Decline of a Population of Wild Seeded Breadfruit (*Artocarpus mariannensis*) on Guam, Mariana Islands[1]

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Abstract: Seeded breadfruit (*Artocarpus mariannensis*) was historically a dominant tree in native forests on Guam and Rota in the Mariana Islands. Censuses conducted during 1989–1999 showed a large decline in the population of this species in northernmost Guam, with the number of trees at one study area decreasing from 549 to 190 trees, or 65.4%. Mean annual decline rates were far higher from 1989 to 1996 (9.2% per year) than from 1996 to 1999 (2.6% per year). Size structure of the population was strongly skewed toward larger trees, with 83.3% of measured individuals having trunk diameters ranging from 31 to 70 cm. Virtually no seedlings or saplings were present. Experiments at this site revealed high rates of fallen seed and fruit consumption and browsing on seedlings by introduced Philippine deer (*Cervus mariannus*) and feral pigs (*Sus scrofa*). In contrast, breadfruit populations elsewhere on Guam and Rota exhibited much less mortality. One population in an area without deer and pigs displayed considerable regeneration and a size structure composed mainly of younger plants. The decline of *A. mariannensis* in northern Guam appeared to be caused primarily by a combination of high mortality associated with an unusually severe typhoon season in 1992 and a nearly complete lack of recruitment due to excessive seed predation and herbivory by deer and pigs. Ungulate control is strongly urged to restore populations of *A. mariannensis* and other native plants, and to prevent further alteration of Guam's forests.

Indigenous plant communities on many Pacific islands have experienced extensive alteration in floristic composition and structure due to direct human activity, fragmentation, the invasion of exotic plants and animals, and losses of pollinators and seed dispersers (Fosberg 1960, 1992, Cuddihy and Stone 1990, Thaman 1992, Cox and Elmqvist 2000, Burney et al. 2001). A frequent outcome of broad habitat change is increased rarity, and in some cases extinction, of native plant species (Adsersen 1989, Jaffre et al. 1998). In Micronesia, little effort has thus far been devoted to identifying plant species at risk or the causes behind their declines (Schreiner 1997). This is a major reason for the general lack of conservation planning aimed at plant preservation in the region.

On Guam in the Mariana Islands, a number of native plants are probably declining on either a local or islandwide scale for reasons that are poorly understood (Wiles et al. 1996, Ritter and Naugle 1999; L. Raulerson, pers. comm.; G.W., pers. obs.). One of these species is the seeded breadfruit (*Artocarpus mariannensis* [family Moraceae]), which is native to the Marianas and Palau but distributed through Micronesia (Fosberg et al. 1979, Ragone 1997). It is one of the largest native trees in the region, attaining heights of 15–20 m and trunk diameters of greater than 1 m. Mature trees feature spreading crowns that are typically emergent above the surrounding forest canopy. Other traits include large but-

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tresses, lobed or elliptic leaves 10–30 cm long, milky sap, staminate flower spikes 8–10 cm long, and cylindric fruit weighing 150–1,000 g (Stone 1970, Raulerson and Rinehart 1991; G.W., unpubl. data). *Artocarpus mariannensis* is widespread on Guam, growing on both limestone and volcanic substrates. The species was once common on much of the island (Safford 1905, Fosberg 1960, Stone 1970) but has declined in abundance during recent decades. A second species, the seedless breadfruit (*A. altilis*), has been widely introduced in Micronesia and other Pacific islands and is an important human food source on many islands.

The fruits of *A. mariannensis* are a favored food of the endangered Mariana fruit bat (*Pteropus mariannus*) (Wiles 1987). During the mid-1990s, numerous dead breadfruit trees were noted in northern Guam in a primary foraging area for fruit bats, raising concern that a decline in this tree species might alter the diet of the bats. This study was initiated to determine the extent and possible causes of the decline of seeded breadfruit.

MATERIALS AND METHODS

Study Area

The study was conducted primarily in the Munitions Storage Area (MSA) on Andersen Air Force Base in northern Guam (13° 37′ N, 144° 53′ E) (Figure 1). The site is 8 km^2 in size and occurs at an elevation of 140–160 m on the northern fringe of an extensive limestone plateau. Secondary-growth limestone forest (Fosberg 1960, Stone 1970) covers most of the area. Common tree species include *Hibiscus tiliaceus*, *Vitex parviflora*, *Aglaia mariannensis*, *Guamia mariannae*, *Pandanus tectorius*, *Cycas micronesica*, *Neisosperma oppositifolia*, *Premna obtusifolia*, *Morinda citrifolia*, and *Leucaena leucocephala*. The forest's canopy ranges from 5 to 10 m in height, with taller emergent trees, such as *Elaeocarpus joga*, *Tristiropsis obtusangula*, *Artocarpus mariannensis*, *Ficus prolixa*, and *F. saffordii*, fairly common. The MSA has served as an ammunition storage area since the late 1940s, when an extensive 46-km-long grid of roads was built. Most of the roads run along an approximately north-south axis and are spaced 125–250 m apart. The MSA has thin well-drained soils derived from coralline limestone substrates (Young 1988). Both Philippine deer (*Cervus mariannus*) and feral pigs (*Sus scrofa*) occur at high densities in the area (Wiles et al. 1999; S. Vogt, pers. comm.).

Mean annual rainfall on Andersen Air Force Base is 2,360 mm. Daily temperatures are warm and relatively constant throughout the year, ranging from 24 to 33 °C. Guam lies in a major typhoon zone running through the western tropical Pacific, with an average of 3.5 storms per year passing within 330 km of the island (USNOCC/JTWC 1991). Major typhoons causing severe and widespread damage to buildings and vegetation strike the island about once per seven years on average.

Additional observations were recorded in other areas of Guam that were either forested or partially urbanized. One of these sites was an isolated 55-ha patch of secondary limestone forest at the Guam International Airport, which was fenced and did not support deer or pigs. One survey was also made on the adjacent island of Rota (14° 9′ N, 145° 13′ E), which lies 60 km north of Guam and is 85 km^2 in size. It has extensive areas of primary and secondary limestone forest, which were heavily damaged by Typhoon Roy in January 1988.

Census Methods

Six censuses of *A. mariannensis* were conducted in the MSA, including one in October 1989 and five others from August 1996 to June 1999. The 1989 census covered a 39-km-long core area of roads. Subsequent counts were expanded to cover the entire study area. During each census, roads were slowly driven at speeds of 10–20 km/hr, with the locations of all visible living and standing dead trees mapped. Most trees were easily detected because their large crowns protruded above the surrounding forest canopy. Breadfruit snags were distinguished from other dead trees by a combination of features, including trunk, limb, and buttress shape; color and softness of the wood; and other traits. Complete counts of trees were possible in the eastern half of the study area because of

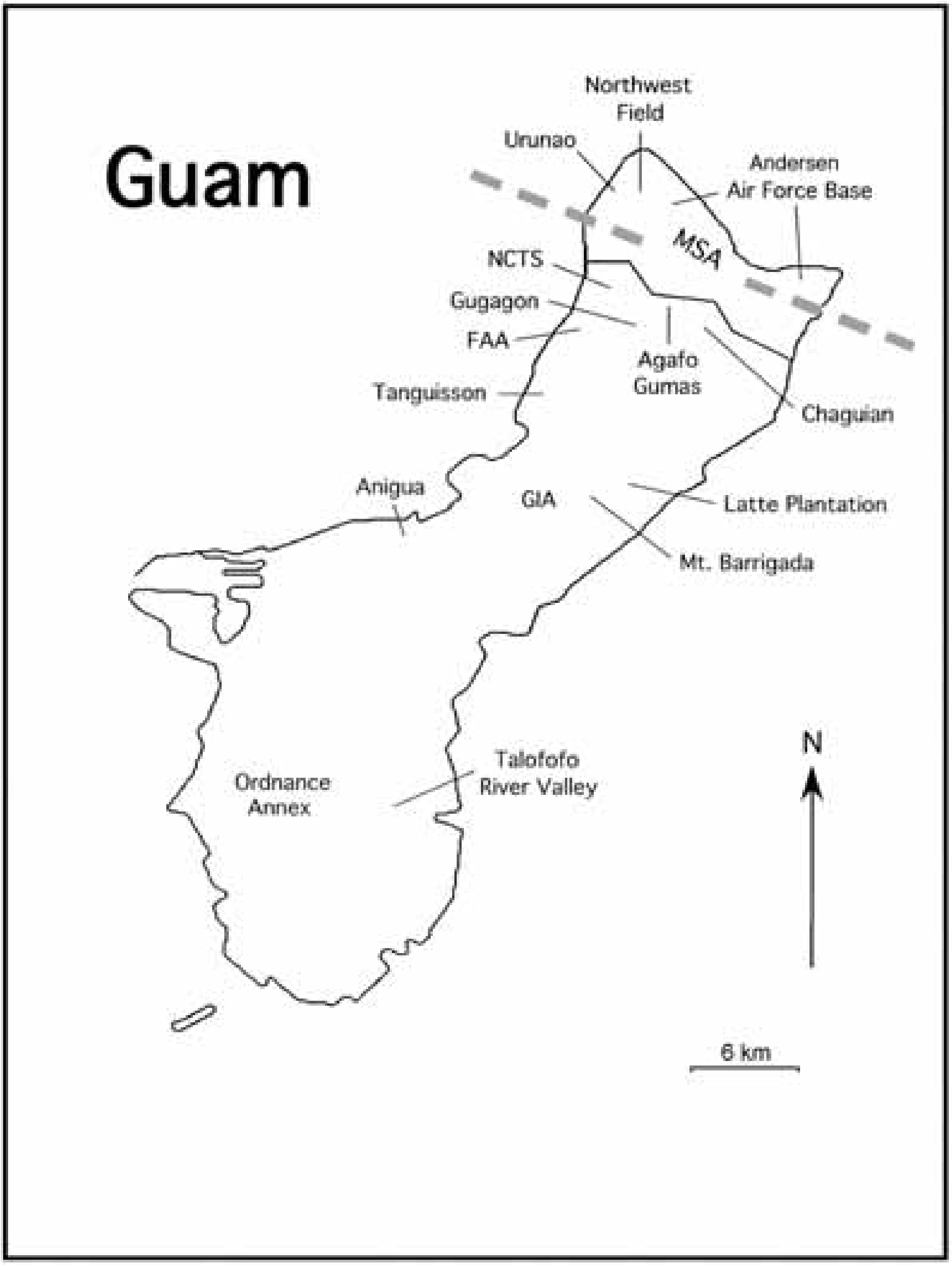

Figure 1. Locations of study sites on Guam, Mariana Islands. Abbreviations are as follows: MSA, Munitions Storage Area; NCTS, Naval Computer and Telecommunications Station; FAA, Federal Aviation Administration; GIA, Guam International Airport. The dashed line indicates the path of the northern eye wall of Typhoon Omar in August 1992 (USNOCC/JTWC 1992).

the good visibility between roads. However, tall, dense roadside vegetation blocked the viewing of some breadfruit trees in the western MSA. Overall, I estimated that 80–90% of the breadfruit trees in the MSA were detected during counts. This was confirmed by the finding of an additional 28 mature trees during the 1996 census that were obviously missed in 1989, probably because of blocking vegetation. In addition, during visits to mature trees, a small percentage (<4%) of individuals had a second smaller mature tree growing close by (0.6–3.0 m) that was overlooked in the 1989 survey. These trees were added to the 1989 totals. Observations of the tree population did not take place between the 1989 and 1996 counts. Cursory roadside surveys of living and dead *A. mariannensis* and *A. altilis* were conducted elsewhere on Guam and Rota in 1996 to determine broader patterns of tree mortality. On Rota, a single survey was made along an 18-km-long route that began at Songsong village, followed the north coastal highway and main road to the Sabana, and ended at the Peace Memorial atop the Sabana.

In May 1997, 120 living *A. mariannensis* and 60 snags in the MSA from the 1996 count were selected using a random numbers table and measured for trunk diameter at breast height (DBH; defined as stem diameter at 1.3 m or directly above buttresses taller than 1.3 m). For dead trees without bark, DBH measurements were increased by 4 cm, the approximate thickness of living bark on both sides of the trunk combined. DBH measurements and visual height estimates were recorded for the airport population in June 1999. The presence of seedlings, saplings, and ungulate sign (i.e., trampled ground, trails, feeding evidence, and feces) in the vicinity of each measured tree was also recorded in both areas.

Typhoon Damage

Typhoon damage was assessed for 120 randomly selected trees 8 weeks after Supertyphoon Paka, which occurred in December 1997. Damage was classified for each tree, using the following categories modified from Gresham et al. (1991) and Walker (1991): (1) undamaged (bole unbent and vertical, little crown damage); (2) bent (roots intact, lower bole intact, terminal leader intact); (3) limbs broken (many limbs broken, with one of three size subcategories [<5 cm, 5–15 cm, and >15 cm diameter] assigned based on size of the largest broken limb; terminal leader intact); (4) top broken (many limbs broken, terminal leader broken); (5) broken bole (bole broken between ground and crown base); (6) uprooted (tree partially uprooted and bole leaning); and (7) downed (tree mostly uprooted with bole lying on ground). Percentage defoliation was also visually estimated for each tree. Poststorm tree mortality was assessed 6, 12, and 18 months after the typhoon.

Assessment of Fruit Consumption and Herbivory

In September 1997, I conducted a 6-day experiment to assess the feeding rates of deer and feral pigs on fallen fruit, seeds, and leaves of *A. mariannensis* in the MSA. The experiment occurred during the species' regular fruiting period (i.e., April to November) and therefore reflected natural conditions in the availability of alternate foods for deer and pigs. Six mature trees distributed across the study area were chosen as test sites. Two sets of seeds, mature leaves, and pieces of fruit pulp were placed under the canopy of each tree on opposite sides of the trunk. Each set of material contained four seeds, one leaf, and two fruit pieces measuring about 5 by 10 cm. Fruit pulp and seeds were spread over a 50-cm-diameter area of ground to simulate a portion of a freshly fallen fruit. At 2-day intervals, items were checked for removal by animals and enumerated, with the surviving material collected and replaced by an entire set of fresh items.

Browsing pressure on seedlings was assessed by placing 26 nursery-reared seedlings of *A. mariannensis* in the wild during the dry season from December 1999 to April 2000. Pairs of seedlings were set out under 13 mature trees located throughout the MSA. Individual seedlings were placed on opposite sides of each trunk at distances of 3–8 m from

TABLE 1

Counts of *Artocarpus mariannensis* in Two Areas of the Munitions Storage Area in Northern Guam

	Core Area				Entire Area			
Survey Date	No. of Living Trees[a]	No. of New Trees	No. of Standing Dead Trees	Total No. of Standing Trees[b]	No. of Living Trees[a]	No. of New Trees	No. of Standing Dead Trees	Total No. of Standing Trees[b]
October 1989	549	—	28	577	—	—	—	—
August 1996	205	11	113	318	235	—	125	360
November 1997	205	0	15	220	235	0	18	253
June 1998	196	0	4	200	225	0	4	229
December 1998	194	0	6	200	222	0	6	228
June 1999	190	0	5	195	218	0	5	223

[a] Includes overlooked trees recorded during subsequent counts.
[b] Includes both living and dead trees.

the trunk. They were kept in 8 by 8 by 8 cm propagation pots that were staked to the ground to prevent tipping. Seedlings had a mean (±SD) of 11.1 ± 2.0 leaves (range, 8–16) per individual at the start of the experiment. They were visited once per week to measure height and note any damage (i.e., browsing of leaves and stems, uprooting) that had occurred. Seedlings were watered each week to prevent drying.

Statistical Analyses

Variable distributions were tested for normality using Kolmogorov-Smirnov tests for goodness of fit. Populations were compared using a nonparametric Mann-Whitney *U*-test when distributions were nonnormal or a *t*-test when distributions were normal. Differences in the ratios of dead to living trees among populations in the MSA, elsewhere on Guam, and on Rota were examined using a 2×2 *G*-test of independence (Sokal and Rohlf 1981).

RESULTS

Trends and Characteristics of the MSA Population

A total of 549 living *A. mariannensis* trees was recorded in the MSA's core area during the 1989 census. Trees were unevenly distributed, with most (79.4%) located in the western half of the study area, where a mean density of 1.7 trees per hectare was recorded.

Numbers of *A. mariannensis* in the core area declined from 549 to 190 living trees (65.4%) from October 1989 to June 1999 (Table 1). Abundance decreased fairly consistently throughout the area. Rate of decline was by far the greatest from October 1989 to August 1996, when tree numbers fell 62.7% overall (mean of 9.2% per year), but was much less from August 1996 to June 1999, when numbers further decreased by only 7.3% (mean of 2.6% per year [Table 1]). Similar rates of decline occurred in both the core and entire areas (7.3 versus 7.2% overall, respectively) from 1996 to 1999 (Table 1). Trees censused in 1989 had a mortality rate of 64.7% through 1996 (mean of 9.5% per year) and 7.7% from 1996 to 1999 (mean of 2.7% per year). Of the 17 trees that died from November 1997 to June 1999, only one appeared unhealthy before Supertyphoon Paka, and at least eight suffered major damage during the storm.

Recruitment of new trees was poor during the study. Only 11 trees entered the population from 1989 to 1996 (Table 1), eight of which were probably saplings or seedlings before 1989. No new individuals, including seedlings and saplings, were observed from 1996 to 2000.

Standing dead trees comprised 4.9% of all *A. mariannensis* stems recorded in the core

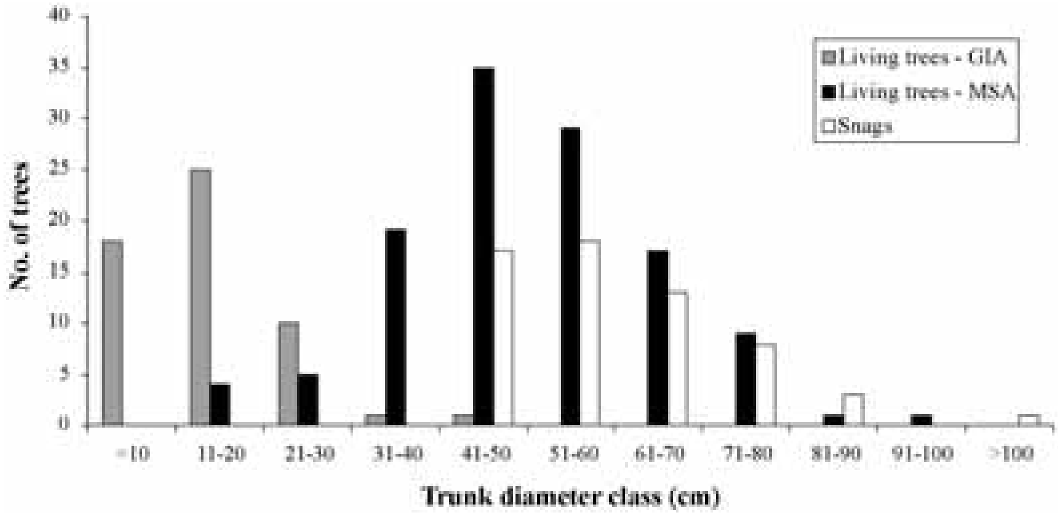

FIGURE 2. Frequency distribution of trunk diameters (DBHs) of living *Artocarpus mariannensis* trees and standing snags at the Munitions Storage Area (MSA) ($n = 120$ trees and 60 snags) in 1997 and at Guam International Airport (GIA) ($n = 55$ trees) in 1999 on Guam.

area in 1989, 35.5% in 1996, 6.8% in November 1997, and ≤3.0% in 1998 and 1999 (Table 1). No older snags remained standing after Supertyphoon Paka.

In 1997, the surviving population of *A. mariannensis* in the entire MSA had a mean DBH of 50.3 ± 14.7 cm (range, 12–96, $n = 120$), with most (83.3%) individuals having diameters ranging from 31 to 70 cm (Figure 2). Only 7.5% of the population had girths of less than 30 cm. Trunk size was normally distributed ($D = 0.987$, $P = 0.860$). Snags averaged 59.9 ± 13.6 cm (range, 42–108, $n = 60$) in DBH, with most (80.0%) having trunk diameters ranging from 42 to 80 cm (Figure 2). The size distribution of snags was not normal ($D = 0.904$, $P < 0.0001$). Snags were larger in girth than living trees ($U = 4{,}902$, $P < 0.001$).

The MSA's small population of *A. altilis* declined from nine to seven trees from 1989 to 1999, with both trees lost between 1989 and 1996.

Typhoon Damage

All *A. mariannensis* in the MSA sustained moderate to severe damage during Supertyphoon Paka. Damage was classified for 120 trees, as follows: limbs broken (5–15 cm), 50.8% of all trees; limbs broken (>15 cm), 30.8%; top broken, 7.5%; limbs broken (<5 cm), 5.8%; bole broken, 2.5%; and downed, 2.5%. No trees occurred in the categories of no damage, bent, or uprooted. Defoliation was complete on nearly all (95%) trees, and the remaining individuals retained only 1–5% of their leaves after the storm.

Fruit Consumption and Herbivory by Ungulates

Ungulate sign was ubiquitous in the MSA. During visits to measure living trees in 1997, I found evidence of deer or feral pig activity underneath or within 25 m of 83.2% of all trees.

Animals removed 66.7% of the seeds and 54.2% of the fruit pieces within 2 days of being placed under study trees. Deer and pigs did not feed on the blade portion of leaves but did consume the stems of 11.1% of all leaves. During the cumulative 6-day test period, seeds and fruit were eaten at each of the six study trees, and leaf stems were consumed at three trees.

Browsing by deer or pigs killed half of

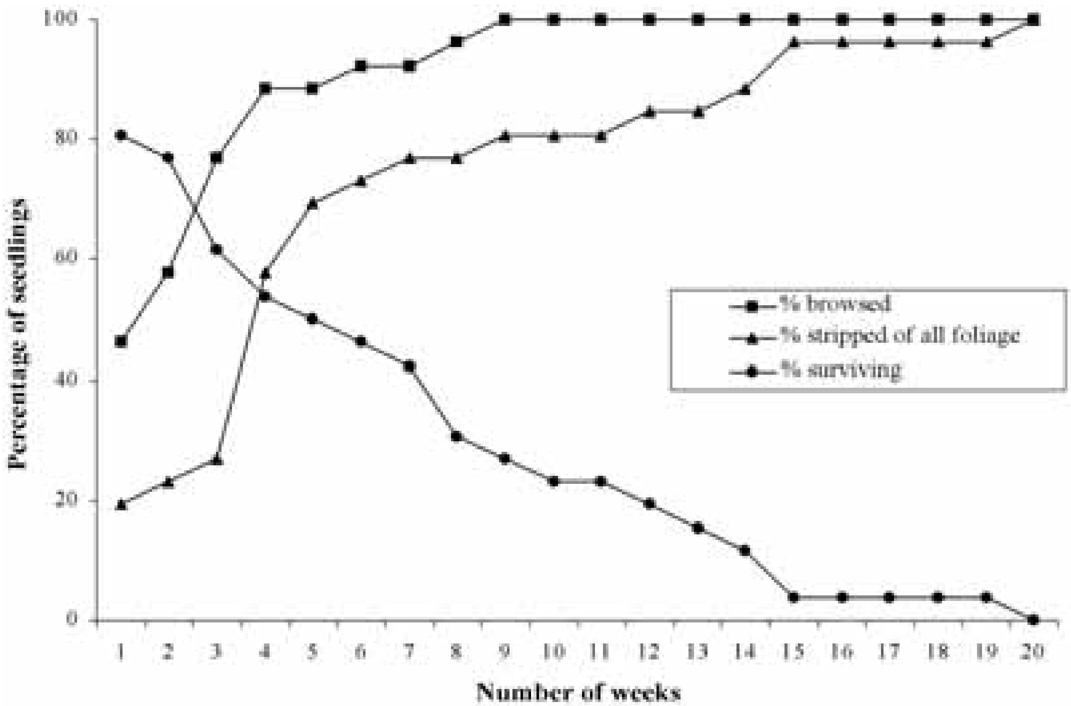

Figure 3. Percentage of *Artocarpus mariannensis* seedlings browsed, stripped of all foliage, and surviving under experimental conditions during 20 weeks of exposure to deer and feral pigs in the Munitions Storage Area, Guam.

the test seedlings within 5 weeks and all seedlings within 20 weeks (Figure 3). More than half of all seedlings were fed on within 2 weeks and stripped of all foliage within 4 weeks. Mortality resulted from heavy browsing of stems and leaves ($n = 16$) or uprooting ($n = 10$). Mean stem height of seedlings was reduced from 51.8 $\pm$ 7.8 cm (range, 26–62) at the start of the experiment to 22.2 $\pm$ 9.1 cm (range, 0–36) at the time of death ($U = 666.5$, $P < 0.001$).

Deer or pigs occasionally used their incisors to scrape small sections of bark off the buttresses and trunks of mature trees, with the bark presumably eaten. Five trees were damaged in this fashion, but in no case did it appear to harm the trees.

Characteristics of Other Populations

Roadside observations revealed considerable mortality among *A. mariannensis* at three other locations near the north end of Guam in 1996. Snags comprised 27.1–35.7% of all *A. mariannensis* trunks at the Northwest Field airfield, along the Northwest Field highway and Urunao cliffs, and at Naval Computer and Telecommunications Station (Table 2, Figure 1). When pooled, the ratio of dead to living trees at these sites did not differ ($G = 1.76$, df = 1, $P = 0.19$) from that in the MSA in 1996. Snag numbers were much reduced at more southerly locations, including some that were only 1–6 km farther south (Table 2). The difference in the ratios of dead to living trees between these sites combined and the MSA was significant ($G = 102.75$, df = 1, $P < 0.0001$). A formal count was not made at Latte Plantation (Adacao) in northern Mangilao, but this location also showed few if any dead *A. mariannensis*. Similarly, no dead *A. altilis* were present along the Anigua cliffline in Hagatña. A survey on Rota also found far fewer ($G = 197.01$, df = 1,

TABLE 2

Numbers of *Artocarpus mariannensis* and *A. altilis* Trunks (Living Trees and Snags Combined) and Percentage of Snags Present at Sites on Guam (Figure 1) and Rota in 1996

	No. of Trunks Counted		
Site	*A. mariannensis*	*A. altilis*	% Snags Present
Munitions Storage Area	360	7	34.1
Northwest Field airfield	14	0	35.7
Northwest Field highway and Urunao cliffs	54	1	27.3
Northern one-third of Naval Computer and Telecommunications Station	59	0	27.1
Federal Aviation Administration housing area, Dededo	33	0	9.1
Agafo Gumas and Chaguian, Yigo	97	0	7.2
Gugagon, Dededo	17	0	5.9
Tanguisson cliffline	20	0	0
Amantes Point	12	0	0
Ordnance Annex	31	11	7.1
Talofofo River valley	18	90	1.8
Rota	310	103	0.5

$P < 0.0001$) *Artocarpus* snags than in the MSA (Table 2).

The Guam airport population was composed almost entirely of saplings and small trees. Mean DBH (14.5 ± 8.5 cm; range, 1–46; $n = 55$) was smaller than in the MSA ($t = -16.81$, df $= 173$, $P < 0.0001$), with 78.2% of all individuals having diameters ≤ 20 cm (Figure 2). Tree size was normally distributed ($D = 0.113$, $P = 0.08$). Virtually all individuals displayed vigorous growth and nearly all exhibited unbrowsed shoots or branches within 1.5 m of the ground. Fallen fruits or seeds were recorded beneath at least nine trees in June 1999 and were sometimes abundant. Mean estimated tree height (4.8 ± 1.6 m; range, 1.5–9) was considerably shorter than in the MSA, where most trees were about 10–16 m tall. The low height of the airport population reflected both its young age distribution and the substantial damage caused by Supertyphoon Paka. Many of the saplings and trees in the area displayed broken tops or stems; however, no snags were present.

DISCUSSION

Historical accounts describe seeded breadfruit as once being a dominant tree in Guam's forests (Safford 1905, Fosberg 1960, Stone 1970), but in recent decades the species has become less common in many parts of the island. By 2000, I was aware of only three moderately dense stands still remaining, none of which covered more than several square kilometers of land. These occurred in the western half of the MSA, at Latte Plantation in Mangilao, and on the southern slopes of Mt. Barrigada. Land clearing is probably responsible for much loss on Guam, but this study shows that other factors are also involved. Poor recruitment appears to be a widespread problem, but the presence of young trees at some sites demonstrates that this is not an islandwide phenomenon. In comparison, the species remains considerably more common on Rota, especially along sections of the north-central coast up to higher elevations and at other areas such as Finata, Payapai, and Palii.

This study documented a dramatic decline in *A. mariannensis* in the MSA and nearby areas of northernmost Guam during 1989–1999, with tree numbers decreasing 65% in the MSA. Major features of the decline were that (1) mortality was heavily concentrated from 1989 to 1996 and was largely restricted to this section of the island, and (2) the population exhibited little regeneration of new trees. Unfortunately, I did not conduct field

TABLE 3

Attributes of Typhoons Causing Substantial Damage to Native Forests in Northern Guam during the 1980s and 1990s

Storm Name	Date	Estimated Wind Speeds (km/hr)[a] Sustained Winds	Gusts	Path of Storm	Area of Most Vegetative Damage and Level of Damage[b]
Typhoon Roy	12 January 1988	122	182	Passed over Rota, 59 km north of Guam	Northern Guam, moderate damage
Typhoon Omar	28 August 1992	195	241	Eye passed over much of northern, southern Guam	Damage severe throughout Guam, somewhat worse at north end
Typhoon Hunt	18 November 1992	111	139	Passed 20 km north of Guam	Northern Guam, minor damage
Typhoon Gay	23 November 1992	158	195	Eye passed over all but southern end of Guam	Severe defoliation islandwide, other damage fairly minor
Supertyphoon Paka	16 December 1997	241	297	Southern wall of inner eye passed over MSA, southern wall of outer eye passed over central Guam	Northern to south-central Guam, severe damage

[a] Estimated wind speeds are reported for northern Guam.
[b] Describes the portion of the island receiving the greatest vegetative damage, with a qualitative assessment of vegetative damage in northern Guam.

observations during the period of greatest mortality and cannot report conclusively on the cause(s) of death for most trees. The study provided adequate evidence to suggest two likely explanations for the decline, but other factors cannot be ruled out as contributing agents.

Causes of Mortality

Because the Mariana Islands are subject to frequent typhoons, native emergent tree species should be adapted for surviving the extreme conditions associated with storms. During high winds, *Artocarpus* readily lose their foliage and many of their smaller branches, which helps them avoid more serious structural damage (T. Marler, pers. comm.; D. Ragone, pers. comm.). In most instances, typhoons kill only small numbers of breadfruit, as illustrated by two examples. Supertyphoon Paka inflicted heavy damage on most *A. mariannensis* in the MSA but killed no more than 16 (6.8%) of the 235 trees in the area. Paka was the strongest storm to strike Guam since 1962, with typhoon-force winds (>119 km/hr) lasting 12–15 hr (Table 3) (USNOCC/JTWC 1997), and was immediately followed by a 5-month dry season with exceptionally low rainfall (27% of normal). Similarly, *A. mariannensis* remained abundant on Rota in 1996 despite the tremendous forest damage caused by Typhoon Roy in 1988. Nevertheless, I believe that unusually severe storm damage best explains the large number of *A. mariannensis* dying during this study.

Aside from Supertyphoon Paka, the 1992 typhoon season was the only other major weather event to substantially damage forests in northern Guam during the 1980s and 1990s (Table 3). It involved an unusual succession of storms during a 3-month span, including three that passed directly over the island and two others that approached within 100 km (USNOCC/JTWC 1992). The season began with Typhoon Omar, which was the first major storm to hit northern and central Guam since 1976, and closed with Typhoon Gay, which had typhoon-force winds lasting 8–10 hr. In addition, Gay carried little rain and left abnormally heavy deposits of airborne salt spray on plants, resulting in extensive defoliation throughout the island within a few days of the storm's passage (Kerr 2000). A harsh dry season of 7 months (41% of normal rainfall) also followed Gay. Forest refoliation eventually returned to normal by late 1993; however, a crown dieback of 1–3 m was widely evident on most canopy and emergent trees islandwide (Kerr 2000; G.W., pers. obs.).

The abundance of *A. mariannensis* snags in the MSA in August 1996 and the subsequent collapse of most of these by November 1997 provides a useful time reference in matching the 1992 typhoon season with the large numbers of trees lost in the area. Breadfruit wood quickly decays and softens after dying, causing most snags to fall within probably 2–5 yr of a tree's death. Thus, most *A. mariannensis* in the MSA likely died between 1992 and 1995. As noted after Supertyphoon Paka, many trees probably were not killed outright by high storm winds in 1992 but instead gradually succumbed over the next several years. Snag numbers in 1996 represented just one-third of the total trees dying during the study and presumably reflects that many snags had already deteriorated and collapsed by that date.

The extensive breadfruit mortality seen in northern Guam is perhaps most likely the result of a combination of characteristics of the 1992 typhoon season, rather than any single feature. The path of Typhoon Omar's northern eye wall (Figure 1) closely corresponds with the boundary between the zones of high and low snag occurrence noted in 1996. Westerly-moving tropical cyclones north of the equator characteristically have their strongest winds on their northern flanks (Simpson and Riehl 1981), thus Omar's heaviest winds probably passed over the MSA and Northwest Field. Before that storm, northern Guam experienced a 16-yr period without severe typhoons, during which time *A. mariannensis* trees would have increased their stature and crown fullness, perhaps making larger individuals increasingly vulnerable to the next major storm. Successive defoliations during the 1992 typhoon season, salt damage from Typhoon Gay, and the abnormal dry spell afterward are other potentially key factors that may have contributed to the poor recovery and high mortality of trees. Salt stress in plants causes increased foliage loss, decreased root uptake of water and nutrients, and may result in vegetation death (Blood et al. 1991, Gardner et al. 1991). Trunk measurements from 1996 suggested that larger breadfruit were more vulnerable to mortality than smaller individuals, as might be expected from strong winds, but this pattern is perhaps equally attributable to smaller snags collapsing sooner than larger ones.

This scenario is consistent with evidence from a die-off of *Artocarpus*, presumably mostly *A. altilis*, during the 1960s when up to 80% of the trees on Guam and some other Micronesian islands died (O'Connor 1969). The cause was originally ascribed to a condition known as "Pingelap disease" but was subsequently attributed to a combination of typhoon damage, drought, aging of trees, salinity, and other environmental problems (Trujillo 1971*a*). Similar factors have also caused breadfruit losses on several Caribbean islands (Ragone 1997).

Pathogens and insects offer two alternative hypotheses for the dramatic die-off of *A. mariannensis* in northern Guam from 1989 to 1996. However, resident plant pathologists and entomologists were unaware of any specific diseases or plant pests known to be killing unusual numbers of *Artocarpus* on the island or elsewhere in Micronesia during that period (I. Schreiner, D. Nafus, F. Cruz, and G. Wall, pers. comm.). Furthermore, these causes would be more likely to induce a broader pattern of tree mortality, both spatially and temporally, on the island than that found in this study. Species of *Artocarpus* are generally considered to be fairly hardy against diseases and pests (Ragone 1997). At least eight pathogens infect the genus in Micronesia (Trujillo 1971*a*, *b*, Hodges and Tenorio 1984).

Mortality rate in the MSA from 1989 to 1996 (mean of 9.5% per year) was substantially higher than from 1996 to 1999 (mean of 2.7% per year). The latter rate resembles the annual death rates of <4% reported in many tropical trees under ordinary conditions (Swaine et al. 1987, Condit et al. 1995). This suggests that mortality in the MSA breadfruit population had returned to normal levels during the second interval, despite the minor additional tree loss caused by Supertyphoon Paka.

Causes of Recruitment Failure

Growth rates as well as trunk diameter distributions must be considered when evaluating the population trends of tropical trees, especially larger climax species (Condit et al. 1998). Size class data from undisturbed populations of *A. mariannensis* do not exist for comparison against the MSA population. My cursory observations suggest that seeded breadfruit has a fairly rapid growth rate, thus there may be a tendency for smaller size classes to be underrepresented in natural populations, as seen at the Guam airport. However, the overwhelming scarcity of seedlings and young trees, and resulting skewed size distribution, in the MSA implies that the population has experienced substantial regeneration problems dating back to at least the 1980s.

Ripened fruit were commonly observed on *A. mariannensis* trees during the study; thus recruitment did not appear to be limited by inadequate seed production. Instead, my results suggest that most fruits and seeds are eaten by ungulates after falling to the ground and that heavy browsing eliminates the few seedlings that may sprout. Fruit and seeds of *Artocarpus* are highly nutritious (Ragone 1997), with the seeds being particularly rich in oil (Safford 1905). Micronesians have long recognized that breadfruit trees are susceptible to intense browsing and bark ringing by livestock, and that young plants require protection from cattle, horses, and goats to survive (Christian 1899, Safford 1905). The use of *A. atilis* leaves and fruit as a primary livestock feed by farmers (Safford 1905) also illustrates that breadfruit is a highly palatable food source for ungulates. In addition, the abundance of young *A. mariannensis* trees at the Guam airport, where deer and pigs were absent, further supports the belief that moderate to high densities of these animals are detrimental to regeneration.

Extensive herbivory and seed predation by deer and feral pigs have seriously damaged Guam's forest communities (Conry 1988, Wiles et al. 1999), which evolved without native mammalian herbivores. Deer were introduced to the island by the Spanish in the 1770s (Wiles et al. 1999), and feral pigs are most likely descended from domestic stock first brought to the island in the 1600s (Intoh 1986). Both species are common to abundant on much of the island, especially on military lands where hunting levels are inadequate to control numbers (Conry 1989, Wiles et al. 1999). Some of Guam's highest deer densities occur in the MSA and other parts of Andersen Air Force Base because legal hunting is largely prohibited and illegal hunting has been reduced due to security measures. Surveys in 2001 indicated that the MSA supported astonishingly high densities of as many as 183 deer per square kilometer (95% confidence interval = 144–215) and 38 pigs per square kilometer (95% CI = 20–55) (S. Vogt, pers. comm.). Deer are generally much less common off-base, where hunting pressure is considerably greater (Wiles et al. 1999).

One other factor that may affect breadfruit regeneration, but was not assessed, is the impact on seed viability of the large scarab beetle (*Protaetia ?orientalis*), which was introduced to Guam in about 1972 (Schreiner and Nafus 1986). Small swarms of these insects commonly consumed most of the soft pulp on the ripened fruits of *A. mariannensis* in the MSA, allowing the exposed seeds to fall to the ground. Although their feeding superficially resembles that by fruit bats, it may result in unrecognized problems such as seed damage and premature desiccation of seeds and thus cause lowered germination rates.

Conservation Implications

An accurate understanding of a species' population trends is fundamental for effective management, yet such information is rarely available for indigenous plant populations in the tropical Pacific. Clearly, *A. mariannensis* abundance is declining in the MSA, most likely due to the combined effects of adult mortality from typhoons and a failure to regenerate because of herbivory and seed predation by exotic ungulates. Under current conditions, eventual extirpation of the species from the MSA and other military lands in northern Guam is likely. Fortunately, *A. mariannensis* is not dependent on primary forest but also regenerates and grows well in some disturbed habitats, including young secondary limestone forest and along forest edges (e.g., at the Guam airport). Prospects for recovery seem good given adequate protection from ungulates and overdevelopment.

Restoration of *A. mariannensis* to its former levels of abundance in the MSA is desirable because of its extensive use by native wildlife (Jenkins 1983, Wiles 1987, Marshall 1989). My observations provide additional evidence implicating Philippine deer and feral pigs in the decline of native plant populations. Eradication or substantial long-term reductions of both species is highly recommended for preserving Guam's forests (Wiles et al. 1999).

This study illustrates that insular plant populations can rapidly decline in just a decade or two. Without monitoring programs, changes in forest composition and plant abundance can be easily overlooked, especially when they are more gradual. In addition to *A. mariannensis*, a number of other trees are known or thought to be declining throughout Guam or in localized areas, including *Serianthes nelsonii*, *Elaeocarpus joga*, *Heritiera longipetiolata*, *Pisonia grandis*, *Pipturus argenteus*, *Dendrocnide latifolia*, *Barringtonia asiatica*, *Intsia bijuga*, *Tristiropsis obtusangula*, and *Tabernaemontana rotensis* (Wiles et al. 1996, Ritter and Naugle 1999; L. Raulerson, pers. comm.; C. Aguon, pers. comm.; G.W., pers. obs.). Some of these species are also characterized by poor recruitment (Wiles et al. 1996, Schreiner 1997, Ritter and Naugle 1999, Morton et al. 2000). These declines raise the issue of how closely Guam's contemporary forests resemble those originally present before human arrival about 3,500 yr ago. My observations during the 1980s and 1990s suggest that the island's forests are evolving toward a short-statured scrubby condition of lower diversity that will be dominated by a small number of tolerant native and introduced species, with many formerly widespread native taxa becoming uncommon, rare, or absent. Such extensive change will almost certainly have major negative impacts on the island's ecology.

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