Historical Population Increases and Related Inciting Factors of Agrilus anxius, Agrilus bilineatus, and Agrilus granulatus liragus (Coleoptera: Buprestidae) in the Lake States (Michigan, Minnesota, and Wisconsin)

Robert A. Haack
USDA Forest Service, robert.haack@usda.gov

Toby Petrice

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Haack, Robert A. and Petrice, Toby 2019. "Historical Population Increases and Related Inciting Factors of Agrilus anxius, Agrilus bilineatus, and Agrilus granulatus liragus (Coleoptera: Buprestidae) in the Lake States (Michigan, Minnesota, and Wisconsin)," The Great Lakes Entomologist, vol 52 (1)
DOI: https://doi.org/10.22543/0090-0222.2337
Available at: https://scholar.valpo.edu/tgle/vol52/iss1/7

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Acknowledgments The authors thank the many forest health staff of the Departments of Natural Resources in Michigan, Minnesota, and Wisconsin for preparing the annual forest pest reports for the past several decades; Val Cervenka for supplying many of the early Minnesota forest pest reports; Andrea Diss-Torrance, Michael Hillstrom, Eduard Jendek, and Daniel Young for providing personal communications and unpublished data, and Daniel Herms, Brian Schwingle, Richard Westcott and two anonymous reviewers for commenting on an earlier version of this paper.
The genus *Agrilus* (Coleoptera: Buprestidae) is considered the most speciose in the Animal Kingdom with over 3200 recognized species worldwide as of April 2019 (Jendek and Poláková 2014; E. Jendek, pers. comm.). The continental United States is known to have at least 194 recognized *Agrilus* species and subspecies, of which 13 species are exotic to the USA (Chamorro et al. 2015; Hoebeke et al. 2017, DiGirolomo et al. 2019).

In the Lake States [a collective term for Michigan (MI), Minnesota (MN), and Wisconsin (WI)] there are at least 60 known *Agrilus* species, of which 4 are exotic (Wellso et al. 1976, Jendek 2013a, 2014). Among the native tree-infesting *Agrilus*, there are three species that regularly reach outbreak levels in the Lake States: *Agrilus anxius* Gory (bronze birch borer), *A. bilineatus* (Weber) (twolined chestnut borer), and *A. granulatus liragus* Barter & Brown (bronze poplar borer). The main host trees for these *Agrilus* are species of Betula for *A. anxius*, Castanea and Quercus for *A. bilineatus*, and *Populus* for *A. granulatus liragus*. Based on 197 annual forest health reports for Michigan (1950–2017, 66 years), Minnesota (1950–2017, 64 years), and Wisconsin (1951–2017, 67 years), *A. bilineatus* was the most often reported *Agrilus* species in all three states (mentioned in 90 annual reports), with *A. anxius* second (71 reports) and *A. granulatus liragus* third (21 reports). Drought was the most commonly reported inciting factor for outbreaks of all three *Agrilus* species, with defoliation events ranking second. The top two defoliators reported as inciting outbreaks of each species were, in decreasing order, *Fenusa pumila* Leach (Hymenoptera: Tenthredinidae; birch leafminer) tied with *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae; forest tent caterpillar) for *A. anxius*; *M. disstria* and *Alsophila pometaria* (Harris) (Lepidoptera: Geometridae; fall cankerworm) for *A. bilineatus*; and *M. disstria* and *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae; large aspen tortrix) for *A. granulatus liragus*. Other environmental factors occasionally listed as inciting *Agrilus* outbreaks included late spring frosts, ice storms, and strong wind events.

**Keywords:** Jewel beetles, flatheaded borers, aspen, birch, oak, environmental stress, outbreak
late summer. In the Lake States, or other areas of similar latitude, adult emergence of these three species usually starts in late May or early June, peaks in late June, and then diminishes through July and August. Adults feed on host foliage for several days to become sexually mature and then mate and oviposit in bark cracks and crevices along the major branches and trunks of host trees. Eggs are laid singly or in small clusters. Upon eclosion, larvae tunnel through the bark and feed in the cambial region, constructing zig-zag galleries that score both the inner bark (phloem) and outermost sapwood (xylem). There are four larval instars and larvae often enter the outer sapwood to molt.

Eggs are laid singly or in small clusters. Over the past several decades, many changes have occurred in the taxonomic status of these three Agrius species. 

Agrilus anxius was initially described by Gory (1841), and included what we now refer to as A. granulatus liragus. Over a century later, Barter and Brown (1949) named Agrius liragus as a new species, separating it from A. anxius based on color, male genitalia, and larval host plants. Carlson and Knight (1969) reevaluated the Agrius anxius complex and reclassified A. liragus as a subspecies of A. granulatus. Later, Bright (1987) recognized A. liragus as a distinct species, then Nelson et al. (2008) once again recognized the subspecies A. granulatus liragus. Although both combinations have appeared in recent scientific literature, we use A. granulatus liragus in the present paper. Agrius bilineatus was first described in 1801 under the name Buprestis bilineata Weber (Fisher 1928). For many years, two subspecies of A. bilineatus were recognized based on their larval hosts and subtle morphological differences, with A. bilineatus bilineatus larvae feeding in Castanea and Quercus, and larvae of A. bilineatus carpini, Knnull, feeding in Carpinus (hornbeam), Fagus (beech), and Ostrya (hop hornbeam) (Knnull 1923). This latter subspecies was later elevated to species status under the name Agrius carpini Knnull (Nelson and Hesper heide 1998). Given the above history, it is understandable that there has been some confusion in the literature on the actual larval hosts of these three Agrius species.

Since the discovery of the Asian species Agrius planipennis Fairmaire (emerald ash borer) in North America in 2002 and in European Russia in 2005 (Haack et al. 2002, 2015), there has been growing concern in Europe, as well as in other countries, that various exotic species of Agrius could enter and greatly impact European urban and forest trees (Ple et al. 2015). For example, as of April 2019, EPPO (European and Mediterranean Plant Protection Organization) has conducted formal pest risk analyses (PRAs) for four Agrius species, including A. anxius in 2010 (EPPO 2011), A. planipennis in 2013 (EPPO 2013), A. bilineatus in 2018 (EPPO 2019a), and Agrilus fleischeri Obenberger in 2018 (EPPO 2019b). We were team members of the Expert Working Groups that conducted the above four Agrius PRAs: RAH for A. anxius and A. planipennis and TRP for A. bilineatus and A. fleischeri. During the PRAs for A. anxius and A. bilineatus, we provided the team members of the Expert Working Groups with details on the outbreak history of these two species in the Lake States, and in turn the team members encouraged us to summarize these data into a formal publication. In addition, the recent discovery of A. bilineatus in Turkey (Hızal and Arslangün doğdu 2018), has further increased interest in A. bilineatus and its potential threat to European Castanea and Quercus trees (EPPO 2019a, Haack and Petrice 2020). Given the above, we reviewed several decades of annual forest pest reports from the Lake States and recorded the number of times each native Agrius species was mentioned as reaching pest status, as well as any biotic and abiotic factors that could have incited the outbreaks.

Materials and Methods

We reviewed all annual forest pest reports that we could locate from Michigan (1950–2017, 66 reports, missing 1951 and 1973), Minnesota (1950–2017, 64 reports, missing 1956, 1963, 1967, and 1973), and Wisconsin (1951–2017, 67 reports). Formal forest pest surveys, often involving aerial surveys, ground surveys, and on-site visits in response to calls from foresters and the public, have been conducted in Wisconsin since 1949, and in Michigan and Minnesota since 1950 (WI CD 1953). Therefore, our dataset represents nearly all published forest pest reports for these three US states. Moreover, in 1951, forest health staff from the Lake States met in Madison, WI, to coordinate their reporting and survey methods for forest pests of mutual concern (WI CD 1953), therefore we feel comfortable comparing infestation records across the Lake States. We located most reports in our USDA Forest
Service library on the Michigan State University campus, where our Insect Research Unit has been located since 1956 (Haack 2006). For any missing years, we contacted the individual states, and in most cases they had copies available. Many of the reports since the 1990s are now online for the Lake States as well as all other US states (FHP 2018). Although the structure of state government has changed over time in the Lake States, these reports were typically prepared by the Forest Health staff within each state’s Department of Natural Resources (DNR). The titles of these DNR reports changed over the decades, usually starting as Forest Pest Reports in the 1950s and 1960s, changing to Forest Insect and Disease Reports in the 1970s and 1980s, and then to Forest Health Reports in the 1990s to the present.

When reviewing each report, we looked for any mention of Agrilus beetles, either by scientific name or common name. We concentrated on native Agrilus species, but after discovery of the exotic species A. planipennis in each state (2002 in MI, 2008 in WI, 2009 in MN), A. planipennis was mentioned in every subsequent annual report. For each mention of a native Agrilus species, we recorded the year of the report, where in the state the species reached pest status, and information on the severity of the infestation.

As a simple means to visualize the infestation levels for each species over time, we assigned a value of 1 to infestations ranked low and a value of 2 to infestations ranked moderate to severe by year and state. The ranking of “low” was given when the description of the infestation was described in terms of being local, scarce, light, spotty, scattered, etc. By contrast, a ranking of “moderate to severe” was given to infestations that were described as abundant, widespread or statewide, and usually causing severe tree dieback or mortality. On a few occasions, however, a ranking of low was given to situations where infestations occurred statewide but were restricted to urban situations, such as when A. anxius infested primarily ornamental birch trees.

Given that populations of many native Agrilus species increase when host trees are weakened by various inciting factors such as drought and defoliation (Millers et al. 1989, Solomon 1955), we also recorded any mention in the reports of the possible inciting factors that could have triggered the Agrilus outbreaks. We recognize that changes in staffing, funding, and priorities have taken place in each DNR Forest Health Unit in the Lake States, but feel confident that the major forest pests were recorded each year and therefore the annual forest health reports represent a good approximation of changes in Agrilus populations over time.

### Results

Agrilus anxius, A. bilineatus, and A. granulatus liragus were the only three native Agrilus species that were reported multiple times as forest pests in the Lake States. Agrilus bilineatus was reported most often in all three states, being mentioned in 90 of the 197 annual reports (16 MI, 34 MN, and 40 WI reports; Table 1). Agrilus anxius was the next most frequently reported species, being mentioned in 71 reports (11 MI, 33 MN, and 27 WI reports). Agrilus granulatus liragus was mentioned in 21 annual reports (7 MI, 11 MN, and 3 WI reports). Based on all 197 reports, A. anxius was first reported in 1951 in Minnesota, and A. bilineatus and A. granulatus liragus were both first reported in Wisconsin in 1966 and 1977, respectively.

Various weather-related phenomena and several defoliators were listed as suspected inciting factors that could have weakened trees and thereby led to population increases of A. anxius, A. bilineatus, and A. granulatus liragus in the Lake States (Table 2). Inciting factors were presented for 72% of the 182 listings of when these three Agrilus species reached reportable levels (62% of the 71 A. anxius listings, 74% of 90 A. bilineatus listings, and 95% of 21 A. granulatus liragus listings). Drought was the most commonly reported inciting factor for all three Agrilus species combined (listed 119 times), as well as individually for A. anxius (44 times), A.
Table 2. Frequency (number of annual reports by state) of various inciting factors that were associated with population increases of *Agrilus anxius*, *A. bilineatus* and *A. granulatus liragus* in Michigan (MI; 66 reports during 1950–2017), Minnesota (MN; 64 reports during 1950–2017), and Wisconsin (WI; 67 reports during 1951–2017) based on each state’s published annual forest health reports.

<table>
<thead>
<tr>
<th>Inciting factor by <em>Agrilus</em> species (including defoliator species, family, and common name)</th>
<th>MI (66 yr)</th>
<th>MN (64 yr)</th>
<th>WI (67 yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Agrilus anxius</em>, bronze birch borer</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>10</td>
<td>18</td>
<td>16</td>
</tr>
<tr>
<td>Late spring frost</td>
<td>1</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Fenusa pumila</em> Leach, Tentheredinidae, birch leafminer</td>
<td>–</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bucculatrix canadensisella</em> Chambers, Bucculaticridae, birch skeletonizer</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td><em>Malacosoma disstria</em> Hübner, Lasiocampidae, forest tent caterpillar</td>
<td>–</td>
<td>5</td>
<td>–</td>
</tr>
<tr>
<td><em>Agrilus bilineatus</em>, twolined chestnut borer</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>16</td>
<td>19</td>
<td>23</td>
</tr>
<tr>
<td>Hail or ice storm</td>
<td>–</td>
<td>–</td>
<td>2</td>
</tr>
<tr>
<td>Late spring frost</td>
<td>–</td>
<td>–</td>
<td>2</td>
</tr>
<tr>
<td>Strong wind event</td>
<td>–</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Orthoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dendroctonus quercus</em> Packard, Acrididae, post–oak locust</td>
<td>–</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Acleris semipurpurana</em> (Kearfott), Tortricidae, oak leafhopper</td>
<td>–</td>
<td>–</td>
<td>2</td>
</tr>
<tr>
<td><em>Alsophila pomatia</em> (Harris), Geometridae, fall cankerworm</td>
<td>–</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td><em>Archips argyrospila</em> (Walker), Tortricidae, fruittree leafroller</td>
<td>–</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td><em>Archips semiferanus</em> (Walker), Tortricidae, oak leafroller</td>
<td>5</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Bucculatrix ainsliella</em> Murtfeldt, Bucculaticridae, oak skeletonizer</td>
<td>–</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td><em>Erannis tiliaria</em> (Harris), Geometridae, linden looper</td>
<td>–</td>
<td>3</td>
<td>–</td>
</tr>
<tr>
<td><em>Lochmaeus manteo</em> Doubleday, Notodontidae, variable oakleaf caterpillar</td>
<td>–</td>
<td>–</td>
<td>2</td>
</tr>
<tr>
<td><em>Lymnastra dispar</em> (L), Erebidae, gypsy moth</td>
<td>1</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td><em>Malacosoma disstria</em> Hübner, Lasiocampidae, forest tent caterpillar</td>
<td>2</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td><em>Symmerista canicosta</em> Franclemont, Notodontidae, redhumped oakworm</td>
<td>–</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td><em>Symmerista leucitys</em> Franclemont, Notodontidae, orangehumped mapleworm</td>
<td>–</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td><em>Phasmda</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Diapheromeria femorata</em> (Say), Diapheromeridae, northern walkingstick</td>
<td>–</td>
<td>–</td>
<td>3</td>
</tr>
<tr>
<td><em>Agrilus granulatus liragus</em>, bronze poplar borer</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>7</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Charistoneura conflictana</em> (Walker), Tortricidae, large aspen tortrix</td>
<td>4</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td><em>Malacosoma disstria</em> Hübner, Lasiocampidae, forest tent caterpillar</td>
<td>4</td>
<td>7</td>
<td>1</td>
</tr>
</tbody>
</table>

*bilineatus* (58 times), and *A. granulatus liragus* (17 times; Table 2). Other weather events listed as inciting factors for population increases of these *Agrilus* (mostly for *A. bilineatus*) included late spring frosts, hail, ice storms, and strong wind events (Table 2). Several of the reports also mentioned tree age (i.e., overmaturity) as well as sandy soils and shallow soils as predisposing factors that increased tree vulnerability to *Agrilus* infestation, especially during periods of drought. The greatest diversity of defoliators listed as inciting factors for population increases of the three *Agrilus* species was associated with *A. bilineatus* (13 defoliator species, representing 8 families in 3 orders), followed by *A. anxius* (3 defoliators in 3 families and 2 orders), and *A. granulatus liragus* (2 defoliators in 2 families in 1 order; Table 2). The top two defoliators mentioned as inciting factors for each *Agrilus* species were, in decreasing order, *Fenusa pumila* Leach [formerly *F. pusilla* (Lepeletier)] and *Malacosoma disstria* Hübner (both tied) for...
Figure 1. Stacked bar graph (within years) showing the cumulative severity rankings (0–2 for each state by year) of Agrilus anxius, A. bilineatus, and A. granulatus liragus infestations in Michigan, Minnesota, and Wisconsin during 1968–2017 based on annual forest pest reports from each state. A value of 0 signifies that the insect was not reported as a pest, 1 represents an infestation ranked low, and 2 represents an infestation ranked moderate to severe within each state by year. See text for more details.
A. anxius; Alsophila pometaria (Harris) and M. disstria for A. bilineatus; and M. disstria and Choristoneura conflictana (Walker) for A. granulatus liragus. The insect order, family and common name for each defoliator are listed in Table 2. Malacosoma disstria was the only defoliator listed as an inciting factor for all three Agrilus species (Table 2).

The historic timeline of A. anxius, A. bilineatus, and A. granulatus liragus reaching pest status in the Lake States is depicted for the 50-year period during 1968–2017 in Fig. 1. For the years not shown in Fig. 1 (1950–1967), there were no reports for any of the three Agrilus species in Michigan, six reports for A. anxius in Minnesota (1951, 1955, 1958–59, 1961, and 1964), and eight reports for A. anxius (1953, 1959–62, and 1965–67) and two reports for A. bilineatus (1966–67) in Wisconsin. Agrilus anxius was reported as a pest in all three states in the same year only twice, in 1968 and 1970 (incited by drought and late frost), and only once for A. granulatus liragus in 2008 (incited by drought and C. conflictana and M. disstria defoliation; Fig. 1). By contrast, there were 12 years when A. bilineatus was reported as a pest in all three states: 1978–80, 1988–91, 1993, 2004, 2007, 2009, and 2013; usually with drought and various combinations of defoliators listed as the inciting agents (Fig. 1). Moreover, during the 3-yr period 1988–1990, A. bilineatus infestations were reported as moderate to severe in all three states, with drought and defoliation listed as the main inciting factors (Fig. 1).

Four additional native Agrilus species were mentioned in the 197 reports we reviewed and all in Wisconsin, including A. otiosus Say, which was reared from dying hickory (Carya) trees that were also infested with the bark beetle Scolytus quadrispinosus Say (Curculionidae: Scolytinae) and the canker fungus Ceratocystis smalleyii Johnson and Harrington (WI DNR 2005). The other three Agrilus species were A. arcuatus (Say), A. cliftoni Knell, and A. transimpressus Fall, all of which were reared in 2012 from dead and dying branches of declining black walnut trees (Juglans nigra L.) (WI DNR 2012; Andrea Diss-Torrance and Michael Hillstrom, pers. comm.). Two of these three walnut-infesting species (A. cliftoni and A. transimpressus) were recognized recently as new state records for Wisconsin (Hoftiezer 2011). Collections of the above hickory- and walnut-infesting Agrilus species resulted from targeted surveys of declining hickory and walnut stands in Wisconsin (WI DNR 2005, 2012).

Discussion

It is not surprising that A. anxius, A. bilineatus, and A. granulatus liragus were the most commonly reported Agrilus species in the Lake States, given that their respective hosts, Betula, Populus and Quercus, are among the most common hardwood trees (i.e., broadleaf trees, dicots) in the region (MN DNR 2017, Pugh et al. 2017, WI DNR 2018), and that these three Agrilus species are the most damaging Agrilus species that infest these host trees in the Lake States (Millers et al. 1989, Solomon 1995). As background, consider that the land areas of the Lake States are heavily forested (56% of MI, 32% of MN, and 49% of WI), and that hardwood forest types dominate the forestland in each state (73% in MI, 69% in MN, and 80% in WI) (MN DNR 2017, Pugh et al. 2017, WI DNR 2018). The aspen-birch forest type is the most common forest type in Minnesota, it ranks second in Michigan and third in Wisconsin. By contrast, the oak-dominated forest types rank first in Wisconsin, second in Minnesota, and third in Michigan. The most common forest type in Michigan is the sugar maple/beech/yellow birch type (Pugh et al. 2017).

There are also many conifers (e.g., softwood trees, gymnosperms) in the Lake States, but none serve as larval hosts for any Agrilus species in this region (Jendek and Poláková 2014). In fact, the only Agrilus species worldwide to be reared from a conifer host is A. schwerdtfegeri Schwerdtfeger, which emerged from a dead branch of Pinus maximinoi Moore (= P. tenuifolia Bentham) in Guatemala (Jendek 2013b).

The relationship of defoliation and drought with population increases of A. anxius, A. bilineatus, and A. granulatus liragus in the Lake States (Table 2), has been documented for many other Agrilus species worldwide (Ohgushi 1978, Vansteenikste et al. 2004, Sever et al. 2012, Sallé et al. 2014, Chamorro et al. 2015). Tree responses to defoliation and drought can be highly variable, depending on factors such as seasonality of the stress event (early summer vs. late summer), severity (mild vs. severe), and duration (one year vs. multi-year) (Kulman 1971, Kozlowski et al. 1991). Some typical early responses to defoliation include a reduction in tree carbon balance, fine root growth, and water uptake, followed by mobilization of stored reserves to develop and expand replacement foliage, which often reduces subsequent stem growth and concentrations of various defensive compounds present in stem tissues (Kulman 1971, Wright et al. 1979, Ericsson et al. 1980, Heichel and Turner 1983, Herm and Mattson 1992, Wargo 1996, Kroeke 2015). Similarly, the response
of phytophagous insects to drought-stressed trees can vary widely by feeding guild, with borers usually being favored by drought (Mattson et al. 1988, Larsson 1989, Huberty and Denno 2004, Rouault et al. 2006, Haa-vik et al. 2015, Showalter et al. 2018). For example, severe drought can reduce a tree’s ability to develop callus tissue, which can engulf and kill young wood-boring larvae such as Agrilus larvae (Sallé et al. 2014).

The greater frequency of A. bilineatus outbreaks in the Lake States as compared with A. anxius and A. granulatus liragus (Table 1, Fig. 1) may reflect differences in xylem structure of their host trees, with A. bilineatus infesting Quercus with ring-porous xylem, while A. anxius infests Betula and A. granulatus liragus infests Populus, which both have diffuse-porous xylem. This is an important difference, given that water moves primarily in the outermost annual ring of xylem in ring-porous trees, compared with several annual rings in the outermost sapwood in diffuse-porous trees (Kozlowski 1961, Wiant and Walker 1961, Kozlowski and Winget 1963). This difference also helps explain why ring-porous trees are more vulnerable to girdling insects like Agrilus larvae as well as pathogens that invade the outer xylem and cause wilt diseases such as chestnut blight, Dutch elm disease, and oak wilt (Zimmermann and McDonough 1978).

As an example consider the study in Wisconsin by Haack and Benjamin (1982) where the current-year annual ring of xylem along the main trunk of mature red (Q. rubra L.) oaks measured 0.8–1.8 mm in width, whereas the average width (measured at the widest point between the dorsal and ventral surfaces of the enlarged prothorax, Chamorro et al. 2015) of third instar A. bilineatus larvae measured 0.9 mm and fourth (last) instars measured 1.3 mm, indicating that late-instar A. bilineatus larvae could easily girdle the outermost annual ring of xylem in many host trees.

Differences in xylem structure also influence the within-tree attack pattern of Agrilus species as well as the ease in detecting infested trees. For example, in ring-porous trees, once the xylem tissue of a portion of a branch or the trunk is completely girdled, all foliage above the girdled area usually wilts and dies that same year. For A. bilineatus, this usually happens in late summer when most larvae are last instars and their feeding galleries are sufficiently deep to girdle the outer annual-ring of xylem (Haack and Benjamin 1982, Haack and Acciavatti 1992). Since A. bilineatus females apparently lay eggs only on live portions of a host tree, the area of current-year infestation moves downward from the crown to the lower trunk in each subsequent year of attack (Haack and Benjamin 1982, Haack et al. 1983, Petrice and Haack 2014). By contrast, the first appearance of wilting foliage and dieback on birch and aspen, which have diffuse-porous xylem, usually requires multiple years of infestation by A. anxius and A. granulatus liragus before enough annual rings of the outer conducting xylem have been effectively girdled to reduce translocation and cause dieback (Barton 1957, 1965, Solomon 1995, Muilenburg and Herms 2012). Moreover, given that dieback is more gradual in birch and aspen, infestation can occur throughout the entire tree as well as in the same area of a tree for several consecutive years until that portion of the tree dies (Loerch and Cameron 1984). As an example of the difference in timing of crown dieback in response to a stress event, consider the widespread severe drought that occurred in 1988 throughout the Lake States (Trenberth et al. 1988, Haack and Mattson 1989, Jones et al. 1993), with widespread oak mortality reported in all three Lake States in 1988 and continuing through to 1991 (Fig. 1), compared with fewer and more delayed infestations reported for A. anxius or A. granulatus liragus (Fig. 1).

In recent years, most aerial surveys for forest pests in the Lake States occur in early summer, which enhances detection of current-year, early-season defoliators. However, given that foliar wilting and discoloration of Agrilus-infested trees usually does not occur until late summer, this practice would usually lead to an underestimate of the actual number of Agrilus infestations that took place in the Lake States. Another difference between ring-porous and diffuse-porous trees that can influence the results of early-season aerial surveys is that ring-porous trees tend to leaf out later than diffuse-porous trees in any given area (Panchen et al. 2014). This occurs because in ring-porous trees, current-year earlywood xylem, which contains mostly large-diameter vessels that transport the bulk of the water, is produced before budburst, whereas in diffuse-porous trees, most current-year xylem is produced after leaf elongation (Umebayashi et al. 2008, Takahashi et al. 2013, Foster 2017).

Nonetheless, even in situations where late-summer aerial surveys are conducted, it would be easiest to detect first-season infestations of A. bilineatus because foliage will wilt and discolor during the first year of attack if the infested portion of the tree is completely girdled. By contrast, Agrilus-infested birch and aspen usually require multiple years of infestation before showing
dieback and if infestations only occur for one or two years the trees may callus-over old galleries and recover (Balch and Preble 1940, Anderson 1944, Barter 1957, 1965). Given this situation, it is likely that Agrilus infestations of birch and aspen occur more often than depicted in Fig. 1.

Many species of Agrilus, as well as other borers, preferentially infest overmature trees, especially during periods of stress (Balch and Preble 1940, Kozlowski 1969, Dunbar and Stephens 1976, Solomon 1995, Williams et al. 2013, Brown et al. 2015). Such a relationship, along with the forest history of the Lake States, is important to consider when viewing the pattern of Agrilus outbreaks depicted in Fig. 1. Consider that most of the virgin forests in the Lake States were logged during the late 1800s and early 1900s, with many large-scale forest fires soon following (Stearns 1997, Dickmann and Leefers 2003). Much of the cut-over land was soon abandoned, or farmed for short periods of time and then abandoned. Many of these degraded lands were then colonized by “pioneer” tree species, such as aspen (P. grandidentata Michx. and P. tremuloides Michx.) and paper birch (B. papyrifera Marshall), which are short-lived trees that reach physiological maturity at 50-70 years (Burns and Honkala 1990). Although some oaks in the Lake States are relatively short-lived (Q. ellipsoidalis E.J. Hill), most oaks are moderate to long-lived species (Loehle 1988, Burns and Honkala 1990, Barnes and Wagner 2004). Forest surveys conducted in the Lake States in the early 1990s indicated a skewed distribution with a large “wave” of forest stands then 55–75 years old (Stone 1997). More recent forest surveys in the Lake States (2014 for MI, 2016 for MN, and 2015 for WD) indicate sharp reductions in aspen and birch acreage, especially in older age classes, compared with increases in acreage of oak-dominated forests, especially in older age classes (Pugh et al. 2017, MN DNR 2017, WI DNR 2018). Such shifts in the species composition and age structure of forests in the Lake States may explain, in part, the decline in A. anxius outbreaks in recent years, the recent spike in the early 2000s of A. granulatus liragus activity, and the near steady activity of A. bilineatus over the past several decades (Fig. 1).

The defoliators listed in Table 2 are common throughout the Lake States as well as in much of eastern North America, and a few also occur in the West (e.g., C. conflictana, F. pumila, and M. disstria; Drooz 1985). At times, outbreaks of C. conflictana and M. disstria cover millions of hectares and can continue for multiple years before subsiding (Prentice 1955, Drooz 1985, Ciesla and Kruse 2009, Schowalter 2017). Of the defoliators listed in Table 2, only two are exotic to North America (F. pumila and Lymantria dispar (Linnaeus)), and both are far less outbreak prone today than in the past as a result of introduced natural enemies: mostly parasitoids for F. pumila (Kirichenko et al. 2019), and a fungus and virus for L. dispar (Solter and Hajek 2009). In addition, all of the defoliators listed in Table 2 initiate larval feeding in early summer, with the exception of the two Symmerista species, which are late-season defoliators (Drooz 1985). Early-season defoliation typically reduces same-year tree growth more than late-season defoliation because trees often use stored reserves to refoliate after early-season defoliation, but seldom refoliate after late-season defoliation (Kulman 1971, Ericsson et al. 1986). However, severe late-season defoliation can have a greater impact on stem growth the following year, compared with early season defoliation (Mattson et al. 1988). With respect to Agrilus adult activity, early-season defoliation would usually occur prior to peak Agrilus oviposition, whereas late-season defoliation would usually occur after most Agrilus oviposition had ended for the year. Outbreaks of many defoliators are also favored during periods of drought (Mattson and Haack 1987, Millers et al. 1989), and drought plus defoliation would likely even more significantly weaken trees, which would further increase tree susceptibility to borer infestation (Thomas et al. 2002).

Now that A. bilineatus has become established in Turkey (Hızal and Arslangünaydın 2018, EPPO 2019a), it is difficult to predict how damaging this species will be to European chestnut and oak trees. Drought and widespread defoliation of hardwood trees are also common in Europe (Gibbs and Greiggi 1997, Moraal and Hilszczanski 2000, Thomas et al. 2002, Sallé et al. 2014, Tiberi et al. 2016) and will likely make European host trees susceptible to A. bilineatus attack. However, throughout Europe there are several native species of Agrilus that utilize chestnut and oak trees as larval hosts (Jendek and Poláková 2014). Among these, A. biguttatus Fabricius is considered the most destructive, especially on oaks, which also commonly reaches outbreak levels in response to defoliation and drought (Moraal and Hilszczanski 2000, Sallé et al. 2014). Therefore, if European host trees are not highly susceptible to A. bilineatus, then A. bilineatus will likely encounter high levels of competition from native European Agrilus for hosts and consequently A. bilineatus may only become a minor pest in Europe. On the other hand, if some European chestnut and oak species are highly susceptible to A. bilineatus infestation, such as was the case when European Quercus robur L. trees were...
planted in Michigan (Haack 1986, Haack and Petrice 2020), then *A. bilineatus* could become a major pest in Europe. Nonetheless, given that drought is predicted to increase in frequency and severity in the future, outbreaks of *Agrilus* species and many other forest insects are expected to become more common in the United States and worldwide (Allen et al. 2010, Kolb et al. 2016).

**Acknowledgments**

The authors thank the many forest health staff of the Departments of Natural Resources in Michigan, Minnesota, and Wisconsin for preparing the annual forest pest reports for the past several decades; Val Cervenka for supplying many of the early Minnesota forest pest reports; Andrea Diss-Torrance, Michael Hillstrom, Eduard Jendek, and Daniel Young for providing personal communications and unpublished data, and Daniel Herms, Brian Schwingle, Richard Westcott and two anonymous reviewers for commenting on an earlier version of this paper.

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