MODEL OF WHITE OAK FLOWER SURVIVAL AND MATURATION

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Abstract: A stochastic model of oak flower dynamics is presented that integrates a number of factors which appear to affect the oak pistillate flower development process. The factors are modeled such that the distribution of the predicted flower populations could have come from the same distribution as the observed flower populations. Factors included in the model are; the range of peak crop intervals, relative humidity in the pollination period (Wolgast 1972), number of severe storms (Cecich 1997), tree hopper (Kopp and Yonke 1973a, 1973b) and acorn weevil population (Gibson 1964), genetic factors related to the fertilization process, and summer drought (Sork and Bramble 1993).

We propose this probabilistic model as a research tool to explore how the included factors affect acorn production. Because the model uses distributions similar to those obtained from bootstrap analysis of the observed data, realizations of the model are generated using a stochastic modeling methodology and then summarized for presentation. With this methodology, the output will be drawn from the distributions similar to the original data and fit statistics are relatively meaningless.

INTRODUCTION

Flower development in oak trees is the defining process in determining the abundance of the acorn crop in a particular year. A large amount of research has been conducted on insect damage to developing acorns (Kearby and others 1986), relatively less attention has been focused on the size of the flower crop and the steps in the pollination and maturation process that may limit acorn crop size (Cecich 1993). Only a few studies have monitored annual oak flower production over a long time frame (Sharp and Sprague 1967; Sork and others 1993; Sork and Bramble 1993; Koenig and others 1994, 1996). Of these, Koenig's study is 16 years long, Sharp and Sprague's study extended 11 years, and Sork's data set covers 9 years. Only Koenig's study and the data used in this study are continuing to collect data. These studies and others indicate that the process of oak flower development is highly stochastic and influenced by both tree specific flower production, average climatic trends, specific weather events and insect populations. Because the process is highly variable and only one observation is added annually, we developed a model of the hypothesized processes to explore its consequences. Correlation analysis indicated a number of factors that are negatively correlated with abundance of oak flower crops at various times (Sork and Bramble 1993, Cecich 1997). Our model describes how these factors affect overall oak flower abundance and tests the predictions against empirical data.

Because the various species of oak have a variety of phenologies, white oak (*Quercus alba* L.) was chosen for the initial model building process. White oak completes the flower to acorn cycle within a single year, an advantage for developing this model. Additionally, our sample dataset contains a number of white oak trees that vary in flower populations and acorn crop sizes.

In this paper, we present a model of the white oak flower development process as four major steps: size of the pre-pollination flower population, May and June survival, June and July survival, and the July and September survival. The hypothesized distribution of flower survival reflects the distribution of observed flower survival in the original sample. These hypothesized distributions are modeled as a function of the dominant factors that can affect flower survival, as identified by the authors above.

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The model is designed with two key considerations: (1) it must accurately reflect the distributions in the observed data and (2) it must provide a flexible method of evaluating alternative hypotheses affecting those distributions. The model follows the general form of first generating a hypothetical population of white oak flowers at the start of the pollination period. Then the survival of oak flowers is predicted for each of three time periods, May-June, June-July, July-September. The survival in each of these periods is influenced by a variety of factors that can reduce the population of oak flowers. The proposed causes of oak flower survival are not an exhaustive list of causes, just those that reflect the author's view of the oak flower survival and maturation process. Figure 1 diagrams the components of the model and the factors that effect each.

$$n_t = \left(\left(\left(\beta(v,w) \cdot \max \right) \cdot \frac{\sum p_i}{n_{p_i}} \right) \cdot \sqrt[n_{p_j}]{\prod p_j} \right) \cdot \frac{n}{\sum \frac{1}{p_k}}$$

where n_t is the number of oak flowers that will survive and mature into acorns in September for that year, $\beta(v,w)$ is a beta distribution with parameters v and w which describe the shape of the beta distribution. If the parameters are the same value the distribution is symmetrical, as the values increase kurtosis increases and as the w increases relative to v the distribution skews to the left. The values generated are between 0 and 1. The constant max in the maximum potential flower crop per tree sample. Variable p_i, p_j and p_k are the proportional reduction by the various factors in the model at times i, j, k, which correspond to May-June, June-July, and July-September time periods. While this model seems quite complicated it is really quite simple, we will describe each part separately to clarify the purpose of each component.

The model must first generate an oak flower population for the year at the start of the pollination period. We chose to start at this point because the processes governing flower initiation are much less distinct and harder to quantify. The pollination period for the study data is typically a 1 week period in late April or early May. This period can vary by a week earlier in some years and a week later in other years. The number of flowers for a particular year varies greatly but tends to have a cyclic pattern. The probability of a large number of white oak flowers in a year decreases after a peak year. The probability increases as the number of years after a peak year increase. This relationship is described by the following equations:

$$n = \beta(v,w) \cdot \max$$

In this equation, v, w are parameters of a beta distribution (β) and max is the maximum flower sample taken in manner of Cecich, (1997). The parameters $v = 3.0$ and $w = 9.0$ were used in this study as they approximate the distribution of initial flower populations determined from a bootstrap analysis of the observed data.

The second component of the model predicts the proportional reduction in the flower population given causes that happen within the period May-June. This period includes factors that affect the pollination process. We model three causes for flower reduction in the May-June period; pollination weather (relative amount of time below 60% relative humidity during the 1 week pollination period), favorable weather (1 - relative frequency of severe storms that cause flower damage (e.g, hail storms or sever winds)), 1 - (the relative number of tree hoppers (*Membracidae*)). All these measures are relative (values between 0 and 1) with 1 being a positive condition for oak flowers. For this component, the arithmetic mean of the three components produce the proportional reduction in the oak flower population. It was found that the original frequency distribution had little or no skewness and this mean reflects that property. The model is:

$$s_1 = \frac{1}{n} \sum_{i=1}^{n} p_i$$

where n is the number of factors being averaged (3 in this case) and p_i is the proportion remaining for each factor.

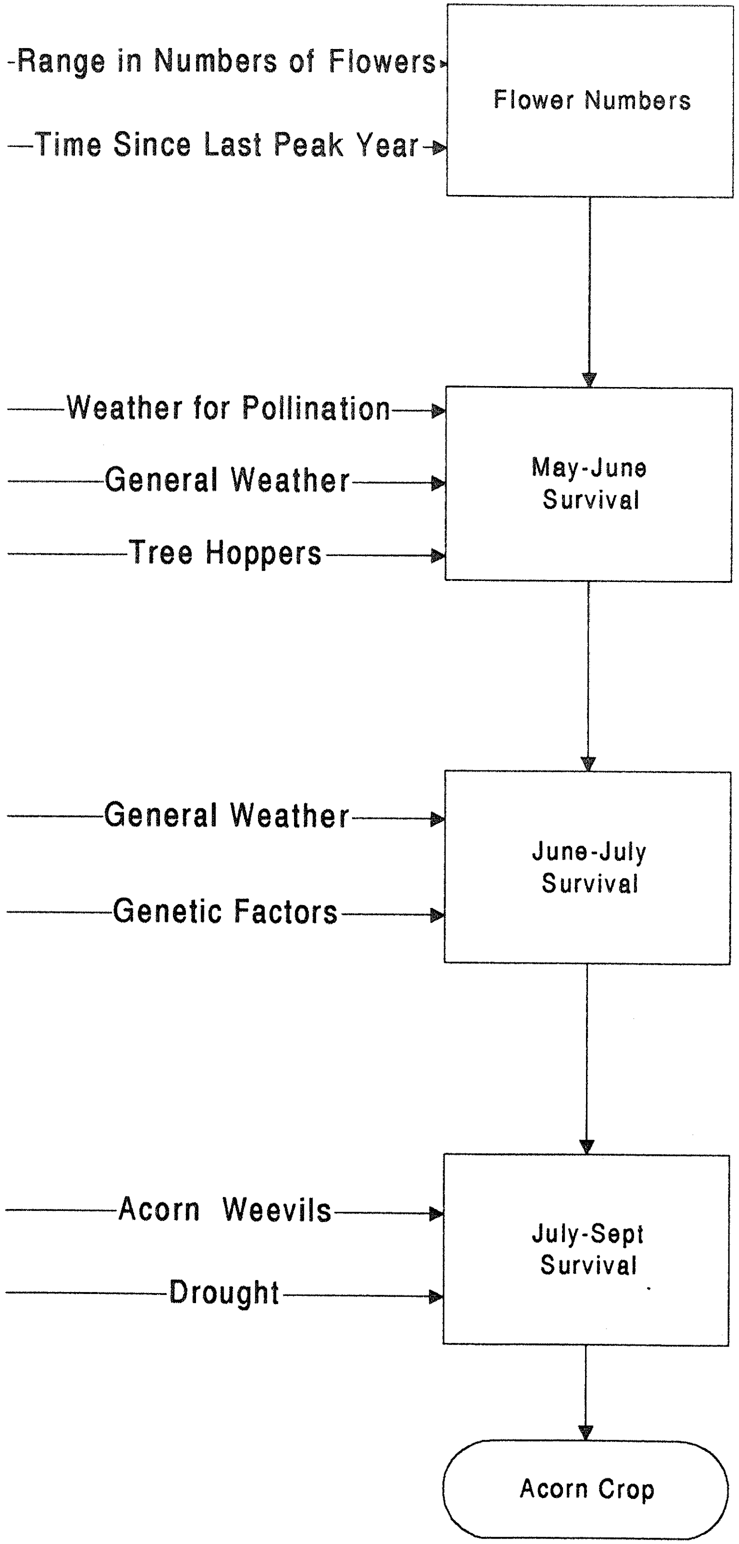

Figure 1. Diagram for the component of the oak flower development model and the factors affecting each component. The distributions in each box are constrained to produce distributions similar to those observed in Missouri white oaks over a 6 year period.

The third component of the model describes the June-July survival and is hypothesized to be driven by two factors; favorable weather in this period, and genetic factors relating to the fertilization process (Cecich, 1997). The favorable weather component is again 1 - (the relative frequency of severe storms that cause flower damage). Genetic factors relate to the success of the fertilization process. This is the period in which fertilization occurs and the growth and maturation of the acorn starts. Lethal gene combinations would disrupt the embryogenic process. These factors are combined by taking the geometric mean. This mean can be skewed to the left of the proportional range similar to the observed data at this time period. The equation is:

$$s_2 = \sqrt[n]{\prod_{j=1}^{n} p_j}$$

where n is the number of factors (2 in this case) and p_k is the proportion remaining for each factor.

The fourth component of the model described the survival of flowers/acorns from July to September and includes two traditional causes of acorn population reduction: acorn weevils and summer drought. Again, we changed these factors so that a value of 0 indicates poor survival for oak flowers/acorns and a value of 1 indicates the best survival of the flowers/acorns. In this component, the harmonic mean of the relative proportions is used to describe the survival as this produces a highly skewed distribution similar to the observed frequencies at this time period. The equation for the third component is as follows:

$$s_3 = \frac{n}{\sum \frac{1}{p_k}}$$

where n is the number of factors (2 in this case) and p_k is the proportion remaining for each factor.

These three type of means used in this study have the property that the harmonic mean ≤ geometric mean ≤ arithmetic mean. If the proportions are equal all three means have the same value otherwise each of the means is skewed to the left as indicated. In terms of the model, the negative effect of several factors is the arithmetic mean of the factors in the first component, with each successive component the mean negatively skewed relative to the arithmetic mean except in the case there the proportions are equal in which case the means are equal.

This model was calibrated using a data set fromnine white oak trees on the Baskett Wildlife Area in central Missouri. Each tree was sampled weekly through the flower development period April-June and then periodically for the remainder of the season. Five branch ends (the past 2 years) are sampled on each tree from the top and sides of the crown. These data were collected since 1990. The year 1996 was not included in the analysis as the data collection was not completed at the time of analysis. The data are summarized as average per tree values for all trees in the stand. A more complete description of this data can be found in this volume (Cecich 1997). The model used the tree sample as the unit of estimation.

RESULTS AND DISCUSSION

Because the model was built in components that matched the empirical observations, each component was designed to allow a varying number of input factors while maintaining the general distributions observed in the data set. The behavior of this model is constrained to the general range of the empirical data.

The model of flower populations is designed to be a highly stochastic. The estimated pattern is assumed to be the combination of two factors. Annual variation in the general weather pattern, such as sufficient moisture and the presence or absence of violent storms with the cyclic pattern is assumed to be due to the energy required to produce a large acorn crop provide the basis for the stochastic effects. Figure 2 illustrates the behavior of these equations for a 100 year period. This prediction assumed a average of 50 flowers per tree sample, and a maximum of 400 flowers per tree sample (an extremely good year).

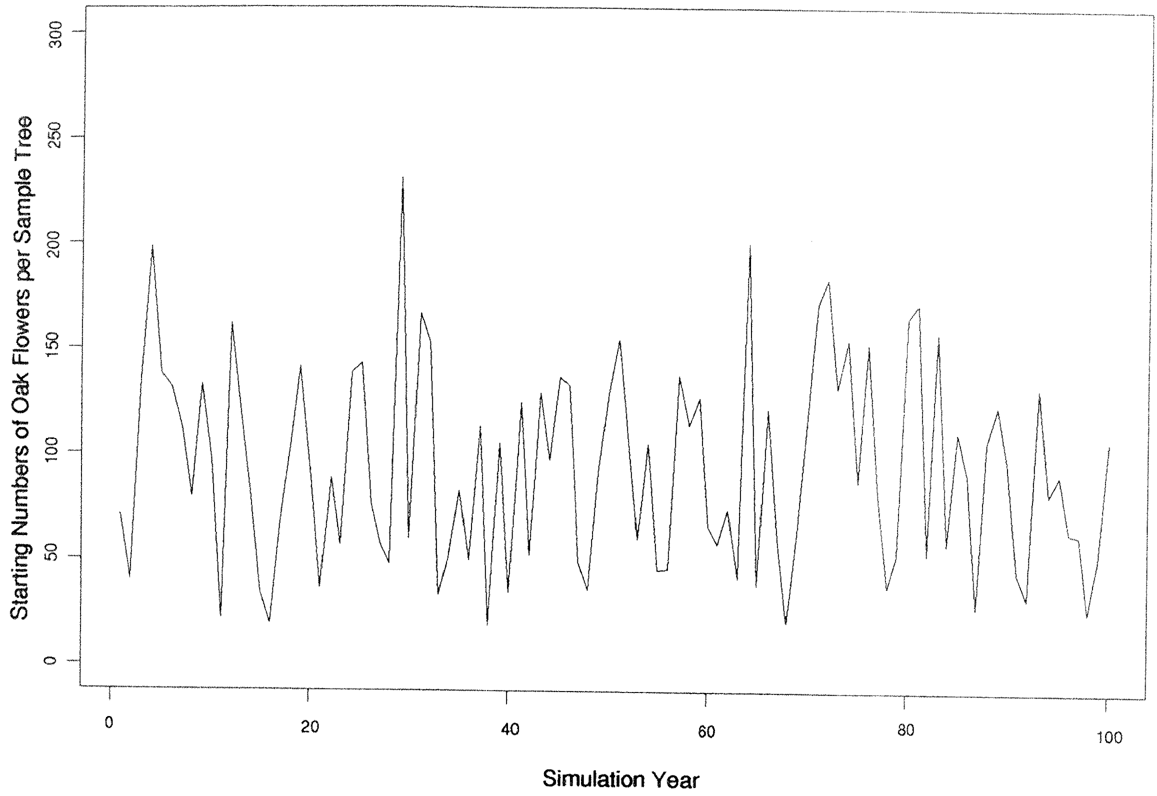

Figure 2. The predicted white oak flower population for a 100 year period using the parameters listed in the paper. The numbers on the y axis indicate the number of oak flowers per five samples of 2 year old branch units.

The values produced in this manner can be considered to come from the same population as the observed data, however, because the observed data is only for 6 years, it is difficult to say that this model completely describes the process. This method of modeling may not be familiar to many of the readers, the intent is to describe a distribution from which the observed data *could have come*. The true distribution will remain unknown until all possible white oak trees are measured for their entire life span. Additionally the distributional approach does not attempt to predict the exact number of flowers in a particular year as in deterministic models. Rather the intent is to describe the probable frequency distribution of possible outcomes over a long period of time.

The three mean components of the model produce proportional reductions to the flower population that parallel the observed distributions. Because the factors are considered independent, large reductions can occur in one period with very small reductions in the next period. On average in the first period oak flowers are reduced by 50%, the second period the remaining flowers are reduced by an additional 35% and the third period the remaining flowers are reduced by another 11%.

To illustrate the overall behavior of the model, 100 simulations were generated to illustrate the range of outcomes. Figure 3 summarizes these simulations with maximum and minimum lines as well as the average line for the simulations. The observed data is presented for reference. Note that in most years, only modest numbers of flowers are initiated, which are further reduced through the season. There are some years in which large numbers of oak flowers are initiated. In some of those years the flower populations are severely reduced and in other years they are not.

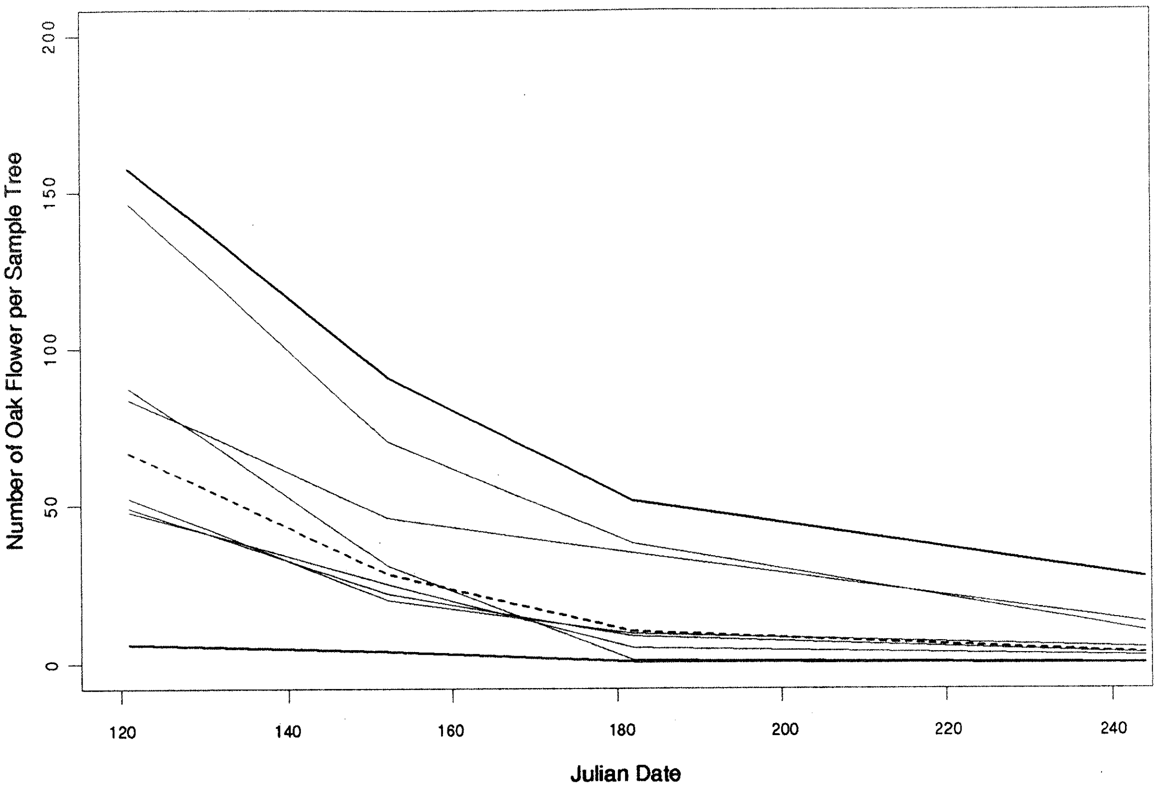

Figure 3. The predicted white oak acorn development process as illustrated by the model. 100 simulations are summarized as the maximum and minimum values (double weight solid lines), the smoothed average of the simulations (double weight dashed line) to illustrate the range of outcomes predicted by the model. The observed data is includes for reference (single weight solid lines). The numbers on the y axis indicate the number of oak flowers per five samples of 2 year old branch units.

CONCLUSION

The proposed model generates distributions of white oak flower populations through a growing season that have the similar distributions, at several intermediate points, to the observed data. These distributions incorporate factors suggested by others to effect changes in flower/acorn populations. While it is not possible to determine that this model is the "correct" characterization of the process, it is possible to use the model to explore the consequences of change in the included factors. If it is assumed to contain major factors affecting the process, the model becomes a useful tool to explore the limits of these factors in explaining the variations in white oak acorn crop production.

This model integrates background periodicity of the acorn production process, weather at specific periods in the pollination, fertilization and maturation process, and other factors that decrease potential acorn crop size. Weather factors that are considered to be important include the amount of time below 60% relative humidity during the pollination period, the number of severe storms with high winds or hail during the growing season, and summer drought that may effect maturation. Other factors include the size of the tree hopper population in the June-July period and the size of the oak weevil population in late summer.

This model could provide a valuable research tool for exploring the consequences of assumed changes in the factors affecting acorn production.

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