

Table 2.

| | Viejo | Medio |
|-----------------------------|-------|-------|
| Postcranial lesions present | 3 | 15 |
| Postcranial lesions absent | 17 | 58 |

figures from Weaver's summed expected Medio frequency multiplied by the total number of cases in Viejo for all skeletal pathology, and subtracting the cranial pathologies. Thus, true incidences are as shown in Table 2. Therefore, chi-square now equals 0.31, much less than the figure of 5.33 manufactured by adding unrelated cells. Thus the test for infectious lesions is remotely removed from significance, the opposite of Weaver's desired conclusion. This seductive method of producing significant results where none exist recalls Thomas's (1976:283) comment: "I nominated chi-square for anthropology's most abused statistic."

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OBSERVATIONS ON MAYA SUBSISTENCE AND THE ECOLOGY OF A TROPICAL TREE

Charles M. Peters

The results from an autecological study of the growth, reproduction, and population dynamics of Brosimum alicastrum (ramón) in southern Mexico are applied to the controversy surrounding the use of this species in Maya subsistence practice. The frequent occurrence of B. alicastrum near ruins is explained by its competitive advantage on shallow limestone soils coupled with a continual input of bat-dispersed seed. Populations of the tree at Tikal are then compared with other naturally occurring populations as an example of how a detailed ecological analysis may furnish valuable insight into the historical use of a plant species. The Tikal populations are shown to be atypical in terms of phenology, productivity and breeding systems, suggesting that some form of artificial selection may have been practiced by the Maya.

In recent years I have watched with interest the growing controversy surrounding the supposed importance of *Brosimum alicastrum* (*ramón*) in the subsistence of the Classic Maya. The primary basis for these arguments appears to lie in the tendency of this species to occur in dense aggregations on or near Maya ruin complexes. Early observations of this association (Thompson 1930; Cook 1935; Lundell 1937; Rupert and Denison 1943) were later quantified at Tikal by Puleston (1968) and expanded into the hypothesis that not only was the tree frequently used by the Classic Maya, but that it was a primary subsistence crop that was deliberately cultivated. The dense stands of the tree found in the vicinity of ruins, therefore, were interpreted to be relicts of ancient Maya orchards. These ideas were developed further by Puleston and others (Puleston 1971, 1976, 1982; Folan et al. 1979) and *ramón* arboriculture came to be viewed as an established component of Maya subsistence practice. On the basis of this assumption, revised population estimates for

Tikal were derived using linear programming and the amazing productivity of this tree crop (Dickson 1980, 1981).

Not being an archaeologist, I have followed the development of these theories with fascination, but the nagging question always arises as to the validity of the assumption upon which all of these theories rest. How indicative of use by the Maya is the present-day distribution of this species? The recent article by Lambert and Arnason (1982:298) serves to increase these doubts further by reporting that the high densities of *B. alicastrum* are "probably the result of their requirements for growth and reproduction, which are optimal on the ruins, and not because they are descendants of trees planted by the Maya aristocracy."

For the past three years I have been studying the growth, reproduction, and population dynamics of *B. alicastrum* in southern Mexico. Several aspects of this study, I believe, can be profitably applied to the Maya-ramón question. In this note, therefore, I elaborate on the ideas of Lambert and Arnason (1982) and present an autecological interpretation of the occurrence of *B. alicastrum* near ruins. I then propose a different approach to the subsistence alternative controversy by examining the structure and function, rather than the spatial distribution, of the ramón populations at Tikal.

AGGREGATION NEAR RUINS

A first point that needs to be made is that *B. alicastrum* is known to form almost pure stands in areas other than near ruins, some of which may contain up to 400 individuals/ha (Rzedowski 1963; Gomez-Pompa 1973). These associations characteristically occur on limestone substrates with steep slopes, and become increasingly more common in the northern part of the species' range where there is a marked dry season, e.g., in Mexico, the states of San Luis Potosí, Tamaulipas, and Veracruz. Investigations that I have conducted in one such forest near Papantla, Veracruz, indicate that these aggregations are stable, self-regenerating populations that are capable of maintaining such high densities.

The significant contribution of the Lambert and Arnason (1982) paper is their suggestion that similar ecological processes occur on the shallow calcareous soils found on and near ruins. While I disagree with their contention that the conditions for the growth and reproduction of ramón are optimal on these sites, local edaphic factors undoubtedly play an important role by limiting the establishment of other species. *Brosimum alicastrum* possesses an extensive root system, which is heavily infected with vesicular-arbuscular mycorrhizae, and water and nutrient uptake are facilitated on well-drained, high-pH soils. This type of substrate, however, is characteristic of large areas of Yucatan, Guatemala, and Belize. How can we account for the frequent occurrence of dense aggregations near ruin sites?

Miksicek et al. (1981:917) speculate that "this association could simply reflect the ecological preadaptation of ramón to disturbed habitats, because it is a *disclimax* species with poorly dispersed fruits" (emphasis added). First, although *B. alicastrum* can be an extremely aggressive colonizer, there is no aspect of its life cycle that indicates an adaptation to disturbed habitats. The seeds lack a well-developed dormancy mechanism, the seedlings exhibit an extremely shade-tolerant photosynthetic response—i.e., low light saturation and compensation point—and contrary to that reported by Puleston (1968), the growth rate of the adult trees is relatively slow. In short, *B. alicastrum* is a characteristic example of a tropical tree adapted to growth and regeneration in a closed forest situation. Secondly, a large quantity of the fruits of *B. alicastrum* fall directly under the crown, but this certainly does not imply that the tree has not evolved a mechanism for the long-distance dispersal of at least a portion of its seed crop. Here, perhaps, lies the key to the ruin-ramón association.

Most of the animals which feed on the fruit of *B. alicastrum* eat the seed as well, and, therefore, function more as seed predators than as dispersal agents. Frugivorous bats, however, display the interesting behavior of collecting the fruit, flying to their roosts, and later eating only the fleshy pericarp and dropping the seed intact. Bats of the genus *Artibeus* have been shown to disperse large quantities of *B. alicastrum* seed in this manner, the fruit comprising the major part of their

diet when available (Vazquez-Yanes et al. 1975). Puleston (1968:56-57) reviewed the dispersal of *ramón* seeds by *Artibeus* bats but later rejected the possibility that they were an important seed vector to the ruins. This is surprising in light of his observations that "large numbers of bats occupy the inner chambers and vaults of the larger palaces and temples," that "their nests are littered with whole *ramón* seeds" and that "the seeds can apparently be carried great distances if the bats have young." I have seen similar accumulations of seeds and seedlings around the ruins of Palenque and Bonampak in Chiapas, and under bat roosts in mango plantations in Veracruz where the nearest *ramón* tree was more than 5 km away. A more reasonable explanation for the commonly observed aggregations of *B. alicastrum* near ruins, therefore, is the competitive advantage this species possesses on limestone soils coupled with the continual input of bat-dispersed seed.

USE BY THE MAYA

Accepting the hypothesis that the clustering of *B. alicastrum* around ruins is a result of normal ecological process does not in itself negate the possibility that the tree was used by the Maya. Brief reference is made to its use in several Postclassic documents such as Landa's *Relación* (Tozzer 1941), yet other approaches commonly used to establish the historical use of a plant species, i.e., the study of the fossil pollen record or the recovery of datable plant remains, have failed to provide supporting evidence (Turner and Miksicek 1981). Nevertheless, it is counterintuitive to think that such an abundant, protein-rich food source would not be used in some manner. The question here appears to be one of the extent or magnitude of its use. Were *ramón* seeds casually collected from the forest only in times of famine, or was some form of deliberate cultivation, silviculture, or selection practiced? If the tree was a cultivated staple food, it is highly possible that evidence of artificial selection by the Maya can still be detected by a detailed analysis of the structure and dynamics of the dense populations of *B. alicastrum* that occur near large Maya centers.

Much of the work that has been conducted on the historical use of *ramón* has necessarily focused on Tikal, and, consequently, the majority of the ecological information available for the species is from this region. Data that I have collected from dense aggregations in other parts of the species' range reveal that, in fact, the Tikal populations are strikingly atypical.

Phenology

Phenological data from various parts of its distribution indicate that fruit production in *B. alicastrum* is usually annual, with peak seedfall occurring at the onset of the rainy season (Croat 1978; Pennington and Sarukhán 1968; Peters and Pardo-Tejeda 1982). In contrast, several authors have reported that trees at Tikal bear fruit twice a year (Gonzales 1939; Puleston 1968), while others suggest that fruiting is continuous throughout the year with three periods of peak abundance (Coelho et al. 1976; Schlichte 1978). It should be noted that these reports are qualitative in nature and do not indicate if the fruiting peaks are at the population or individual level. This is an important distinction given that the three fruiting peaks may result from the independent phenologies of the three varieties of *ramón* reported at Tikal, i.e., *ramón blanco*, *ramón amarillo*, and *ramón colorado* (Puleston 1968:11). In any case, the important point is that the reproductive phenology of *B. alicastrum* at Tikal is quite distinct from that in other regions. I should point out that a population I am studying in Veracruz, which is growing under environmental conditions almost identical to Tikal (similar elevation, mean temperature and precipitation, and substrate), produces fruit only once a year.

Productivity

Estimates of fruit production by *B. alicastrum* are extremely scarce, and those data that are available have been reported in a form that makes comparative measurements almost impossible. Puleston's (1968:96-97) estimate of 56.4 kg/tree is based on a single fruiting event from one tree

“which was rather old and evidently suffered from competition.” Coelho et al. (1976:Table 6), using data largely collected by Puleston and supplemented by their own observations, report a mean annual productivity for the species at Tikal of 4,235 kg/ha. This estimate is based on data from 25 sample plots that were monitored over a period of 10 years. Unfortunately, the study area was only described as containing “a relatively low density of *ramón*,” and the actual number of trees was not reported.

For the purpose of this discussion, both of these estimates can be crudely converted to provide a value of mean production/tree/year. Based on his report of two fruiting periods, doubling Puleston’s estimate gives an annual production of 112.8 kg/tree. Dividing Coelho’s production figure by 38.2 trees/ha, the reported mean density of *B. alicastrum* at Tikal (Puleston 1968), yields an annual production of 109.7 kg/tree, a result surprisingly similar to that derived from Puleston’s data.

These approximations should obviously be viewed with skepticism given the innumerable variables that control the reproductive output of trees. The point to be made, however, is that the results I have obtained in Veracruz using litter traps under marked individuals of differing size indicate that the maximum annual production in this region by a large tree is 65 kg, or approximately half of that derived for the Tikal trees.

Breeding Systems

There is considerable confusion in the literature concerning the distribution of the sexes within individuals of *B. alicastrum*. Swartz’s (1797) original description of the species reports that male and female flowers are found on separate individuals, i.e., that the species is dioecious. Later reports have classified the species as monoecious (Standley and Steyermark 1946; Pennington and Sarukhán 1968; Croat 1978), dioecious (Berg 1972), or both (Woodson and Schery 1960). My own observations in Mexico have indicated that the tree is very plastic in its sex expression and that indeed all of these possibilities can occur.

Brosimum alicastrum is pollinated by wind, and as wind is a poor carrier of pollen, the distance between conspecific individuals appears to exert a controlling influence on the breeding system of a given population. In very dense populations with the mean distance between individuals being relatively short, I have found that the sexes are usually separate and that outcrossing is obligate. In less dense populations, for example, in the southern part of the species’ range, the tree is monoecious and the outcrossing requirement is less strict. A fundamental difference between these two breeding systems is that in one, every tree can potentially produce fruit, while in the other, fruit production is limited to the female trees in the population.

As a result of the general pattern I have described above, one would expect the dense populations of *B. alicastrum* surrounding Tikal to be dioecious. This apparently is not the case, however, as the tree is consistently described as being monoecious in this region (Standley and Steyermark 1946; Puleston 1968), with all trees being capable of producing fruit.

What we seem to be presented with in Tikal, therefore, is a dense population of *B. alicastrum* in which fruit is produced in extremely large quantities at frequent intervals by every mature individual. The curious feature is that similar forests of the tree in other regions do not exhibit this behavior.

One possible explanation is that the regeneration of the tree is severely limited for some reason at Tikal, and an abundant reproductive output is necessary to maintain the population. A second interpretation, however, is that such a high level of fruit production is in excess of what is actually required, and the curious reproductive dynamics of *B. alicastrum* at Tikal are manifestations of relict genotypes deliberately selected for by the continued use and management of the tree. Simple collections of the seeds during the times of famine would not produce such a marked effect. What appears to be suggested is the conscious mixing of diverse genotypes with the objective of producing an abundant, year-round supply of seeds.

Rather than trying either to refute or to substantiate the tree’s importance to the Maya with scanty data, I wish to point out with this note the potential value of the type of analysis that I have

used. As the genotypes produced by the forces of natural selection are markedly different from those produced by man's continued use, the comparative examination of the autecology of a species can provide an additional focus to archaeologists and botanists studying the historical use of a plant species. Clearly, the relation between *B. alicastrum* and the Maya is far from being resolved, yet I am hopeful that my comments here will stimulate further investigation of this interesting and important tropical tree.

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A COMMENT CONCERNING “TESTING FLOTATION RECOVERY RATES”

Michael W. Pendleton

Since carbonized seed species differ in buoyancy characteristics, and since certain conditions may cause carbonized seeds to become nonbuoyant, the use of both buoyant and nonbuoyant modern carbonized seed species as a recovery standard is suggested in order to provide a more representative measure of flotation device effectiveness. Recovery standards utilizing modern carbonized seeds should be viewed as probable, rather than absolute, determinations of flotation device recovery efficiency because the effectiveness of flotation systems can be significantly altered by subtle changes in technique.

The recovery rate of modern carbonized poppy seeds (*Papaver somniferum*), which have been introduced into soil samples prior to processing by flotation, is suggested by Gail E. Wagner (1982:127) as the measure of the effectiveness and consistency of any flotation system. For this comment, the term “seed” is used in the layman’s sense. Since poppy seeds normally float, their rate of recovery provides an excellent general indication of a flotation unit’s recovery efficiency for those botanical remains that are naturally buoyant. However, nonfloating modern carbonized seed species should be added to these poppy seeds so that a flotation unit’s efficiency of recovery of nonbuoyant botanical material may also be indicated. A determination of nonbuoyant seed recovery rates for flotation systems is important because: (1) not all carbonized seed species normally float (Pendleton 1979a, 1979b, 1980, 1982; Schock 1971:231; Yarnell 1963:548); (2) smaller seeds and fragments may not float due to their lowered bulk densities (Renfrew 1973:15); (3) porous or damaged seeds may tend to sink (Renfrew 1973:15; William 1973:289); (4) carbonized material may become waterlogged during flotation processing and lose buoyancy (French 1971:62); and (5) in arid regions, it is common for calcium carbonate to coat carbonized plant material and prevent it from floating (Minnis and Le Blanc 1976:492).

Two species of modern nonbuoyant carbonized seed that can provide a recovery test of