Susceptibility of English Oak (*Quercus robur*) to the Twolined Chestnut Borer, *Agrilus bilineatus* (Coleoptera: Buprestidae): Observations from Michigan

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Abstract

The twolined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae), is a native North American buprestid beetle that normally infests oak (*Quercus*) trees stressed by drought or defoliation. However, during the 1980s and early 1990s, *A. bilineatus* preferentially infested English oak (*Quercus robur* L.) trees that initially appeared healthy at two experimental plantings in southern Michigan as well as on the Michigan State University (MSU) campus in East Lansing, Michigan. At both experimental plantings the English oaks were intermixed with native white oaks (*Quercus alba* L.) and had a border of native northern red oaks (*Quercus rubra* L.). At both locations, only the English oaks showed evidence of *A. bilineatus* infestation. Significantly more *A. bilineatus* adults were captured on sticky band traps on English oaks with low or depleted root starch levels compared to trees with medium to high starch levels. For one of the experimental plantings that was monitored for five consecutive years, 29 English oak trees eventually died that appeared healthy during the first year of observation: 3 (10%) died in one year, 20 (69%) in two years, 4 (14%) in three years, and 2 (7%) in four years. Of 403 English oak trees at MSU that were rated for crown dieback typical of *A. bilineatus* infestation, 37% showed some level of dieback in 1990, and 60% in 1991. As of 2024, as many as 157 of the original 403 English oak trees were still alive on the MSU campus, with most living trees having been treated with systemic insecticides. These results are discussed in terms of the "naïve host" theory in which plants may have lower resistance to herbivores that they did not coevolve with.

Keywords: *Agrilus*, wood borer, oak, *Quercus*, naïve host, coevolution

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The concept of the "naïve host" is one where the host plant lacks a coevolutionary history with a particular herbivore and thus the plant may have limited resistance to that herbivore (Gandhi and Herms 2010, Duan et al. 2024). When considering insects, such novel encounters can happen when either a host plant or an insect is moved between continents, or even within the same continent if a geographical barrier has kept them separate for millennia. In North America, there are buprestid beetles (Coleoptera) in the genus *Agrilus* that exemplify each of these scenarios. For instance, North American ash (*Fraxinus*) trees are highly susceptible to the Asian emerald ash borer, *Agrilus planipennis* Fairmaire (Herms 2015), which was first discovered in the United States in 2002 (Haack et al. 2002). Similarly, Asian and European species of birch (*Betula*) when planted in North America are highly susceptible to the North American bronze birch borer, *Agrilus anxius* Gory (Miller et al. 1991, Nielsen et al. 2011). And lastly, many species of oaks (*Quercus*) that are primarily native to California are highly susceptible to the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer, which was likely introduced from Arizona and thereby bridged the mountains that historically served as a barrier to natural spread by *A. auroguttatus* (Coleman and Seybold 2011). A similar intracontinental example is now unfolding in China where *Agrilus mali* Matsumura, a pest of apple (*Malus*) native to eastern China, has become established in northwestern China where it is causing severe damage on wild apples (Volkovitsh et al. 2020).

Another example of an agrilid and a naïve host appears to be the interaction between *Agrilus bilineatus* (Weber) (twolined chestnut borer), a North American species, and *Quercus robur* L. (English oak or pedunculate oak), which is native to much of Europe and western Asia (Eaton et al. 2016). To date, the only two reports on this interaction were both short publications from conference proceedings (Feder et al. 1980, Haack 1986). Feder et al. (1980) reported on *A. bilineatus* infesting and killing 10–40 cm diameter English oaks in Massachusetts, whereas Haack (1986) reported that English oaks were preferentially attacked by *A. bilineatus* in two mixed plantings of English oaks and native white oaks *(Quercus alba* L.) in southwestern Lower Michigan.

In 2018, *A. bilineatus* was reported in Europe for the first time, specifically in Turkey (Hizal and Arslangündogdu 2018, Ruzzier et al. 2023). Soon following that discovery, the European and Mediterranean Plant Protection Organization (EPPO) placed *A. bilineatus* on EPPO's Pest Alert List (EPPO 2018), followed by a formal pest risk assessment (EPPO 2019) and publication of a pest datasheet (EPPO 2020). In both the risk assessment (EPPO 2019) and the datasheet (EPPO 2020), the possible susceptibility of English oak to *A. bilineatus* was mentioned, citing "R. A. Haack, unpublished data." The aim of this publication is to provide much of the background data from Michigan that was the basis for citing RAH in those EPPO publications.

Agrilus bilineatus is a major pest of oaks and American chestnut, *Castanea dentata* (Marsh.) Borkh., in eastern North America (Haack and Acciavatti 1992, EPPO 2020). The native range of *A. bilineatus* matches closely with the native range of the eastern oaks, including the area from the Canadian Maritime Provinces, westward to the Great Plains, and southward to include the US states from Texas to Florida. Host trees impacted by various environmental stresses such as drought and defoliation are most susceptible to *A. bilineatus* infestation (Dunbar and Stephens 1976, Cote and Allen 1980, Haack and Benjamin 1982, Dunn et al. 1986a, Muzika et al. 2000, Haack and Petrice 2019). Infestation typically begins in the upper crown and proceeds downward along the main trunk in subsequent years, with tree death often occurring within three years (Dunbar and Stephens 1976, Haack and Benjamin 1982, Haack et al. 1983). An individual branch or an entire tree dies once the larval galleries completely encircle and thereby girdle a particular region of a tree (Haack and Benjamin 1982, Haack et al. 1983).

The life cycle of *A. bilineatus* has been studied for over a century (Chittenden 1897, Chapman 1915). Since those early years, many more studies have focused on various aspects of *A. bilineatus* life history (Dunbar and Stephens 1974, 1975, 1976; Cote and Allen 1980; Haack and Benjamin 1980, 1982; Haack et al. 1981, 1983; Dunn et al. 1986a, 1986b, 1987, 1990; Dunn and Potter 1988; Petrice and Haack 2014; Haack and Petrice 2019; Rutledge and Keena 2019). Briefly, *A. bilineatus* is univoltine throughout its geographic range. Most individuals overwinter as fully developed larvae in pupal cells constructed in the outer bark or outer sapwood, depending on bark thickness. Pupation occurs in late spring or early summer. New adults emerge through the bark by chewing a D-shaped exit hole, and then fly to the crowns of trees and feed on foliage to become sexually mature. Adults usually mate on the bark or foliage of host trees. Females lay eggs in bark cracks and crevices. After hatching, larvae immediately tunnel through the bark to the cambial region, scoring both the inner bark (phloem) and outer sapwood (xylem). There are four larval instars. Larvae construct meandering galleries that individually can extend over 80 cm in length (Chapman 1915, Dunbar and Stephens 1976, Cote and Allen 1980, Haack and Benjamin 1982).

In the 1980s, *A. bilineatus* appeared to preferentially infest and kill English oaks over white oaks in two mixed plantings at Michigan State University's (MSU) W. K. Kellogg Forest Experiment Station (Kalamazoo County, 42.36° N, 85.36° W) and Fred Russ Forest Experiment Station (Cass County, 42.01° N, 85.96° W), which are both managed by the MSU Department of Forestry. In addition, in the late 1980s and early 1990s, *A. bilineatus* infested several English oak trees on the main MSU campus in East Lansing (Ingham County, 42.73° N, 84.48° W). The objectives of the present study were to (1) monitor tree mortality over time at the English oak-white oak planting at Kellogg Forest, (2) relate trapping density of *A. bilineatus* adults on sticky bands to tree condition and root starch levels at Kellogg Forest and Russ Forest, and (3) summarize *A. bilineatus* infestation levels of English oak trees on the MSU campus in the early 1990s, and compare those early planting records with data from 2024.

Materials and Methods

Study sites and planting history. Two mixed plantings of English oak and white oak were established in southwestern Lower Michigan in April 1962. One planting was at Kellogg Forest and the other at Russ Forest (Wright et al. 1973). The Kellogg Forest planting started with 101 English oaks and 97 white oaks. The Russ Forest planting started with 94 English oaks and 88 white oaks. These trees had been grown from acorns collected in 1959 and grown for 2 years at a nursery on the MSU campus in East Lansing, MI. The English oak acorns had been collected from three English oaks trees growing on the MSU campus that had originated from acorns acquired from native English oaks growing in the Sherwood Forest near Nottinghamshire, England (Wright et al. 1973, Telewski 2023). The white oak acorns were collected from a single, large, native white oak tree growing in a natural forest setting at Russ Forest (Wright et al. 1973).

On the MSU campus, the first record of an English oak tree being planted was in 1935 (Wright et al. 1973). After observing how well English oak trees grew on the MSU campus, hundreds more were acquired from various arboreta and commercial nurseries and planted on campus starting in the 1950s (Wright et al. 1973). Current tree planting records on the MSU campus are maintained by MSU staff at the MSU Beal Garden and Campus Arboretum (https://bealbotanicalgarden.msu.edu/).

Early stand history at Kellogg Forest and Russ Forest. At both locations, seedlings of the two oak species were intermixed randomly and planted on sandy loam sites. Each planting had a single-tree border of native northern red oak (*Quercus rubra* L.), that had been grown from acorns collected at Russ Forest. The seedlings were planted on a 6 × 10 ft spacing (1.8 × 3.0 m) at Kellogg Forest, and an 8 × 8 ft spacing (2.4 × 2.4 m) at Russ Forest (Wright et al. 1973). Weed control was practiced at both locations for the first four years. At both locations, English oaks grew much faster than the white oaks. For example, average tree height 11 years after planting was 7.0 m for the English oaks and 4.6 m for the white oaks at Kellogg Forest (Wright et al. 1973). Similarly, average DBH for English oaks and white oaks was 11.1 cm and 5.4 cm, respectively, at Kellogg Forest at age 12, and 18.3 cm and 7.7 cm at Russ Forest at age 23 (Kowalewski 1985, Stadt et al. 1985).

Crown dieback of several English oak trees was first observed at both sites in the early 1980s (Kowalewski 1985, Stadt et al. 1985). No obvious stress event was identified that could have initiated the dieback. Staff at Kellogg Forest scored all English oaks and white oaks for crown dieback in early October 1984 and 1985, using a 1–4 rating system. The criteria were: (1) tree apparently healthy with no obvious crown dieback or wilting foliage, (2) trees with some crown branches dead or with some wilted foliage, but less than 50% of crown affected, (3) trees with more than 50% of the crown branches dead or with wilted foliage, but with at least some live branches remaining, and (4) all crown branches dead or with all foliage wilted, indicating tree death. The staff at Kellogg Forest did not thin or remove any of the oak trees. However, at Russ Forest, all white oaks were removed in 1985, along with most English oaks, especially those showing evidence of crown dieback, leaving 32 well-spaced English oak trees in the stand and the red oak border trees (Kowalewski 1985).

1986 sampling at Kellogg Forest. On 7 April 1986, a single sample of root wood (ca. 2 × 2 × 1 cm) was removed from one major root of 28 English oaks at Kellogg Forest. The sample was removed from the upper side of each root about 30 cm from where the soil line met the trunk. Each sample was placed individually in a labelled plastic bag, placed on ice in a cooler, returned to the laboratory, and stored in a freezer at –10 °C until processing. On 22–23 May 1986, root samples were prepared and rated visually for starch using the methods given in Wargo (1978). After allowing a sample to thaw, cross-sections 120-µ-thick, were cut with a sliding microtome, and stained with an I_2KI solution. After about 5 min, the excess iodine solution was wicked away, and the sample washed with water. The section was then placed on a labelled glass slide with cover slip, viewed under a dissecting microscope, and rated for starch content. Starch levels were categorized as high, medium, low, or depleted based on the standards shown in Wargo (1975) for northern red oak. Wargo (1975) had determined that the starch concentrations, calculated on a dry-weight basis, for the roots of red oaks were 15–30% starch for samples rated high, 7–12% for medium, 3–6% for low, and 0–1% for depleted.

On 11 April 1986, a 5-inch-wide (ca. 13 cm) plastic band was wrapped around the trunk of 25 English oaks at the study site, using only trees from which root starch samples had been taken. Each band was placed about 1.5 m above groundline, secured to the bark using a staple gun, and then coated with Tree Tanglefoot (Tanglefoot Company, Grand Rapids, MI), an adhesive material that catches insects when they land or walk on the surface. All traps were inspected for *A. bilineatus* adults during each site visit, which was usually 1–2 times per week from late May through July, and then every 2 weeks through September. During each visit, all *A. bilineatus* adults were removed and counted. Other items such as leaves and other large insects were also removed during each visit to keep the trapping surface mostly clean. New bands and tanglefoot were installed on all trees on 26 June 1986. The surface area of each trap was measured and used to calculate the density of captured *A. bilineatus* adults for each collection period and the entire trapping season.

We used the same 1–4 rating system to score the oak trees for degree of crown dieback on 8 September 1986. All English oaks, white oaks, and the red oak border trees were scored. As background to understanding the rating system, note that foliage on branches that are currently infested with *A. bilineatus* typically wilt and turn brown soon after larvae completely girdle the branch in late summer (Haack and Benjamin 1982, Haack and Acciavatti 1992). In the Great Lakes region, wilting of foliage on infested branches usually starts in August and peaks by early September, which coincides with the time when *A. bilineatus* larvae have become last (fourth) instars and are girdling deeper into the outer sapwood. In oaks, upward water conduction occurs primarily in the outermost annual ring in red oaks, and in the outermost 1 or 2 annual rings in white oaks (Kozlowski and Winget 1963, Kramer and Kozlowski 1979). When using a rating system based on foliage color in late summer it is important to complete the survey before the onset of normal fall leaf colors, which usually occurs in late October in southern Lower Michigan.

1987 sampling at Kellogg Forest. Sampling protocols in 1987 were the same as those described for 1986. Root samples for starch analyses were taken from 47 English oak trees on 7 April 1987, and prepared and scored for starch on 8 April 1987. Plastic bands, 5-in-wide, were installed around the lower trunk of the same 47 English oaks on 16 April 1987 and coated with tanglefoot. All traps were checked for *A. bilineatus* adults at 6–10 day intervals through July and then every 2–3 weeks until 10 September 1987. New sticky traps were installed on all trees on 19 June 1987. As in 1986, the trap surface area was used to calculate *A. bilineatus* density for each collection period and the entire flight season by tree. All English, white, and red oaks were rated for current-year dieback on 15 September 1987, using the same 1 (healthy) to 4 (dead) scale as described for 1986.

1988 sampling at Kellogg Forest. Again, the sampling protocols used in 1988 were similar to the preceding two years. However, no root samples were taken for starch analysis in 1988. Plastic bands, again 5-in-wide, were installed around the lower trunk of 32 English oaks on 21 April 1988 and typically checked weekly for *A. bilineatus* through July, and then at about 2-week intervals until 9 October 1988. New sticky traps were installed on all trees on 24 June 1988. Season-long trapping densities of *A. bilineatus* adults were calculated as above for each tree. All oaks were rated for current-year dieback on 9 October 1988.

Russ Forest sampling. By late summer 1986, crown dieback typical of *A. bilineatus* was observed on several of the 32 English oak trees that remained at Russ Forest after the 1985 thinning. Using the methods described above for root starch analyses, we removed a single sample of root wood from a major root of all 32 English oaks on 10 April 1987 and then processed the samples on 13 April 1987. Sticky bands as described above were installed around the lower trunk of all 32 English oaks on 16 April 1987. Tree diameter was recorded at the center of each band trap, and then the plastic was coated with tanglefoot. As above, *A. bilineatus* were collected from the traps periodically and counted. The sticky traps were removed on 27 July 1987, which was after *A. bilineatus* peak flight had occurred. Trapping densities of *A. bilineatus* adults were calculated as above for each tree.

English oak sampling at Michigan State University. Starting in the late 1980s several of the English oak trees on the MSU campus, were showing evidence of crown dieback. Dry conditions during 1987 and a severe regional drought in 1988 (Kunkel and Angel 1989, Michigan Weather Center 2023) could have impacted the English oaks more than the native oaks on the MSU campus. Given that our USDA Forest Service Insect Unit is located on the MSU campus, we were asked to evaluate some of the campus English oaks in late summer 1989. On all declining English oak trees examined, we found dead or dying branches with characteristic *A. bilineatus* exit holes on the bark surface, as well as *A. bilineatus* larvae and their galleries under the bark. In early May 1990, we worked with MSU Landscape and Grounds Department staff to develop a map locating all English oak trees on the main campus (403 trees), which had been planted at various times and from various sources over the preceding 55 years. These trees had been planted in a variety of settings, including along streets, in open areas, and near buildings. During 16–22 May 1990, we evaluated all 403 English oaks on the main campus, recording DBH and percent crown dieback in six general categories (0, 1–10, 11–25, 26–50, 51–75, >75% dieback). Crown condition of all English oak trees was again recorded in July 1991.

To document the presence of *A. bilineatus* and possibly other bark- and wood-infesting insects, we placed a single sticky trap in the lower crown of 138 English oak trees on campus during 1–4 June 1990. Trees in all crown dieback categories were sampled. The trap consisted of a 5-inch-wide band of plastic that was wrapped around and stapled to the base of a major crown branch or around the trunk but within the lower crown. Diameter of the trunk or branch was recorded near the midline of each trap. Next, the plastic band was coated with tanglefoot. Although placing the traps lower along the trunk would have been preferred, the lower crown was selected to reduce potential interactions with the public. All traps were recovered in September 1990 and examined for *A. bilineatus* adults and other borers.

Data management and statistical analyses. The *A. bilineatus* adult flight season was determined by first summing all adults collected on each collection day by year. Next, since the exact collection dates varied from year to year, we combined the data into five general collection periods: late May, and then early (1–15) and late (16–31) June, July, and August. Historical temperature data were used to calculate growing degrees for selected dates in 1986–1988, using the "averaging method" [(max. + min.) / 2–base temp], using a base temperature of 10 °C and start date of 1 March. Temperature data were obtained from weatherunderground.com for the Augusta, MI station (42.34 °N, 85.35 °W), which is about 3 km from the Kellogg Forest study site. For the few days with missing temperature data, other nearby weather stations were used. A planting map of the English oaks and white oaks at Kellogg Forest was developed to depict the late summer crown condition of each tree from 1984 to 1988 based on the annual surveys. The percentage of English oak trees in each crown condition category was calculated by year.

Mean sticky trap densities of captured *A. bilineatus* adults were analyzed for trees by their (a) initial spring 1986 and 1987 root starch ratings and (b) their dieback ranking as of September 1987. In these analyses the data were first log10 (x + 1) transformed. Afterwards, means were compared using the non-parametric Kruskal-Wallis rank sum test followed by the Dunn's test for post-hoc pairwise comparisons (https://astatsa.com). An alpha level of 0.05 was used in all analyses. The relationship between the initial spring root starch rating for a given tree and its subsequent late summer crown condition in the same year was explored by simple linear regression. For each of the 25 trees sampled for root starch in spring 1986 and the 47 trees sampled in 1987, we used a 1 (depleted) to 4 (high) rating for starch level and a 1 (dead) to 4 (healthy) rating for crown condition.

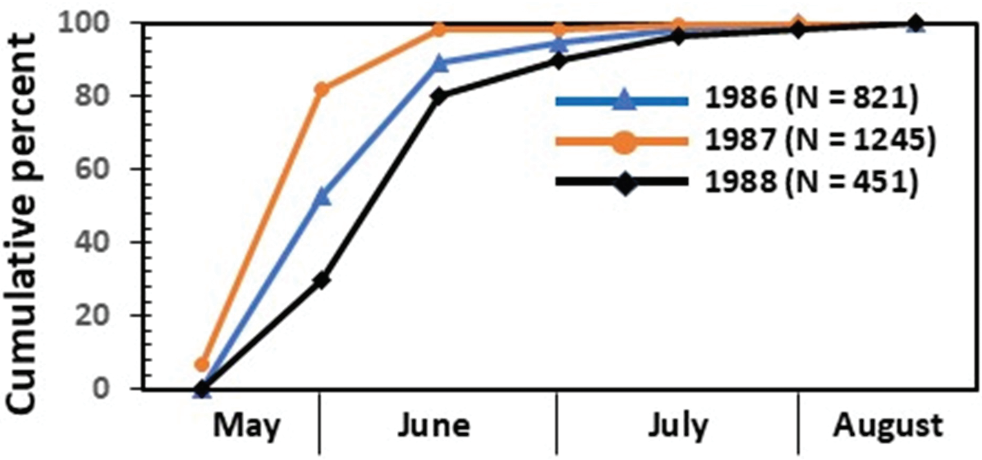
For the English oak surveys conducted on the MSU campus, the percentage of trees in each crown dieback condition was calculated. Average *A. bilineatus* trapping density were compared among the English oak trees in the various crown dieback categories. The number of English oak trees on the MSU campus in 1990–1991 was compared to current (2024) campus tree records obtained from staff at the MSU Beal Garden and Campus Arboretum to estimate percent survival of the English oaks that were present in 1990. The campus tree database has information on current trees by species, location, planting date, and condition, as well as notes on past treatments (e.g., application of systemic insecticides and fertilizer). Similar data for trees recently removed are also in the database, often with information about the reason for a tree's removal (e.g., construction).

Results

1986–1988 *A. bilineatus* flight at Kellogg Forest. The *A. bilineatus* flight season was similar in all three years sampled, beginning in late May, and ending in mid- to late August (Fig. 1). Peak flight (i.e., when the greatest percentage of *A. bilineatus* were collected) occurred during the first week of June in 1987, but closer to mid-June in 1986 and 1988. The earlier timing of peak flight in 1987 reflected the warmer spring conditions that year as noted by the greater degree-day accumulation as of 1 June 1987 compared to 1986 and 1988 (Fig. 1). There was wide variation in the density of *A. bilineatus* adults captured each year on the trees that had sticky traps, i.e., 0–16 adults/dm^2 of trap surface area in 1986, 0–18 in 1987, and 0–6 in 1988.

1984–1988 oak decline at Kellogg Forest. In spring 1984, 91 of the original 101 English oaks and 90 of the original 97 white oaks were present at Kellogg Forest, although their crown condition in spring 1984 was not recorded. By late summer 1984, 23 of the 91 English oaks were classified as dead (25.3% mortality), and similarly, 31 of the 91 trees had died by late summer 1985 (34.1%), 43 by 1986 (47.2%), 56 by 1987 (61.5%), and 65 by 1988 (71.4%; Fig. 2, Table 1). During this same 5-year period, none of the 90 white oaks died, nor any of the red oak border trees, or showed evidence of any crown dieback typical of *A. bilineatus* infestation. Of the 56 English oaks that showed no crown dieback at the end of the 1984 growing season, 29 eventually died over the following four years. Three of the 29 trees died in one year (dead in late summer 1985), 20 in two years (1986), 4 in three years (1987), and 2 in four years (1988) (Fig. 2).

Root starch levels in relation to *A. bilineatus* flight at Kellogg Forest. Of the 25 English oaks tested for starch levels in spring 1986, and which also had sticky traps, 12 had starch ratings of depleted, 9 low, 3 medium, and 1 high. In absolute terms, the average season-long trapping densities of *A. bilineatus* adults were greater on the trees with depleted or low starch levels, compared to trees with medium or high starch levels, although the differences were not significant (Table 2). Of the 47 English oaks tested for starch levels in spring 1987, 9 were rated as



Year	Cumulative degree days by date				
	1 June	15 June	1 July	15 July	1 Aug
1986	317	439	618	796	1067
1987	402	595	802	978	1224
1988	336	510	730	972	1209

Figure 1. Cumulative percent of *Agrilus bilineatus* adults captured per year during 2-week periods from May through August in 1986–1988 at the Kellogg Forest in Kalamazoo County, MI. Data based on the number of adult beetles captured on sticky band traps placed around the lower trunks of English oak trees. Numbers in parentheses are the total number of adults captured on all trees by year. Below the figure are the cumulative degree days (base 10°C) for selected dates in 1986–1988 based on weather records for Augusta, MI, which is about 3 km from the study site (see Methods for details).

depleted, 24 low, 12 medium, and 2 high. On average, season-long trapping density of *A. bilineatus* in 1987 was significantly greater on the trees with depleted or low starch levels compared with the trees with medium or high starch levels (Table 2).

Using data from 1987, which was the year when the largest numbers of English oak trees were sampled (47 trees), *A. bilineatus* adults tended to be captured at higher densities throughout the flight season on trees with depleted or low starch levels compared with trees with medium or high starch ratings (Fig. 3a). For example, on Julian day 155 (4 June 1987), which was the period of peak flight that year, mean (± SE) *A. bilineatus* densities were significantly greater on trees with depleted (3.5 ± 1.3 adults/dm^2) and

Table 1. Percent of English oak trees (N = 91) in an experimental planting at Kellogg Forest grouped by their late-summer crown condition for each year from 1984 to 1988.

Tree crown condition in September*	Percent (%) of English oaks by crown condition and year				
	1984	1985	1986	1987	1988
Healthy	61.5	42.9	25.3	16.5	12.1
< 50% dieback	7.7	16.4	14.3	16.5	5.5
> 50% dieback	5.5	6.6	13.2	5.5	11
Dead	25.3	34.1	47.2	61.5	71.4

* See Methods or Figure 2 caption for details on the crown condition categories.

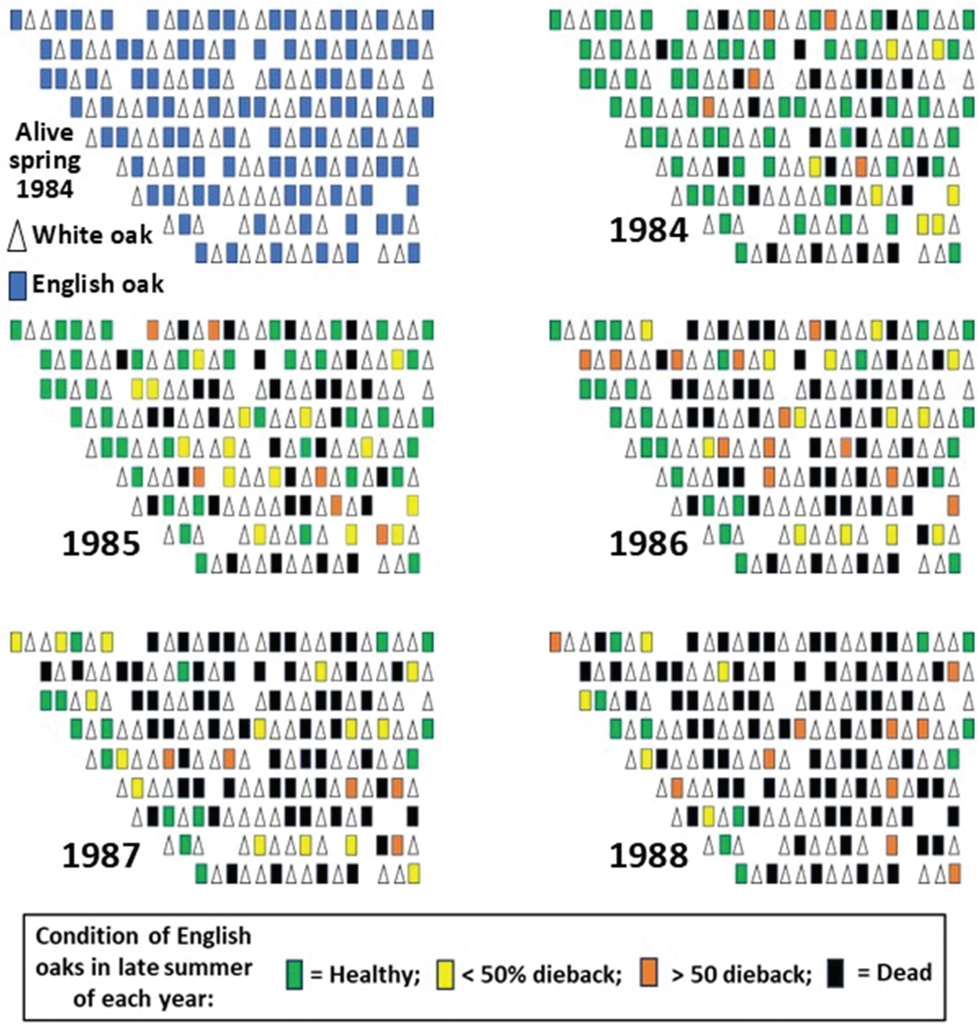


Figure 2. (Upper left) Planting map of the English oak (rectangles) and white oak (triangles) trees that were present and apparently alive at the Kellogg Forest study site in 1984, with open gaps representing where trees had been removed prior to 1984. Next, annual maps depicting the late-summer crown condition of each English oak tree from 1984 through 1988. The crown condition categories were: (1) tree apparently healthy with no obvious dieback or wilted foliage, (2) trees with less than 50% of crown showing dieback or wilted foliage, (3) trees with more than 50% of the crown dead or with wilted foliage, but with some green foliage remaining, and (4) all crown branches dead or with wilted foliage, All white oak trees appeared healthy (no wilted foliage) during 1984–1988, and are not color-coded.

low (2.4 ± 0.6) starch levels compared to trees with medium (0.1 ± 0.04) or high (0.2 ± 0.1) starch levels trees (Fig. 3a; Kruskal-Wallis $H = 27.6$; df = 3; $P = 0.000004$).

When the 1987 flight season data for the 47 sampled trees was grouped based on each tree's crown condition as of September 1987, *A. bilineatus* adults tended to be captured at higher densities on trees that ended the growing season with over 50% crown dieback (5 trees) or were considered dead (13), compared with trees that were ranked healthy (15) or having less than 50% crown dieback (14; Fig. 3b). As above, on Julian day 155 an average of 4.8 ± 2.0 *A. bilineatus* adults/dm^2 were collected on trees with >50% crown dieback at the end of the growing season, and similarly 4.1 ± 0.9 for trees that died in 1987, which were both significantly greater than the average densities of adults captured on trees with less than 50% dieback

Table 2. Season-long trapping density of *A. bilineatus* adults on English oak trees during the summers of 1986 and 1987 by tree root-starch level at Kellogg Forest (see methods for details).

	A. bilineatus adults / dm² [mean ± SE (range; No of trees)]				
Year	High starch	Medium starch	Low starch	Depleted starch	Kruskal-Wallis statistic
1986	0 ± 0 (0; N = 1) a*	1.4 ± 0.9 (0–3.1; N = 3) a	3.4 ± 1.3- (0.2–11.2; N = 9) a	5.5 ± 1.4 (0.9–16.5; N = 12) a	$H = 6.3$; df = 3; $P = 0.0998$
1987	0.3 ± 0.1 (0.2 – 0.5; N = 2) b	0.4 ± 0.1 (0.001–1.0; N = 12) b	4.2 ± 0.9 (0.3–16.3; N = 24) a	5.8 ± 2.0 (0.6–18.4; N = 9) a	$H = 23.6$; df = 3; $P = 0.00003$

*Means followed by the same letter (within rows) are not significantly different (Dunn's test).

(0.7 ± 0.2) or were classified as healthy at the end of the 1987 growing season (0.17 ± 0.06) ($H = 27.6$; df = 3; $P = 0.000004$; Fig. 3b).

Spring root starch levels relationship to late-summer crown condition. A significant linear relation was found between decreasing root starch levels and declining crown condition at Kellogg Forest for the pooled data from 1986 and 1987 (N = 72 trees; $F = 115.7$; df = 1,70; $P < 0.00001$; $r^2 = 0.62$). For example, for the three trees with high starch levels in spring, all had healthy appearing crowns at the end of summer of the same year. By contrast, for the 25 trees with depleted starch levels in spring, three had over 50% crown dieback, and 22 had died by the end of summer.

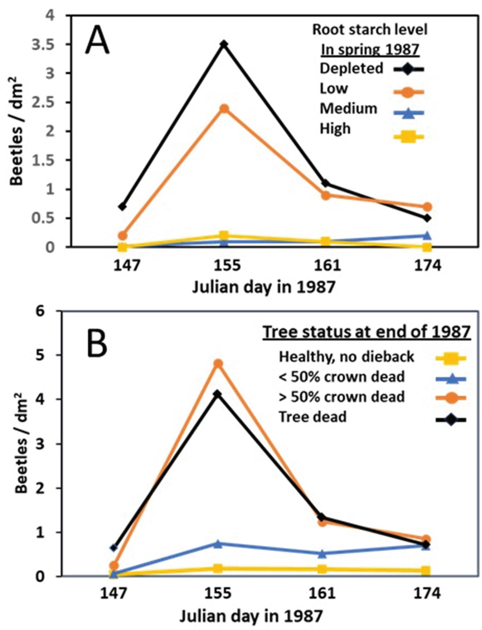


Figure 3. Trapping density of *Agrilus bilineatus* adults on sticky band traps placed around the lower trunk of English oak trees during the start of the 1987 flight season at the Kellogg Forest in Kalamazoo County, MI, with data presented by (A) tree root-starch rating in spring 1987 for 47 trees (9 rated as depleted, 24 low, 12 medium, and 2 high), and (B) tree crown condition in late summer 1987 for the same 47 trees. Calendar days in 1987 were 27 May for Julian day 147, 4 June for 155, 10 June for 161, and 23 June for 174.

Spring root starch levels over two consecutive years. For the 28 English oak trees at Kellogg Forest that were sampled for root starch in spring of both 1986 and 1987, all trees had either the same starch rating in both years (16 trees) or declined in starch level from 1986 to 1987 (12). There were three trees that had medium starch ratings in both years, ten with low ratings both years, and three with depleted ratings both years. For the 12 trees that showed a change in starch rating, five went from high to medium, one from high to low, three from medium to low, and three from low to depleted.

Root starch levels in relation to *A. bilineatus* flight at Russ Forest. In spring 1987, 5 of the 32 English oaks at Russ Forest had depleted root-starch levels, 7 were rated low, 9 medium, and 11 high. The 1987 average season-long trapping density of *A. bilineatus* was significantly higher on trees with depleted (3.3. ± 1.4 *A. bilineatus*/dm²) or low starch levels (3.3 ± 1.7) compared with trees with medium (0.4 ± 0.2) or high starch levels (0.2 ± 0.1) ($H = 17.7$; df = 3; $P = 0.0005$).

***A. bilineatus* infestations on the MSU campus in 1990–1991.** Of the 403 English oak trees rated for crown dieback in 1990, 215 (53%) showed no evidence of crown dieback, while 188 (37%) showed various levels of dieback. Overall, 33% of the 403 trees had 1–10% dieback in September 1990, 6% had 11–25% dieback, and 8% had 26–50% dieback. By July 1991, only 161 (40%) of the 403 English oak trees showed no evidence of crown dieback, while 242 trees (60%) had

Table 3. Average density of *A. bilineatus* adults captured on sticky traps placed on 138 English oak trees on the Michigan State University campus during summer 1990 by crown dieback category.

Percent crown dieback category	No. of trees	*A. bilineatus* adults / dm^2 Mean ± SE (range)	Dunn's test results
0%	51	0.02 ± 0.01 (0–0.4)	b
1–10%	34	0.18 ± 0.14 (0–4.8)	b
11–25%	22	0.43 ± 0.23 (0–4.0)	ab
25–50%	31	1.01 ± 0.55 (0–15.9)	a
Kruskal-Wallis test	H = 11.5; df = 3; P = 0.0092		

some dieback. Of all 403 trees in July 1991, 35% were in the 1–10% dieback category, 13% had 11–25% dieback, 10% had 26–50%, and 1% had 51–75%. In 1990, DBH for the 403 English oak trees on the MSU campus varied from 13 to 75 cm. Some trees of all sizes showed evidence of crown dieback in both 1990 and 1991, i.e., DBH values from 14 to 75 cm in 1990 and 13 to 75 cm in 1991.

Adult *A. bilineatus* were captured on 26 (19%) of the 138 sticky band traps placed in the lower crown of the English oak trees at MSU in 1990. No other bark- or wood-infesting adult beetles were recovered from the sticky traps at MSU, although other borers are commonly associated with *A. bilineatus* (Haack et al. 1983). Overall, *A. bilineatus* adults were captured on 8% (4 of 51) of the trees with no obvious crown dieback, 18% (6 of 34) of trees with 1–10% dieback, 23% (5 of 22) of trees with 11–25% dieback, and 35% (11 of 31) of trees with 26–50% dieback. When the number of *A. bilineatus* captured was expressed on a per area basis (adults/dm^2), trapping density increased significantly with increasing crown dieback severity (Table 3).

Numbers of English oaks on the MSU campus in 1990 and 2024. Although records for all tree plantings and removals on the MSU campus were not complete, current tree inventory data showed 157 live English oak trees in the same area of campus where the original 403 English oak trees were sampled in 1990 and 1991. These 157 trees did not include any trees with planting dates after 1991. The inventory data often do not provide details for why a tree was removed. Nevertheless, for the English oaks, infestation by *A. bilineatus* can be assumed as the reason for removal for most of these trees (Frank Telewski, MSU Beal Gardens, pers. comm). However, records for 26 of the likely original 403 English oaks state that they were removed during various campus construction projects. Additional notes in the database for the 157 English oaks still alive in 2024 state that at least 91 of them had been treated with various systemic insecticides for *A. bilineatus* over the years (initially with imidacloprid-based products and in more recent years with emamectin benzoate) (Katie Fry and Carolyn Miller, MSU Beal Gardens, pers. comm.).

Discussion

The English oaks at Kellogg Forest, Russ Forest, and on the MSU campus appeared to have been preferentially infested by *A. bilineatus* over nearby native oaks. At both Kellogg Forest and Russ Forest, the white oaks that were intermixed with the English Oaks showed no symptoms (i.e., wilted foliage) typical of *A. bilineatus* infestation during the study period, nor did any of the red oak trees that served as a border of each planting. Nevertheless, oviposition could have occurred on some of the white and red oaks at various times, but the resulting larvae died or never were in numbers great enough to girdle any individual branches and thereby cause premature wilting of the foliage.

English oaks grow best on fertile, well-drained soils, but are well-adapted to grow under a wide variety of conditions (Timbal and Aussenac 1996, Eaton et al. 2016). Given that the soils at the Kellogg and Russ Forest planting sites were both sandy loams, and that early growth of the English oaks at both sites was exceptional (Wright et al. 1973), we do not consider that poor site conditions led to the higher *A. bilineatus* infestation rates of English oak compared to the native oaks. In addition, we suspect that *A. bilineatus* infestation of the English oak at Kellogg Forest began some years before 1984, but went unnoticed, given that 25% of the English oaks were classified as dead by the Kellogg staff by autumn 1984, which was the first year surveys were made.

At MSU, besides English oaks, there were 1629 other oak trees planted on the MSU campus as of 2024, representing 22 distinct *Quercus* species (Carolyn Miller, MSU Beal Gardens, pers. comm.). Of these 1629 oak trees, 1548 represented 16 North

American species (*Q. alba, Q. bicolor* Willd., *Q. coccinea* Muenchh., *Q. ellipsoidalis* E. J. Hill, *Q. ilicifolia* Wangenh., *Q. imbricaria* Michx., *Q. macrocarpa* Michx., *Q. michauxii* Nutt., *Q. montana* Willd., *Q. muehlenbergii* Engelm., *Q. palustris* Münchh., *Q. phellos* L., *Q. rubra, Q. shumardii* Buckland, *Q. stellata* Wangenh., and *Q. velutina* Lam.) and 45 represented 6 exotic species (*Q. acutissima* Carruth., *Q. aliena* Blume, *Q. cerris* L., *Q. dentata* Thunb., *Q. mongolica* Fisch. ex Ledeb., and *Q. serrata* Murray). Of all the oak trees on the MSU campus over the past few decades, *A. bilineatus* has been a pest almost exclusively of the English oak trees, with some native oak trees infested when they were stressed by nearby construction projects (Jerry Wahl, MSU Campus Arborist, personal communication).

Many authors have reported that oak trees usually die in 1–3 years after initial infestation by *A. bilineatus* (Dunbar and Stephens 1976, Haack and Benjamin 1982, Dunn et al. 1986a, Haack and Acciavatti 1992), and that infestation begins primarily in the upper trunk and crown (Haack and Benjamin 1982, Haack et al. 1983). Our observations at Kellogg Forest support these reports given that 10% of 29 trees that appeared healthy and uninfested at the end of the first year of the study died the following year, 69% died in two years, 14% in 3 years, and 7% in four years. Such differences in timing likely result from variation in local *A. bilineatus* populations, general tree health, and the branching pattern of individual trees. Typically, an individual branch dies when *A. bilineatus* larval galleries completely encircle the branch and effectively girdle it. Similarly, an entire tree will die when the larval galleries encircle some region of the trunk below the first live branch (Haack and Benjamin 1982). If *A. bilineatus* larval galleries, especially those created by the last two instars, do not completely encircle a branch or a particular trunk area, then wilting of the foliage above that area will not occur (Haack and Benjamin 1982). Therefore, it is likely that some oaks in our study that appeared healthy in late summer (i.e., had no wilted foliage) actually had *A. bilineatus* larvae in some branches, but the galleries were not dense enough to effectively girdle that portion of the tree.

Temperate-zone deciduous trees typically store reserve carbohydrates in their roots during winter in the form of starch (McLaughlin et al. 1980, Kozlowski 1992). Winter starch levels are considered a good indicator of tree vigor, with higher levels reflecting a more vigorous tree (Wargo 1976, 1981; McLaughlin et al. 1980). In Kentucky, for white oaks showing no evidence of *A. bilineatus* infestation in late summer, but varying levels of stored root starch during the following winter, Dunn et al. (1987, 1990) found that trees with low starch levels attracted significantly more *A. bilineatus* adults (on sticky traps placed on the lower trunk) the next summer and had significantly more *A. bilineatus* larvae beneath the bark the following fall than trees with high starch levels. Our results agree with Dunn et al. (1987, 1990). However, it should be noted that in the present study and in the studies by Dunn et al. (1987, 1990), sticky band traps were placed along the lower trunk of the test trees (1.4 to 2 m above groundline). Such trap placement, although convenient, may not detect initial years of infestation by *A. bilineatus* on trees where oviposition occurs mostly in the upper trunk and crown (Haack and Benjamin 1982, Haack et al. 1983).

Adults of many *Agrilus* species are known to be visually attracted to various colors as well as to bodies of dead adults (or simply elytra) of conspecifics when used as decoys (Domingue et al. 2011, 2013; Duan et al. 2024). Given such information, it is likely that some *A. bilineatus* adults captured on the sticky traps in the present study were attracted to other *A. bilineatus* adults already stuck on the traps rather than being attracted by host volatiles (Dunn et al. 1986b) or possible pheromones (Dunn and Potter 1988).

Following the report by Wright et al. (1973) that English oaks grew faster than native oaks in Michigan, other researchers documented similar performance for English oak at test sites in Illinois (Clausen 1983a, 1983b) and Missouri (Johnson 1981). English oak is the most widely planted exotic oak in the United States, and dozens of English oak cultivars are available in the nursery industry (McArdle and Santamour 1985).

Although the results of this study suggest that English oaks are highly susceptible to *A. bilineatus*, it should be noted that the English oaks involved in these Michigan plantings likely represent only a small fraction of the genetic diversity present in *Q. robur* given its large geographic range that covers much of Europe and western Asia (Eaton et al. 2016). For the Kellogg Forest and Russ Forest plantings, we know that the English oaks came from acorns collected from trees that originated in the Sherwood Forest of England. However, for most of the English oaks on the MSU campus, the geographic origin of the parent trees is unknown.

Given the above, it is not clear if *A. bilineatus* will be a lethal threat to most English oaks or only a few seed sources. By comparison, most species of North American ash are highly susceptible to the Asian buprestid *A. planipennis* (Herms 2015), and similarly most Asian and European species of birch are highly susceptible to the North American buprestid *A. anxius* (Miller et al. 1991, Nielsen et al. 2011). Such examples of extreme susceptibility can be explained in terms of the "naïve host" theory which states that plants may be particularly susceptible to herbivores for which they lack a history of coevolution (Gandhi and Herms 2010, Showalter et al. 2018). Planting native woody plants is one way to avoid situations where a native borer exists that is lethal to non-native hosts. However, even native woody plants will become susceptible to native bark- and wood-infesting insects when stressed (Haack and Petrice 2019). In addition, favoring native plants will help support many native insects that use them as host plants (Tallamy 2009, Tallamy and Shropshire 2009).

Nevertheless, the potential threat posed by *A. bilineatus* to English oaks in Europe, as well as other species of *Castanea* and *Quercus* throughout Europe, warrants caution given the recent introduction of *A. bilineatus* in Turkey (Hizal and Arslangündogdu 2018). There are 78 species of *Agrilus* in Europe (Jendek and Grebennikov 2023), of which 11 species are known to use English oak as a larval host (Jendek and Poláková 2014). Time will tell if *A. bilineatus* becomes a major pest in Europe, exploiting some of the European *Castanea* and *Quercus* species as naïve hosts, or if *A. bilineatus* will be only a minor pest because it will need to compete with several other European agrilids for stressed host trees.

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Literature Cited

Chapman, R. N. 1915. Observations on the life history of *Agrilus bilineatus*. Journal of Agricultural Research 3: 283–294.

Chittenden, F. H. 1897. The twolined chestnut borer (*Agrilus bilineatus* Weber). United States Department of Agriculture, Division of Entomology Circular 24.

Clausen, K. E. 1983a. English oak grows better than white oak of comparable seedling size. Tree Planter's Notes 34(4): 17–19.

Clausen, K. E. 1983b. Variation between and among English oak and white oak families in survival and early growth. Pages 60–67 in: Proceedings, 28th Northeastern Forest Tree Improvement Conference, July 7–9, 1982, Durhan, New Hampshire.

Coleman, T. W. and S. J. Seybold. 2011. Collection history and comparison of the interactions of the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), with host oaks in southern California and southeastern Arizona, USA. The Coleopterists Bulletin 65: 93–108.

Cote, W. A. and D. C. Allen. 1980. Biology of two-lined chestnut borer, *Agrilus bilineatus*, in Pennsylvania and New York. Annals of the Entomological Society of America 73: 409–413.

Domingue, M. J., G. Csóka, M. Tóth, G. Vétek, B. Pénzes, V. Mastro, and T. C. Baker. 2011. Field observations of visual attraction of three European oak buprestid beetles toward conspecific and heterospecific models. Entomologia Experimentalis et Applicata 140: 112–121.

Domingue, M. J., J. P. Lelito, I. Fraser, V. C. Mastro, J. H. Tumlinson, and T. C. Baker. 2013. Visual and chemical cues affecting detection rate of the emerald ash borer in sticky traps. Journal of Applied Entomology 137: 77–87.

Duan J. J., T. D. Johnson, J. K. O'Dea, T. R. Petrice, and R. A. Haack. 2024. The ecology, economics, and management of *Agrilus* beetles. Current Forestry Report 10: 487–509.

Dunbar, D. M. and G. R. Stephens. 1974. Twolined chestnut borer: effects of storage conditions, processing, and insecticides on its survival in oak logs. Journal of Economic Entomology 67: 427–429.

Dunbar, D. M. and G. R. Stephens. 1975. Association of two-lined chestnut borer and shoestring fungus with mortality of defoliated oak in Connecticut. Forest Science 21: 169–174.

Dunbar, D. M. and G. R. Stephens. 1976. The bionomics of the two-lined chestnut borer. Pages 73–83 in: J. F. Anderson and H. K. Kaya (eds.), Perspectives in forest entomology, Academic Press, New York.

Dunn, J. P. and D. A. Potter. 1988. Evidence for sexual attraction by the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae). The Canadian Entomologist 120: 1037–1039.

Dunn, J. P., T. W. Kimmerer, and G. L. Nordin. 1986a. The role of host tree condition in attack of white oaks by the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae). Oecologia 70: 596–600.

Dunn, J. P., T. W. Kimmerer, and G. L. Nordin. 1986b. Attraction of the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae), and associated borers to volatiles of stressed white oak. The Canadian Entomologist 118: 503–509.

Dunn, J. P., T. W. Kimmerer, and D. A. Potter. 1987. Winter starch reserves of white oak as a predictor of attack by the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae). Oecologia 74: 352–355.

Dunn, J. P., D. A. Potter, and T. W. Kimmerer. 1990. Carbohydrate reserves, radial growth, and mechanisms of resistance of oak trees to phloem-boring insects. Oecologia 83: 458–468.

Eaton, E., G. Caudullo, S. Oliveira, and D. De Rigo. 2016. *Quercus robur* and *Quercus petraea* in Europe: distribution, habitat, usage and threats. Pages 160–163 in: J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant, and A. Mauri (eds.) European atlas of forest tree species. Publications Office of the European Union, Luxembourg.

EPPO (European and Mediterranean Plant Protection Organization). 2018. Pest Alert List: *Agrilus bilineatus* (Coleoptera: Buprestidae). Available from: https://gd.eppo.int/taxon/AGRLBL/documents

EPPO. 2019. Document 19-24767 Pest Risk Analysis for *Agrilus bilineatus*. Available from: https://gd.eppo.int/taxon/AGRLBL/documents

EPPO. 2020. *Agrilus bilineatus*, data sheets on pests recommended for regulation. EPPO Bulletin 50: 158–165.

Feder, W. A., G. W. Moorman, and T. A. Tattar. 1980. English oak decline on Cape Cod, MA. Phytopathology 70: 462.

Gandhi, K. and D. A. Herms. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biological Invasions 12: 389–405.

Haack, R. A. 1986. English oaks in Michigan: Are they susceptible to two-lined chestnut borer? Newsletter of the Michigan Entomological Society 31(4): 6.

Haack, R. A. and R. E. Acciavatti. 1992. Twolined chestnut borer. Forest Insect and Disease Leaflet 168. USDA Forest Service, Washington, D.C.

Haack, R. A. and D. M. Benjamin. 1980. Influence of time of summer felling of infested oak trees on larval development and adult emergence of the twolined chestnut borer, *Agrilus bilineatus*. University of Wisconsin, Forestry Research Note 236.

Haack, R. A. and D. M. Benjamin. 1982. The biology and ecology of the twolined chestnut borer, *Agrilus bilineatus* (Coleoptera: Buprestidae), on oaks, *Quercus* spp., in Wisconsin. The Canadian Entomologist 114: 385–396.

Haack, R. A. and T. R. Petrice. 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 52: 21–33.

Haack, R. A., D. M. Benjamin, and B. A. Schuh. 1981. Observations of the biology of *Phasgonophora sulcata* (Hymenoptera: Chalcididae), a larval parasitoid of the twolined chestnut borer, *Agrilus bilineatus* (Coleoptera: Buprestidae), in Wisconsin. The Great Lakes Entomologist 14: 113–116.

Haack, R. A., D. M. Benjamin, and K. D. Haack. 1983. Buprestidae, Cerambycidae, and Scolytidae associated with successive stages of *Agrilus bilineatus* (Coleoptera: Buprestidae) infestations of oaks in Wisconsin. The Great Lakes Entomologist 16: 47–55.

Haack, R. A., E. Jendek, H. P. Liu, K. R. Marchant, T. R. Petrice, T. M. Poland, and H. Ye. 2002. The emerald ash borer: a new exotic pest in North America. Newsletter of the Michigan Entomological Society 47: 1–5.

Herms, D. A. 2015. Host range and host resistance. Pages 65–73 in: R. G. Van Driesche and R. Reardon (eds.), Biology and control of emerald ash borer. USDA Forest Service Forest Health Technology Enterprise, Technical Bulletin FHTET 2014–09, Morgantown, WV.

Hizal, E. and Z. Arslangündogdu. 2018. The first record of two-lined chestnut borer *Agrilus bilineatus* (Weber, 1801) (Coleoptera: Buprestidae) from Europe. Entomological News 127: 333–335.

Jendek, E., and V. V. Grebennikov. 2023. Summary of native geographic distribution of all 3,341 species of the most speciose animal genus *Agrilus* (Coleoptera: Buprestidae). Journal of Insect Biodiversity 39: 32–78.

Jendek, E., and J. Poláková. 2014. Host plants of world *Agrilus* (Coleoptera, Buprestidae)—a critical review. Springer, Cham.

Johnson, P. S. 1981. Early results of planting English oak in an Ozark clearcut. USDA Forest Service, North Central Forest Experiment Station, Research Paper NC-204. St. Paul, MN.

Kowalewski, G. 1985. Oak performance at Russ Forest. Unpublished report submitted to the Department of Forestry, Michigan State University, East Lansing, MI.

Kozlowski, T. T. 1992. Carbohydrate sources and sinks in woody plants. The Botanical Review 58: 107–222.

Kozlowski, T. T. and C. H. Winget. 1963. Patterns of water movement in forest trees. Botanical Gazette 124: 301–311.

Kramer, P. J. and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York.

Kunkel, K. E. and J. R. Angel. 1989. Perspective on the 1988 midwestern drought. Eos 70(36): 817–819.

McArdle, A. J. and F. S. Santamour. 1985. Cultivar checklist for English oak (*Quercus robur*). Jorunal of Arboriculture 11: 307–315.

McLaughlin, S. B., R. K. McConathy, R. L. Barnes, and N. T. Edwards. 1980. Seasonal changes in energy allocation by white oak (*Quercus alba*). Canadian Journal of Forest Research 10: 379–388.

Michigan Weather Center. 2023. Michigan droughts. Available from: https://michigan-weather-center.org/michigan-droughts#:~:text=The%201987%20to%201990%20drought,the%201987%20to%201990%20period

Miller, R. O., P. D. Bloese, J. W. Hanover, and R. A. Haack. 1991. Paper birch and European white birch vary in growth and resistance to bronze birch borer. Journal of the American Society for Horticultural Science 116: 580–584.

Muzika, R. M., A. M. Liebhold, and M. J. Twery. 2000. Dynamics of twolined chestnut borer, *Agrilus bilineatus*, as influenced by defoliation and selection thinning. Agricultural and Forest Entomology 2: 283–289.

Nielsen, D. G., V. L. Muilenburg, and D. A. Herms. 2011. Interspecific variation in resistance of Asian, European, and North American birches (*Betula* spp.) to bronze birch borer (Coleoptera: Buprestidae). Environmental Entomology 40: 648–653.

Petrice, T. R. and R. A. Haack. 2014. Biology of the European oak borer in Michigan, United States of America, with comparisons to the native twolined chestnut borer. The Canadian Entomologist 146: 36–51.

Rutledge, C. E. and M. A. Keena. 2019. Mating behavior and reproductive biology of emerald ash borer (Coleoptera: Buprestidae) and two of its native congeners, the twolined chestnut borer and the bronze birch borer. Journal of Economic Entomology 112: 2620–2631.

Ruzzier, E., R. A. Haack, G. Curletti, A. Roques, M. G. Volkovitsh, and A. Battisti. 2023. Jewels on the go: exotic buprestids around the world (Coleoptera, Buprestidae). NeoBiota 84: 107–135.

Showalter, D. N., K. F. Raffa, R. A. Sniezko, D. A. Herms, A. M. Liebhold, J. A. Smith, and P. Bonello. 2018. Strategic development of tree resistance against forest pathogen and insect invasions in defense-free space. Frontiers in Ecology and Evolution 6: 124. doi: 10.3389/fevo.2018.00124

Stadt, T., J Hill, and B. O'Neal. 1985. Silvicultural and genetic experiments at W. K. Kellogg Experiment Station. Unpublished report submitted to the Department of Forestry, Michigan State University, East Lansing, MI.

Tallamy, D. W. 2009. Bringing nature home: how you can sustain wildlife with native plants. Timber Press, Portland, OR.

Tallamy, D. W. and K. J. Shropshire. 2009. Ranking lepidopteran use of native versus introduced plants. Conservation Biology 2: 941–947.

Telewski, F. W. 2023. The Sherwood Forest English oak *Quercus robur*. Available from: https://bealbotanicalgarden.msu.edu/campus-arboretum/tree-tour/english-oak

Timbal, J. and G. Aussenac. 1996. An overview of ecology and silviculture of indigenous oaks in France. Annals of Forest Science 53: 649–661.

Volkovitsh, M. G., A. V. Kovalev, and M. J. Orlova-Bienkowskaja. 2020. Current distribution and diagnostic features of two potentially invasive Asian buprestid species: *Agrilus mali* Matsumura and *A. fleischeri* Obenberger (Coleoptera: Buprestidae). Insects 11(8): 493. Available from: https://doi.org/10.3390/insects11080493

Wargo, P. M. 1975. Estimating starch content in roots of deciduous trees-a visual technique. USDA Forest Service, Northeastern Forest Experiment Station, Research Paper NE-313, Upper Darby, PA.

Wargo, P. M. 1976. Variation of starch content among and within roots of red and white oak trees. Forest Science 22: 468–471.

Wargo, P. M. 1978. Judging vigor of deciduous hardwoods. USDA Combined Forest Pest Research and Development Program, Agriculture Information Bulletin No. 418, Washington, D.C.

Wargo, P. M. 1981. Measuring response of trees to defoliation stress. Pages 248–267 in: C. C. Doane and M. L. McManus (eds.), The gypsy moth: research toward integrated pest management. USDA Forest Service Technical Bulletin 1584, Washington, D. C.

Wright, J. W., W. A. Lemmien, J. N. Bright, and G. W. Parmelee. 1973. English oak—A versatile tree. Michigan Agricultural Experiment Station, Research Report No. 207. East Lansing, MI.