USDA United States Department of Agriculture

Forest Service

Northeastern Research Station

General Technical Report NE-316

Proceedings

14th Central Hardwood Forest Conference

March 16-19, 2004
Wooster, Ohio

14th

CENTRAL HARDWOOD
FOREST CONFERENCE

NOTICE:

File size is 9.5MB, 539 pages

To access the Table of Contents linked to individual papers suitable for reprints, go to:
http://www.fs.fed.us/ne/newtown_square/publications/technical_reports/pdfs/2004/316papers/gtr316toc.pdf

OAK SEED PRODUCTION, WEEVIL (COLEOPTERA: CURCULIONIDAE) POPULATIONS, AND PREDATION RATES IN MIXED-OAK FORESTS OF SOUTHEAST OHIO

Cynthia L. Riccardi, Brian C. McCarthy and Robert P. Long[†]

ABSTRACT.—Oaks have dominated much of the central hardwood forest region for thousands of years. However, there have been geographically widespread reports of its failure to regenerate on many types of sites for many decades. Most studies have approached the oak regeneration problem through the examination of direct effects. There are many indirect ecological effects that have not been well studied. Anecdotal evidence suggests that Native Americans may have used fire for many reasons including control of insect predators and/or pathogens. We chose to examine how fire and/or thinning may *directly* influence oak seed production and how those treatments may *indirectly* impact seed quality by influencing the major species of pre-dispersal oak seed predators (curculionid weevils). Weevils have been known to destroy > 90% of a typical acorn crop. Two mixed-oak forests were selected for study in southeastern Ohio. Within each forest, four stands were selected and randomly assigned a control and a treatment: prescribed fire, thinned, thinned & followed by fire. Thinning treatments were executed during the fall-winter of 2000-2001, followed by controlled burns in the spring of 2001. After the treatments were executed, we selected two species for study: black oak (*Quercus velutina*) and chestnut oak (*Q. prinus*). We selected nine trees of each species (144 trees total) within each unit and erected two 0.25 m^2 seed traps beneath each tree. Traps were sampled monthly throughout the growing season and for a period after leaf drop (August-December) during 2001 and 2002 to collect seeds. Acorns were destructively sampled and scored as sound, aborted, weevil-depredated, or other. Treatments did not appear to strongly influence seed production or predation rates in the first growing season (floral buds had already initiated and treatment effect was likely minimal). However, during the second season, treatment influence was dramatic. Both oak species responded by producing considerably more seeds in the combined thin-burn units. Any unit receiving a burn also produced a significantly greater number of sound acorns (weevil depredation was lowest in burn units). Long-term studies are continuing to help work out the details of how silvicultural treatments may influence periodic seed-producing (masting) species such as oaks.

Based on stand composition and structure, numerous studies have concluded that there is the potential for large-scale conversion of mixed oak forests in the central Appalachians to domination by more mesic species. In stands where the overstory is dominated by oaks and hickories, the understory is often dominated by more shade tolerant maples and beech (Lorimer 1984, McCarthy and others 1987, Crow 1988). In addition, recent studies have begun to document the decline of oak in the overstory. The cause of decline in the overstory appears to be multi-causal and is likely the result of combined factors such as drought, acid deposition, atmospheric pollution, two-lined chestnut borer, and *Armillaria* fungi (Millers and others 1989, LeBlanc 1998). The seriousness of the overall problem has been recognized for almost two decades and examined in considerable detail (Loftis and McGee 1993); however, few immediate solutions have been forthcoming and many details are still not well understood.

The failure of oak to regenerate naturally has prompted an interest in the role of prescribed fire as a silvicultural tool. The suppression of fire for the past 60-80 years is correlated to the period of oak regeneration failure (Loftis and McGee 1993). The role of fire is still not well understood and there may be a variety of direct and indirect effects. Moreover, during this same time frame, there have been dramatic

[†]Research Ecologist (CLR) Pacific Wildland Fire Sciences Laboratory, USDA Forest Service, PNW Research Station, 400 N. 34th Street, Suite 201, Seattle, WA 98103-8600; Professor of Forest Ecology (BCM), Department of Environmental and Plant Biology, Ohio University, Athens, OH 45701-2979, and Research Plant Pathologist (RPL), Northeastern Research Station, USDA Forests Service, 359 Main Road, Delaware, OH 43015. BCM is corresponding author: to contact, call (740-593-8182) or e-mail at mccarthy@ohio.edu

shifts in wildlife populations (e.g., deer, turkey, and squirrel). The direct role of wildlife in the hardwood regeneration has been fairly well studied. Deer can have an enormous negative impact when their densities are sufficiently high (Harlow and others 1975, Marquis and others 1976, Tilghman 1989, Gill 1992, Healy and others 1997, Horsley and others 2003). Rodents may have a remarkable effect on pre- and post-dispersal seed mortality, often > 90% (Barnett 1977, Sork 1983, McCarthy 1994). And likewise, insects may negatively influence oak regeneration via pre- and post-dispersal seed depredation (Gibson 1972, Galford et al. 1991).

The relationship between fire, wildlife, and oak regeneration has received considerably less attention. With the exception of one study by Wright (1986) we are unaware of any other work that has experimentally evaluated the role of prescribed fire in controlling insect populations in mixed oak forests with the goal of increasing oak regeneration. While Galford et al. (1991) found that there were a number of acorn predators including acorn weevils (*Conotrachelus posticactus*), nitidulids (*Stelidota octomaculata*), and acorn moths (*Valentia glandulella*) that destroy great numbers of acorns in Pennsylvania oak stands, we concentrate here on the role of acorn weevils as they have been observed (BC McCarthy, *personal observation*) as being particularly problematic in southeastern Ohio mixed oak stands.

Several studies have examined the masting nature of seed production in oaks and hickories (Collins 1961, Christisen and Kearby 1984, Sork and Bramble 1993, Healy and others 1999, Greenberg 2000, Kelly and Sork 2002). Factors that influence mast production in oaks include weather during anthesis (Sharp and Chisman 1961, Cecich and Sullivan 1999), tree onotogeny (Greenberg 2000), genetics and site quality (Wolgast 1978, McCarthy and Quinn 1989), weather during maturation (Sharp and Sprague 1967), and predators (Gibson 1972, Short 1976, Barnett 1977, Lewis 1980, Gibson 1982, Weckerly and others 1989, Galford and others 1991). The effects of management strategies, e.g., mechanical thinning and prescribed fire, on seed production are not as clear. Healy and others (1999) suggest seed production is influenced more by individual tree and annual variation than by thinning. Additionally, the increased acorn production in thinned areas was a short term response and production returned to unthinned levels in ca. 6 years.

Historically, fire has been an integral component of the disturbance regime of many central Appalachian mixed-oak forests (Rouse 1986, Abrams 1992, Sutherland 1997, Brose and Van Lear 1998). Forest fire suppression since the turn of the century has changed the natural disturbance regime and may very well turn out to play a pivotal role in oak regeneration and forest conversion. What is less clear is whether fire plays a direct role or an indirect role in oak regeneration. Certainly, wildland fires open up the midstory, allow more light penetration, produce a flush of nitrogen in the system, and reduce herbaceous competition. Several large studies have been launched in Missouri (MOFEP) and Ohio (USFS) to better understand the role of fire in oak regeneration. The role of fire may involve a variety of direct and indirect effects.

We hypothesize that the role of fire in oak regeneration may be strongly tied to acorn weevil population dynamics and a concomitant increase in the availability of viable seed. Weevils have been found to kill up to 90% of oak (Barnett 1977, Galford et al. 1991, Gribko 1995) and hickory (McCarthy and Quinn 1989, McCarthy 1994) seed crops and have been implicated as a primary cause of oak regeneration failure (Marquis and others 1976, Weckerly and others 1989) in certain forests. The *Curculio* weevil life-cycle begins while the acorn is developing on the tree. The adult weevils emerge from late spring to early summer, after pollination has occurred. Females drill a hole into the developing nutmeat and eggs are deposited into a channel (Gibson 1969). The larvae consume the remaining nutmeat generally before the acorn detaches from the tree (Marquis and others 1976). Full-grown larvae hatch in 5 to 14 days (Brooks 1910). The *Curculio* larvae emerge from the acorn after it has fallen and will burrow up to 20 cm into the soil to over-winter. The adults emerge the following year and the process repeats. Adult *Conotrachelus* weevils tend to emerge later and will not oviposit through an acorn shell (Gibson 1964). Oviposition occurs in damaged, cracked, sprouted or previously infested acorns. Interestingly, the prime time for forest fires in southeastern Ohio is the autumn and spring—the same time that weevil larvae are emerging from the nuts (autumn) or from the soil as adults (spring). Fires during this time would result in major population declines for the weevil and decreased nut predation during fruit ripening in the summer and fall. Thus, the role of fire may be in

controlling the major seed predator of oak. If we are to manage oak forests for maximum wildlife abundance, we must begin to understand the relationship between fire, weevils (and other arthropods), and oak mast.

The objectives of this research are to examine the role of fire and thinning with respect to acorn production and to *Curculio* and *Conotrachelus* populations and survival. Specifically, we wish to test several hypotheses. To test the effects of silvicultural treatments on acorn production the null and several alternative hypotheses are:

H_{10}: Silvicultural treatments do not affect oak seed production.
H_{1A}: Thinning treatment will increase production vs. the control due to increased light.
H_{1B}: Burning treatment will increase production vs. the control due to increased nutrients.
H_{1C}: Thinning and burning combined will produce a greater effect than either thinning or burning alone.

To examine factors affecting the variability of acorn production and the silvicultural treatments, the null and alternative hypotheses are:

H_{20}: Reproduction among trees will be more or less uniform due to population masting habit.
H_{2A}: Considerable variability among trees in seed production because of genetics or differences in moisture levels (Integrated Moisture Index: IMI (Iverson and others 1997)).
H_{2B}: Variability will be greater in treatments vs. the control due to the interaction of genetics and patch effect.

To examine the effect of treatments on weevil acorn depredation we tested the hypotheses that:

H_{30}: Weevil predator abundance will be similar among silvicultural treatments.
H_{3A}: Weevil abundance will be lower in burn treatments due to mortality incurred by weevils.

Finally, we wanted to test the effect of treatments on viable acorn production and the hypotheses that:

H_{40}: Proportion of sound seed produced will be similar among treatment applications.
H_{4A}: Proportion of sound seed will be greater in treatment units because of increased resources.
H_{4B}: Proportion of sound seed will be greater in burn treatments because of fewer weevils.

Study Areas

This study was conducted in Vinton County, OH in the mixed-oak forests of the Raccoon Ecological Management Area (REMA: Vinton Furnace Experimental Forest) and Zaleski State Forest (ZAL). The region lies within the unglaciated Allegheny Plateau physiographic province (Fenneman 1938) of Ohio and has been designated as part of the Mixed Mesophytic Forest Region by Braun (1950). Southeast Ohio exhibits a humid continental climate with mean yearly temperatures of 12.2°C (NOAA 2003). July is the warmest month (mean 23.7°C), and January is the coldest (mean -0.5°C). Mean annual precipitation is 106.7 cm with October being the driest month and July the wettest month.

Methods

The study areas are part of a landscape-scale ecosystem restoration project, Fire and Fire Surrogate Study (FFS), using mechanical thinning and prescribed fire as management tools to restore ecosystem structure, function and composition. Within each forest, four stands ca. 20 ha each were selected and were randomly assigned into three treatments and a control (control unit). The treatments consisted of a shelterwood thin aimed at reducing basal area by ca. 30% (thin), prescribed fire (burn) and a combination thin and prescribed fire (thin & burn).

Seed Traps

To assess the level of seed predation and to evaluate treatment effect on acorn production, 288 seed traps (36 traps in each unit) were placed under mast trees of black (*Quercus velutina* Lam.) oak (BO) and

Table 1.—Number of chestnut oak and black oak acorns collected during 2001 and 2002 at two forests in southeast Ohio. Category 1: sound & filled; 2: unfilled/aborted (immature & small); 3: depredated (weevil or exit hole present); and 4: other (e.g., fungi).

Year	Species	Category				Total
		1	2	3	4	
2001	Chestnut oak	1	3	10	3	17
	Black oak	1029	704	2160	64	3957
2002	Chestnut oak	332	680	267	47	1326
	Black oak	57	958	553	68	1636

chestnut (*Q. prinus* L.) oak (CO). Two 0.25 m^2 conical seed traps were placed ca. 1.5 m aboveground under each oak tree and every four weeks, the seeds were collected and returned to the laboratory. Seed traps were installed in July and mid-month sampling occurred from August–December during 2001 and 2002. Seeds were identified and scored as (1) filled and sound, (2) unfilled/aborted (immature and small), (3) depredated (weevil or exit hole present), and (4) other (e.g., fungi).

Emergence Traps

To elucidate the phenology of weevil populations, several methods were employed during 2001 and 2002 to capture weevils as they emerged from the soil. First, 10 white oak (*Q. alba*) and 10 black oak (*Q. velutina*) in each unit (160 trees total) were selected and a 15-20 cm ring of Tanglefoot™ was applied to each bole. Trees were monitored at weekly intervals to see if weevils were trapped in the Tanglefoot™. Second, emergence traps were built (Raney and Eikenbary 1969) and placed under 3 white oak and 3 black oak trees in each unit for a total of 48 traps. To avoid confounding effects, different trees were used for each study. Emergence traps were placed in the field in late February 2002 and checked on a weekly basis through June 2002. Captured weevils were returned to the laboratory and identified.

Statistical Analysis

Mixed model analysis of variance (ANOVA) with orthogonal contrasts (Hintze 1997) was used to test for treatment effects on acorn production. Orthogonal contrasts included the control vs. thin, control vs. burn, and thin and burn combination vs. thin and burn only, respectively. Log-linear analysis (Hintze 1997) was utilized to test seed viability among sites, treatments and oak species. Data collected during 2001 was not included in the analysis because treatments were applied after bud formation so any effect of treatment would have been missed. ANOVA (Hintze 1997) was used to test for treatment effects on weevil populations and to examine differences between collection methods. The study areas were treated as random while treatments were fixed effects. All data conformed to normality and equal variance assumptions.

Results

In 2001, a total of 3974 chestnut oak and black oak acorns were collected of which only 17 were CO acorns (table 1). One sound and 10 weevil depredated CO acorns were recorded. Of the 3957 BO acorns produced, 26 percent (1028) were sound and 54.6 percent (2160) were weevil depredated. The remaining 19.6 percent (769) were inviable for other reasons (aborted, fungi, etc.).

In 2002, a total of 2962 CO and BO acorns were collected, 1326 were CO and 1636 were BO acorns (table 1). More CO acorns were sound than weevil depredated (25.0 vs. 21.0 percent, respectively) but more BO acorns were weevil depredated than sound (33.8 vs. 3.5 percent, respectively).

Chestnut oak acorn production responded significantly to the silvicultural treatments (table 2). CO acorn production increased in response to thinning and burning (fig 1A). Greater variability was recorded in CO

Table 2.—Analysis of variance testing for differences in Q. prinus and Q. velutina acorn production among site and treatment units in 2002. C: control, T: thin; TB: thin and burn; and B: burn. Significance (P < 0.05) is indicated by an asterisk.

	Quercus prinus				*Quercus velutina*			
Source	df	MS	*F*	*P*	df	MS	*F*	*P*
Unit	3	0.55	4.24	0.007*	3	0.197	2.91	0.037*
C vs. T	1		0.65	0.516	1		0.59	0.553
C vs. B	1		0.37	0.711	1		2.83	0.005*
TB vs. T+B	1		3.23	0.001*	1		0.92	0.358
Site	1	0.05	0.40	0.528	1	0.586	8.62	0.004*
Total	114				138			

Table 3.—Log-linear analysis of chestnut and black oak acorn seed viability in 2002 at two forests in southeast Ohio subjected to three treatments. S:site; T: treatment; and O: oak species.

Effect	df	Partial Chi-Square	Probability
Site	1	51.48	0.0001
Treatment	3	127.55	0.0001
Oak species	1	46.45	0.0001
S × T	3	11.26	0.0104
S × O	1	1.16	0.2818
T × O	3	144.72	0.0001
S × T × O	3	62.16	0.0001

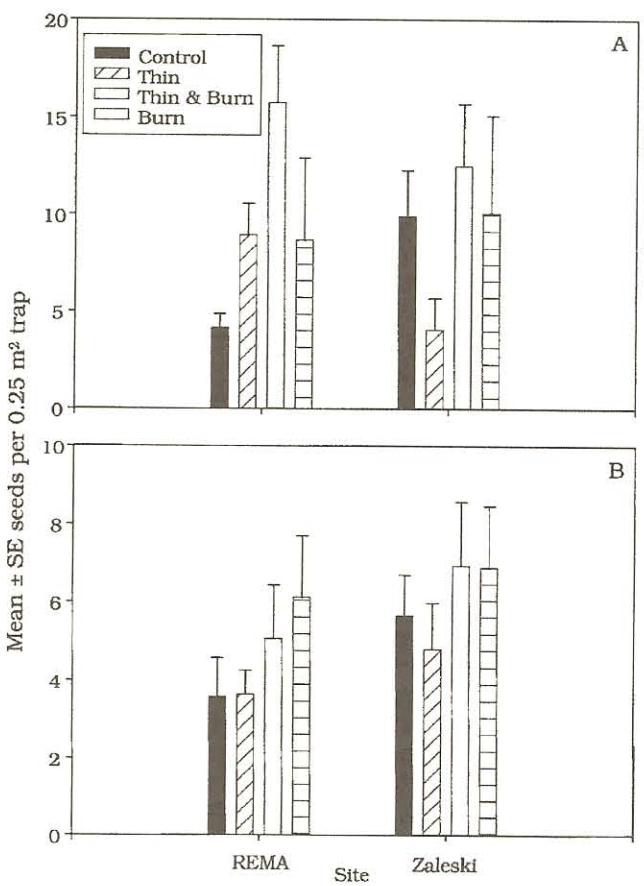

Figure 1.—Mean ± SE of chestnut (A) and black (B) oak acorns produced in different treatment units in two forests in southeast Ohio Note that panels are on different scales.

production in the burn vs. the thin & burn unit. CO acorn production responded differently at each site in the control and thin units (fig. 1A).

Black oak acorn production responded significantly different at each site and to the silvicultural treatments (fig. 1B). BO acorn production increased in response to the thinning and burning and was greater than CO production.

Log-linear analysis indicated that seed viability at each site, for each treatment and between oak species was significantly different (table 3). More sound seeds were produced in the thin and burn and burn units than in the control and thin units (287 vs. 102 acorns, respectively).

A total of 35 *Curculio* weevils were trapped representing eight species and one unknown (table 4). Fourteen of the 25 were caught in the emergence traps (ET). The remaining *Curculio* weevils serendipitously appeared in the seed mast traps (ST). The dominant species was *Curculio strictus* with 15 individuals. Two rare species, *C. iowensis* and *C. orthorhynchus* (L.P. Gibson, personal communication), were collected only from Zaleski.

A total of 16 *Conotrachelus* weevils were caught representing 3 species (table 4). The most abundant was *Conotrachelus naso* with 11 individuals while the least abundant was *C. carinifer* represented by only one individual. *C. naso* weevils found in seed traps were generally associated with chestnut oak trees.

There was no difference in the number of weevils caught between the forests ($F = 0.90$, $P = 0.379$) or among the units ($F = 0.86$, $P = 0.529$). There was no difference in the number of weevils caught in emergence traps or weevils found in mast traps ($F = 0.61$, $P = 0.465$). No weevils were caught using Tanglefoot™ on tree boles.

Discussion

Many factors influence seed production. Increased seed production results from increased crown area (Greenberg 2000) and potentially from fire (Abrahamson and Layne 2002). We found that seed production increased in response to prescribed fire and to thinning combined with prescribed fire. Thinning reduced standing basal area, creating more space for existing oak trees; however, we did not record increased acorn production in thinned units.

Studies indicate that there is a high level of variability in acorn seed production among individual trees and even populations (Healy and others 1999, Greenberg 2000). McCarthy and Quinn (1989) suggest that most variability results from individual and annual variation in trees, rather than as a response to thinning (Healy and others 1999). While Healy and others examined the effects of thinning, our study combines the results of increased light produced by thinning with increased nutrients produced by fire. We found a great deal of variability among trees and forest sites but our data indicate that thinning and prescribed fire combined increased variability of acorn production greater than thinning alone.

Acorns are an important food source for wildlife. Native Americans also consumed acorns as part of their diet. McCarthy (1993) suggests that Native Americans in California burned in order to control invertebrate acorn infestation rates. Wright (1986) found evidence to support the role of prescribed fire in controlling acorn weevils in southeastern Ohio. We found that weevil populations were distributed evenly throughout the units but that sound seeds increased in the burn & thin relative to the control and thin units. Indeed, prescribed fire may decrease *Curculio* populations as a result of mortality. Since most weevil emergence occurred after the spring prescribed fire season in Ohio, weevil mortality is more likely to occur as a result of fall burning. During the fall fire season, generally October to November, there is an increased likelihood that weevils would be killed while exiting from fallen acorns or while in the forest floor layers while attempting to reach the soil. However, it may be possible for spring fire to have an effect on weevil survival as well. Some weevils may overwinter in the acorn and emerge the following spring (Gibson 1969). Likewise, absence of a litter layer due to burning in any season may influence predation rates.

Table 4.—*Curculio* and *Conotrachelus* species emergence dates, unit locations and collection method in two forests in southeastern Ohio. C: control, T: thin; TB: thin and burn; B: burn; ET: emergence trap; and ST: seed trap.

Species	Date	Site	Unit	Qty	Collection Method	Associated Oak mast tree
Curculio strictus Casey.	05/15/02	REMA	T	2	ET	
	05/20/02	ZAL	TB	4	ET	
	05/20/02	ZAL	B	3	ET	
	05/24/02	ZAL	TB	1	ET	
	05/26/02	REMA	B	1	ET	
	05/29/02	ZAL	T	1	ET	
	08/15/02	ZAL	TB	1	ST	Black
	08/19/02	REMA	T	1	ST	Chestnut
	10/12/02	ZAL	C	1	ST	Black
	Total			15		
Curculio confusor Horn.	05/24/02	ZAL	B	1	ET	
	05/26/02	REMA	TB	1	ET	
	Total				2	
Curculio proboscideus Fab.	05/26/02	REMA	T	1	ET	
	10/05/02	ZAL	C	1	ET	
	10/09/02	REMA	TB	1	ST	Chestnut
	10/12/02	ZAL	C	1	ST	Black
	Total			4		
Curculio iowensis Casey.	08/15/02	ZAL	B	1	ST	Chestnut
	Total			1		
Curculio pardalis Chttn.	09/09/02	REMA	C	1	ST	Black
	09/09/02	REMA	B	1	ST	Chestnut
	10/09/02	REMA	T	1	ST	Black
	Total			3		
Curculio sulcatulus Casey.	09/09/02	REMA	C	1	ST	Black
	09/10/02	ZAL	C	1	ST	Black
	10/05/02	ZAL	TB	1	ET	
	0/09/02	REMA	T	1	ST	Black
	Total			4		
Curculio orthorhynchus Casey.	09/10/02	ZAL	T	1	ST	Chestnut
	09/25/02	ZAL	B	1	ET	
	10/12/02	ZAL	C	1	ST	Black
	Total			3		
Curculio nasicus Say.	10/05/02	ZAL	C	1	ET	
	10/05/02	ZAL	TB	1	ET	
	Total			2		
Curculio sp.	10/12/02	ZAL	B	1	ST	Chestnut
Conotrachelus naso Lec.	04/17/02	REMA	B	1	ET	
	05/26/02	REMA	TB	2	ET	
	06/04/02	ZAL	C	2	ET	
	06/04/02	ZAL	T	2	ET	
	08/15/02	ZAL	B	1	ST	Chestnut
	08/19/02	REMA	TB	1	ST	Chestnut
	09/09/02	REMA	TB	2	ST	Chestnut & black
	Total			11		
Conotrachelus posticatus Boh.	04/17/02	REMA	B	1	ET	
	05/26/02	REMA	C	1	ET	
	05/26/02	REMA	TB	1	ET	
	08/19/02	REMA	C	1	ST	Chestnut
	Total			4		
Conotrachelus carinifer Casey	09/09/02	REMA	C	1	ST	Black
	Total			1		
Total *Curculio*				35		
Total *Conotrachelus*				16		

The position of the weevil larvae in the soil/litter horizons during a fire may be the key to their survival. Weevils that emerge from acorns earlier in the fall and descend into the soil will most likely escape the effects of an autumn fire. Prescribed fire temperatures in mixed-oak forests of southeast Ohio rarely exceed 30°C 2 cm below the soil surface (Riccardi and McCarthy, unpublished data) and will not cause weevil mortality. Weevils present in the forest floor litter layer during a fire will most likely be killed since forest floor fuels are the major fuel sources of prescribed fires in mixed-oak forests of southeast Ohio. Consumption of the forest floor removes potential hiding areas for weevils and could lead to greater predation by small forest mammals, also resulting in a reduction of weevil populations.

Three species of *Conotrachelus* are known to infest acorns in the United States (Gibson 1964) and we recorded all three species in our study. *Conotrachelus* weevils began emerging in April, before *Curculio* weevils. *Conotrachelus* weevil populations potentially would be affected by spring fires; however, because they infest damaged or otherwise open acorns, their effects on acorn viability are probably less crucial than *Curculio* weevil damage.

Our data suggest that the combination of thinning, to increase light levels and to increase spatial availability for tree crowns, coupled with a flush of nutrients resulting from prescribed fires can increase acorn oak production. Furthermore, prescribed fire, particularly during the autumn, may result in weevil mortality leading to an increase in the production and survival of sound acorns.

Acknowledgments

This is contribution 39 of the National Fire and Fire Surrogate Research (FFS) Project. This research was funded by the USDA Forest Service through the National Fire Plan and the U.S. Joint Fire Science Program (JFSP) to BCM. CLR is grateful to the many field assistants and especially to L.P. Gibson for assistance with weevil identification.

Literature Cited

Abrahamson, W.G.; Layne, J.N. 2002. **Post-fire recovery of acorn production by four oak species in southern ridge sandhill association in south-central Florida.** American Journal of Botany 89(1):119-123.

Abrams, M.D. 1992. **Fire and the development of oak forests.** BioScience 42(5):346-353.

Barnett, R.J. 1977. **The effect of burial by squirrels on germination and survival of oak and hickory nuts.** The American Midland Naturalist 98(2):319-330.

Braun, E.L. 1950. **Deciduous Forests of Eastern North America.** New York: Hafner. 596 p.

Brooks, F.E. 1910. **Snout beetles that injure nuts.** West Virginia Agriculture Experiment Station Bulletin 128:143-185.

Brose, P.H.; Van Lear, D.H. 1998. **Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands.** Canadian Journal of Forest Research 28:331-339.

Cecich, R.A.; Sullivan, N.H. 1999. **Influence of weather at time of pollination on acorn production of *Quercus alba* and *Quercus velutina*.** Canadian Journal of Forest Research 29:1817-1823.

Christisen, D.M.; Kearby, W.H. 1984. **Mast measurements and production in Missouri (with special reference to acorns).** Terrestrial Series #13. Missouri Department of Conservation. Jefferson City, MO:34 p.

Collins, J.O. 1961. **Ten year acorn mast production study in Louisiana.** Louisiana WildLife and Fisheries Commission:73 p.

Crow, T.R. 1988. **Reproduction mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—a review.** Forest Science 34:19-40.

Fenneman, N.M. 1938. **Physiography of Eastern United States.** New York: McGraw-Hill Book Company. 714 p.

Galford, J.; Auchmoody, L.R.; Smith, H.C. and Walters, R.S. 1991. **Insects affecting establishment of northern red oak seedlings in central Pennsylvania.** Pages 271-280 In: Proceedings 8th Central Hardwood Forest Conference, University Park, Pennsylvania. USDA Forest Service, GTR NE-148.

Gibson, L.P. 1964. **Biology and life history of acorn-infesting weevils of the genus Conotrachelus (Coleoptera: Curculionidae).** Annals of the Entomological Society of America 57:521-526.

Gibson, L.P. 1969. **Monograph of the genus Curculio in the New World (Coleoptera: Curculionidae) Part I. United States and Canada.** Miscellaneous Publications of the Entomological Society of America:241-285.

Gibson, L.P. 1972. **Insects that damage white oak acorns.** USDA Forest Service Research Paper NE-220. NE Forest Experiment Station, Upper Darby, PA:8.

Gibson, L.P. 1982. **Insects that damage northern red oak acorns.** USDA Forest Service Research Paper NE-492. NE Forest Experiment Station, Broomall, PA:6.

Gill, R.M.A. 1992. **A review of damage by mammals in north temperate forests: 1. Deer.** Forestry 65(2):145-169.

Greenberg, C.H. 2000. **Individual variation in acorn production by five species of southern Appalachian oaks.** Forest Ecology and Management 132:199-210.

Gribko, L.S. **The effect of acorn insects on the establishment and vigor of northern red oak seedlings in north-central West Virginia.** In: Gottschalk KW, Fosbroke SLC, editors; 1995 March 5-8, 1995; Morgantown, WV. Gen. Tech. Report NE-197, U.S.D.A. Forest Service. p 430-441.

Harlow, R.F.; Whelan, J.B.; Crawford, H.S.; Skeen, J.E. 1975. **Deer foods during years of oak mast abundance and scarcity.** Journal of Wildlife Management 39(2):330-336.

Healy, W.M.; deCalesta, D.S.; Stout, S.L. 1997. **A research perspective on white-tailed deer overabundance in the northeastern United States.** Wildlife Society Bulletin 25(2):259-263.

Healy, W.M.; Lewis, A.M.; Boose, E.F. 1999. **Variation of red oak acorn production.** Forest Ecology and Management 116:1-11.

Hintze, J. 1997. **Number Cruncher Statistical System 2000.** Kaysville, Utah.

Horsley, S.B.; Stout, S.L. and DeCalesta, D.S. 2003. **White-tailed deer impact on the vegetation dynamics of a northern hardwood forest.** Ecological Applications 13:98-118.

Iverson, L.R.; Dale, M.E.; Scott, C.T.; Prasad, A. 1997. **A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (U.S.A.).** Landscape Ecology 12:331-348.

Kelly, D.; Sork, V.L. 2002. **Mast seeding in perennial plants: Why, How, Where?** Annual Review of Ecology and Systematics 33:427-447.

LeBlanc, D.C. 1998. **Interactive effects of acidic deposition, drought, and insect attack on oak populations in the midwestern United States.** Canadian Journal of Forest Resources 28:1184-1197.

Lewis, A.R. 1980. **Patch use by gray squirrels and optimal foraging.** Ecology 61(6):1371-1379.

Loftis, D.L.; McGee, C.E. 1993. **Oak regeneration: serious problems, practical solutions.** Gen Tech. Report SE-84, U.S.D.A. Forest Service, Ashville, NC.:319 pp.

Lorimer, C.G. 1984. **Development of the red maple understory in northeastern oak forests.** Forest Science 30(1):3-22.

Marquis, D.A.; Eckert, P.L.; Roach, B.A. 1976. **Acorn weevils, rodents, and deer all contribute to oak-regeneration difficulties in Pennsylvania.** Research Paper NE-356, U.S.D.A. Forest Service:5 pp.

McCarthy, B.C. 1994. **Experimental studies of hickory recruitment in a wooded hedgerow and forest.** Bulletin of the Torrey Botanical Club 121(3):240-250.

McCarthy, B.C.; Quinn, J.A. 1989. **Within- and among-tree variation in flower and fruit production in two species of *Carya* (Junglandaceae).** American Journal of Botany 76:1015-1023.

McCarthy, B.C.; Hammer, C.A.; Kauffman, G.L.; Cantino, P.D. 1987. **Vegetation patterns and structure of an old-growth forest in southeastern Ohio.** Bulletin of the Torrey Botanical Club 114(1):33-45.

McCarthy, H. 1993. **Managing oaks and the acorn crop.** In: Vane SB, Bean LJ, editors. Before the wilderness: environmental management by native Californians. Menlo Park: Ballena Press. p 213-228.

Millers, I.; Shriner, D.S.; Rizzo, D. 1989. **History of hardwood decline in the Eastern United States.** Gen. Tech. Report NE-126, U.S.D.A. Forest Service, Broomall, PA:75 pp.

NOAA. 2003. **Area Climate Information:** National Climatic Data Center/National Oceanic and Atmospheric Administration.

Raney, H.G.; Eikenbary, R.D. 1969. **A simplified trap for collecting adult pecan weevils.** Journal of Economic Entomology 62(3):722-723.

Rouse, G. 1986. **Fire effects in Northeastern Forests: Oak.** Gen. Tech. Report NC-105, U.S.D. A. Forest Service, St. Paul, MN:7 pp.

Sharp, W.M.; Chisman, H.H. 1961. **Flowering and fruiting in the white oaks. I. Staminate flowering through pollen dispersal.** Ecology 42(2):365-372.

Sharp, W.M.; Sprague, V.G. 1967. **Flowering and fruiting in white oaks. Pistillate flowering, acorns development, weather, and yields.** Ecology 48(2):243-521.

Short, H.L. 1976. **Composition and squirrel use of acorns of black and white oak groups.** Journal of Wildlife Management 40(3):479-483.

Sork, V.L. 1983. **Mammalian seed dispersal of pignut hickory during three fruiting seasons.** Ecology 64:1049-1056.

Sork, V.L.; Bramble, J. 1993. **Ecology of mast-fruiting in three species of North American deciduous oaks.** Ecology 74(2):528-541.

Sutherland, E.K. **History of fire in a southern Ohio second-growth mixed oak forest.** In: Pallardy SG, Cecich RA, Garrett HE, Johnson PS, editors; 1997 March 23-26, 1997; Columbia, MO. U.S.D.A. Forest Service. p 401.

Tilghman, N.G. 1989. **Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania.** Journal of Wildlife Management 53(3):524-532.

Weckerly, F.W.; Sugg, D.W.; Semlitsch, R.D. 1989. **Germination success of acorns (Quercus): insect predation and tannins.** Canadian Journal of Forest Research 19:811-815.

Wolgast, L.J. 1978. **Effects of site quality and genetics on bear oak mast production.** American Journal of Botany 65(4):487-489.

Wright, S.L. 1986. **Prescribed burning as a technique to manage insect pests of oak regeneration.** Pages 91-96 In: A.L. Koonce, editor, Prescribed Burning in the Midwest: State-of-the-Art. Proceedings of a Symposium in Stevens Point, WI, March 3-6, 1986.