Quercus costaricensis Liebm. and the problem of multi-seeded acorns

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Abstract. *Quercus costaricensis* Liebm, growing near Cerro de la Muerte, Cartago Province, Costa Rica has been found to produce 42% multi-seeded acorns. With the addition of *Q. costaricensis* there are now 10 species of *Quercus* known to produce acorns that contain more than one seed. The only published explanation suggests that insect seed predation may be the selective agents producing an advantage to trees that make multi-seeded acorns period. *Q. costaricensis* was found to experience little insct predation, forcing us to generate an alternative explanation for the multi-seeded acorn habit of some oaks. We hypothesize that thc production of multi-seeded acorns is selectively neutral, being found only in oaks that produce a wide range of seed weights even within the single seeded acorns they produce. Abnormalities in cotyledon number within acorns are also noted.

It has been more that a century since Meehan (1871) noted that *Quercus robur* produced acorns containing multiple seeds, yet our understanding of the origin of the multi-seeded habit in oaks is still unclear. The developmental aspects of multi-seeded acorn production are simple enough; *Quercus* flowers contain six ovules of which only one usually develops into a seed (Mogensen 1975). What is lacking is an evolutionary explanation for why acorns are variable in the number of seeds they contain.

Garrison and Augspurger (1983) present clear evidence that the multi-seeded acorns produced by *Quercus macrocarpa* are beneficial in reducing the level of insect seed predation experienced by the tree. Acorns with multiple seeds suffer the same frequency of seed damage as single-seeded acorns, but due to satiation of the insect larvae within single acorns, at least one seed escapes insect damage more often in double-seeded than in single-seeded acorns. While the data are convincing, they leave open the question of whether or not multi-seeded acorns have evolved in response to pressure from seed predators. While presently advantageous in the *Q. macrocarpa* population of east-central Illinois, USA, the production of multi-seeded acorns by oaks may be the product of genetic drift, selection for variable seed size, etc., and not an evolutionary response to insect seed predation (an "aptation" and not an "adaptation" [Gould and Vrba 1982]).

Our goal is to explore the evolution of the multi-seeded acorn habit of oaks. Two approaches are taken to the problem. The first is to investigate the acorn production of a high elevation tropical oak that experiences little insect damage to its acorns. If multi-seeded acorns have only evolved in response to insect seed predation, then oaks without insect seed predators would not be expected to produce multi-seeded acorns. The second investigative approach is to compile the published reports on "abnormalities" in acorn development and search for taxonomic or ecological differences between the species for which multi-seeded acorns are recorded and those for which it is unknown.

MATERIAL AND METHODS

Quercus costaricensis Liebm. acorns were collected from the ground beneath trees near the Cerro de la Muerte, Cartago Province, Costa Rica (near Km 88 of the Inter-American Highway, ca. 3,200 m elevation) on 1 January 1985. *Q. costaricensis* isfound only at elevations greater than 2,700 m in Costa Rica (Burger 1983). The cool higlands of Costa Rica are depauperate in insects requiring "substrate warmth" during immature stages (e.g., wood-boringinsects, seed eating weevils, etc., [Janzen 1983]). As a consequence, the acorns of *Q. costaricensis* were found to be nearly free from insect damage.

We collected acorns haphazardly and without reference to the canopy boundaries of trees so our sample is a mixture of the acorn crops of at least 4 trees. Germinating acorns were plentiful, being found at a density of approximately 3 to 10 acorns per square meter. Only two nongerminated acorns were found and these were not included in our sample. The collected acorns were placed in plastic bags to reduce water loss and were weighed within 12 hours. The seedlings growing from each acorn were gently removed from the soil to avoid breaking the major roots and were wrapped separately. Weights were measured with a Pesola brand spring balance read to the nearest 0.1 gram. Acorns were excluded from the weighing if they were found to be damaged by vertebrate feeding.

Statistical treatment of the comparisons of seedling weights were complicated by the non-independence of seedlings within the same acorn. The data for double-seeded acorns that are presented are only one weight drawn at random from the two available for each doubly-seeded acorn. This method eliminates the artificial inflation of the sample and prevents the potential problem of non-independence of observations within the sample.

To compare the fruiting habits of oaks known to produce some multi-seeded acorns with those not yet known to do so, we used the sizes of the acorns of North American species listed in Rehder (1949) and Sargent (1905). Synonomies in these lists were merged with the aid of Sudworth (1927). The extremes of the values of acorn size reported by both of these authors were used as our estimate of acorn size variability within a species.

RESULTS AND DISCUSSION

Of the 83 acorns collected beneath the canopies of *Q. costaricensis* trees, 48 contained one seed 30 had two, four had three, and one had four seeds inside. Sixteen of the 99 acorns collected were damaged by vertebrates and were excluded from further consideration. Of the sixteen collected and then rejected because of vertebrate damage, six had one seed, eight had two, and two had three seeds. There was no indication that vertebrate seed predation was in any way associated with the number of seeds within the acorn.

The number of cotyledons attached to the young seedlings also varied within the sample. Of the 124 seedlings investigated, two had a single cotyledon, 109 had the normal two cotyledons, 11 had three, and two had four attached cotyledons. There was no tendency for the unusual numbers of cotyledons to be associated with multi-seeded acorns. The phenomenon of variable cotyledon number will not be discussed further.

Only one insect larva was found in the 120 or so acorns dissected during this survey. This unidentified beetle larva was found feeding in a cotyledon of an acorn picked up before detailed record keeping had begun. In contrast, Garrison and Augspurger (1983) found 43 to 100% of the acorns of *Q. macrocarpa* were damaged by insects. The existence of some insect seed damage, even at the very low level observed here, does not allow complete elimination of insect seed predation as a relevant selective pressure.

Vertebrate seed predation occurs much more frequently than insect seed predation in *Q. costaricensis.* Vertebrate damage differs from the feeding of insects in that vertebrates are not as easily satiated as insect larvae, therefore, multi-seeded acorns probably do not give any protection against damage due to vertebrates. In *Q. costaricensis* at the Cerro there is no strong tendency for acorns containing more seeds to escape with at least some seedlings intact. With such a small sample of damaged acorns it is not possible to say more. In the very least, *Q. costaricensis* can serve as a counter-example to the claim that all oaks with multi-seeded acorns experience high levels of insect seed predation.

The average weight of seedlings derived from double-seeded acorns appears to be less than

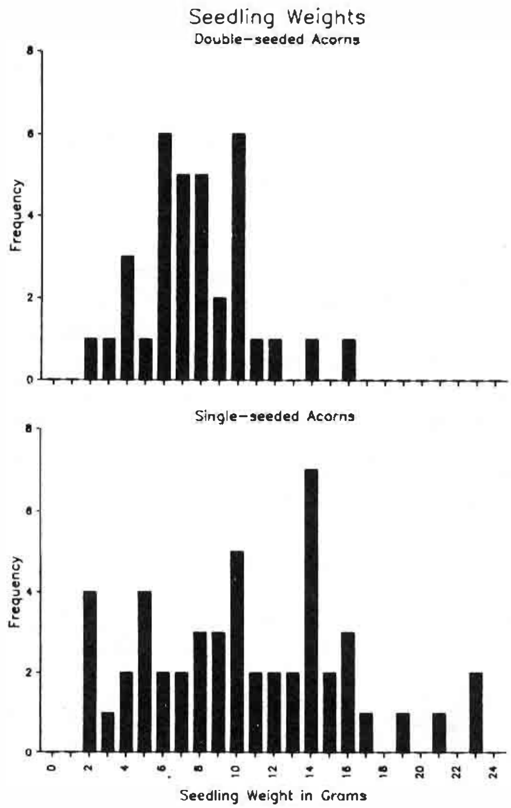

Fig. 1: Seedling wet weight distributions for double-seeded (top) and single-seeded (bottom) acorns. The midpoints of the distributions are significantly different (Mann-Whitney U test, $P = 0.0153$), but notice that the range of values is nearly the same. Double-seeded acorns do not produce seedlings of smaller size than single-seeded acorns even though on average their seedlings are smaller.

those from single-seeded acorns (Figure 1), but the ranges of values are not notably different. While this observation is based on germinated acorns and therefore not a direct measure of seed weight, it is clear that the range of weights of double-seeded acorns is contained within the range of single-seeded acorns. The production of multi-seeded acorns by *Q. costaricensis* does not increase the range of seedling sizes produced over what would be found if all acorns contained just a single seed. In fact, the variance in seed size would be reduced if only multiple-seeded acorns were made; the very largest acorns are all single-seeded. Unless these largest acorns are those that tend to survive, the production of multi-seeded acorns may not influence the number of seedlings produced by the tree.

The great variability in seed size of these oaks suggests an alternative explanation for the production of multi-seeded acorns in some oak species. The production of multi-seeded acorns may not carry a "cost" to the parent plant. Given that there is already a wide range of seed sizes within the acorn crop of the tree, placement of several seeds within the same acorn may not be maladalptive. Certainly seeds from multi-seeded acorns are smaller, but if they fall within the natural range of variation in single-seeded acorns their small size may not matter. At the outset, it would seem that linking the fates of two or more offspring in the same dispersal unit (here the acorn) would be detrimental. Competition would surely result from the germination of all seeds within the acorn. This line of reasoning is quickly set aside once it is realized that many if not most seed plants produce multi-seeded dispersal structures. If the non-independence of offspring is so detrimental why has it evolved so many times in other plant groups?

This non-adaptive (not maladaptive or adaptive) view of multi-seeded acorn production can be tested by comparing the acorn production of oaks of different species. Multi-seeded acorns would only be expected in oaks that produce a range of acorn sizes wide enough to span the variation that results from producing multi-seeded acorns. In other words, multi-seeded acorns would only be expected in oaks where natural selection has not constrained the range of acorn sizes produced to only a few values. Given the observation that there is a positive correlation between maximum acorn length and the range of lengths reported in the literature ($r = 0.62$, $N = 57$, $P < 0.05$) it should be expected that multi-seeded acorns would be found primarily in species that produce large acorns.

The oaks known to produce multi-seeded acorns are not a random subset of oaks in general, but are those oaks that produce acorns of intermediate to large size (Figure 2). These oaks are not strikingly similar in phylogeny, being derived from both subsections of the *Quercus* genus. Ecologically, they also do not share habitats or distributional ranges to a great extent so it seems unlikely that simple ecological factors are the sole cause of the phenomenon.

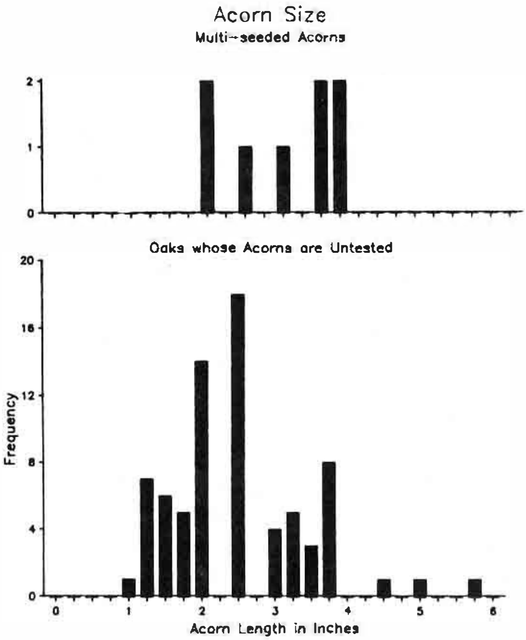

Fig. 2: Frequency histogram of maximum acorn length for *Quercus* known to produce multi-seeded acorns (top) and for those species of North America that have not yet been tested (data from Sargent [1905] and/or Rehder [1949]). These two distributions are significantly different in their position along the size axis (Kolmogorov-Smirnov D statistic = 0.35, P = 0.04). Data from Buchlotz 1941; Buda and Schepotiev 1973; Coker 1904, 1912; Harvey 1917; Hosner 1959; Meehan 1871 Reines 1969; Smith 1914.

In summary, the evolution of multi-seeded acorns is far from clearly understood. The primary limitation to our understanding is an adequate survey of multi-seeded acorn production in oaks. This problem could be easily corrected with simple observations made by local botanists on the presence or absence of multi-seeded acorns in local populations. Most needed are estimates of the frequency of multi-seeded acorn production within and between trees, with a count of the total number of acorns inspected by the observer. Insect seed predation is widespread in the genus, but oaks known to produce multi-seeded acorns are not always found to be heavily attacked by insects. (*Q. costaricensis* is the only known exception). Non-adaptive explanations for the habit have not yet been adequately explored.

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RESUMEN

El roble *Quercus costaricensis*, que crece cerca del Cerro de la Muerte en Costa Rica, produce un 42% de nueces con varias semillas cada una (solamente se conocían hasta ahora nueve especies en el mismo fenómeno). Se desecha la hipótesis de que éste sea resultado de la depredación, la cual es rara en esta población. Más bien podría tratarse de una característica selectivamente neutra.

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