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Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp.)

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Abstract

Mast-seeding is the synchronous production of large seed crops within a population or community of species every two or more years. This paper addresses three non-mutually exclusive hypotheses explaining the evolution of mast-seeding in temperate tree species, especially the genus *Quercus*: (1) mast-seeding is a consequence of mast-flowering which evolves to increased pollination efficiency in mast-flowering years; (2) mast-seeding has evolved as an anti-predator adaptation by which large seed crops during mast years satiate the seed predators and allow survival of some of the seeds; (3) selection on seed size by habitat can indirectly affect the evolution of masting if trees with large seeds require more time to accumulate reserves to mature those seeds. I find support for the pollination hypothesis in several wind-pollinated temperate tree species but not oaks. However, oaks show evidence favoring the predation and seed size hypotheses. I then develop a model to illustrate the relationships among the three hypotheses in their effects on the evolution of masting. Finally, using data from herbaria and Floras, the influence of selection via flowering, fruiting, and seed size in the evolution of masting in tropical oaks is discussed. I conclude that the need for a supra-annual cue to synchronize flowering and fruiting as well as the larger seed size found in many tropical oak species should contribute to the evolution of masting to a greater extent than seen among temperate oaks.

Introduction

Mast-seeding is the synchronous production of large seed crops within a population or community of tree species every two or more years (Janzen 1969, 1971, 1974; Silvertown 1980; Waller 1979). This phenomenon is most likely to occur in trees which, as long-lived plants, are less affected by the costs of delayed reproduction (Waller 1979). Mast-seeding has been best documented in north temperate tree species (Silvertown 1980; Waller 1979) but is also well-known for tropical dipterocarpaceae (Janzen 1974; Ash-

ton *et al.* 1988) and possibly other tropical species (Janzen 1978; Wheelwright 1986). In general, it appears that mast-seeding has evolved by postponing seed production during some years to accumulate the resources necessary to produce a large crop in other years. Thus, there are two aspects of this reproductive phenomenon: size of seed crop during a mast year and length of inter-mast interval, that is, the number of years between mast years.

The most parsimonious explanation for year-to-year fluctuations in seed production is weather (Sork *et al.* in press; Norton & Kelly 1988). Plant

populations may simply be responding to variation in climatic conditions that are most suitable to the production of large seed crops (Norton & Kelly 1988). In fact, several studies have shown various weather variables to be associated with large seed crops (Mathews 1955; Wenger 1957; van Vredenburg and la Bastide 1969; Sork *et al.* in press). When a large seed crop is part of a mast-seeding reproductive strategy, there should be a reallocation of resources rather than only a matching of the seed crop size to current resource levels (Norton & Kelley 1988; Sork *et al.* in press). Evidence of resource allocation would include a negative correlation between crop size one year and crop size during one or more previous years, or a trade-off between vegetative and reproductive growth. For many species, vegetative growth is reduced during mast years (Kozłowski 1971; Kozłowski & Keller 1976). In Missouri oaks, we found that size of acorn crop was inversely correlated with prior acorn production, suggesting that individual trees must accumulate new resources after a mast year before they can produce another large crop (Sork *et al.* in press). Moreover, we also found that weather clearly influences the size of the crop, but internal cues determine when the next mast crop will occur (Sork *et al.* in press). It is likely that this pattern of interaction between weather cues and internal physiological cues will be observed in many masting species.

There are several non-mutually exclusive hypotheses that may account for the evolution of masting. The first hypothesis states that masting in wind-pollinated species has evolved owing to the proportional increase in fertilization (especially by outcross pollen) and seed set during mast years (Nillson & Wastljung 1987; Norton & Kelly 1988; Smith *et al.* 1990). A second hypothesis proposes that mast-seeding is an anti-predator adaptation that allows survival of seeds by periodically satiating seed predators (Janzen 1969, 1971, 1974; Smith 1970; Silvertown 1980). A third hypothesis concerns the potential impact of selection on seed size, a factor that may indirectly affect the evolution of masting. This hypothesis proposes that selection for increased seed size

could indirectly select for greater intermast interval owing to the physiological need to accumulate resources for a longer period of time to produce a large seed. A likely selection pressure is habitat selection for increased seed size to enhance survival of seedlings under low light conditions (Grime & Jeffrey 1965; Gross 1984; Winn 1985; Mazer 1989). Support for this possibility comes from observations like those of Mazer (1989) of an Indiana dune community and Foster and Janson (1985) of moist forest communities who found that large seeded species are more likely to occur in closed canopy conditions. Thus, the evolution of masting may have been influenced by selection at any or all of the flower, fruit, and seedling stages of the species' life history.

In this paper, I will discuss the potential role of selection at three life-history stages in the evolution of mast-seeding in temperate tree species with special emphasis on oaks. I will then develop a model illustrating the interactions of these factors for temperate oaks. Oaks also occur in tropical habitats where the climate can be much less seasonal than found in the temperate zone. Consequently, the reproductive biology may not be identical to that of temperate oaks. While little is known about tropical oaks, I will use information gathered from herbaria and regional Floras to summarize current knowledge on their reproductive biology. These findings will be used to make predictions about which oak species are most likely to have evolved a mast-seeding reproductive pattern. I hope that these predictions will pave the way for future research on tropical oaks.

Evolutionary ecology of masting in temperate trees

Pollination efficiency in temperate tree species

In this paper, pollination efficiency will be defined as the percentage of flowers that are fertilized. Because most wind-pollinated tree species are highly outcrossing (Loveless & Hamrick 1984), we would expect fertilization success to be higher from outcross rather than self-pollination owing

to the effects of inbreeding depression. Within a season, selection for pollination efficiency should favor synchronization of flowering by trees within a population to maximize opportunity for cross-pollination. For temperate tree species, pollination usually occurs during early spring over a relatively short time period probably using a combination of daylength and temperature as a cue.

Across years, pollination efficiency may result in the synchronization of flowering so that all trees within a population produce their larger flower crops during the same year. Thus, pollination may play a role in the evolution of masting. The pollination-efficiency hypothesis states that masting has evolved to favor the increased fertilization success that occurs when more pollen is available (Norton & Kelley 1988; Smith *et al.* 1990). Since the majority of mast-fruited species in temperate forests are wind-pollinated, it may be that selection has acted through the flowering stage in addition to or instead of other stages. In other words, masting may have evolved through selection for mast-flowering due to increased efficiency of pollination during mast-flowering years. Alternatively, masting may be common in wind-pollinated species not because of selection for increased flower production but because wind-pollination, in contrast to animal pollination, does not lose effectiveness with increasing flower production. For example, animal-pollinated tree species may have an upper limit on size of the flower crop caused by pollinator limitation while size of flower crop in wind-pollinated species is limited only by the internal resources needed to mature a seed crop.

Smith *et al.* (1990) developed a model to evaluate the potential advantages of mast-flowering for pollination efficiency in wind-pollinated species. The two most important assumptions of their model are that (1) fluctuations in male and female flower production are positively correlated across years; and (2) that cost of sexual reproduction through female function is the same regardless of fertilization. This second assumption refers to the fact that many plant species produce the reproductive structure (e.g., a cone) whether or not the

ovules within it are fertilized or matured. Because the cost of producing a flower includes the production of fruit, selection should favor increased pollination efficiency through mast-flowering to minimize wasted reproductive effort. They conclude that mast-flowering is particularly advantageous in gymnosperms because (a) many species invest in production of cones regardless of fertilization and (b) gymnosperm species often occur in monodominant stands where mast pollen production can dilute self-pollen and increase cross-fertilization.

Several types of evidence would provide support for the pollination-efficiency hypothesis: (1) percentage fertilization of a flower crop should be greater during a mast-flowering year; (2) male and female flower production should be temporally correlated across years; and (3) high percent fertilization is correlated with mast-fruited years. The first type of evidence is required to demonstrate that pollination efficiency could select for mast-flowering. The second type of evidence also would result if masting is a consequence of selection for mast-flowering because we would expect that male and female flower production should be synchronized to the same year. The third type of evidence is necessary but not sufficient to support the pollination efficiency hypothesis. If the other two types of evidence are absent, then high fertilization success only demonstrates that large crop size can result from flowering success; it would not indicate increased pollination efficiency resulting from mast flowering (Sork & Bramble, *manuscr.*).

Data from several gymnosperm and angiosperm species were reviewed to test the pollination-efficiency hypothesis (Table 1). As predicted by the Smith *et al.* (1990) model, in all cases where mast flowering was found to enhance fertilization success, the plant produces a reproductive structure regardless of fertilization. For example, *Pinus*, *Dacrydium*, *Betula*, and *Fagus* all mature a cone or fruit even when the seeds are absent or undeveloped. Because the reproductive structure is produced regardless of seed set, it is easy for the investigators to estimate percentage fertilization by counting hollow seeds or fruit. Al-

Table 1. Studies examining the three kinds of evidence in support of the pollination efficiency hypothesis to account for the evolution of masting in temperate tree species. See text for discussion of criteria.

Species	Reference	Increased fertilization success during years with high flowering?	Correlation of male and female flowering during mast year?	Increase seed set in mast years?
<i>Dacrydium cupressinum</i>	Norton & Kelly 1988	yes	–	yes
<i>Fagus sylvatica</i>	Nilsson & Wastljung 1987	yes	–	yes
<i>Betula pubescens</i> & <i>B. verrucosa</i>	Sarvas 1952	yes	yes	yes
<i>Picea abies</i>	Sarvas 1957	yes	–	yes
<i>Pinus silvestris</i>	Sarvas 1955	no	–	yes
<i>Quercus alba</i> , <i>Q. rubra</i> , & <i>Q. velutina</i>	Sork & Bramble, in prep.	no	no	yes

– = data not available.

though only two of the studies which showed fertilization success also measured male and female flowering, in only one case male and female flowering correlated temporally (Table 1).

The pollination-efficiency hypothesis was also examined using collections of aborted flowers and fruit from individual trees of *Quercus alba*, *Q. rubra*, and *Q. velutina* from spring through autumn of 1984–1988 (Sork & Bramble, *manusc.*). To test the hypothesis that percent fertilization is greater during mast years, we estimated number of flowers initiated and number of flowers fertilized and then calculated percent fertilized. Unlike the species discussed above, it is not possible to determine fertilization success by counting hollow fruit. Oaks often have two peaks of premature abscission. The first one occurs in June, which coincides with a period after fertilization should have taken place, and the second one occurs in midsummer just prior to fruit enlargement (Shellburne 1983; Sork *et al.* in press). Assuming that the number of abscised flowers falling prior to late June represents unfertilized flowers, we used the first early peak as an estimate of the unfertilized flowers. To test the hypothesis that male and female reproduction is synchronized across years, we measured the catkin biomass that fell into traps (cone-shaped plastic bags with a 0.5 m² opening) placed beneath the canopy of individual trees. This provides us a relative estimate of pollen production, which we correlated with total number of flowers. Finally, we assessed the size of the mature acorn crop by counting the mature acorns in the fall.

Our results do not support the pollination-efficiency hypothesis (Table 1). Percent fertilization was not greater in years of high pistillate flower production or years of high pollen production (Sork & Bramble, *manusc.*). Total number of female flowers was not correlated with male catkin biomass. Although the pollination-efficiency hypothesis was supported in beech (Nilsson & Wastljung 1987) another member of the Fagaceae (Table 1), we cannot draw the same conclusions for oaks. A major difference between the two genera is that oaks do not allocate energy to the fruit if the seed is unfertilized. Indeed, large proportions of the flower crop are aborted quite early. In spite of our observation that mature acorn crop size correlated with percent fertilization, this finding alone without the other two types of evidence should not be interpreted as support for the pollination-efficiency hypothesis.

Role of seed predation in temperate tree species

The predation hypothesis proposes that mast-seeding is an anti-predator adaptation that allows survival of seeds by satiating their predators (Janzen 1969, 1971, 1974; Smith 1970; Silvertown 1980). In Janzen's view, both the ability to satiate seed predators during mast years and to suppress predator populations during nonmast years are important factors in the evolution of masting. In his review of a wide range of species, Silvertown (1980) found evidence supporting predator satiation, but was unable to find support for Janzen's hypothesis about the importance of the in-

termast interval for the reduction of predator populations. Silvertown (1980) suggested that masting is most likely to evolve in populations subject to intense predation. His principal support for this was a significant correlation between the coefficient of variation of crop size (an index of masting) and the highest observed percent pre-dispersal mortality (an index of intensity of predation). An alternative explanation for the intermast interval is that it is simply a physiological consequence of producing a large crop and is unrelated to suppression of predator populations (Silvertown 1980; Sork *et al.* in press).

The best evidence demonstrating that high crop size reduces seed predation is increased percent seed survival from either insect and/or vertebrate predators during mast years. Several mast-fruited species show evidence of predator satiation. Silvertown (1980) reanalyzed data from mast-seeding species to determine those cases in

which probability of seed survival is correlated with log crop size for data sets with five or more years of crop size data. He examined 59 cases for 25 tree species, but the majority ($n = 39$) of the cases did not report the cause of mortality (whether animal or something else), thus preventing any test of the predator-satiation hypothesis. In Table 2, I list the significant cases in which either insect or vertebrate predation was identified as a source of mortality. These seven species provide an indication of the range of species in which masting results in predator satiation. In Table 2, I also list six species in which the predator-satiation hypothesis was specifically examined. Of those studies, only Nilsson and Wastljung (1987) measured seed predation by both insect and vertebrate predators. In fact, this study is the only one that I am aware of in which both the pollination and predator hypotheses are tested. They concluded that both pollination and

Table 2. Evidence addressing the predator-satiation hypothesis in temperate mast-fruited tree species. The studies cited by Silvertown (A) presented data that he reanalyzed to test for a relationship between percent survival from predation and crop size. The second group of studies (B) were specifically designed to address the predator satiation hypothesis.

Species	Reference	Increased seed survival from insect predators during mast years?	Increased seed survival from vertebrate predators during mast years?
A. Studies cited in Silvertown (1980) ^a			
<i>Abies concolor</i>	Fowells & Schubert 1956	yes	no
<i>Fagus grandifolia</i>	Gysel 1971	yes	no
<i>Fagus sylvatica</i>	Nielsen 1977	yes	–
<i>Pinus banksiana</i>	Kraft 1968	yes	–
<i>Pinus palustris</i>	McLemore 1975	yes	–
<i>Pinus ponderosa</i>	Fowells & Schubert 1956; Schubert 1970	yes	yes
<i>Pinus resinosa</i>	Matson 1971	yes	–
B. Studies directly testing predator satiation			
<i>Fagus sylvatica</i>	Nilsson and Wastljung 1987	yes	yes
<i>Hammamelis virginiana</i> ^b	De Steven 1983	yes	–
<i>Carya glabra</i>	Sork 1983	no ^c	no
<i>Quercus alba</i>	Sork & Bramble, manusc.	no ^c	–
<i>Quercus rubra</i>	Sork & Bramble, manusc.	yes	–
<i>Quercus velutina</i>	Sork & Bramble, manusc.	yes	–

^a References cited by Silvertown 1980 who reanalyzed their data.

^b Shrub species.

^c More seeds escaped seed predation during mast years but there was not a proportional advantage of mast years as found in other studies in this table.

– = not available.

predation contribute to the evolution of masting in beech.

In a study of three temperate oak species, we examined the relationship between crop size and insect infestation in 1981–1988 (Sork & Bramble, *manusc.*). We found that percent infestation shows a negative exponential relationship with log crop size in *Quercus rubra* and *Q. velutina*, members of the black oak subgenus. For *Quercus alba*, a member of the white oak subgenus, a proportional advantage of large acorn crops did not occur, but numerically more acorns survived during a mast year than a non-mast year. Thus, *Quercus alba* is less efficient in satiating its seed predators than the other two species but in all three species large acorn crop enhances escape from seed predators. When seed predation is more intense, as in *Quercus alba*, it may cause stronger selection for increased masting (Silvertown 1980). So, current directional selection may be acting on *Quercus alba* to increase crop size even further until proportional satiation of predators occurs. It is interesting to note that in some areas, the masting interval of *Quercus alba* can be as high as ten years (Schopmeyer 1974) rather than the three years observed in one Missouri population.

Because the two subgenera of oaks have such different patterns of reproduction in North America, I decided to evaluate the extent to which masting has evolved in each. The differences in reproductive patterns include the following: 1) members of the white oak subgenus mature fruit in one season while the North American members of the black oak subgenus require two seasons; 2) acorns of the white oak subgenus germinate in the fall immediately upon falling while black oak acorns are dormant until the following spring; and 3) acorns of the white oak subgenus tend to have greater moisture content (Korstian 1927). To examine the differences between the two subgenera, we utilized data from Schopmeyer (1974) on length of the intermast interval in common eastern North American deciduous oak trees. The length of the intermast interval provides an index of masting. When Schopmeyer reported a range of years, the midpoint of the range was used.

The eighteen tree species in Schopmeyer's review includes 13 species which show intermast intervals of two or more years (Table 3). Our analysis showed that intermast interval varied across species but that, on the average, white oak species have a greater interval than black oak species (Table 3). This suggests that selection has been stronger for greater masting in the white oak subgenus than in the black oak subgenus among North American oaks.

In conclusion, the temperate deciduous oaks show evidence that masting succeeds in predator satiation of insect seed predators. In general, species of the white oak subgenera show greater masting, as indicated by length of intermast interval, than species of the black oak subgenus, which may be due to greater selective pressure by seed predators. Further research is needed to understand how phylogenetic constraints contribute to the evolution of masting. Nonetheless, the predator-satiation hypothesis is supported by several North American oak species.

Seed size, habitat selection and masting in temperate forest trees

Seed size can play an important role in the successful establishment of seedlings: larger acorns produce more vigorous seedlings than small acorns (Korstian 1927; Beaman 1981). It has been shown for a range of species that larger seeds are favored under conditions of shading (Grime & Jeffrey 1965; Gross 1984; Winn 1985), drought (Baker 1972; Wulff 1986) and in high latitudes characterized by short growing seasons (McWilliams *et al.* 1968). Aizen and Patterson (1990) found seed size in temperate deciduous oaks to be correlated with geographical range and concluded that large seed size enables those species to colonize a broader range of habitats. Selection on seed size could affect masting indirectly because size of the seeds may influence the length of time to accumulate reserves for seed production. A large seed may require more local reserves to develop than a small seed.

Using data from Schopmeyer (1974), Waller

(1979) reported that, within six genera (*Acer*, *Betula*, *Fraxinus*, *Pinus*, *Prunus*, and *Quercus*), species that had an intermast interval greater than 1.5 years had significantly larger seed size than those producing seeds every year. Using Schopmeyer's (1974) data for oak tree species, I estimated seed size by transforming the average number of cleaned acorns per pound to mean grams per acorn. I found a positive correlation between log of intermast-interval and log seed size (Fig. 1, $r = 0.617$, $n = 18$, $P < 0.01$). Moreover, white oak species have significantly larger acorns than black oak species (Table 3).

In spite of the seed size differences between the two North American subgenera, some members of the black oak subgenus do produce large acorns and show long masting intervals. For example, *Quercus rubra*, a large seeded species, tends to occupy late successional habitats that typically are associated with larger seed size. It appears that phylogenetic constraints alone do not explain the evolution of seed size or masting in *Quercus*. To examine whether habitat correlates with seed size, I categorized seed size into small (less than 2.5 g) and large (greater than 2.5 g) after examining the size distribution of seed weights. Then I used information from Fowells (1965) to categorize each species according to successional status (mid- or late succession). I found that large seeded species are more likely to be classified as late successional species $\chi^2 = 5.84$, $df = 1$, $P < 0.05$) than small-seeded species. *Quercus alba*

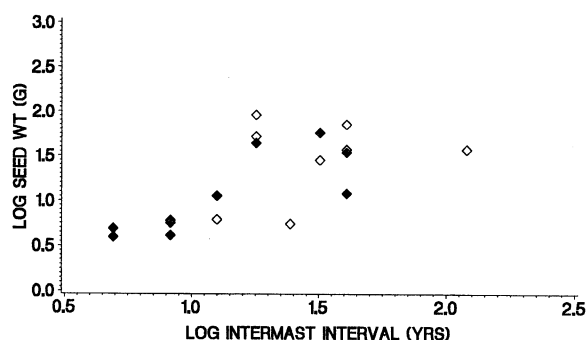


Fig. 1. Acorn weight versus intermast interval for 18 species of North American eastern deciduous oaks in the white oak subgenus (hollow diamond) and the black oak subgenus (solid diamond). Data were taken from Schopmeyer (1974).

and *Q. rubra* in Missouri have larger seeds than *Quercus velutina* and show significantly greater indices of masting (Sork *et al.* in press). Those former two species are mature forest co-dominants whereas *Q. velutina* is distributed in the more xeric and open sites.

What we cannot determine with current information is whether (a) selection for increased seed size puts increased selective pressure on masting because a crop of the same magnitude but with larger seeds requires a longer intermast interval to store the necessary resources; or (b) whether factors which have selected for masting such as seed predation have also favored large seed size. Normally, seed predation should favor a tree to produce more and presumably smaller seeds (Janzen 1969). However, if masting has evolved, the tree may have the resources to produce both large crops and large seeds. Given that masting species produce fewer crops than non-masting species, there may also be selection to increase the probability of seedling survival through large seed size. Consequently, selection for large crop size with a long mast interval may also select for larger seeds. Further research is needed to understand the relationship between seed size, masting, and habitat selection. Moreover, because white oak species have larger seeds than black oak species, future work should include an analysis of possible phylogenetic constraints on the evolution of seed size and masting (e.g. Donohue 1989).

General model for temperate deciduous oaks

This discussion has shown that selection could have acted during several life history stages. These possible effects are not mutually exclusive and probably include interactions among them. To summarize the relationships among flower phenology, seed predation, selection on seed size and mast-fruiting, I have developed a schematic diagram (Fig. 2).

Selection via pollination efficiency could contribute to the evolution of masting either through its effect on the intermast interval or on acorn crop size. Selection to maximize pollination effi-

Table 3. Successional stage, intermast interval, and seed size in selected species of eastern North American oaks.

Subgenus	Species	Successional stage	Mast interval (yrs)	Seed size (g)
White oaks	<i>Q. alba</i>	mid	7.0	3.28
	<i>Q. bicolor</i>	late	4.0	3.46
	<i>Q. lyrata</i>	late	3.5	3.53
	<i>Q. macrocarpa</i>	mid	2.5	5.24
	<i>Q. michauxii</i>	mid	4.0	3.99
	<i>Q. prinus</i>	late	2.5	3.67
	<i>Q. stellata</i>	mid	2.0	1.10
Black oaks	<i>Q. coccinea</i>	mid	4.0	1.80
	<i>Q. falcata</i>	mid	1.5	0.83
	<i>Q. imbricaria</i>	mid	3.0	0.83
	<i>Q. laurifolia</i>	late	1.0	0.85
	<i>Q. niger</i>	mid	1.5	0.98
	<i>Q. nuttalli</i>	mid	3.5	4.61
	<i>Q. palustris</i>	mid	1.5	1.07
	<i>Q. phellos</i>	mid	1.0	0.95
	<i>Q. rubra</i>	late	4.0	2.77
	<i>Q. shumardii</i>	late	2.5	4.45
<i>Q. velutina</i>	mid	2.0	1.75	
White oak	MEAN (S.E.)		3.64 (0.64)	3.42 (0.47)
Black oak	MEAN (S.E.)		2.32 (0.35)	1.90 (0.43)
	W.O. vs B.O. ^a		P < 0.05	P < 0.05

^a T-test for unequal variances using log-transformed data.

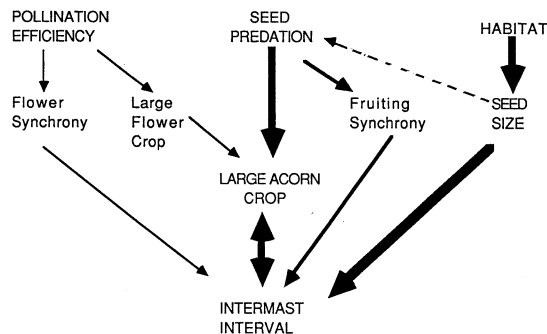


Fig. 2. General model for the evolution of mast-fruiting in temperate deciduous oaks. Thickness of line indicates hypothesized relative importance of the relationship between the two variables. See text for description.

ciency via outcrossing may act on flowering synchrony across years so that year-to-year variation in flower production is synchronized. This later process could potentially influence the intermast interval if such synchronization requires some specific cue that occurs every so many years.

However, because synchronization of flower production within a year is strongly cued to early spring in North American oaks, I do not expect that the need for flower synchrony would be the most important factor contributing to the intermast interval. I have indicated this with thin arrows (Fig. 2). Pollination efficiency could contribute to the evolution of masting by selecting for larger flower crop which could result in an increased crop size. However, my research on three temperate oak species does not provide strong support for this path, so I have drawn thin arrows (Fig. 2) to indicate the extent of importance.

For predator satiation to be effective, acorn maturation should be synchronized within a season and among years. In the temperate zone, oaks mature acorns during early fall. Among years, some cue is necessary to synchronize acorn production within a population to the same year. My research has shown that each of the three species (a) produce large and small crops synchronously

across years within a species, and (b) has its own internal cue for the production of a mast year (Sork *et al.* in press). Selection via seed predation should affect both the crop size and mast interval components of masting. However, I suggest that the major impact of selection by seed predators is on increased crop size, as indicated by the thick line (Fig. 2). Then, as selection continues on crop size, the need for greater resources to produce a mast crop could cause a concomitant increase in the intermast interval. Moreover, if the intermast interval is due to physiological needs to accumulate sufficient resources for another large crop, then selection on intermast interval should be a function of crop size times seed size or total biomass allocated to acorn production.

The significant correlation between habitat and seed size, combined with the significant correlation of seed size and intermast interval, suggests that habitat also may influence the evolutionary ecology of masting. I suggest that seed size influences the intermast interval component rather than the crop size component of masting as indicated by the line between seed size and intermast interval (Fig. 2). The effect on the mast interval would occur because as seed size increases more resources are needed to mature a seed which could in turn affect the masting interval if simultaneously selection favors increased crop size. I speculate that large seed size could indirectly affect the crop size component of masting (indicated by dashed line in Fig. 2) by increasing the vulnerability of seeds to predators, which then causes selection for increased crop size. Clearly, the relationship among these factors requires direct investigation.

In summary, selection through predation and seed size but not pollination efficiency seem to be quite important in the evolutionary ecology of masting in temperate deciduous oaks.

Applications to tropical oaks

Although more than half of the world's species of oaks occur in the tropics, we know very little about them. Like their temperate zone counter-

parts, tropical oaks, especially in Central America, are ecologically significant in that they often dominate the forests in which they occur and they provide a major food source for wildlife. Montane tropical oak forests are disappearing as fast as lowland rain forest enhancing the need to understand the factors contributing to the production of seeds so important for tree regeneration. In this section, I will utilize existing, albeit scanty, information about Central American tropical oak species to modify the temperate oak model of the evolutionary ecology of masting for application to tropical oaks. My prediction is that masting has evolved in many of these species.

Pollination and masting

Unlike the temperate zone where spring provides a sharp cue for flowering, tropical oaks, especially those in less seasonal climates, do not have such a strong seasonal cue. In this way, the tropical oaks may be similar to the dipterocarps in Malaysia, which have a large, high-lipid fruit like *Quercus* (Janzen 1974; Ashton *et al.* 1988). Although *Quercus* spp. are wind-pollinated and dipterocarp species are insect-pollinated, both types of pollination would require a cue to synchronize flowering to achieve fertilization, especially in aseasonal environments. Apparently, in Malaysia mast-fruiting is more common in the aseasonal dipterocarp species than in the seasonal species from which they probably evolved. Ashton *et al.* (1988) proposed that because the aseasonal species have no clear seasonal cue, they must have evolved to respond to a supra-annual cue that can be detected by a large number of individuals. Flowering in the aseasonal species is hypothesized to be cued by El Niño years (Ashton *et al.* 1988) but flower synchrony has probably evolved through selection for mast-fruiting (Janzen 1974; Ashton *et al.* 1988) rather than mast-flowering. Because dipterocarps are insect-pollinated, mast-flowering is unlikely to improve fertilization success (Smith *et al.* 1990).

We have no data on the relationship between supra-annual weather cues and mast-flowering or

mast-fruiting in tropical oaks. To evaluate whether oaks use a reliable seasonal cue, I first wanted to determine whether they flower at the same time each year. For this purpose, herbarium specimens were examined for the oaks of Costa Rica and Panama from herbaria at the Instituto Nacional de Biodiversidad in Costa Rica, the Missouri Botanical Garden, and the California Academy of Science. Although herbarium data do not have the same reliability as data collected systematically in the field, they are the best data currently available on flowering and fruiting phenology of neotropical oaks. I found that wet-forest species in Costa Rica were collected in flower in a range of months throughout the year (Table 4A). For most species, 75% of the flowering record fell in one of the six potential months of the dry season (December through May) with March being the most common month of flowering. Breedlove (pers. comm.) hypothesizes that for flowering of many oaks are keyed to a three day dry spell followed by rain, which may explain why flowering occurs during so many months because that dry spell could occur anytime in the dry season. For one species in Costa Rica, (*Quercus bumelioides*, I found specimens with flowers in nine

months of the year (Table 4A). This species occurs in high elevation cloud forest with no clear dry season. In contrast to temperate oaks in which flowering occurs consistently within the same month each year, tropical oaks seem to flower in different months across years. If within year cues for flowering are not highly predictable, which is probably true for species in less seasonal habitats, then mast-flowering which is synchronized to a strong supra-annual cues might evolve to improve pollination efficiency. In spite of the fact that temperate oaks show little evidence in support of the pollination-efficiency hypothesis (Sork & Bramble, *manusc.*), tropical oaks that occupy wet habitats (even in the 'dry' season) may have strong selective pressure to flower synchronously during years when environmental conditions are unusually good. Probably the first cue that should be tested is the El Niño years.

Predator satiation and masting

Only one study that I am aware of has examined seed predation in tropical oaks. Boucher (1981) demonstrated that the synchronous production of

Table 4. Observations of herbarium collections recording flowering and fruiting times for six wet-forest species of Costa Rica oaks. Each observation represents a different plant.

Species	Dec	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sep	Oct	Nov	Total
A. Flowering observations													
<i>Q. benthamii</i>	1	1		3									5
<i>Q. bumelioides</i>	1	1	1	5	2		1	1		1		2	15
<i>Q. costaricensis</i>		2	2	3	1		1						8
<i>Q. insignis</i>			1	2								2	5
<i>Q. lancifolia</i>				1									1
<i>Q. salicifolia</i>	4		4	2			1		2	1			14
Total flowering	6	4	7	16	3	0	3	1	2	2	0	4	48
A. Fruiting observations													
<i>Q. benthamii</i>						3			1				4
<i>Q. bumelioides</i>			2	3					1			1	8
<i>Q. costaricensis</i>		2			2					1			5
<i>Q. insignis</i>						1		1	1				3
<i>Q. lancifolia</i>					1		1			1			3
<i>Q. salicifolia</i>				1		2		2	1	1	1		8
Total fruiting	0	2	2	4	3	6	1	3	4	3	1	2	31

acorn crops by several individuals within a population was necessary to satiate mammalian seed predators of *Quercus oleiodes*. While other tropical trees can exhibit a mast-fruited reproductive pattern (e.g. Wheelwright 1986), only a few cases of predator satiation have been demonstrated. Research on other large-seeded tropical tree species, including the understory tree *Gustavia superba* (Sork 1987) and the canopy species *Dipteryx panamensis* (De Steven & Putz 1984; Clark & Clark 1984), demonstrate that high seed density is critical for escape from predation. Consequently, we should expect predation by seed predators to play as much a role in the evolution of mast-fruited in tropical oaks as it does in temperate oaks.

Synchronization of fruit maturation in tropical oaks should be extremely important to achieve predator satiation. As with flowering synchrony, we might expect species without a clear seasonal cue to rely on a supra-annual cue in order for individuals within a species to synchronize to the same year and time of year. To evaluate fruiting phenology, I used herbarium specimens for Costa Rica and Panama oaks to determine whether there was any seasonal pattern of acorn production. I recorded date for a mature fruit only if I had evidence that it was attached to the specimen at the time of sampling or the label stated that mature fruit were present in the trees. Although the sample sizes are not always large, it is apparent that the timing of fruit maturation is highly variable from year to year (Table 4B). Thus, one might predict that if predator satiation is necessary for seed survival, we should see the evolution of mast-fruited by synchronizing fruit production to supra-annual cues as observed in the Malaysian dipterocarps in such a way that tropical oak populations produce large acorn crops in the same year and during the same time of year.

Given that we have no reason to believe that tropical oaks are any less vulnerable to seed predators than temperate oaks, I predict that selective pressure through predation has contributed to the evolution of masting in these species. At this point, we need data on insect infestation, predation by vertebrates, dispersal agents as well as

patterns of acorn production in tropical oak species to evaluate their vulnerability to predation and the extent of masting. It will be interesting to see whether the tendency for members of the white oak genus to show greater masting intervals than those of the black oak genus as has been observed among North American oaks.

Seed size and habitat

Tropical oaks show tremendous variation in seed size both within and across species. Because moist conditions sometimes select for smaller seeds (Grime & Jeffrey 1974), one possible hypothesis is that wet-forest species should have smaller seed size than dry-forest species. However, if differences in forest type also affect light conditions, then because low light environments usually are associated with larger seed size (Grime & Jeffrey 1974; Foster & Janson 1985; Mazer 1989), one could hypothesize that larger seeds would be associated with wet forest which tend to have more closed canopy.

I examined three flora – (1) Costa Rica, (2) Nicaragua, and (3) State of Chiapas, Mexico – to evaluate whether seed size correlated with habitat in tropical oaks and whether there were differences between subgenera. Using data from herbaria and Floras, I measured length and width of mature acorns and recorded the date, location, and elevation of each observation. The dependent variable of acorn size (log transformed) was estimated by calculating the volume from length and width measurements. Most oak species could be classified as inhabitants of either wet forest or dry forest. The nomenclature is that of D. Breedlove (pers. comm.).

For the Costa Rican oaks, I utilized the individual observations from herbaria on six wet-forest species of oaks to test for differences across species as well as subgenera. Seed size differed significantly among species (ANOVA, $F(4,33) = 13.4$, $P < 0.0001$) and was significantly greater for species in the white oak subgenus than those in the black oak subgenus (ANOVA, $F(1,33) = 11.0$, $P < 0.01$). Because elevation pro-

vides an environmental gradient, I included this variable in the ANOVA model as a covariate and found that acorn volume co-varied inversely with elevation (ANOVA, $F(1,33) = 4.8$, $P < 0.05$). Thus, seed size may be affected by environmental factors associated with elevation (e.g. temperature, precipitation, length of growing season). If moisture increases with elevation then selection on smaller seeds in mesic environments may account for the trend. Alternatively, some evidence suggests that length of growing season may decrease with elevation. Using data on date of collection on specimens with young staminate or pistillate flowers and mature attached acorns where December 1 was day 1 and November 30 was day 365, I found that mean day of fruiting within a year was negatively correlated with elevation ($r = -0.388$, $n = 27$, $P < 0.05$) even though day of flowering was not correlated with elevation ($r = -0.125$, $n = 55$, $P > 0.10$). These two observations together suggest that higher-elevation trees have a shorter period of time to mature their acorns and thus produce smaller acorns. Regardless of the explanation, the relationship between elevation and seed size in Costa Rican oaks indicates that habitat may also put selective pressure on seed size.

For Nicaragua oaks, I estimated acorn volume using the midpoint of the range of length and width measurements reported in the Flora of Nicaragua (Breedlove, pers. comm.). Many of the species are also found in Costa Rica but additional dry-forest species are also present. Again,

I found that the white oak subgenus had significantly larger acorns than the black oak subgenus (dependent variable = log transformed acorn volume: ANOVA, $F(1,9) = 7.17$, $P < 0.05$; Fig. 3A). I also found that wet-forest species had significantly larger acorns than dry-forest species (ANOVA, $F(1,9) = 9.17$, $P < 0.05$, Fig. 3B). This finding runs counter the observation that mesic environments select for small seed size. However, because other studies have found large seeded species to be associated with closed habitats (Mazer 1989) or more mature forest (Foster & Janson 1985), perhaps light availability is lower in wet forests than in dry forests.

As an additional test of the habitat hypothesis, I examined data from the Flora of Chiapas, Mexico which contains a larger number of species than Nicaragua. Breedlove (pers. comm.) has identified 24 species, but I chose to use only the 17 species occupying wet and dry forest and to omit those found in the cold, high elevation forest. Based on information from Breedlove (pers. comm.), species were assigned to either the small (volume less than 5 cm^3) or large (volume greater than 5 cm^3) seed size class. Using a goodness of fit test, I found that more species within the black oak subgenus had small acorns than did members of the white oak subgenus $\chi^2 = 7.244$, $df = 1$, $P < 0.01$; Fig. 4A) and that dry-forest species were more likely to have small acorns than wet-forest species $\chi^2 = 4.735$, $df = 1$, $P < 0.05$; Fig. 4B).

In conclusion, tropical oaks show a similar phylogenetic constraint observed in temperate

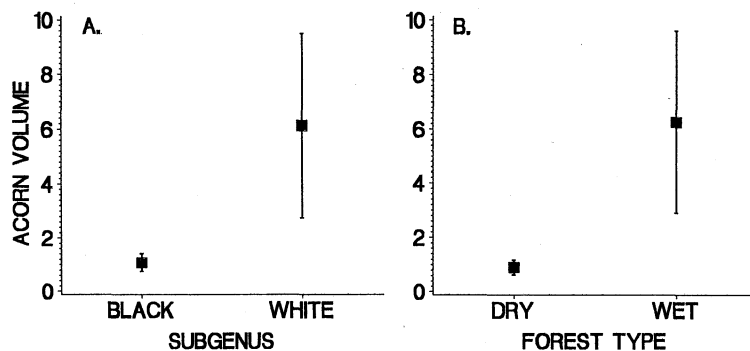


Fig. 3. Mean acorn volume (± 1 SE) of 5 species in the black oak subgenus and 9 species of the white oak subgenus for Nicaraguan oaks (A) and for 6 dry-forest and 6 wet-forest species from Nicaragua (B).

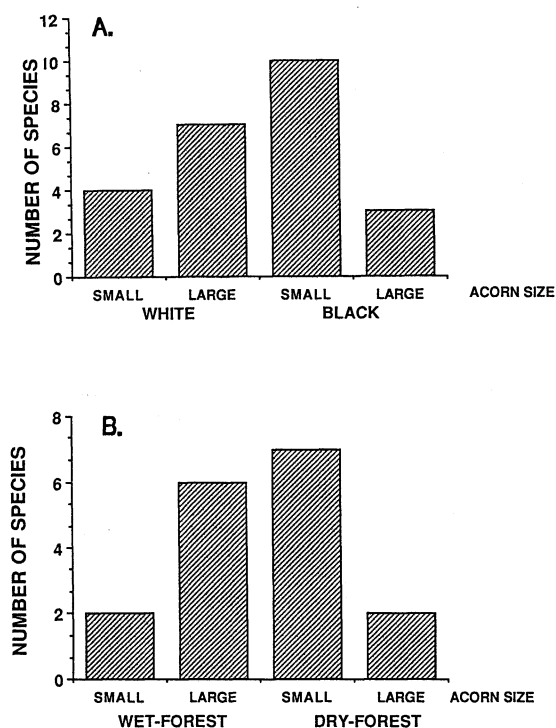


Fig. 4. Number of species from Chiapas, Mexico with small and large acorns which belong to the two subgenera (A) and occur in dry-forest and wet-forest.

oaks that the white oak subgenus has larger acorn size, on the average, than the black oak subgenus. They also show that acorn size is associated with habitat. Moreover, some tropical oaks have much larger acorns than any among the temperate deciduous oaks. For example, the large-seeded *Quercus insignis* in Costa Rica has a mean seed volume of 25.6 cm³ which is much greater than that of a large-seeded North American oak, *Quercus rubra*, which has an acorn volume of 10.4 cm³. If seed size directly or indirectly selects for mast crop size and intermast interval in tropical oaks as it appears to do in North American oaks, then we should expect the tropical large-seeded species to have even longer intermast intervals than observed among temperate masting species. Thus, I predict that one should look for the evolution of masting in species that are in the white oak subgenus, occupy wet forests habitats, or are known to have large acorns.

General model for tropical oaks

The general model of the evolutionary ecology of masting in temperate oaks should probably be modified for tropical oaks. As before, I have indicated important relationships with thick lines (Fig. 5). While the nature of the relationships should be similar between temperate and tropical oaks, I think certain differences in the strengths of the relationships are likely to occur. The major difference concerns the role of pollination. As stated above, the need for increased pollination efficiency in less seasonal climates should select for a response to a supra-annual cue. Because of the importance of tight synchronization within a year, this cue must be strong enough to trigger flowering within the same year and time of year. Thus, the scale of the intermast interval will be influenced by the type of cue that is used. Unlike temperate oak species, I predict that selection for pollination efficiency should have a strong effect on the evolution of mast-flowering. Such mast-flowering will result in mast-fruiting.

Like temperate oaks, predator satiation will play a strong role in the evolution of mast-fruiting. Again, because tropical climates tend to be less seasonal, there may be selection to respond to a supra-annual cue in order to ensure that individuals within a population mature fruit in the same year and season. Because of the need for sufficient reserves to produce a mast crop, especially in the large-seeded tropical oaks, a mast year will

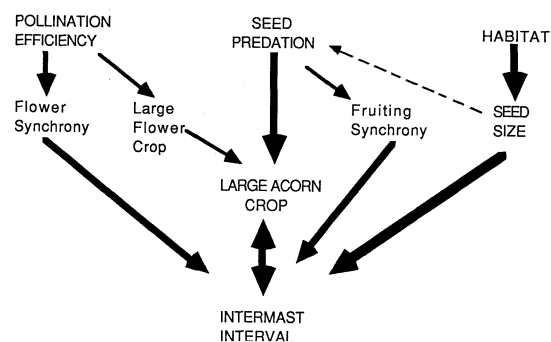


Fig. 5. General model for the evolution of mast-fruiting in Central American tropical oaks. Thickness of line indicates hypothesized relative importance of the relationship between the two variables. See text for description.

require a number of elapsed years since the last mast crop as well as a strong external cue. In temperate oaks, a good acorn crop was a function of both internal cues and weather conditions (Sork *et al.* in press). In tropical oaks, I expect this interaction between internal physiological and external cues to be at least as strong.

In summary, I wish to make four predictions concerning tropical oaks. Like temperate oaks, I do not anticipate that all species will have evolved the same degree of mast-fruiting. However, I do believe it is going to be found to be quite common. First, improved pollination efficiency through mast-flowering will be more prevalent among tropical oaks than temperate oaks owing to the less seasonal nature of tropical environments creating a greater need for a supra-annual cue for flowering. Second, I predict that predator satiation will also be important in tropical oaks thus creating a need for mast-fruiting to be tied to a supra-annual cue to insure the synchronous production of acorn crops for the less seasonal species (e.g. Ashton *et al.* 1988). In fact, if a supra-annual cue is found to be associated with masting in tropical oaks, it might be difficult to distinguish whether it evolved through the flowering or fruiting life-history stages. Third, I predict that white oak species will have greater intermast intervals than black oak species, on average. Determining whether this is true because of their larger seed size or phylogenetic tendency toward longer intermast interval can only be sorted out with a phylogenetic analysis of character-state evolution (e.g. Donoghue 1989). Fourth, I predict that because wet-forest species have larger seed size, they will also show longer intermast intervals than dry-forest species.

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