INFLUENCE OF WEATHER ON POLLINATION AND ACORN PRODUCTION IN TWO SPECIES OF MISSOURI OAKS

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Abstract: The process by which oak pistillate flowers become acorns is reasonably understood from an anatomical perspective; however, the way that various factors influence this process is still unclear. This study examined acorn production in a small population of white oak and black oak trees in central Missouri, from 1990 to 1995, in relation to weather variables (maximum and average temperature, relative humidity, fog, rain, and hail) at the time of pollination. There was large tree-tree and year-year variation in the size of flower crops and the dates when the flowers aborted. In the white oaks, acorn production was never high in relation to the number of flowers produced; most flowers aborted by July every year. The black oaks generally produced more acorns than the white oaks, but some individual trees never produced a mature acorn from their large flower crops. This variation in acorn production is correlated with certain weather variables at the estimated time of pollination and for the 1 or 2 weeks before and after those dates. Significant negative correlations with black and white oak acorn production were found for maximum temperature and the number of days with hail during pollination. Rain during pollination was negatively correlated with white oak flower survival in July. In both the black and white oaks, flower survival in early July, following pollination, was positively correlated with acorn production.

INTRODUCTION

Reliably predicting an acorn crop more than a few weeks before the acorns drop from a tree has proven to be a difficult task (Cecich 1993, Gysel 1958, Koenig and others 1994b). Feret and others (1982) concluded that production of white oak acorns could best be predicted from the number of peduncles borne per shoot. Sork and Bramble (1993) and Sork and others (1993) studied flower and acorn production in the same populations of northern red (*Q. rubra* L.), black (*Q. velutina* Lam.), and white (*Q. alba* L.) oaks for 8 years and provided evidence that these three species have inherent cycles of reproduction that are affected by weather and previous reproductive history—black oak with a 2-year cycle, white oak with 3-year cycles, and northern red oak with 4-year cycles. Koenig and others (1994a) have provided similar results for oaks in the Western United States. Although numerous pistillate flowers in the spring do not guarantee a large acorn crop (Sharp 1958, Sharp and Chisman 1961, Wright 1953, Gysel 1956, Cecich and others 1991), few-to-no flowers means a small to nonexistent acorn crop (Sork and Bramble 1993).

A necessary step to developing confidence in predicting an acorn crop is an awareness of major yield components of the acorn production process. These include: (1) *flower initiation*, 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*, the structural manifestation of the initiation process; e.g., the development of the staminate and pistillate inflorescences and their flower primordia (Merkle and others 1980); (3) *emergence* of the flowers in spring (the first visible phase of the flowering process) associated with receptivity of the stigmas and shedding of pollen; (4) *fertilization* of the egg by the male gamete; and (5) *maturation*, the development of the flower and embryo into an acorn. In central Missouri, pollination occurs in late April to early May. 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, in press). Mortality occurs at every stage of development, but up to 100% of flower loss can occur by the time of fertilization (Williamson 1966, Kossuth 1974, Cecich 1991).

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Weather affects acorn production. Emergence of staminate inflorescences and shedding of pollen increase or hasten with rising temperatures and the associated lower relative humidity (Romashov 1957, Sharp and Chisman 1961, Jovanovic and Tucovic 1975). Relative humidity (rh) can limit the size of an acorn crop. When Wolgast and Stout (1977) controlled rh at the time of pollen shed and stigma receptivity in a growth chamber, no acorns matured when rh exceeded 61%, but about half the flowers matured into acorns when rh was lower. Sharp and Sprague (1967) found no correlation with rh and acorn yields in field studies and concluded that temperature was a 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, Cecich 1993). Sharp (1958) found that low temperatures in the spring did not affect flowering unless there was a freeze sufficient to damage shoots and leaves. Late-spring freezes can kill first-year (Sork and Bramble 1993) or second-year (Wolgast and Trout 1979) pistillate flowers in the Erythrobalanus subgenus. Sharp and Sprague (1967) considered the impact of drought on differentiation of flowers and developing acorns to be inconclusive; however, Sork and others (1993) found a negative correlation of summer drought, a combination of temperature and rainfall effects, with acorn production.

How can we predict the size of an acorn crop more efficiently? Since most flower abortion occurs between pollination and fertilization, what weather factors are most likely to affect the pollination process? How might these factors and their timing or duration be related to the development of the flower? Any such speculation should be accompanied by some notation of time; i.e., during what specific time period is that factor operational? This study examines the impacts of several weather factors (maximum and average temperature, relative humidity, rain, and hail) 1 and 2 weeks before, during, and 1 week after the time of pollination, on the survival of flowers into acorns.

METHODS

Study trees (12 black oaks and 9 white oaks), from 10 to 25 m tall, were located along a forest road on the Thomas S. Baskett Wildlife Research and Education Area, Ashland, Missouri (38°N, 92°W). Sampling of the oak flowers was done from a bucket lift on a truck equipped with a 13-m hydraulic boom that reached to a maximum height of 16 m. Flower populations from 1990 to 1995 and their survival were monitored weekly from pollen shed to acorn maturation. On each tree, 5 current-year branches on a major branch system were selected for monitoring flower survival. The total flower survival of the five branches was recorded each week. For this study, 1994 was the last flower crop for black oak (acorns matured in 1995) and 1995 was the last year for white oak.

The dates of pollen shed for the study trees varied by species, from tree to tree within a species, and by year. Since controlled pollinations were not used to evaluate the timing of developmental events, an approximate date of pollen shed was recorded each year. Each species at the experimental site shed pollen for about 1 week, with peaks of activity for black oak several days earlier than that for white oak.

Climatological data for the months of April and May during the years 1988 to 1995, recorded at the nearby Columbia Regional Airport, were evaluated. Daily weather variables were average temperature (Ave C), maximum temp. (Max C), relative humidity (Hum), days with fog (Fog), days with rain (Rain), and days with hail (Hail). Only 1 night dropped to a low of 0° C, so the minimum temperature data were not used. Since the 2-month period was still too broad a timeframe for evaluating 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 on May 1, 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. The EPD's for black and white oaks were generally about 2-3 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 weather data were daily averages and the hourly variation could not be assessed, the data were pooled into weekly EPD values that were correlated with stages of flower development and acorn production. Statistical evaluation was done with the JMP software package for the Macintosh (SAS 1994).

RESULTS

Flower and acorn production in the black and white oaks varied by year and among individual trees (Tables 1, 2). In both species, the largest total flower crop was produced in 1990 and was about 2-3 times as large as subsequent flower crops. The coefficient of variation (cv) for the flower crops over the period of study was the same for both species, but the cv for acorn production was twice as large for white oak (Tables 1, 2).

Most of the black oak flowers in 1990 were produced on five trees (#4, 5, 10, 11, and 12). In subsequent years, trees 11 and 12 remained the "best" flower producers. Although tree 11 was the best acorn producer, the adjacent tree 12 never produced an acorn crop during this study (nor in the 1996 crop not reported here). A large percentage of tree 12's reproductive potential was lost every July and August of the second growing season during the stages of cotyledon and embryo enlargement, indicating the possible expression of late embryonic lethal alleles (Fisher 1965) carried by tree 12. As a contrast to good flowering, tree 7 was not a good flower-producing tree, except for 1993. In 2 consecutive years it did not have pistillate flowers or pollen catkins. Trees 2 and 6 did not have flowers in either 1991 or 1994. Acorn production, when considered as a percent of the number of flowers, varied between 7 and 15%, with an average of about 10% for all years (Table 3).

The heavy white oak flower crop in 1990 was produced on six of the nine trees (Table 2). Tree 8 came closest to regularly producing a good flower crop, but only produced a relatively good acorn crop in 1995. Acorn production for these white oaks, when considered as a percent of the initial flower crop, averaged about 7% over all years (Table 4).

Flower crops for all the black oaks were pooled by year and correlated with survival at the subsequent developmental stages (Table 5). The general tendency within a year was that all correlations with the flower crops were reduced the farther in time the developmental stage got from the flower stage. When the black oak developmental stages were examined across all flowering years, correlations with the acorn crop were significant for the J1 and S1 stages (Table 6).

White oak flower survival in July (J1) for all trees was negatively correlated with acorn production in the previous year ($r = -0.909$) and positively correlated with acorn production 2 years prior ($r = 0.913$). Percent survival of white oak acorns was highly correlated with the percent flower survival in July ($r = 0.956$), but weakly correlated with initial flower numbers ($r = 0.536$).

The weather variables, assembled as weekly averages, are shown in conjunction with the EPD classes in Table 7. Flower survival values between 1990 and 1995 were correlated with days of hail occurrence during the pollination season (includes all the EPD classes). White oak flower survival in July ($r = -0.867$) and acorn production in September ($r = -0.878$) both had significant negative correlations. For black oak, only survival at the J2 stage (July of the second growing season) showed a strong, but non-significant, negative correlation ($r = -0.856$) with hail during pollination; all other stages were weakly correlated.

The daily averages for relative humidity (rh) were generally above the 60 percent threshold described by Wolgast and Stout (1977). Therefore, no further direct investigation of the relationship of rh to pollen shedding and acorn production could be conducted. If hourly values of rh were available, then the "4 hr-low relative humidity" period or window that Sharp and Chisman (1961) described as necessary for pollen release could also have been evaluated. However, the two EPD's that contain rh values below 60% (EPD-1 and EPD-2 in 1994) were associated with the poorest white oak acorn crop during this study (3.6%).

Table 1. Number of black oak pistillate flowers (F) and acorns (A) on 5 branch tips per tree

Tree	Year and stage of development										r[1]	
	90-F	91-A	91-F	92-A	92-F	93-A	93-F	94-A	94-F	95-A		
1	50	2	34	0	57	11	64	17	40	4	0.898	*
2	79	10	0	0	63	21	42	8	0	0	0.810	
3	24	0	44	11	53	2	67	14	62	12	0.747	
4	190	14	19	0	29	1	52	3	66	0	0.954	**
5	220	0	55	0	53	0	78	1	63	0	-0.124	
6	49	9	0	0	58	6	34	7	0	0	0.901	*
7	13	0	0	0	0	0	68	5	36	6	0.850	
8	42	1	54	12	72	15	50	2	54	5	0.865	
9	41	3	0	0	32	4	55	4	42	0	0.572	
10	262	22	39	4	62	24	50	0	49	8	0.593	
11	233	49	127	25	93	19	96	18	52	1	0.985	**
12	318	0	70	0	60	0	86	0	68	0	0.000	
Mean	126.8	9.2	36.8	4.3	52.7	8.6	61.8	6.6	44.3	3.0		
sd	109.2	14.4	37.7	7.9	23.5	9.0	18.3	6.4	23.1	4.0		

r[1] Correlation coefficients for flower and acorn crops between 1990 and 1994.
*, ** indicate P>0 .05 and 0.01, respectively.
Coefficient of variation for population means over 5 year period: F = 56%, A = 42%.

Table 2. Number of white oak pistillate flowers (F) and acorns (A) on 5 branch tips per tree

Tree	Year and stage of development												r[1]	
	1990		1991		1992		1993		1994		1995			
	F	A	F	A	F	A	F	A	F	A	F	A		
1	74	6	43	4	36	0	38	0	101	0	65	6	0.141	
2	82	5	60	15	30	4	27	8	95	0	40	8	-0.366	
3	248	4	16	3	60	1	0	0	50	0	0	0	0.614	
4	158	0	65	0	83	1	0	0	46	0	139	11	0.466	
6	203	8	37	3	83	5	85	6	65	3	94	16	0.350	
7	34	0	86	1	26	0	50	2	47	0	63	9	0.373	
8	103	1	56	1	45	0	66	4	107	0.	167	32	0.814	*
9	220	6	30	0	30	1	55	1	146	0	39	6	0.376	
11	195	62	0	0	37	9	44	13	127	0	61	15	0.722	
Mean	146.3	10.2	43.7	3.0	47.8	2.3	40.6	3.8	87.1	0.3	74.2	11.4		
sd	75.3	19.6	26.4	4.7	22.4	3.1	28.3	4.5	36.9	1.0	51.8	9.1		

r[1] Correlation coefficients for flower and acorn crops from 1990 to 1995.
* = P> 0.05.
Coefficient of variation for population means over 6-year period: F = 55%, A = 87%.

Table 3. Percent survival at various stages of black oak flower development into acorns

	Tree No.												
Stage*	1	2	3	4	5	6	7	8	9	10	11	12	Mean
90-F	100	100	100	100	100	100	100	100	100	100	100	100	100
90-J1	28	51	38	55	55	31	46	43	56	38	71	43	46
90-S1	20	39	21	47	46	27	46	40	29	29	61	39	37
91-M2	20	32	17	45	43	22	38	36	22	26	60	38	33
91-J2	16	24	13	31	39	22	31	29	22	16	42	33	27
91-A	4	13	0	7	0	18	0	2	7	8	21	0	7
91-F	100		100	100	100			100		100	100	100	100
91-J1	44		84	63	87			74		46	63	66	66
91-S1	41		80	53	87			72		46	60	64	63
92-M2	41		57	16	82			72		46	56	57	53
92-J2	12		27	5	55			26		31	43	50	31
92-A	0		25	0	0			22		10	20	0	10
92-F	100	100	100	100	100	100		100	100	100	100	100	100
92-J1	58	84	70	55	77	36		75	59	77	78	97	70
92-S1	53	81	60	52	74	34		65	50	73	72	97	65
93-M2	49	70	55	17	68	26		50	28	50	42	58	47
93-J2	26	56	9	7	51	14		33	22	47	32	57	32
93-A	19	33	4	3	0	10		21	13	39	20	0	15
93-F	100	100	100	100	100	100	100	100	100	100	100	100	100
93-J1	56	57	72	27	79	53	37	30	38	48	79	65	53
93-S1	50	36	57	23	77	35	32	20	29	40	69	59	44
94-M2	41	24	30	13	60	32	28	6	13	10	54	35	29
94-J2	34	19	30	10	49	24	12	4	9	8	31	30	22
94-A	27	19	21	6	1	21	7	4	7	0	19	0	11
94-F	100		100	100	100		100	100	100	100	100	100	100
94-J1	80		71	27	76		58	56	48	45	15	40	52
94-S1	73		61	27	76		53	43	40	43	12	40	47
95-M2	10		53	18	51		47	28	14	20	4	38	28
95-J2	10		44	12	44		31	15	7	20	2	26	21
95-A	10		19	0	0		17	9	0	16	2	0	7

* Stage of development for the pistillate flowers, as indicated by month and growing season:
F = flowers; A = acorns; J, S, and M = July, September, and May, respectively;
1 and 2 indicate the first and second growing seasons.
Average survival of flowers to acorns is 10%.

Table 4. Variation in percentage of flower survival and acorn production in white oak

Stage*	Tree No. 1	2	3	4	6	7	8	9	11	Mean**
90-F	100	100	100	100	100	100	100	100	100	100
90-J	27	18	31	5	23	12	15	22	55	25.9
90-A	8	6	2	0	4	0	1	3	32	7.0
91-F	100	100	100	100	100	100	100	100	0	100
91-J	37	35	25	0	27	5	23	3	0	17.6
91-A	9	25	19	0	8	1	2	0	0	6.4
92-F	100	100	100	100	100	100	100	100	100	100
92-J	0	37	5	1	12	4	2	17	35	10.5
92-A	0	13	2	1	6	0	0	3	24	5.0
93-F	100	100	0	0	100	100	100	100	100	100
93-J	16	30	0	0	12	12	17	15	39	18.1
93-A	0	30	0	0	7	4	6	2	30	9.3
94-G	100	100	100	100	100	100	100	100	100	100
94-J	1	1	0	0	8	4	1	0	0	1.3
94-A	0	0	0	0	5	0	0	0	0	0.4
95-F	100	100	0	100	100	100	100	100	100	100
95-J	65	43	0	17	49	40	44	26	66	42
95-A	9	20	0	8	17	14	19	15	25	15

* F = flowers, J = flower survival on July 1, A = acorns.
** Average survival of flowers to acorns is about 7 percent.

Table 5. Correlation coefficients of individual black oak flower crops with their subsequent developmental stages during the two growing seasons

Flowering year	Stage and growing season J1	S1	M2	J2	AC
90-F	0.940*	0.935*	0.927*	0.921*	0.429
91-F	0.976**	0.972**	0.970**	0.952*	0.780
92-F	0.911*	0.892*	0.847	0.731	0.631
93-F	0.895*	0.913*	0.861	0.801	0.260
94-F	0.724	0.724	0.692	0.649	0.232
All years-F	0.966**	0.939*	0.931*	0.962**	0.709

*, ** = P> 0.05 and 0.01, respectively (n = 12).

Table 6. Correlations of black oak flower development stages with each other for the flowering years 1990 to 1994

	J1	S1	M2	J2	AC
J1	---	0.980**	0.792	0.741	0.955*
S1		---	0.825	0.748	0.879*
M2			---	0.974**	0.638
J2				---	0.619
AC					---

*, ** = P > 0.05 and 0.01, respectively. (n = 5)

Maximum temperature during pollination season (EPD-2 to EPD+1) was negatively correlated with black oak flower survival at the J1 and S1 stages (r = - 0.907* and - 0.950*, respectively). In white oak, maximum temperature was also negatively correlated with flower survival in July (r = - 0.950**) and with acorn production (r = -0.851*). Average temperature or days with fog, an indirect measure of humidity, showed no significant correlations with any developmental stages of either the white or black oak flowers.

Rain during the EPD was negatively correlated (P> 0.811) with white oak flower survival in July (r = - 0.829*). For black oak, there were negative correlations (r values between - 0.706 and - 0.837, ns) for rain during EPD+1 in relation to flower survival at all stages of development.

DISCUSSION

Certain components of weather (days with hail and maximum temperature) during the pollination period were found to be negatively correlated with acorn production. Hail (Table 7) may potentially affect flower survival and acorn production in several ways: it may (1) damage or remove leaves, which reduces total leaf area and, thereby, reduces production of photosynthates for export to the developing acorns; (2) remove the fragile catkins (and, thus, the pollen source) if the hail occurs before shedding; and (3) damage or remove pistillate flowers, especially those of white oaks which, because of the long and slender peduncle, tend to be more fragile than those of black oak, which are tightly appressed to the branch. However, the long styles of the black oaks are probably more susceptible to hail damage than the sessile styles of white oaks. It is not unusual to observe black oak flowers in their first or second growing season with missing styles. If styles are broken off before pollen tubes cease growing in mid-May (Cecich and Haenchen 1995; Cecich, in press), then the flower will not be fertilized in the second growing season and will abort. Since pollen tubes cease growth just below where the style fractures (the visible portion of the perianth (Cecich, in press)), they have the potential for resuming growth to accomplish fertilization.

The negative correlation of maximum temperature during the pollination season for black and white oak flower survival at J1 may indicate that the elevated temperature put pollen development out of synchrony with the receptivity of the pistillate flowers, causing the females to abort from lack of pollen. For instance, Sharp and Sprague (1967) speculated that a warm late April and a cool early May were related to early catkin emergence and delayed pollen dispersal, respectively. At their site, pollen usually was shed in late May. Under those weather conditions, pollen shed and pistillate flower receptivity were considered to be more closely aligned and thus related to good acorn crops. Similarly, in the current study, with pollen shed usually occurring in late April or early May, the relatively dry and warm conditions for EPD-1 and EPD-2 in 1994 may have altered the time relationship between pollen shed and pistillate flower receptivity, especially if considered in conjunction with the lower temperature and higher relative humidity during the EPD (Table 6). In white oak, maximum temperature was also negatively correlated with acorn production, which is highly correlated to flower survival at J1.

Table 7. Weekly averages of weather variables in relation to the EPD classes for black and white oak

			Weather variables					
EPD's	DATE		AVE C	MAX C	HUM	FOG	RAIN	HAIL
EPD-2	4/23/90		20.8	27	68	3	0	
	4/23/91		11.3	27	71	1	1	
	4/9/92		14.7	22	61	3	2	
	4/23/93		12.5	19	68	4	2	
	4/16/93	a	10.0	15	82	4	1	2
	4/16/94		16.6	25	51	0	1	1
	4/16/95		14.4	20	64	3	3	
EPD-1	4/30/90		12.4	17	72	2	1	
	4/30/91		16.5	17	65	2	4	
	4/16/92		18.0	23	71	3	3	1
	4/30/93		17.5	22	78	2	0	
	4/23/93	a	12.5	19	68	4	2	
	4/23/94		17.4	24	55	2	3	1
	4/23/95		11.1	17	68	3	2	
EPD	5/7/90		14.2	21	69	3	1	
	5/7/91		16.6	21	73	4	1	
	4/23/92		9.9	15	74	1	2	
	5/7/93		20.2	26	78	0	2	
	4/30/93	a	17.5	22	78	2	0	
	4/30/94		10.0	15	72	3	2	1
	4/30/95		9.9	14	75	5	0	
EPD+1	5/14/90		15.3	21	78	6	1	
	5/14/91		23.5	20	76	5		
	4/30/92		16.8	23	58	1	0	
	5/14/93		16.2	22	71	0	2	
	5/7/93	a	20.2	26	78	0	2	
	5/7/94		15.2	21	72	2	1	
	5/7/95		14.7	19	80	6	2	

a. The EPD dates and associated weather data for black oak in 1993 are 1 week earlier than those of white oak.

The negative correlation for white oak acorn production in the previous year and flower survival in July (r = - 0.909) may indicate that storage reserves in the tree are critical to the acorn development process only until the time of fertilization in mid-June. Then, as the acorn grows, primarily during cotyledon enlargement, the current-year photosynthates may become important as the energy source. Kossuth (1974) found that developing leaves and pistillate flowers of white oaks were not competitive sinks for photosynthates. The positive correlation of July flower survival with acorn production 2 years prior (r = 0.913) and the negative correlation for the previous year (r = - 0.909) can be viewed as evidence for biennial-bearing in white oak. However, this view must be tempered with the fact that, because of the number of years of data, the threshold for a significant r-value is 0.950. Sork and others (1993) provided evidence of a 3-year fruiting cycle in white oak and a 2-year cycle in black oak by using 8 years of individual tree data. Since there is little loss of white oak flowers between July and September, the July 1 value appears to be a good estimator of current-year acorn production.

There are two possible causes for the high flower counts in 1990: (1) an increase in the number of peduncles with 3 pistillate flowers (normally, the black oaks in this population have 2 pistillate flowers per peduncle; a few have 1 or 3); (2) an increase in the number of leaves per branch with flowers in their axils. That is, those leaves that usually would have vegetative buds in their axils could have had pistillate flowers. This assumes there was no increase in the number of leaves per branch in 1990. Unfortunately, a record of this potential variation was not kept during the study.

Genetic control over seed production has been examined by numerous investigators (Cecich 1993). For instance, Farmer (1981) found that in a given year acorn production in white oak was highly correlated with the percentage of fertilized pistillate flowers, while year-to-year differences were associated with variation in the number of flowers. The current study also provides evidence of tree-to-tree variation in white and black oak for both flower production and acorn production (Tables 1, 2). But, the data also suggest that weather factors may mediate the pollination process and eventually affect fertilization and acorn development. The coefficients of variation for flower production of the two species are identical (Tables 1, 2), but the twofold difference in cv's for acorn production indicates that factors such as weather are affecting subsequent development. The difference in cv's for acorn production in the black and white oaks (42% and 87%, respectively) also reflects the year-to-year consistency of acorn production in black oak (Sork and Bramble 1993).

Since the visible portions of the reproductive cycles in white and black oaks require one and two growing seasons, respectively, can one realistically ascribe the success or failure of the development of pistillate flowers into acorns to factors such as weather? That is, how and when does the weather affect differentiation? Although the data were evaluated differently, the present findings support the position of Sork and others (1993) and Koenig and others (1994a) that weather and previous reproductive history affect seed production. Furthermore, the results of this study provide evidence that weather at the time of a specific developmental event, such as pollination, can be correlated to acorn production.

LITERATURE CITED

Cecich, R.A. 1991. Seed production in oak. In (S. Laursen and S.L. Philips, eds.) The oak resource in the upper midwest - implications for management. June 3-6, 1991. Winona, MN: University of Minnesota. p. 125-131.

Cecich, R.A. 1993. Flowering and oak regeneration. In (D.L. Loftis and C.E. McGee, eds.) Oak regeneration: serious problems, practical recommendations. USDA Forest Service Gen. Tech. Rep. SE-84. p. 79-95.

Cecich, R.A. (in press). Pollen tube growth in *Quercus*. For. Sci.

Cecich, R.A. and W.W. Haenchen. 1995. Pollination biology of northern red and black oak. In (K.W. Gottschalk and S.L.C. Fosbroke, eds.) 10th Central Hardwood Forest conference. USDA Forest Service Gen. Tech. Rep. NE-197. p. 238-246

Farmer, R.E., Jr. 1981. Variation in seed yield of white oak. For. Sci. 27(2): 377-380.

Feret, P.P., R.E. Kreh, S.A. Merkle, and R.G. Oderwald. 1982. Flower abundance, premature acorn abscission, and acorn production in *Quercus alba* L. Bot. Gaz. 143(2): 216-218.

Fisher, R.A. 1965. The theory of inbreeding. Academic Press, New York. 150 p.

Gysel, Leslie W. 1956. Measurement of acorn crops. For. Sci. 2(1): 305-313.

Gysel, Leslie W. 1958. Prediction of acorn crops. For. Sci. 4(3): 239-245.

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

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

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

Kossuth, S.V. 1974. Premature acorn abscission in white oak (*Quercus alba* L.). New Haven, CT: Yale University. 127 p. Dissertation.

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

Merkle, S.A., P.P. Feret, J.G. Croxdale, and T.L. Sharik. 1980. Development of floral primordia in white oak. For. Sci. 26(2): 238-250.

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

Romashov, N.V. 1957. Laws governing fruiting in oak. Botanicheskii Zhurnal 42: 41-56. [Translated by Israel Program for Scientific Translation.]

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

Sharp, W.M. 1958. Evaluating mast yields in the oaks. Penn. Agric. Exp. Stn. Bull. 635. 22 p.

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

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

Sork, V.L. and J.E. Bramble. 1993. Prediction of acorn crops in three species of North American oaks: *Quercus alba, Q. rubra* and *Q. velutina*. Annales des Sciences Forestieres. 50 (Suppl 1): 128s-136s.

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

Weigel, D. and O. Nilsson. 1995. A developmental switch sufficient for flower initiation in diverse plants. Nature 377: 495-500.

Williamson, M.J. 1966. Premature abscissions and white oak acorn crops. For. Sci. 12(1): 19-21.

Wolgast, L.J. and B.B. Stout. 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 J.R. Trout. 1979. Late spring frost affects yields of bear oak acorns. J. Wild. Manag. 43(2): 239-240.

Wright, J.W. 1953. Notes on flowering and fruiting of northeastern trees. USDA Forest Service Sta. Pap. 60. 38 p.