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A Review of Bronze Birch Borer (Coleoptera: Buprestidae) Life History, Ecology, and Management

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ABSTRACT Bronze birch borer (Agrilus anxius Gory) (Coleoptera: Buprestidae), a specialist wood-borer endemic to North America, is prone to periodic outbreaks that have caused widespread mortality of birch (Betula spp.) in boreal and north temperate forests. It is also the key pest of birch in ornamental landscapes. Amenity plantings have extended the distribution of birch in North America, for which we report an updated map. Life history and phenology also are summarized. Larvae feed primarily on phloem tissue of stems and branches, which can girdle and kill trees. Stressors such as drought, elevated temperature, and defoliation predispose trees to bronze birch borer colonization and trigger outbreaks, which implicates the availability of suitable host material in the bottom-up regulation of populations. Stress imposed by climate change may increase the frequency of outbreaks and alter the distribution of birch. Bronze birch borer has a diverse array of natural enemies, but their role in top-down population regulation has not been studied. There is substantial interspecific variation in resistance to this insect. North American species share a coevolutionary history with bronze birch borer and are much more resistant than Eurasian species, which are evolutionarily naïve. Potential resistance mechanisms are reviewed. The high susceptibility of Eurasian birch species and climatic similarities of North America and Eurasia create high risk of widespread birch mortality in Eurasia if the borer was inadvertently introduced. Bronze birch borer can be managed in amenity plantings through selection of resistant birch species, plant health care practices, and insecticides.

KEY WORDS Betula, forest decline, insect outbreaks, population dynamics, host plant resistance

The metallic wood-boring beetles (Coleoptera: Buprestidae) constitute a diverse and widespread taxa, with an estimated 12,000–15,000 species worldwide, most of which are tropical or subtropical (Bright 1987, Evans et al. 2007). ~700 species are native to North America (Bright 1987). Most are saproxylic, depending on dead or dying trees for development (Speight 1989, Grove 2002), but some, including many species in the genus Agrilus, colonize living trees (Bright 1987, Solomon 1995, Evans et al. 2007). Of the >120 Agrilus species native to North America, a few have caused substantial tree mortality in natural and urban forests of North America. Twolined chestnut borer (A. bilineatus (Weber)) outbreaks in oak (Quercus spp.) forests (Dunbar and Stephens 1975, Haack and Benjamin 1982, Dunn et al. 1986) and bronze poplar borer (A. liragus Barter & Brown) outbreaks in aspen (Populus spp.) forests (Barter 1965, Carlson and Knight 1969) have been associated with stress events such as drought and defoliation that weaken host defenses. Recent invasions of eastern North America by emerald ash borer (A. planipennis Fairmaire) and of southwestern California by A. auroguttatus Schaefeler have resulted in extensive mortality of ash (Fraxinus spp.) (Cappaert et al. 2005, Pugh et al. 2011) and oak (Coleman et al. 2011), respectively. Larvae of these species construct galleries just under the bark as they feed, which can girdle and ultimately can kill the tree.

Perhaps the most ecologically and economically important Agrilus species endemic to North America is bronze birch borer (A. anxius Gory), a specialist wood-borer of birch (Betula spp.) (Slingerland 1906, Barter and Brown 1949, Bars and Brown 1957, Carlson and Knight 1969). This insect first was recognized as a pest of amenity trees by Chittenden (1898) and as a forest pest by Swaine (1918). Bronze birch borer is prone to expansive outbreaks that have been associated with periodic episodes of widespread birch (Betula spp.) decline and mortality throughout the 20th century in north temperate and boreal forests (Swaine 1918, Balch and Prebble 1940, Hawboldt and Skolko 1948, Barter 1957, Jones et al. 1993). Outbreaks consistently have followed large-scale stress events such as drought and high temperatures (e.g., Balch and Prebble 1940, Jones et al. 1993) that are thought to have compromised host resistance (Anderson 1944, Barter 1957, Carlson and Knight 1969).

Bronze birch borer colonizes most species of birch (Carlson and Knight 1969), but there is substantial interspecific variation in resistance to this insect (Miller et al. 1991, Nielsen et al. 2011). North American species, which share a coevolutionary history with bronze birch borer, are resistant to colonization unless stressed (Anderson 1944, Miller et al. 1991, Nielsen et al. 2011). In contrast, Eurasian species, which are evolutionarily naïve, are much more susceptible (Miller et al. 1991, Nielsen et al. 2011). The high susceptibility of Eurasian birch species and climatic similarities of North America and Eurasia where Betula spp. exist, suggest a high risk of establishment and spread throughout Eurasia if bronze birch borer were to be inadvertently introduced (EPPO 2011, Nielsen et al. 2011, Økland et al. 2012).

The European and Mediterranean Plant Protection Organization (EPPO) recently completed a comprehensive Pest Risk Assessment (PRA) that measured the risk of introduction of bronze birch borer to Europe. The PRA (EPPO 2011) and accompanying technical report (Muilenburg and Herms 2011) reviewed the biology of bronze birch borer as it relates to questions of regulatory significance, including potential pathways and vectors of introduction, probability of establishment and methods of prevention, survey and detection methods, and approaches to eradication should it become established. Here, we also review bronze birch borer biology and life history, but in ecological context, emphasizing host interactions and resistance, forest decline, population dynamics, potential effects of climate change, and pest management strategies in urban forests and ornamental landscapes.

Host Plants and Distribution. Bronze birch borer is endemic to the boreal and northern hardwood forests of North America. The range of bronze birch borer historically overlapped with the natural distribution of its evolutionary hosts: paper birch (Betula papyrifera Marshall), sweet birch (B. lenta L.), yellow birch (B. alleghaniensis Britton), gray birch (B. populifolia Marshall), and water birch (B. occidentalis Hook.) (Fisher 1929, Balch and Prebble 1940, Barter and Brown 1949, Carlson and Knight 1969). River birch (B. nigra L.) is considered to be immune (Nielsen et al. 2011). Among these host species, paper birch is the most widely distributed, endemic throughout Canada and the northern United States (Safford et al. 1990). Sweet birch, yellow birch, and gray birch are endemic to the northeastern United States and southeastern Canada (Erdmann 1990, Lamson 1990), whereas water birch is endemic to western North America, typically existing in mountainous or riparian regions (Gucker 2012). Betula species are the only documented larval hosts. Earlier reports of bronze birch borer larvae infesting species of poplar (Populus spp.) (Anderson 1944) subsequently were shown to be of a separate species described as the bronze poplar borer (Barter and Brown 1949). Bronze birch borer larvae infest trees of all sizes (Barter 1957) and have been observed to colonize branches as small as one cm in diameter (Slingerland 1906). Consequently, bronze birch borer can be a pest of nursery stock (Wohlers 1990, D. A. Herms, unpublished data).

Bronze birch borer also readily colonizes birch species that are exotic to North America, including varieties and cultivars of Asian white birch (Betula platyphylla Sukaczew), downy birch (B. pubescens Ehrh.), European white birch, Himalayan birch (B. utilis variety jacquemontii D. Don), monarch birch (B. maximowicziana Regel), and Szechuan white birch (B. szechuanica Jansson) (Dirr 2009, EPPO 2011, Nielsen et al. 2011). The high susceptibility of these Eurasian species (Nielsen et al. 2011) coupled with the climatic similarities of North America and Eurasia where Betula spp. exist, suggest a high risk of establishment and spread throughout Eurasia if bronze birch borer were to be inadvertently introduced (EPPO 2011, Nielsen et al. 2011, Økland et al. 2012). To date, however, bronze birch borer has not been detected outside of North America.

The current range of bronze birch borer in North America now extends beyond the natural distribution of its host plants into the southern and western United States (Fig. 1) because of planting of birch species as amenity trees. For example, exotic species such as European white birch and Himalayan birch (Ball and Simmons 1980, Dirr 1981, Katovich et al. 1997), and native species such as paper birch and gray birch (e.g., Johnson et al. 2001, Gu et al. 2007, Dirr 2009), have been planted as ornamental and shade trees throughout much of the United States (Table 1).

Previously published descriptions of the distribution of bronze birch borer have been derived from a combination of primary and secondary sources (Slingerland 1906, Balch and Prebble 1940, Carlson and Knight 1969, Bright 1987, EPPO 2011). It is possible that distribution lists published before taxonomic separation of bronze birch borer and bronze poplar borer in 1949 (Barter and Brown 1949) may represent the combined distributions of the two species. Here, we provide an updated distribution (Fig. 1) based on published reports and expert testimony falling into three categories of certainty: present, unknown, or no record of presence (Fig. 1; Table 1). “Present” indicates confirmation of bronze birch borer in that geographic area either in a publication or by expert testimony. “Unknown” indicates lack of confirmation of presence in a published record or by expert testimony,
but its absence cannot be considered conclusive as suitable hosts are known to exist in those locales. "No record of presence" indicates that bronze birch borer has not been documented in that geographic location and that suitable hosts are rare or absent, suggesting that bronze birch borer presence in that locale is unlikely. Hence, this final categorization represents a stronger certainty of the status of bronze birch borer than "unknown."

**Life History and Behavior.** The life cycle of bronze birch borer can be annual or biennial depending on climate and host condition, with 2-yr life cycles more prevalent in cooler climates and on more vigorous hosts (Slingerland 1906, Balch and Prebble 1940, Anderson 1944, Nash et al. 1951, Barter 1957, Carlson and Knight 1969). Adult emergence begins in May in Kentucky (Mussey and Potter 1997); May or June in Ohio and Michigan (Akers and Nielsen 1984, Herms 2004); and late June or early July in New Brunswick, Canada (Balch and Prebble 1940, Barter 1957). Emergence may begin earlier or later at more southern and northern extremes of its distribution, respectively. Emergence is relatively synchronized, occurring over a period of 10–12 wk and peaking 2–4 wk after first emergence (Fig. 2, D. A. Herms, unpublished data) (Barter 1957, Akers and Nielsen 1984, Loerch and Cameron 1984).

Several studies have modeled the phenology of bronze birch borer adult emergence based on degree-day accumulation (Akers and Nielsen 1984, Mussey and Potter 1997, Herms 2004). In 5-yr studies conducted in Wooster, OH and Midland, MI, adult emergence began on average at 547 (from 1985 to 1989) and 550 cumulative degree-days (DD) (from 1997 to 2001), respectively, using a starting date of 1 January and a base temperature of 50°F (corresponding to 276 and 278 DD, respectively, using a base temperature of 10°C) (Herms 2004). In Kentucky, adult emergence occurred on average at 1,807 cumulative DD, using a starting date of January 1 and base temperature of 35°F (corresponding to 1,004 DD, using a base temperature of 1.7°C) (Mussey and Potter 1997). Akers and Nielsen (1984) characterized adult emergence at three locations from southern to northern Ohio and found that a different model was most accurate at each location.

Adults, which live for 2–5 wk (Barter 1957, Akers and Nielsen 1990), are narrow and subcylindrical with coppery-bronze metallic coloration. Beetles are 7–12 mm long, with females being slightly larger than males (Barter 1957). Males have a ventral groove on the first and second abdominal segments that are absent in females (Barter 1957). Adults must feed on foliage to achieve reproductive maturity (Barter 1957, Akers and Nielsen 1990), and in natural and laboratory conditions, have been observed to feed on several species including birch, willow (*Salix*), and poplar for 7–25 d, depending on species (Akers and Nielsen 1990). Tree defoliation is negligible (Britton 1923).
No pheromones have been reported from bronze birch borer and mate location is not well understood but is thought to be facilitated by host selection (Barter 1957, Akers and Nielsen 1992). Males have been reported to arrive on host plants before females, where they actively seek and “ambush” females with which they copulate (Barter 1965). Females have the potential to produce ∼75 eggs in a lifetime (Barter 1957), but fecundity varies depending on the host plant upon which the adult female has fed (Akers and Nielsen 1990). Mating with multiple females increased reproductive output of males, but repeated matings did not increase female fecundity, and most females mated only once (Akers and Nielsen 1992). Small (1.5 by 0.75 mm), white to cream-colored, oval-shaped eggs are oviposited singly or in clusters of up to 14 under flakes of outer bark and in bark cracks and crevices (Hutchings 1923, Barter 1957, Loerch and Cameron 1984). Eclosion occurs approximately 2 wk after oviposition (Barter 1957).

Upon hatching, neonates immediately bore through the outer bark where they feed primarily on phloem and outer xylem. Feeding creates frass-filled galleries that disrupt transport of photosynthate and to some

### Table 1. Reports of bronze birch borer (A. anxius) in North America

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<th>Reference</th>
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<tr>
<td>Alberta</td>
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<td>Northwest Territories</td>
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<td>Prince Edward Island</td>
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<td>Quebec</td>
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<td>Yukon</td>
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<td>United States</td>
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PC, personal communication.
degree water (Anderson 1944, Barter 1957, Carlson and Knight 1969). Although bronze birch borer has been referred to as a cambial borer, Carlson and Knight (1969) consider this terminology to be technically incorrect, as the single-cell cambial layer is much too thin to be nutritionally significant. Gallery length is dependent on host condition and species, with shorter galleries (~25 cm) associated with unfavorable hosts (more resistant trees) and longer, more sinuous galleries (~127 cm) associated with more susceptible hosts (Anderson 1944, Barter 1957). When larval density is high enough, galleries girdle the tree, resulting in decline and eventual death (Anderson 1944, Barter 1957).

In Pennsylvania, morphological characteristics, including the width of the peristoma, indicated that larvae complete four instars (Loerch and Cameron 1983a). Five and six instars also have been reported but without indication of how these numbers were determined (Hutchings 1923, Barter 1957). Larvae are white to cream-colored, dorso-ventrally flattened, and have eight abdominal segments proceeded by two caudal segments (Barter 1957). Larvae are 8–20 mm long when mature (Loerch and Cameron 1983a). The final caudal segment terminates in a pair of sclerotized, tooth-like styles that are characteristic of Agrius spp. (Slingerland 1906). These terminal structures traditionally have been termed urogomphi; however, Chamorro et al. (2012) have proposed that they are more appropriately termed terminal processes, as they are not truly homologous with urogomphi.

All instars overwinter, but prepupal larvae (fourth instars that have completed development and constructed pupal cells) are most common (Barter 1957). Prepupal larvae must experience freezing temperatures before pupation can occur (Barter 1957), suggesting that early instars that overwinter will not pupate until after they experience obligatory chilling requirements as prepupae the next winter. This results in a 2-yr life cycle for larvae that do not reach the prepupal stage before overwintering and apparently is important for the relatively synchronized phenology of bronze birch borer adult emergence (Fig. 2).

During late summer or early fall, pupal cells are constructed by fourth instars in the outer xylem just interior to the cambial layer (Barter 1957, Loerch and Cameron 1984). Pupae initially are creamy-white and darken as pupation progresses, achieving adult coloration before emergence (Barter 1957). Pupation is initiated in April–June and takes 2–3 wk, after which adults emerge from trunks and branches (Barter 1957, Akers and Nielsen 1984, Loerch and Cameron 1984).

Signs, Symptoms, Impact, and Pattern of Colonization. Infested trees typically possess at least one of the following signs or symptoms: distinctively D-shaped adult emergence holes (3–5 mm wide), frass-filled larval galleries at the phloem-xylem interface just under the bark, and serpentine ridges (“welts”) visible externally on the trunk and branches caused by growth of wound periderm (callus tissue) over galleries (Anderson 1944, Barter 1957). In addition, bronze birch borer larvae may girdle branches, which induces branch dieback that generally commences in the upper crown, progresses downward, and is sometimes preceded by chlorotic foliage, thinning foliage, or both (Barter 1957, Ball and Simmons 1980). Other symptoms of bronze birch borer infestation include sprouting at the base of the trunk and damage to trunk and branches caused by woodpeckers as they excavate larvae. Trees often decline over several years, although death can occur more rapidly when trees are overwhelmed by large numbers of beetles (Barter 1957).

Ball and Simmons (1980) adopted the system of Barter (1957) to classify the vigor of birch based on the degree of crown dieback. Five vigor classes were recognized: 1) stem and crown healthy with no dieback; 2) crown contains flagging and twig dieback; 3) crown contains twig and small branch dieback; 4) crown contains three branches, at least 1 m in length, exhibiting dieback; 5) greater than half of the crown exhibiting dieback (Barter 1957, Ball and Simmons 1980). Trees in classes 1 and 2 contained only a few bronze birch borer larvae, whereas trees in more advanced classes of decline contained high densities of larvae. In some years, trees in class 2 exhibited improved vigor, resulting in reassignment to class 1. However, trees in class 3 or greater did not show signs of improved vigor and continued to decline. In addition, trees in class 4 contained small areas of dead, darkened phloem tissue, and trees in class 5 contained large areas of dead phloem tissue (Ball and Simmons 1980). Although larval development is severely protracted or ceases in dead phloem tissue (Anderson 1944, Barter 1957), class 5 trees still had the highest larval densities and were the only trees to contain high numbers of emergence holes on the stem (Ball and Simmons 1980, Nielsen et al. 2011).

There are conflicting descriptions of the pattern of colonization of birch by bronze birch borer. Balch and Prebble (1940) suggest that bronze birch borer preferentially colonizes weakened branches of yellow, gray, and paper birch until tree vigor diminishes to a degree that the lower bole is also suitable to support larval growth; however, it is not apparent how they
came to this conclusion. In contrast, after careful dissection of the main stems of European white birch, Loerch and Cameron (1984) found that the vertical distribution of bronze birch borer larvae was random and that the lower stem is as readily colonized as the upper stem. In addition, Ball and Simmons (1980) found that larvae successfully colonized the main stem rather than branches first, but it is not evident if this pattern occurred in all birch species or just in the highly susceptible European white birch. A potential explanation for these seemingly incongruous observations is that patterns of bronze birch borer colonization may be different in more resistant versus more susceptible species. In inherently susceptible European species (Nielsen et al. 2011), vertical colonization of the stem was random (Loerch and Cameron 1984). However, in more resistant North American species (Nielsen et al. 2011), larvae may colonize upper parts of the stem first (Balch and Prebble 1940), perhaps because of increased preference by ovipositing females, increased susceptibility of tissue, or both.

Bronze Birch Borer Outbreaks and Birch Decline. Periodic episodes of widespread birch decline in North America (Swaine 1918, Balch and Prebble 1940, Hawboldt and Skolko 1948, Redmond 1957, Millers et al. 1959, Jones et al. 1993, Auclair 2005) have been associated with expansive outbreaks of bronze birch borer (Balch and Prebble 1940, Nash et al. 1951, Barter 1957, Houston 1987). These episodes of forest decline and bronze birch borer outbreaks have been associated with stress events (Redmond 1957) including drought and elevated temperatures (Balch and Prebble 1940, Hawboldt and Skolko 1948, Clark and Barter 1958, Jones et al. 1993); defoliation (Balch and Prebble 1940); logging (Spaulding and MacAloney 1931, Hawboldt 1947); spring frost (Braathe 1995, Bourque et al. 2005, Auclair et al. 2010); and age-related tree senescence (Balch and Prebble 1940, Auclair et al. 1997), all of which were considered to have weakened host resistance and thus dramatically increased the availability of susceptible hosts.

The pattern of birch decline and bronze birch borer outbreak dynamics conform to the model of tree decline outlined by Sinclair (1964) and expanded by Manion (1981). This model identified three successive and interactive factors that together result in tree mortality: 1) predisposing factors (e.g., tree age, soil conditions, tree genetics, air pollution) that are general, long-term stresses; 2) inciting factors (e.g., drought, defoliation) that are specific, short-term stresses; and 3) contributing factors (e.g., insect borers, root rot, cankers) that are opportunistic colonizers of weakened trees. Manion (1981) conceptualized these categories into a disease spiral. In this model, decline events will minimally involve one factor from each category. Predisposing factors initiate the spiral of decline, and inciting and contributing factors further stress trees, ultimately leading to tree death (Manion 1981). Stressors such as drought (Hawboldt and Skolko 1948, Jones et al. 1993) and defoliation (Balch and Prebble 1940) were considered to increase susceptibility of yellow and paper birch to bronze birch borer, which ultimately killed the trees.

Some birch decline events could also conform to the theory of cohort senescence (Mueller-Dombois 1986, Mueller-Dombois 1992, Auclair et al. 1997). Paper birch is a relatively short-lived, early successional species that often forms even-aged, monospecific stands following disturbances such as fire and logging (Perala and Alm 1990, Lavoie and Saint-Louis 1999). Following a period of vigorous growth, cohorts enter a stage of maturity. Mature trees then exhibit decreased energy as a result of intrinsic genetic factors, which when coupled with extrinsic environmental stressors, can lead to large-scale dieback and mortality (Mueller-Dombois 1986). Consistent with this hypothesis, Auclair et al. (1997) proposed that large scale episodes of birch decline and mortality were a function of a shared history. Major disturbances such as fires, clear-cutting, or high winds can result in regeneration of homogeneous stands of trees dominating large areas of forest or can result in a mosaic of different cohorts across the forest landscape. A demographic cohort of trees, sharing a similar physiological experience, can mature, decline, and ultimately senesce simultaneously in response to an abiotic or biotic stress such as a drought or widespread defoliation that triggers a wood-borer outbreak. The trigger itself is not the sole causal agent of dieback, but rather a secondary or tertiary factor that occurs in synchrony with intrinsic stand factors (e.g., maturation) (Mueller-Dombois 1986, Auclair et al. 1997). Under this model, observed stand mortality is not viewed as a disease, but a normal process of forest decline etiology and succession dynamics (Mueller-Dombois 1992).

The most recent expansive bronze birch outbreak, which followed the severe drought of 1988 and resulted in mortality of over 105 million birch trees in the Great Lakes region of North America (Jones et al. 1993; MN DNR 1993, 1994), was consistent with the cohort senescence model. Many birch stands were aged similarly because of extensive logging and fires in the 1920s and 1930s. Mature stands were stressed because of droughts and high temperatures (Jones et al. 1993), which led to outbreaks of bronze birch borer and widespread birch dieback (MN DNR 1993, 1994).

Female reproductive effort of paper birch has been hypothesized as playing an important role in sustaining some bronze birch borer outbreaks (Herns and Mattson 1991). Birch species are monoecious, meaning that pistillate (female) and staminate (male) catkins are produced as separate reproductive structures on the same plant. Female reproductive effort is costly in that it can decrease vegetative growth (Caesar and MacDonald 1983, Herms 1991), and heavy seed set has been associated with tree decline (Gross 1972, Houston 1987). A trade-off also was documented between allocation to production of female structures (which require more resources than male structures) and resistance to bronze birch borer (Herns 1991, Herms and Mattson 1991). Slow vegetative growth may stimulate increased allocation of resources to female reproduction, which further reduces vegetative growth
because of within-plant resource competition (Herms and Mattson 1991). Increased female reproductive effort was negatively correlated with rate of wound-periderm formation (Herms 1991, Herms and Mattson 1991), a putative resistance mechanism to bronze birch borer (Miller et al. 1991). Therefore, a positive feedback loop involving reduced growth and increased female reproduction may progressively increase tree susceptibility to bronze birch borer (Herms and Mattson 1991).

Climate Change and Bronze Birch Borer. As natural disturbance events in forest ecosystems (Katovich et al. 2000), bronze birch borer outbreaks are integral components of ecosystem function that alter successional patterns and regulate nutrient cycling (Mattson and Addy 1975). However, interactions between birch species and bronze birch borer may be increasingly mediated by anthropogenic forces. Birch species are physiologically sensitive to environmental stressors such as drought (Raney et al. 1991, Jones et al. 1993, Darbah et al. 2010) and high temperature (Perala and Alm 1990, Davis and Zabinski 1992, Jones et al. 1993, Darbah et al. 2010). Because mean temperatures are projected to increase globally and rainfall patterns also are predicted to change, resulting in reduced rainfall in some regions (IPCC 2007), global climate change has been predicted to affect the distribution of birch species (Pastor and Post 1988, Overseck et al. 1991, Solomon and Bartlein 1992, Jones et al. 1994, Haack 1996). Models predict that distribution of paper birch will contract in the United States as its range migrates northward (Iverson et al. 1999, Iverson and Prasad 2001). Increased host stress resulting from climate change is predicted to increase susceptibility of paper birch to bronze birch borer, leading to increased frequency and intensity of borer outbreaks (Haack 1996). This may be especially pronounced at the southern edge of the natural distribution of paper birch, potentially accelerating its northward migration (Haack 1996). Other northern birch species in North America may respond similarly to climate change.

Population Dynamics

Tree Stress and Bronze Birch Borer Outbreaks. Bronze birch borer populations usually exist at low densities, with population growth presumably constrained by a limited supply of susceptible host material consisting of weakened, declining trees or branches (Balch and Prebble 1940, Barter 1957). During the past century, however, periodic wide-scale stress events have been implicated in weakening host resistance and thus dramatically increasing the availability of susceptible hosts, leading to expansive outbreaks of bronze birch borer (Balch and Prebble 1940, Nash et al. 1951, Barter 1957, Houston 1987, Jones et al. 1993). Stress imposed experimentally by girdling (Anderson 1944, Barter 1957, Herms 1991) and drought (Herms 1991) also increased larval colonization and growth, further implicating the role of stress in population outbreaks (Herms 1991) and the role of host availability in bottom-up regulation of bronze birch borer populations.

Bronze birch borer generally is considered a secondary, opportunistic colonizer of trees that first have been weakened by another biotic or abiotic stress (Spaulding and MacAloney 1931, Anderson 1944, Hawboldt 1947, Carlson and Knight 1968). Other authors have hypothesized that bronze birch borer can exist as both a secondary and primary colonizer, with its ecological role dependent on whether it exists at endemic or epidemic population densities, respectively (Balch and Prebble 1940, Nash et al. 1951, Barter 1957, Herms and Mattson 1991). Under this latter scenario, widespread stress dramatically increases the availability of suitable hosts and populations of bronze birch borer increase to outbreak densities, which then allows high numbers of colonizing beetles to overwhelm defenses of even healthy trees. However, the role of positive density dependence in bronze birch borer population dynamics is a hypothesis that requires further testing.

Natural Enemies. The primary natural enemies of bronze birch borer include woodpeckers and diverse egg and larval parasitoid species (Nash et al. 1951, Barter 1957, Loerch and Cameron 1983b, Taylor et al. 2012). In some cases, natural enemies have caused substantial bronze birch borer mortality. In studies in Maine and New Brunswick, parasitism of bronze birch borer eggs averaged over 50% (Nash et al. 1951, Barter 1957), whereas larval parasitism was <10% (Barter 1957). However, in Pennsylvania, egg parasitism was only 7%, but larval parasitism was 18% and woodpecker predation of overwintering larvae was 60% (Loerch and Cameron 1983b). Woodpecker predation also caused 51% larval mortality in individual trees in New Brunswick (Barter 1957). Density-dependent responses of natural enemies to bronze birch borer populations have not been investigated.

Three Asian parasitoid species have been released in North America to provide classical biological control of emerald ash borer (Bauer et al. 2010), which is a congener of bronze birch borer. No-choice tests indicate that two of these species, *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae) and *Spathius agrilli* Yang (Hymenoptera: Braconidae), can successfully parasitize bronze birch borer eggs and larvae, respectively (USDA APHIS 2007). The impact these parasitoids may have on field populations of bronze birch borer remains unknown. However, as emerald ash borer populations decline because of high mortality of their host plants (Pugh et al. 2011), increased parasitism of alternate hosts such as bronze birch borer and other native buprestids may occur.

There is little information regarding entomopathogens of bronze birch borer, but a microsporidian species recently was isolated from bronze birch borer adults that had been reared from infested trees in Ontario, Canada (Kyei-Poku et al. 2011).

Population Regulation: The Relative Role of Top-Down and Bottom-Up Effects. Although both top-down and bottom-up forces are considered to contribute to regulation of bronze birch borer popu-
lations, their relative importance has not been established (Barter 1957). The clear association of outbreaks with stress events that increase the availability of susceptible host plants implicates a primary role for bottom-up regulation of bronze birch borer populations (Barter 1957). Further evidence of bottom-up regulation is provided by differential survival of larvae among resistant and susceptible host species (Ball and Simmons 1990, Miller et al. 1991, Nielsen et al. 2011) and by larval mortality in resistant trees before pupation (Anderson 1944, Barter 1957, Nielsen et al. 2011).

The role of natural enemies in top-down regulation of bronze birch borer populations has received less attention and remains unclear. We are not aware of any evidence that documents a density-dependent effect of natural enemies or that natural enemies can prevent outbreaks when suitable host material is present. Nor are we aware of any evidence that natural enemies can protect highly susceptible host species such as European white birch when planted in North America. It is possible that natural enemies may respond in a delayed density-dependent manner to bronze birch borer outbreaks and thus play a role in suppressing bronze birch borer populations to endemic levels. Natural enemies also may contribute to regulation of low-density populations, but these hypotheses require more study.

**Interspecific Variation in Host Plant Resistance.**

There is dramatic variation among birch species in their resistance to bronze birch borer (Miller et al. 1991, Nielsen et al. 2011). North American species that have coevolved with bronze birch borer are much more resistant than evolutionarily naïve Eurasian species, which are highly susceptible (Miller et al. 1991, Nielsen et al. 2011). For example, in a 20-yr common garden study in Ohio, bronze birch borer colonization caused complete mortality of Eurasian species (European white birch, downy birch, monarch birch, and Szechuan white birch). North American species (paper birch, gray birch, and river birch), however, exhibited high survival throughout the study even without irrigation during the severe drought of 1988 and despite being planted outside their natural range (Nielsen et al. 2011). River birch, which is native to more southern reaches of North America, was not colonized, suggesting that it is immune to bronze birch borer (Nielsen et al. 2011). However, *Agrilus betulaniigrae* MacRae, which is morphologically very similar to bronze birch borer, has been observed to colonize dead branches of river birch in Missouri (MacRae 2003).

This pattern of variation in birch resistance to bronze birch borer is consistent with biogeographic theory of plant defense, which predicts that degree of resistance will correspond with selection pressure imposed by key herbivores (Bryant et al. 1994). A parallel pattern has been documented for the congenic emerald ash borer: Manchurian ash (*F. mandshurica* Rupr.), which shares a coevolutionary history with emerald ash borer in Asia (Liu et al. 2003), is much more resistant than the North American green (*F. pennsylvanica* Marshall) and white ash (*F. americana* L.), which do not share a coevolutionary history with the borer (Rebek et al. 2008).

Accurate characterization of degree of resistance of some birch species to bronze birch borer has been muddled by conflicting reports and taxonomic inaccuracies (Santamour 1999). For example, monarch birch and gray birch have been characterized as both susceptible and resistant (Kozel and Toth 1975, Santamour and Clausen 1979, Santamour 1982). Similarly, the birch ‘Whitespire,’ which was introduced to nursery industry as resistant to bronze birch borer (Hasselkus 1984), initially was classified as *B. platyphylla* variety *japonica* (Miq.) (Santamour and Mc Ardle 1989), a species indigenous to Japan, but later was identified as a cultivar of gray birch based on chemotaxonomic evidence (Santamour and Lundgren 1997). Despite substantial variation in their bark and foliage morphology, monarch birch has been confused with the much more resistant paper birch (Dirr 1981).

Considering the high susceptibility of European and Asian birch species planted in North America to bronze birch borer (Nielsen et al. 2011), the inadvertent introduction and establishment of this beetle to Eurasia could threaten birch species there on a continental scale (EPPO 2011, Muilenburg and Herms 2011, Nielsen et al. 2011, Ökland et al. 2012), just as the establishment and spread of emerald ash borer in North America threatens the survival of ash species in North America (Poland and McCullough 2006). Birch species exist throughout most of Europe and Asia and are dominant in some areas, comprising as much as 28% of the total volume of growing stock (Hynynen et al. 2010). Moreover, the wide geographic distribution of bronze birch borer in North America (Fig. 1) indicates that bronze birch borer can tolerate a wide range of climatic conditions and could be physiologically preadapted to establish throughout much of Eurasia where *Betula* species exist (EPPO 2011, Ökland et al. 2012).

**Potential Mechanisms of Birch Resistance to Bronze Birch Borer.**

The mechanisms underlying interspecific variation in resistance among woody angiosperms to wood-boring beetles, including variation in resistance among birch species to bronze birch borer, are not well understood. It has been hypothesized that both chemical and physical mechanisms, of which many could be constitutively expressed, induced, or both, by larval feeding, may play a role (Herms 1991, Muilenburg 2010). In birch species, phenolics, including simple phenolics, tannins, and lignin, are dominant secondary metabolites that have been implicated as defenses in other birch-herbivore interactions (e.g., Julkunen-Titto et al. 1996, Kopper et al. 2002, Laitinen et al. 2004, Mattson et al. 2005, Tiimonen et al. 2005) and may be important in birch resistance to bronze birch borer. Comparison of phenolics from stem phloem of susceptible European white birch and more resistant paper birch showed that they had unique phenolic profiles (Muilenburg et al. 2011). Three phenolics found in paper birch were not detected in European white birch, and concentrations of six other phenolics were higher in paper birch.
Evolutionary history between paper birch and bronze bircher.

Previously, it was hypothesized that rhododendrol played a key role in birch resistance to bronze bircher borer, putatively functioning as an oviposition stimulant in the inner bark of susceptible birch species (Santamour 1990, 1999, Santamour and Lundgren 1997). This hypothesis was based on the presumption that river birch and monarch birch, which both lack rhododendrol, were resistant to bronze bircher borer, whereas more susceptible species contained this compound. However, monarch birch subsequently was found to be much more susceptible to bronze bircher borer than North American birch species (Nielsen et al. 2011), demonstrating that the absence of rhododendrol is not a reliable indicator of bronze bircher borer resistance. Furthermore, paper birch (resistant to bronze bircher borer) was found to contain much higher concentrations of the rhododendrol precursors—betuloside (also known as rhododendrin) and betuloside pentoside—than European white birch (susceptible to bronze bircher borer), which is further evidence that rhododendrol, its glycosides, or both, do not mediate susceptibility of birch species to bronze bircher borer (Muilenburg et al. 2011).

Previous research indicates that growth of wound periderm (i.e., callus tissue) induced by larval feeding may be important in birch resistance to bronze bircher borer (Anderson 1944, Herms 1991, Miller et al. 1991). Serpentine ridges frequently are visible externally on the bark surface and result from growth of wound periderm over larval galleries. In many cases, failure of emergence holes to form in the vicinity of bark ridges is common, indicating that larvae died before completing development (Miller et al. 1991, Nielsen et al. 2011). Dissection of these galleries frequently reveals dead larvae encapsulated within wound periderm tissue (V.L.M. and D.A.H., unpublished data).

The rate of wound periderm formation by paper birch has been associated positively with resistance to bronze bircher borer (Anderson 1944, Herms 1991). Herms (1991) observed that resistance of paper birch declined rapidly when the rate of wound periderm formation fell below a threshold value approximately equal to the rate of larval movement through the phloem. Consistent with this threshold hypothesis, the relationship between the rate of wound periderm formation and bronze bircher borer colonization was best represented mathematically by a negative power function (Herms 1991). However, when comparing paper birch and European white birch, the rate of wound periderm growth did not vary between species (Muilenburg 2010). Collectively, these findings suggest that the rate of wound periderm formation is necessary but not sufficient to confer resistance. This implies that birch resistance may result from the integration of physical and chemical defense mechanisms, which is consistent with the distinct chemical differences between paper birch and European white birch (Muilenburg et al. 2011). For instance, the co-evolutionary history between paper birch and bronze birch borer may have led to selection of targeted defenses that slow bronze birch borer feeding enough to facilitate encapsulation of larvae by wound periderm. Conversely, the lack of targeted defenses in European white birch, which do not share a coevolutionary history, may allow larvae to move more quickly through phloem, thus escaping encapsulation by wound periderm.

### Bronze Birch Borer Management

Host plant resistance has been recognized as an ideal management tool for insect pests of trees (Hanover 1975, Nielsen 1989) and has been recognized specifically as an effective strategy for managing bronze birch borer in urban forests and ornamental landscapes (Harms 2002a, 2003). Planting North American birch species that are resistant to bronze birch borer (Nielsen et al. 2011) reduces the need for insecticide applications and other interventions, which can be costly and thus often are limited to high value trees. However, planting trees in sites to which they are poorly adapted (e.g., far outside their natural range) could impose physiological stress and predispose them to borer colonization. Cultural practices that maintain tree health, such as planting shade-intolerant birch trees in full sun, irrigating during drought, and preventing severe defoliation, are considered important components of plant health care programs for amenity plantings of birch (Nielsen 1985, Katovich et al. 1997, Herms 2003). Although commonly recommended, there is no evidence that fertilization increases tree resistance to bronze birch borer or other wood-borer species (Herms 2002b).

Several insecticides, including systemic products (e.g., azadirachtin, dinethoate, emamectin benzoate, dicrotophos, dinotefuran, imidacloprid) and prophylactic bark sprays (e.g., bendiocarb, bifenthrin, carbaryl, chlorpyrifos, lindane, permethrin), have been shown to control Agrilus species to varying degrees (Appley et al. 1973; Petrice and Haack 2006; Herms et al. 2009; Herms 2010; McKenzie et al. 2010; Smitley et al. 2010a,b; McCullough et al. 2011; D. G. Nielsen, unpublished data). Systemic insecticides target larvae feeding under the bark and adults feeding on foliage, and depending on the label, are applied as soil drenches, soil injections, trunk injections, or basal trunk sprays. Protective cover sprays target feeding adults and neonate larvae as they enter the tree and are applied to the trunk, branches, and foliage (Herms et al. 2009). Optimal timing of insecticide application depends on the product being used. In studies in Ohio, soil drenches and injections of imidacloprid were effective against bronze birch borer when applied mid- to late spring (D. G. Nielsen and D. A. Herms, unpublished data). Protective cover sprays most effectively controlled bronze birch borer when applied twice, with the first application made just before adult emergence and the second application 4 wk later (D. G. Nielsen, unpublished data). In Ohio and Michigan, first emergence of bronze birch borer occurs between first and full bloom of Robinia pseudoacacia L. (black locust tree) (Herms 2004).
Concluding Thoughts. White-barked birches have obtained an unfavorable reputation as high maintenance trees unsuitable for amenity plantings in the United States because of high susceptibility to bronze birch borer. However, the generalization that all white-barked species are highly susceptible to bronze birch borer is inaccurate (Miller et al. 1991, Nielsen et al. 2011). Species native to North America, such as paper birch and gray birch, are highly resistant to bronze birch borer and are grown successfully in urban forests and ornamental landscapes without substantial management inputs (Nielsen et al. 2011). Cognizance on the part of urban foresters, landscape designers, and homeowners to avoid planting in unfavorable sites and preventing acute stress (e.g., droughty soils, shady aspects, defoliation) that would predispose otherwise resistant species to bronze birch borer colonization will further promote resistance. However, Eurasian birch species are much more susceptible and should not be planted in North American landscapes (Miller et al. 1991, Nielsen et al. 2011). Furthermore, the high susceptibility of Eurasian species to bronze birch borer coupled with climatic similarities of North America and Eurasia where Betula species exist, suggest that if bronze birch borer were inadvertently introduced to Europe or Asia, there may be a high risk of establishment, spread, and birch mortality on a continental scale (EPPO 2011, Økland et al. 2012).

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