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Author(s): Victoria L. Sork, Judy Bramble, Owen Sexton
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ECOLOGY OF MAST-FRUITING IN THREE SPECIES OF NORTH AMERICAN DECIDUOUS OAKS[1]

VICTORIA L. SORK AND JUDY BRAMBLE[2]
Department of Biology, University of Missouri–St. Louis, St. Louis, Missouri 63121-4499 USA

OWEN SEXTON
Department of Biology, Washington University, St. Louis, Missouri 63130 USA

Abstract. We conducted an 8-yr study of flower and acorn production in three species of oak in east-central Missouri: white oak (*Quercus alba*), red oak (*Q. rubra*), and black oak (*Q. velutina*). The goal was to evaluate whether mast-fruiting, the synchronous production of large seed crops followed by small seed crops, is simply a response to weather conditions or is actually an evolved reproductive strategy. In this paper, we address four specific questions: (1) Are annual fluctuations in acorn crop size the result of synchronous production of acorns by individuals? (2) Are large acorn crops the result of large flower crops and/or high survival of those flowers to mature fruit? (3) To what extent do weather variables account for variation in acorn production among years? (4) Does acorn crop size correlate negatively with prior acorn production?

Red oak and white oak showed a greater degree of mast-fruiting than did black oak. Within a species, individuals tended to produce large acorn crops in the same years, but each species differed in which years they produced large crops. The size of a given acorn crop was determined by both flower abundance and survival of flowers to fruit. Principal components and multiple-regression analyses were used to describe the relationship between weather variables and acorn production. The first principal component explained the largest amount of the variation in black oak ($R^2 = 0.55$) and red oak ($R^2 = 0.89$). In white oak, two principal components combined to explain 77% of the variation in acorn production. The weather variables that were associated with these principal components included spring temperature (positive effect) and summer drought (negative effect).

Past acorn production had a major impact on the size of the current acorn crop, with each species showing a different pattern. In black oak, the current acorn crop was negatively correlated with the crop 3 yr prior but positively correlated with the crop 2 yr prior. In red oak, acorn crop size 1, 2, and 3 yr prior had negative correlations with current acorn crop, while acorn crop size 4 yr prior was positively correlated. In white oak, there were negative correlations between acorn crop size and crop size 1, 2, and 4 yr prior but a positive correlation with the acorn crop size 3 yr prior. These data are consistent with the hypothesis that mast-fruiting species must store resources during some years in order to produce a mast crop. We discuss the possibility that these three species may have inherent cycles of reproduction that are modified by the impact of weather conditions, black oak with 2-yr cycles, white oak with 3-yr cycles, and red oak with 4-yr cycles. We conclude that the patterns of acorn production for black oak, red oak, and white oak are not simply responses to weather events but are also a function of prior reproductive events. This suggests that masting is an evolved reproductive strategy.

Key words: acorn production; Fagaceae; mast-fruiting; masting; Missouri, USA; oaks; predator satiation; Quercus alba; Quercus rubra; Quercus velutina; *resource allocation; wind pollination.*

INTRODUCTION

Some oak species show high year-to-year variation in acorn production (Downs and McQuilken 1944, Christisen 1955, Christisen and Korschgen 1955, Tyron and Cavell 1962, Beck 1977, Carmen et al. 1987). The synchronous production of large seed crops every two to several years within a population of trees is called mast-seeding or simply masting (Janzen 1969, 1971, Silvertown 1980). A commonly cited hypothesis (Janzen 1969, 1971, Smith 1970, Silvertown 1980) is that mast-seeding is an antipredator adaptation that satiates seed predators because more seeds are produced than can be consumed. Evidence of predator satiation by masting exists for several tree species (Silvertown 1980), although such evidence does not demonstrate that masting evolved in response to predation. Moreover, among wind-pollinated species, increased fertilization efficiency with synchronous flowering could

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[2] Present address: Department of Biology, St. Louis University, St. Louis, Missouri 63103 USA.

also contribute to patterns of masting (Nilsson and Wastljung 1987, Norton and Kelly 1988, Smith et al. 1990). Before postulating adaptive significance of masting for a given species, it is important to determine the extent to which the observed variation in seed production is a response to annual variation in weather conditions and to what extent variation in seed production is an intrinsic physiological response. The latter would indicate that fluctuations in seed production are an evolved reproductive strategy. The objective of this paper is to evaluate these two possible explanations for variation in acorn production in three species of Missouri oaks, black oak (*Quercus velutina* Lam.), red oak (*Q. rubra* L.), and white oak (*Q. alba* L.).

The most parsimonious explanation of annual variation in acorn production is that seed crop size is dictated by weather conditions. Norton and Kelly (1988) hypothesized that weather conditions in certain years promote greater photosynthate production and/or are less stressful, and therefore enable the plants to produce more seeds. They call this the resource matching hypothesis because the trees are matching their reproductive output to the resources available each year. Weather might also determine seed crop size because certain aspects of the reproductive biology require specific weather conditions (for example, adequate fruit set may require dry weather conditions at the time of pollination). Both of these hypotheses could be categorized as weather tracking hypotheses because the annual variation in acorn production is a response to the weather conditions.

Several weather factors have been proposed to cause fluctuations in tree seed crops (Baldwin 1942, Baker 1950, Wenger 1957, Mathews 1963, van Vredenburch and la Bastide 1969). Factors that have been suggested or shown to have an impact on acorn production are: late spring frost (Goodrum et al. 1971, Minima 1954, Romashov 1957); winter cold (Baldwin 1942); temperature, humidity, and wind at time of pollination (Minima 1954, Sharp and Chisman 1961, Sharp and Sprague 1967, Wolgast and Stout 1977); and drought and high temperatures (Sweet 1973). Within the genus *Quercus,* each species may respond to different environmental factors (Gysel 1956, Olson and Boyce 1971), and species responses may vary among sites.

Weather conditions can produce a tendency towards population synchrony of flowering or fruiting, but such synchrony would not by itself demonstrate that annual fluctuations are an evolved reproductive strategy. For it to be an evolved strategy, one would expect to find an alteration in the allocation of resources between mast and nonmast years (Norton and Kelly 1988). For example, if a mast-fruiting strategy requires that the tree expend all or much of its resources to produce a large seed crop, then much lower acorn production would be expected in subsequent years. To our knowledge, no one has tested whether large seed production negatively affects future production in mast-seeding species. Thus, strong evidence supporting the hypothesis that mast-fruiting is more than just a response to weather would be an inverse relationship between acorn crop size and prior acorn production.

During the 8-yr period, 1981–1988, we monitored individual tree acorn production of black, red, and white oaks in a Missouri oak–hickory forest. We addressed the following questions: (1) Are annual fluctuations in acorn crop size in these three species due to mast-seeding, e.g., synchronous acorn production, or are different individuals producing large crops in different years? (2) Is large acorn crop size due to large flower crop size and/or high survival of those flowers to mature fruit? (3) To what extent do weather variables account for year-to-year variation in acorn production? (4) Is acorn crop size inversely related to prior acorn production? Answers to these questions should clarify the extent to which masting is an evolved reproductive trait in these oak species.

METHODS

Site description.—The study was conducted in an oak–hickory forest located at Tyson Research Center, Eureka, St. Louis County, Missouri, an 800 ha area owned by Washington University. This site is on the northeastern end of the Ozark plateau (38°31′ N, 90°33′ W) and has never been glaciated (Braun 1950, Wuenscher and Valiunas 1967, Thom and Wilson 1980). The Tyson forest is within a contiguous forest of ≈2000 ha. The major canopy species are white oak (*Quercus alba* L.), red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam), and pignut hickory (*Carya glabra*) (Zimmerman and Wagner 1979, Hampe 1984).

Floral biology of study species.—The study species belong to two different subgenera of oaks: white oak is in the subgenus *Quercus* (=*Leptobalanus*), while black and red oak are in the subgenus *Erythrobalanus.* Among temperate species, the two subgenera differ in length of time between flowering and fertilization (Romashov 1957). White oaks produce flowers in spring, which are fertilized and develop into mature fruit in autumn of the same year as they were pollinated. In contrast, black and red oak produce staminate and pistillate flowers during the spring of one year, but ovules are fertilized and the fruit mature in the following year. For all species, the staminate floral buds are initiated in the spring of the year prior to flowering and the pistillate floral buds are initiated in late summer of the year prior to flowering (Minima 1954, Turkel et al. 1955, Romashov 1957, Merkle et al. 1980). Thus, the full development of flower primordia to mature acorns spans 2 yr in white oaks and 3 yr in black and red oak.

Field methods.—During the spring of 1981, 15 reproductive trees of each oak species were chosen. For each tree, we measured the dbh (diameter at breast height) and the area beneath the canopy drip line in 1981 and again in 1987. Canopy area was estimated by segmenting the area defined by the canopy drip line into an octagon and calculating the resulting area covered by the canopy. In 1982 and 1983, some of these trees were dropped from the study because they were not reproductive and were replaced with new ones. Consequently, for analyses based on the full 8-yr period, samples were 13 black oaks, 12 red oaks, and 15 white oaks.

We placed eight seed-collecting traps (trap area = 0.5 m^2) under the canopy of each tree in sites not overlapped by the canopies of adjacent conspecific oaks. The cone-shaped seed traps were constructed of clear plastic sheeting 150 μm (6 mil) thick with the mouth of the frame held open by galvanized wire (after Christisen and Kearby 1984). The traps were suspended above the ground and small drain holes were placed at the bottom of each trap.

From 1981 to 1988, trap contents were collected once weekly from July until mid-November when acorn fall has ceased. In 1984–1988, we began the collections in late April to assess female flower production and early fruit abortion. Lacking a way to determine when a female flower is fertilized and becomes an acorn, we group female flowers and acorns together in our analyses. Because the female reproductive structures were collected throughout the season, the total number of flowers and acorns provides an estimate of the total number of flowers initiated. For all three species, our seed traps underestimate the number of early season flowers because these small-sized flowers are blown in a larger area than that sampled by our traps. This problem may be even greater in black and red oak because these small flowers are held for an additional season. Nonetheless, our estimates of total flower crop size provide a good index of the year-to-year variation in flower number.

From April through July, female flowers and acorns were air-dried and counted, and the entire sample was weighed. After July, acorns were weighed individually and divided into two classes, immature and mature, based on size of the fruit and the position of the fruit with respect to the cap. They were then categorized further into one of three categories: (1) viable (including those with small amounts of vertebrate damage); (2) insect infested; or (3) maldeveloped (e.g., incomplete embryo development, fungal attack, or some unidentifiable source of mortality).

Daily precipitation and daily maximum and minimum temperature were recorded at Tyson Research Center throughout the 8 yr. Mean daily temperature was estimated as the average of maximum and minimum temperatures for that day.

Data analyses.—Data from field collections were used to calculate several variables. Mature Acorn Density is the number of viable and infested mature acorns per m^2 that fell into the seed traps. The size of the Mature Acorn Crop for a tree is the Mature Acorn Density multiplied by the 1987 canopy area. From 1984 to 1988, we were able to estimate Total Flower Crop per tree by counting all flowers and acorns that fell in the seed traps from mid-April through November, and then adjusting this density value for canopy area. Percent Flower Survival was obtained by dividing Mature Acorn Crop by Total Flower Crop per tree.

Daily weather information was used to test several weather variables for their influence on flower initiation, flower development, and fruit production. This list of weather factors (Table 1) takes into account the critical periods of flower and fruit development. Most variables are self explanatory. Summer drought, a variable that combines temperature and rainfall, was included because it is possible that neither of those variables alone measures water stress to the plant. To evaluate drought, we used an index (Walter 1973) calculated for each month as follows: Drought = (mean daily temperature per month, in degrees Celsius) − [0.333 × (mean daily rainfall per month, in millimetres)]. Negative values indicate no drought and were set to zero. Positive values provide a relative index of water stress, with the higher index indicating higher stress. To estimate drought stress over several months, we averaged the monthly drought indices over the specified time interval.

To analyze the effect of weather on acorn production, we first conducted a principal components analysis on the set of weather variables to reduce the large number of weather variables into a smaller number of independent, orthogonal composite variables. This approach was used because our 8-yr study provides only seven degrees of freedom and many of the weather variables were correlated with each other. The weather variables used were related to the period from the beginning of flower bud initiation through acorn maturation, 3 yr for red and black oak and 2 yr for white oak (see Table 1). The 17 weather variables for red and black oak and the 12 weather variables for white oak were reduced to 7 principal component variables.

To address the question of the effect of weather on Mature Acorn Crop, we conducted a forward stepwise regression separately for each species using the seven principal components as the independent variables but only using up to three principal components in the model at one time. For each species, the dependent variable was the average Mature Acorn Crop per year. The analyses for each species were based on yearly means rather than individual tree values of Mature Acorn Crop to avoid problems of pseudoreplication (Hurlbert 1984).

To identify individual weather variables that may be useful predictors of acorn crop size, we included a correlation analysis of all weather variables with Mature Acorn Crop size. Given the large number of tests involved, this analysis is intended to illustrate potentially important variables rather than to statistically test the extent to which weather accounts for variation in acorn production.

To evaluate the impact of prior acorn production on

TABLE 1. Description of weather variables and their abbreviations used in the correlation tests and principal components analyses between weather variables and measures of flower and acorn crop size.

Variable	Abbreviation	Description
Spring max. temp	SPRTEM	Spring maximum temperature during the time of pollination calculated as the mean maximum daily temperature during 15 April–7 May of the year of acorn maturation.
Spring max. temp. (−1)	SPRTEMP(−1)	Same as above except calculated for 1 yr prior to the year of acorn maturation, when pollination occurs for red and black oak.
Spring temp (w/o rain)	SPRTEMNR	Same as Spring Max. Temp. except that temperature is included only for days without rain, when pollen dispersal could easily occur.
Spring rain	SPRRAIN	Mean daily rainfall during 15 April–7 May of the year of acorn maturation.
Spring rain days	SPRRDAYS	Number of days with rain during 15 April–7 May of the year of acorn maturation.
Spr. rain days (−1)	SPPRDAYS(−1)	Same as Spring Rain Days except measured 1 yr prior.
Late spring frost	SPRFROST	Calendar date of the latest spring minimum temperature < −5°C.
Late spr. frost (−1)	SPRFROST(−1)	Same as above but 1 yr prior.
Summer max. temp.	APJULTEM	Mean daily temperature for the period of 1 April–30 July during the year of acorn maturation.
Sum. max. temp. (−1)	MAYSEPTEM(−1)	Mean daily temperature during 1 May–30 September during year prior to acorn maturation.
Summer temp. (−2)	MAYSEPTEM(−2)	Same as above but 2 yr prior.
Summer rain	APJULRN	Mean daily rainfall for the period of 1 April–30 July during the year of acorn maturation.
Summer rain (−1)	MAYSEPRN(−1)	Mean daily rainfall during 1 May–30 September of previous year.
Summer rain (−2)	MAYSEPRN(−2)	Same as above but 2 yr prior.
Summer drought	APJULDRT	Mean daily drought during 1 April–30 July during year of acorn maturation.
Summer drought (−1)	MAYSEPDRT(−1)	Mean daily drought during 1 May–30 September during year prior to acorn maturation.
Sum. drought (−2)	MAYSEPDRT(−2)	Same as above but 2 yr prior.
Winter cold	WINCOLD	Mean minimum daily temperature during 16 November–15 March of the year of acorn maturation.
Winter cold (−1)	WINCOLD(−1)	Same as above but 1 yr prior.

current acorn crop size, we correlated Mature Acorn Crop with lagged values of Mature Acorn Crop for 1, 2, 3, and 4 yr prior for each tree. For example, the correlation coefficient for tree 1 for current acorn crop size and acorn production 1 yr ago was based on the following pairs of crop sizes: 1981 vs. 1982, 1982 vs. 1983, 1983 vs. 1984, etc.; through 1987 vs. 1988. We used the correlation coefficients for all individual trees to perform a t test of the null hypothesis of no correlation at the population level (i.e., the mean correlation coefficient over all trees equals 0). If there was no impact of prior acorn production on current acorn production, the mean correlation coefficient should not differ significantly from zero. Separate t tests were conducted for each lag of 1, 2, 3, and 4 yr for each species using the number of trees minus one as the degrees of freedom. By using individual trees as replicates, we can evaluate trends within the population of each species. To determine whether any weather variables also show cycles, we repeated this analysis by autocorrelating each weather variable with itself 1, 2, 3, and 4 yr prior for the years 1981–1988. The Pearson correlation coefficients were used to test significance.

All data analyses were conducted through SAS Version 5 (SAS 1985). Log transformations were used throughout regression and ANOVA tests when necessary to meet assumptions of the models and are indicated in tables and text.

RESULTS

Evidence for mast-fruiting

To estimate the extent of mast-seeding by each species, we used each tree's coefficient of variation (CV) for Mature Acorn Crop as an index of masting (Silvertown 1980). The CVs of red oak (133.6 ± 9.2% [mean ± 1 SE]) and white oak (135.8 ± 6.0%) were significantly greater than that of black oak (105 ± 7.9%; ANOVA, $F = 5.5$, df = 2, 37, $P < .01$; Scheffé a posteriori contrasts, $P < .05$).

All three species showed significant year-to-year variation in size of Mature Acorn Crop (Fig. 1; Table 2), a pattern consistent with masting. While the three species produced their lowest crop sizes during 1983 and 1984, they differed in the years of greatest acorn production (Fig. 1). The best year for black oak was 1987, when 11 out of 14 trees produced their largest crop during the 8-yr interval (Table 3). The best year for red oak was 1981, when 5 out of 6 trees sampled during that year produced their largest crop (Table 3). The best years for white oak were 1985 and 1988, during which 13 of 15 trees produced their largest crop

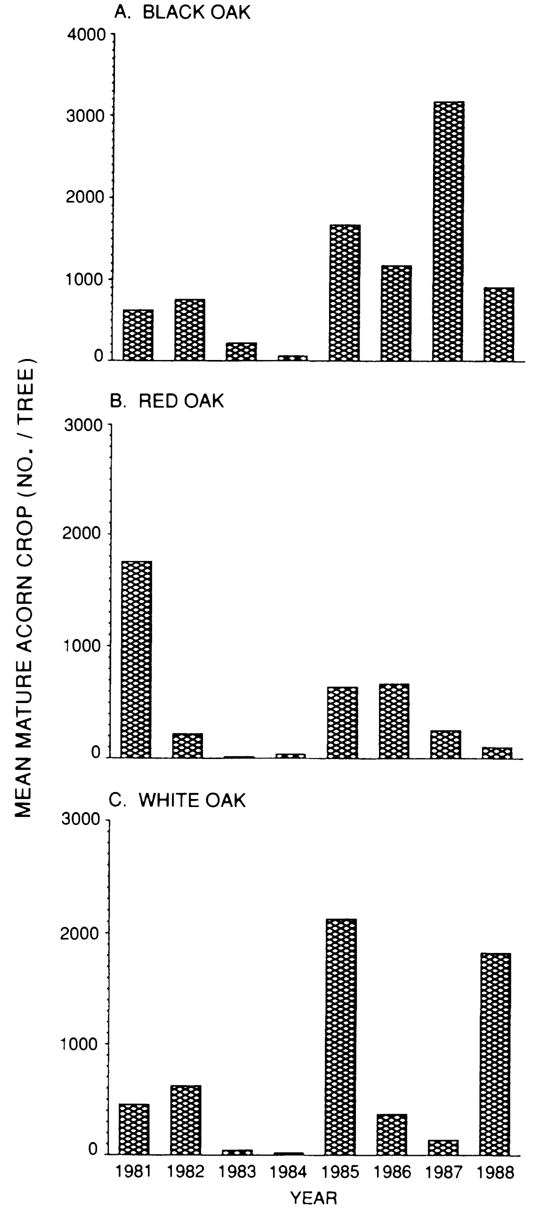

FIG. 1. Annual mean mature acorn production for black oak (n = 13 trees), red oak (n = 12 trees), and white oak (n = 15 trees) sampled at Tyson Research Center, St. Louis County, Missouri, from 1981 to 1988.

in one of those years (Table 3). These results illustrate that "mast years" are due to the synchronous production of large crops during the same years.

Within each species, individual trees showed tremendous variation (Table 3), which resulted in a significant effect due to tree (Table 2). Mean Mature Acorn Crop per tree was correlated significantly with canopy size for black oak (r = 0.75, df = 13, P < .01) and red oak (r = 0.83, df = 11, P < .001) but was not correlated with dbh. In white oak, the mean size of the Mature Acorn Crop was not correlated with either canopy area or dbh.

Proximate causes of masting

To address whether mast-fruiting is due to large flower crops or high flower survival to fruit, we used the 5 yr of data in which we estimated Total Flower Crop and Mature Acorn Crop. Total Flower Crop and Percent Flower Survival were significant predictors of Mature Acorn Crop for all three species (Table 4). In black oak and red oak, percent flower survival explained much more of the variation in acorn crop size than did the size of the flower crop (Table 4). In contrast, total flower crop explained most of the variation in acorn crop size of white oak (Table 4).

The pattern of flower/acorn fall within a year illustrates the ecological dynamics that contribute to a mast year (Fig. 2). In an exceptionally poor year for acorn production, 1984, flowers were initiated for all three species, but there was an early peak of prematurely abscised acorns collected from the seed traps (Fig. 2). In contrast, during a mast year, such as that of white oak 1985 or black oak 1987, the late season peak of acorn fall was greater than acorn fall during the early season (Fig. 2). Remembering that the y axis is $\log_{10}$ transformed, one can see that within a species, nonmast years were associated with high early season abscission and low-to-medium density of acorns in the late season. Black oak has late season peaks in 1985 and 1987, which were both good acorn production years (Fig. 2, left column). During 1984–1988, red oak never shows a late season peak (Fig. 2, middle column); this pattern is consistent with our observation that red oak did not have a superabundant acorn crop during those years as compared to the average crop size of 1981 (Fig. 1).

TABLE 2. ANOVA results for the effect of year and tree on the dependent variable, Mature Acorn Crop (log transformed), in black, red, and white oak during 1981–1988. The effect of year is tested across all trees while the effect of tree is tested across all years with no interaction possible. The degrees of freedom given are those of the numerator and denominator of the F ratio.

Source of variation	Black oak			Red oak			White oak		
	df	MS	F	df	MS	F	df	MS	F
Year	7, 91	44.7	22.5***	7, 77	38.9	14.7***	7, 98	64.9	27.6***
Tree	13, 91	12.7	6.4***	11, 77	5.1	1.9*	14, 98	18.6	7.9***

* P < .05; *** P < .001.

TABLE 3. Descriptive information on tree and crop sizes for individual study trees within black oak, red oak, and white oak during the period 1981–1988. (Trees marked with asterisks were sampled starting in 1982.)

Tree ID no.	dbh (cm)	Canopy area (m^2)	Mean crop size	Minimum crop size	Year of minimum	Maximum crop size	Year of maximum	CV (%)
				Black oak				
*3	39.2	56	74.0	0.0	1984	224.0	1987	132.8
6	52.4	87	2277.3	0.0	1983	6177.0	1985	103.9
9	40.8	62	2258.0	15.5	1983	7440.0	1987	110.9
11	35.4	56	419.7	0.0	1984	1120.0	1987	103.4
16	30.8	21	313.5	10.5	1983, 1984	1286.3	1985	130.1
*21	28.5	54	977.8	40.5	1984	1647.0	1987	57.8
*23	31.7	35	675.0	0.0	1984	1216.3	1987	72.3
25	41.0	46	566.4	0.0	1984	2461.0	1987	144.1
*40	37.6	39	182.5	0.0	1983, 1988	1111.5	1987	225.5
41	40.4	61	1782.3	0.0	1984	7792.8	1987	139.9
42	57.5	50	906.7	266.1	1981	2612.5	1987	85.1
*43	34.5	41	654.5	10.3	1983	1250.5	1985	75.0
*46	40.6	48	1164.6	60.0	1983	3588.0	1987	76.7
*49	39.4	87	2575.8	43.5	1984	8700.0	1987	117.8
				Red oak				
*2	46.2	54	102.2	0.0	1982, 1983	324.0	1986	120.8
5	24.5	22	335.9	5.5	1983	1356.2	1981	143.5
7	29.1	43	336.7	0.0	1983	1350.2	1981	131.1
15	57.5	76	1033.2	19.0	1982	3154.4	1981	127.3
17	36.1	54	734.2	0.0	1983, 1984	3322.4	1981	161.3
18	27.7	35	134.9	0.0	1983, 1985	860.7	1981	218.4
*33	24.1	33	129.6	0.0	1982	404.3	1985	106.5
*34	31.5	40	321.4	0.0	1983, 1988	920.0	1986	117.6
*35	45.3	40	61.4	0.0	1983	190.0	1988	103.6
44	50.1	71	390.1	35.5	1983	1082.8	1987	104.5
*50	28.5	40	87.1	10.0	1983	360.0	1986	141.3
*51	38.0	111	701.7	0.0	1983	1998.0	1982	126.9
				White oak				
1	49.2	77	1508.0	57.8	1984	3850.0	1985	96.9
*4	41.5	39	441.5	0.0	1983, 1984	1452.8	1985	141.9
10	37.5	38	914.9	38.0	1984	3211.0	1988	118.7
12	34.0	46	638.3	0.0	1983	3105.0	1985	182.2
13	32.3	47	474.4	0.0	1983	1668.5	1985	142.9
14	37.5	67	498.9	0.0	1983, 1984	2445.5	1988	162.9
19	47.8	97	1124.6	0.0	1981, 1984	4656.0	1985	168.5
*22	35.6	39	542.2	0.0	1984	2408.3	1985	158.2
24	33.7	42	1114.1	10.5	1984	2992.5	1985	119.6
26	24.7	61	47.7	0.0	1981, 1983, 1984	152.5	1986	116.6
28	28.3	63	250.0	0.0	1983, 1984, 1987	819.0	1988	125.1
30	40.6	88	1531.8	66.0	1984	4928.0	1985	120.4
32	47.7	60	1022.8	60.0	1983	3660.0	1985	131.8
*47	41.3	50	392.9	0.0	1984	1250.0	1988	126.1
*48	45.6	87	9.3	0.0	1983–1986	21.8	1982	124.7

TABLE 4. Results of stepwise regression model of mean Mature Acorn Crop on Total Flower Crop and Percent Flower Survival for black, red, and white oak during 1984–1988.† (All data were log transformed or arcsine transformed.) Partial R^2 (expressed as a percent of total variation) is the incremental contribution for each variable to the model.

	Black oak ($N = 70$, $R^2 = 0.891$)		Red oak ($N = 60$, $R^2 = 0.904$)		White oak ($N = 70$, $R^2 = 0.885$)	
Variable	Partial R^2 (%)	F	Partial R^2 (%)	F	Partial R^2 (%)	F
% flower survival	75.3	207.3***	60.9	90.2***	30.5	178.1***
Total flower crop	13.8	84.7***	29.5	175.1***	58.1	94.2***

† Note that, for white oak, the first variable entered was Total Flower Crop.
*** $P < .001$.

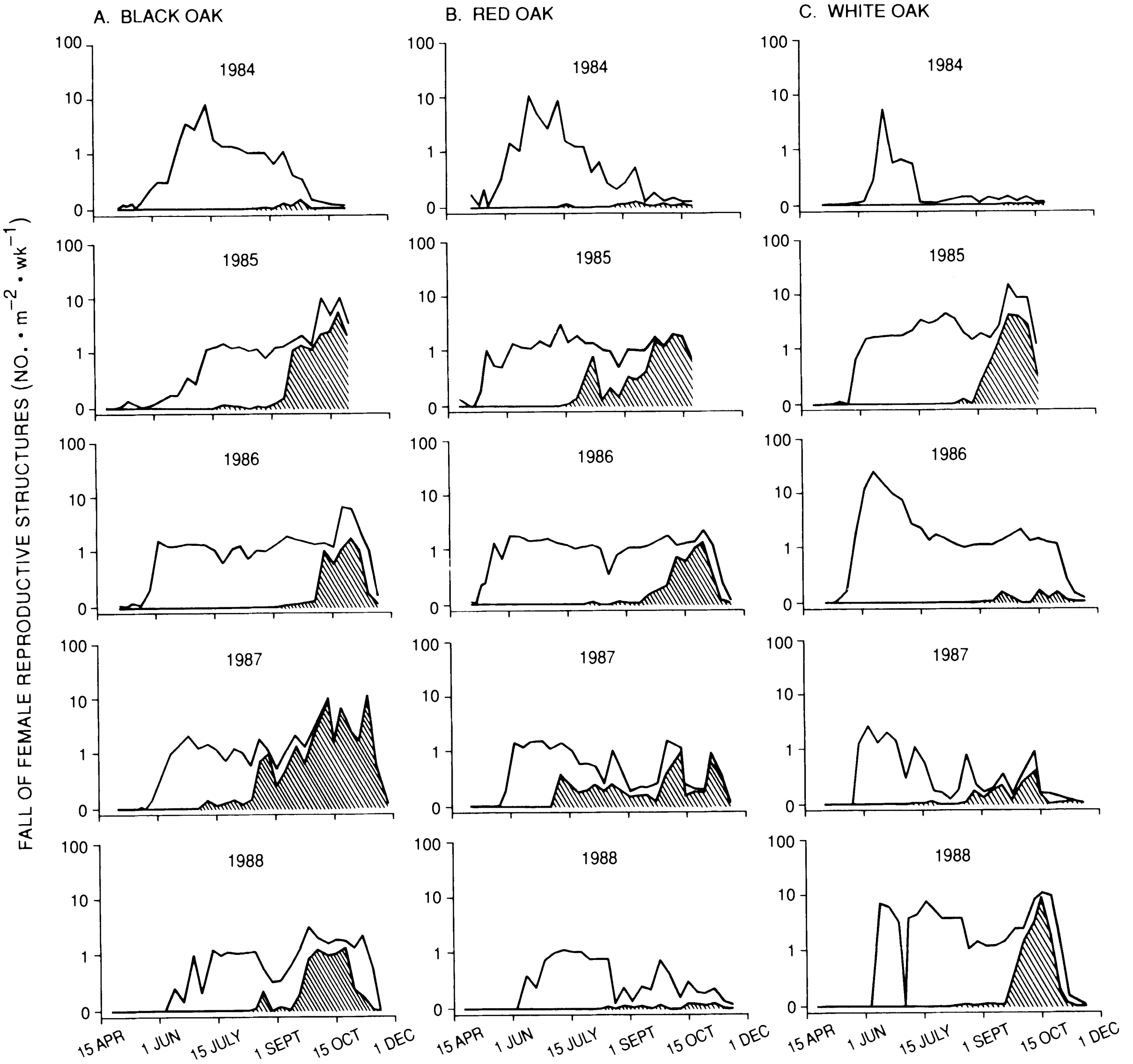

FIG. 2. Pattern of weekly fall of all female reproductive structures (upper line) and mature-sized acorns (hatched area) into seed traps from mid-April through December for all three oak species during 1984–1988.

In white oaks, Fig. 2 (right column) shows high early season acorn abscission during 1984, 1986, and 1987 when mature acorn production was low. In contrast, during 1985 and 1988, mast years, there were two peaks of acorn drop of which the second one exceeded the early one. Thus, a significant factor contributing to a mast or nonmast year is both the total flower crop and the pattern of survival of those flowers to mature acorns.

Impact of weather

The 17 weather variables used for the weather analyses involving black and red oak were reduced to seven principal components (Appendix A). The first principal component accounted for 30.3% of the total variation and was loaded highly with spring temperature during the year of fruiting, summer drought during the year of fruiting, and late spring frost during the previous year (Appendix A). The white oak weather analyses used 12 weather variables, which also were reduced to seven principal components (Appendix B). In this analysis, the weather variables loaded slightly differently than for the first set of variables used for red and black oaks. For example, the first principal component, which accounted for 32.2% of the variation, was correlated most strongly with mean daily maximum spring temperature on days without rain, mean daily maximum spring temperature, and summer temperature.

For black oak, the first principal component significantly accounted for the variation in mean annual Mature Acorn Crop size (Fig. 3A; $R^2 = 0.55$, $P < .05$).

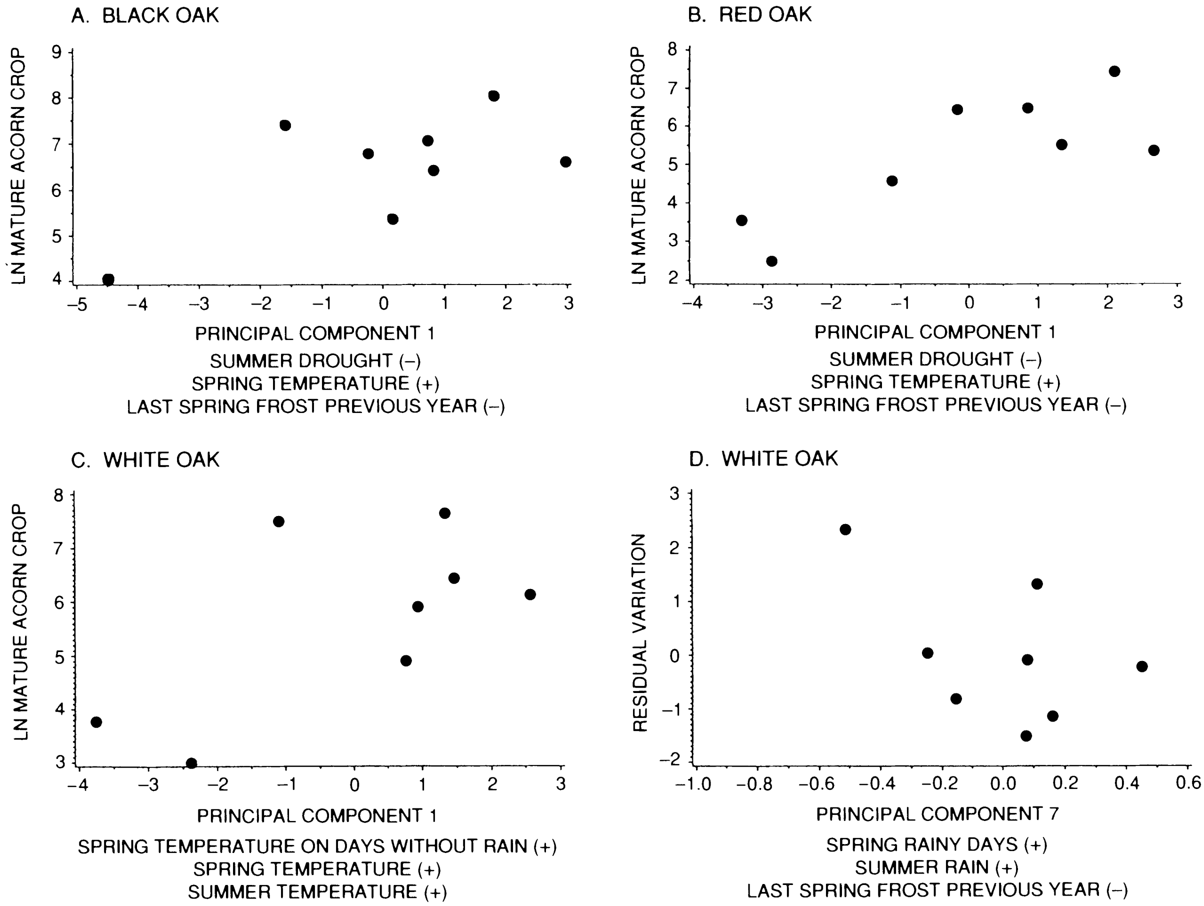

FIG. 3. Mean annual Mature Acorn Crop per tree (log transformed) plotted against the most significant principal component for each oak species. The three weather variables that are highly correlated with this principal component are given beneath each graph, with the sign of the correlation. (A) Black oak: $r = 0.552$, df $= 1,6$, $F = 7.4$, $P < .05$. (B) Red oak: $r = 0.894$, df $= 1,6$, $F = 50.5$, $P < .001$). (C, D) White oak, the first principal component and its residual variation plotted against the seventh principal component: overall model $R^2 = 0.771$, df $= 1,6$, $F = 8.4$, $P < .05$.

Biologically, this result implies one or more of the following relationships: (1) that the warmer the spring temperature during time when ovule maturation and fertilization takes place, the larger the size of mature acorn production; (2) the latter the date of spring frost during spring when anthesis occurs, the lower the viable acorn production; (3) the greater the summer drought, the lower the viable acorn production. Of course, it is important to point out that because the variables are correlated with each other, it is difficult to select the single weather variable that is most important; indeed, all could be contributing to the observed pattern.

For red oak, the first principal component was also the best predictor of viable acorn production (Fig. 3B; $R^2 = 0.89$, $P < .05$). Again, while it is not possible to identify which weather variable is most responsible, it is striking that this composite weather variable accounts for nearly 90% of the variation in mature acorn production.

In white oak, the impact of weather is a little more complex (Fig. 3C, D). Principal component 1 explained the largest portion of variation but only accounted for 39% of the variation in Mature Acorn Crop size and was not significant. The regression model of Mature Acorn Crop that was significant included principal components 1 and 7 ($R^2 = 0.77$, df $= 2,5$, $F = 8.42$, $P < .05$). The variables that were most highly associated with these two principal components are listed on Fig. 3C, D. Three of these variables are associated with spring: mean daily maximum spring temperature, mean daily maximum spring temperature on days without rain, and number of spring days with rain. Other variables that loaded high with these principal components can be seen in Appendix B. Similar to that of black and red oak, white oak acorn production appears to be positively influenced by spring temperature.

To examine how single weather variables were associated with the developmental stages of flower initiation to mature acorn, we included the correlation

TABLE 5. Pearson correlation coefficients calculated between mean Mature Acorn Crop size (natural log transformed) for black oak (B), red oak (R), and white oak (W) acorn crops produced during 1981–1988 and single weather variables associated with different stages of flower and fruit development during the seasons of reproductive development. Weather

		Weather variables			
		Temperature			Rainfall
Season‡	Fruit stage	B	R	W	B
Summer −2	Flower initiation§	0.148	0.330	NA	−0.530
Winter −1		−0.426	−0.106	NA	···
Spring −1	Pollination§	0.652†	0.543	NA	···
Summer −1		−0.148	0.339	0.124	0.331
Winter 0		0.089	−0.347	−0.261	···
Spring 0	Ovule dev., fert. (poll.‖)	0.803*	0.884**	0.743*	−0.499
Summer 0	Acorn development	0.529	0.577	0.303	0.138
Autumn 0	Acorn fall	···	···	···	···

† $P < .10$; * $P < .05$; ** $P < .01$.

‡ Numbers associated with season indicate the number of years prior a given acorn crop that the variable was lagged (see Table 1). The year of acorn maturation is considered year 0.

§ Red and black oak only.

‖ White oak only.

coefficients for all three species (Table 5). Although we recognize that this approach can result in spurious correlations, it is interesting that spring temperature during the year of acorn development (Spring 0) was highly significant for all three species in spite of the fact that they have different bumper crop years and different lengths of acorn development. The three species also showed a negative correlation between summer drought and mature crop size (Table 5). The series of correlations also point to some potential differences among species. In red oak, the variables of rainfall and summer drought at the time of flower initiation (Summer −2) were significantly correlated with Mature Acorn Crop size. However, the strong correlations between these two weather variables and spring temperature ($r = -0.90$, $P = .002$; $r = 0.67$, $P = .07$, respectively) complicate interpretation of which variables might be causal.

Masting and resource allocation

The data showed that current acorn production was negatively correlated with prior acorn production but in a different pattern for each species (Fig. 4). In black oak, there was a significant positive correlation between the size of the acorn crop 2 yr prior, and current acorn production (Fig. 4). In addition, there was a highly significant negative correlation with the size of the acorn crop 3 yr prior (Fig. 4). Thus, it appears that the acorn crop during the fall prior to flower bud initiation has a negative impact on acorn production. In red oak, the most significant correlation was a negative one between current acorn production and acorn production 3 yr prior (Fig. 4). In addition, acorn production 1 and 2 yr prior was negatively correlated with current acorn production, while acorn production 4 yr prior was significantly positively correlated. In white oak, there was a significant positive correlation between current acorn production and acorn production 3 yr prior (Fig. 4), while all other correlations were significantly negative. Thus, for the 8 yr of crop sizes included in this study, the data suggest that black oak had a positive association between crop sizes every 2 yr, red oak had positive association between crops every 4 yr, and white oak had positive association between crop sizes every 3 yr.

To determine whether the lag effects described above could be caused by concurrent cycles of weather variables, we examined the autocorrelation of all weather variables in Table 1 for the period 1981–1988 with the variables 1 through 4 yr prior. Only 4 out of 48 correlations were significant. These were: Spring Rain Days lagged by 1 yr ($r = 0.89$, $n = 7$, $P < .01$); Late Spring Frost lagged by 2 yr ($r = -0.84$, $n = 6$, $P < .05$); May–September Drought lagged 2 yr ($r = -0.88$, $n = 6$, $P < .05$); Maximum April–July Temperature lagged 4 yr ($r = -0.99$, $n = 4$, $P < .01$); and April–July Drought lagged 4 yr ($r = 0.96$, $n = 4$, $P < .05$). It should be noted that these latter two variables are correlated with each other because the drought index includes temperature.

DISCUSSION

All three species showed year-to-year variation in acorn production, and individual trees within each population did so in a synchronous manner. These patterns are consistent with mast-fruiting. Of the three, red oak and white oak had larger indices of masting (CVS) than black oak. In contrast to community-wide synchrony found in other oak studies (Downs and McQuilken 1944, Burns et al. 1954, Beck 1977, Christisen and Kearby 1984), the three species in this study produced their bumper crops in different years. Silvertown (1980) suggested that the fact that different species do not share good and bad years proves that climatic conditions are not a primary determinant of seed production. However, it could also mean that each species masts in response to different weather cues. In this discussion, we will first address whether number data were recorded for 1979–1988. NA indicates the correlations for white oak that are not appropriate. Ellipses (· · ·) indicate variables that were not tested.

Weather variables							
Rainfall		Drought			Late spr. frost		
R	W	B	R	W	B	R	W
−0.923**	NA	0.597	0.800*	NA	· · ·	· · ·	NA
· · ·	NA	· · ·	· · ·	NA	· · ·	· · ·	NA
· · ·	NA	· · ·	· · ·	NA	−0.416	−0.803*	NA
0.059	0.183	−0.204	0.072	0.100	· · ·	· · ·	· · ·
· · ·	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·
−0.322	−0.228	· · ·	· · ·	· · ·	0.272	−0.218	−0.185
0.546	0.141	−0.665$^+$	−0.705$^+$	−0.627$^+$	· · ·	· · ·	· · ·
· · ·	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·

of flowers or flower and fruit survival are the proximate causes of acorn crop size, then discuss the role of weather, and finally examine whether acorn crop size during one season affects future acorn production. Our ultimate goal is to determine the extent to which all these factors contribute to patterns of mast-fruiting and whether mast-fruiting can be considered an evolved reproductive character.

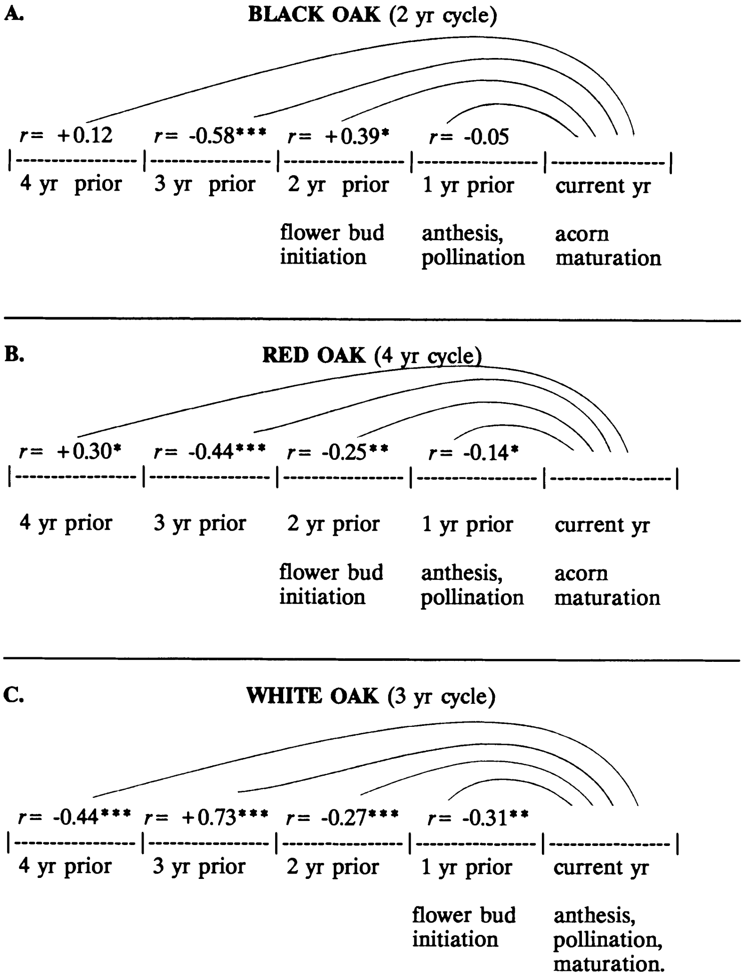

FIG. 4. Summary of mean autocorrelation values of current acorn production with prior acorn production. Major biological events occurring for each species are listed beneath the year of occurrence. The hypothesized cycle is listed in parentheses next to each species. Significant correlation coefficients are indicated as: * $P < .05$, ** $P < .01$, *** $P < .001$. See *Methods: Data analyses* for description of statistical analyses.

Proximate causes of mast-fruiting

There are contrasting ideas in the literature about whether the number of flowers (Feret et al. 1982) or the survival of those flowers to fruit (Williamson 1966, Farmer 1981) are the proximate causes of masting. Our data demonstrate that both number of flowers in spring and the survival of those flowers to fruit have a significant effect on crop size in all three species of oaks. However, the three species did not respond identically. Variation in mature acorn crop size for red and black oaks, the species with two season flower to fruit development, was explained largely by premature abscission of flowers during their final season of development. In white oak, the number of flowers initiated explained more of the variation in mature acorn crop than did flower survival. This result may reflect a fundamental difference in crop size regulation between the two subgenera.

The pattern of fruit abscission as indicated by the weekly seed trap collections showed that mast and nonmast years were dramatically different. Nonmast years, in contrast to mast years, are associated with a high premature abscission in late June and early July, a pattern also reported by Williamson (1966) and by Feret et al. (1982) in *Quercus alba.* This early period of abscission corresponds to the time during which fertilization takes place; thus, the premature abscission could be due to fertilization failure. Sometimes there is additional abscission (Shellburne 1983), which may reflect the abortion of excess fruit that the tree does not have the resources to mature (Lloyd 1980).

Role of weather in mast-fruiting

A major question we addressed in this study is the extent to which weather conditions contribute to mast-fruiting in these oak species. To answer this question we included a broad range of weather variables covering the critical periods in flower initiation and development and acorn maturation for the mature acorn crop size during 1981–1988. In all three species, we found that weather explained a large proportion of the variation in acorn production. In black oak and red oak, the first principal component accounted for 55 and 89% of the variation in mature acorn crop size, respectively. Three single weather variables were highly correlated with the first principal component: summer drought, spring temperature, and date of last spring frost during the previous year. For white oak, a significant regression model, which required two weather variables, principal component 1 and principal component 7, accounted for 77% of the variation in acorn production. These principal components also included several spring weather variables. Thus, we find that not only can weather factors explain the majority of year-to-year variation in crop size, but the models point to spring weather conditions as important.

When we look at the single variable correlations with acorn crop size, spring temperature during the season of fruit maturation (Spring 0) was significantly correlated with acorn crop size for all three species. This pattern again suggests that this factor might be a crucial one. This finding is consistent with those of Sharp and Chisman (1961) and Sharp and Sprague (1967), who report that spring temperatures are crucial to acorn production in white oak (*Q. alba*). In their work, they attribute the positive effect of spring temperature to its impact on pollen dehiscence and pollination success. However, because we found a positive effect of spring temperature for black and red oaks during the spring when fertilization but not pollination occurs, we suggest that spring temperature has a positive affect on ovule development and fertilization rather than pollination events. Of course, neither their study nor ours can identify causal mechanisms, but both concur that spring weather is a critical factor.

In contrast to our findings that the most important weather variables occur during the same year of acorn maturation, other studies have found that weather during previous seasons may be important. Long-term studies of beech nut production (Mathews 1955), seed production in loblolly pine (Wenger 1957), and cone crop size of Douglas-fir (van Vredenburch and la Bastide 1969) all report significant correlations with weather events 1 or 2 yr prior. These findings indicate that weather may affect flower initiation. Thus, it appears that weather has a significant impact on seed production for a range of species. In the three species of oaks we studied, the impact is through flower to fruit survival rather than through flower initiation.

Mast-fruiting as a reproductive character

The next crucial question to address is whether the synchronous production of large and small seed crops by a population of trees is solely due to the impact of weather or is an evolved reproductive character. We agree with Norton and Kelly (1988) that mast-fruiting should be considered more than a response to weather conditions if it can be shown that a large seed crop is due to resource allocation. Our data demonstrate that acorn crop size is negatively correlated with prior acorn production. Moreover, the fact that each of the species fits a different pattern provides further support that mast-fruiting is an evolved trait that has been acted upon through selection differently for each of the three species.

The pattern of masting that we observed showed strong tendencies for certain year intervals to have negative correlations with current acorn crop and other year intervals to have positive correlations. We believe the most likely interpretation for these correlations is that the negative correlations indicate that a large crop x years prior will have an inhibiting effect on crop size during the current year. We also suggest that the significant positive correlations between crop size y years prior with the current acorn crop indicate that these species may have inherent cycles of producing mast crops. This possibility is seen most clearly in red oak and white oak. In red oak, the data support the interpretation of a tendency to produce mast crops every 4 yr: there were significant negative correlations between current crop and acorn production 1, 2, and 3 yr prior but a positive correlation between current acorn crop and acorn production 4 yr prior. In white oak, the autocorrelation analyses support the hypothesis that this species is on a 3-yr cycle; we observed negative correlations between current acorn crop size and acorn production 1, 2, and 4 yr prior, but we also observed a positive correlation between current acorn crop size and acorn production 3 yr prior.

A potentially confounding effect in our analysis of mast-fruiting cycles is the observation that some weather variables also showed significant autocorrelations. We found four significant correlations. The interdependence of two of those results in only three significant independent correlations, one more than we would expect due to chance at the 5% level, given the number of correlations we examined. It is impossible to rule out the possibility that one of these factors truly is responsible for synchronizing the masting cycles of the oak species. Two points nevertheless support the hypothesis that mast cycles are inherent rather than externally induced. First, that the three species showed different cycles and different mast years indicates that weather alone is not the only factor. Second, none of the weather variables showed a significant 3-yr autocorrelation that could account for the 3-yr cycle of white oak. Thus, we have one species without an identified weather factor to account for its cycling. Additional years of data should clarify the contributing role of weather in mast cycles.

Comments on the interaction of weather and reproductive cycles

Having demonstrated that certain weather variables are correlated with copious acorn production and that these oak species have tendencies to produce large acorn crops at specific intervals, the question remains as to how these two factors interact. We consider both factors to be important. We suggest that each species has its own tendency to produce large acorn crops at certain intervals: black oak every 2 yr, red oak every 4 yr, and white oak every 3 yr. Perhaps it takes approximately that interval of time to store or restore the resources needed for the next big acorn crop. However, because the trees are influenced by weather conditions, we do not expect to observe perfect mast cycles at the population level. The ability of trees to either build up resources for future acorn production or recover from the depletion of energy due to the last acorn crop will be influenced by weather conditions. Once a flower crop is initiated, subsequent weather conditions may modify the size of the resulting acorn crop. Therefore, we propose that weather is a critical factor, but it acts on top of the inherent tendencies of each species to produce acorn crops at certain intervals.

This information about the importance of weather and the hypothesized mast cycles can be used to predict good acorn crops. As long as the critical weather variables are average to above average in what should be a mast year, one should be able to predict crop size based on the inherent pattern for a given species at a given site. Black oaks, which show the lowest masting index, would be easy to predict because they will probably produce a larger than average crop every other year. In red oaks, one should expect a large acorn crop every 4 yr. White oaks have the tendency to produce a good acorn crop every 3 yr. Using these predictions, we anticipated bumper crop years for red oak in 1989 and white oak in 1991 with low intervening years. Indeed, these predictions were met (V. L. Sork, *unpublished data*).

In conclusion, the year-to-year variation we observe in these and probably other species of oaks is clearly more than a response to weather conditions. Although weather conditions influence acorn production, these species' inherent tendencies to produce bumper crops in different cycles support the notion that selection has favored the evolution of masting. Future work needs to address why masting has evolved in some oak species (see Sork, *in press*).

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APPENDIX A

Correlation coefficients of 17 weather variables with the first seven principal components (PCs) used in regression model for black oak and red oak. Eigenvalues and proportion of variation explained for each principal component are also given.

Variable*	PC1	PC2	PC3	PC4	PC5	PC6	PC7
SPRTEM	0.383	−0.152	−0.023	−0.063	−0.013	0.111	0.663
SPRTEMNR	0.307	0.200	0.253	−0.024	−0.116	−0.463	−0.239
SPRTEM(−1)	−0.147	0.023	−0.504	−0.166	−0.142	0.177	−0.117
SPRRAIN	−0.145	0.125	−0.279	0.515	−0.032	−0.029	−0.097
SPRFROST	0.022	0.381	0.026	−0.392	0.093	0.380	0.094
SPRFROST(−1)	−0.345	0.104	0.234	0.161	0.063	−0.185	0.455
APJULTEM	0.231	−0.122	0.462	−0.080	−0.036	0.015	−0.200
MAYSEPTEM(−1)	0.096	−0.205	0.148	0.334	0.494	0.083	0.038
MAYSEPTEM(−2)	0.222	0.188	−0.329	0.072	0.240	−0.527	0.002
APJULRAIN	0.236	0.055	−0.066	0.479	0.157	0.448	−0.155
MAYSEPRN(−1)	0.160	0.422	−0.117	−0.180	0.206	0.047	0.091
MAYSEPRN(−2)	−0.353	0.291	0.098	0.023	0.022	−0.072	−0.120
APJULDRT	−0.385	−0.220	0.079	−0.115	−0.009	0.033	−0.107
MAYSEPDRT(−1)	−0.080	−0.432	−0.227	−0.006	−0.196	−0.196	0.211
MAYSEPDRT(−2)	0.308	−0.164	−0.037	0.014	−0.443	0.111	−0.223
WINCOLD	−0.133	0.219	0.316	0.261	−0.367	−0.130	0.125
WINCOLD(−1)	−0.110	−0.310	0.088	−0.235	0.461	0.031	−0.233
Eigenvalue	5.159	3.748	3.000	2.237	1.944	0.596	0.317
Proportion	0.303	0.220	0.176	0.132	0.114	0.035	0.019

* See Table 1 for definitions of abbreviations.

APPENDIX B

Pearson correlation coefficients of 12 weather variables with the first seven principal components (PCs) used in regression model for white oak. Eigenvalues and proportion of variation explained for each prinicipal component are also given.

Variable*	PC1	PC2	PC3	PC4	PC5	PC6	PC7
SPRTEM	0.416	0.183	0.175	−0.205	0.254	0.335	−0.052
SPRTEMNR	0.474	0.007	0.097	−0.175	0.181	0.344	0.157
SPRRDAYS	−0.346	−0.070	0.420	−0.143	−0.104	−0.181	0.457
SPRRAIN	−0.376	−0.089	0.374	0.035	0.280	0.147	−0.278
SPRFROST	−0.148	0.456	−0.283	−0.159	0.154	0.305	−0.389
APJULTEM	0.399	0.073	−0.141	0.416	−0.137	−0.388	0.243
MAYSEPTEM(−1)	0.203	−0.079	0.380	0.272	−0.623	0.274	−0.348
APJULRN	0.047	0.192	0.555	0.230	0.067	0.081	0.447
MAYSEPRN(−1)	−0.161	0.523	0.016	−0.236	−0.077	0.026	0.294
APJULDRT	−0.184	−0.432	−0.254	−0.009	−0.310	0.538	0.253
MAYSEPDRT(−1)	0.169	−0.486	0.041	−0.311	0.248	−0.084	0.061
WINCOLD	−0.169	0.031	−0.159	0.654	0.463	0.305	−0.005
Eigenvalue	3.868	2.911	2.493	1.466	0.808	0.244	0.152
Proportion	0.322	0.243	0.208	0.122	0.067	0.020	0.013

* See Table 1 for definitions of abbreviations.