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Seed Predation by Mammals and Forest Dominance by *Quercus oleoides*, a Tropical Lowland Oak

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Summary. *Quercus oleoides* Cham. and Schlecht is an unusual tree in several respects: it is an oak found in neotropical lowland forests. its distribution is not continuous but rather divided into many patches of various sizes, and it is a dominant in all the forests in which it occurs, attaining densities far higher than most species of tropical trees. This density pattern is related to the vulnerability of *Q. oleoides* acorns to predation by mammals. Observations of agoutis, deer, peccaries, squirrels, pocket mice and other seed consumers in Santa Rosa National Park, Costa Rica, showed that these mammals act only as predators, not dispersers, of *Q. oleoides* acorns. Experiments which involved placing acorns in deciduous forest where *Q. oleoides* does not occur, demonstrated that, due to high predation rates, the number of acorns produced by an isolated tree is far too low for adults to replace themselves.

In oak forest, on the other hand, where the combined acorn crops of many oaks satiate the seed predators, acorn survivorship until germination is high enough to maintain the population. Furthermore, acorn survivorship in oak forest areas is inversely proportional to the apparent mammal density in those areas. Thus the pattern of forest dominance and patchy distribution is related to positively density-dependent acorn survivorship: where *Q. oleoides* is the forest dominant, it will survive, but if its density falls to the level typical of tropical trees, it will go locally extinct.

Oaks, or for that matter nut-producing trees of any kind, are rare in tropical lowlands. The striking dominance of nut-producing families (predominantly the Fagaceae, Juglandaceae, and Hippocastanaceae) in temperate zone forests and in many tropical montane forests contrasts sharply to the extremely poor representation of these families in tropical lowland forests (Janzen 1971). One of the few nut-producing trees that does occur in the lowland tropics is *Quercus oleoides* Cham. and Schlecht, which ranges from Mexico to Costa Rica in both the Atlantic and Pacific lowlands. While dozens of *Quercus* species occur in tropical Mexico and Central America (e.g. over a hundred in Mexico: Martinez 1974; 26 in Guatemala; Standley and Steyermark 1952; and 12 in Costa Rica: Burger 1977) all except *Q. oleoides* are predominantly or exclusively species of mountains above 1,500 m. *Q. oleoides*, on the other hand, occurs from sea level up to only about 1,400 m (Montoya 1966).

Two other ecological characteristics of *Q. oleoides* also make it unusual. Its distribution is not continuous over its range, but rather is divided into a large number of extensive distinct "patches" of various sizes. from less than 1 km to perhaps 100 km wide. [Highly detailed vegetation maps exist only for the northern (Puig 1976) and southern (Von Borries 1967; Montoya 1966) ends of the range.] These patches generally correspond in a rough way to areas of "poor soil" but the specific type of soil poverty is extremely variable. ranging from pseudogleys with periodic inundations to excessively drained latosols and volcanic tuffs (Gomez-Pompa 1966; Montoya 1966; Pennington and Sarukhan 1968; Puig 1972; Puig 1976; Von Borries 1967).

Another notable feature is that *Q. oleoides* is almost invariably the dominant tree species within these patches, and attains densities and importance values far greater than is usual for tropical lowland trees. Von Borries (1967), for example, found importance values (relative density − frequency − basal area) for Costa Rican stands ranging from 30% to 71%. These values can be compared with mixed deciduous forests in the same area, in which generally no species had an importance value above 15% (Holdridge et al. 1971; Hubbell 1979; Von Borries 1967). The general pattern of tropical forests is to have a large number of tree species, none of which attain dominance (Richards 1964), but *Q. oleoides* forests are an exception to this rule throughout the species' range (Bartlett 1935; Gomez-Pompa 1965; Gomez-Pompa 1966; Martinez y Ojeda and Gonzalez 1977; Miranda 1952; Montoya 1966; Pennington and Sarukhan 1968; Puig 1972; Puig 1976; Sarukhan 1968; Sousa 1963; Von Borries 1967).

Furthermore, *Q. oleoides* forests differ from most other tropical lowland forests which have clear dominance of one or a few species (e.g. mangroves, swamp forests of *Prioria copaifera*, *Pterocarpus officinale*, *Parkinsonia aculeata*. *Haematoxylon campechianum*, *Raphia taedigera*, etc.: Holdridge et al. 1971; Janzen 1978; Richards 1964; Pennington and Sarukhan 1968; Miranda and Hernandez 1963) in that there are often a large number of other tree species besides *Q. oleoides* present. In Santa Rosa National Park, Costa Rica, for example, most of the two hundred-plus species of trees found in the mixed deciduous forest are also found in the *Quercus oleoides* forest. Forty-four species of trees were found in a 4 hectare plot in the "Area G" oak forest of the O.T.S. Comparative Ecosystem Study on the Comelco Ranch near Bagaces, Costa Rica (Hartshorn and Hathaway 1972). While other *Q. oleoides* forests may have fewer tree species than nearby non-oak forests (Puig 1976), they still contain dozens of tree species, and it is clear that the dominance and distribution pattern of *Q. oleoides* cannot be explained simply by physiological exclusion of other species from the soils on which it grows.

Thus there are at least two aspects of *Quercus oleoides* ecology which are unusual for a lowland tropical tree: it is a nut-producing species from a "temperate-zone" family, and it dominates

the forests in which it occurs. I propose that these points are intimately related, and that the abundance and distribution pattern of *Q. oleoides* can be explained by the activity of mammals as predators on *Q. oleoides* nuts.

The hypothesis, in brief, is the following: *Q. oleoides* acorns are extremely vulnerable to mammal predation, and their survival to germination depends on satiation of mammalian consumers. The number of acorns required for effective satiation is far beyond the number produced by an individual tree; thus successful reproduction depends on there being a substantial density of oaks in a given area. When it occurs in low densities, *Q. oleoides* will fail to reproduce successfully and will go locally extinct; it will only be found surviving where it occurs in high densities. In sum, the dominance pattern of *Q. oleoides* is related to its need for population-level satiation of mammalian seed predators (Janzen 1971, 1974b).

The following sections will present observational and experimental data to establish the plausibility of the major elements of this hypothesis:

1) Mammals act almost exclusively as predators on *Q. oleoides* acorns, not as dispersers.

2) The number of acorns produced by individual *Q. oleoides* trees is insufficient to satiate these mammals.

3) Sufficient satiation of the mammals occurs in areas of high *Q. oleoides* density so that some acorns survive.

4) Survival of acorns in *Q. oleoides* forest is substantially increased when mammal populations are reduced.

The Study Area

There are three areas of *Q. oleoides* forest in Costa Rica (Montoya, 1966; personal observation). The largest, centered around Liberia, is about 25 km in diameter, and corresponds roughly to the Liberia soil formation. The second patch, about 5 km in diameter, is in and around the northern part of Santa Rosa National Park, while the smallest patch is only about 2 km across and is along the PanAmerican Highway about 5 km south of La Cruz. In Costa Rica the species generally occurs on plateaus but not in valleys, and often is on thin soils with limited root space to bedrock (Von Borries 1967).

Most of my experimental and observational studies were done in the 10,000 ha. Santa Rosa National Park, in Guanacaste province of northwestern Costa Rica (Servicio de Parques Nacionales, 1977). Figure 1 is a map of the region, indicating the location of Santa Rosa National Park at approximately 10°50′N latitude and 85°37′W longitude. About half of the park, and all of its oak forest, lies on a plateau of about 300 m̄ elevation which slopes gently to the north and east.

The park, and most of Guanacaste province, has a tropical seasonal climate with year-round warm temperatures and roughly six months of rain and six months of drought. Rainfall is well below 100 mm from December through April, and is generally zero for January, February and March. The rains begin with a few light showers in April, and the rainy season begins in earnest in May.

Mixed tropical deciduous forest originally covered most of Guanacaste, and substantial areas of it still remain in Santa Rosa National Park. Much of my work done in a stand of this type measuring about 0.75 km² which stretches north along the Entrance Road from near the Casona Historica to the head of the Quebrada Puercos valley. The area which I studied on a more or less daily basis was about 10 ha, at the southern end of the stand. No species in this deciduous forest has an importance value greater than 10%. The oak forest, on the other
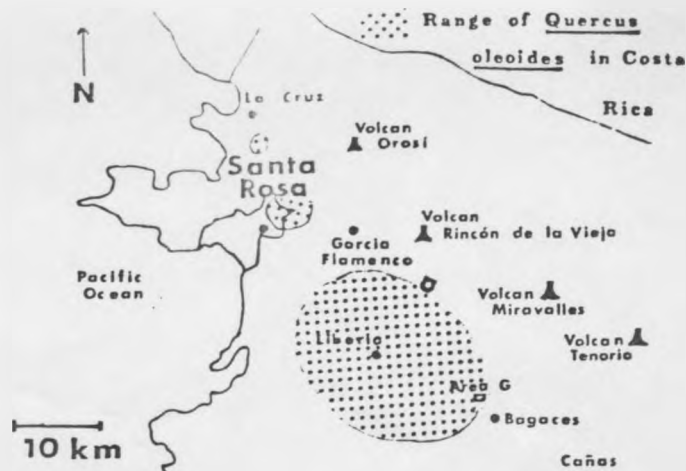

Fig. 1. Map of northwestern Guanacaste, Costa Rica, showing the distribution of *Quercus oleoides*

hand, is strongly dominated by *Q. oleoides*, which makes up from 30% to nearly 100% of the canopy trees.

Life History of Quercus oleoides

Q. oleoides, called "encino" in Costa Rica, is unusual among dry forest trees in being evergreen, as are its closest relatives, the live oaks of the southeastern U.S. (Muller 1961). The acorns are thin-walled, somewhat bitter, and about $2\frac{1}{2}$ cm long with a shallow cap. The radicle elongates rapidly after germination and reaches a depth of 4 to 8 cm, after which it thickens into a small carrot-shaped tuber as the seed reserves are transferred into it from the acorn.

Flowering time varies both from place to place and from year to year in a complicated and as yet not well described manner. The Santa Rosa population generally flowers in June, with the acorns falling to the ground around the end of the wet season and not germinating till the following rainy season. On the other hand, the Comelco Area G population, near Bagaces (Fig. 1), generally flowers in December and January, with acorns dropping to the ground soon thereafter. There are often exceptions to these patterns, however, and in fact herbarium specimens from Costa Rica show flowering in seven different months. For the entire range, I have seen 62 herbarium specimens which indicate flowering in the wet season (April to October) and 33 which indicate flowering in the dry season (November to March).

An unidentified microlepidopteran seed predator occasionally destroys substantial numbers of acorns. This insect sometimes oviposits in the cracks formed by the radicle breaking the tip of the shell upon germination, but it has also been found inside ungerminated acorns. The Costa Rican populations apparently lack the Curculionid beetle seed predators found on North American oaks.

Quercus oleoides Seed Predators

This section describes the ecology of the vertebrate species which, according to my observations, are the major predators on *Q. oleoides* acorns. Due to the relatively large size of the acorns, only a small proportion of the bird and mammal species of the park can prey on them effectively. However these species can destroy very large numbers of acorns.

Agoutis, squirrels, peccaries, and white-faced monkeys were directly observed eating *Quercus oleoides* acorns either in the

... ... in mixed deciduous forest (acorns placed there in the experiments described below). In addition, caged *Liomys salvini* pocket mice ate acorns in feeding tests, and a white-tailed deer was frightened at a spot where many shells of recently eaten acorns were found, although it was not actually observed eating them. In all these cases the shells were broken and the kernel cracked, and only small pieces of the seed were left behind. Of the thousands of acorns observed being eaten by mammals, none appeared even remotely likely to have remained viable afterward, whether swallowed or left in pieces on the ground.

Agoutis (*Dasyprocta punctata*) were observed eating acorns both in oak forest and mixed deciduous forest. They ate the acorns one at a time, holding them in the front paws and pulling the shell from the kernel with the incisors, then eating the kernel in a few bites. The agoutis generally ate the acorns at the spot where they found them, and often ate only five or ten acorns from a pile before moving on. Many of the shells of acorns put in deciduous forest in the experiments described below, were found in pieces which looked similar to the shells of acorns eaten by agoutis.

Collared peccaries (*Tayassu tajacu*) were observed eating acorns placed in deciduous forest on several occasions. The peccaries generally consumed all the acorns they found before they moved on, and one was seen to consume 336 acorns in 13 min. They ate acorns noisily, cracking them with their molars and swallowing the pieces. Only small pieces of kernel and shells were left behind after a peccary had eaten.

Variegated squirrels (*Sciurus variegatoides*) were seen feeding on acorns in oak trees, picking them from the branches or cutting them loose with the teeth. They ate them singly, holding them in the front paws and cutting off pieces of shell with the incisors, and then biting off pieces of kernel. Although they often ate sloppily and dropped many pieces, including nearly whole acorns on occasion, they were never seen carrying whole acorns more than a few meters. This species is very arboreal; in nearly a hundred hours of observation, it was observed on the ground only once, and then only for a few seconds while it crossed a small open area. Squirrels thus appear to be most important as predispersal seed predators on large-seeded fruits; there was no sign of them ever caching food either in trees or on the ground. The only study of the species is a taxonomic monograph (Harris 1937) which does not give ecological information.

On three different occasions white-faced monkeys (*Cebus capucinus*) were seen to descend from trees to take acorns which I had placed in deciduous forest (twice observed by me, once by Dora M. Rodriguez). In each case they filled one or both hands with acorns and reascended a tree, then sat on a branch to eat them. In each case all the acorns were eaten before the troop left the area, with seven, five and one monkey eating them on the three different occasions; however the largest number of acorns available was only 40. As with the squirrels, the monkeys ate sloppily and dropped many pieces of acorn to the ground, some almost whole. The longest horizontal distance that acorns were moved was approximately 20 m.

Spiny pocket mice (*Liomys salvini*) are the most common rodents at Santa Rosa. I estimated their density by live-trapping in April-June 1977, and arrived at a figure of 5.5 per ha. This is quite comparable to the estimates of Fleming for this species at Finca La Pacifica, Guanacaste (4 to 8/ha in March through June; Fleming 1974) and for *L. adspersus* in central Panama (5.5 to 8/ha; Fleming 1971). *Liomys* will cache a variety of seeds, but since they cache in their burrows, this is effectively equivalent to predation, since even uneaten seeds are unable to establish themselves. Feeding tests done with captive *Liomys*

... ... that they generally take acorns to the nest before removing the shell, and then eat small pieces of the kernel.

In summary, peccaries, agoutis and probably deer are major predators on fallen acorns, while variegated squirrels eat large numbers of acorns from the tree. White-faced monkeys and pocket mice are also known to be consumers. None of these mammals eat acorns in a way that allow more than a very few to remain viable, nor were any seen to disperse them more than a few meters. The mammals must be considered as effectively seed predators on *Q. oleoides* but not dispersers of it.

Experimental Methods

The knowledge that the major consumers of *Q. oleoides* acorns act as predators, not dispersers, allowed me to perform experiments on acorn removal rate in which removal was assumed to be equivalent to predation. These experiments took advantage of the proximity of the oak forest in Santa Rosa National Park to deciduous forests in which no oaks are found. Thus I could place known numbers of acorns in the deciduous forest study area and be certain that these were the only acorns which the mammals of that forest would encounter.

The experiments were done at two times: one set of experiments, using 10 and 100 acorn "piles", began 15 December 1976, and the other, using piles of 10, 100, 500, and single acorns, started on 5 April 1977. The data are combined in the following analysis.

"Piles" of acorns were actually lines or square grid arrangements to facilitate censusing. They were placed in densities of 100 per m², a density well within the range of densities found under trees in oak forests. Acorns were placed on the litter and their locations mapped with reference to nearby trees or stakes; no identifying markers of any kind were used. All experiments in a set were started at dusk on the same day, and locations were chosen on a map in advance so that all acorn piles would be at least 50 m from each other.

The piles were censused at dawn and at dusk each day until all acorns were gone. The only exception was a single acorn in the April experiment which had not been removed when the experiment was terminated on 10 June. The raw data (number remaining versus time) were fitted to an exponential decay curve of the form:

$$dN/dt = -kN$$

where N is number remaining, t is time in days, and k is a constant which I will call the "instantaneous removal rate". This simple equation has been found adequately to represent nut removal data in previous studies (Sork and Boucher 1977). It gave the best fit to the data of several curves tried. The equation can be integrated to give:

$$N = N(0)\exp(-kt)$$

where $N(0)$ is the original pile size. The integrated form was used to estimate the number which would remain after 150 days, a minimum estimate of the time from fall of acorns to the ground around the end of the wet season, to their earliest possible germination date at the beginning of the next wet season.

Q. oleoides acorns are composed of two parts which eventually separate: the cupule or cup (a modified involucre) and the nut itself. Since there is always one and only one cup per nut, the number of cups remaining at the end of the fruiting season can be used as an estimate of the number of acorns produced. The assumptions of this method, that all cups become separated from the nut and are later found by the investigator, are quite

reasonable for *Q. oleoides*, since the majority of nuts separate from the cups while still on the tree, and the cups fall to the ground below in the next few months. The only way that the inedible cups might be destroyed by predators is if predation took place on the tree while the acorns were still small and green. Since only cups 1 cm in diameter or larger were counted (this is approximately the minimum possible size of acorn that could germinate, in my experience), the bias introduced should not be great.

Mature *Q. oleoides* trees were chosen for sampling in three oak forest areas. The ground area below their canopies was measured to the nearest square meter. A sample area of approximately a third of the below-canopy ground area (in no case less than 15%) was laid out under the canopy, in at least three separate plots scattered below the tree.

Samples were taken in three different oak forest areas which varied in their mammal populations. The first, called "Santa Rosa Main", was in the main part of the Santa Rosa oak forest; 10 trees were sampled here. The second area was a small clump of about 15 oak trees in the savanna at Santa Rosa, isolated from the main part of the oak forest by about 50 m of *Hyparrhenia rufa* savanna. In this area, called "Santa Rosa Isolated", 3 trees were sampled. It was felt that, since this clump of trees was far too small to sustain even single individuals of any of the mammal predators discussed above, its average population of mammals over a long period of time would be smaller than that of the main forest, being composed only of occasional animals which crossed the savanna to forage there. Finally, 10 trees were sampled in the Organization for Tropical Studies "Area G" study site on the Comelco Ranch, about 10 km west of Bagaces and about 50 km southwest of the Santa Rosa site (Fig. 1). This area is surrounded by cattle pastures which are burned annually, and its mammal population has been greatly reduced by disturbance. Few squirrels, and probably no deer, peccaries or agoutis now inhabit this area.

The three areas sampled were assumed to form a sequence in terms of mammal population sizes, from "Santa Rosa Main", where the mammals are found in close to natural numbers, to "Santa Rosa Isolated", which is occasionally visited by agoutis, deer, and perhaps other species, to "Area G", which has greatly reduced mammal populations. The cups in the Santa Rosa sample areas were collected and counted between 21 and 23 May 1977, at the start of the wet season. No germination of acorns had yet taken place. Examination of the trees confirmed that no cups remained on the trees at this time. All sound acorns found in the May census were marked by placing a colored plastic toothpick about 2 cm away from them in the soil. These areas were resampled on 8 June and the acorns remaining were collected and cut open to assess whether they were viable. The cup counting method was used in the same way at "Area G", which was sampled only once on 9 June.

Total crop size $N(0)$ was estimated by multiplying the proportion of the ground area beneath the tree being sampled by the number of cups found. Instantaneous removal rates (k) were calculated assuming $t = 150$ for 9 June, that is, that the entire crop fell from the tree on 10 January. Since almost all the acorns had fallen before this date, the calculated k values will be maximum estimates.

Experimental Results

Figure 2 shows the estimated crop sizes of the 23 trees sampled. The distribution is strongly skewed to the right, with a median of 594 and a range from 156 to 10,274. Over 60% of the trees produced fewer than 1,000 acorns.
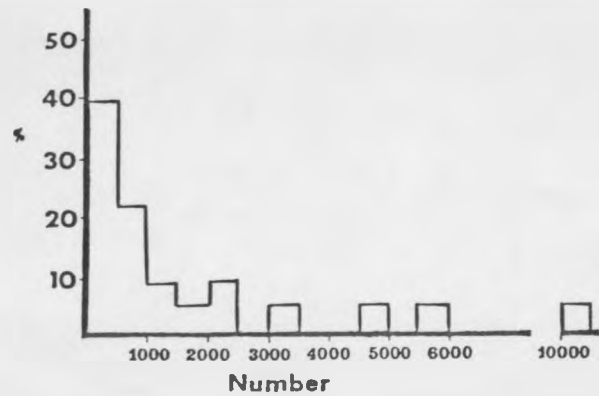

Fig. 2. Frequency distribution of estimated acorn crops of 23 *Q. oleoides* trees (all three areas combined)

Table 1. Pile sizes and removal rates for acorns in the deciduous forest experiments

$N(0)$	Sample size	Instantaneous removal rate k	Standard deviation of k	150-day survivorship (%)
1	10	0.026		2.0
10	10	0.426	0.248	1.77×10^{-26}
100	9	0.306	0.239	1.16×10^{-18}
500	1	0.154		9.29×10^{-9}

Table 1 shows instantaneous removal rates (k), their standard deviations, and the estimated percentage remaining after 150 days, for the experimental piles of acorns placed in the deciduous forest. It is clear that removal for piles of 10 or more acorns was extremely rapid; all of these piles were removed in $7\frac{1}{2}$ days or less. Single isolated acorns, on the other hand, survive much better, and an estimated 2.0% would remain from a sample of isolated acorns after 150 days. The 150-day survivorships for the other pile sizes are miniscule; the best survivorship, for piles of 500, is less than one in ten billion.

The decrease of instantaneous removal rates with increasing pile size shows that there is some satiation effect. However, the calculations of the 150-day survivorship percentages make it clear that this satiation is totally insufficient to prevent destruction of all acorns during the minimum period of time they would be exposed to terrestrial predators. A regression of k against $N(0)$ can be used to estimate instantaneous removal rates for larger crop sizes, and then these k values can be used to estimate 150-day survivorship. The best fit regression of k against $N(0)$, excluding the single acorn data, is a power function:

$$k = 0.55 \times N(0)^{-0.19}$$

for which $r = 0.34$ ($n = 20$, $P > 0.05$). Using this equation I calculated the expected number of acorns surviving 150 days for various crop sizes. For a crop of 10,274 acorns, the maximum found among the 23 trees, the estimate is that 0.0064 acorns would survive for 150 days. A crop of over 40,000 acorns would be needed to have just one acorn survive for 150 days. Furthermore, these are actually low estimates, since they assume that k will continue to decrease with $N(0)$ according to the power function given above, even though this regression is not statistically significant at the 0.05 level.

A quite different situation is found in the oak forest areas (Table 2). The removal rates are much lower, and appreciable percentages of the acorns are left at the start of the wet season.

Table 2. Crop sizes and removal rates for acorns in three oak forest areas

Forest	Sample size	Mean $N(0)$	Median $N(0)$	Mean k	Standard deviation of k	Survivorship to 9 June (%)
Santa Rosa Main	10	2247	845	0.026	0.00710	1.5
Santa Rosa Isolated	3	2086	216	0.016	0.00110	6.1
Area G	10	1047	561	0.007	0.00004	33.2
Overall	23	1704	594			

Table 3. Estimated number of acorns remaining after 150 days from acorn crops of various sizes in three different forests

Acorn crop. $N(0)$	Forest		
	Deciduous forest	Santa Rosa main oak forest	Area G oak forest
50	4.23×10^{-16}	0.98	16.23
100	1.08×10^{-13}	1.96	32.47
594	1.28×10^{-8}	11.67	192.84
1,000	2.17×10^{-7}	19.60	324.65
10,274	0.0064	201.82	3,335,48
50,000	1.27	982.18	16,232.62
100,000	9.37	1,964.37	32,465.25

Furthermore, survivorship increases inversely with the assumed gradient in mammal populations, from 1.5% in the main Santa Rosa forest, to 6.1% in the isolated Santa Rosa clump, to 33.2% in Area G. In none of the three areas is there a significant correlation between survivorship to June and estimated acorn crop per tree. However the differences among the three areas in survivorship to June are all statistically significant ($P < 0.05$ using the Mann-Whitney U test); indeed the ranges hardly overlap.

The k values calculated for each area were used to estimate 150-day survivorship for acorn crops of various sizes as before, except that simply the mean values of k were used rather than estimates from the power curve as in the deciduous forest experiments. Table 3 compares the estimated number of acorns remaining after 150 days from various crop sizes, in deciduous forest, Santa Rosa main forest, and Area G. The differences are dramatic; survival of a single acorn to the end of the wet season requires crop sizes of about 3 in Area G, about 50 in the main Santa Rosa forest, and over 40,000 in deciduos forest.

An average of 82.2% of the acorns in the main Santa Rosa forest, and 52.7% of those in the isolated Santa Rosa clump, were infested by the unidentified microlepidopteran moth, and could not have germinated. Thus the potential number of seedlings is about a fifth of the numbers shown in Table 3. However, even if there were 100% germination of the deciduous forest acorns, the number of seedlings would still remain about 8 orders of magnitude below that in the main Santa Rosa forest for a normal tree's crop. The survivorship of acorns in the various oak forest areas is of the same order of magnitude as for other tree species in this area (Boucher, in preparation); that in the deciduous forest appears far too low for a population to maintain itself.

Discussion

The data presented provide evidence which corroborates the hypothesis that survival of patches of *Quercus oleoides* forest is dependent on satiation of mammalian seed predators at the population level. Individual-tree-level satiation does occur to some extent, as shown by the decrease in instantaneous removal rate with increasing crop size in the deciduous forest experiments. However the survivorship of the acorns of an isolated tree is still much too small to permit reproduction. Thus if *Q. oleoides* occurred in the low densities typical of tropical lowland trees, it would probably go extinct in a generation.

Only the combined crops of many trees can provide sufficient acorns to satiate the mammals. Thus only oaks in high density concentrations will successfully reproduce. Furthermore, reproductive success is increased when the mammal populations are reduced. These data thus provide a partial explanation for the patchy distribution and dominance of *Q. oleoides*. The phenomenon is of course dependent on the extreme vulnerability of *Q. oleoides* to its mammalian seed predators (see also Shaw 1968). This suggests the possibility that the variation in vulnerability of nuts of different species to mammals may explain differences in those species' adult densities. This idea is explored in more detail elsewhere (Boucher 1979 and in preparation). Of course, the present explanation does not tell us how the dominance of *Q. oleoides* in lowland patches was originally established, only how it persists.

In forests such as those of *Q. oleoides* the fitness of an individual tree is affected much more by variations in the density and reproductive behavior of its conspecific neighbors than by its own behavior. Thus, for example, the lack of correlation between an individual tree's acorn crop size and the survivorship of these acorns in the oak forest – that is, the lack of a satiation effect at the individual level – is not surprising, since satiation is operating at the population level. Variation in acorn numbers between individual trees can hardly be expected to have much effect on an agouti if the entire area is coverd with acorns. This is not to say that these data support either side of a group versus individual selection argument. Indeed, the process does not hypothesize any kind of adaptation being selected for. Living in high density is not an adaptation of either individuals or groups; it is simply the result of the selection against those individuals which lived in low density. The process occurs rapidly, over ecological time rather than evolutionary time, and the present distribution is not a reflection of evolutionary adaptation, but rather a direct result of natural selection itself. Genetic variation, a basic assumption of evolutionary explanations, is not a necessary part of the hypothesis.

There are various alternative explanations for the pattern of distribution and abundance of *Q. oleoides*. That of adaptation to poor soils was not examined in this study; I can only add that, while it is not a sufficient explanation of why *Q. oleoides* occurs only in high density patches, it most certainly has a great deal to do with where those patches are. The correlation of *Q. oleoides* distribution with poor soils reflects an additional selective force which affects the seedling, sapling and adult stages of the life cycle. Thus it is complementary rather than contradictory to the process discussed here, which acts on the seed stage.

A related explanation, not yet investigated, concerns the fact that *Q. oleoides* is mutualistic with ectomycorrhizal fungi. This is in contrast to most tropical trees, which associate with vesicular-arbuscular mycorrhizal fungi. If survivorship is dependent on mycorrhizal association, as is true of many tropical trees, *Quercus oleoides* may have to maintain sufficient populations of its mycorrhizal associate in the soil in order to survive. In other words, the relationship would be an obligate mutualism, whose dynamics can involve threshold effects (extinction at low densities, survival at high) similar to that discussed here (Vandermeer and Boucher 1978). This explanation is of course closely related to the " poor-soil-adaptation" hypothesis, and is similarly complementary to the seed predator satiation hypothesis. However it would go beyond either of these hypotheses in that it explains both occurrence in high-density patches and those patches' location.

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