

Correlates of interspecific synchrony and interannual variation in seed production by deciduous trees

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Received 23 October 2006; received in revised form 31 January 2007; accepted 31 January 2007

Abstract

Eastern deciduous forests are populated with a variety of hardwood species, with composition at large scales determined by a complex interplay of temperature, moisture, and disturbance. An understanding of seed production is important in the context of forest regeneration and wildlife management. We analyzed time series data obtained from the literature to investigate (1) the effects of life-history characteristics on interannual covariation in seed production; (2) the environmental drivers of interannual variation in seed production; (3) the effects of spatial relations on seed production. Life-history attributes accounted for between 9% and 29% of annual covariation in interspecific seed production. Phylogenetic similarity was an important determinant of covariation in seed production across species groups. Similarity in geographic range had a positive effect on covariation among oak species, but a negative effect on covariation among non-oak species. Weather accounted for 18.1% of the variation in seed production for oaks of the *Lobatae* section and 12.2% of the variation in seed production for oaks of the *Quercus* section. Climate was only significant for oaks of the *Quercus* section, with climate variables accounting for 14% of the variation in seed production. For two species, red and white oak, there was a significant east–west gradient in acorn production, possibly indicating the presence of a precipitation gradient. These results provide a comprehensive overview of seed production across eastern North America through time.

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Keywords: Hardwoods; Interannual covariation; Interannual variation; Masting; Non-oaks; Oaks; *Quercus* spp.; Seed production

1. Introduction

Eastern deciduous forests contain a variety of hardwood species, with composition at large scales determined by complex interplay of temperature, moisture, and disturbance. In terms of basal area, nut-producing species, particularly oaks (*Quercus* spp.) dominate all regions except New England and the Great Lakes states (McWilliams et al., 2002). In such systems, nut-producing trees are important drivers of community and ecosystem processes (Ellison et al., 2005; McShea and Healy, 2002). However, regeneration failure has been noted worldwide for many of these species, particularly for oaks (Watt, 1979; Abrams, 2003; Li and Ma, 2003; Aldrich et al., 2005). The loss of such foundation species (*sensu*; Ellison et al.,

2005) from ecosystems has dramatic effects on the functioning of these ecosystems, including changes to energy and nutrient dynamics, food web structure, hydrology, and forest biodiversity (Ellison et al., 2005).

Given the importance of nut-producing trees, understanding seed production is essential. Forest regeneration depends almost exclusively on natural regeneration from seed (Carvell and Tryon, 1961; Ward, 1966; Arend and Scholz, 1969; Crow, 1988; Kelty, 1988). The observed annual variation in the production of seeds such as acorns is partially due to environmental factors (Johnson et al., 2002). Managers interested in fostering forest regeneration need to understand not only periodicity in seed production, but also the environmental factors influencing variation in seed production. Management operations designed to improve forest regeneration are often more effective when conducted during mast years (Johnson et al., 2002). However, the timing of such management activities requires an ability to predict seed crops, which in turn requires an understanding of the factors influencing seed production.

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Nuts, especially oak acorns, are an important source of food for forest wildlife. Deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), and various squirrel species (*Sciurus* spp., *Glaucomys volans*) rely on acorns and other nuts as a staple food source (Feldhamer, 2002; Kirkpatrick and Pekins, 2002; Steffen et al., 2002; Smith and Stapanian, 2002). Changes in wildlife populations often track fluctuations in seed production (Wolff, 1996; Johnson et al., 2002; Kirkpatrick and Pekins, 2002; Boutin et al., 2006). Therefore, understanding the dynamics of seed production provides natural resource managers greater insight into the dynamics of wildlife populations (cf. Clark et al., 2005).

Covariation of seed production between species has important implications for wildlife. Koenig and Knops (2002) reported significant, positive correlations in seed production between species requiring the same number of years for seed maturation and negative, but non-significant, correlations between species requiring different numbers of years for seed maturation. With a mixture of seed-producing species, therefore, it is less likely that a seed-crop failure of any one species will negatively affect wildlife populations. Prescriptions for managing oak-dominated forest stands for seed production commonly include recommendations for maintaining a diversity of seed-producing species (Healy, 2002). Acorn woodpeckers (*Melanerpes formicivorus*), for example, do not occupy oak monocultures, but instead inhabit forest stands composed of at least two different oak species (Bock and Bock, 1974; Koenig and Haydock, 1999; Koenig and Knops, 2002). Liebhold et al. (2004) reported that total seed production was less variable through time than the production of seed by any individual species in a forest stand. Tree species composition is important for maintaining viable wildlife populations, particularly in landscapes affected by forest fragmentation and loss (Rice et al., 1983; Kurki et al., 2000). To ensure the value of these stands to wildlife species, covariation in seed production should be minimal, thereby reducing the likelihood of concurrent seed-crop failures among species. However, little is known about the factors influencing covariation in seed production among species.

Many studies of interannual seed variation within a single species have focused on variability among locations, but few have examined patterns of variation across space and time concurrently (Koenig and Knops, 2002). Synchrony among spatially disjunct populations has important practical implications for management of wildlife species. For example, widespread, synchronous seed-crop failure could affect regional abundance of wildlife. Seton (1920) discussed early observations of squirrel migrations in response to low food abundance. Schorger (1947) reported migrations of gray (*Sciurus carolinensis*) and fox (*Sciurus niger*) squirrels in Wisconsin in 1946 resulting from acorn shortages. More recently, Smith (1968, 1970) reported wide-scale migrations of red squirrels (*Tamiasciurus hudsonicus*) in response to seed-crop failures in boreal forests. Similar migrations were observed for gray squirrels in the eastern United States over the same period (Flyger, 1969).

We investigated (1) the effects of species life-history characteristics on interannual covariation in seed production; (2) environmental drivers of interannual variation in seed production; (3) the effects of spatial relations on seed production, using 32 time series collected from across the northeastern United States.

2. Methods

We obtained time series of seed production from the published literature (17 time series), from government agency reports (12 time series), and from other unpublished sources (3 time series) (Appendix A). These time series included data for 8 oak species and 13 non-oak species with sufficient data for analysis (i.e., species with ≥ 14 cases; Table 1). Several studies included in our sample did not identify oaks below the sectional level and were, therefore, included as *Lobatae* (red oak section) and *Quercus* (white oak section) in the database. Studies were

Table 1

Genus, species, group, and common names for most producing species included in the analyses

Scientific name	Common name
<i>Lobatae</i> oaks group	
<i>Quercus rubra</i>	Northern red oak
<i>Q. coccinea</i>	Scarlet oak
<i>Q. falcata</i>	Southern red oak
<i>Q. velutina</i>	Black oak
<i>Q. marilandica</i>	Blackjack oak
<i>Quercus</i> oaks group	
<i>Q. alba</i>	White oak
<i>Q. prinus</i>	Chestnut oak
<i>Q. stellata</i>	Post oak
Non-oaks species group	
<i>Acer rubrum</i>	Red maple
<i>A. saccharum</i>	Sugar maple
<i>Betula alleghaniensis</i>	Yellow birch
<i>B. papyrifera</i>	Paper birch
<i>Carya glabra</i>	Pignut hickory
<i>Carya ovata</i>	Shagbark hickory
<i>Carya tomentosa</i>	Mockernut hickory
<i>Celtis occidentalis</i>	Common hackberry
<i>Crateagus</i> spp.	Hawthorn
<i>Elaeagnus angustifolia</i>	Russian olive
<i>Fagus grandifolia</i>	American beech
<i>Fraxinus americana</i>	White ash
<i>Fraxinus nigra</i>	Black ash
<i>Juglans nigra</i>	Black walnut
<i>Liriodendron tulipifera</i>	Yellow poplar
<i>Lonicera tatarica</i>	Tatarian honeysuckle
<i>Morus rubra</i> ^a	Red mulberry
<i>Populus grandidentata</i>	Bigtooth aspen
<i>Populus tremuloides</i>	Quaking aspen
<i>Prunus serotina</i>	Black cherry
<i>Sassafras</i> spp.	Sassafras
<i>Tilia americana</i>	American basswood
<i>Ulmus americana</i>	American elm

Studies from which data were obtained and the length of individual time series are located in Appendix A.

^a This species produces multiple seeds per fruit, so fruit production was quantified.

conducted between 1937 and 2003, and ranged between 3 and 39 years in duration. We focused on studies located in the upper Midwest and the northeastern United States, from Wisconsin and Missouri in the west, to Maine and Virginia in the east (Appendix A).

These data were used in three separate analyses. The first factors that we examined related to covariation in seed production among species. Thus, only studies that indexed seed production for ≥ 2 species were included in the database. We estimated the pair-wise correlation in annual seed production among all possible species combinations within studies and used these comparisons as response variables for the covariation in seed production. Predictors included phylogenetic similarity, the duration of the study, and similarities in species phenology, age at first reproduction, successional stage, growth rate, longevity, seed weight, and geographic range. Phylogenetic similarity between taxa i and j was calculated as $1 - (d_{ij}/d_{\max})$, where d_{ij} is the amount of divergence between the taxa and d_{\max} is the amount of divergence between the most phylogenetically distinct taxa within the group considered (Freckleton et al., 2002). This similarity index ranged from 0 for taxa least related to each other to 1 for conspecifics. We obtained data on phylogenetic similarity from the published literature (Appendix B). However, published phylogenetic trees did not resolve relationships beyond the family level, and taxa within our database consisted of congeneric pairs and pairs of species within sections. For these pairs, we arbitrarily assigned $d_{ij} = 0.90$ for congeneric pairs and $d_{ij} = 0.95$ for species within sections. Phenology was computed as the average of the mean date of flowering, in months, and the mean period of time, in months, over which flowering occurred. For instance, a score of 4.5 for flowering date indicated that the species typically flowers in mid-April, whereas a score of 5.5 for flowering period indicated that the species was in flower for 5.5 months. This species would, therefore, receive a score of 5.0 for phenology $([4.5 + 5.5]/2)$. Age at first reproduction was defined as the age at first fruiting in years (Loehle, 1988; Young and Young, 1992). We were unable to determine the age at first reproduction for *Fraxinus nigra*, so we used the mean age at first reproduction of its congeners. Successional stage represented the spectrum of shade tolerance of the species and ranged between one and five (Barrett, 1994; Preston and Braham, 2002; Loehle, 1988). A score of one indicated shade intolerance characteristic of an early successional species, whereas a score of five indicated shade tolerance characteristic of a late-successional, closed canopy species. Growth rate described the rapidity with which a species typically reached mature stature and ranged from one for very fast to five for very slow growing species (Barrett, 1994; Preston and Braham, 2002; Loehle, 1988). Longevity described the mean lifespan in years. Seed weight was the mean weight of seed in grams (Young and Young, 1992). Geographic range was scored based on the region in which the species' range was centered (Preston and Braham, 2002), with values of 1–3 assigned to species with range centers in the northeastern, southeastern, and midwestern United States, respectively. Finally, study duration, the number of years of

data included from the original study, was included as a nuisance variable. Gower's coefficients of similarity were calculated for these variables following the methods of Legendre and Legendre (1998, pp. 258–259).

Least-squares regression for the analysis of covariation was done using Matlab v7.0.1. Our response variable was correlation in production between a pair of species in a study. Independent variables were the coefficients of similarity for each of the attributes described in the preceding paragraph. We used randomization tests with 999 randomizations to determine significance of the regression model and coefficients (Legendre and Legendre, 1998, pp. 20–22). Randomizations were carried out within studies to avoid problems associated with varying study methods and indices. Statistical significance was assigned as the proportion of randomizations that were as extreme as, or were more extreme than, the absolute value of the observed coefficient, with $\alpha = 0.05$. Separately, we analyzed data for all species comparisons, comparisons between oak species, comparisons between non-oak species, and comparisons of non-oak and oak species.

The second analysis investigated the effects of weather and climate variables on interannual variation in seed production. The yearly seed production of each individual species was the focus of this analysis. We used all studies that reported >1 year of seed production for >1 species. Because each study included in the sample quantified seed production in a different manner, raw seed production indices were not directly comparable across studies. Therefore, we converted the seed production indices to a z -score by subtracting the mean from each value and dividing the difference by the standard deviation, and used the z -score as the response variable in the models (see below). We extracted weather and climate data from the National Oceanic and Atmospheric Administration's National Climate Data Center (NCDC) records. Weather data consisted of observed meteorological conditions recorded during the biological year. The biological year was defined as the preceding fall (September–November of the previous year), and winter (December–February), spring (March–May), and summer (June–August) of the current year, where the current year is the year in which seed production was recorded. We included mean maximum and minimum seasonal temperature, mean season diurnal temperature difference (difference between daily mean maximum and minimum temperatures), and total seasonal precipitation. Climate data consisted of the difference between the long-term climate normals and yearly weather values specified above. Climate normals are defined as the mean value of a meteorological element over a 30-year period, and are recalculated every 10 years. Climate normals serve as the basis against which current conditions can be compared (Whitehurst and Owen, 2003). We included climate data because prior research (Tapper, 1996; Schaubert et al., 2002) suggested that plant species might adapt to prevailing climate conditions and be affected more strongly by deviations from these climate conditions. We also included the previous year's (*Quercus* oak and non-oak species) or the previous 2 years' (*Lobatae* oak species) seed production index as model predictors.

Because of severe multicollinearity among temperature variables, we elected not to use a standard regression technique. Instead, we applied a neural network modeling approach (Smith, 1996; Fielding, 1999). Neural networks are a type of machine-learning algorithm originally intended to mimic learning in the human brain (Rumelhart et al., 1986), and can be considered a form of multivariate, non-linear regression (Goodman and Harrell, 1998). Neural network models are non-parametric, can account for both linear and non-linear relationships without *a priori* specification of the form of the relationship, and, most importantly for our purposes, are unaffected by multicollinearity (Smith, 1996). This technique has been applied to a number of ecological problems, including modeling occurrences of algal blooms (Recknagel et al., 1997; Maier et al., 1998), presence/absence of small-bodied fish (Mastrorillo et al., 1997), production of biomass in the tallgrass prairie (Olson and Cochran, 1998), abundance of northern bobwhites (*Colinus virginianus*; Lusk et al., 2001, 2002), and nest-site selection of lark sparrows (*Chondestes grammacus*; Lusk et al., 2003) and northern bobwhites (Lusk et al., 2006).

We used a multi-layered, back-propagation neural network architecture (Hagan et al., 1996; Smith, 1996), consisting of three layers: input, hidden, and output. The input layer contains nodes representing each of the predictor variables, which are each connected to every node in the hidden layer. The hidden layer contains a variable number of processing elements, called hidden nodes, which predict the dependent variable. The more hidden nodes a model contains, the more complex the relationships it is able to approximate (Smith, 1996). The process of predicting the dependent variable begins when the values for each of the independent variables for a particular case are passed to the hidden node, where a weight is applied and the values are summed. The sum is then transformed using one of several transfer functions. We used a logistic transfer function. The transformed sums from each hidden node are passed to the output node, where they are weighted, summed, and transformed to produce a prediction of the dependent variable (Smith, 1996). The prediction is compared to the actual value of the dependent variable represented by the output node and the root-mean-square error is calculated. This error is back-propagated through the model and is used to adjust the model weights. This process continues iteratively until the error is minimized or some arbitrary threshold error is achieved (Smith, 1996).

Neural network models were developed using Statistica Neural Network v.4.0 (StatSoft, Inc., Tulsa, OK, USA). The optimum number of hidden nodes was determined automatically in an attempt to balance model complexity with predictive power. The software also automated the process of selecting predictors, retaining only those predictors that increased predictive power. We withheld ~40% of the available data for model validation; these data were not used in model development and allowed us to gauge the performance of the model when presented with novel data. Cases with missing values were not included in the analysis. Performance was measured as the percentage of variation in the seed production index accounted for by the predictors. We measured the

importance of each predictor by calculating the relevance scores. A relevance score measures the relative influence of each variable in a set of predictors on a response variable. It is calculated from the set of model weights as the sum of weights for the variable of interest divided by the sum of all weights (Özesmi and Özesmi, 1999). This proportion is then expressed as a percentage and referred to as percent relevance.

We used predicted responses to interpret the output of the neural models. Predicted responses allowed us to visualize the effects of each predictor variable across the observed range of that predictor on the response variable, with all other predictors held constant at their mean value.

The final analyses investigated the role of spatial processes in the variation in seed production among oak species. Since red (*Quercus rubra*) and white (*Q. alba*) oaks were the most common species in the databases compiled here, these species were selected for analysis in order to maximize the sample size. We conducted separate analyses for red and white oak. Prior to analysis, we examined time series from each study to determine whether the series trended through time, and excluded those studies in which there was a significant temporal trend. We also removed any series <5 years in duration. This process resulted in 16 cases suitable for analysis for white oak and 15 cases for red oak. For each of the remaining time series, we estimated the mean *z*-score seed production-index over the period of study. We used these mean *z*-score indices as the response variable in our regression models. Explanatory variables included the UTM coordinates of the study site or of the closest weather station to the study site, if the study site coordinates were not available. We also included the duration of each study as a predictor in the regression models. Randomization tests with 999 randomizations were used to determine model and coefficient significance as above (Legendre and Legendre, 1998).

3. Results

The database used for seed covariation analysis contained 354 between-species comparisons, each comprised of correlations among the seed-production time series of two species. The regression model for seed covariation among all species in the database accounted for 9.7% ($R^2 = 0.097$, $F = 4.01$, $P_{\text{random}} = 0.001$) of the variation (Table 2). Among the predictors, phylogenetic similarity, and similarity of species longevity were highly significant, and study duration was marginally significant (Table 2). The correlation of seed production between species increased with increasing phylogenetic similarity and with increasing similarity in species' longevity. There was a weak positive effect of study duration on the correlation of seed production.

When considering only comparisons between oak species ($n = 152$), the regression model's performance improved substantially, accounting for 25.7% ($R^2 = 0.257$, $F = 5.12$, $P_{\text{random}} = 0.001$) of the variation in covariation in seed production among oaks (Table 2). Again, phylogenetic similarity and similarity of species longevity were significant predictors (Table 2). In addition to these predictors, geographic

Table 2
Regression results for models of the effects of life-history attributes on seed-production covariation

Predictors	Regression coefficients			
	All species ^a	Oak only ^b	Non-oak ^c	Oak vs. non-oak ^d
Intercept	-0.1307	-4.8315	-0.1627	0.2747
Phylogenetic similarity	0.3593***	5.6867**	0.6578***	0.0879
Study length	0.0071*	0.0066	0.0094	-0.0031
Phenological similarity	-0.1265	-0.2460	-0.0772	0.0989
Similarity in age at first reproduction	-0.1403	-0.4737	-0.2061	0.0566
Similarity in successional type	-0.0023	-0.2829	0.2759	0.1132
Growth-rate similarity	0.0682	0.4068**	0.0012	0.0093
Similarity in longevity	0.3149***	0.4189*	0.2465	-0.2677
Similarity in seed weight	0.0964	-0.6239	0.2387	0.0578
Similarity in geographic range	-0.0579	0.9408***	-0.4607***	-0.1938

Significance was determined using randomization tests with 999 randomizations.

^a $R^2 = 0.0974$, $F = 4.01$, $P_{\text{random}} = 0.001$.

^b $R^2 = 0.2571$, $F = 5.12$, $P_{\text{random}} = 0.001$.

^c $R^2 = 0.2867$, $F = 4.87$, $P_{\text{random}} = 0.001$.

^d $R^2 = 0.0609$, $F = 0.52$, $P_{\text{random}} = 0.677$.

*** $P < 0.01$.

** $P < 0.05$.

* $P < 0.10$.

similarity was a significant predictor, and similarity of species growth rates was marginally significant (Table 2). All of these relationships were positive.

The regression model for non-oak species ($n = 120$) also had a better fit than the model including both oak and non-oak species. The non-oak regression accounted for 28.7% ($R^2 = 0.287$, $F = 4.867$, $P_{\text{random}} = 0.001$) of the variation in seed-production covariation (Table 2). Only phylogenetic and geographic similarities were significant predictors of the correlation between species' seed production (Table 2). Like oaks, as the similarity in phylogeny increased, so did the correlation of seed production among species (Table 2). However, the correlation of seed production among non-oak species decreased with increasing similarity in geographic range (Table 2).

There were 82 comparisons between oak and non-oak species (see above) in the database. However, the model accounted for only 6% ($R^2 = 0.061$, $F = 0.519$, $P_{\text{random}} = 0.677$) of the variation in seed-production covariation and was not statistically significant (Table 2).

The optimal neural model of the relationship between the variation in seed production of red oak (*Lobatae*) species ($n = 365$) and weather contained six hidden nodes and 10 predictors (Table 3). The neural model accounted for 18.1% of the variation in the training data and 18.3% of the variation in the validation data. Of the 10 variables that were selected for inclusion in the model, five had relevance scores greater than expected if all weather variables were equally good predictors of seed production variation (Table 3). Of these five, the mean maximum summer temperature in year-2 had the highest percent relevance (17.6%), followed by seed production in year-2 (12.0%), mean minimum spring temperature in year-2 (11.3%), seed production in year-1 (11.2%), and mean maximum fall temperature in year-2 (10.5%) (Table 3). We report the predicted responses for these five variables, since they are the most influential. The index of seed production

tended to increase above mean production with increasing mean maximum fall temperature in year-2 (Fig. 1). The seed-production index also increased with increasing mean maximum summer temperature in year-2, but only for temperatures >29 °C (Fig. 1). As the mean minimum spring temperature in year-2 increased, the index of seed production declined (Fig. 1). Together, seed production over the previous 2 years had a combined relevance of 23.2%. The seed-production index for the current year was negatively related to the seed-production index 2 years previous. That is, above average seed production in year-2 tended to be followed by below average production in the current year (Fig. 2). In contrast, above average seed production in the immediately preceding year (year-1) tended to be followed by above average seed production in the current year (Fig. 2).

None of the neural-network models of the relationship between climate and red-oak seed-production variation performed better than a 17-predictor model containing 11

Table 3
Percent relevance for each predictor in the neural network model of the effects of weather on red oak (*Lobatae* section) seed production

Predictor variable	Relevance (%)
Mean maximum summer temperature year-2	17.64
Seed production year-2	11.97
Mean minimum spring temperature year-2	11.26
Seed production year-1	11.23
Mean maximum fall temperature year-2	10.54
Total winter precipitation year-2	8.73
Total spring precipitation year-1	8.09
Mean minimum spring temperature year-1	7.91
Total winter precipitation year-1	7.16
Total fall precipitation year-2	5.47

Percent relevance gives a relative measure of each variable's influence on model predictions. The neural network model accounted for 18.1% of the variation in the training data and 18.3% of the variation in the validation data. Variables with $\geq 10\%$ relevance were most important in influencing model predictions.

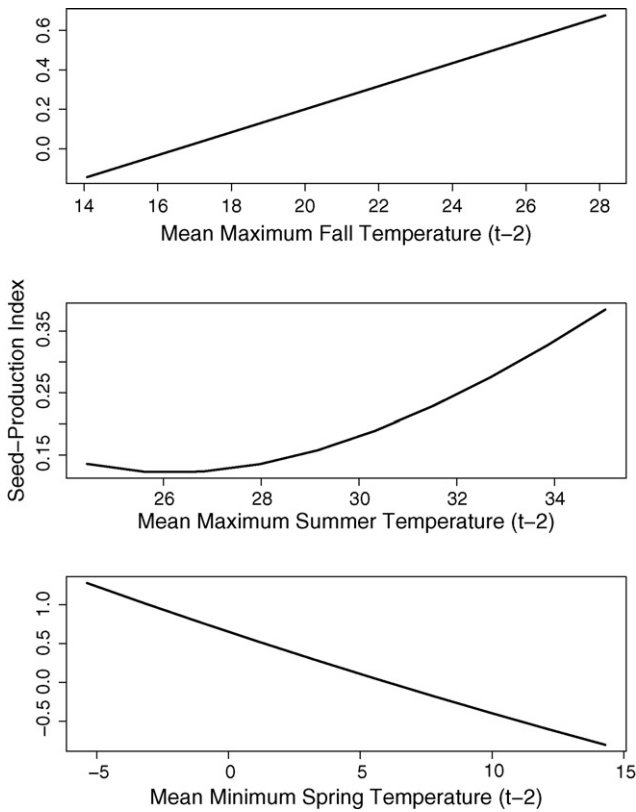


Fig. 1. Predicted responses from the neural network model of variation in acorn production by red oaks (*Lobatae* section) in relation to weather for selected weather variables. Variables shown here had relevance scores $\geq 10\%$, indicating that they contributed more to the model predictions than expected.

hidden nodes, which accounted for only 0.06% of the variation in the training data. Since this model lacked predictive power, we do not consider it further here.

The optimal neural model of the relationship between seed-production variation of white oak (*Quercus*) species ($n = 393$) and weather contained five hidden nodes and nine predictors (Table 4). This model accounted for 12.2% of the variation in the training data and 6.7% of the variation in the validation data. Of the nine variables selected for inclusion in the neural model,

Table 4
Percent relevance for each predictor in the neural network model of the influence of weather variables on white oak (*Quercus* section) seed production

Variable	Relevance (%)
Mean maximum fall temperature	15.62
Total fall precipitation	12.38
Mean maximum summer temperature	11.73
Total winter precipitation	11.15
Study year	11.13
Total spring precipitation	10.91
Mean minimum spring temperature	10.65
Previous year's seed production	9.16
Total summer precipitation	7.27

Percent relevance gives a relative measure of each variable's influence on model predictions. The neural network model accounted for 12.2% of the variation in the training data and 6.7% of the variation in the validation data. Variables with $\geq 11\%$ relevance were most important in influencing model predictions.

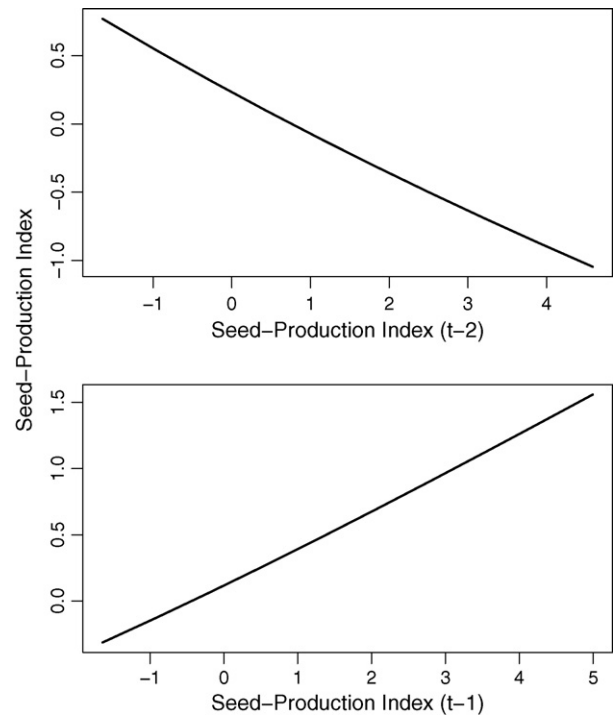


Fig. 2. Predicted responses from the neural network model of variation in acorn production by red oaks (*Lobatae* section) in relation to weather for acorn production during the previous 2 years. These variables had relevance scores $\geq 10\%$, indicating that they contributed more to the model predictions than expected.

four had greater than expected percent relevance (Table 4). Mean maximum fall temperature had the highest percent relevance (15.6%), followed by total fall precipitation (12.4%), mean maximum summer temperature (11.7%), and total winter precipitation (11.2%) (Table 4). The relevance score for year was equal to expectation (11.1%), indicating the strength of its effect on model predictions was borderline (Table 4). The index of seed production for white oaks increased with increasing mean maximum fall temperatures, and declined with both mean maximum summer temperature and total winter precipitation (Fig. 3). The seed-production index increased with increasing total fall precipitation until approximately 400 mm, after which the relationship was negative (Fig. 3). Because of the importance of spring weather previously reported for white oak seed production, we discuss the predicted results for spring weather variables. The index of seed production increased with increasing mean minimum spring temperature and with total spring precipitation (Fig. 3). There was a negative trend in the overall seed-production index through time (Fig. 4), indicating that the seed production index has progressively declined during the period over which data were collected (1948–2003).

The optimal neural model relating *Quercus* seed production to climate variables contained 13 predictor variables and six hidden nodes. The neural model accounted for 14.0% of the variation in the training data and 14.1% of the variation in the validation data (Table 5). Six of the predictors in the model had relevance scores greater than expected, with the deviation of mean maximum spring temperature from long-term climate normals having the greatest influence over model predictions

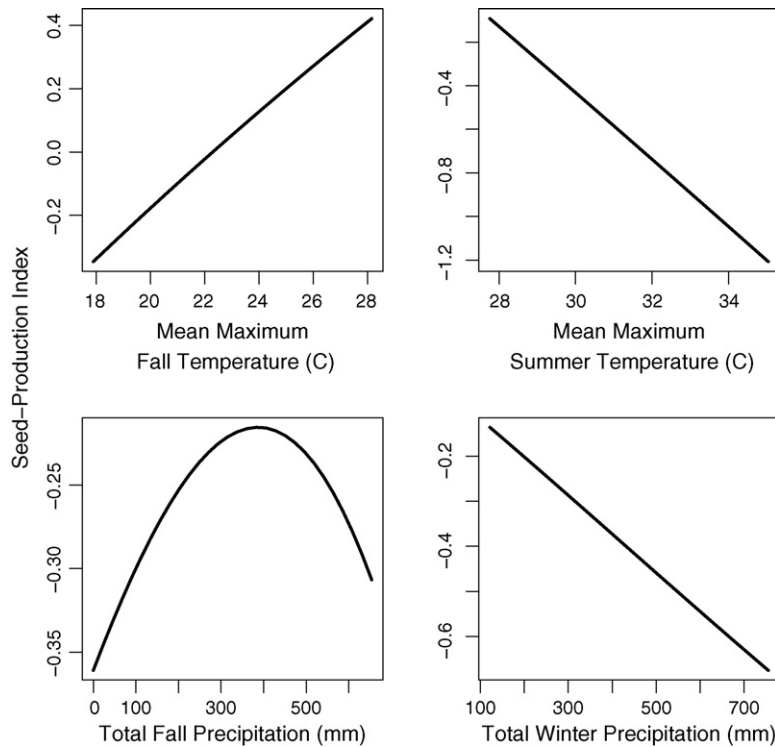


Fig. 3. Predicted responses from the neural network model of variation in seed production by white oaks (*Quercus* section) in relation to weather for selected weather variables. Variables shown here had relevance scores >11%, indicating that they contributed more to the model predictions than expected.

(11.7%). Other influential predictors include the deviation of mean maximum summer temperature (10.1%), mean winter (8.7%) and summer (8.6%) diurnal temperature shift, and total spring precipitation (8.2%) from their long-term climate

normals (Table 5). The effect of year was also an influential predictor (8.8%). The index of acorn production increased as the mean maximum spring temperature and mean winter diurnal temperature increased above the long-term average (Fig. 5). Seed production declined as mean maximum summer temperature, mean summer diurnal temperature shift, and total spring precipitation increased above long-term averages

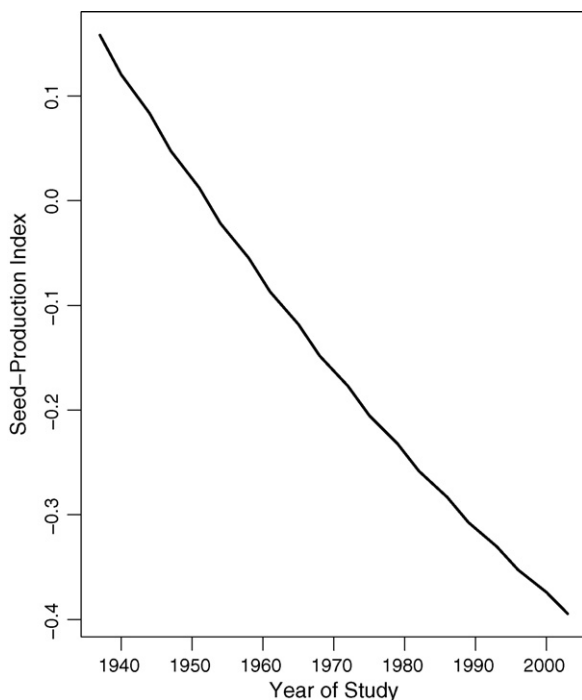


Fig. 4. Predicted responses from the neural network model of variation in seed production by white oaks (*Quercus* section) in relation to weather for the variable “year.” This variable had a relevance score $\geq 10\%$, indicating that it contributed more to the model predictions than expected.

Table 5

Percent relevance of variables selected for inclusion as predictors in the neural network model of the influence of climate variables on white oak (*Quercus* section) seed production

Variable	Relevance (%)
Deviation from mean maximum spring temperature (°C)	11.65
Deviation from mean maximum summer temperature (°C)	10.05
Study year	8.77
Deviation from mean winter diurnal temperature change (°C)	8.74
Deviation from mean summer diurnal temperature change (°C)	8.60
Deviation from mean total spring precipitation (mm)	8.22
Deviation from mean total winter precipitation (mm)	7.38
Previous year's seed-production Index	7.20
Deviation from mean minimum fall temperature (°C)	7.20
Deviation from mean minimum summer temperature (°C)	6.12
Deviation from mean minimum winter temperature (°C)	5.99
Deviation from mean minimum spring temperature (°C)	5.80
Deviation from mean total fall precipitation (mm)	4.31

Climate variables represent the deviation of yearly weather values from the long-term climate normals for the climate region in which the study was located. Percent relevance gives a relative measure of each variable's influence over model predictions. The neural model accounted for 14% of the variation in the training data and 14.1% of the variation in the validation data. Variables with $\geq 7.69\%$ relevance were the most important for model predictions.

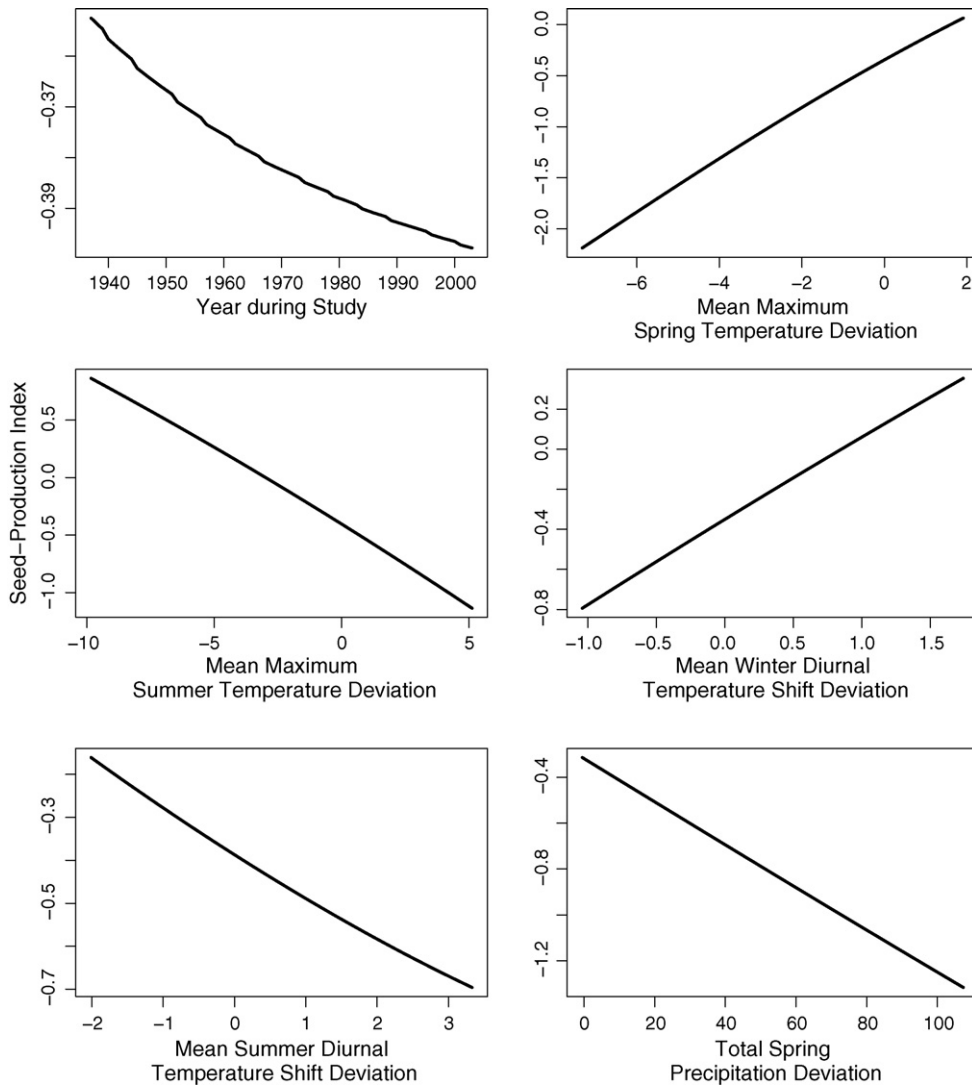


Fig. 5. Predicted responses from the neural network model of variation in seed production by white oaks (*Quercus* section) in relation to climate for selected variables. These variables had relevance scores >7.7%, indicating that they contributed more to the model predictions than expected.

(Fig. 5). As with the weather model, there was a negative trend in the index of acorn production through time (Fig. 5).

Neural models of the response of *Quercus* to climate and weather both indicated that the seed-production index declined with time. In both cases the relationship showed a deceleration for later years. We also detected significant negative trends in mean maximum summer and fall temperatures, and in mean minimum spring temperature (Fig. 6), which accounted for between 25% and 45% of the variation in the temperature time series.

Interspecific differences in seed production were revealed by estimation of the mean seed production indices for the spatial analysis. For *Q. alba*, the mean seed-production index for each study tended to be negative, whereas for *Q. rubra* the mean seed-production index for each study tended to be positive. The main effects of spatial position were not significant predictors of mean seed-production indices for red oaks, but the number of years each study was conducted and the interaction of spatial coordinates were significant predictors (Table 6; $R^2 = 0.568$,

$P_{\text{random}} = 0.058$). Similarly, the number of years in a particular study was a significant predictor of mean seed production indices for white oaks (Table 6; $R^2 = 0.497$, $P_{\text{random}} = 0.085$). In the case of white oak, the first UTM coordinate also was a

Table 6
Results of the regression analysis of the effects of spatial location on the mean seed production for *Q. alba* and *Q. rubra*

Variable	Regression models	
	<i>Q. alba</i> ^a	<i>Q. rubra</i> ^b
Intercept	0.277	-0.124
UTM 1 (x)	-0.206*	0.155*
UTM 2 (y)	0.062	0.160
Length of time series	-0.024**	0.028**
UTM 1 × UTM 2	0.109	-0.227**

^a $R^2 = 0.497$, $F = 2.72$, $P = 0.0851$.

^b $R^2 = 0.568$, $F = 3.29$, $P = 0.0579$.

* $P < 0.10$.

** $P < 0.05$.

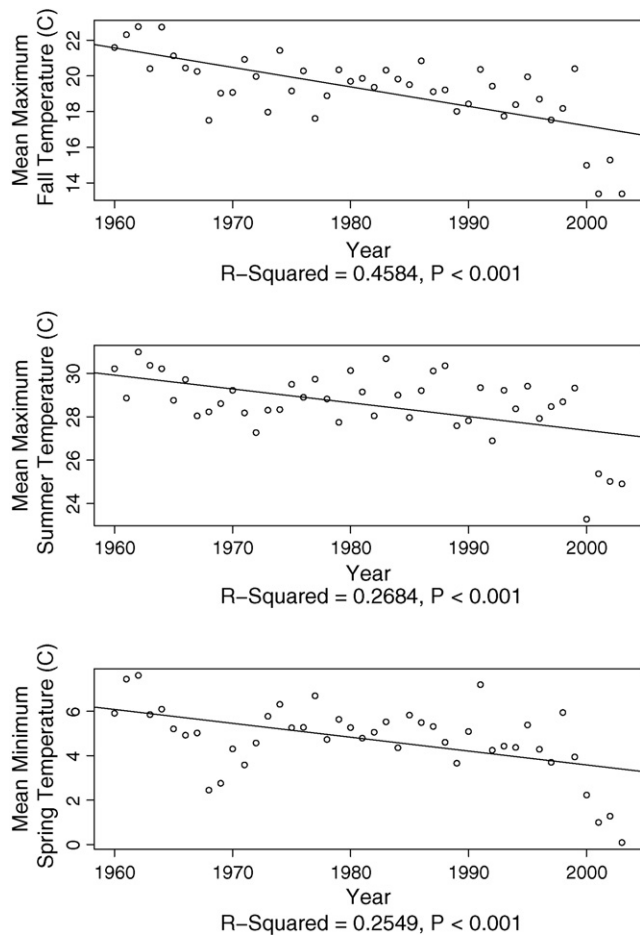


Fig. 6. Results of the regression of year on mean maximum summer and fall, and mean minimum spring temperatures across study sites over the duration of the time series.

marginally significant predictor ($P < 0.10$), but neither the second UTM coordinate nor their interaction term were significant (Table 6).

4. Discussion

Seed production of many North American trees can be characterized by extreme interannual variation, interspecific asynchrony, and intraspecific synchrony at large spatial scales (Koenig and Knops, 2002). Here, we examined potential factors governing seed production over a large spatial (upper Midwest and northeastern United States), temporal (1937–2003), and taxonomic extent. Our investigation focused in part on potential endogenous, life-history factors influencing seed-production covariation. The relationship between life-history characteristics and covariation in seed production was significant when considering all species simultaneously; however, the model accounted for only a small amount of the variation in the data (9.7%). Covariation in seed production was greater in more closely related tree species. The role of phylogeny perhaps was expected, given the broad taxonomic distribution considered in the overall analysis. Yet the importance of phylogeny persisted even when subsets of the larger data set were considered.

Phylogeny typically has not been addressed explicitly in studies of seed production, but our results indicate that shared evolutionary history of tree species is a more important determinant of annual covariation in seed production than the life-history traits we considered.

Phylogenetic similarity was significantly, positively related to covariation in acorn production when analysis was restricted only to species of oak. Other studies also have reported interspecific synchrony (positive covariation) among oak species requiring the same number of years to mature acorns, and interspecific asynchrony (negative covariation) among species requiring different numbers of years to mature acorns (Koenig and Knops, 2002; Liebhold et al., 2004). The synchronizing effects of regional weather are thought to influence patterns of covariation in oaks (Koenig and Haydock, 1999; Koenig and Knops, 2000; Liebhold et al., 2004). According to this scenario, weather conditions in a given year affect aspects of the reproductive ecology of oaks, such as pollen dispersal or acorn development. The effects of these weather conditions are manifested in the current year's acorn production for oaks in the section *Quercus* and are manifested the following year for oaks in the section *Lobatae*. Liebhold et al. (2004) reported nearly identical autocorrelation functions with 1-year lag for *Q. douglasii* and *Q. lobata*, indicating that the species had similar endogenous dynamics.

Our analysis including all species comparisons and oak-only comparisons indicated that similarity in species' longevity was an important factor influencing covariation in seed production, although it was not a significant factor when comparing non-oak species. In all cases, the relationship was positive, indicating that the more similar species were in their maximum life-expectancy, the greater the correlation in annual seed production. The mechanisms generating this pattern are not readily apparent, but such an association suggests that strategies for allocating resources to reproduction are similar, even in phylogenetically disparate species of trees.

Several studies have investigated the effects of weather variables on variation in mast production and synchrony among locations and species (Koenig et al., 1996; Piovesan and Adams, 2001; Koenig, 2002; Koenig and Knops, 2002; Schaubert et al., 2002). Koenig and Knops (2002) summarized studies of the effects of weather on annual variation in acorn production. They reported often-conflicting responses between selected weather variables and acorn production. For example, each of the studies of red oak species covered by Koenig and Knops (2002) had different sets of correlations between weather and acorn production. For white oaks, one study reported negative effects of warm spring temperatures on acorn yield (Cecich, 1997), whereas the relationship was positive for another study (Sork et al., 1993). However, biological organisms often filter environmental signals in a non-linear manner to produce a biological response (Laasko et al., 2001). The nature of the relationship between environmental signal and observed response (i.e., positive or negative correlations) will depend on the structure of the filter

and where along the continuum of values an environmental signal ranges (Laasko et al., 2001). For example, if oak trees process certain weather variables in a symmetric fashion with a clear optimum, then the differences in the results could simply result from the range of values for the weather variable observed in the different studies. If the weather signal has a mode to the left of the optimum in one region, then there will be a positive correlation between the weather variable and the response in that region (here, acorn production). Likewise, if the weather signal's mode is to the right of the optimum in a particular region, there will be a negative correlation between the weather variable and the response in that region (Laasko et al., 2001). Neural network models, rather than distilling relationships to a single value, map the response of the system under study to the range of variation observed in the predictors, thus enabling us to investigate non-linearities in the relationship between response and predictors. This characteristic is extremely useful when the exact form of the non-linear relationship is not known.

Koenig et al. (1996) outlined several types of weather conditions that potentially could affect acorn and seed development. One of these conditions was overall water availability. They reported that mean annual rainfall on their study site in the current year was positively related to acorn crop size for *Q. agrifolia* and *Q. chrysolepis* and also during the previous year for *Q. chrysolepis* (Koenig et al., 1996; Koenig and Knops, 2002). The relationship was slightly stronger for the 1-year species (*Q. agrifolia*; $r_s = 0.65$) than for the 2-year species (*Q. chrysolepis*; $r_s = 0.59$). However, at the same sites, a negative relationship existed between mean annual rainfall and acorn crop size for *Q. douglasii* and *Q. lobata*, both 1-year (white oak) species (Koenig and Knops, 2002). In the current study, seasonal precipitation variables were used to represent water availability. Winter precipitation in the current year and the previous year, fall precipitation the previous year, and spring precipitation in the current year contributed to the neural network model of *Lobatae* response to weather. However, their relevance scores (Table 3) indicated that they were not the most important variables in the model. For *Quercus*, precipitation variables for all four seasons were selected as predictors of seed production (Table 4), but only fall and winter precipitation contributed more than expected to the model's predictions, based on relevance scores. The negative relationship between seed-production indices and winter precipitation could result from damage sustained from heavy accumulations of snow and ice on branches at the temperate latitudes in our study. Such damage might reduce the overall investment in the next acorn crop in favor of investing in new growth to compensate for the loss of photosynthetic tissues. Alternatively, reduction in seed-production indices could result from a reduction in viable buds from ice damage. Total fall precipitation had a strong unimodal relationship with the seed-production index; annual production increased with total fall precipitation until approximately 350 mm and then declined sharply for greater values (Fig. 3). Fall is the time when flower-bud initiation occurs (Johnson et al., 2002). Excessive moisture during this

time appears to negatively affect the acorn crop the following year.

Weather conditions that could affect acorn development include those during the fertilization period, which occurs in the spring, and during acorn development, which occurs during the summer (Koenig et al., 1996). A general consensus exists regarding the effects of late spring freezes on acorn production (Johnson et al., 2002; Koenig et al., 1996; Koenig and Knops, 2002; Neilson and Wullstein, 1980). Late freezes in Missouri reduced white oak flower density by 80% of expected (Cecich and Sullivan, 1999). However, Sharp and Sprague (1967) found that killing frosts occurred too infrequently in Pennsylvania to be a major cause of mast failure and reductions. We included mean minimum spring temperatures in the neural models as surrogates for late frosts, under the assumption that such frosts would be reflected in lower mean minima. For oaks in section *Quercus*, the relationship was as expected: the seed-production index increased with increasing minimum spring temperature. Among species in section *Lobatae*, however, as minimum spring temperature increased, the seed-production index decreased. This result is opposite what we initially expected based on the effects of frost on fertilization, which occurs in the previous year among *Lobatae*. However, warmer spring minimum temperatures are positively correlated with relative humidity. Humidity is thought to decrease pollen availability, resulting in low fertilization rates and subsequent acorn production (Johnson et al., 2002; Koenig et al., 1996). Of course, this does not explain the presence of the opposite relationship in *Quercus* unless the effect of humidity on *Quercus* is fundamentally different from that for *Lobatae*. A similar pattern was observed for the effects of summer temperature on species in the red and white oak groups. Among species of *Quercus*, seed-production index was negatively related to mean maximum summer temperature and the deviation from maximum summer temperature normals. Among *Lobatae*, the relationship was non-linear, with relatively little effect at low maximum summer temperatures during the previous year, but a positive relationship after temperatures surpassed 28 °C. The observed relationship for *Lobatae* is in agreement with previously reported results, which found that high summer temperatures were associated with larger acorn crop sizes (Koenig and Knops, 2002; Sork et al., 1993). Again, it is not clear why the pattern of response differed between species of the two sections.

Seed-production indices for the previous 2 years were strong contributors to the current year's seed-production index for members of *Lobatae*. The relationship between current year seed-production index and the seed-production index 2 years previous was negative. This pattern is consistent with the cyclicity in mast production among red oaks (Koenig and Knops, 2002), and implies that high reproductive output in a given year negatively affects reproductive output initiated that year (i.e., production of acorns that will mature the following year declines with increases in the current year's crop). The relationship between current year's production and the previous year's seed-production index was positive.

For *Q. alba*, longitude was negatively related to the mean seed-production index. Therefore, the mean seed-production index increased in a westerly direction, suggesting effects of a possible precipitation gradient. For *Q. rubra*, the mean seed-production index increased along a spatial gradient from north to south, possibly related to an underlying gradient in temperature. Acorn viability declines with desiccation (Dey, 2002). Thus, greater allocation to seed production could be warranted in areas where acorns are more susceptible to mortality from hot, dry conditions during seed fall. We might have detected a stronger spatial effect had we not used the mean of each time series as the response in the regression models. However, there was insufficient temporal overlap in our database for testing the effects of spatial location.

Seed production by *Q. alba* was consistently below average production of all species at a site, whereas seed production by *Q. rubra* was consistently above the average for all species. Differences were not likely attributable to species composition; both species occurred in 12 of 16 studies. These results have implications for white oak regeneration for two reasons. First, white oak acorns are more palatable than red oak acorns because red oak acorns contain higher concentrations of tannin (Servello and Kirkpatrick, 1987; Chung-MacCoubrey et al., 1997; Kirkpatrick and Pekins, 2002). Second, white oak acorns typically are consumed upon first encounter rather than being cached, because, unlike red oak acorns, they do not experience a period of winter dormancy and, therefore, germinate in the fall (Steele and Smallwood, 1994, 2002). Taken together, these factors suggest a cause for reported regeneration failures of *Q. alba* (Abrams, 2003; Aldrich et al., 2005), if consumer demand reduces already below-average seed availability. Alternatively, the below-average seed production noted for *Q. alba* could result partially from unobserved depredation of white-oak acorns prior to seed-production surveys.

5. Conclusion

Using time series collected over the latter half of the 20th century, we were able to develop a long-term and large-scale picture of the dynamics of seed production in the north-eastern United States. Our results show that over a wide range of seed-producing tree species in the northeastern United States, phylogeny was a more important determinant of covariation in annual seed production than life history traits. This implies that taxonomically related species exhibit stronger synchrony in seed production than more distantly related species. Forest management for wildlife species, therefore, should focus on promoting taxonomic diversity to protect against total seed-production failure and its negative effects on wildlife. To a more modest extent, covariation also could be explained by similarities in species life-history attributes and geographic ranges. Species within *Lobatae* and *Quercus* sections of the genus *Quercus* exhibited contrasting responses to certain weather variables. These results suggest

that forest regeneration activities might benefit white oaks most when mean minimum spring temperatures are high. Higher mean minimum spring temperatures will tend to have a negative effect on red-oak seed production the following year, possibly favoring the establishment of white oaks. We found evidence for a spatial gradient in acorn production, a decline over time in production of white-oak acorns, and lower average acorn production by *Q. alba* versus *Q. rubra*. It is important, therefore, that regeneration activities occur during years of high seed production for white oaks, to maximize their chances of establishment. Our results should help forest managers better predict when high seed production is likely. These results, taken together, improve our understanding of the factors governing between and within-year variation in seed production, and offer avenues for future research. We suggest that a coordinated framework be established for collecting contemporaneous data on seed production and local weather conditions, including tree- and stand-level measurements, across a broad geographic area. Data obtained from such a framework would help to clarify further the effects of environment, life history, and intraspecific variation on local and regional seed production.

Acknowledgments

The authors wish to thank Nathan Lichti for reviewing an early draft of this manuscript, and C. Canham, S. Elias, J. Witham, M. Hunter, Jr., W. Jakubas, R. Ostfeld, and C. Smith for providing seed-production time series for analysis. The Maryland and West Virginia Departments of Natural Resources, and the Virginia Department of Inland Fisheries and Game also provided time-series data. We thank two anonymous reviewers for thoughtful review of our manuscript. Funding for this study was provided by the John S. Wright Fund and the James S. McDonnell Foundation.

Appendix A. Citations and time-series lengths for seed-production studies used in analyses

Barni, R.T., 1980. Production and utilization of acorns on the Quehanna Wild Area. MS Thesis, Pennsylvania State University (3 years).

Beck, D.E., 1977. Twelve-year acorn yield in southern Appalachian oaks. US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, North Carolina, Forest Service Research Note SE-244 (12 years).

Canham, C.D., Institute for Ecosystem Studies, Millbrook, New York (8 years).

Cecich, R.A., Sullivan, N.H., 1999. Influence of weather at time of pollination on acorn production of *Quercus alba* and *Quercus velutina*. Can. J. For. Res. 29, 1817–1823 (7 years).

Christisen, D.M., 1955. Yield of seed by oaks in the Missouri Ozarks. J. For. 53, 439–441 (6 years).

Christisen, D.M., Kearby, W.H., 1984. Mast measurement and production in Missouri (with special reference to acorns).

Missouri Department of Conservation, Jefferson City, Missouri, Terrestrial Series #13 (4 years).

Christisen, D.M., Korschgen, L.J., 1955. Acorn yields and wildlife usage in Missouri. *N. Am. Wildl. Conf.* 20, 337–357 (5 years).

Cypert, E., Webster, B.S., 1948. Yield and use by wildlife of acorns of water and willow oaks. *J. Wildl. Manage.* 12, 227–231 (3 years).

Downs, A.A., McQuilkin, W.E., 1944. Seed production of southern Appalachian oaks. *J. For.* 42, 913–920 (7 years).

Elias, S.P., Witham, J.W., Hunter Jr., M.L., 2004. *Peromyscus leucopus* abundance and acorn mast: population fluctuation patterns over 20 years. *J. Mammal.* 85, 743–747 (20 years).

Godman, R.M., Mattson, G.A., 1976. Seed crops and regeneration problems on 19 species in northeastern Wisconsin. US Department of Agriculture, Forest Service, Research Paper NC-123, St. Paul, Minnesota (13 years).

Goodrum, P.D., Reid, V.H., Boyd, C.E., 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. *J. Wildl. Manage.* 35, 520–532 (3–18 years).

Greenberg, C.H., 2000. Individual variation in acorn production by five species of southern Appalachian oaks. *For. Ecol. Manage.* 132, 199–210 (5 years).

Grisez, T.J., 1975. Flowering and seed production in seven hardwood species. US Department of Agriculture, Forest Service, Research Paper NE-315 (6 years).

Gysel, L.W., 1957. Acorn production on good, medium, and poor oak sites in southern Michigan. *J. For.* 55, 570–574 (5 years).

Gysel, L.W., Lemmien, W.A., 1964. An eight-year record of fruit production. *J. Wildl. Manage.* 28, 175–177 (8 years).

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McQuilkin, R.A., Musbach, R.A., 1977. Pin oak acorn production on green tree reservoirs in southeastern Missouri. *J. Wildl. Manage.* 41, 218–225 (7 years).

Nicholas, N.S., White, P.S., 1984. Great Smoky Mountains National Park hardmast survey: an evaluation of the current survey, analysis of past data, and discussion of alternatives for future surveys. US Department of Interior, National Park Service, Resources Management Report SER-68, Gatlinburg, Tennessee (4 years).

Nixon, C.M., McClain, M.W., Donohoe, R.W., 1975. Effects of hunting and mast crops on a squirrel population. *J. Wildl. Manage.* 39, 1–25 (9 years).

Nixon, C.M., McClain, M.W., Hansen, L.P., 1980. Six years of hickory seed yields in southeastern Ohio. *J. Wildl. Manage.* 44, 534–539 (6 years).

Palmer, W.L., 1998. Acorn production in a mixed-oak stand in central Pennsylvania: twenty-seven years of data. Pennsylvania Game Commission, Final Project Report 06210, Job 21004. Harrisburg, Pennsylvania (23 years).

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Tryon, E.H., Carvell, K.L., 1962. Acorn production and damage. West Virginia University Agricultural Experiment Station, Bulletin 466T. Morgantown, West Virginia (6 years).

Maryland Department of Natural Resources, 1980–2000. Red oak and white oak group mast production (21 years).

Virginia Department of Inland Fisheries and Game, 1970–2000. Red and white oak group mast production (31 years).

West Virginia Division of Natural Resources, 1970–2000. Mast production of several species of hardwoods (31 years).

Appendix B. Citations used in determining phylogenetic relatedness of species used in the analyses

Campbell, C.S., Donoghue, M.J., Baldwin, B.G., Wojciechowski, M.F., 1995. Phylogenetic relationships in Maloideae (Rosaceae): evidence from sequences of the internal transcribed spacer of nuclear ribosomal DNA and its congruence with morphology. *Am. J. Bot.* 82, 903–918.

Chen, Z.-D., Manchester, S.R., Sun, H.-Y., 1999. Phylogeny and evolution of the Betulaceae as inferred from DNA sequences, morphology, and paleobotany. *Am. J. Bot.* 86, 1168–1181.

Gunter, L.E., Kochert, G., Giannasi, D.E., 1994. Phylogenetic relationships of the Juglandaceae. *Pl. Syst. Evol.* 192, 11–29.

Kalkman, C., 1988. The phylogeny of the Rosaceae. *Bot. J. Linn. Soc.* 98, 37–59.

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Wallander, E., Albert, V.A., 2000. Phylogeny and classification of the Oleaceae based on *RPS16* and *TRNL-F* sequence data. *Am. J. Bot.* 87, 1827–1841.

Wiegrefe, S.J., Sytsma, K.J., Guries, R.P., 1994. Phylogeny of elms (*Ulmus*, Ulmaceae): molecular evidence for a sectional classification. *Syst. Bot.* 19, 590–612.

Appendix C. Values used in the analysis of the effects of life-history attributes on covariation in seed production for each species used. Studies from which data were obtained and the length of the individual times series are reported in Appendix A. Common names and group membership are reported in Table 1. Definitions of each variable are provided in the text.

Species	Phenology	Age at first reproduction	Successional type	Growth rate	Longevity	Seed weight	Geographic range
<i>Quercus rubra</i>	4.00	50	3	4	200	3.64	3
<i>Q. coccinea</i>	4.50	20	2	3	50	1.24	2
<i>Q. velutina</i>	4.00	40	3	3	100	1.86	3
<i>Q. marilandica</i>	5.00	NA	2	4	100	NA	1
<i>Q. alba</i>	5.00	50	3	2	300	4.46	3
<i>Q. prinus</i>	4.00	20	3	3	300	1.20	2
<i>Q. stellata</i>	4.00	25	2	2	250	1.20	2
<i>Acer rubrum</i>	3.00	4	3	3	115	0.02	3
<i>A. saccharum</i>	3.25	60	5	2	300	0.07	2
<i>Betula alleghaniensis</i>	2.75	40	3	4	150	0.001	1
<i>B. papyrifera</i>	5.25	15	2	2	170	0.0008	1
<i>Carya glabra</i>	4.50	30	3	3	200	2.27	3
<i>Carya ovata</i>	4.50	40	4	3	275	4.55	3
<i>Carya tomentosa</i>	4.50	25	2	2	200	5.00	2
<i>Celtis occidentalis</i>	4.50	15	3	2	150	0.08	1
<i>Crataegus spp.</i>	5.25	NA	2	5	40	33.00	3
<i>Fagus grandifolia</i>	4.25	60	5	2	300	3.50	2
<i>Fraxinus americana</i>	4.50	37	3	2	260	0.03	3
<i>Fraxinus nigra</i>	5.50	28	2	2	175	0.06	2
<i>Juglans nigra</i>	5.00	12	2	3	150	11.10	2
<i>Liriodendron tulipifera</i>	5.00	15	3	2	200	0.055	2
<i>Morus rubra</i>	4.50	7	4	4	100	0.0013	2
<i>Populus grandidentata</i>	4.50	15	1	2	80	0.0002	1
<i>Populus tremuloides</i>	4.50	4	1	2.5	100	0.0001	1
<i>Prunus serotina</i>	5.50	15	2	4	100	0.11	3
<i>Sassafras spp.</i>	4.00	25	1	4	100	0.08	2
<i>Tilia americana</i>	6.50	15	4	4	100	0.11	1
<i>Ulmus americana</i>	3.50	28	3	3	175	0.006	3

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