A DENDROCHRONOLOGICAL ANALYISIS OF RED OAK BORER ABUNDANCE

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Abstract—Unprecedented outbreaks of red oak borer (*Enaphalodes rufulus* Haldemann) have occurred in the lower Midwestern United States. Although generally not a mortality agent, red oak borer appears to contribute to general oak decline and mortality. The objective of this project was to explore dendrochronology as a means of determining the role of tree age, tree growth and climate in long-term red oak borer activity and to quantify the historic importance of red oak borer. In a *Quercus* (oak) dominated forest in Missouri, 31 oak trees were sampled and dendrochronological methods used to develop a red oak borer chronology. Borer activity in the stand has increased over the past 70 years with large increases occurring over the last 25 years. The abundance of wounds was related to tree age, ring width, annual mean temperature, and annual mean minimum temperature. Red oak borer wound abundance was not related to tree basal area increment, mean maximum temperature nor precipitation.

INTRODUCTION

Enaphalodes rufulus (Haldeman) Coleoptera: Cerambycidae, (red oak borer) is a wood boring insect that occurs throughout a wide range of deciduous forests in North America (Donley and Acciavatti 1980). In the past, damage associated with this insect has resulted in log degrade and overall decrease in wood quality. Recently very high population levels of the red oak borer have coincided with oak decline sites, and although not a primary mortality agent, it is clear that an abundance of red oak borer damage occurs in oak dominated forests with high tree mortality. Many explanations have been invoked to explain recent and unprecedented outbreaks of *E. rufulus* in the Ozark Highlands of Missouri and Arkansas. Among these, the abundance and age of host tree species, principally *Quercus* species (oaks), may provide an explanation. It is more likely, however, that the outbreaks are a result of host abundance coupled with the potential effect of climate on the development of *E. rufulus*. Historically, borer populations may have been limited by the sporadic occurrence and mixed age distribution of host tree species in the Missouri Ozarks. Forest harvesting regimes (ca. 1900), however, have resulted in extensive tracts of even-aged forests consisting predominantly of host species, namely *Quercus* sect. *Lobatae* (red or black oaks). On many sites these tree species have replaced shortleaf pine (*Pinus echinata*). A complete understanding of oak decline and specifically red oak borer abundance is lacking; in particular the relationship of red oak borer and site, climate, stand history has yet to be clarified. There is a need to understand tree, forest, and environmental conditions that influence such outbreaks.

Dendrochronology has been used often in entomology research to evaluate the frequency and timing of defoliator outbreaks (e.g., Fritts and Swetnam 1989, Swetnam and Lynch 1993), or the influence of defoliators on growth loss (Muzika and Liebhold 1999). The use of dendrochronology to examine wood boring insects, however, is relatively uncommon. Notable exceptions include a study by McManus and Giese (1968) that revealed that precipitation, temperature and flooding, were positively related to population fluctuations of the Columbian timber beetle (*Corthylus columbianus* Hopkins). Cambium mining insects (Diptera: Agromyzidae) create scars, sometimes referred to as pitch flecks, and have been used to evaluate population dynamics over a period of several decades (Schimitschek 1935, Ylioja and others 1999).

For this study, our primary goal was to document historic red oak borer occurrences as a way to examine the presence and abundance of red oak borer relative to a variety of abiotic factors. The intent is to begin to decipher the components of oak decline. Specifically, we examined the response of oak borers to climate, tree growth, tree age and stand age. We used dendrochronologically-dated xylem wounds made by oak borer larvae to construct borer activity chronologies at an oak decline site in the Missouri Ozarks.

METHODS

The study area was located in the Mark Twain National Forest, approximately 5 km east of Bixby, Missouri. The stand was a designated salvage site where most of the trees were to be removed soon after our study was complete. The 70-year old stand was dominated by scarlet oak and black oak. We established two 20 m belt transects and sampled each scarlet and black oak that fell within the transects. Thirty-one trees were sampled. Each sampled tree was felled and cut into one meter intervals, beginning at 1 m.

In the lab cross sections were prepared by sanding. Annual tree growth increments were cross-dated (Stokes and Smiley 1986) and tree stem initiation dates determined. Injuries were identified as borer damage by the wound configuration and characteristics (size, xylem wound shape, holes in bark, excelsior fibers), the presence of borer tunnels and tunnel stain traces, and infrequently, the occurrence of live larvae in tunnels. Although all borer wounds can be dated, not all borer tunnels on a cross-section are datable. The dimensions of each dated wound were measured and used as confirmation and stratification of wounds. These include: tangential extent of callus tissue and cambial death, the radial extent of callus tissue, presence/absence of tunnels, tunnel width and length. Borer wounds from all thirty-one

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trees were then compiled into a frequency distribution with annual resolution. Specifically, this oak borer chronology represents a time series of oak borer activity as preserved in the tree-ring record by the larval scarring of the cambium.

Radial growth chronologies of sampled trees were constructed in order to examine the relationships between borer activity and tree growth. Growth chronologies were calculated as raw ring-width (mm) and annual basal area increment (cm^2) was constructed. Basal area chronologies were used to assess tree growth and vigor while ring-width chronologies were used as an indirect estimate of change in wood density. Correlation analysis was used to determine the strength of relationship between red oak borer abundance and several stand and climate variables.

RESULTS

We tree-ring dated a total of 743 oak borer wounds on the 31 trees that grew in a declining oak forest in southeastern Missouri. From these data we developed a red oak borer chronology that described the levels of larval activity for a period extending more than 60 years (fig. 1). The red oak borer has a synchronized two-year life cycle (Solomon 1995). The predominance of wounds (89 percent) occurred biennially, supporting our supposition that red oak borer caused most cambial injuries.

Borer wounds increased abruptly during the late 1970's and remained at high levels to such an extent that red oak borer abundance was consistently greater than at any time since stand initiation in 1935 (fig. 1). The dramatic increase in red oak borer wounds occurred at a stand age of approximately 50 years.

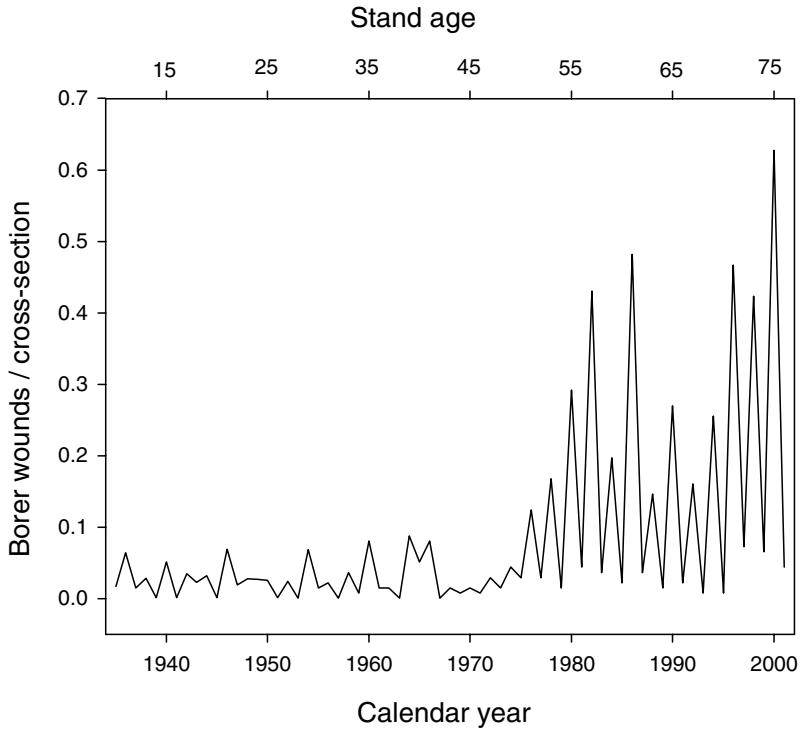

Figure 1—An annual frequency distribution of larval borer wounds dated on 137 cross sections from 31 oak trees near Bixby, MO.

Table 1—Correlation coefficients for the relationship between growth variables and tree-ring dated borer wounds

Growth variables	All dated wounds	Dated wounds/tunnels
Mean ring-width	-0.47**	-0.43**
[ln] ring-width	-0.51**	-0.47**
Basal area increment	0.17	0.15
Forest stand age	0.50**	0.46**

* = $p < 0.05$; ** = $p < 0.01$.
Dated wounds/tunnels are wounds that were associated with characteristic red oak borer tunnels. Mean ring-width is the raw nonstandardized width of the rings. Analysis includes all years of record (1920–2000).

Table 2—Correlation coefficients for the relationship between climate variables and tree-ring dated borer wounds

Climate variables	All dated wounds	Dated wounds/tunnels
Annual mean temperature	0.49*	0.56**
Annual mean max temperature	-0.22	-0.12
Annual mean min temperature	0.54*	0.59**
Annual total precipitation	0.18	0.06

** = $p < 0.05$; ** = $p < 0.01$.
Dated wounds/tunnels are wounds that were associated with characteristic red oak borer tunnels. Analysis is for even calendar years only during the period of recent red oak borer abundance (1956–2000). Even years are the years of synchronous red oak borer larval injury to the cambium.

We examined the correlations between growth variables and red oak borer activity. Correlations were performed on all dated wounds, as well as only those wounds that co-occurred with tunnels. The latter category of wounds represents a more conservative estimate of red oak borer activity. Basal area increment was not significantly related to the frequency of borer wounds (table 1), but mean ring-width and logarithmic transformed ring-width were both inversely related to red oak borer abundance, and forest stand age was positively related to red oak borer abundance.

Annual mean temperature and annual mean minimum temperature were positively related to red oak borer activity (table 2). Neither annual mean maximum temperature nor annual total precipitation was significantly related to red oak borer activity. Results were similar whether all dated wounds were used or dated wound with tunnels only.

DISCUSSION

These data indicate that the large increases in the frequency of borer wounds occurred in the mid to late 1970s (fig.1) despite the fact that this wood boring beetle has gained attention only during the late 1990's. Furthermore, red oak borer wounds did not correlate with basal area increment, an index that quantifies the amount of basal area that accrues on a tree or in a forest, i.e. the cross sectional area of wood produced by the tree annually. The lack of a relationship indicates that red oak borer outbreaks are not simply related to decreases in tree vigor. There was an inverse association between mean ring-width and increases in wound frequency (table 1). This association may be related to several direct and indirect factors such as reductions in wood density. Although outbreaks of red oak borer are associated with stressed trees that eventually succumb, these data suggest that individual trees and entire stands can support substantial populations of red oak borer for decades before the stand exhibits signs of decline.

Correlation analyses indicate that temperature, ring width, and stand age were most strongly related to the frequency of borer attacks. Minimum temperature was most strongly related to the frequency of red oak borer wounds (table 2). The effect of temperature on red oak borers is corroborated by previous laboratory experiments that found increases in temperature (21.1 to 32.2 °C) were positively related to the survival and fecundity of laboratory reared red oak borer (Galford 1974). We found no significant relationships between precipitation (table 2) and borer activity, despite the purported influence of drought on reduction in tree resistance.

Climatic factors can strongly influence insect populations, and substantial evidence exists to demonstrate how fecundity, survival, and dispersal are affected by temperature, precipitation, wind or humidity. Over long time periods, rainfall has been the most consistent predictor of insect populations, at least defoliators (Swetnam and Lynch 1993). Our data suggests that although drought may play a role in general oak decline, there seems to be no relation between precipitation at our study sites and red oak borer abundance.

Considering the potential implication of climate change and red oak borer, among other insects (Williams and Liebhold 2002), it is critical to examine trends in temperature in order to develop predictions. Although the magnitude of increase in mean temperatures has been modest, change in mean minimum temperature has been much larger. In the region of the case study, minimum temperatures have increased about 2.8 °F since the 1960s. Minimum temperatures could be most limiting to borer development, growth, reproduction, and fecundity (Galford 1974).

Whole wood density and ring-width have been shown to be strongly related in ring-porous angiosperms (Panshin and Zeeuw 1970). Large-diameter vessel elements that occur only in earlywood have large empty lumens that make the earlywood less dense. Since earlywood width tends to be consistent among rings, irrespective of total width; proportionally, more earlywood (low-density) occurs in narrow rings. Since ring width size is negatively related to red oak borer wounds, wood density could be a direct and important variable concerning the temporal, spatial, and stem distribution of larval wounds. Wood density might reflect host quality from both a physical and chemical perspective. As density decreases the proportion of early wood within rings increases as does the proportion of readily hydrolyzed hemicellulose (Wu and McGinnes 1974). Further research may explain the significance of this factor.

CONCLUSIONS

Our research has provided insight into the evaluation of historical abundance of red oak borer and of factors controlling its activity. Oak borer wound chronologies offer us a new tool. The sectioning of trees and dating of wounds provides data on insect larval populations in an exact location for from 50 to 150 years. The data compiled is high resolution (tree wounds dated to the year), relatively long-term (many generations of insects), and abundant (many single trees have over one hundred borer wounds). This type of research will greatly improve our ability to sample and interpret both short and long-term changes in the abundance of wood boring insects and decipher basic biological limitations on insects.

This research represents a case study providing some indication about the factors that influence red oak borer activity and consequently oak decline. Further research will provide greater information about these and other factors that may ultimately assist in developing predictive models and influence management activity.

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