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RISE AND FALL OF RED OAK BORER (COLEOPTERA: CERAMBYCIDAE) IN THE OZARK MOUNTAINS OF ARKANSAS, USA

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ABSTRACT

Oak-hickory forests of the Arkansas Ozarks recently incurred extensive tree mortality due in part to a native wood-boring beetle, the red oak borer *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae). Historically, red oak borer has existed throughout southeastern U.S. forests at relatively low population levels, but Arkansas infestation estimates in 2001 and 2003 reported much higher populations. Red oak borer has a two-year generation with adult emergence occurring synchronously only in odd numbered years. We report here results of whole-tree estimates of pre-emergent red oak borer population numbers from 7 stands in 2005 and 3 stands in 2003 and 2007 in the Ozark National Forest. Trees were felled at each sampling site, cut into 0.5 m sections, split on site with hydraulic log splitters, and a count of live red oak borers was recorded for each tree. In 2001 and 2003, red oak borer population estimates indicated emerging populations much higher than any previously reported. An exponential decrease during a single cohort between 2003 and 2005, and even lower populations in 2007 suggest that red oak borer populations have returned to historic densities.

Key Words: *Enaphalodes rufulus*, forest entomology, insect outbreak, population dynamics, population sampling, *Quercus rubra*

RESUMEN

Los bosques de roble-nogal de las montañas Ozark del estado de Arkansas recientemente sufrió una mortalidad de árboles extensiva debido en parte a un escarabajo nativo barrenador de madera, el barrenador de roble rojo *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae). Históricamente, el barrenador de roble rojo ha existido por todos los bosques del sureste de los Estados Unidos con niveles de población relativamente bajos, pero los informes del nivel de infestación en Arkansas en el 2001 y 2003 indica una población mucho más alta. El barrenador de roble rojo cumple una generación en dos años con la emergencia de los adultos, ocurriendo sincrónicamente durante los años de número impar. Reportamos los resultados de los números aproximados de la población pre-emergente del barrenador de roble rojo de los árboles totales de 7 grupos de árboles en 2005 y 3 grupos de árboles en 2003 y 2007 del Bosque Nacional de Ozark. Los árboles en cada uno de los sitios de muestreo fueron tumbados, cortados en secciones del tamaño 0.5 m, partidos con un rajador hidráulico de troncos y se noto el numero de barrenadores de roble rojo vivos encontrados por cada árbol. En el 2001 y 2003, los aproximados de la población del barrenador de roble rojo indicaron la emergencia de poblaciones mucho más altas que las reportadas anteriormente. Una disminución exponencial durante un solo cohorte entre el 2003 y 2005, y aun poblaciones mas bajas en el 2007 sugerieron que la población del barrenador de roble rojo ha vuelto a las densidades históricas.

The Ozark highlands in northern Arkansas encompass approximately 6.5 million forested hectares, most of which are made up of oak-hickory forest type (Guldin et al. 1999). Overall, the red oak group (*Quercus*: Section Lobatae), and primarily northern red oak *Q. rubra* L., comprise approximately 25% of these forests (Guldin et al. 1999). Widespread oak decline was discovered in the Arkansas, Missouri, and Oklahoma Ozarks in 1999 (Starkey et al. 2000). Resulting tree mortality was widespread, with significant impacts on forest conditions and resources such as economy, ecology, and aesthetics. During the period of peak decline, at least one-third of mature northern red oaks (*Quercus rubra* L.) died in stands throughout the Ozarks (Guldin et al. 2006). Red oak borer, *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae), was implicated as the primary contributing agent to this oak mortality event (Stephen et al. 2001). Red oak borer is native to eastern North America, and prior to the recent outbreak in Arkansas, was only reported as a minor pest of oaks throughout its range (Hay 1974; Donley & Acciavatti 1980; Galford 1983). Before

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the current outbreak, stands exhibiting 1 emerging beetle per tree were considered highly infested (Hay 1974).

Despite more than 50 oak decline events in the eastern United States in the last 150 years (Millers et al. 1989), neither an associated red oak borer outbreak nor widespread red oak borer-related tree mortality has previously been reported (Stephen et al. 2001). No definitive causative agents have been identified in the red oak borer outbreak. However, some evidence indicates that anthropogenic disturbance in the form of widespread logging from 1890 to 1920 (Faulkner 1997) and long-term fire suppression (Faulkner 1997) may have contributed to this outbreak by creating large areas of densely-stocked, even-aged, overmature northern red oak dominated stands (Oak et al. 1996; Aquino et al. 2008).

During the recent outbreak in Arkansas, estimated density of emerging red oak borers during 2001 sampling peaked as high as ~174 per tree when data reported by Stephen et al. (2001) are extrapolated to the whole tree level. Ongoing red oak borer life-table research and population monitoring in 2004 and 2005 yielded far fewer red oak borers and indicated a probable decrease in red oak borer population density at 3 primary monitoring sites (F.M.S., unpublished data). The overall goal of our research was to document this decrease and determine if it was localized or more widespread. Three primary field locations were sampled in 2003, 2005, and 2007, and 4 additional field locations were selected for monitoring during 2005. Our objective was to estimate preadult red oak borer (late-stage larvae, pupae, pharate adults) populations before adult emergence by felling trees and immediately dissecting them to obtain a direct count of live red oak borers at multiple locations in the Ozark National Forest. Total counts of all live red oak borers in each whole-tree sample likely provide the best estimate of red oak borer emerging adults, as mortality in the short time between our sampling and adult emergence in the protected environment of the pupal chamber is likely very low.

Red oak borers exhibit a 2-year life cycle, emerging synchronously in odd-numbered years throughout most of their range (Donley & Acciavatti 1980). Emergence during even-numbered years occurs only in the far southern portions of the range, where a small percentage of the population emerges during even years (Hay 1969; Hay 1972). Adults are nocturnal and usually emerge mid-Jun through mid-Aug (Donley 1978; Donley & Acciavatti 1980; Fierke & Stephen 2007). Females deposit an average of 119 eggs singly in bark crevices and under lichen on boles of host trees (Donley 1978; Donley & Acciavatti 1980). After hatching, larvae burrow horizontally through outer bark into phloem and initiate a feeding gallery in which they overwinter (Hay 1969; Fierke et al. 2005a). Actively foraging larvae enlarge phloem galleries to approximately 18 cm^2 and initiate galleries into xylem tissues (heartwood) during late spring of the following year (Hay 1969). Larvae burrow into and upwards through the heartwood before their second winter (Fig. 1A). Larvae enclose themselves in cylindrical pupal chambers approximately 3.75 cm long at the apex of heartwood galleries, with wood shavings and frass forming gallery plugs (Hay 1969). Pupae complete metamorphosis during late spring and early summer of odd-numbered years (Hay 1969; Fierke et al. 2005a). Adults retreat down the heartwood gallery after eclosion and exit the tree via characteristically-shaped oval holes in the outer bark, directly over the original phloem gallery site. Life histories similar to those reported previously have been observed during this outbreak in Arkansas (Stephen et al. 2001; Fierke et al. 2005a; Crook et al. 2007).

Herein, we describe emergence densities of red oak borers during 3 separate cohorts, and compare these findings with previous reports of red oak borer population density. This information is critically important because it is the first detailed, multi-cohort description of red oak borer density during the first reported outbreak of the species, and provides evidence that the recent outbreak has subsided.

Materials and Methods

Research areas were initially chosen in 2001 during studies to develop sampling methods (Fierke et al. 2005a; Fierke et al. 2005b). Trees were selected from those locations (White Rock, Fly Gap and Oark) during 2003, 2005, and 2007. Trees were also selected at 4 additional widely-distributed stands (Pilot Rock, Pedestal Rocks, Dickie Junction, and Ozone) to expand the geographic area of population estimates for the 2005 cohort. The geographic location and topography of each sampling location are illustrated in Fig. 2. Observations based on additional field sampling conducted in the same locations following 2005 adult emergence confirmed population decline in 2005. Only the highest density stands originally chosen in 2003 (White Rock, Fly Gap and Oark) were selected for the 2007 sampling effort. Focusing on these most severely affected areas allowed a "worst-case" estimate of red oak borer populations. These locations were chosen based on specific site and stand characteristics (ridges, high northern red oak stocking, tree age greater than 50 years, and visual evidence of red oak borer activity) because prior studies suggested association of these characteristics with increased red oak borer hazard (Fierke et al. 2007; Aquino et al. 2008). Specific descriptions of vegetation communities and stand variables have been previously described by Fierke & Stephen (2007).

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Fig. 1. Early-instar red oak borer larva phloem gallery (A) and cross-section of red oak borer xylem galleries (B).

All areas were systematically visited before red oak borer adult emergence, and potential sample trees were categorized into 1 of 3 infestation-history classes based on a rapid estimation procedure (Fierke et al. 2005b). This procedure was designed to estimate red oak borer infestation severity as a function of red oak borer emergence holes in the basal 2 m of the tree and visual estimates of percent crown dieback. Trees were felled at each site, cut into 0.5-m long bolts, beginning 0.5 m above the ground and terminating at the highest sign of red oak borer infestation (neonate attack holes and/ or emergence holes). Total tree height, diameter at breast height (DBH), and diameter at midpoint of each 0.5-m sample bolt were recorded for each tree. All bolts were dissected on site with gasoline-powered hydraulic log splitters. A total count of live red oak borer larvae, pupae, and pharate (pre-emergent) adults (hereafter collectively referred to as "live red oak borer") was recorded.

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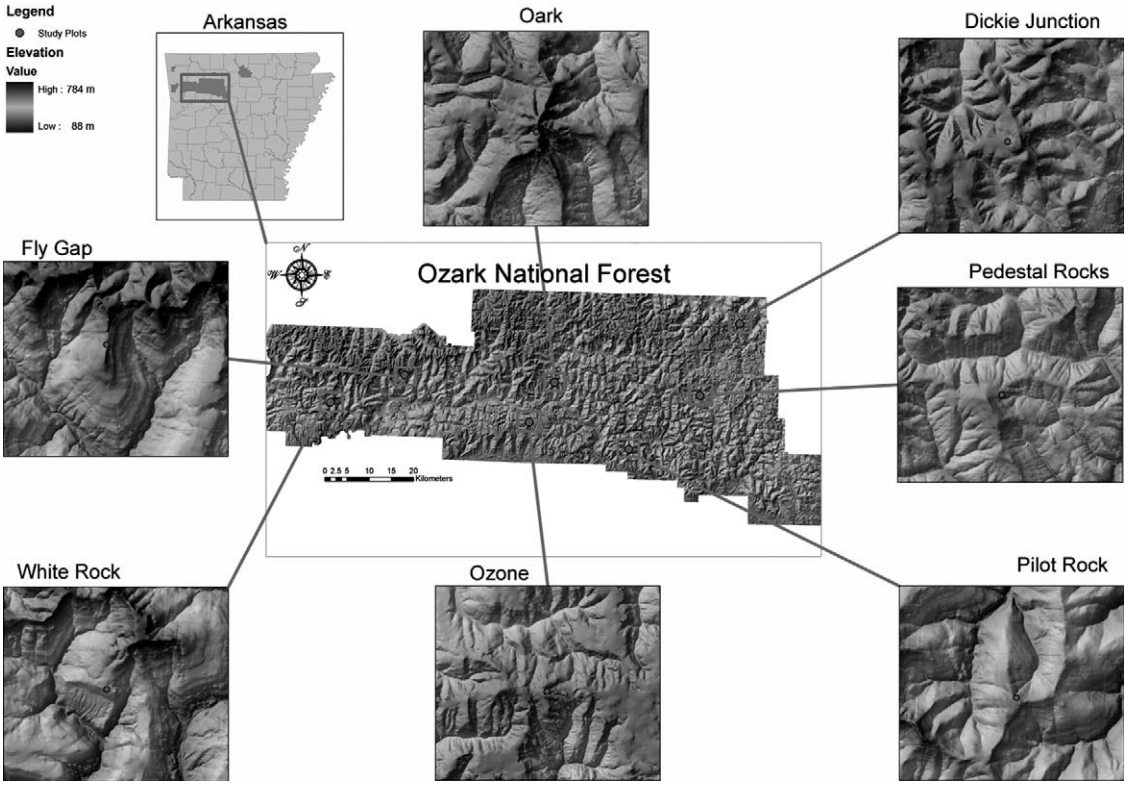


Fig. 2. Geographic location and topography of sampling sites in Ozark National Forest of Arkansas, U.S.A.

Logistical challenges during preliminary sampling in 2003 resulted in a slightly late start, with some samples being taken after earliest emergence had begun in Jun. As a result, in 2003 a number of current generation emergence galleries were counted in lieu of their recently departed inhabitants. These recently-vacated galleries were easily distinguished from previous generation emergence galleries by absence of fungus or any appearance of necrotic tissue in the heartwood gallery lining. They were also easily distinguished from unsuccessful heartwood galleries by the presence of frass plug remnants and the absence of cadavers. While sample timing may have introduced small error into 2003 counts, the estimates of red oak borer density form an important baseline for subsequent sampling years, and the aforementioned absence of fungus or necrotic tissue allowed us to differentiate between empty current generation emergence galleries and galleries from previous red oak borer cohorts. We assume that their inclusion in the total counts for 2003 provides a more accurate estimate of emerging red oak borer in 2003 than would be possible if those data were excluded. We cannot exclude the possibility that some of these galleries were formed by other closely related species such as *E. atomarius*, which could have slightly skewed 2003 counts. However, no other large pharate cerambycids were recorded during data collection, suggesting that effects due to this were minimal.

During all tree dissections, care was taken to completely uncover and examine all signs of red oak borer presence, whether in the form of phloem galleries with entrances to heartwood galleries, or heartwood galleries on the basal cross-section of each sample bolt (Fig. 1B). Bolt dissections began with complete removal of all outer bark to expose any potentially occupied heartwood galleries. Each visible heartwood gallery, including those continually discovered during successive splitting, was then fully exposed to its apical terminus to determine if a living red oak borer was present. Second-year larvae are approximately 2.5-4.0 cm in length (F.M.S., unpublished data) and are readily visible once trees are dissected. Bolts without externally obvious heartwood galleries were thoroughly dissected to minimize omitting any red oak borers. Because of our previous experience and the robust nature of late-stage larvae and their correspondingly large and obvious heartwood galleries (Figs. 1A and 1B), we assume that very few red oak borer were omitted from counts.

A count of live red oak borers in each tree was divided by total bark surface area for that tree.

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Bark surface area was calculated from diameter measurements of each sample bolt. Densities of red oak borers were expressed per square meter of bark surface area to provide a standardized unit that could be compared among locations and years despite variation in the number and size of trees sampled. Analysis of variance with JMP 7.0® (SAS Institute, 2007) was conducted, and significance was judged at $\alpha = 0.05$ with Tukey-HSD used for mean separation when appropriate.

Results

DBH for all 98 trees sampled ranged from 14.5-42 cm, and mean DBH was 29.8 cm (±0.54 SE). Mean total tree height was 18.9 m (±0.26, range 12.5-24.5 m). Mean total height of infestation was 13.6 m (±0.24, range 7.5-19.5 m). The average total bark surface area of the 98 trees sampled in this study was 9.4 m^2 (±0.32, range 2.3-17.2). There were no significant differences in mean DBH, total tree height, height of infestation, or bark surface area among different years of the study ($P \geq 0.1, F < 2.4$).

Overall mean density of live red oak borer was significantly higher in 2003 than in either 2005 or 2007 ($F_{2,97} = 45.37, P = <0.0001$) at 4.11, 0.18, and 0.10 per sq. m, respectively, (Table 1). All locations exhibited red oak borer population declines from the 2003 to 2005 cohort, but there was no statistically significant decrease from the 2005 to 2007 cohort (Table 1). Red oak borers were encountered much more frequently and in greater numbers per tree in 2003 than in subsequent sampling years (Fig. 3). In 2003, mean number of red oak borer per tree was 31.7 (±7.9 SE). Mean number of red oak borer per tree was 1.6 (±0.37) in 2005 and 1.0 (±0.25) in 2007.

Discussion

Estimates of the population density of live red oak borers immediately before adult emergence in the Arkansas Ozarks were derived from 3 separate cohorts (2003-2007) inhabiting 98 northern red oaks that were felled and completely dissected. The earliest estimates of red oak borer within-tree population density were made during the 1999-2001 cohort by Stephen et al. (2001). Their sample size was small; 15.1-m long bolts collected from 2 trees, and resulted in an estimated average emergence density of 18.5 (±4.3) red oak borers per sq. m. This estimate is more than 4 times higher than the average density of the 2003 cohort, and when extrapolated to average whole tree size calculated for the present study (9.38 sq. m), would result in an approximate density of 174 emerging adults per tree during the 2001 cohort. Populations of red oak borers may have declined approximately 88% from the 2001 to 2003 cohort and declined again (96%) between the 2003 and 2005 cohort. The extent of this reduction in density can be visualized by examining frequency distributions of total numbers of red oak borers per tree, which show that ~ 53% of trees sampled in 2003 contained more than 20 live red oak borers per tree (Fig. 3A). In 2005 and 2007 combined, only 2 of the 81 trees sampled contained 10 or more red oak borers, and 38 trees contained no red oak borers (Figs. 3B and C).

Hay (1974) described endemic red oak borer populations as averaging less than 1 larva per tree. Given our average tree size and bark surface area, Hay's (1974) description of endemic population densities can be estimated at approximately 0.11 larvae per sq. m of bark surface area. In 2003 the average density of 4.11 larvae emerging per sq. m of surface area from 17 sample trees was

Table 1. Mean density (number per square meter of bark surface area) of live red oak borers recorded from northern red oak trees at locations in Ozark National Forest during the 2001-2003, 2003-2005, and 2005-2007 cohorts.

	2003		2005		2007				
Location	Density	*n*	Density	*n*	Density	*n*	*F*	*df*	*P*
Fly Gap	5.74 a	10	0.30 b	8	0.15 b	8	14.13	2, 25	<0.0001
White Rock	2.35 a	3	0.19 b	9	0.06 b	8	42.50	2, 20	<0.0001
Oark	1.01 a	4	0.35 ab	8	0.09 b	8	3.56	2, 18	0.0525
Pedestal Rocks	n/a	0	0.01	8	n/a	0	n/a	n/a	n/a
Pilot Rock	n/a	0	0.03	8	n/a	0	n/a	n/a	n/a
Dickie Junction	n/a	0	0.39	8	n/a	0	n/a	n/a	n/a
Ozone	n/a	0	0.05	8	n/a	0	n/a	n/a	n/a
Overall	4.11a	17	0.18b	57	0.10b	24	45.37	2, 97	<0.0001

*The column labeled *n* indicates number of trees dissected during each location-year combination.

Means were considered significantly different at *P* d 0.05. Rows labeled with different lower-case letters represent significantly different mean cohort densities ($\alpha = 0.05$).

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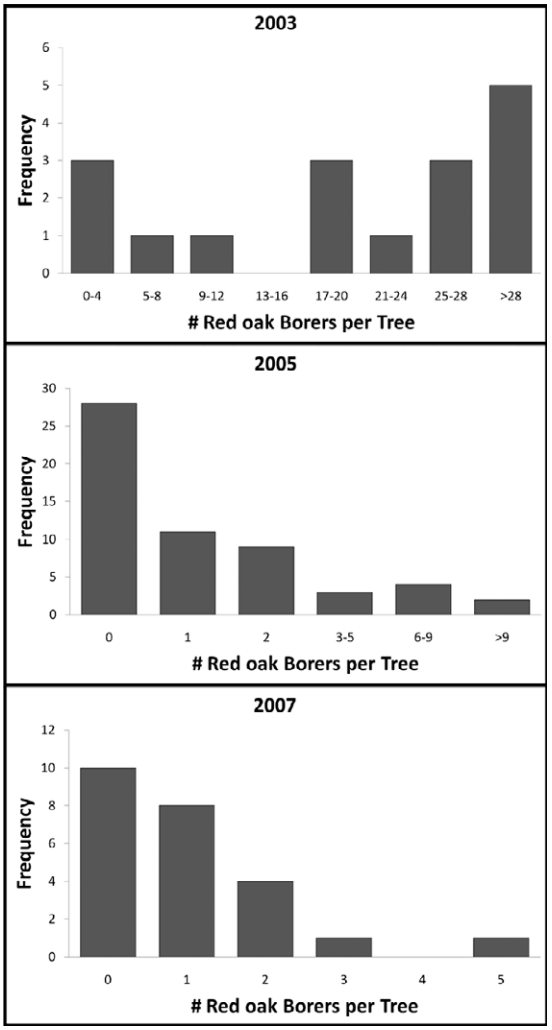


Fig. 3. Red oak borer frequency distribution based on total counts of live red oak borer per northern red oak tree dissected in the field during three successive cohorts in Ozark National Forest of Arkansas, U.S.A.

about 37 times greater than endemic levels. After the abrupt decline of red oak borer populations during the 2003-2005 cohort, overall average density of red oak borers (0.18/ sq. m) was only slightly higher than expected at endemic levels (0.11/ sq. m). Live red oak borer density immediately before emergence in 2007 (0.10 /sq. m) was not statistically lower than in 2005. This density estimate indicates that red oak borer populations at our sampling locations in Ozark National Forest in 2007 have returned to population levels consistent with those reported by Hay (1974), indicating that the recent outbreak event is over.

This insect outbreak is unusual because red oak borer is a widely-distributed native species, but has never been reported in high numbers anywhere in its range throughout hardwood forests of the eastern United States and southeastern Canada. More than 57 oak decline events have been documented in the eastern United States between 1856 and 1986 (Millers et al. 1989), including 1959 and 1980 in Arkansas (Toole, 1960; (Toole 1960; Bassett et al. 1982). In none of these decline events has red oak borer been described as a major contributing factor to tree mortality.

Cohort senescence theory (Mueller-Dombois 1987) predicts this type of insect and pathogen activity in a mosaic across the landscape as hosts begin to senesce due to the accumulation of stress over their lifetimes. Physiological age is the ultimate "score-keeper" of sorts, as the effects of a myriad of predisposing, inciting, and contributing factors (e.g., topographic position, acute drought, and insects, respectively) accumulate throughout trees' lives. The decline-disease spiral eventually culminates with tree death (Manion 1991). Conditions associated with oak decline are high red oak stocking density, ridge topographic position, poor site quality, older age (>60 years), advanced physiologic age (as measured by the ratio of site index/ stand age), and xeric soils (Starkey et al. 1989; Oak et al. 1996; Starkey et al. 2000; Heitzman & Guldin 2004; Kabrick et al. 2008). Red oak borer populations could potentially resurge if conditions favorable to oak decline are eventually replicated. Berryman (1986, 1987) characterized insect outbreaks in 2 general forms: (1) gradient responses to changes in environmental favorability (e.g., abundance of resources, predators, and parasitoids); and (2) eruptive outbreaks that begin in epicenters of highly favorable conditions and have the ability to spread into less susceptible areas and eventually infest vast areas of hosts (Valenti et al. 1999). Classifying red oak borers into 1 of these categories of outbreak pest is complicated because studies outlining its long-term population dynamics are lacking. However, the speed of onset, severity, and size of the outbreak suggests an eruptive pest, as is the apparent ability to successfully attack healthier host trees. However, it is more likely this outbreak fits into the framework of a graded response to a landscape-level superabundance of host trees beginning to senesce at the same time.

Conclusion

The dramatic outbreak of red oak borer first reported in northern Arkansas in 1999 appears to have subsided in 2005 and populations remain low in 2007. Red oak borer numbers increased exponentially, and then abruptly returned to endemic levels almost entirely during the course of 2 generations. The oak decline event that accompanied the outbreak (Starkey et al. 2004) was unique given the role of red oak borer as a major contributing factor (Manion 1991). At this time we remain un-

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certain of the cause of the outbreak and subsequent red oak borer population decline. It is likely, based on current understanding of oak decline etiology, that direct (forest management practices) and indirect anthropogenic disturbance (e.g., climate change) were both involved with this event.

Continued monitoring of red oak borer population abundance and dynamics may help anticipate future outbreaks. Ongoing remote sensing and spatial modeling may provide near real-time assessment of relative forest health and predictive hazard assessment at individual tree, stand, and landscape levels (Franklin 2001; Wang et al. 2007; Aquino et al. 2008; Riggins et al. 2009). Silvicultural treatments such as alteration of species composition, thinning, selective removal of infested trees, and prescribed fire are management practices which have been prescribed by forest managers in an attempt to improve the species diversity and age structure of Ozark National Forest (Donley 1981; Guldin et al. 2006). Removal of infested oaks in Ohio resulted in a 50% reduction of red oak borer population within the following generation, and about 90% during the second generation after silvicultural control was applied (Donley 1981). Prescribed fire and selective thinning both serve to remove poor specimens from the stand and should provide similar results. These practices may help to lessen future widespread red oak borer activity in the Arkansas Ozarks.

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