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Influence of weather at time of pollination on acorn production of *Quercus alba* and *Quercus velutina*

Robert A. Cecich and Neal H. Sullivan

Abstract: Pistillate flower development and acorn production were observed in small populations of white oak (*Quercus alba* L.) and black oak (*Quercus velutina* Lam.) in central Missouri from 1990 to 1997. There were significant year–year differences in the size of flower crops for both species and significant tree–tree differences in black oak. About 7% of the white oak flowers matured into acorns; most flowers aborted by early July, just after fertilization. About 12% of the black oak flowers matured into acorns, but some individual trees never or rarely produced a mature acorn. The number of fertilized flowers in white oak and black oak in early July was positively correlated with acorn production. Over all trees and years, the number of flowers and acorns were significantly correlated. Acorn production varied in relation to weather variables during the time of pollination. Simple regression models were good predictors of white oak acorn production but not of black oak acorn production. Maximum temperature and the number of days with hail had negative effects on acorn production. The number of days of rain during the pollination period was positively correlated with flower survival in black oak but not with white oak.

Résumé : Le développement des fleurs femelles et la production de glands ont été observés dans de petites populations de chêne blanc (*Quercus alba* L.) et de chêne noir (*Quercus velutina* Lam.) dans le centre du Missouri de 1990 à 1997. Il y avait des différences significatives entre les années dans la production de fleurs chez les deux espèces et des différences significatives entre les arbres chez le chêne noir. Environ 7% des fleurs produisaient des glands chez le chêne blanc; la plupart des fleurs avortaient tôt en juillet, immédiatement après avoir été fertilisées. Environ 12% des fleurs produisaient des glands chez le chêne noir, mais certains arbres n'ont jamais ou rarement produit de glands matures. Le nombre de fleurs fertilisées tôt en juillet chez le chêne blanc et le chêne noir était positivement corrélé à la production de glands. Pour l'ensemble des arbres et des années, le nombre de fleurs et le nombre de glands étaient significativement corrélés. La production de glands variait en fonction des variables climatiques pendant la période de pollinisation. Des modèles simples de régression sont de bons outils pour prédire la production de glands chez le chêne blanc mais pas chez le chêne noir. La température maximale et le nombre de jours avec de la grêle avaient un effet négatif sur la production de glands. Le nombre de jours de pluie pendant la période de pollinisation était positivement corrélé avec la survie des fleurs chez le chêne noir mais pas chez le chêne blanc.

[Traduit par la Rédaction]

Introduction

The process by which oak pistillate flowers become acorns is understood reasonably well from an anatomical perspective (Cecich 1993). However, the way that various factors influence that process is not always clear. Weather does affect acorn production (Sork et al. 1993; Koenig et al. 1994*a*, 1996; Cecich 1997*b*). The emergence of staminate inflorescences and shedding of pollen hasten with rising temperatures and lower relative humidity (Romashov 1957; Sharp and Chisman 1961; Jovanovic and Tucovic 1975; Wolgast and Stout 1977). Sharp and Sprague (1967), finding no correlation with relative humidity and acorn yields in field studies, concluded that spring temperature was the primary factor in determining the success of acorn crops. Temperature may directly or indirectly influence the time of flower emergence through branch and leaf elongation (Minina 1954). Low temperatures in the spring do not affect the amount of flowers unless there is a freeze sufficient to damage shoots and leaves (Sharp 1958). Late-spring freezes can kill both first-year (Sork and Bramble 1993) and second-year (Wolgast and Trout 1979) pistillate flowers in oaks of the *Erythrobalanus* subgenus. Sork et al. (1993) found that acorn production was negatively correlated with the severity of summer drought, a combination of temperature and rainfall effects. Genetic control of acorn production has been examined previously (Cecich 1993). For instance, Farmer (1981) found that in a given year acorn production in white oak (*Quercus alba* L.) was highly correlated with the percentage of fertilized pistillate flowers, while year-to-year differences were associated with variation in the number of flowers that emerged.

Most abortion during the acorn production process occurs between the stages of flower emergence and fertilization (Cecich 1993). Up to 100% of the flowers that emerge can abort during that time (Williamson 1966; Kossuth 1974; Cecich 1997*b*). Pollen catkins appear about 1 week before new shoots begin to elongate and leaves unfold. Thus, successful

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pollination may be subject to environmental conditions for at least 2 weeks before pollination occurs (Neilson and Willstein 1980). Determining what weather factors affect specific physiological and structural processes during this time should prove useful in increasing our understanding of acorn production and in predicting acorn yields. This study evaluates acorn production and the percent survival of pistillate flowers into acorns for white oak and black oak (*Quercus velutina* Lam.) in relation to several weather factors, 1 and 2 weeks before, during, and 1 week after the time of pollination.

Methods

Study trees. 12 black oaks and 9 white oaks from 12 to 25 m tall, were located in a closed-canopy forest on the Thomas S. Baskett Wildlife Research and Education Area, Ashland, Mo. (38°N, 92°W). Sampling of the oak flowers was done along a forest road with a "cherry picker," a truck equipped with a 13-m hydraulic boom that reached to a maximum height of 16 m.

The elongating branches from five terminal branch buds, and any subtending lateral buds, were selected on each tree from 1990 to 1997. For black and white oak, the total flower count was recorded and survival of the pistillate flower populations was monitored. Black and white oak flowers were counted weekly from the time of pollen shed to early July and then monthly until early September. However, since black oak flowers require two growing seasons to become acorns, their "second-year" flowers were counted monthly, beginning in late April or early May and ending in September. Therefore, 1996 was the last black oak flower year, since their acorns matured in 1997. The last year for observing white oak flowers was 1997, since their acorns mature in the same season as pollination. An approximate date for the completion of pollen shed was recorded each year based on the change in catkin color from bright yellow to dull brown once pollen was shed. Both species shed pollen for about 1 week, with peaks of activity for black oak several days earlier than the peak for white oak.

A necessary step to understanding the acorn production process is an awareness of some of its yield components. For the purpose of this study, these components include the following.

(1) Flower initiation is the process whereby chemical, genetic, and abiotic factors interact during a critical time period to cause a meristem to commit itself to become a flower or flower part (Mandel and Yanofsky 1995; Weigel and Nilsson 1995).
(2) Differentiation is the structural manifestation of the initiation process. In white oak, the male inflorescence was first observed in late May and the female inflorescence in late summer (Merkle et al. 1980).
(3) Emergence of the flowers in spring is associated with receptivity of the stigmas and shedding of pollen. In central Missouri, pollination of white oak and black oak occurs from late April to early May, depending on the year.
(4) Fertilization occurs in mid-June of the first growing season in white oak (*Lepidobalanus* subgenus) and in late June of the second growing season in black oak (*Erythrobalanus* subgenus) (Cecich 1997*a*).
(5) Maturation encompasses the development of the flower and its embryo into an acorn.

The yield components for white oak acorn production were classified as the number of flowers at emergence (*F*) and flower survival on July 1, following fertilization in mid-June (*J*). Since black oak requires two growing seasons from flower emergence to acorn maturation, the growing seasons were designated with a 1 or 2. Thus, for the first growing season, the number of flowers at emergence is *F*, flower survival on July 1 following pollination is J1, and flower survival in early September is S1. For the second growing season, flower survival on or about May 1 is M2, and flower survival on July 1 following fertilization in late June is J2.

An estimate of acorns per tree was calculated with the procedure of Cecich and Larsen (1998). The number of branch forks from the ground to a terminal bud at the crown perimeter was found to be 8.9 ± 1.1 (mean ± SD). This value is used to estimate the number of branch tips on the surface of the crown of an average oak tree. Assuming there is dichotomous branching, the number of branch ends would be two to the power equal to the number of forks ($2^{8.9}$ or 478 terminal branch ends). The mean number of acorns per tree was estimated by multiplying 478 times the mean number of acorns from the five-branch sample originating within one of these terminal ends.

Climatological data for the months of April and May during the years 1988–1997 were retrieved from data bases at the nearby Columbia Regional Airport. Daily weather variables of interest were average temperature (°C), maximum temperature (°C), minimum temperature (°C), relative humidity (RH), days with fog, days with rain, and days with hail. Except for 1997, the temperature dropped to a low of 0°C on only one night during April and May of the study years. Since the April and May time period was considered too long to evaluate the effects of weather on the pollination process, the weather data for a given year were separated into weekly increments defined by the estimated pollination date (EPD) for that year. For example, if pollen were shed with a peak of activity on May 1, the 7 days including the 3 days before and after May 1 would make up the week of the EPD. One and 2 weeks earlier are noted as EPD − 1 and EPD − 2, respectively; the week after the EPD is noted as EPD + 1. Thus, the pollination season in a given year was defined by the period from EPD − 2 to EPD + 1. The EPDs for black and white oaks were generally about 3 or 4 days apart but are shown as the same dates each year for convenience, except for 1993, when black oak shed pollen about 1 week ahead of white oak. Since the recorded weather data were daily averages, the variation within a day could not be assessed, and so the data were pooled into weekly EPD values that were evaluated in relation to percent flower survival and acorn production. Ultimately, the analysis of weather effects on acorn production was based on the 4-week EPD totals or means, since we were interested in the overall effects, rather than the individual tree effects.

Data were examined with analysis of variance, linear regression, the Pearson product–moment correlation, and the Bonferroni multiple comparison test (SAS Institute Inc.1994). Differences in responses among categorical variables (species, tree, and year) were tested using ANOVA. Differences in response among these categorical variables and the continuous variables (weather) were tested using analysis of covariance. However, for a given year, the same weather data was applied to all the trees since only one source of weather data was available. Thus, both weather and year were implicitly connected and could not be modeled simultaneously. Differences among trees was minimal. Since inclusion of the categorical variables was not possible or considered necessary, regression techniques became an equivalent method of testing for the influence of weather. Before analysis, percentage data were arcsine transformed, and data sets with numerous zeros were transformed to $(y + 0.5)^{0.5}$ (Steel and Torrie 1980).

Results

Flowering and acorn production data from the 12 black oak and 9 white oak trees are presented in Tables 1 and 2, respectively. In black oak and white oak there were significant differences between years in the number of flowers produced ($P < 0.0002$ for black oak and $P < 0.0001$ for white oak). In both species, the largest flower crop, about two to

Table 1. The number of pistillate flowers and resulting acorns on five branch tips per tree in black oak, 1990–1997.

Tree	Year and stage of development[a]													
	90-F	91-A	91-F	92-A	92-F	93-A	93-F	94-A	94-F	95-A	95-F	96-A	96-F	97-A
1	50	2	34	0	57	11	64	17	40	4	28	2	47	19
2	79	10			63	21	42	8			62	3	44	21
3	24	0	44	11	53	2	67	14	62	12	37	9	32	3
4	190	14	19	0	29	1	52	3	66	0	43	3	35	12
5	220	0	55	0	53	0	78	1	63	0	52	0	34	0
6	49	9			58	6	34	7			47	1	36	8
7	13	0					68	5	36	6	16	0	36	0
8	42	1	54	12	72	15	50	2	54	5	65	7	51	18
9	41	3			32	4	55	4	42	0	73	5	41	20
10	262	22	39	4	62	24	50	0	49	8	56	9	39	15
11	233	49	127	25	93	19	96	18	52	1	91	12	58	19
12	318	0	70	0	60	0	86	0	68	0	100	0	65	0
Mean	126.8	9.2	55.3	6.5	57.5	9.4	61.8	6.6	53.2	3.6	55.8	4.3	43.2	11.3
SD	109.2	14.4	32.8	9.0	17.4	9.0	18.3	6.4	11.4	4.2	24.5	3.4	10.3	8.6
Percent[b]		7		12		16		11		7		8		26
Acorns per tree		4242		3172		4398		3249		1780		2134		5369

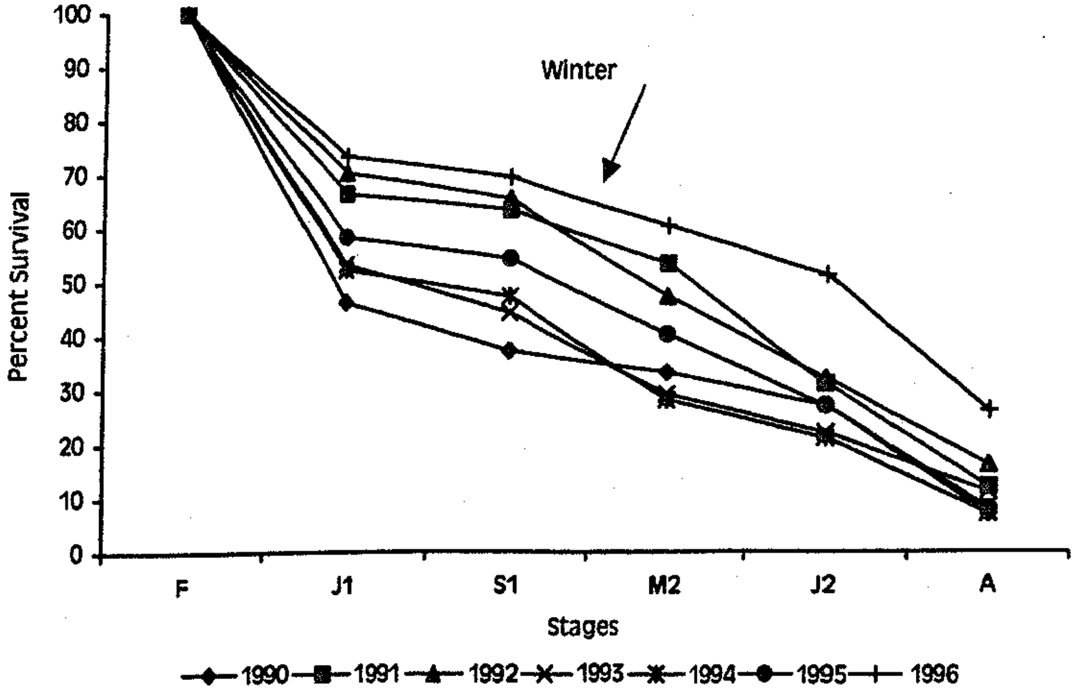
[a]Missing values indicate there was no flower crop that year and, thus, no acorn crop. F, number of pistillate flowers; A, number of acorns.
[b]Percent flower survival into acorns.

Table 2. The number of pistillate flowers and resulting acorns in white oak, 1990–1997.

Tree	Year and stage of development[a]															
	90-F	90-A	91-F	91-A	92-F	92-A	93-F	93-A	94-F	94-A	95-F	95-A	96-F	96-A	97-F	97-A
1	74	6	43	4	36	0	38	0	101	0	65	6	70	4		
2	82	5	60	15	30	4	27	8	95	0	40	8	38	9	4	0
3	248	4	16	3	60	1			50	0						
4	158	0	65	0	83	1			46	0	139	11	85	0	17	0
6	203	8	37	3	83	5	85	6	65	3	94	16	28	4	13	0
7	34	0	86	1	26	0	50	2	47	0	63	9	39	1		
8	103	1	56	1	45	0	66	4	107	0	167	32	34	6	23	0
9	220	6	30	0	30	1	55	1	146	0	39	6	32	3	6	0
11	195	62			37	9	44	13	127	0	61	15	47	23		
Mean	146.3	10.2	49.1	3.4	47.8	2.3	52.1	4.9	87.1	0.3	83.5	12.9	46.6	6.3	12.6	0.0
SD	75.3	19.6	22.1	4.9	22.4	3.1	19.1	4.6	36.9	1.0	46.8	8.6	20.3	7.3	7.8	0.0
Percent[b]		7		7		5		9		0		15		14		0
Acorns per tree		4895		1502		1142		2316		1665		5987		2985		0

[a]Missing values indicate there was no flower crop that year and, thus, no acorn crop. F, number of flowers; A, number of acorns.
[b]Percent flower survival into acorns.

Fig. 1. Percent survival of black oak pistillate flowers during the 1990–1996 flowering years. Acorns mature in the second growing season.



three times as large as subsequent flower crops, was produced in 1990. Most of the black oak flowers in 1990 were produced on five trees (Nos. 4, 5, 10, 11, and 12). In subsequent years, trees 11 and 12 continued to be, relative to the other black oaks, the "best" flower producers (Table 1). As a contrast, tree 7 produced few flowers, except for 1993. In two consecutive years it did not have pistillate flowers or pollen catkins. The among-tree differences in black oak flower number were significant ($P < 0.02$).

The large number of white oak flowers in 1990 occurred on six of the nine trees (Table 2). Tree 8 came closest to annually producing a good flower crop but only produced a relatively good acorn crop in 1995. The smallest white oak flower crop, about 20% as large as the study average, was observed in 1997, the year of a severe late spring freeze. There were no significant among-tree differences in flower number for white oak.

Black oak

There were significant differences among the black oak trees for both acorn production ($P < 0.0001$) and the percent survival of flowers into acorns ($P < 0.02$). However, the source of the variation differed between these response variables. A Bonferroni multiple comparison test for acorn production among trees indicated that tree 11, which produced the most acorns per branch, was the major source of the variation. Tree 12, the other consistently good flower producer, never produced a mature acorn during the years of this study, and tree 5 produced only one acorn. A large percentage of tree 12's reproductive potential was lost every year during July of the second growing season during the initial stages of cotyledon and embryo enlargement, indicating the possible expression of late embryonic lethal alleles (Fisher 1965) carried maternally by tree 12. The estimated number of black oak acorns per tree ranged from 1780 in 1994 to 5369 in 1996 (Table 1). These values are within the range estimates reported by Burns et al. (1954).

Percent flower survival averaged about 12% over all trees and years (Fig. 1). A Bonferroni test for flower survival indicated that no paired tests among the trees were significant but that the major sources of variation were tree 12 (no survival) and tree 5 (low survival). There was not an overall significant difference ($P < 0.05$) among years in terms of acorn production for black oak, but there were significant differences ($P < 0.0003$) in terms of percent flower survival, with more flowers surviving in 1996.

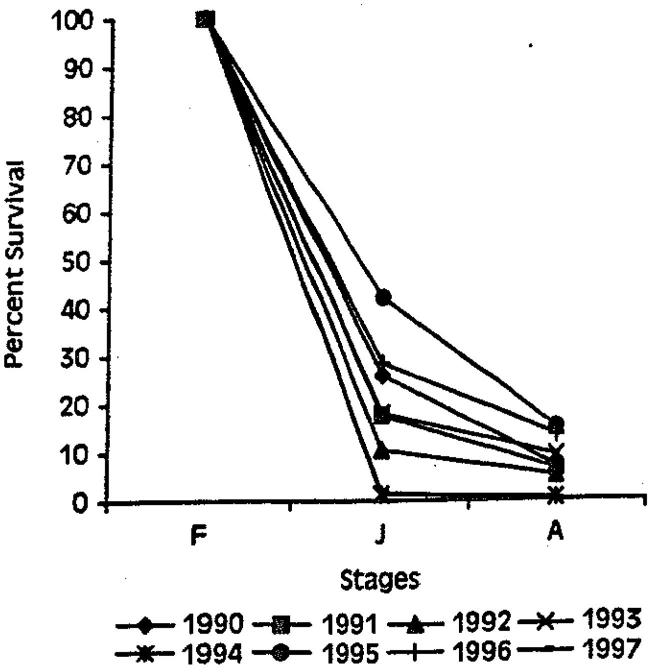
When flower and acorn crops were pooled by year, the number of flowers was not significantly correlated with the number of acorns ($P < 0.05$). However, the correlation of flower number and acorn production over all trees and years was highly significant ($P < 0.0002$). This result is most likely related to an increase in the degrees of freedom (82 vs. 7).

White oak

There was not an overall significant difference ($P > 0.34$) among the white oak trees for the number of acorns produced or the percentage of flowers surviving to the acorn stage. The percentage of flowers surviving to the acorn stage in September averaged about 7% over all years. On average, about 80% of the flower loss for all white oak trees occurred between the time of pollination and shortly after fertilization (Fig. 2). There were significant differences among years in terms of white oak acorn production ($P < 0.04$) and percent flower survival ($P < 0.01$). The low survival values in 1994 and 1997 (Table 2) appear to account for this result.

The number of acorns was highly correlated with the number of fertilized pistillate flowers on July 1 ($r = 0.964$,

Fig. 2. Percent survival of white oak pistillate flowers during the 1990–1997 growing seasons.



$P \leq 0.0002$). This relationship is consistent with that observed in black oak where flower survival in July of the second year (post-fertilization) was highly correlated with acorn production ($r = 0.918$, $P < 0.0001$). As with black oak, the initial white oak flower numbers, when pooled by years, are not significantly correlated with the number of acorns ($P < 0.05$). However, the correlation of flower number and acorn production over all trees and years was highly significant ($P < 0.0004$). The estimated number of white oak acorns per tree ranged from zero in 1997 to 5987 in 1995 (Table 2). These values are within the range estimates reported by Burns et al. (1954).

Estimated pollination date (EPD)

There were both positive and negative effects of the weather variables during the period of the EPD on acorn production and percent of flowers surviving to the acorn stage. The significant models predicting white oak acorn production typically had one or two parameters. Maximum temperature had a significant negative effect upon acorn production ($P = 0.05$). Relative humidity (RH) alone had a significant positive effect ($P = 0.009$). The models with RH along with one temperature parameter were also significant and produced the best fit ($R^2 = 0.14$). When RH was regressed in association with one of the temperature variables, the parameter coefficient for RH was always positive and the coefficients for each of the temperature variables were always negative. The number of days with fog was the only significant predictor ($P = 0.006$) among the "event" variables (rain, fog, and hail), and its effect was positive.

The significant models predicting percent flower survival in white oak were also one- or two-parameter models. Fog and RH alone had positive effects, while hail had a negative effect. Combinations of two of the three temperature parameters produced a better model fit ($R^2 = 0.20$) than fog, hail, or RH.

Simple models were not good predictors of black oak acorn production. Significant relationships could be found, but the models required five parameters to be significant ($P < 0.05$) and the R^2 was low (0.04). However, simple models were successful at predicting percent flower survival. Both fog and rain were positively correlated with survival ($R^2 = 0.05$ and 0.20, respectively).

Discussion

During the 4-week pollination season, as defined by the EPD, certain weather factors affected acorn production and percent flower survival. The number of days with hail was negatively correlated ($P = 0.03$) with the percentage of white oak flowers surviving to the acorn stage. Hail may affect flower survival and acorn production in several ways: (*i*) it can damage or remove leaves, thereby reducing the total leaf area and the production of photosynthates for export to the developing flowers and acorns; (*ii*) it can remove the fragile catkins (and, thus, the pollen source) if the hail occurs before the pollen is shed; and (*iii*) it can damage or remove pistillate flowers, especially those of white oak. Because of their relatively long peduncle, they tend to be more fragile than those of black oak, which are tightly appressed to the branch. However, the long stigma–styles of the black oak flowers are probably more susceptible to hail damage than the flattened or sessile stigma–styles of white oak. It is not unusual to observe black oak flowers in their first or second growing season with all three styles broken. If styles are broken before pollen tubes cease growing in mid-May (Cecich and Haenchen 1995; Cecich 1997*a*), then the flower will not be fertilized in the second growing season and will abort. Since pollen tubes cease growth in mid-May just below the point where the style usually fractures, the visible portion of the perianth (Cecich 1997*a*), they can resume growth to accomplish fertilization.

The effects of the late spring freeze of 1997 on acorn production depended upon species. Flower differentiation, which continues through the period of emergence (Cecich 1993), appeared to have been disrupted by the late spring freeze in 1997. Vegetative tissues, such as bud scales, leaf primordia, and unelongated stems, at the distal ends of the branches were also frozen. The number of emerging white oak flowers in 1997 was only about 20% of the average for all the other years and their emergence was delayed about 2 weeks later than the average date (May 1). These observations agree with Sharp (1958) who concluded that low temperatures in the spring did not affect flowering unless there was a freeze sufficient to damage shoots and leaves. There was a complete loss of the white oak acorn crop in 1997. However, the second-year black oak flowers (those pollinated in 1996) did not appear to suffer freezing damage in 1997. This is opposite to what Wolgast and Trout (1979) observed in *Quercus ilicifolia* Wangenh. The mean number of black oak flowers in 1996 was the smallest (43.2), but the percent survival was the best (26%). Perhaps the reduction of dry matter that would normally have been required for the production of pistillate flowers and pollen in the spring of 1997 (data not included in this paper) lead to a shunt of resources toward acorn development in the summer of 1997.

High daily maximum temperature always had a negative effect on white oak acorn production and flower survival and on black oak flower survival. Sork and Bramble (1993) and Sork et al. (1993) showed that warm spring temperature was positively correlated with good acorn crops. However, in northern red oak (*Quercus rubra* L.) and black oak, they found that the high correlation occurred during the year of acorn maturation (the second growing season), not during the year of pollination. They suggested that the warm spring weather might affect ovule development and fertilization. In the current study, the effect of average temperature on white oak acorn production and flower survival was both positive and negative, depending on parameters associated with it in the models. Sork and Bramble (1993) found that average temperature alone in late April and early May was positively correlated with white oak acorn production.

The effects of RH, rain, and fog during the EPD are not so easily reconciled in terms of their impact on the acorn production or flower survival. Those parameters were expected to have negative impacts on the acorn production process. Relative humidity, a significant contributor to the variation in white oak acorn production and flower survival, had no measurable effect on black oak. The daily averages for RH were generally above the 60% threshold described by Wolgast and Stout (1977) as necessary for pollen release. If hourly values of RH were available, then the "4 h, low relative humidity" period or window that Sharp and Chisman (1961) described as necessary for pollen release could also have been evaluated. Rain had a significant positive effect on black oak flower survival ($P = 0.0001$) but no effect on white oak. The effects of rain during the EPD may be on the overall vigor of the trees, rather than negatively affecting pollen dispersal in association with high rh (Wolgast and Stout 1977). Fog had positive effects on flower survival of both white and black oak. Since it demonstrated a weak autocorrelation with both RH and rain, its inclusion in the regression models is not surprising.

Reliably predicting the size of an acorn crop more than a few weeks before acorn drop has proven to be a difficult task (Cecich 1993; Gysel 1958; Koenig et al. 1994*b*). Numerous pistillate flowers in the spring do not guarantee a large acorn crop (Sharp 1958; Sharp and Chisman 1961; Wright 1953; Gysel 1956; Jovanovic and Tucovic 1975; Feret et al. 1982; Sork and Bramble 1993; Cecich 1997*b*). Since there was little loss of white oak flowers in the present study between July and September, the July 1 value appears to be a good estimator of current-year acorn production. The percentage of white oak flowers surviving to July 1 accounts for 93% of the variation in acorn production ($R^2 = 0.928$). In black oak, the regression coefficient for flower development in July of the second year and acorn production ($R^2 = 0.869$) was also highly significant. These observations support the conclusions of Romashov (1957) and Farmer (1981) that the flowers remaining on the tree after fertilization were a good index of the future acorn crop. These projections do not include the negative impact that insects can play in the loss of acorns, reduction in germination, or seedling viability (Oak 1993; Gribko 1995; Post et al. 1998).

References

Burns, P.Y., Christisen, D.M., and Nichols, J.M. 1954. Acorn production in the Missouri Ozarks. Univ. Mo. Agric. Ext. Bull. No. 611.

Cecich, R.A. 1993. Flowering and oak regeneration. *In* Proceedings, Oak Regeneration: Serious Problems, Practical Recommendations, 8–10 Sept. 1992, Knoxville, Tenn. *Edited by* D.L. Loftis and C.E. McGee. USDA For. Serv. Gen. Tech. Rep. No. SE-84. pp. 79–95.

Cecich, R.A. 1997*a*. Pollen tube growth in *Quercus*. For. Sci. **43**: 140–146.

Cecich, R.A. 1997*b*. The influence of weather on pollination and acorn production. *In* Proceedings of the 11th Central Hardwood Forest Conference, 23–26 Mar. 1997, Columbia, Mo. *Edited by* S.R. Pallardy, R.A. Cecich, H.E. Garrett, and P.S. Johnson. USDA For. Serv. Gen. Tech. Rep. GTR-NC-188. pp. 252–261.

Cecich, R.A., and Haenchen, W.W. 1995. Pollination biology of northern red and black oak. *In* Proceedings of the 10th Central Hardwood Forest Conference, 5–8 Mar. 1995, Morgantown, W.V. *Edited by* K.W. Gottschalk and S.L.C. Fosbroke. USDA For. Serv. Gen. Tech. Rep. NE-197. pp. 238–246.

Cecich, R.A., and Larsen, D.R. 1998. Bud demography and bifurcation in *Quercus alba* L., and *Quercus velutina* Lam. *In* Proceedings of a Conference on Diversity and Adaptation in Oak Species, 12–17 Oct. 1997, University Park, Pa. *Edited by* K.C. Steiner. Pennsylvania State University, University Park. pp. 68–75.

Farmer, R.E., Jr. 1981. Variation in seed yield of white oak. For. Sci. **27**: 377–380.

Feret, P.P., Kreh, R.E., Merkle, S.A., and Oderwald, R.G. 1982. Flower abundance, premature acorn abscission, and acorn production in *Quercus alba* L. Bot. Gaz. **143**: 216–218.

Fisher, R.A. 1965. The theory of inbreeding. Academic Press, New York.

Gribko, L.S. 1995. The effect of acorn insects on the establishment and vigor of northern red oak seedlings in north-central West Virginia. *In* Proceedings of the 10th Central Hardwood Forest Conference, 5–8 Mar. 1995, Morgantown, W.V. *Edited by* K.W. Gottschalk and S.L.C. Fosbroke. USDA For. Serv. Gen. Tech. Rep. NE-197. pp. 430–431.

Gysel, L.W. 1956. Measurement of acorn crops. For. Sci. **2**: 305–313.

Gysel, L.W. 1958. Prediction of acorn crops. For. Sci. **4**: 239–245.

Jovanovic, M., and Tucovic, A. 1975. Genetics of common and sessile oak (*Quercus robur* L., and *Q. petraea* Liebl.). Ann. For. 7: 23–53.

Koenig, W.D., Mumme, R.L., Carmen, W.J., and Stanback, M.T. 1994*a*. Acorn production by oaks in central coastal California: variation within and among years. Ecology, **75**: 99–109.

Koenig, W.D., Knops, J.M.H., Carmen, W.J., Stanback, M.T., and Mumme, R.L. 1994*b*. Estimating acorn crops using visual surveys. Can. J. For. Res. **24**: 2105–2112.

Koenig, W.D., Knops, J.M.H., Carmen, W.J., Stanback, M.T., and Mumme, R.L. 1996. Acorn production by oaks in central California: influence of weather at three levels. Can. J. For. Res. **26**: 1677–1683.

Kossuth, S.V. 1974. Premature acorn abscission in white oak (*Quercus alba* L.). Ph.D. dissertation, Yale University, New Haven, Conn.

Mandel, M.A., and Yanofsky, M.F. 1995. A gene triggering flower formation in *Arabidopsis*. Nature (London), **377**: 522–524.

Merkle, S.A., Feret, P.P., Croxdale, J.G., and Sharik, T.L. 1980. Development of floral primordia in white oak. For. Sci. **26**: 238–250.

Minina. E.G. 1954. Biological bases of flowering and fruit-bearing in oak. Tr. Inst. Lesa Akad. Nauk SSSR. **17**: 5–97. [*Translated by* Indian National Scientific Documentation Centre. Delhi, India.]

Neilson. R.P., and Willstein, L.H. 1980. Catkin freezing and acorn production in gambel oak in Utah. 1978. Am. J. Bot. **67**: 426–428.

Oak. S.W. 1993. Insects and diseases affecting oak regeneration success. *In* Proceedings. Oak Regeneration: Serious Problems, Practical Recommendations. 8–10 Sept. 1992. Knoxville, Tenn. *Edited by* D.L. Loftis, and C.E. McGee. USDA For. Serv. Gen. Tech. Rep. SE-84. pp. 105–111.

Post. L.S., Schlarbaum, S.E., Cecich. R.A., Barber. L.R., and Barrett. D. 1998. The effect of insecticide application on acorn quality in northern red oak (*Quercus rubra* L.). *In* Proceedings of the 7th Workshop on Physiology and Growth Problems in Oak Plantings, 28–29 Sept. 1998. South Lake Tahoe, Calif. *Edited by* D. McCreary. University of California, Berkeley, Calif. (Abstr.).

Romashov, N.V. 1957. Laws governing fruiting in oak. Bot. Zh. **42**: 41–56. [*Translated by* Israel Program for Scientific Translation.]

SAS Institute Inc. 1994. JMP. Statistics for the Apple Macintosh. SAS Institute Inc., Cary, N.C.

Sharp, W.M. 1958. Evaluating mast yields in the oaks. Penn. Agric. Exp. Stn. Bull. 635.

Sharp, W.M., and Chisman, H.H. 1961. Flowering and fruiting in the white oaks. I. Staminate flowering through pollen dispersal. Ecology, **42**: 365–372.

Sharp, W.M., and Sprague, V.G. 1967. Flowering and fruiting in the white oaks. Pistillate flowering, acorn development, weather, and yields. Ecology, **48**: 243–251.

Sork, V.L., and Bramble, J.E. 1993. Prediction of acorn crops in three species of North American oaks: *Quercus alba*, *Q. rubra* and *Q. velutina*. Ann. Sci. For. **50**(Suppl 1): 128s–136s.

Sork. V.L., Bramble, J., and Sexton, O. 1993. Ecology of mast-fruiting in 3 species of North American deciduous oaks. Ecology, **74**: 528–541.

Steel, R.G.D., and Torrie, J.H. 1980. Principles and procedures of statistics. McGraw-Hill, New York.

Weigel, D., and Nilsson, O. 1995. A developmental switch sufficient for flower initiation in diverse plants. Nature (London), **377**: 495–500.

Williamson, M.J. 1966. Premature abscissions and white oak acorn crops. For. Sci. **12**: 19–21.

Wolgast, L.J., and Stout, B.B. 1977. The effects of relative humidity at the time of flowering on fruit set in bear oak (*Quercus ilicifolia*). Am. J. Bot. **64**: 159–160.

Wolgast, L.J., and Trout, J.R. 1979. Late spring frost affects yields of bear oak acorns. J. Wildl. Manage. **43**: 239–240.

Wright, J.W. 1953. Notes on flowering and fruiting of northeastern trees. USDA For. Serv. Northeast. For. Exp. Stn. SP-60.