produced an estimated 4,712,000 flowers. After both of these flowerings, there were still an estimated 2,059,000 unopened buds on the tree; many of these flowers opened over a 2–3 day period starting on 6 November 1982. This estimated total of 18,570,400 flowers represented about 59 kg of wet mass (14.9 kg dry mass) after the pollen had been shed. Exceptionally large and fully emergent male trees may bear as many as ten times the number of flowers recorded in the example above; 3-m-tall juveniles may bear as few as 1–5 flowering terminal inflorescences, each with 1,000–3,000 flowers.

Juvenile trees

Young female trees sometimes have a few male flowers scattered through their inflorescences. The reverse case has not been encountered.

In nature, the age at first flowering (males and females) of fully insolated saplings is about 5–6 years. They are 3–4 m tall at this time. However, in the Oxford University (England) heated greenhouses, B. Styles and C. Hughes planted Nicaraguan seed on 2 February 1985, and the first plant opened flowers on male inflorescences borne on a single branch on 5 December 1985. Likewise, 2-m-tall 3-year-old *Ateleia herbert-smithii* seedlings/saplings grown from Santa Rosa seed at Kew Gardens produced male flowers. Since at Kew the plant was growing almost year-round, it had about as many months of growth before its first flowers as does a wild Santa Rosa plant that first flowers at an age of 6–7 years but experiences only a 6-month growing season each year. The Oxford plants, however, displayed inexplicably early flowering.

Young males often produce smaller inflorescences with fewer lateral branchlets than do adult males (as was also observed by Styles, Hughes, and Stirton in the English greenhouse trees). Young females, however, tend to make large inflorescences and even set large numbers of seeds per inflorescence, but they produce relatively few inflorescences.

Heavily shaded *Ateleia herbert-smithii* Santa Rosa saplings produce only a few leaves each year and barely increase in size. They do not flower even after 6–7 years of growth, and I suspect they eventually die unless they become insolated as the result of a tree fall.

IV. SEED PREDATION

PRE-DISPERSAL SEED PREDATION BY WEEVILS

Natural history of weevils

As a population and within most individuals' crops in most years, *Ateleia herbert-smithii* sustains the greatest percent pre-dispersal seed predation (Figs. 8, 9, 13–19; Tables 2–4, 6; Appendices I, V–VII) that I have witnessed for any tropical tree. It is so great that the positive correlation between the fruit crop size and the absolute number of surviving seeds (Fig. 8d) is severely obscured (e.g., Fig. 9) because the fruit crop sizes are enormous in comparison with the absolute number of surviving seeds in a crop. The bigger the seed crop borne by an *A. herbert-smithii* crown, the larger will be the absolute number of surviving seeds that it generates (e.g., Fig. 8d), but the variation among trees and years is very great. A small fruit crop can contain a relatively large absolute number of viable seeds and an enormous fruit crop can contain almost no viable seeds (e.g., Fig. 8d). Virtually all of this seed predation is committed by a 2-mm-long black and gray curculionid weevil (Fig. 6), *Apion johnschmitti* Whitehead (Whitehead, 1985). The weevils may be easily observed by close scrutiny of very young *A. herbert-smithii* infructescences (early November) day or night. They also are found climbing through male inflorescences. There is, however, no aspect of their natural history that suggests that they may be regular pollinators of *A. herbert-smithii* by carrying pollen to the female stigmas (although this certainly could occur if they had appropriate

TABLE 6. Percent of the surviving *Ateleia herbert-smithii* seeds that survived because they were in two-seeded fruits, 1974–1985 in Santa Rosa National Park.

	1974	1976	1978	1980	1982	1984	1985
Average	13.41	10.18	not available	6.67	12.91	5.58	23.59
s.d.	22.6	19.57		9.37	19.39	8.34	21.16
n	20	33		25	101	37	60
Maximum	71.43	66		37.58	78.71	29.44	79.7
Minimum	0	0		0	0	0	0
Range	71.43	66		37.58	78.71	29.44	79.7
Median	0	0		3.2	5.13	1.35	17.67
Skewness	1.29	1.62		1.69	1.99	1.36	0.79
Kurtosis	0.17	1.11		2.44	3.1	0.48	−0.28
Probability distribution normal	0.047	0.007		0.117	0.006	0.043	0.149

behavior). I have never even seen one on a newly opened flower, even though they are common on the adjacent new green fruits. I suspect that the weevil uses the strong odors of *A. herbert-smithii* vegetation to locate the trees and does not discriminate between male and female plants. Additionally, it may be feeding on the pollen when it is on male inflorescences.

The weevil walks across the green fruits and oviposits on the lateral surfaces, in the vicinity of the seed. Oviposition occurs when the expanding seed is not much more than 1 mm wide (i.e., within 4–10 days after flowering). The fruit is 5–10 mm wide at this time. I have not determined if she breaks the surface of the fruit in the act of ovipositing. She walks away from the fruit after ovipositing on it. Inferring from the oviposition regime of other weevils (Curculionidae) and bruchids (Bruchidae), she lays 50–200 eggs in a few weeks and then dies.

The first instar larva mines through the fruit wall, lodges partly inside the seed at the point of intersection of the funiculus with the seed, and appears to be eating the embryo as it develops. This means that the larva may have little or no contact with the secondary and potentially defensive compounds found in the mature seed (see below under seed chemistry). Little or none of the seed coat is eaten, and it continues to expand to nearly full-size (Figs. 6, 7). That the larva can feed on the embryo as the embryo grows (or attempts to grow) suggests that the parent plant does not physiologically distinguish between an intact growing seed and one with a weevil larva in it. There is no suggestion that *A. herbert-smithii* fruits with weevil larvae in them are aborted or shed by the plant earlier than are those with intact seeds in them.

There is never more than one larva per fruit. Either the weevil avoids oviposition in those fruits in which oviposition has already occurred, or the first larva to arrive consumes the latecomers (the latter kind of cannibalism is committed frequently by seed predator bruchid beetle larvae, but it is only indirectly suggested in this case). The weevil larva pupates or is ready to do so within about 4 weeks after the egg was laid (in early November or late October). If the attacked green fruits are picked from the tree (in early December or later) and begin to dry up, within 2–10 days the weevil completes development and emerges through a small circular exit hole cut by the adult weevil through the side of the fruit (Fig. 6). At this time in the season, unattacked seeds are full-sized and solidly filled with green embryo and endosperm (Fig. 6). However, if the attacked fruits are left on the tree, the weevils emerge as late as early January, at about the time that the fruits on the tree begin to dry and turn from bright green to yellowish.

After emerging, the weevils wait as adults in the habitat for 10 or 22 months before the next *Ateleia herbert-smithii* crop appears. If there was a crop failure for three years in a row, perhaps the weevil would have to live 34 months. The larvae of this weevil develop in no other species of plant in Santa Rosa (this statement is based on the extensive and ongoing rearing of pre-dispersal seed predators from all potential hosts; Janzen, 1980). The waiting adults have never been located at Santa Rosa, but many other species of weevils and bruchids with similar biologies spend the waiting period at Santa Rosa as quiescent adults in sheltered places (e.g., rolled leaves, crevices in tree bark, abandoned insect nests, etc.). These adults sometimes visit flowers, extrafloral nectaries, and new green foliage for moisture and food, but it is not known if the *A. herbert-smithii* weevil does this. No weevil larvae have been found in *A. herbert-smithii* flower buds (although flower buds of other legume species are often attacked by other species of weevil larvae, and an *Apion* has been found in *Ateleia arsenii* flower buds in Mexico [Whitehead, 1985]).

Sampling pre-dispersal seed predation

The intensity of pre-dispersal seed predation by the weevil is easy to determine and not labor-intensive, even for large samples. A fruiting branch end is cut from the tree and the 1–2-month-old fruits are stripped off. I then spread the translucent fruits on a glass or plastic sheet, with a strong light shining through from below. Intact seeds appear as solid black-green discs, whereas a seed containing a weevil larva (or its parasitoids) is semitranslucent gray and lighter green (Fig. 7). An experienced person with a high tolerance for boredom and a good stereo can thus survey thousands of fruits per hour for weevil damage (two-seeded fruits are also easily detected during this "candling"). Fruits that are still attached to the tree can also be examined (more laboriously) in the field by looking through the fruit held up against a beam of sunlight. Once the fruits are dried and the weevils have left, a rough minimum damage estimate can be obtained by counting fruits with exit holes (the "exit hole of a moth larva" in the *A. herbert-smithii* fruit wall in fig. 1 in Janzen, 1978, is in fact the exit hole of the adult weevil). Such a method, however, yields a serious underestimate if many weevils have died in the fruits or if there is a high rate of parasitism (hymenopterous parasitoids of the weevil larvae sometimes leave only tiny exit holes and sometimes die in the fruit). Mature dry fruits can also be scored for damage as described above with the immature fruits, but full-sized aborted seeds are difficult to distinguish from intact seeds when the fruit is examined by transmitted light.

Sampling fruits for weevil attack and determining fruit crop sizes has some subjective components but is moderately reliable. Fruit crop sizes were determined by directly counting the number of infructescences over 5–10% of the crown and then estimating how many such large areas there were in the crown. A sample of 20–60 infructescences was then cut haphazardly out of the tree crown by a climber or with a 6 m pole-pruner. The numbers of fruits in the infructescences were used to calculate a mean number of fruits per infructescence for each tree. Since there is only one infructescence per leafy branch end, the shorter word "branch" is used throughout this paper as synonymous with "infructescence." The numbers of fruits in each infructescence in this sample were counted directly at the same time that the fruits were candled for weevil damage. In the 1982 and 1984 crops, the fruits on three large trees were collected entirely and all fruits counted; the estimates were 92, 94, and 106 percent of the actual number of fruits. Very large samples were recorded for three other trees (Appendices V–VII). The infructescences were randomized and sampled in cumulative samples of 20, and from these the average number of fruits on a branch (Fig. 10), average percent of fruits attacked on a branch (Fig. 11), and average number of unattacked fruits on a branch (Fig. 12) were calculated. In most cases a sample of 40 infructescences is a more accurate representation of the true value than is a sample of 20. However, 20 gives a value within 1–2% of the mean in almost all cases, which is certainly accurate enough for the level of resolution of crop parameters discussed here.

In many of the comparisons below, I use the data from three very large samples (tree 181, 1982; tree 11, 1982 and 1985) for examination of within-crown processes. This eliminates worry about small sample sizes in interpreting processes and data. However, I should also add that the observations on the hundreds of other and smaller samples were unambiguously consistent with the results from the three large samples.

Throughout the description of weevil attack, I distinguish between seed death and fruit attack.

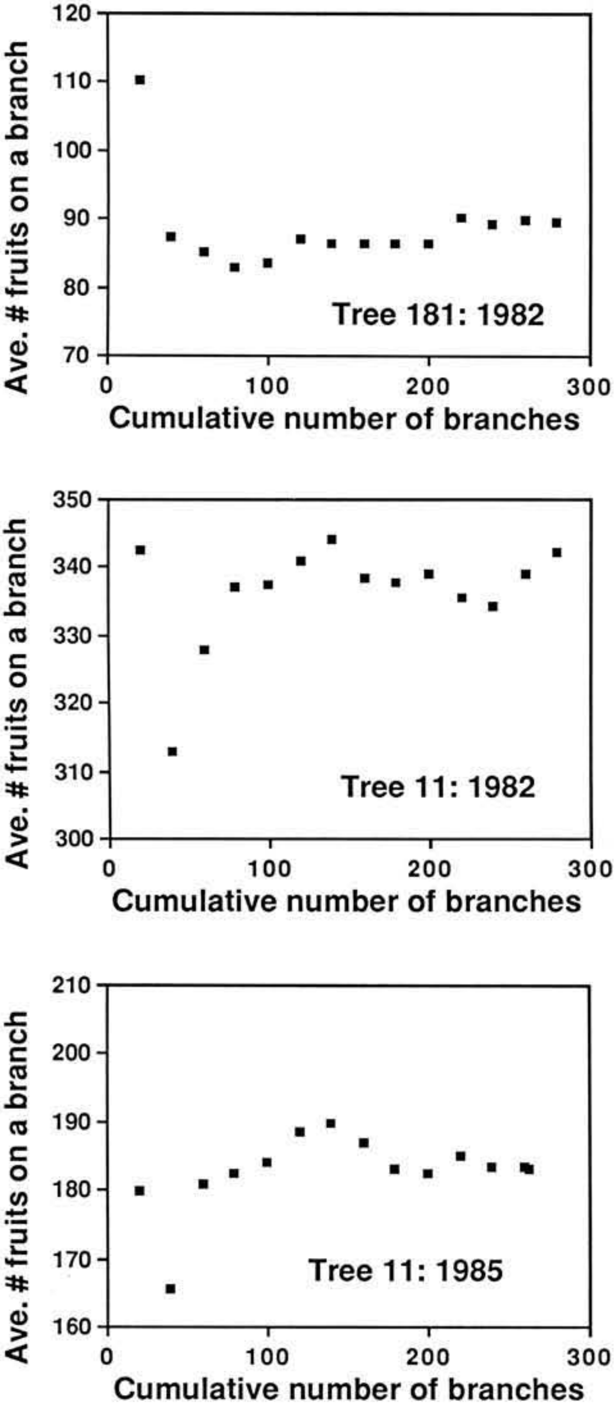

FIGURE 10. Relationship of average number of fruits on a branch (in an infructescence) to the cumulative number of branches sampled within three large samples of *Ateleia herbert-smithii*. Same locale as Figure 1.

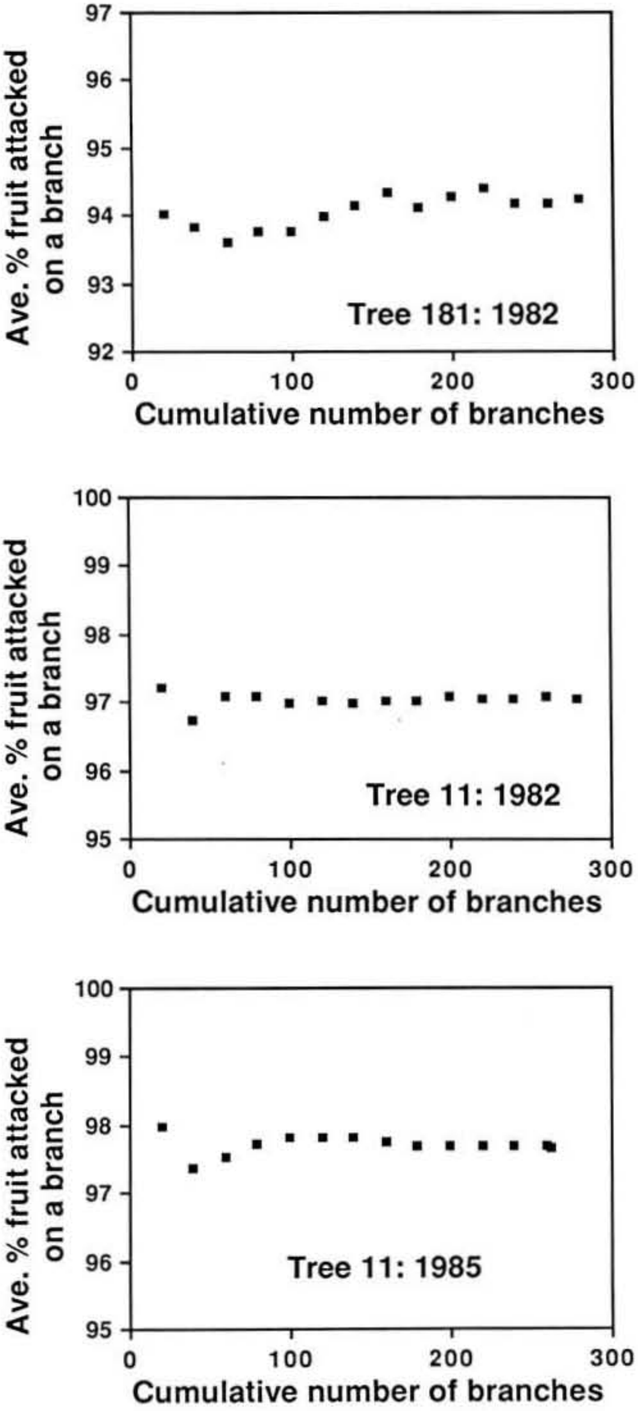

FIGURE 11. Relationship of the average of the percent of fruits attacked on a branch (in an infructescence) to the cumulative number of branches sampled. Same branches and locale as in Figure 10.

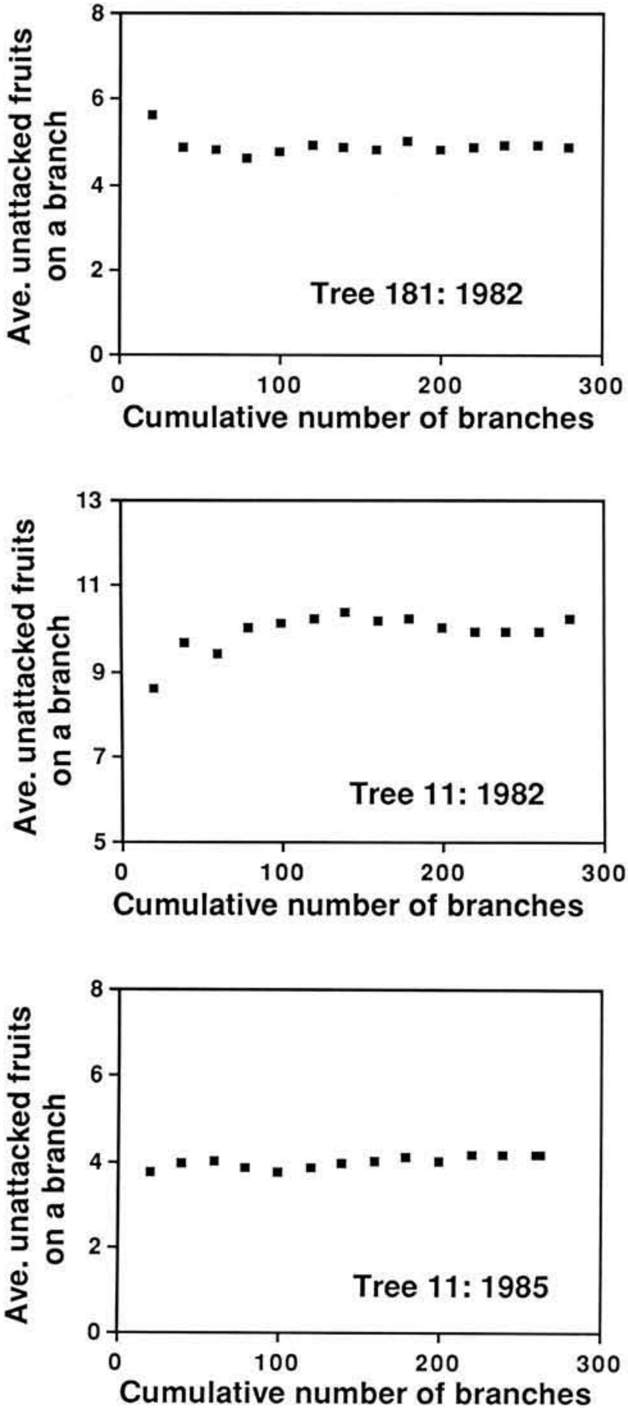

FIGURE 12. Relationship of the average number of unattacked fruits on a branch (in an infructescence) to the cumulative number of branches sampled. Same branches and locale as in Figure 10.

The former is determined unambiguously by observation. Only a minimum estimate can be determined for the latter, since a fruit may be attacked without its seed being killed. Also, observable fruit attack does not equal seed death because the fruit may be attacked but only one of a pair of seeds killed.

Intensity of pre-dispersal seed predation

The average percent seed predation by the weevil usually ranges from 80–98% over a large sample of trees (Table 4), but it is commonplace for individual trees to have more than 98% of the seed crop killed by weevils (Figs. 8b, 18; Appendix I). On rare occasions, a crown suffers only a moderate percent seed predation by the weevil (see next section below). The average of the percent of seeds killed by the weevil seems to increase from 1974 to 1985 (Table 4). The two highest percentages were recorded in 1984 and 1985 and could well represent the highest attainable given that the weevil makes some errors and is so abundant that there is no predator satiation (see below). I stated in Janzen (1978) that the *Ateleia herbert-smithii* at Santa Rosa did not flower in 1972 and 1973, and thus the 1974 low in percent predation could be the result of two successive years without a seed crop (meaning that the weevils that oviposited in 1974 had to have survived for 34 months). However, I have since come to have reduced faith in the source of the information that there was no flowering in 1972, so it is best to simply recognize a low percent mortality in the 1974 crop and leave the cause undetermined. At the high end of the scale, the high percent of seed mortality in 1984 and 1985 could be due to both small overall seed crops (= poor seed predator satiation) and high weevil survival during the single year between seed crops.

Causes of seed survival

The fruits that contained intact seeds were not clustered together at a point within an infructescence (Fig. 6), but rather were scattered among the fruits that had weevils in their seeds. The processes that led to surviving seeds were obviously multiple, and many of them co-occurred in the same seed crop; they ranged from weevil errors to population-wide seed predator satiation:

1. In 1-seeded fruits

a) A weevil can oviposit (and therefore probably render a fruit unsuitable for oviposition from the viewpoint of other weevils) but then her egg or newly hatched larva suffer developmental failure. If the failure of a weevil to develop in a marked fruit is the sole cause of a seed's survival, the percent of seed survival in trees with greater than 95% seed attack by the weevil is probably equal to the percent of weevil immatures that have developmental failure. In other words, seed predator satiation is not occurring at the high levels of percent of seed attack. Such failure should be randomly distributed over the branches unless a female largely confines her oviposition activities to a single infructescence and the eggs of certain females are more prone to developmental failure than are those of others. In the three large crops (Appendices V–VII), the number of fruits attacked on a branch was perfectly correlated with the number of fruits on a branch (Fig. 13). There was a conspicuous uniform increase in the number of unattacked fruits as the number of fruits on a branch increased (Fig. 15). Likewise, there was no correlation between the percent of fruits attacked on a branch and the number of fruits on a branch (Fig. 14). These results are consistent with a random distribution of weevil developmental failures among the branches, but could be caused by other processes as well.

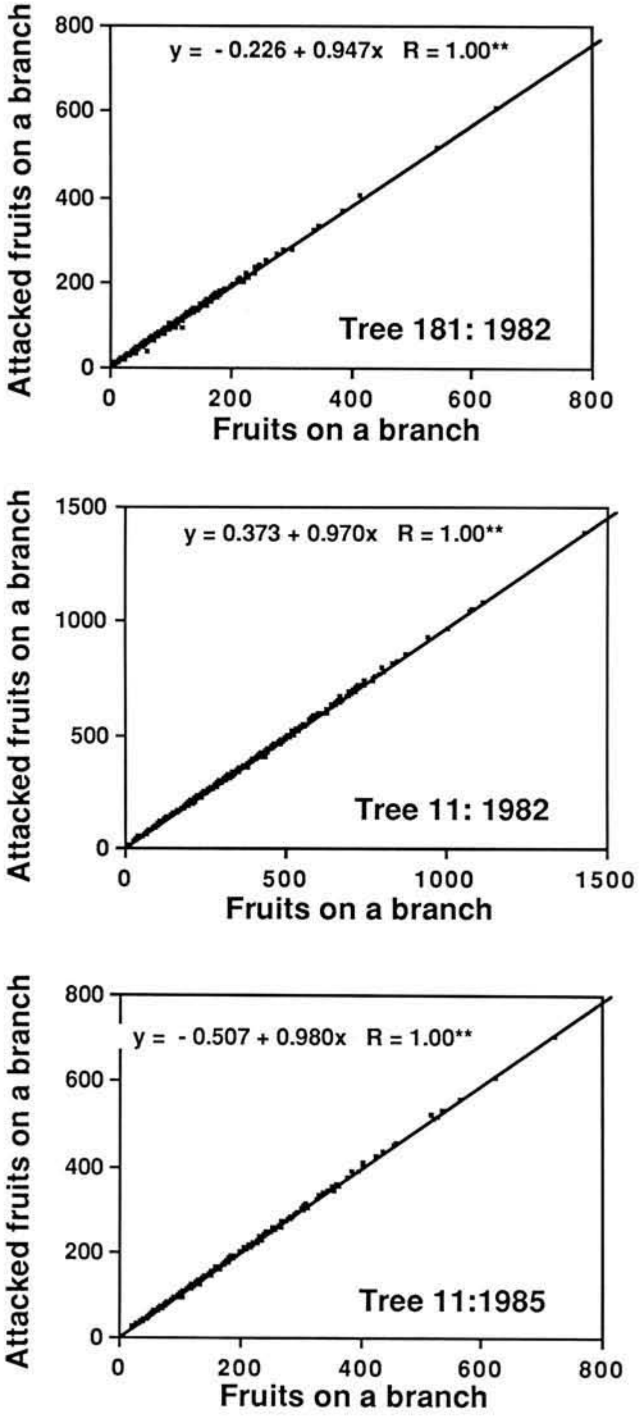

FIGURE 13. Relationship of number of attacked fruits on a branch to the number of fruits on a branch within three large samples of *Ateleia herbert-smithii* (see Appendices V–VII for sample sizes). Same locale as in Figure 1.

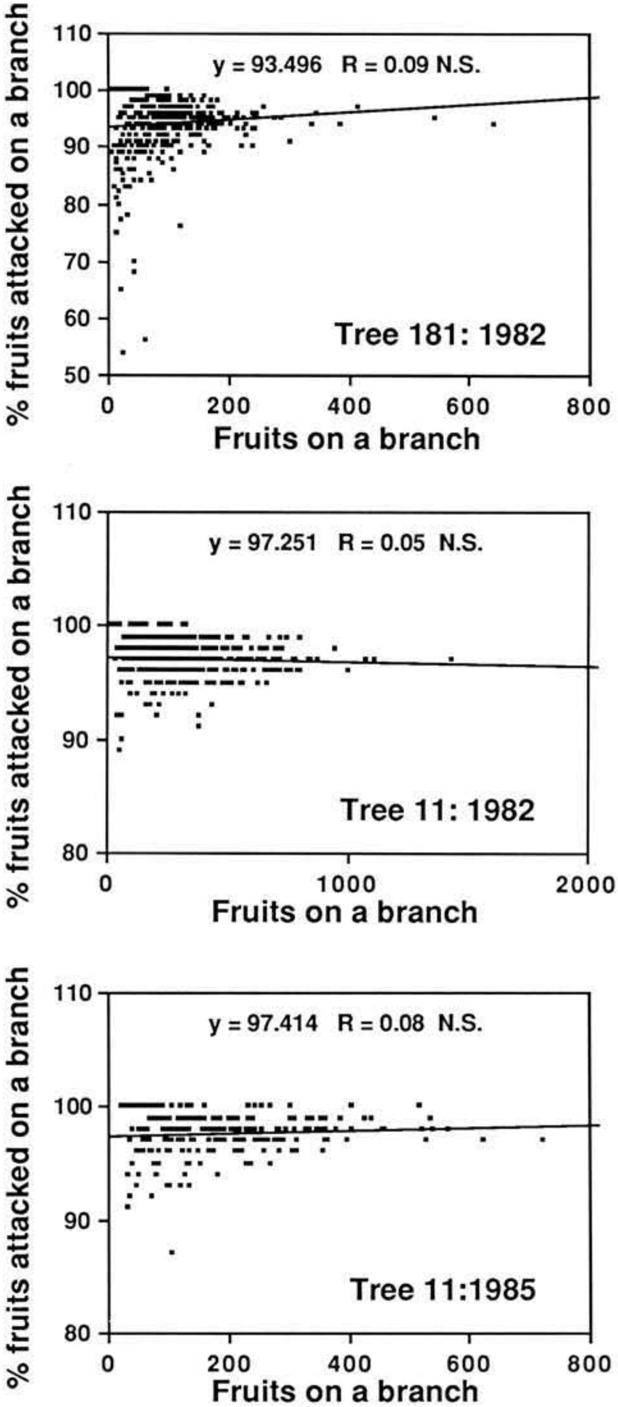

FIGURE 14. Relationship of percent fruits attacked on a branch to the number of fruits on a branch. Same tree and locale as in Figure 13.

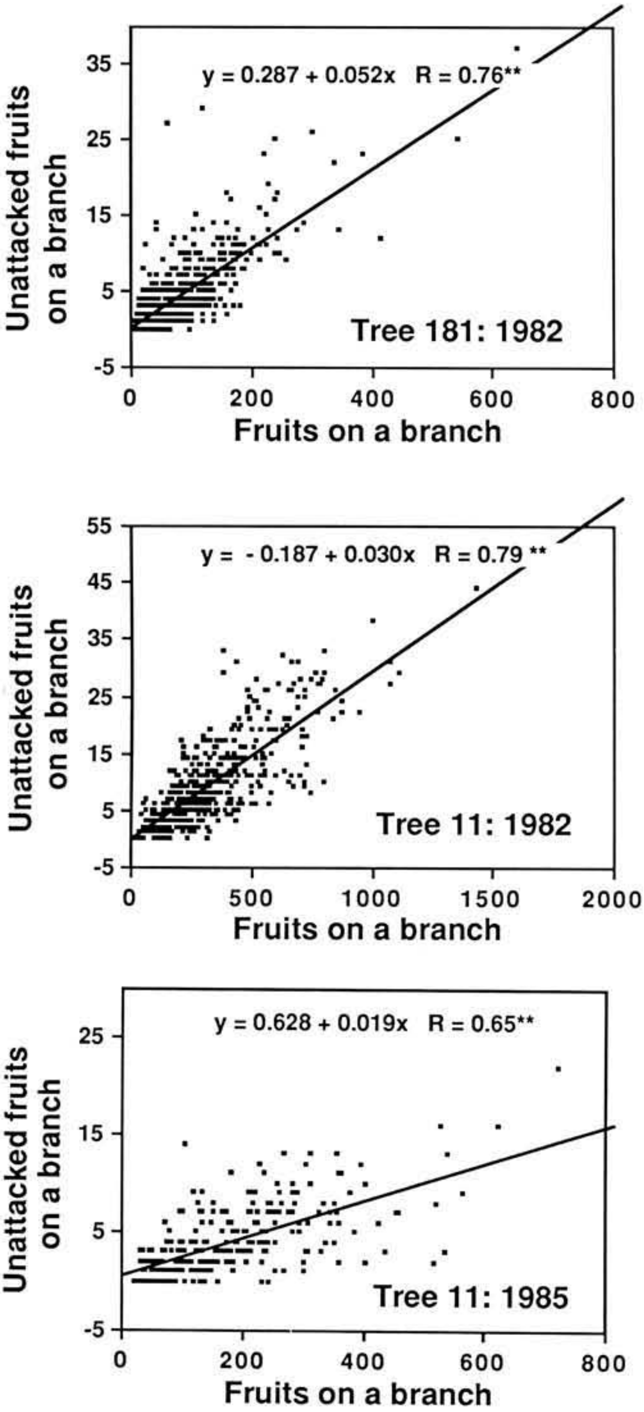

FIGURE 15. Relationship of the number of unattacked fruits on a branch to the number of fruits on a branch. Same tree and locale as in Figure 13.

b) A fruit may be overlooked by all ovipositing females. This might occur when an infructescence bears hundreds of fruits, and therefore the fruits are very tightly packed together (Fig. 6). Likewise, it might occur when there are only a few fruits in an infructescence, rendering the infructescence olfactorily inconspicuous in comparison with more normal infructescences in the same crown. These processes should result in there being slightly lower percentages of attacked fruits in very small and very large infructescences. There are more infructescences with slightly reduced percentages of attacked fruits among the small infructescences in Figure 14 than among the others, suggesting that small infructescences might be occasionally overlooked or bypassed (in the presence of a large number of other potential oviposition sites). Likewise, very young trees with only a few fruits in their crops are the source of exceptionally high seed survival within a crown (e.g., Fig. 8a, b). Interestingly, this relationship occurs even when the young tree is only a few tens of meters from a large adult bearing a large fruit crop.

c) In crops with greater than 95% seed predation, surviving seeds are commonly in fruits where some other insect has eaten small amounts out of the thin bladelike margin of the fruit wall. This implies that the adult weevils avoid ovipositing in fruits damaged in this manner. If there truly is avoidance, it may be that the herbivore damage mimics the cues that a weevil uses to avoid ovipositing in a fruit in which oviposition has previously occurred (if this is indeed why only one weevil develops per fruit). Response to such signs seems likely in the case where only one larva can develop in a fruit and there is an abundance of fruits in which to oviposit. Alternatively, the weevil may simply avoid ovipositing in damaged fruits (the selection for such behavior might have been that such fruits have a reasonable probability of containing no seed or of being aborted by the parent on a later date).

d) I have seen no sign of egg parasitoids (which also would leave some attacked fruits without larvae), but they could occur. The weevil larvae are attacked by hymenopterous parasitoids, but the wasp larvae do not kill the weevil larvae until after the seeds have been killed (see below).

2. *In 2-seeded fruits*

Two-seeded fruits (Table 5) are an obvious source of surviving seeds in some crowns (e.g., Fig. 16). There is no suggestion that a pair of weevils can co-occur in a two-seeded fruit. When there are two seeds in a fruit, the weevil larva usually kills only one of them (Fig. 7). This means that attacked 2-seeded fruits have a much higher chance of producing one surviving seed than do 1-seeded fruits. The total percent seed survival that is due to 2-seeded fruits varies from 0–80% among trees (Fig. 16; Table 6; and see tree 20 in 1985 in Appendix I). This percentage is a function of two different processes: the percent of the crop that is 2-seeded (Table 5) and the behavior of the larvae in the fruits. First, most trees have so few 2-seeded fruits that even a high percent of survival due to 2-seeded fruits makes relatively little contribution to the total percent of seed survival. However, if attack is intense, even a few survivors contributed by 2-seeded fruits may be a large proportion of the surviving seeds (e.g., many trees in 1985 had less than 5% 2-seeded fruits in the crop, but 20–50% of the seed survival was due to escape of one of the seeds in 2-seeded fruits; Appendix I; see also Fig. 8e).

Second, in some crowns in some years the single larva frequently mined into both seeds, thereby eliminating increased survival due to 2-seeded fruits; the cause of variation in whether 1 or 2 seeds are killed is not obvious. The outcome of these two different processes acting in concert is that when a small percent of a tree's fruit crop is 2-seeded, it is not possible to predict either the percent of surviving seeds or what percent of the surviving seeds will be in 2-seeded fruits. However, when a tree's fruit crop has many 2-seeded fruits, the percent of seeds surviving in the crop will be somewhat greater than the population average, and a high percent of the surviving seeds will be in

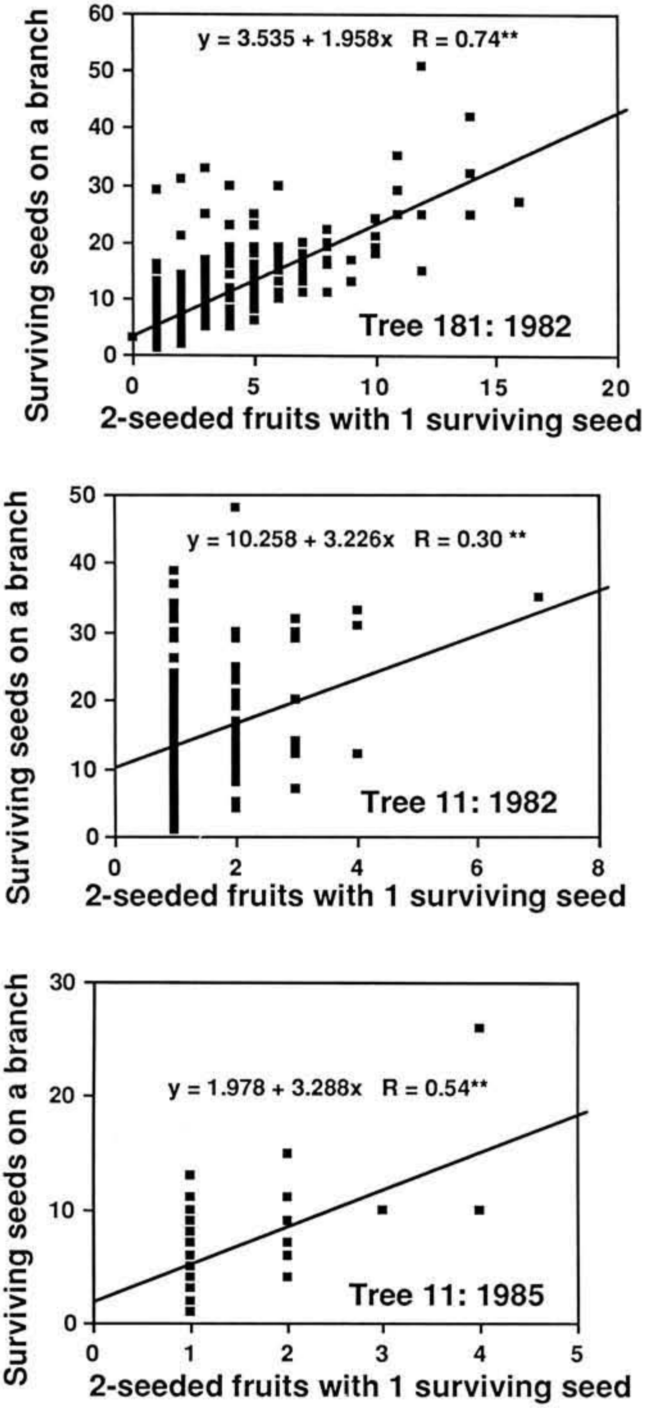

FIGURE 16. Relationship of the number of surviving seeds on a branch to the number of two-seeded fruits with one surviving seed. Same tree and locale as in Figure 13.

2-seeded fruits (Fig. 16; Appendix I). The large number of trees sampled in 1982 allows an overall comparison between crowns; there is a barely significant negative regression of the percent of seeds killed in all of a crop against the percent of the fruits in that crop that are 2-seeded (Fig. 8f).

In general, 2-seeded fruits are not common enough to seriously alter the pattern of seed predation by weevils that is obtained by considering the fruits attacked (Figs. 13–15) and that obtained by considering the actual number of seeds killed (Figs. 17–19). However, there is a slight increase in slope in Figure 19 as compared with Figure 15. This increase is due to the presence of 2-seeded fruits, which results in some attacked fruits still bearing a viable seed. Overall, the outstanding relationship is that as the number of seeds in an infructescence increases, the number of surviving seeds in that infructescence increases (Fig. 19; Table 7). It is also true that as the number of 2-seeded fruits in an infructescence increases, the number of surviving seeds on that branch increases (Fig. 16; and see 1982, 1984, and 1985 in Table 7). This is partly because the overall number of surviving seeds is so low that the proportional contribution from 2-seeded fruits is very high, and partly because the number of 2-seeded fruits on an infructescence increases as the total number of fruits on that infructescence increases. Note, however, that the larger absolute number of surviving seeds in 1-seeded fruits per branch increases as the number of fruits on that branch increases.

3. Seed predator satiation

If an increase in weevils or weevil oviposition capacity within a crown or tree population leads to an increase in the percent of seed mortality within a crown or tree population, seed predator satiation is occurring. However, even when there are so many weevils that satiation is no longer occurring, the bigger the seed crop borne by an *Ateleia herbert-smithii* crown, the larger will be the absolute number of surviving seeds that it generates (e.g., Fig. 8d). The intertree variation in absolute number of surviving seeds is very great (Appendix I; Fig. 8d) though not nearly as great as is the intertree variation in total crop size. A small fruit crop and an enormous fruit crop may produce the same (small) number of viable seeds.

a) *Satiation within a tree's crown.* Within any given year, the percent of fruit attack in a tree's crop was not correlated with fruit crop size except in 1982 (nonparametric test, Table 7). I suspect that in 1982 there were so few weevils that the massive population-wide fruiting resulted in some seed predator satiation in certain tree crowns. However, even in 1982 the regressions of the percent of fruits attacked or the percent of seeds killed on the estimated fruit crop size (Fig. 8a, b) were significant. The very largest crops recorded (1–2 million fruits) suffered about the same percent of seed predation within the crown as did more normal crops. Since the percent of seed predation within a crown is uniformly high (e.g., Fig. 8a, b), it is likely that either a tree usually attracts weevils in proportion to the number of fruits that it bears (over a wide range of crop sizes) or large numbers of weevils arrive at all trees. If the latter is the case, many of these must then leave the smaller crops in search of larger crops (with the consequence of an accumulation of weevils on a tree in proportion to the size of its crop).

There are cases in which the ovipositing females that arrive at a tree's crown appear to collectively lack sufficient eggs to be able to oviposit on all the fruits (i.e., intracrown seed predator satiation has occurred). This is the most likely primary cause of cases of seed mortality less than about 90% (e.g., Appendix I). For example, the fruit crop of tree 130 was of two age groups in 1984 (Appendix I). Its older fruits (from the first flowers) matured in synchrony with the majority of the *Ateleia herbert-smithii* population, and 99% of those seeds were killed by weevils. Its younger fruits (from a late pulse of flowering) matured long after most weevils had (presumably) laid their eggs; the younger fruits suffered only 58% seed loss. Again, tree 296 in 1982 flowered at the end of the general flowering period in a year in which virtually all female trees made full-sized crops; its fruits were therefore maturing at the time when the weevil population should have nearly exhausted its

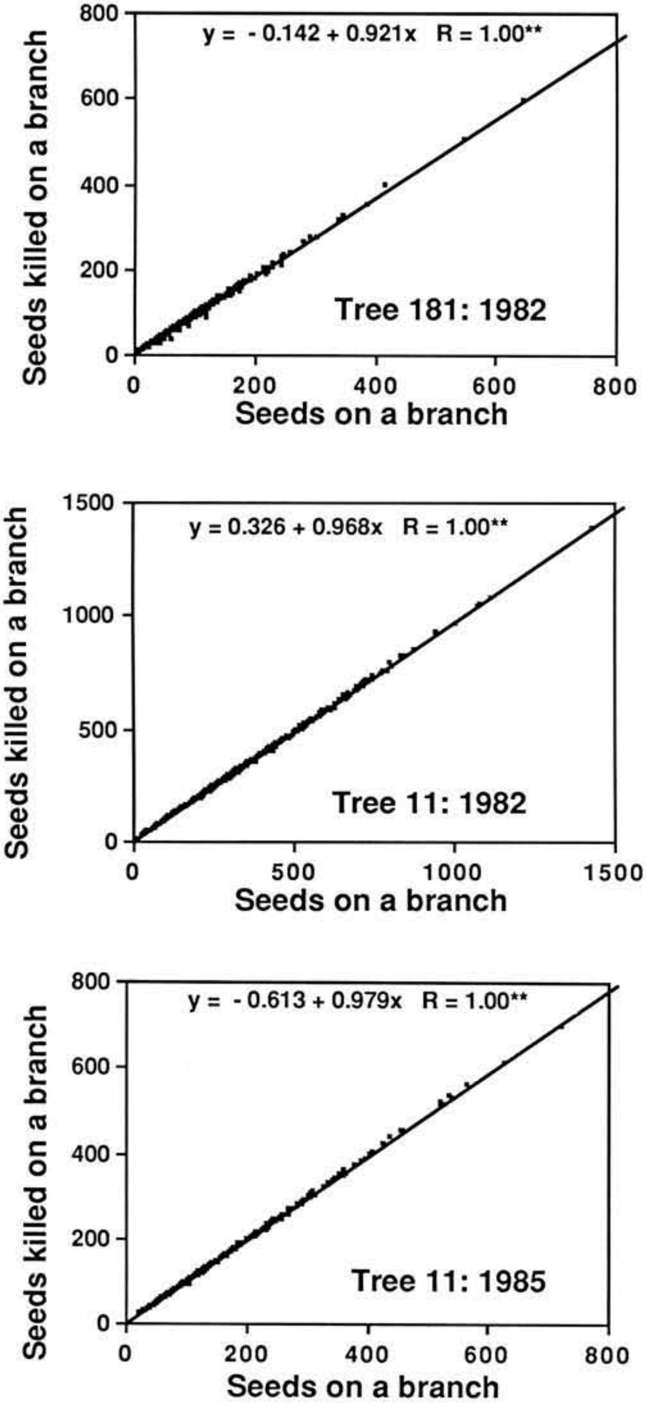

FIGURE 17. Relationship of the number of seeds killed on a branch to the number of seeds on a branch. Same tree and locale as in Figure 13.

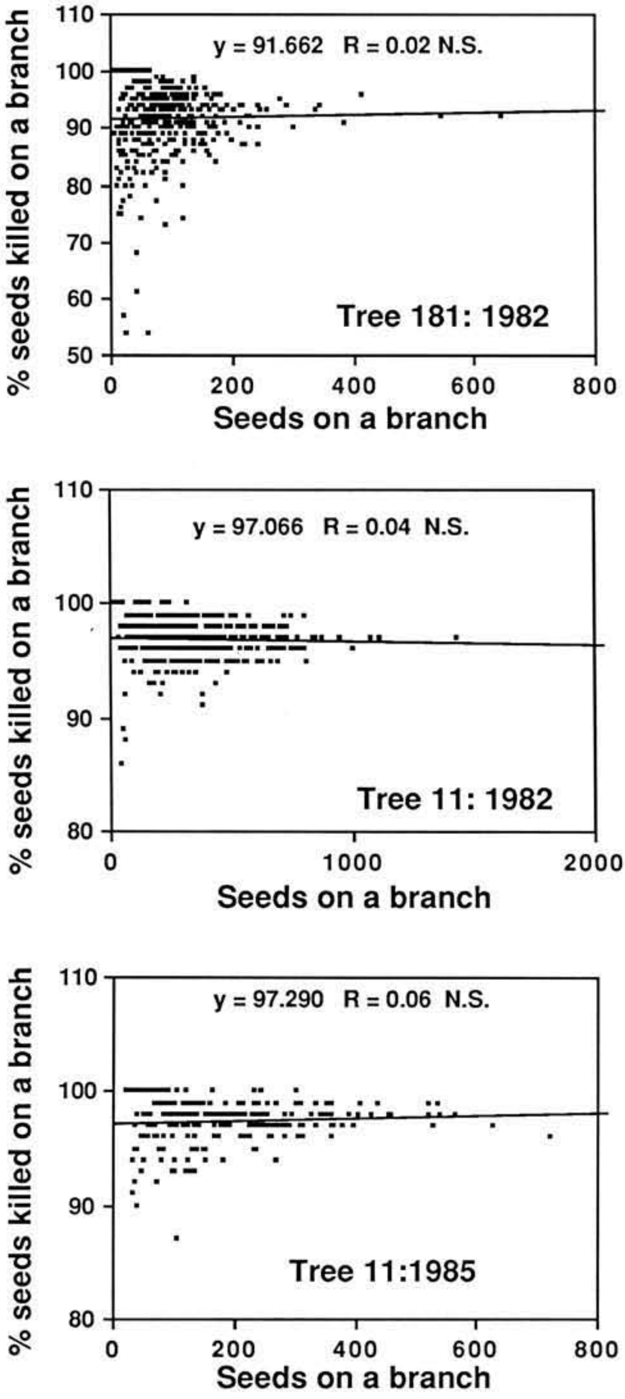

FIGURE 18. Relationship of the percent of the seeds killed on a branch to the number of seeds on a branch. Same tree and locale as in Figure 13.

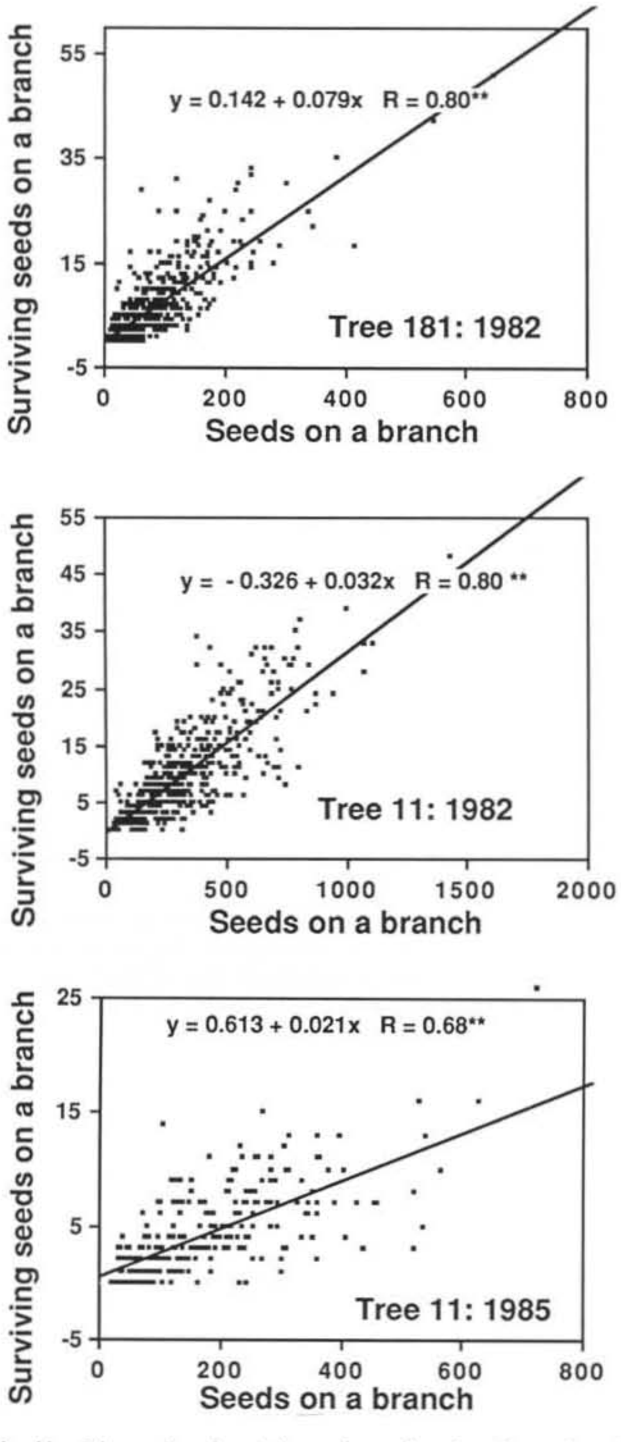

FIGURE 19. Relationship of the number of surviving seeds on a branch to the number of seeds on a branch. Same tree and locale as in Figure 13.

TABLE 7. Results of Spearman rank correlation tests of *Ateleia herbert-smithii* fruit and seed crop variables in Santa Rosa National Park from 1974 to 1985.

Figure number and subject	1974	1976	1978	1980	1982	1984	1985
1. % fruits attacked × fruit crop size	ns	ns	ns	ns	***	ns	ns
2. % seeds killed × fruit crop size	ns	ns	ns	ns	***	ns	ns
3. Number of seeds surviving × number of fruits attacked	***	***	ns	ns	ns	ns	***
4. % seeds killed × % fruits two-seeded	ns	ns	NA	ns	***	ns	***
5. Number of seeds surviving × number of fruits two-seeded	ns	ns	NA	ns	**	***	***
6. Number of seeds surviving × seed crop size	***	***	***	***	***	***	***

oviposition capacity, and it suffered only 25–31% seed predation. In this case, both within-crown and within-population seed-predator satiation occurred.

There is a second cause of seed survival that appears to be within-crown pre-dispersal seed predator satiation but is not necessarily so. Very young trees often have very small fruit crops. These small crops, often containing only a few infructescences, sometimes have a quite low percent of seed mortality (e.g., Fig. 8a, b, and especially tree 184 in 1982). This mortality is, however, of a quite distinctive kind. Most of the surviving seeds are in one or two of the few infructescences, strongly implying that those infructescences were simply missed or located infrequently by weevils (e.g., seed survival due to errors), or the weevils that arrived had few eggs left to lay. Strictly speaking, only the latter case is seed predator satiation at the level of the individual fruit crop. Large trees bearing exceptionally small seed crops show no sign of diminished levels of seed predation. I suspect that the vegetative tree itself provides the odor cue to the weevils, and therefore many arrive irrespective of whether the fruit crop is large or small.

b) *Within the population*. The percent of attack by the weevil has been generally increasing over the past 11 years at Santa Rosa (Tables 3, 4). That is to say, the percent of seed predator satiation across the population as a whole has been declining at least through 1982. The 1984 and 1985 percent of seed survival may be as great as can occur once the weevil population has reached such a high relative level that it cannot be satiated. As mentioned earlier, the 1985 record percent of seed predation levels may represent the combined effects of a relatively small seed crop for the population as a whole and only a single year between crops. These two things suggest that an excessive number of weevils probably arrived at a relatively small number of fruits. When all trees in the population suffer greater than 92% seed mortality, as occurred in 1985, there is essentially no population-wide predator satiation, and almost all seed escape appears to be due to errors by the weevils, 2-seeded fruits, etc.

The few trees that partly escape the weevil may produce as many viable seeds as will tens to hundreds of other fruiting trees combined (Table 2). The overall number of surviving seeds per tree has a distribution that does not seriously deviate from normal, but the few individuals that partly escape make a contribution to the population-level seed production that is many standard deviations from the mean. For example, during this study, the single tree with the largest number of surviving seeds in its year made up the following percentages of the total surviving seed crop censused in each year (Table 2): 16, 35, 44, 29, 8, 40, and 29 (note, however, that this percent is a function of how many trees are contained in the sample). If a large seed crop in a particular tree suffers a low percent of seed predation, it is quite possible for that particular tree to produce as many seeds as do all the combined female members of the population within several kilometers of that tree. On the other hand, since the fruits are wind-dispersed, the few trees with high seed survival do not encroach on the seed shadows generated by other trees nearly as much as would be the case were *Ateleia herbert-smithii* dispersed by animals.

The Nicaraguan *Ateleia herbert-smithii* population in the region of El Bordo de las Tinajas suffers only trivial pre-dispersal seed predation by insects (C. Hughes and B. Styles, pers. comm.). Since the population grows in a severely disturbed area that contains only fragments of badly disturbed secondary successional deciduous forest that are widely scattered over much pasture and cropland, the low percent of seed predation could well be due to a lack of adequate sites in which the adult weevils can pass the time between fruit crops. Depression or elimination of insect seed predator density in agriculturized habitats is commonplace to the south of Santa Rosa National Park in Guanacaste Province (unpublished collection records). It even occurs on the boundary between SRNP and Hacienda Rosa Maria, where the few *A. herbert-smithii* that have been left in tiny patches of forest among the extensive cotton and sorghum fields suffer little pre-dispersal seed predation (e.g., tree 402, 1984). Both habitat destruction and agrochemicals are probably responsible for depression of seed predator density in Guanacaste. However, it is possible that the pristine original Nicaraguan population initially lacked a substantial degree of pre-dispersal seed predation by the weevil, but that is now unknowable.

3. *Parasitoids*. I have reared hundreds of thousands of adult weevils from fruits that were collected in the crowns of *Ateleia herbert-smithii* trees in Santa Rosa's forests and abandoned pasture margins. The number of hymenopterous parasitoids emerging from the fruits along with the weevils show that weevil larvae suffer an attack frequency of about 0–2%. These tiny parasitoids have not yet been identified, but there are at least six species, and they appear to be species I have reared from other species of weevils and bruchid beetles whose larvae develop in Santa Rosa flower buds and seeds in maturing fruits. The wasp species reared from *Apion johnschmitti* are probably maintained most of the time by successive generations in prey species other than this weevil. However, they move onto the huge food resource of weevils that is produced when there is an *A. herbert-smithii* crop, and during that year enormous numbers of wasps are produced by the crop (more than by any other species of woody plant in the habitat). The *A. herbert-smithii* crop probably generates more parasitoids than do all the other hosts combined.

The seeds that are attacked by parasitized weevil larvae are killed and as thoroughly consumed as are those attacked by unparasitized weevil larvae. Since there is only one weevil generation per *A. herbert-smithii* crop, the weevil mortality due to these hymenopterous parasitoids within a crown and year is irrelevant to the biology of *A. herbert-smithii* in that year. Furthermore, its intensity is determined by the numbers of parasitoids generated by the non-*Apion johnschmitti* hosts in the previous year. However, these parasitoids may increase survival of *Ateleia herbert-smithii* seeds in the population as a whole. For example, if parasitoids reduce the number of weevils produced overall by the *A. herbert-smithii* population in a given year, somewhat fewer weevils may be available to oviposit in the subsequent fruit crop. Even a slight reduction in the percent attack in the subsequent crop can be highly significant if pre-dispersal seed predation is very high (as it is in *A. herbert-smithii*); a reduction in percent of seed predation from 99% to 98% represents a doubling in the size of the crop of viable seeds. However, it is also probable that a few percent of reduction in the weevil population by parasitoids will not lead to an observable reduction in the percent of seed predation, when that percent of seed predation is set by errors rather than by seed predator satiation.

PRE-DISPERSAL SEED PREDATION BY OTHER ORGANISMS

No other species of weevil (or other seed predator beetle) has ever been reared from *Ateleia herbert-smithii* in Santa Rosa (or elsewhere). However, the Nicaraguan population at El Bordo Las

Tinajas has not been examined for weevils or other seed predators in general; the same lack of attention applies to other *Ateleia* spp. populations.

A minute fraction of the *A. herbert-smithii* fruit crop at Santa Rosa is also attacked by the larvae of a phyticine pyralid moth. The larva mines inside the fruit and consumes the seed. A larva is normally restricted to one seed and starts feeding on it after the seed is full-sized. However, in the laboratory, a larva may move from fruit to fruit if the fruits with intact seeds are clumped together in a container. This moth usually attacks fewer than 0.01% of the fruits on a tree, but the larvae are found exclusively in the few seeds that have been missed by the weevils (some of which are in 2-seeded fruits). The result is that they may kill as many as 5% of the surviving seeds in some crops, although the usual amount is less than 1%. Damage by this pyralid moth was not systematically recorded and is not included in the mortality figures in Appendix I (e.g., if a tree is recorded as having 91 surviving seeds, three of them might have been in fact killed by the larvae of the pyralid).

In a few cases an unidentified orthopteran eats the seed-containing centers of fruits. I do not know if it feeds on all kinds of *Ateleia herbert-smithii* fruits or only those with intact seeds. Unidentified parrots opened a few green fruits with intact seeds in the 1982 fruit crop, but this damage, like that of the orthopteran, was trivial.

POST-DISPERSAL SEED PREDATION

No animal regularily attacks or moves *Ateleia herbert-smithii* fruits (or dormant seeds) once they have been dispersed. In a single unique case, I found that a small rodent had removed the seeds from several hundred fruits below tree 11 in 1978. The response of animals to newly germinated *A. herbert-smithii* seeds has not been examined.

The habitat into which *Ateleia herbert-smithii* seeds fall is thoroughly foraged by a small rodent seed predator, *Liomus salvini* (Heteromyidae). When *A. herbert-smithii* fruits or clean seeds are placed at a *L. salvini* feeding station, they are left undisturbed. When the seeds are given to an *L. salvini* in the laboratory, it chooses to die of starvation rather than eat them. 2,4-methanoglutamic acid and 2,4-methanoproline extracted from Santa Rosa *A. herbert-smithii* seed (provided by R. Nash, and see Bell et al., 1980) was mixed into laboratory chow at 0.5% and 1.0%, respectively (the concentrations at which they occur in *A. herbert-smithii* seed); *L. salvini* in the laboratory at Santa Rosa (five adult males and five adult females, August 1984) ate the adulturated chow with gusto and grew fat on it. These two uncommon amino acids are clearly not the major cause of rejection of *A. herbert-smithii* seeds by *L. salvini*. Ground up *A. herbert-smithii* seeds did not show any protease inhibitor activity nor show a hemagglutinating response to rabbit or type B human blood (Janzen et al., 1986); however, these results certainly do not exclude the possibility that *A. herbert-smithii* seeds contain a toxic protein, since some hemagglutinins (lectins) are toxic to *L. salvini* (Janzen, 1981), and many more kinds of blood would have to be screened against *A. herbert-smithii* seeds before it could be stated that they contain absolutely no lectins. So the rejection of *A. herbert-smithii* seeds by *L. salvini* remains very much a mystery.

V. GROWTH

As described earlier, male and female *Ateleia herbert-smithii* have somewhat different life forms (Figs. 1, 2). Trees of both sexes may attain an age of at least 200 years. This figure is based on counting the conspicuous annual rings in the sapwood; *A. herbert-smithii*, like numerous other species of Santa Rosa trees, have conspicuous annual rings that are associated with the cessation of growth during the six-month dry season. Additionally, tree ages have been estimated by extrapolating from diameter increments (Appendices I–IV). Trees of 200 years of age are 0.8–1.3 m dbh and usually grow in small old pastures where they have received full sunlight and other trees have not grown up because annual grass fires have kept them out. These fires have, however, not killed the *A. herbert-smithii* for two reasons. First, the area directly below a large old *A. herbert-smithii* is often choked with woody shrubs that eliminate grass by their shade, and therefore protect the lower trunk and limbs of the *A. herbert-smithii* from grass fires. Second, grazing by cattle helps the *A. herbert-smithii* by minimizing the amount of grass fuel; following removal of cattle from Santa Rosa in 1978–1979, many large *A. herbert-smithii* in pastures or on pasture edges were killed by the very intense fires in subsequent years. However, it is not clear why truly old *A. herbert-smithii* that are protected from wind and fire die in Santa Rosa.

A more common size for reproductive adults in forest is 30–70 cm dbh (i.e., 50–150 years old). However, trees greater than about 40 cm dbh on shallow soils are subject to being uprooted by early dry season (January) winds. I have encountered at least 50 recently dead *A. herbert-smithii* in the past 12 years, and all but one death was due to wind-throw or to trunk breakage following fire damage to the lower trunk. Wind-thrown trees were usually uprooted following the breakage of major surface roots 1–2 m from the bole and during the period of intense winds in January. The fire-killed trees were growing on a pasture–forest interface, and a strong downwind fire moved into the forest from the pasture. The cambial layer near ground level was killed by the heat, leaving a patch of dying tissue. The next fire, in some later year, then had access to the dead core area and burned through the base of the tree; the subsequent (third) fire to pass by consumed the newly fallen tree.

A large *Ateleia herbert-smithii* that is subjected to only 1 or 2 ground-level fires often develops a hollow core, and this core is a roosting and nesting area for animals. Roots often grow from the inner lower walls of the tree directly into this (presumably) nutrient-rich dung heap (Fig. 20b, c). Likewise, if the hollow core extends upward through the bole, these internal roots grow upwards to moist pockets caused by rain oozing in the core from places where the core hollow breaks through the bole (usually in the forks of large branches).

During the period from about 2–3 years of age to senescence, healthy *Ateleia herbert-smithii* with insolated crowns add an average of about 0.5 cm to their dbh per year. Seventy-eight healthy adult female trees were observed for two years, and their annual dbh increment was an average of 0.5 cm (s.d. = 0.5, range 0–2.9 cm; initial diameters 6.1–71.4 cm, average 32.4 cm, s.d. = 1.5) (Appendix III). Nine males observed during the same period had an average diameter increment of 0.4 cm per year (s.d. = 0.2, range 0.1–0.7 cm; initial diameters 31–63 cm, average 48.9 cm, s.d. = 9.2) (Appendix II). Sixteen healthy adult females were observed for eight years, and their average diameter increment was 0.5 cm (s.d. = 0.4, range 0.1–1.5 cm, average initial diameters 10.4–87.1 cm, average 39.5 cm, s.d. = 20.9) (Appendix IV). None of these three increment rates are significantly different from each other (Spearman rank correlation test). In all three sets of wood increment records, the slope of the regression of annual diameter increment against the initial diameter of the trunk was not significantly different from zero, and the three correlation coefficients were also not significant. All these statements were also true of the subset of the female trees that were watched for two years and that fell within the diameter range of the male trees in Appendix II. The very large *A. herbert-smithii* with a dbh of greater than 1–1.5 m have highly fluted trunks (Fig. 20a, b), and diameter increment measurements are difficult to record and interpret. Younger trees sometimes have less severely fluted trunks.

Ateleia herbert-smithii are as tall or taller than are any of the trees with which they grow. Even though they sprout on bare soil (or in herbaceous growth) in the earliest stages of succession, the adults are not shaded out at a later stage. The slower-growing evergreen species of later succession that form a substantial part of the canopy of pristine forest (e.g., *Manilkara, Hymenaea, Mastichodendron, Swartzia, Swietenia, Quercus*) do not grow taller than do *A. herbert-smithii* adults at Santa Rosa. The same applies to the many species of deciduous trees that co-occur with *A. herbert-smithii* both in the early stages of succession and later. However, these large and tall adult *A. herbert-smithii* produce virtually no surviving seedlings and saplings in the forest understory, even when it is a vegetation that is very deciduous in the dry season. As the old adults die through

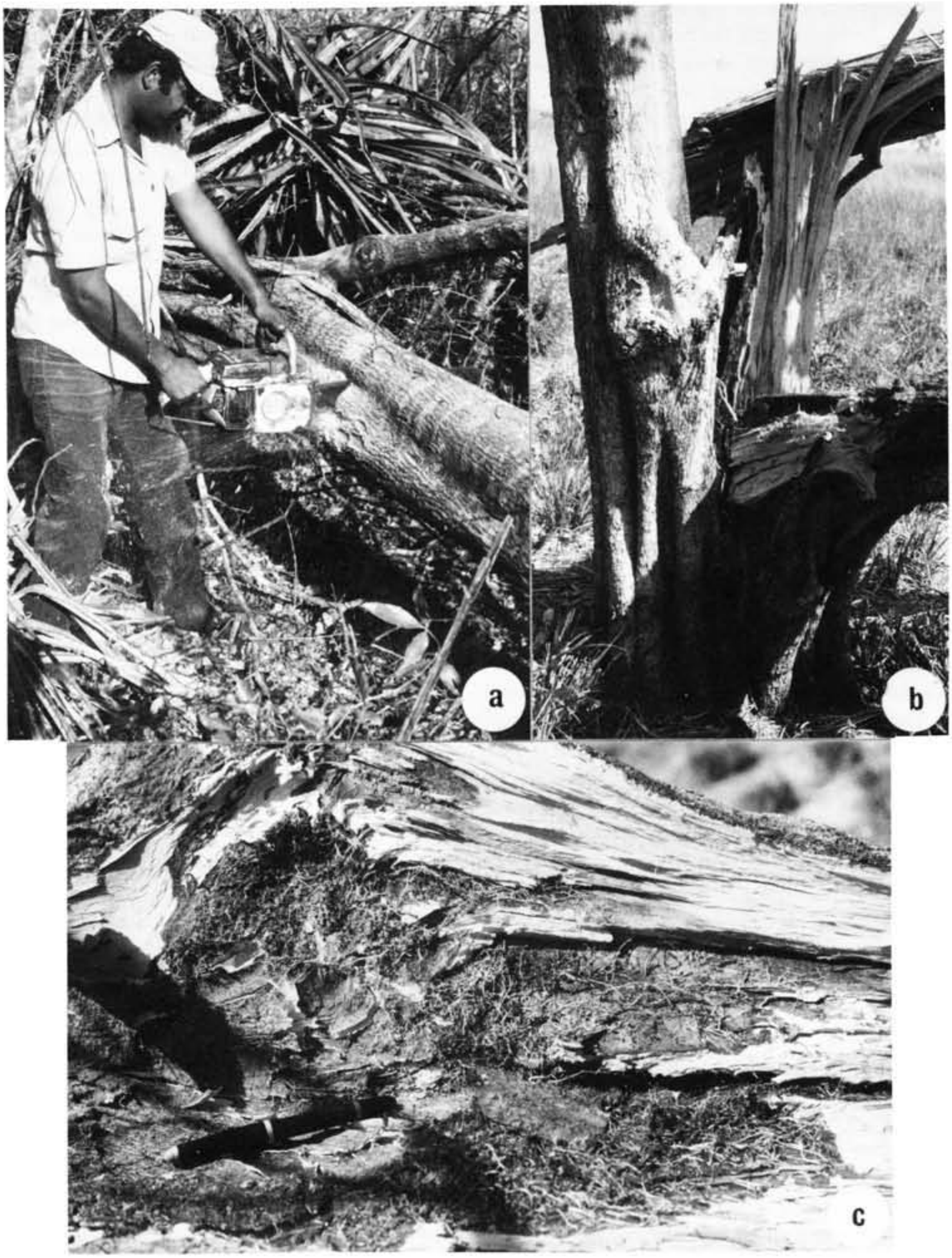

FIGURE 20.—a. Forty-year-old *Ateleia herbert-smithii* immediately after being uprooted by January winds in same locale as Figure 1.—b. Fifty-year-old forked *A. herbert-smithii* split by January winds 3 km south of Figure 1 locale; the split at the fork was made likely by a rotten core that got started in an old fire scar. At the center of the photograph is a root extending from the left-hand standing portion of the tree into the downed portion.—c. Center of downed trunk in b above, filled with rotted wood and guano, and thoroughly penetrated by adventitious roots of *A. herbert-smithii* growing out of the sides of the cavity in the trunk.

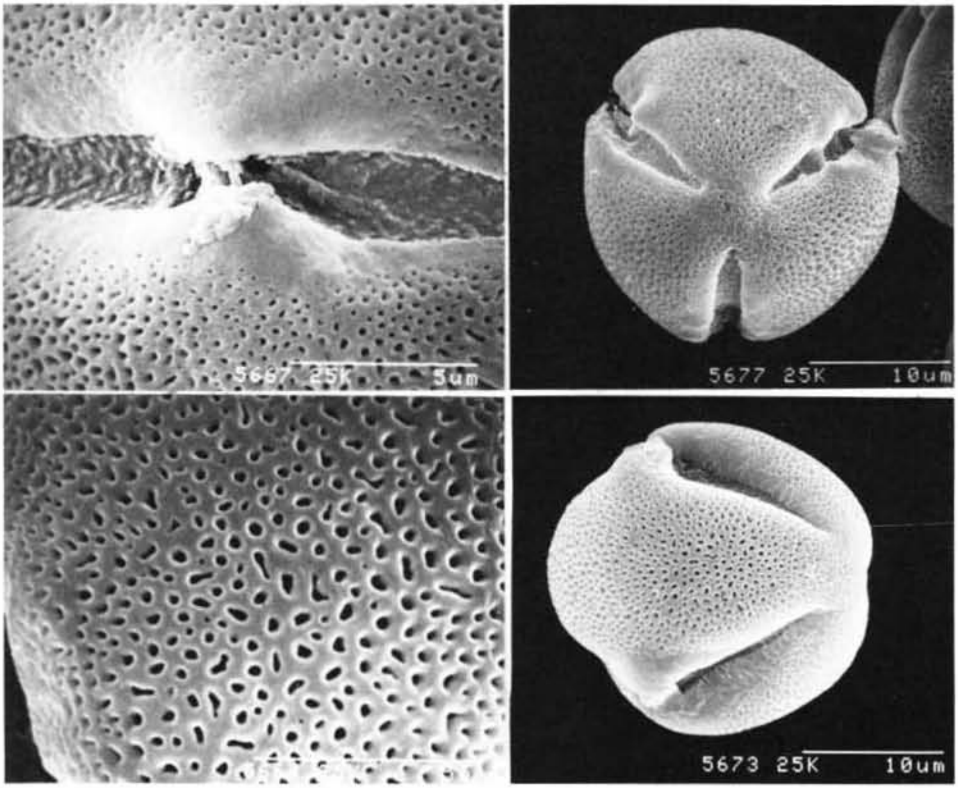

FIGURE 21.—a. Polar view of a representative tricolporate *Ateleia herbert-smithii* pollen grain.—b. Lateral view of a above.—c, d. Fine detail of a and b Specimens (DHJ 11511) from Santa Rosa National Park, prepared by C. Batchelor and I. K. Ferguson (1986).

being wind-thrown, they are replaced by other species, except in a very restricted set of habitats. It appears that *A. herbert-smithii* was originally a common deciduous member of the disturbed sites and tree falls of relatively evergreen oak forest *(Quercus oleoides)* and perhaps a rare member of semi-evergreen to nearly purely deciduous forest in a few very rocky sites in the eastern end of Santa Rosa. When such a mosaic of oak and semideciduous forest is patchily and incompletely agriculturized (selectively logged or patchily burned, pastured, and browsed), seedling and sapling survival conditions for *A. herbert-smithii* are greatly improved. It is likely that the tree has become much more common during the last 300 years and even occupies some forest succession on very moist and very dry sites that were probably not originally occupied by it. It becomes the most abundant where pasture or road edges are cleared of forest within about 100 m of large adult *A. herbert-smithii* and then allowed to return to woody vegetation through prevention of fires. In such sites, it may form monospecific stands of 10–30 m diameter. As such forest again returns to its original state, *A. herbert-smithii* again becomes a rarer and more habitat-specific tree. This is currently happening to most of its population in Santa Rosa, where it was and is a rapid and frequent colonizer of pastures that were abandoned when the park was formed in 1968–1972. It is not replacing itself in most sites in 50- to 200-year-old secondary successional forest.

Ateleia herbert-smithii usually does not sprout from the bole, roots, or branches when wind-thrown or burned. However, a young to middle-aged tree that has been cut off near ground level may produce sucker shoots if the site is insolated. Saplings with their crowns cut or smashed out of and fungi; there is no obvious difference in hardness or chemical composition between the cream-colored heartwood and sapwood. Freshly cut or broken *Ateleia herbert-smithii* branches may be located within a few hours as an oviposition site by a yellow and black cerambycid beetle (*Placosternus crinicornis* Chev.).

VII. DISCUSSION

Ateleia herbert-smithii is the only legume in the world that is known to be wind-pollinated. However, I strongly suspect that the approximately 17 other species of *Ateleia* (Dillon, 1980; Rudd, 1968) are also wind-pollinated. Their flowers look just like those of *A. herbert-smithii* (e.g., see drawings of *A. arsenii* in Polhill [1981: 219], and descriptions in Rudd [1968]). I suspect that the drawings showing well-developed *Ateleia* anthers positioned next to a comparatively huge and fully exposed discoid stigmatic surface should be viewed as the product of artistic license and a temptation to draw shriveled stamens or stigmas in a fully expanded manner. I also suspect that all *Ateleia* are dioecious, just as is *A. herbert-smithii;* those descriptions that mention *Ateleia* stigmas describe them as discoid, sessile, and/or peltate. It is likely that descriptions that ignore the stigma are based on material from a male tree (where the stigma is always severely shrunken) but it was simply assumed that the flowers were poorly preserved.

Discussion of the pollination systems of other potentially wind-pollinated legumes should be done by those who know them in the field. Arroyo (1981) suspected that "some Australian acacias might be anemophilous, at least facultatively"; however, P. Bernhardt (pers. comm.) is of the opinion that Australian acacias would be at best wind-pollinated only in the sense of being selfed by pollen falling from one flower to the next. C. Stirton (pers. comm.) suspects that *Colophospermum*, which grows in widespread monospecific stands in the Zambesi River basin, is a candidate for wind-pollination. Faegri & van der Pijl (1979) state that, "The corolla has been lost in [the Indian tree] *Hardwickia* (Caesalpiniaceae) and the blossom in anemophilus"; however this conclusion cannot be used without knowing its basis. Likewise, the *Ceratonia* and *Gleditsia* inflorescences figured on the back cover of Polhill & Raven (1981) are not only dioecious but look suspiciously like those of wind-pollinated plants.

There has been some question as to whether *Ateleia* should be placed within the papilionoid or caesalpinoid legumes (Rudd, 1968). While Polhill (1981: 213) firmly planted *Ateleia* in the Sophoreae (Papilionoideae), he noted that the Sophoreae "is a tribe of convenience between the Caesalpinioideae and the bulk of the Papilionoideae, sharply defined from neither." *Ateleia herbert-smithii* has a number of traits that are generally associated with caesalpinioids:

1. There are 8–10 stamens in most flowers, but flowers of *A. herbert-smithii* with 11–12 stamens are commonplace (and both C. Stirton and I have counted up to 13–14 in some); Rudd (1968: 391) noted that "instability of stamen number is a character more often found in caesalpinioid genera."
2. The peltate stigma of *Ateleia* (including *A. herbert-smithii*) would be "unique among the Faboideae, so far as I know, but it occurs in a few caesalpinioid genera such as *Arcoa, Bauhinia, Ceratonia,* and *Peltophorum*" (Rudd 1968: 391).
3. The strongly exserted stamens and radially symmetrical flower are strongly suggestive of the form of many caesalpinioid flowers (and see *Gleditsia* and *Ceratonia* photographs on the back cover of Polhill & Raven [1981]). This, along with (4) below, is why I earlier and naively placed it in the Caesalpinioideae (Janzen, 1978).
4. The embryo in the mature dormant seed is sandwiched between two layers of translucent and hard polysaccharide-rich endosperm. This trait is common in caesalpinioids (e.g., *Bauhinia, Cassia, Schizolobium, Delonix*), but I know of no papilionoids with this trait.
5. The single petal has the general shape of the stalked petals of many caesalpinioid flowers and does not resemble the petals of papilionoid flowers.
6. The severe reduction in petals (without even rudimentary ontogenetic initiation of petals) has

occurred on a number of occasions in caesalpinioids, but almost never in papilionoids (Tucker, 1989).

7. The floral organs are not initiated unidirectionally from the abaxial side, in contrast to the case with papilionoid legumes (Tucker, 1989).

8. In papilionoid legumes, the carpel usually arises along with the second whorl of stamens; in *A. herbert-smithii* it appears before the stamens do (Tucker 1989).

With the respect to the floral traits mentioned above, it is easy to view *Ateleia* as simply an ordinary caesalpinioid dish-shaped entomophilous flower that moved evolutionarily into wind pollination. For example, a single flowering branchlet of an *A. herbert-smithii* inflorescence superficially resembles an (insect-pollinated) *Mora megistosperma* (Caesalpinioideae) inflorescence. The loss of petals is the removal of an unrewarded cost and the removal of an obstruction to pollen launching and reception by the many small flowers. The peltate and sessile stigma is one of several possible solutions to the problem of how the size of the stigmatic surface can be increased in a habitat that is sufficiently dry to pose desiccation problems for a foliose stigma. On the other hand, it is also easy to imagine evolutionarily inventing an *Ateleia* flower from insect-pollinated Sophoreae such as *Acosmium*, *Myroxylon*, and *Lovanafia* (see figures in Polhill [1981: 219]).

But what about *Cyathostegia*, a close relative of *Ateleia*? Rudd (1968) felt most comfortable keeping *Cyathostegia* as a (perhaps monotypic) genus in a similarily uncertain position between the Caesalpinioideae and Papilionoideae. As noted earlier, R. Nash (pers. comm.) finds that the seeds (which Rudd viewed as morphologically very similar to those of *Ateleia*) contain the same uncommon amino acids as do those of *Ateleia* (Bell et al., 1980). While this will not help to understand its subfamily status, it is not difficult to view *Cyathostegia* as simply an *Ateleia* (or as having a common ancestor with *Ateleia*) with stamen multiplication in order to increase the amount of pollen produced. The pollinator of *Cyathostegia* is not known, but judging from the large number of strongly exposed anthers, it is either visited by a large hairy (or feathery) animal or wind-pollinated. In this context, it is interesting that it grows in xerophytic deciduous woodlands (Peru and Ecuador; Rudd, 1968), the same type of habitat occupied by *Ateleia* throughout its range (Rudd, 1968).

In view of the very central role given to floral parts in defining legume genera and higher groups, it is hard to avoid the conclusion that if more legumes were to have started down the road of wind-pollination, we would have considerably more groups as confusing as is *Ateleia*. Furthermore, genera such as *Ateleia* are prime suspects as the base for the evolution of major higher taxa. Assume that the evolutionary roots of *Ateleia* lie in some ordinary appearing legume. Through and during the evolution of wind-pollination coupled with dioecy, a rather unlegumelike flower has been evolutionarily invented. However, it is still similar enough to other legumes that its placement in the Leguminosae is incontestable. The argument lies in what subfamily or tribe it should be placed. Now, imagine that it were to find itself in a circumstance whereby there was intense realized selection for an insect-pollinated *Ateleia*. A variety of floral traits would be evolutionarily reinvented, but they would come from a highly modified legume flower. The evolutionary solutions to the standard problems in insect-pollination might well involve the production of traits viewed as decidedly nonlegume. The result would be a new family of plants, by what is hardly a profound evolutionary chain of events.

The extremely local distribution of *A. herbert-smithii* (and of the other *Ateleia*; Rudd, 1968) in Mesoamerica is probably intimately related to their dioecy and wind pollination. 1) One *A. herbert-smithii* does not a colonizer make. Since the sex ratio of adult plants is roughly 50:50, even two *A. herbert-smithii* will not be a colonizing population at least half of the time. This means that following any habitat change, the population has to expand and survive as a unit rather than as individuals making relatively long dispersal hops. 2) If there are to be equivalent levels of pollen donation and reception, the individuals of *A. herbert-smithii* must be much closer together in space and/or time than is generally the case for animal-pollinated tropical plants. It is striking in this context that *A. herbert-smithii* co-occurs with *Quercus oleoides*, the only other wind-pollinated tree in lowland Costa Rica that makes forests with single-species dominance. 3) Owing to the general unidirectionality of wind flow (from the east) in Santa Rosa, male plants that are arranged in the population so that the downwind habitat lacks conspecifics are effectively sterile. 4) The conspecifics growing downwind from a male have a greater than random chance of being his daughters, since it is the females growing downwind from him that will be his mates and simultaneously the producers of the seeds that have moved yet further downwind.

I suspect that the above biological traits explain at least in part why *Ateleia herbert-smithii* has not spread out of its very local range as humans have destroyed the forest in the general area. Topographically, *A. herbert-smithii* occupies a ridge–mesa that runs roughly at right angles to the direction of the dry season winds (that disperse the seeds). The tree has probably not spread upwind into pastures and secondary succession simply because the seeds are wind-dispersed. Within Santa Rosa, the tree has spread downwind but has run into two kinds of inhospitable habitats: pastures that for hundreds of years have been burned repeatedly, and deciduous and/or semi-evergreen forest on land so flat that most of the disturbances are only that of tree falls. I suspect, but cannot demonstrate, that the frequency of tree falls in most kinds of pristine forest in Santa Rosa is not great enough to support a population of a dioecious wind-dispersed tree that is also wind-pollinated and does not start major reproduction until it is 20–30 years old.

The upcoming fates of the attempts to introduce it around the world as a firewood tree (Hughes & Stiles, 1984) may well be instructive on the question of why the tree has not spread away from Santa Rosa. If the tree is introduced into areas where the vegetation is relatively intact, it may well be that *Ateleia herbert-smithii* will be a very poor naturalized invader even though it is a ruderal species, in view of its obvious inability to spread in Santa Rosa. On the other hand, once it is tried on many different exotic habitats, it may well find itself in one in which it will maintain a high density irrespective of other desired uses for the site (especially if the weevil does not accompany it).

It is likely that *Apion johnschmitti* and its relatives will be found to be involved with *Ateleia* reproductive biology throughout its natural range. Whitehead (1985) found a closely related species (*Apion analomum* Kissinger) in fruits of *Ateleia gummifera* from the Bahamas, and Kissinger (1974) described this species from wild-caught beetles in Cuba, where *Ateleia gummifera* is widely distributed (Rudd, 1968). A similar but undescribed species of *Apion* was found that had developed in a flower bud of *Ateleia arsenii* (Quinceo, near Morelia, Michoacan, Mexico, 2,800 m) (Whitehead, 1985). Unfortunately, if the high percent of seed survival in the Nicaraguan population is indeed due to the anthropogenic demise of the weevil, the *Apion* that feed on *Ateleia herbert-smithii* seeds may be as endangered as are their host plants.

Apion johnschmitti plays a very large role in the biology of *Ateleia herbert-smithii* in Santa Rosa. It is easy to imagine that the tree would be more abundant within Santa Rosa if the weevil were absent. This implies that *A. herbert-smithii* would expand its range in Costa Rica if its crops of surviving seeds were much larger and it therefore had more tries at recruitment in habitats where the probability of death of a seedling is high. Ironically, the habitat destruction at the Nicaraguan population of *A. herbert-smithii* may result in an increase in recruitment for the species, not only through producing more insolated habitats for colonization, but through increasing the number of surviving seeds by making life very difficult for the weevil. *Ateleia herbert-smithii* is a plant that might do best of all as, for example, a firewood tree in tropical habitats with a strong dry season and virtually all other vegetation cleared off the site (especially vegetation that could form a fuel base for occasional fires in the dry season). It may be ideal for sites where much of the barrier to fuelwood development is collection of woody plant foliage for livestock before the wood biomass can accumulate. On the other hand, there remains the possibility that goats or other domestic herbivores might feed on *A. herbert-smithii* foliage under certain circumstances. Its weed potential in such a circumstance might well be controlled by culling female trees as they first flower. However, introduction of *Apion johnschmiti* as a means of controlling *A. herbert-smithii* does not appear to have much promise unless the vegetation is so intact that it offers sufficient refugia for the weevil between fruit crops.

ACKNOWLEDGMENTS

This study has been supported by NSF grants BMS 75-14268, DEB 77-04889, GB-25189, GB-7819, GB-35032X, DEB 80-11558, BSR 83-08388, and BSR 87-06155 and by the Servicio de Parques Nacionales de Costa Rica. Two Earthwatch teams and the Field Naturalist Program of the University of Vermont contributed substantially to processing seeds in the field. The following people greatly aided in locating references and material, and in identifying specimens: W. D. Stevens, R. Poole, P. Bernhardt, D. R. Whitehead, L. D. Gomez, R. Waid, B. T. Styles, C. E. Hughes, R. M. Polhill, J. L. Zarucchi, I. K. Ferguson, R. Lopez, J. Chemsak, and G. C. Stevens. Field collections and processing of seed crops were aided by G. C. Stevens, M. Johnston, Y. R. Scharf, M. D. Gershman, F. B. Engstrom, G. R. Strimbeck, M. Charny, M. J. Hallwachs, R. G. Hallwachs, P. Harvey, G. Vega, A. Espinosa, R. Espinosa, L. Espinosa, O. Espinosa, and W. Hallwachs. Chemical analyses were provided by E. A. Bell, C. H. Stirton, R. Nash, and L. E. Fellows. D. Boucher first introduced me to *Ateleia herbert-smithii*.

This paper is dedicated to Velva Rudd, whose serious and prompt taxonomic help encouraged me to believe that tropical plants could be seriously treated as distinct species. It is also dedicated to Arthur Bell, who inspired me to think seriously about why plants have secondary compounds in their seeds. Finally, it is dedicated to Brian Styles and Colin Hughes, who are saddled with the horrific responsibility of deciding whether this and many other tropical trees should be introduced into habitats and continents other than their native homes.

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Appendix I. Fruit and seed crop parameters for marked female *Ateleia herbert-smithii* in Santa Rosa National Park, 1974–1985. Each tree has the same number from year to year. Absence of data for a tree in the years after it first appears in the record means that it did not fruit, it was destroyed, or it was impossible to further census it. Absence of data for a tree between years in which it fruited means that it did not flower or fruit in the years in which it is absent from the record.

Tree number	Estimated fruit crop size	Number of fruit sampled	Percent of fruit attacked	Percent of seeds killed	Percent of seeds surviving because in 2-seeded fruit	Percent of crop 2-seeded	Number of seeds surviving
1974							
1	25,000	252	82.54	82.54	0.00	0.00	4,365
2	120,000	232	65.09	65.09	0.00	0.00	41,897
3	100,000	258	23.64	23.64	0.00	0.00	76,357
4	75,000	283	49.12	49.12	0.00	0.00	38,163
5	150,000	294	47.73	47.73	0.00	0.00	79,081
6	50,000	160	85.00	58.12	71.43	46.00	30,625
7	150,000	256	64.84	47.84	50.29	36.00	100,195
8	90,000	288	42.01	42.01	0.00	0.00	52,188
9	50,000	304	63.49	42.23	52.65	50.00	43,421
10	50,000	278	84.89	84.89	0.00	0.00	7,554
11	70,000	1,119	77.12	52.78	38.86	46.00	48,293
12	70,000	363	39.95	39.95	0.00	0.00	42,039
13	200,000	371	78.17	78.17	0.00	0.00	43,665
14	75,000	1,205	89.63	89.63	0.00	0.00	7,780
15	50,000	257	67.70	67.70	0.00	0.00	16,148
16	100,000	245	78.37	78.37	0.00	0.00	21,633
17	20,000	260	61.15	55.79	16.67	9.00	9,692
18	200,000	314	32.80	31.50	5.36	4.00	142,675
19	100,000	305	53.12	53.12	0.00	0.00	46,885
20	50,000	276	44.57	32.80	32.94	36.00	45,652
1976							
1	14,111	611	95.75	92.86	40	3.00	1,039
1A	45,709	709	81.17	81.17	0	0.00	8,317
2	1,197	697	96.27	87.60	66	10.00	163

APPENDIX I. Continued.

Tree number	Estimated fruit crop size	Number of fruit sampled	Percent of fruit attacked	Percent of seeds killed	Percent of seeds surviving because in 2-seeded fruit	Percent of crop 2-seeded	Number of seeds surviving
3	944	444	85.36	67.56	55	12.00	387
4	1,069	569	71.35	71.23	0	0.00	308
5	1,073	573	80.98	68.24	50	19.00	397
6	14,070	570	98.42	98.42	0	0.00	173
7	23,189	689	84.04	84.04	0	0.00	3,702
8	6,137	962	98.75	98.75	0	0.00	77
9	2,946	1,038	99.04	99.31	0	0.00	28
11	270,079	859	99.07	99.07	0	0.00	2,515
12	6,650	1,250	98.56	98.56	0	0.00	96
12A	14,286	786	92.49	92.49	0	0.00	1,072
13	10,711	811	99.38	99.38	0	0.00	66
14	20,886	636	98.59	98.59	0	0.00	230
15	50,595	1,095	98.72	98.72	0	0.00	647
16	23,170	670	94.03	94.03	0	0.00	1,383
17	129,096	786	94.66	94.66	0	0.00	6,898
18	28,823	663	91.70	91.70	0	0.00	2,391
19	51,457	857	73.40	73.40	0	0.00	13,690
20	23,362	4,112	83.29	74.72	33	12.00	4,522
41	135,618	618	86.41	86.41	0	0.00	18,433
47	18,672	672	77.83	77.83	0	0.00	4,140
49	9,535	535	68.22	68.22	0	0.00	3,030
103	2,768	518	76.83	76.83	0	0.00	641
109	23,064	564	87.41	74.36	49	18.00	6,952
111	5,099	599	72.12	72.12	0	0.00	1,422
176	176,271	771	94.81	93.24	21	2.00	12,117
177	153,761	761	55.59	55.59	0	0.00	68,293
180	3,464	764	57.33	57.33	0	0.00	1,460
181	117,589	589	87.95	86.05	14	2.00	16,770
184	6,817	617	49.76	49.76	0	0.00	3,425
185	22,895	695	65.18	63.09	8	3.00	8,450
1978							
LM	67,770	7,915	77.25	77.25	not available	not available	15,420
UM	646,700	8,407	38.60	38.60			397,080
6	4,966	685	19.42	19.42			4,002
7	1,815	363	80.44	80.44			355
8	237,600	3,155	93.66	93.66			15,061
9	13,080	654	74.92	74.92			3,280
11	448,189	3,312	95.35	95.35			20,840
14	633,600	1,760	55.34	55.34			282,959
15	61,562	2,712	45.39	45.39			33,618
16	10,858	855	55.21	55.21			4,864
19	46,203	1,045	73.78	73.78			12,114

APPENDIX I. Continued.

Tree number	Estimated fruit crop size	Number of fruit sampled	Percent of fruit attacked	Percent of seeds killed	Percent of seeds surviving because in 2-seeded fruit	Percent of crop 2-seeded	Number of seeds surviving
123	10	10	0.00	0.00			10
124	16,586	887	87.71	87.71			2,038
137	13,632	568	94.72	94.72			720
138	27,602	1,302	88.40	88.40			3,201
143	18,609	1,311	96.95	96.95			568
145	10,802	867	90.31	90.31			1,047
176	283,792	969	60.68	60.68			111,584
1980							
LM	188,002	3,218	96.99	96.55	12.50	1.00	6,543
UM	426,136	3,101	90.81	90.55	2.72	0.00	40,401
1	140,910	1,281	90.71	90.29	3.20	0.00	13,750
6	43,360	542	97.42	97.42	0.00	0.00	1,120
7	1,329	443	93.45	93.03	6.45	0.00	93
8	117,682	2,029	96.80	95.99	19.51	1.00	4,756
9	9,456	788	95.69	95.32	8.11	0.00	440
11	278,190	2,529	96.13	95.89	1.92	0.00	11,440
13	3,362	747	91.43	90.96	5.88	1.00	306
14	391,416	1,938	97.63	96.98	22.03	1.00	11,916
15	28,496	1,781	90.01	89.96	0.56	0.00	2,864
16	401,866	1,509	94.63	94.44	3.57	0.00	22,370
19	10,238	1,621	79.09	79.09	0.00	0.00	2,141
109	75,590	1,665	84.57	75.16	37.58	14.00	21,383
176	183,820	1,313	86.90	85.05	12.94	2.00	28,140
177	188,416	1,472	59.44	59.44	0.00	0.00	76,418
179	10,050	1,005	90.15	90.15	0.00	0.00	990
181	7,104	592	84.97	84.11	4.21	1.00	1,140
184	26	26	0.00	0.00	0.00	0.00	0
200	100,700	2,090	97.70	97.56	5.88	0.00	2,457
201	20,608	681	96.62	96.62	0.00	0.00	696
202	53,952	1,124	96.09	94.66	19.67	2.00	2,908
203	11	11	0.00	0.00	0.00	0.00	0
207	49,020	817	87.27	87.27	0.00	13.00	1
208	125,184	1,956	94.02	94.02	0.00	0.00	7,489
1982							
LM	354,552	11,130	98.74	98.18	8.87	0.00	6,467
UM	1,204,000	11,113	97.89	97.83	2.49	0.00	26,110
6	83,250	2,775	99.06	99.06	0.00	0.00	780
7	347,131	4,342	96.04	95.88	0.56	0.00	14,311
8	40,964	3,723	99.44	99.41	4.55	0.00	242
9	374,896	3,392	97.94	97.91	0.00	0.00	7,847
11	838,590	35,015	97.54	97.44	3.34	0.00	21,531

APPENDIX I. Continued.

Tree number	Estimated fruit crop size	Number of fruit sampled	Percent of fruit attacked	Percent of seeds killed	Percent of seeds surviving because in 2-seeded fruit	Percent of crop 2-seeded	Number of seeds surviving
12	29,598	4,656	97.23	97.05	2.90	0.00	877
13	64,239	6,375	97.91	97.76	6.99	0.00	1,443
14	217,984	6,212	97.46	97.27	7.65	0.00	5,965
15	89,162	4,501	98.56	98.53	0.00	0.00	1,307
16	288,805	4,355	97.08	96.66	11.64	0.00	9,682
19	255,210	4,593	98.15	98.15	0.00	0.00	4,721
20	616	616	89.61	88.47	6.76	4.00	74
123	33,698	1,489	97.58	91.96	70.87	6.00	2,874
124	108,460	1,972	98.23	95.04	61.39	3.00	5,550
126	45,795	2,130	97.09	96.91	6.06	0.00	1,419
127	111,022	3,747	98.03	95.25	57.38	3.00	5,422
128	4,432	956	95.50	95.20	6.52	0.00	213
129	4,839	1,281	97.11	96.96	5.13	0.00	147
130	1,944,000	4,860	98.79	98.62	11.94	0.00	26,800
137	79,241	2,308	99.22	99.14	10.00	0.00	687
138	45,486	2,909	97.22	97.18	2.44	0.00	1,282
145	35,785	2,302	99.22	99.18	5.26	0.00	295
147	66,814	2,197	97.36	95.84	16.00	2.00	2,281
176	376,800	4,422	97.22	96.61	14.57	1.00	12,867
177	468,545	3,383	98.94	98.91	2.70	0.00	5,124
179	30,712	1,118	98.21	98.21	0.00	0.00	549
180	18,282	2,210	92.53	92.41	1.19	0.00	1,390
181	153,964	39,044	94.39	91.99	28.71	3.00	12,694
184	771	771	76.27	75.77	0.54	1.00	185
185	3,365	3,365	96.46	95.84	13.48	1.00	141
200	120,608	2,774	98.77	98.77	0.00	0.00	1,478
201	238,073	7,132	97.29	97.13	5.37	0.00	6,843
202	314,104	3,976	95.57	94.79	13.88	16.00	16,511
251	30,992	2,945	97.96	97.96	0.00	0.00	631
253	103,785	1,785	97.09	95.23	39.08	2.00	5,058
255	45,408	2,838	94.89	93.66	14.21	2.00	2,928
258	1,421	758	97.49	97.49	0.00	0.00	36
261	75,516	2,436	94.17	93.75	6.54	0.00	4,743
271	6,409	1,989	94.92	93.10	25.00	2.00	451
272	1,721	1,052	93.73	93.46	2.90	0.00	113
273	120,516	5,478	92.95	91.23	19.39	2.00	10,780
274	385,125	5,135	96.92	96.83	3.03	0.00	12,375
275	49,245	3,283	98.45	98.30	8.93	0.00	840
276	21,014	1,501	96.74	96.67	2.00	0.00	700
277	94,826	2,734	98.54	93.97	76.30	5.00	6,000
278	10,246	1,636	95.29	79.54	78.71	20.00	2,530
279	112,087	5,579	96.70	96.67	1.08	0.00	3,737
280	267,599	3,769	97.75	90.77	75.73	8.00	26,625
281	63,842	2,895	96.72	93.59	45.83	3.00	4,234
282	369,840	4,129	97.51	97.20	10.35	0.00	10,390

APPENDIX I. Continued.

Tree number	Estimated fruit crop size	Number of fruit sampled	Percent of fruit attacked	Percent of seeds killed	Percent of seeds surviving because in 2-seeded fruit	Percent of crop 2-seeded	Number of seeds surviving
283	61,327	1,649	94.66	92.00	33.09	3.00	5,058
284	45,128	1,223	93.46	93.38	1.24	0.00	2,989
285	1,102,152	3,909	96.65	95.76	19.64	1.00	47,368
286	330,852	2,830	92.69	91.81	9.83	1.00	27,357
287	124	124	79.03	79.03	0.00	0.00	26
288	69,285	1,455	95.40	93.36	30.30	2.00	4,714
289	42,714	3,051	94.43	93.98	7.57	1.00	2,590
290	69,326	1,384	98.41	97.15	45.00	1.00	2,064
291	36,897	1,757	94.42	83.96	66.04	14.00	6,741
292	293,121	2,969	98.05	97.85	9.09	0.00	6,516
293	23,697	2,633	98.03	97.99	1.89	0.00	477
294	642,488	5,959	97.57	94.93	51.77	3.00	33,531
295	41,198	2,612	98.28	96.52	47.37	4.00	1,498
296	34,960	4,370	25.17	24.96	0.15	1.00	26,512
296 repl.	11,157	11,157	31.16	30.96	0.25	1.00	7,760
297	8,883	1,269	88.57	88.50	0.00	0.00	1,022
298	49,078	2,438	96.39	96.35	1.12	0.00	1,792
299	20,192	5,235	95.91	95.84	0.92	0.00	841
300	66,302	10,664	95.29	95.11	2.87	0.00	3,252
301	12,330	4,110	99.39	99.39	0.00	0.00	75
302	367,392	8,544	99.16	99.15	0.00	0.00	3,139
303	484,763	7,164	98.91	98.83	0.00	0.00	5,684
304	27,293	3,560	99.47	99.47	0.00	0.00	146
305	39,051	4,409	99.07	99.07	0.00	0.00	363
306	167,901	5,916	97.90	97.69	8.03	0.00	3,888
307	314,221	4,096	98.68	98.40	12.12	0.00	5,063
308	56,559	3,327	97.54	97.01	16.00	1.00	1,700
309	111,052	1,214	98.93	98.93	0.00	0.00	1,189
310	2,958	1,450	89.24	84.16	28.57	7.00	500
311	155,545	5260	97.15	97.06	2.58	0.00	4,584
312	236,691	4,434	98.17	97.87	11.58	0.00	5,071
313	47,800	8,365	98.84	98.76	4.81	0.00	594
314	51,554	2,999	96.40	95.51	18.98	2.00	2,355
315	374,595	7,345	98.29	98.22	2.29	0.00	6,681
316	43,927	3,404	97.27	97.21	2.11	0.00	1,226
317	627	627	96.81	96.82	0.00	0.00	20
318	309,886	8,049	97.24	97.16	1.31	0.00	8,816
319	440,510	6,082	98.78	98.70	6.25	0.00	5,794
320	509,929	6,099	98.16	98.04	2.50	0.00	10,033
321	884	884	92.53	92.43	2.99	0.00	67
322	821	821	88.55	88.55	0.00	0.00	94
323	9,557	9,557	96.51	96.46	0.59	0.00	339
324	58,242	3,426	98.57	98.48	1.92	0.00	884
325	144,904	3,304	98.79	98.02	30.30	1.00	2,895

APPENDIX I. Continued.

Tree number	Estimated fruit crop size	Number of fruit sampled	Percent of fruit attacked	Percent of seeds killed	Percent of seeds surviving because in 2-seeded fruit	Percent of crop 2-seeded	Number of seeds surviving
326	175,497	2,887	99.17	98.99	13.79	0.00	1,769
327	7,074	2,358	99.32	99.32	0.00	0.00	48
328	60,418	1,841	98.75	98.64	8.00	0.00	820
329	348,227	19,874	92.58	92.33	2.55	0.00	26,790
330	295,079	3,053	99.44	99.44	0.00	0.00	1,643
1984							
LM	3,972	538	95.72	95.74	0.00	0.400	170
UM	5,642	830	98.44	98.44	0.00	0.200	88
1	34,053	1,570	98.22	97.97	12.50	0.300	694
6	12,738	1,019	97.55	97.55	0.00	0.000	313
8	6,670	2,001	98.25	98.15	5.41	0.100	123
14	9,310	1,330	94.89	93.97	16.05	1.000	567
15	2,413	724	95.72	95.45	6.06	0.300	110
16	165,205	2,423	98.80	98.60	14.71	0.200	2,318
124	181,769	5,857	95.10	93.63	22.16	1.600	1,762
130	14,400	1,008	99.40	99.40	0.00	0.000	86
130 repeat	9,286	650	58.31	58.13	0.73	0.300	3,900
137	25,417	1,112	97.12	97.10	0.00	0.600	731
143	9,786	1,896	95.99	95.94	1.30	0.100	397
145	23,965	2,716	97.94	97.79	3.33	0.200	529
147	74,032	2,311	95.33	94.48	14.73	1.100	4,132
176	139	139	41.73	41.73	0.00	0.000	81
200	760	380	98.95	98.95	0.00	0.000	8
272	38	38	71.05	71.05	0.00	0.000	11
293	129	129	91.47	91.47	0.00	0.000	11
294	444,814	17,189	93.75	92.34	19.07	1.600	34,443
298	1,061	467	97.00	96.18	22.22	0.800	41
302	3,195	703	98.58	98.58	0.00	0.000	45
303	266	266	79.70	79.70	0.00	0.000	54
306	4,915	1,413	97.66	97.60	2.94	0.100	118
309	16,359	1,854	97.20	97.09	1.85	0.100	476
311	9,300	992	99.60	99.60	0.00	0.000	38
312	1,415	566	92.76	92.43	2.33	0.400	108
313	6,065	4,380	98.33	98.33	1.35	0.000	102
314	3,212	835	96.05	94.61	21.74	2.300	177
318	3,765	1,705	95.13	95.13	0.00	0.000	183
319	3,987	1,196	98.33	98.33	0.00	0.000	67
320	13,148	1,157	97.93	97.84	4.00	0.100	284
325	21,071	1,475	84.81	84.81	0.00	0.000	3,200
328	11,616	968	95.45	95.36	2.22	0.100	540
400	161,108	10,155	95.01	94.92	1.36	0.100	8,186

APPENDIX I. Continued.

Tree number	Estimated fruit crop size	Number of fruit sampled	Percent of fruit attacked	Percent of seeds killed	Percent of seeds surviving because in 2-seeded fruit	Percent of crop 2-seeded	Number of seeds surviving
401	51,976	5,291	90.95	90.84	0.82	0.100	4,764
402	47,572	4,061	77.35	68.02	29.44	17.400	17,864
1985							
LM	922,208	5,728	98.20	98.06	8.04	1.00	18,032
UM	565,200	8,851	97.30	95.39	16.83	2.00	26,565
6	9,486	1,165	98.37	98.03	13.04	0.00	187
7	2,187	767	94.92	94.81	2.50	1.00	114
8	2,239	684	98.83	98.83	0.00	0.00	26
11	293,797	48,056	97.77	97.59	6.12	0.00	7,092
12	6,192	1,032	97.77	97.50	7.69	1.00	156
13	17,622	1,958	98.72	98.38	21.88	1.00	288
14	36,835	2,085	97.51	96.85	22.39	2.00	1,184
15	12,047	3,681	98.59	98.43	10.34	0.00	190
16	13,475	1,225	99.35	99.35	0.00	0.00	88
19	15,632	1,839	97.66	97.40	10.42	0.00	408
20	30,243	2,412	98.51	92.94	79.70	18.00	2,533
123	17,919	594	97.64	96.20	30.43	2.00	694
128	76,979	4,586	97.47	93.76	53.42	7.00	5,153
129	36,493	2,546	98.11	98.00	1.96	0.00	731
130	44,678	1,992	97.04	96.43	11.11	1.00	1,615
137	1,863	138	98.55	97.84	33.33	1.00	41
143	4,780	493	98.38	98.38	0.00	0.00	78
147	8,253	917	97.27	96.15	25.00	2.00	324
176	20,108	1,828	97.76	97.25	15.69	1.00	561
177	5,756	999	98.00	98.00	0.00	0.00	115
180	1,439	365	99.18	99.18	0.00	0.00	12
185	3,056	904	92.92	92.65	1.49	1.00	227
200	2,180	1,387	98.92	98.50	28.57	1.00	33
202	40,013	2,200	98.27	96.63	46.75	4.00	1,400
251	2,831	1,514	98.41	98.22	7.41	0.00	50
253	29,499	1,189	97.65	97.02	38.89	3.00	893
255	21,009	2,251	98.62	96.91	52.78	3.00	672
258	22,222	2,292	97.99	97.91	2.08	0.00	465
261	7,836	1,413	98.87	98.39	30.43	1.00	128
263	6,608	1,279	98.05	97.74	13.79	1.00	150
267	84,727	4,660	97.83	96.38	38.15	3.00	3,145
269	13,844	558	98.21	97.35	26.67	1.00	372
270	78,529	6,813	98.55	96.98	51.66	3.00	2,432
271	2,077	1,111	98.83	97.87	45.83	1.00	45
273	62,509	3,677	98.40	96.58	54.26	2.00	2,193
274	11,806	2,654	98.38	97.98	18.52	1.00	240
275	8,780	1,211	97.61	97.05	19.44	1.00	261
281	5,000	1,124	98.58	97.72	38.46	1.00	116

APPENDIX I. Continued.

Tree number	Estimated fruit crop size	Number of fruit sampled	Percent of fruit attacked	Percent of seeds killed	Percent of seeds surviving because in 2-seeded fruit	Percent of crop 2-seeded	Number of seeds surviving
285	57,577	2,062	98.01	96.96	34.38	2.00	1,787
286	12,936	616	98.70	98.71	0.00	0.00	168
295	22,846	2,264	97.66	95.00	48.91	21.00	1,382
296	1,685	822	95.86	93.06	41.67	4.00	123
300	17,908	1,847	97.89	96.82	35.00	2.00	582
301	762	501	97.41	97.41	0.00	0.00	20
302	6,412	1,241	98.07	97.75	7.14	0.00	145
303	19,318	1,862	98.60	98.50	7.14	0.00	291
305	7,568	688	98.26	98.84	0.00	1.00	88
306	28,728	3,078	97.17	96.77	13.00	0.00	933
307	99,424	3,824	98.17	93.73	71.43	11.00	6,916
308	4,412	938	98.40	95.17	66.67	6.00	226
310	1,004	1,004	96.81	89.97	70.94	16.00	117
312	11,331	1,259	98.57	98.10	25.00	0.00	216
313	7,056	2,352	98.81	98.77	0.00	0.00	87
314	7,388	1,019	98.43	97.86	27.27	1.00	160
315	7,185	712	98.03	97.50	16.67	1.00	182
318	4,145	1,306	97.32	97.18	5.41	0.00	117
319	9,477	620	99.03	97.95	38.46	2.00	199
320	30,173	2,235	99.15	99.06	9.52	0.00	284

APPENDIX II. Diameter (dbh) increment per year by healthy adult male *Ateleia herbert-smithii* in Santa Rosa National Park, January 1983 to January 1985.

Tree number	Initial diameter (cm)	Increment/year (cm)
250	62.99	0.64
252	57.91	0.30
254	46.23	0.58
256	49.28	0.41
257	40.89	0.54
259	30.99	0.69
260	51.31	0.07
262	50.55	0.10
265	50.29	0.29

APPENDIX III. Diameter (dbh) increment per year by adult healthy female *Ateleia herbert-smithii* in Santa Rosa National Park, January 1983 to January 1985.

Tree number	Initial diameter (cm)	Increment/year (cm)
LM	35.56	0.71
6	39.12	0.59
7	50.80	0.21
8	20.57	0.39
9	60.71	0.27
13	22.35	1.55
15	26.67	1.08
16	70.36	0.38
123	46.48	1.46
124	50.04	0.07
130	62.23	0.81
176	42.93	0.01
177	35.31	0.14
179	20.83	0.83
180	22.61	0.46
184	12.70	0.37
185	10.92	0.05
200	27.94	0.49
201	24.38	0.51
251	24.89	0.19
253	51.82	0.56
255	29.46	0.61
258	36.32	0.42
261	18.29	0.26
263	17.27	0.89
264	28.45	0.41
267	33.27	0.18
268	11.18	0.23
269	46.48	0.13
270	36.58	2.90
271	21.59	1.79
273	18.54	0.21
274	34.54	0.22
275	26.67	0.45
276	50.80	0.46
277	32.00	0.72
278	17.27	0.26
280	52.07	0.51
281	32.26	0.49
282	31.50	0.48
283	38.86	0.46
284	39.12	0.23
285	56.64	0.14
287	14.73	0.49
288	25.40	0.28
289	23.88	0.25
290	61.47	1.30
291	42.67	0.00
293	21.59	0.47
294	71.37	0.36

APPENDIX III. Diameter (dbh) increment per year by adult healthy female *Ateleia herbert-smithii* in Santa Rosa National Park, January 1983 to January 1985.

Tree number	Initial diameter (cm)	Increment/year (cm)
LM	35.56	0.71
6	39.12	0.59
7	50.80	0.21
8	20.57	0.39
9	60.71	0.27
13	22.35	1.55
15	26.67	1.08
16	70.36	0.38
123	46.48	1.46
124	50.04	0.07
130	62.23	0.81
176	42.93	0.01
177	35.31	0.14
179	20.83	0.83
180	22.61	0.46
184	12.70	0.37
185	10.92	0.05
200	27.94	0.49
201	24.38	0.51
251	24.89	0.19
253	51.82	0.56
255	29.46	0.61
258	36.32	0.42
261	18.29	0.26
263	17.27	0.89
264	28.45	0.41
267	33.27	0.18
268	11.18	0.23
269	46.48	0.13
270	36.58	2.90
271	21.59	1.79
273	18.54	0.21
274	34.54	0.22
275	26.67	0.45
276	50.80	0.46
277	32.00	0.72
278	17.27	0.26
280	52.07	0.51
281	32.26	0.49
282	31.50	0.48
283	38.86	0.46
284	39.12	0.23
285	56.64	0.14
287	14.73	0.49
288	25.40	0.28
289	23.88	0.25
290	61.47	1.30
291	42.67	0.00
293	21.59	0.47
294	71.37	0.36

APPENDIX III. Continued.

Tree number	Initial diameter (cm)	Increment/year (cm)
295	17.53	0.23
296	21.34	1.21
298	29.21	1.25
299	18.03	0.69
300	22.35	1.27
302	33.27	0.39
303	38.35	0.09
304	23.11	0.49
305	23.62	0.07
306	43.94	2.30
307	48.77	0.46
308	28.96	1.16
309	58.93	0.05
310	18.29	1.30
311	35.81	0.60
312	38.10	0.12
313	16.51	0.09
314	29.97	0.21
315	38.61	0.27
316	27.18	0.35
317	10.67	0.42
319	33.27	0.24
320	46.74	0.12
321	7.11	0.54
322	8.38	0.71
323	6.10	0.30
325	35.81	0.92
328	35.56	0.18

APPENDIX IV. Diameter (dbh) increment per year by healthy female *Ateleia herbert-smithii* in Santa Rosa National Park, January 1977 to January 1985.

Tree number	Initial diameter (cm)	Increment/year (cm)
11	55.12	0.32
16	66.04	0.64
124	48.01	0.27
128	37.85	1.47
129	27.69	1.31
130	59.69	0.52
138	87.12	0.39
143	49.02	0.22
145	38.86	0.10
147	33.27	0.35
176	37.34	0.70
177	32.77	0.35
179	15.75	0.84
180	20.57	0.37
184	11.94	0.19
185	10.41	0.08

APPENDIX V. Fruit crop parameters for the 459 terminal infructescences on one major branch of *Ateleia herbert-smithii* number 181 in 1982. All seed death was caused by *Apion johnschmitti*. Blanks are zeros. Note: branch numbers were assigned as the branches were taken from a large but nonrandomized branch pool and should be randomized before subsampling.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
1	99	10	2		
2	25	1	2	1	
3	81	1	12	1	
4	102	5	4	5	
5	115	6	7		
6	87	8	1	1	
7	57	4	4		
8	54	1	0		
9	91	5	1	1	
10	170	6	1		
11	122	5	6	1	
12	124	7	5	1	1
13	124	4	1		
14	139	9	16	1	4
15	81	3	0		
16	54	4	3	1	2
17	50	5	1		
18	57	1	2	1	2
19	39	5	1		2
20	161	12	2		1
21	158	10	6	1	
22	37	5	1		
23	160	9	5		1
24	202	9	5		1
25	133	14	10		4
26	20	1	0		
27	46	5	5	1	1
28	398	12	6		
29	107	4	3		1
30	71	9	3	1	1
31	73	7	1		1
32	57	1	1		1
33	46	2	0		
34	34	2	0		
35	168	11	10		2
36	56	0	0		
37	66	2	0	1	
38	158	8	7		
39	20	4	1		
40	62	4	1		
41	19	1	0		
42	152	8	4		
43	136	11	5	1	2
44	49	0	2		
45	125	4	4		
46	69	4	2		

Appendix V. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
47	65	5	0		
48	29	0	1		
49	18	3	0		
50	33	0	0		
51	67	5	0		
52	98	4	2		
53	106	4	2		
54	32	1	2	1	
55	24	0	0		
56	112	3	0		
57	82	2	3		
58	36	0	0		
59	23	2	0		
60	209	16	14	1	1
61	67	1	2		
62	92	6	1		2
63	84	4	1		1
64	19	2	0		
65	14	0	0		
66	97	2	2		
67	94	1	2		1
68	190	11	8		3
69	103	3	0		1
70	52	1	0		
71	53	1	0		
72	56	6	0	1	
73	22	0	2	1	
74	14	3	0		
75	103	6	1		
76	86	2	0		
77	127	11	7	1	2
78	81	6	4	1	
79	89	4	1		
80	109	7	7	1	
81	123	11	6		
82	16	0	0		
83	63	2	0		
84	27	2	0		
85	18	2	0		
86	70	2	2		
87	47	1	0		
88	21	0	0		1
89	136	11	8		
90	26	0	0		
91	37	1	1		
92	120	14	5		
93	24	2	1	1	1
94	18	2	0		
95	111	6	0		
96	65	0	0		1

APPENDIX V. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
97	9	1	0		
98	30	2	0		
99	90	6	3		
100	43	1	0		
101	24	3	0		
102	58	2	4		4
103	90	2	1	2	
104	230	12	2		
105	77	3	0		
106	25	5	0		
107	63	1	0		
108	66	4	2	1	
109	152	3	2		
110	82	2	0		
111	33	2	2		
112	80	5	1		
113	41	0	0		
114	48	2	1		
115	78	3	4		
116	86	2	2		
117	55	3	3	1	
118	34	1	0		
119	138	8	8	2	
120	88	1	0		
121	13	0	0		
122	8	1	0		
123	110	5	6	2	
124	58	3	0		
125	174	8	9		
126	82	3	1		
127	110	5	3		
128	172	7	5	1	1
129	103	7	4		1
130	67	10	11	2	
131	91	3	3		
132	37	3	4		
133	75	3	1		
134	54	1	1		
135	121	6	10	1	
136	112	4	1		1
137	22	1	0		
138	55	2	1		
139	269	14	4		2
140	65	5	6		
141	65	3	1		
142	69	1	5		1
143	72	2	2	1	
144	114	6	5		
145	59	4	1		
146	221	16	5	2	

APPENDIX V. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
147	233	10	7		
148	156	6	8	1	
149	194	22	6	1	
150	55	6	4		
151	114	3	0		
152	41	0	1		
153	36	3	2		
154	107	3	1	1	
155	158	13	6		1
156	44	3	0		
157	118	9	3		
158	51	2	1	1	
159	69	3	4		
160	24	1	2		
161	71	1	2	1	1
162	54	1	1		
163	84	7	3		1
164	14	2	0		
165	28	6	1		
166	36	2	2		
167	17	0	0		
168	13	8	2		
169	23	4	0		
170	84	5	1		
171	94	1	1		1
172	177	9	14	1	
173	149	15	2	2	1
174	121	5	1		
175	22	0	0		
176	63	4	2	2	
177	117	2	1		
178	84	3	0		
179	204	11	1		
180	154	9	8		1
181	152	8	1		
182	136	2	0		
183	133	4	2		
184	100	8	2		
185	87	3	1		
186	60	3	2		
187	45	9	1		
188	109	5	0	1	
189	160	3	8		
190	119	5	6		1
191	163	4	0	1	1
192	69	2	0	1	
193	155	2	4		
194	66	5	2		1
195	56	3	1		
196	238	9	10		2

APPENDIX V. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
197	43	3	1	1	
198	49	1	1		
199	102	2	0		
200	146	7	7		
201	125	4	6		
202	143	8	4		
203	224	10	5		3
204	121	5	1		
205	20	0	0		
206	501	22	14	3	3
207	13	0	0		
208	32	1	0		
209	354	22	11	1	
210	26	1	1		
211	27	0	0		
212	63	0	0		
213	22	2	1		
214	44	1	0		
215	56	1	0	1	
216	157	8	0		1
217	113	4	7		
218	106	4	0	1	1
219	84	10	5		1
220	63	2	0		
221	92	12	1	1	1
222	95	5	1		1
223	98	0	2		
224	29	2	1		
225	143	7	3	2	1
226	77	7	0		
227	13	3	0		
228	113	1	5		
229	5	0	0		
230	324	12	8	1	1
231	41	0	1		
232	36	1	0		
233	30	4	1		
234	594	35	12	2	
235	174	3	5		
236	45	0	0		
237	19	0	1		
238	53	1	4		
239	26	2	1		
240	13	3	1		
241	50	0	0		
242	54	4	0		1
243	8	1	1		
244	61	5	0		
245	136	18	5		1
246	112	3	0		

Appendix V. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
247	49	3	1		
248	53	3	0		
249	36	1	0		
250	16	0	0		
251	77	6	1		
252	64	6	0		
253	48	0	0		
254	37	3	2		
255	65	1	1		
256	73	5	5		2
257	54	2	2		
258	18	1	0		
259	26	1	1		
260	98	2	1		
261	206	19	4		
262	83	5	2	1	
263	33	4	0		
264	22	2	0		
265	64	1	0		
266	316	22	3		
267	93	15	1		
268	30	0	0		
269	21	0	0		
270	62	3	0		
271	28	2	0		
272	92	2	0		
273	273	26	4		
274	17	1	0	1	
275	58	3	0		
276	264	12	1	1	1
277	25	7	0		
278	38	5	0		
279	26	4	2		
280	206	15	4		
281	37	0	0		
282	40	4	1	1	
283	170	8	1	2	
284	94	1	2		
285	82	8	0		
286	62	8	4		
287	190	12	3		
288	82	4	1		
289	32	2	0		
290	28	1	0		
291	46	2	2		
292	84	6	1		
293	26	1	0		
294	130	11	3	1	
295	13	1	0		
296	56	1	0		

APPENDIX V. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
297	15	4	1		
298	140	8	3	1	
299	76	1	4		1
300	87	5	1		1
301	36	1	0		
302	16	2	0		
303	37	6	0		
304	54	1	1		
305	38	6	0		
306	23	1	0		
307	19	1	1		
308	62	5	3		
309	55	3	0		
310	28	1	0	1	
311	23	1	0		
312	34	26	1	1	
313	17	2	0		
314	58	11	2		
315	37	6	0	1	
316	21	1	0		
317	17	2	0		
318	10	2	0		
319	16	0	0		
320	13	2	0		
321	12	2	0		
322	53	2	1		
323	24	1	0		
324	89	29	2		
325	32	3	0		
326	27	14	3		
327	18	1	0		
328	100	7	3		
329	43	3	0	1	
330	28	5	2		
331	26	0	0	1	
332	13	11	0		
333	38	2	1		
334	14	3	0		
335	30	12	0	1	
336	14	0	0		
337	107	8	4	1	1
338	8	0	0		
339	44	1	1		
340	36	2	0		
341	34	1	0		1
342	41	4	1		
343	20	2	0		
344	12	4	0		
345	9	0	0		
346	17	5	0		

APPENDIX V. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
347	88	2	2		
348	56	3	2		1
349	26	0	0		
350	100	4	1		1
351	69	4	3		
352	58	1	0		
353	41	3	0		
354	116	7	2		
355	56	1	0		
356	166	10	1		
357	126	3	1		
358	37	1	2		
359	35	3	2	1	
360	119	3	3		
361	131	5	2		
362	37	2	0		
363	48	3	3		
364	29	1	0		
365	62	2	0		
366	29	3	0		
367	57	3	2		
368	18	0	0		
369	55	4	0		
370	117	8	3		3
371	50	0	2		
372	136	7	3		
373	42	1	1		
374	64	2	4		
375	110	4	0		
376	98	10	6		
377	66	2	2		1
378	106	9	1		
379	71	4	1		1
380	73	9	8		
381	60	7	0		
382	75	9	6	1	
383	47	6	1		
384	33	2	0		
385	147	6	3		
386	62	0	0		1
387	136	6	5		1
388	212	12	4	1	
389	44	3	1	2	1
390	108	5	1		
391	54	5	2		
392	32	2	0		
393	72	2	1		
394	74	4	1		
395	135	3	1		2
396	130	9	8		1

Appendix V. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
397	60	7	0	1	
398	51	1	0	1	
399	126	9	3		
400	213	20	3	5	
401	77	6	1		
402	61	5	0		
403	148	12	4		1
404	47	4	1	1	
405	106	8	1		
406	23	1	0		
407	58	2	4		
408	209	11	7		1
409	137	1	2		
410	90	3	5		
411	105	6	4	1	
412	18	1	0		
413	65	4	1		
414	41	2	1		
415	187	14	11	2	1
416	101	4	0		1
417	99	6	1		
418	86	7	3	1	
419	89	2	1		
420	68	7	3		2
421	132	9	8	1	
422	172	10	0	1	
423	58	11	4	1	
424	76	1	0		
425	37	2	9	1	
426	97	13	12		
427	28	1	0		
428	62	4	4		
429	65	8	5		
430	39	2	0		
431	57	2	0		
432	98	10	2		
433	86	4	0		1
434	62	1	0		
435	16	0	2		
436	52	0	0		
437	44	3	0		
438	98	1	2		
439	38	1	1		
440	22	1	1		
441	40	1	2		
442	141	4	5		1
443	34	2	0	1	
444	32	2	3		
445	37	2	2		
446	88	5	1		

APPENDIX V. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
447	32	0	0		
448	29	1	0		
449	32	4	0		
450	40	4	1		1
451	113	5	2		
452	91	4	2	2	
453	93	11	2		
454	156	11	5		
455	183	9	2		
456	129	4	2		4
457	71	2	1		
458	86	1	2		1
459	77	4	2		

APPENDIX VI. Fruit crop parameters for the 500 terminal infructescences on a majority and complete subset of one major branch of *Ateleia herbert-smithii* number 11 in 1982. All seed death was by *Apion johnschmitti*. Blanks are zeros. Note: branch numbers were assigned as branches were taken from a large but nonrandomized branch pool and should be randomized before subsampling.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
1	193	3			not available
2	268	9			
3	441	16			
4	210	7			
5	299	17			
6	215	4			
7	662	9	3		
8	147	3			
9	742	29			
10	229	9			
11	525	11			
12	274	4	1		
13	201	14			
14	568	18	1	1	
15	820	26	3		
16	424	19			
17	32	1			
18	352	11			
19	202	6		1	
20	390	10	2	1	
21	150	2	1		
22	274	9	2		
23	224	4			
24	224	6			
25	162	2			

APPENDIX VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
26	341	7			
27	89	2			
28	113	3			
29	315	7			
30	494	11			
31	238	10			
32	158	8			
33	142	4			
34	508	23	2		
35	155	2			
36	211	5		1	
37	608	19			
38	209	4			
39	253	5			
40	194	8			
41	141	3			
42	142	6	1		
43	467	25			
44	133	3			
45	215	4			
46	196	9			
47	215	4			
48	312	10			
49	269	7			
50	360	8	2		
51	564	15	1		
52	573	6			
53	500	24			
54	200	16			
55	214	7			
56	272	9			
57	486	11	3		
58	413	9			
59	367	13	1	1	
60	202	9			
61	384	14			
62	222	6			
63	241	5			
64	275	8			
65	102	1			
66	354	5			
67	257	8			
68	38	1			
69	271	8			
70	404	7	2		
71	215	7			
72	314	19			
73	467	21	1		
74	297	5			
75	300	6			

Appendix VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
76	479	19	1		
77	396	8			
78	210	3			
79	243	11			
80	112	4			
81	86	3			
82	307	11			
83	197	6	2		
84	320	5			
85	152	2	1		
86	224	5	1	1	
87	319	12			
88	248	13		1	
89	99	6			
90	333	17	3		
91	332	15			
92	44	0			
93	179	3			
94	268	7			
95	132	2	1		
96	150	1			
97	73	2			
98	183	7		1	
99	153	12			
100	140	0		1	
101	218	9			
102	72	3			
103	70	1			
104	136	4			
105	151	6			
106	173	5			
107	60	1			
108	59	7	1		
109	130	6			
110	43	4	3		
111	116	2	1		
112	92	2			
113	120	4			
114	163	7			
115	202	8			
116	180	3	2		
117	175	9			
118	182	5	1		
119	194	3		1	
120	188	5			
121	202	15			
122	238	10			
123	145	3			
124	197	9			
125	261	9		1	

APPENDIX VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
126	271	6			
127	163	0			
128	195	7			
129	169	12			
130	121	4			
131	215	4			
132	300	8			
133	255	10			
134	275	7			
135	296	6			
136	254	8			
137	264	5			
138	223	14	1		
139	235	7			
140	193	7			
141	261	14			
142	241	11			
143	225	2			
144	308	9			
145	281	18	1		
146	248	12	2		
147	327	16			
148	392	6	1		
149	422	20	1	1	
150	384	15			
151	312	14			
152	458	14	1		
153	356	11			
154	389	10	1		
155	437	20			
156	543	14	1		
157	393	11			
158	281	7	1		
159	277	13	1		
160	336	12			
161	363	13	1		
162	390	10			
163	555	22			
164	464	14	1		
165	401	19			
166	493	9	2		
167	535	26			
168	651	27	2		
169	496	28			
170	403	11	2		
171	752	26	2	1	
172	583	27	4		
173	720	13	1		
174	759	28	7		
175	593	10	2	1	

Appendix VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
176	719	27	1	1	
177	1,052	26		1	
178	1,386	42	2	2	
179	264	12			
180	366	10			
181	336	10			
182	667	25	1		
183	314	10			
184	363	13	1	1	
185	287	16		1	
186	433	11	1		
187	366	11			
188	234	3			
189	276	7			
190	270	13	2		
191	337	10	1		
192	339	16	1		
193	349	10			
194	352	33	1		
195	414	13	1		
196	309	17			
197	490	24			
198	790	9		1	
199	241	13			
200	271	11			
201	351	29			
202	500	17	1		
203	338	11			
204	532	12	1	2	
205	144	6			
206	276	11	1		
207	965	38	1		
208	699	16			
209	107	4			
210	271	5	1		
211	243	1			
212	283	3			
213	301	9			
214	220	3	1		
215	390	10			
216	180	3			
217	748	21	2	1	
218	83	4			
219	345	8			
220	714	9			
221	274	7			
222	452	16	1		
223	73	1			
224	77	1			
225	211	4			

APPENDIX VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
226	179	5			
227	1,044	30	1	1	
228	353	17	1		
229	252	4		2	
230	155	8			
231	52	0			
232	311	12			
233	103	3			
234	89	5			
235	472	11			
236	405	11		1	
237	132	5			
238	96	4			
239	181	8			
240	144	2			
241	148	6			
242	60	3			
243	424	13		1	
244	639	31	1		
245	259	9			
246	127	0	1		
247	44	1			
248	922	22	2		
249	338	10			
250	185	6	1		
251	450	16	1		
252	545	21	2		
253	219	12			
254	460	23	1		
255	255	12	1		
256	775	29	3		
257	633	21			
258	293	15			
259	229	8	1		
260	1,083	29	4		
261	276	5			
262	228	4			
263	378	16	2	1	
264	364	10	1		
265	391	14	2		
266	232	9			
267	259	16			
268	219	6			
269	325	10			
270	201	9			
271	403	31	1		
272	335	8			
273	360	13			
274	441	14			
275	267	10	1		

APPENDIX VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
276	690	18		1	
277	583	17			
278	422	12	1		
279	517	6			
280	305	4			
281	424	4		1	
282	417	15			
283	138	1			
284	149	6			
285	508	14			
286	539	13			
287	361	10			
288	177	11			
289	266	9	1		
290	206	3			
291	266	1	1		
292	626	20			
293	120	1			
294	462	16	1		
295	542	12			
296	239	5			
297	239	7			
298	343	10		1	
299	220	5			
300	774	30	1	3	
301	853	24			
302	441	14			
303	364	10			
304	307	9			
305	549	11			
306	256	6			
307	711	17	2	1	
308	275	6	2	2	
309	176	8			
310	148	0			
311	408	11			
312	692	26			
313	528	15	1		
314	668	23	1		
315	249	2			
316	413	6			
317	458	24	1	2	
318	457	21	1	1	
319	556	17	2	2	
320	676	28			
321	346	10		1	
322	317	10	1		
323	132	4	1		
324	641	25	3	1	
325	187	10		1	

APPENDIX VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
326	502	13	2	1	
327	409	11		1	
328	596	32			
329	215	4	1		
330	307	13			
331	307	8		2	
332	695	16		2	
333	88	4			
334	383	10	3		
335	394	12	2		
336	436	13			
337	413	10		1	
338	256	10	1		
339	303	8	2		
340	44	0			
341	193	17			
342	415	6	2		
343	79	2			
344	739	8			
345	693	25			
346	81	1			
347	580	19			
348	577	17	2		
349	307	4			
350	114	3			
351	536	26			
352	12	0			
353	285	11			
354	151	7			
355	220	7			
356	405	20			
357	416	12	2		
358	817	21			
359	374	11			
360	49	6			
361	751	27	2		
362	219	12			
363	688	11			
364	405	11			
365	494	16			
366	630	12	1		
367	707	9		1	
368	416	17			
369	666	31	1		
370	400	19			
371	353	4			
372	183	4			
373	56	5			
374	194	3			
375	98	5	1		

APPENDIX VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
376	586	17	1	2	
377	519	19			
378	175	1			
379	489	11			
380	210	2			
381	150	5			
382	150	6			
383	250	12			
384	650	11	2		
385	319	8	1		
386	123	8			
387	257	12			
388	190	7			
389	223	2			
390	341	12			
391	120	0			
392	420	4			
393	309	7	1		
394	88	1			
395	180	5			
396	306	10			
397	318	9			
398	234	11			
399	459	6			
400	130	2			
401	335	7			
402	188	2	2		
403	648	10			
404	150	3			
405	452	14			
406	201	3			
407	243	1			
408	280	9			
409	388	13	1	1	
410	52	2			
411	334	4			
412	194	5			
413	432	3			
414	158	3			
415	489	7	1	1	
416	327	1	1		
417	97	0	1		
418	46	0		1	
419	451	7			
420	197	10			
421	284	2			
422	296	8	4		
423	222	4	1		
424	230	3			
425	104	2	2		

APPENDIX VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
376	586	17	1	2	
377	519	19			
378	175	1			
379	489	11			
380	210	2			
381	150	5			
382	150	6			
383	250	12			
384	650	11	2		
385	319	8	1		
386	123	8			
387	257	12			
388	190	7			
389	223	2			
390	341	12			
391	120	0			
392	420	4			
393	309	7	1		
394	88	1			
395	180	5			
396	306	10			
397	318	9			
398	234	11			
399	459	6			
400	130	2			
401	335	7			
402	188	2	2		
403	648	10			
404	150	3			
405	452	14			
406	201	3			
407	243	1			
408	280	9			
409	388	13	1	1	
410	52	2			
411	334	4			
412	194	5			
413	432	3			
414	158	3			
415	489	7	1	1	
416	327	1	1		
417	97	0	1		
418	46	0		1	
419	451	7			
420	197	10			
421	284	2			
422	296	8	4		
423	222	4	1		
424	230	3			
425	104	2	2		

APPENDIX VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
426	205	3			
427	35	1			
428	303	6			
429	321	7	1	1	
430	174	1			
431	301	10		1	
432	530	9	1		
433	439	6	1		
434	500	6			
435	438	5			
436	303	5			
437	580	8	1		
438	246	7			
439	521	10	3		
440	168	9			
441	410	7	1		
442	292	8			
443	126	1	1		
444	362	5			
445	225	5	1		
446	433	11	1		
447	395	4			
448	621	21			
449	634	24		2	
450	354	4			
451	356	13			
452	425	10			
453	466	12			
454	121	0		2	
455	385	5			
456	321	6			
457	854	22			
458	150	2			
459	401	8	2		
460	403	14			
461	420	5			
462	203	5	1		
463	302	8	2		
464	249	8			
465	287	6			
466	167	3			
467	400	10	2	2	
468	294	3			
469	111	0			
470	322	2			
471	309	8	1		
472	24	0			
473	141	0			
474	76	1			
475	122	4			

APPENDIX VI. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
476	393	11	1		
477	347	6			
478	105	2			
479	306	5			
480	318	0			
481	284	7			
482	252	9			
483	245	1			
484	52	0			
485	237	4		2	
486	265	7	1		
487	237	0			
488	212	5			
489	253	7			
490	325	6			
491	219	7			
492	260	2			
493	186	3			
494	217	1			
495	303	7			
496	146	1			
497	256	8	1		
498	257	3			
499	229	7			
500	365	3			

APPENDIX VII. Fruit crop parameters for the 263 terminal infructescences on one major branch of *Ateleia herbert-smithii* number 11 in 1985. All seed death was caused by *Apion johnschmitti*. Blanks are zeros. Note: branch numbers were assigned as the branches were taken from a large but nonrandomized branch pool and should be randomized before subsampling.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
1	284	9			
2	146	6	1	1	
3	47	2			
4	204	7	1		
5	120	5			
6	290	6	1		
7	140	2			
8	135	1	1		
9	382	4	1	1	1
10	173	4			
11	348	4			1
12	241	4			1
13	67	0			
14	282	7		1	

APPENDIX VII. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
15	60	2			
16	252	4	1		
17	93	0			
18	130	6			
19	60	0			
20	328	8	1		
21	123	3			
22	323	7			
23	80	4			
24	164	5			
25	163	5			
26	513	16			
27	213	4	1		
28	699	22	4		
29	302	6	4		
30	36	1	1		
31	255	13	2		
32	247	10	1		
33	141	6	1		
34	119	8	1		
35	221	7			
36	277	7	2		
37	206	1		1	
38	253	7	1		
39	275	10			
40	213	4	1		
41	339	7			
42	56	0			
43	73	1			1
44	43	3			
45	76	0			
46	253	7			
47	125	9			
48	197	3	1		
49	111	9			
50	160	7			
51	353	11			
52	148	1			
53	301	13			
54	67	1			
55	77	1	1		2
56	416	6	1		3
57	185	4			
58	202	9			2
59	202	5			
60	86	1			
61	342	6			
62	110	2			
63	89	2			
64	56	2			

APPENDIX VII. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
65	190	3			
66	40	0			
67	127	1			
68	128	2			
69	531	2	1	1	1
70	301	1			1
71	268	1	1		
72	609	16			1
73	280	5			
74	329	3	1		1
75	180	3			
76	556	9	1		1
77	131	3	1		
78	181	2			1
79	435	3			1
80	273	7			3
81	90	0			
82	453	7			1
83	350	7			2
84	95	3			
85	96	1			
86	357	2			2
87	144	8			
88	147	2			
89	516	2	1		1
90	46	0			
91	33	0			
92	133	2			
93	182	5			
94	172	6			
95	91	3			
96	35	1			
97	103	3			
98	211	7		1	
99	186	1			
100	135	2	1		
101	129	0	1		
102	206	3			
103	237	7			1
104	226	11			
105	34	3			
106	226	4			
107	116	1			
108	121	0			
109	294	12			1
110	70	0			
111	59	2			
112	141	2			
113	234	5	2		
114	158	2			1

APPENDIX VII. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
115	245	6		1	
116	275	9	2		
117	184	4	2		
118	35	1			
119	23	0			
120	292	5			
121	301	2			
122	98	3			
123	126	1			
124	33	0			
125	107	2			
126	229	2	1		
127	236	3			1
128	229	5	1		
129	37	2	2		
130	214	4			
131	68	6			
132	94	4			
133	79	0			
134	80	4			
135	242	8			
136	31	0			
137	40	2			
138	137	0	1		
139	257	7			
140	70	3			
141	101	2			
142	150	1		1	
143	134	4			
144	86	1			
145	52	0			
146	212	9			
147	234	2	1	1	
148	203	5			1
149	102	1			
150	392	10			2
151	209	4	1		
152	176	6			
153	41	1			
154	304	3			
155	43	0			
156	112	2			
157	81	3			
158	30	2			
159	135	4			1
160	333	4	2		2
161	38	2			
162	303	10			
163	217	5	3	1	
164	55	0			1

APPENDIX VII. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
165	253	8	1	1	
166	91	1			
167	93	1			1
168	252	1	1		
169	105	2			
170	105	0			
171	208	4			
172	160	3			
173	177	3			
174	55	2			
175	109	2			
176	49	1			
177	219	6			
178	115	4			
179	22	0			
180	97	4	2		
181	386	12	1		
182	168	7			
183	259	7		1	1
184	124	7			
185	66	3			
186	139	1	1		
187	88	0			
188	77	5			
189	129	2			1
190	354	6			
191	129	7			
192	138	4			
193	63	1	1		
194	29	3			1
195	167	3			
196	117	3		2	1
197	234	0			
198	128	7			1
199	172	4			
200	73	4			
201	123	3			
202	348	8			
203	343	13			2
204	82	0			
205	90	14			1
206	188	4			
207	185	5			
208	123	1			
209	94	2			
210	347	11			2
211	113	4			
212	68	2			
213	187	5			
214	77	1			1

APPENDIX VII. Continued.

Branch number	One-seeded fruits		Two-seeded fruits		
	Seed killed	Seed missed	One seed killed	None killed	Both killed
215	225	4			
216	126	3			
217	213	3			
218	214	4			1
219	159	2			
220	116	2			
221	173	1		1	
222	237	8			
223	96	7			
224	213	8		1	
225	47	3			
226	134	2	1		
227	183	2	2		1
228	210	3			1
229	370	9	1		
230	161	0			1
231	234	4	1		
232	529	13			
233	21	0			
234	94	2			
235	134	1			
236	121	4			
237	103	1			
238	65	3			
239	199	5			
240	91	7			
241	61	1			
242	208	7	1		
243	96	2			
244	251	6			
245	447	7			2
246	218	12			1
247	172	11			
248	513	8			
249	241	4			
250	64	0			
251	64	2			
252	154	3			
253	63	2			
254	402	2	2		1
255	271	7			
256	57	1			1
257	246	0			
258	309	3			
259	52	2			
260	41	0			
261	93	2			
262	71	0			1
263	217	6			1