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Original article

Prediction of acorn crops in three species of North American oaks: *Quercus alba, Q rubra* and *Q velutina*

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Summary — Many oak species show tremendous year-to-year variation in acorn production. Is this variation completely random or is there some predictable pattern? Using an 8-year data set of individual trees from 3 species of oaks in central-eastern Missouri, we evaluated the patterns of acorn production in order to identify critical external and internal factors. Our results showed that flower counts can be used to predict small acorn crop size but high flower counts do not always predict large acorn crops. In addition, we found that each species differed in the length of the interval between large acorn crops and that acorn crop size was influenced by spring temperature and summer drought. Thus, the combination of physiological constraints, reflected by intermast interval, and key weather factors can be used to predict future acorn crop size.

***Quercus alba* / *Q rubra* / *Q velutina* / mast-fruiting / acorn production**

Résumé — Prédiction de la fructification chez 3 chênes américains : *Quercus alba, Q rubra, Q velutina.* *De nombreux chênes manifestent de très grandes irrégularités annuelles de fructification. Quelle est la nature de ces variations : est-elle purement aléatoire, ou peut-elle être prédite ? La glandée a été observée au niveau d'arbres individuels appartenant à 3 espèces différentes pendant 8 années successives au centre-est de l'État du Missouri de manière à identifier les facteurs critiques internes et externes intervenant dans la glandée. Quand la floraison est faible, la glandée peut être prédite à partir du comptage des fleurs; par contre, les floraisons importantes ne sont pas corrélées à des fructifications élevées. Des différences spécifiques ont été observées dans le délai (nombre d'années) séparant 2 glandées importantes. Le niveau de fructification dépend des températures printanières et de la sécheresse estivale. En conclusion, les contraintes physiologiques, révélées par les délais entre fructifications élévées, et les facteurs climatiques peuvent être utilisés pour prédire le niveau des fructifications.*

Quercus alba / Q rubra / Q velutina / *fructification massive / production de graines*

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INTRODUCTION

It has commonly been observed that many oak species do not produce good acorn crops every year (*eg* Carmen *et al,* 1987; Christisen and Kearby, 1984). While some species of oaks, usually the smaller-seeded ones (Sork, in press), produce at least some acorns almost every year, other species produce acorn crops much more intermittently. In order to assess future acorn availability for wildlife or for seed collections for tree seedling nurseries, it would be advantageous to be able to predict when good acorn crops will occur. This communication presents our recommendations on how to predict acorn crops in 3 Missouri oad species, white oak (*Quercus alba* L), northern red oak (*Q rubra)* and black oak *(Q velutina).* We summarize herein the results of a prior study that examined internal and external factors which influence the size of acorn crops in these 3 species (Sork *et al,* in press) and we present additional results to illustrate the biology of flowering and fruiting in oaks.

Ecologists often call the phenomenon of producing good crops some years and poor crops in other years, mast-seeding or mast-fruiting (Janzen, 1971; Silvertown, 1980). A year of good acorn production is called a mast-year. Because the size of a flower crop constrains the size of the acorn crop, it is critical to evaluate the extent to which flower availability determines acorn crop size. A second potentially important factor in acorn production is the role of weather conditions. Several studies have suggested or demonstrated that weather has strong impact (Goodrum *et al,* 1971; Minima, 1954; Romashov, 1957; Sharp and Chisman, 1961; Sharp and Sprague, 1967). A third factor is the impact of prior acorn production on the resource availability for current acorn crop size. It is possible that production of a large acorn crop depletes the resources of a tree so that it is unable to produce another crop for several years (Koslowski, 1971). For tree species which show a mast-fruiting pattern, a specific length of time between mast crops may be inherent.

MATERIALS AND METHODS

The study site (38° 31' N, 90° 33' W) was Tyson Research Center, an ecological preserve administered by Washington University, located near Eureka, St Louis Co, Missouri. This area is situated on the unglaciated northeastern end of the Ozark plateau and is described in detail in Sork *et al* (in press). The study species belong to 2 different subgenera of oaks. White oak (*Quercus alba* L) belongs to the subgenus *Quereus* while black and northern red oak (*Q velutina* Lam, and *Q rubra* L) belong to the subgenus *Erythrobalanus.* The floral biology of these species is described elsewhere (Minima, 1954; Romashov, 1957; Sork *et al,* in press).

Since 1981, we have been monitoring flower and acorn production in 12-15 individual trees of each species (DBH range = 28,5–57,5 cm, Sork *et al,* in press). To estimates total crop size, we placed 8 0.5-m cone-shaped acorn-collecting traps (see Christisen and Kearby,1984) beneath the canopy of each tree so that they were scattered throughout the canopy but not beneath the canopy of neighboring conspecifics. The total trap area sampled was on average ca 7.5% of the canopy (range: 4–19%). Collections were made on a weekly basis. We opened all the acorns to determine whether they were immature or mature and infested, maldeveloped (unsound) or apparently viable. Our estimates of total crop size are based on the number of mature acorns produced by the entire canopy of a tree as a function of the percentage of the canopy sampled by our collection traps.

In early May and late August of each year, we counted the density of flowers on the outer 75 cm of 5 upper canopy branches/tree by means of a truck with a hydraulically-raised bucket. During the late August sample, we also measured the length of vegetative growth branch for that year.

To address the question of how weather affects acorn crop size, we used minimum temperature, maximum temperature and precipitation which were recorded daily at Tyson Research Center. We used these data to calculate weather variables corresponding to different seasons to identify the critical weather factors (See Sork *et al*, in press, for more complex statistical analysis using principal components and stepwise regressions.)

To evaluate the impact of prior acorn production on crop size for the 3 species, we performed an autocorrelation analysis of mature acorn crop size with acorn crop size 1, 2, 3, 4 years earlier, separately for each individual study tree of each species. For example, to evaluate the 1 year lag autocorrelation, we correlated a tree's acorn crop size for a given year with the acorn crop size 1 year earlier for 8 years of the study. Thus, the autocorrelation for 1 year is based on 7 observations, for 2 years it is based on 6 observations, etc. Then, for the entire population we calculated the average correlation coefficient and used a *t*-test to see whether it was significantly different from zero.

As additional evidence for the hypothesis that acorn crop size is related to resource availability, we evaluated whether the acorn density on upper canopy branches correlated with the vegetative growth on those same branches. If resources are limiting and the tree must partition its energy into sexual *versus* vegetative reproduction, one might expect an inverse relationship between these 2 variables.

RESULTS AND DISCUSSION

Our observations from 1981 to 1988 showed that acorn crop sizes differed dramatically across years and among the 3 species (fig 1). Black oak was the most consistent acorn producer: in almost every year except 1983 and 1984, each study tree produced a moderate (> 500 to > 1000) number of mature acorns. During that same interval, northern red oak had one large crop and two moderate crops, while white oak had two large crops and one moderate crop. Statistical tests revealed that acorn production was synchro-

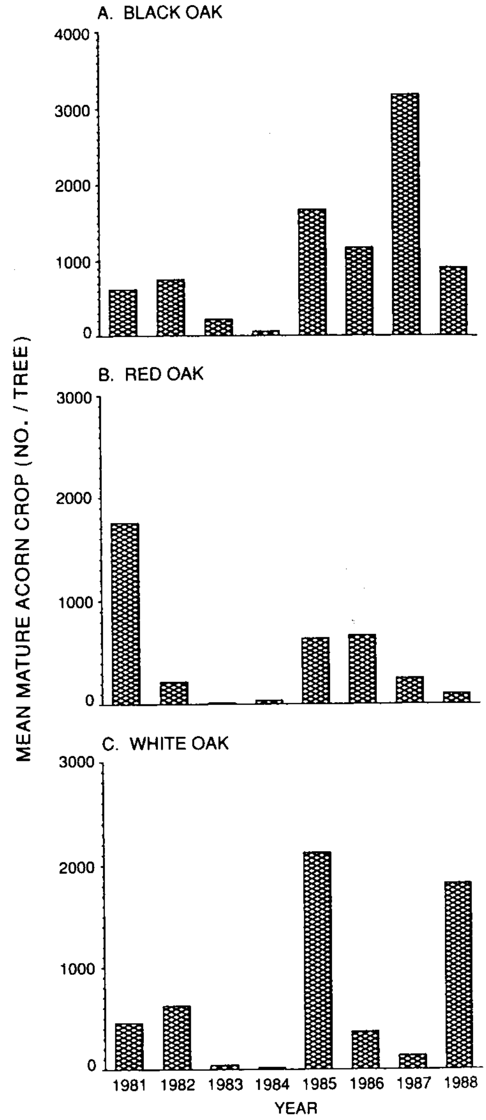

Fig 1. Annual mean mature acorn production for black (n = 13), red (n = 12) and white oak (n = 15) sampled at Tyson Research Center, St Louis Co, Missouri, from 1981 to 1988. Values are estimates of total acorn crop size based on acorn traps placed beneath a portion of the canopy (Figure taken from Sork *et al*, in press).

nous within a species (Sork *et al,* in press). Thus, a good year for one tree was generally a good year for all trees of that species at that study site. The 3 species shared the same bad years but they did not produce their mast crops during the same years (fig 1).

How important is the flower crop?

The data we obtained by monitoring flower initiation and survival in the upper canopy demonstrate that the initial size of the flower crop is a major determinant of acorn crop size (see table I). For each species,

Table I. Mean number of flowers/upper canopy branch at the time of anthesis (May), mean number of mature acorns/branch (August) percent flower-to-mature-acorn/branch (August), percent flower-to-mature-acorn survival and mean density of acorns in ground seed-traps/m^2 for black oak, northern red oak and white oak from 1981 to 1983. Outer 75 cm of 5 branches/tree and 4–5 trees/species were sampled. During 1981, only white oak was sampled. During 1984, no canopy observations were made for any species. na: data not available; – cannot be calculated.

Species	*Acorn crop year*	*Upper canopy branch observations* [a] *n flowers in May*	 *n acorns in August*	 *% flowers survival*	*Ground-trapped acorns (n/m^2)*
Black oak [b]	1982	na	16.1	–	14.3
	1983	11.0	3.3	30.0	3.8
	1984	33.2	na	–	1.1
	1985	na	14.4	–	29.2
	1986	41.5	24.6	59.3	21.1
	1987	77.9	24.4	44.2	53.2
	1988	31.5	12.5	39.7	16.7
Red oak [b]	1982	9.8	0.9	9.2	2.7
	1983	13.4	0.0	0.0	0.2
	1984	83.6	na	–	0.7
	1985	na	5.8	–	11.6
	1986	76.3	14.2	18.7	12.8
	1987	52.3	3.8	7.3	4.8
	1988	27.8	1.1	4.0	2.0
White oak	1981	72.1	9.5	13.2	8.1
	1982	64.0	10.3	16.1	11.8
	1983	24.1	2.2	9.1	0.7
	1984	na	na	–	0.3
	1985	71.7	35.4	49.4	37.0
	1986	39.9	14.2	35.6	6.3
	1987	28.7	9.7	33.8	2.2
	1988	57.0	24.1	42.3	31.9

[a] Data are standardized to *n* / 75 cm of outer branch. [b] Flower observations were made in May of the year prior to acorn maturation.

the correlation between flowers and mature acorns branch was relatively high (black oak: $r = 0.964$, $n = 5$, $P < 0.05$; northern red oak: $r = 0.914$, $n = 5$, $P < 0.05$; white oak: $r = 0.574$, $n = 7$, $P < 0.20$). However, it is also clear that sometimes flower availability is high but the acorn crop size is low (*eg,* black oak and northern red oak in 1984 and white oak in 1981). Thus, survival of those flowers through acorn maturation is a critical variable. In fact, for northern red oak and white oak, branch acorn density was significantly correlated with flower survival (red oak: $r = 0.905$, $n = 5$, $P < 0.05$; white oak: $r = 0.869$, $n = 7$, $P < 0.05$). In sum, low flower counts in spring can reliably predict small acorn crop sizes but high flower counts do not necessarily indicate a large acorn crop.

Impact of weather on acorn production

In a separate paper, the principal-component and single-variable analyses revealed that spring weather variables were important for all 3 species (Sork *et al,* in press). Moreover, the single weather variable that consistently showed the highest correlation coefficients for each oak species was spring temperature during the year of acorn maturation (fig 2). The higher the average maximum temperature during the last 2 weeks of April and the 1 week of May, the greater the number of mature acorns (see Sork *et al,* in press). For all 3 species, this is the period when ovules are maturing and the pollen is growing (Minima, 1954; Romashov, 1957). In white oak, it is also the time when pollination occurs.

The other weather variable that showed relatively high correlation coefficients across the 3 species is summer drought. This variable combines temperature and rainfall (Sork *et al,* in press) and was consistently negatively correlated with acorn production (black oak: $r = -0.665$, $n = 8$, $P < 0.10$; northern red oak: $r = -0.705$, $n = 8$, $P < 0.10$; white oak: $r = -0.627$, $n = 8$, $P < 0.10$). The 2 worst years for acorn production (1983 and 1984) were associated with high levels of drought. It is possible that drought may not be linearly associated with crop size, but may act at some critical level of stress to influence early fruit abscission. More years of data are necessary to further evaluate this hypothesis.

Late spring frost has been hypothesized as a possible limitation on acorn crop size due to frost damage to flowers (Minima, 1954). Northern red oak was the only species which had a significant negative correlation between late spring frost during the year of flower anthesis and acorn crop size ($r = -0.803$, $n = 8$, $P < 0.05$). Of the 3 species, northern red oak is usually the first species to break bud and therefore may be more vulnerable to a late spring frost.

Thus even though these 3 species of North American oaks had different patterns of acorn production across the 8 year sampling period, they showed similar patterns of correlation with weather variables. High spring temperature and low summer drought may both be useful in predicting large acorn crops for these species. For northern red oak in Missouri, late spring frost can have an additional negative impact on acorn crop size.

Impact of prior acorn production

Our final analysis examined the impact of prior acorn production on acorn crop size in order to evaluate whether there are physiological limitations preventing each species from producing good acorn crops every year. The pattern of annual variation in mean crop size demonstrates that each species differs in its degree of fluctuation (fig 1). The autocorelation of individual

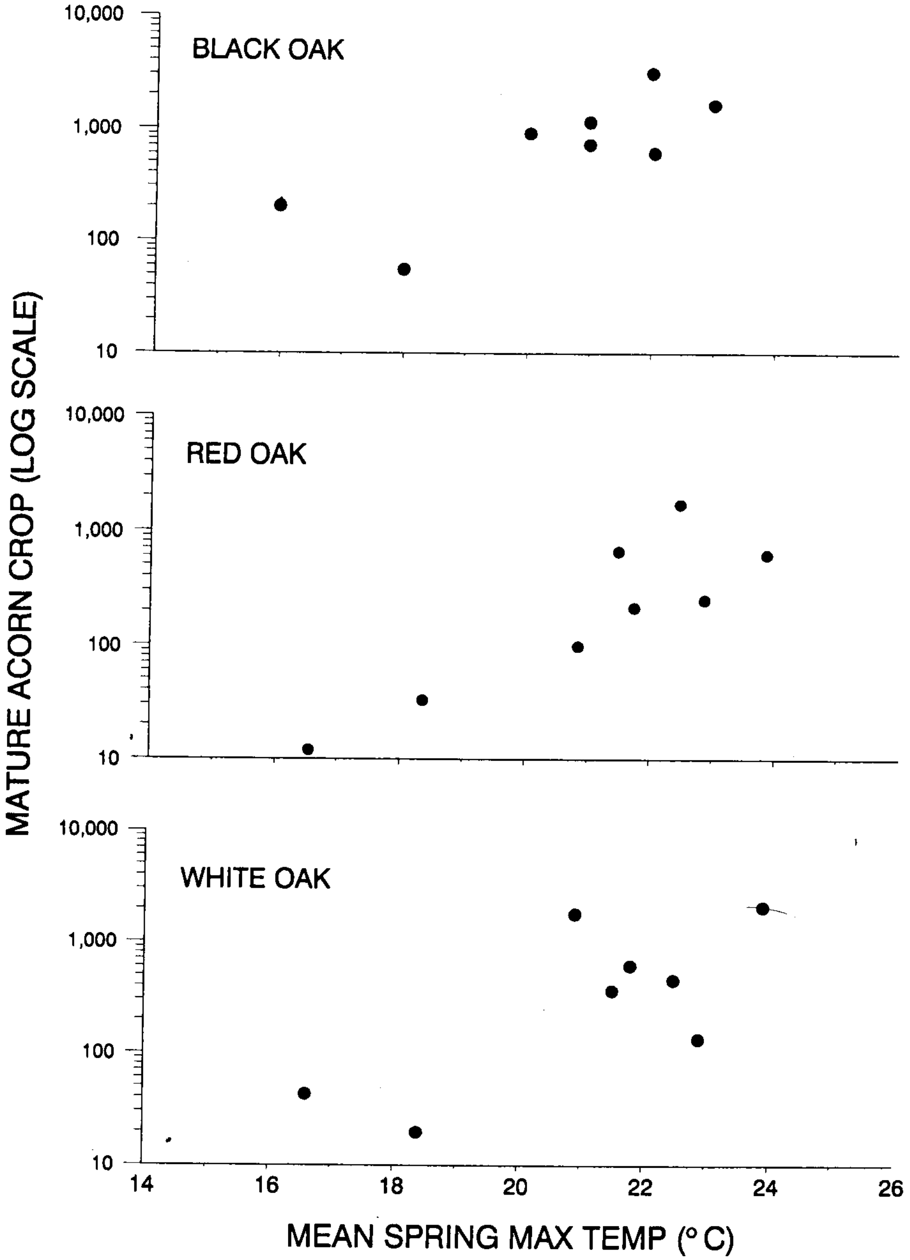

Fig 2. Maximum spring temperature during spring of ovule development and fertilization plotted against mean mature acorn crop size for black oak, northern red oak and white oak during 1981–1988. Black oak: $r = 0.803$, $P < 0.05$; northern red oak: $r = 0.884$, $P < 0.01$; white oak: $r = 0.743$, $P < 0.05$.

trees with prior acorn production showed that all 3 species displayed significant negative correlations with prior acorn production (table II). This suggests that prior acorn production does influence crop size. However, the species differed in their respective patterns. For example, northern red oak showed a negative correlation for crops produced 2 and 3 years earlier, while white oak showed a negative correlation for crops produced 2 and 4 years earlier (table II). We interpret the negative correlations as reflecting physiological constraints on the length of time each species requires to accumulate sufficient resources to produce another large acorn crop, and hypothesize that intervals of positive correlation correspond to an internal cycle of mast years for each species.

If resource availability is a limiting factor in acorn production, then we might expect that, during a mast year, resources should be allocated to sexual rather than vegetative reproduction. In fact, it is likely that developing acorns are a strong sink for photosynthate. This hypothesis is supported by an inverse relationship between vegetative growth and mature acorn density. The data suggest such a relationship for black and northern red oak (fig 3). In white oak, for which we have only 4 years of observations, no relationship is apparent. While the data are suggestive, more years will be needed to statistically evaluate whether these oak species partition energy into either reproductive or vegetative growth.

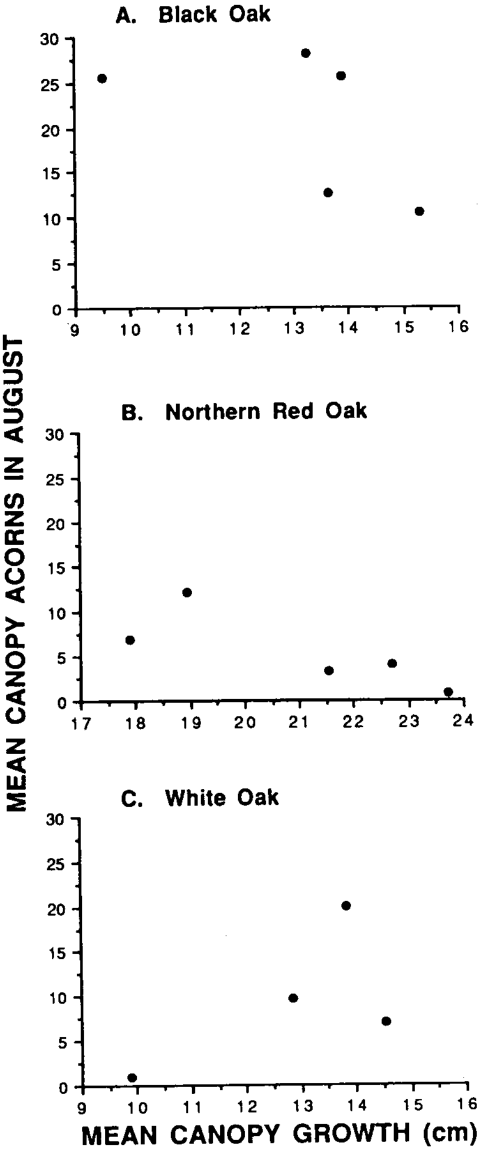

Fig 3. Plot of mean number of mature acorns in August/upper canopy branch/tree/year *versus* length of new vegetative growth during same year for black oak, northern red oak and white oak. Five branches/tree and 5 trees year/species were sampled.

CONCLUSIONS

This intensive study on one Missouri forest stand suggests that acorn production is influenced by both weather conditions and a species-specific inherent cycle of acorn production. Flower availablility and flower

Table II. Summary of mean autocorrelation values of current acorn production with prior acorn production. The hypothesized cycle for frequency of mast years is listed for each species. See text for description of statistical analyses (Results taken from Sork *et al*, in press)

Species	*Correlation coefficient with prior acorn production*				*Hypothesized cycle*
	4-yr prior	*3-yr prior*	*2-yr prior*	*1-yr prior*	
Black oak	+0.12	–0.58[b]	+0.39[a]	–0.05	2 yr
Northern red oak	+0.30[a]	–0.44[c]	–0.25[b]	–0.14	4 yr
White oak	–0.44[c]	+0.73[c]	–0.27[c]	–0.31	3 yr

[a] $P < 0.05$; [b] $P < 0.01$; [c] $P < 0.001$.

survival determine acorn crop size. But the physiological constraints of the tree determine when a mast crop can occur and weather influences the final crop size. Severe weather conditions may completely alter a tree's physiological state. Because populations of trees produce large crops synchronously, the length of the intermast interval is probably similar among trees within a population. However, this inherent cycle within a species may differ across regions. Consequently, it is important to understand the reproductive biology of the local species in order to make accurate predictions about patterns of acorn production.

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