Emerald Ash Borer in North America: A Research and Regulatory Challenge

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The saga of the emerald ash borer, *Agrilus planipennis* Fairmare (Coleoptera: Buprestidae), in North America began on 25 June 2002, when five entomologists representing Michigan State University (MSU), the Michigan Department of Natural Resources (MDNR), and the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (USDA APHIS) visited Detroit to examine declining ash (*Fraxinus* spp.) trees. The visit was prompted by submission of iridescent green beetles to the MSU Department of Entomology the preceding week (Fig. 1). The beetles, reared from ash logs by an extension agent and a landscape consultant in the Detroit area, were readily identified as a member of the genus *Agrilus*, but experienced coleopterists could not determine the species. Within days, specimens were sent to specialists in the United States and Europe, and on 9 July, the beetles were conclusively identified as *A. planipennis* by Eduard Jendek of Bratislava, Slovakia. This phloem-feeding species had not been collected previously outside of its native range in Asia. Published reports indicated that *A. planipennis*, which has several synonyms including *A. marcopoli* Obenberger, *A. marcopoli ulmi* Kurosawa, and *A. feretrius* Obenberger, is native to northeastern China, Korea, Japan, Mongolia, Taiwan, and eastern Russia (Jendek 1994, Haack et al. 2002).

Meanwhile, entomologists and regulatory officials in Michigan continued to assess the infestation in southeastern Michigan and were staggered by the extent of dying and declining ash trees in landscapes and forested areas surrounding Detroit. The Michigan Invasive Species Task Force, comprising government and university scientists, forest health specialists, and state and federal regulatory officials, met in early July 2002. An internal report presented at the meeting noted that many of the affected trees were growing in poor or stressful conditions typical of urban plantings, but healthy ash trees growing under regular irrigation and fertilization regimes also were infested and dying (McCullough 2002). Naturally regenerated ash in woodlots where other overstory species appeared quite healthy were similarly affected (McCullough 2002). Provincial officials in Ontario were notified; and beetles from infested trees in nearby Windsor, ON, were confirmed as *A. planipennis* on 7 August 2002 (Dobesberger 2002, Haack et al. 2002).

On 16 July 2002, following identification of *A. planipennis*, the Michigan Department of Agriculture (MDA) imposed a state quarantine to regulate movement of ash nursery trees, logs, and related products from infested counties. The state regulations were incorporated into a federal quarantine published by USDA APHIS on 14 October 2003 (Federal Register 2003). Additional activities in

Fig. 1. *A. planipennis*, the asian import identified in the United States in 2001. Mating occurs on the bark of ash hosts, in June.

2002 included organization of a New Pest Advisory Group by USDA APHIS in mid-July. Natural resource and regulatory officials from federal and state agencies met in southeastern Michigan to observe and discuss the situation in August, and a national Science Advisory Panel was convened by USDA APHIS in October. Locally, a series of meetings with nursery producers, municipal foresters, arborists, and representatives from other affected industries was initiated in July to explain the situation and regulations associated with the quarantine. Aerial and ground surveys to assess damage were conducted by natural resource and regulatory personnel from several states in the Upper Midwest in late summer. By the end of 2002, it was apparent that at least 5–7 million ash trees were declining, dying, or dead in a six-county area of southeastern Michigan.

How did *A. planipennis* become so widespread before detection? Like many nonindigenous phloem or wood borers, *A. planipennis* was probably transported to the United States in crating or other solid-wood packing material originating in its native range. The country of origin and year of establishment have not been determined. Genetic analyses are underway to ascertain the point of origin of Michigan infestations (Smith et al. 2004, Bray et al. 2005). *A. planipennis* was not reported as a major pest in Asia, and it had not invaded any other country or region. From 1984 to 2000, there were more than 565,000 insect interceptions in baggage and cargo, including solid-wood packing material, during inspections by USDA APHIS personnel at ports of entry and border crossings. Buprestids, however, accounted for <0.33% of the 75,800 Coleopteran records (McCullough et al. 2005a). Nonindigenous *Agrilus* were intercepted only 38 times during the 17-yr period from 1985 to 2000, mostly in cargo originating in Europe (Haack et al. 2002). Of the 38 *Agrilus* interceptions, only 1 was identified to the species level as *A. sulcicollis* Lacordaire (Haack et al. 2002).

History suggests many nonindigenous invasive pests experience a lag phase following initial introduction and establishment, during which populations remain at relatively low levels below detection thresholds. This lag phase may persist for several years before suitable weather, an abundance of hosts, or other factors lead to an exponential increase in density of the invasive population (Shigesada and Kawasaki 1997, Crooks and Soulé 1999, NRC 2002). Recent dendrochronological evidence indicates that *A. planipennis* was established in southeastern Michigan at least 10 years before its discovery (NWS and DGM, unpublished data). Widespread mortality of ash caused by *A. planipennis* was not observed until 2001–2002, suggesting that *A. planipennis* density increased sharply in the late 1990s and 2000.

The difficulty of identifying trees with low-to-moderate *A. planipennis* densities complicates the problem. External symptoms of *A. planipennis* infestation, such as epicormic shoots, canopy dieback, and bark cracks over larval galleries, are rarely present until trees are heavily infested. The lack of obvious symptoms on lightly infested trees exacerbated the artificial spread of *A. planipennis* before official recognition of the problem and implementation of quarantine regulations. Ash, a favored tree for urban settings, was one of the most commonly planted trees in new residential and industrial developments within the southeastern Michigan area. Following identification of *A. planipennis*, trace-backs of ash nursery stock by regulatory agencies found that young ash trees from nurseries in the infested area of southeastern Michigan were planted in distant areas of Michigan and Ohio. This information, combined with data from dendronchronological studies (NWS and DGM, unpublished data), suggests that most of the outlier populations were established years before *A. planipennis* was discovered to be causing tree mortality in 2002. Movement of ash logs and firewood also initiated localized infestations miles beyond the core of the infestation in southeast Michigan.

Fig. 2. Dying green ash on city street. Note epicormic shoots, symptom of terminal *A. planipennis* infestation.

Other factors impeding the discovery of *A. planipennis* included the already widespread occurrence of ash decline in forested and urban areas across much of the upper Midwest and northeastern United States (Castello et al. 1985) during much of the past decade. Symptoms of infested trees may sometimes be similar to those associated with ash yellows, a disease caused by a mycoplasma-like organism (Sinclair and Griffiths 1994). In addition, reports of insects colonizing declining or dying ash were consistent with secondary infestations of the native redheaded ash borer, *Neoclytus acuminatus* (F.) (Coleoptera: Cerambycidae), and native clearwing borers (Lepidoptera: Sessidae), such as banded ash clearwing borer, *Podosesia aureocincta* Purrington & Neilsen; peachtree borer, *Synanthedon exitiosa* (Say); and ash borer, *Podosesia syringae* (Harris). Furthermore, urbanized areas such as Detroit and nearby cities and suburbs are not typically included in routine surveys conducted by forest health specialists, who might have recognized *A. planipennis* as a potential exotic.

Potential Impacts of *A. planipennis* in North America

Continued spread of *A. planipennis* threatens the ash resources throughout North America, including at least 16 endemic ash species, as well as naturalized species and cultivars used in landscapes (USDA NRCS 2004, Wei et al. 2004). Results of damage surveys conducted in late 2004 show that at least 15 million ash trees are dying or have been killed by *A. planipennis* in southeastern Michigan (Fig. 2). The national Emerald Ash Borer Science Advisory Panel (EAB SAP) has reiterated the need to contain *A. planipennis*, reduce population densities, and eventually eradicate this nonindigenous pest (EAB SAP 2002, 2004, 2005). Economic costs associated with *A. planipennis* include the loss of ash trees from city and suburban landscapes, as well as forested settings. Cultivars of green ash (*F. pennsylvanica* Marsh.) and white ash (*F. americana* L.) are hardy, fast-growing trees that have long been valued as landscape and street trees, particularly in Midwestern states. For instance, the 600,000 ash trees in Chicago alone make up 14.4% of the total leaf cover and are valued at $231 million (Federal Register 2003). Potential costs associated with removals of urban ash trees in the United States were estimated at $20–60 billion, a figure that does not include replacement costs. Ash is also an important commercial lumber and pulp species with many uses including tool handles, furniture, crating, cardboard, and paper. Ash constitutes ~7% of sawtimber in the eastern United States, and its stumpage value is estimated to be $25 billion (Federal Register 2003). Several Native American tribes value ash as a cultural resource, and black ash (*F. nigra* Marsh.) is harvested annually for basket making (Reo 2005).

Ecological impacts of *A. planipennis*, while difficult to quantify, could be profound. Ash species are found on a variety of soil and sites in the Upper Midwest and across much of the eastern half of the United States (Eyre 1980). Ash trees are generally prolific seeders; and a variety of ducks, song birds, game birds, small mammals, and insects feed on ash seeds. In many ecosystems, ash trees provide browse, thermal cover, and protection for a variety of wildlife, including white-tailed deer and moose. Beaver, rabbits, and porcupines may feed on the bark of young trees (Heyd 2005). White ash, the most valuable ash lumber species, frequently grows in mixed-species stands with other upland hardwoods and is a major component of at least 26 forest cover types (Burns and Honkala 1990). Green ash is the most widely distributed ash species in the United States and often dominates the overstory on heavy, wet soils and along riparian corridors. Black ash often grows in bogs and swamps, but can also be found in mixed stands dominated by beech–maple. In northern areas, black ash is sometimes the only tree growing in swamps. Effects of widespread black ash mortality in these ecosystems are especially difficult to predict.

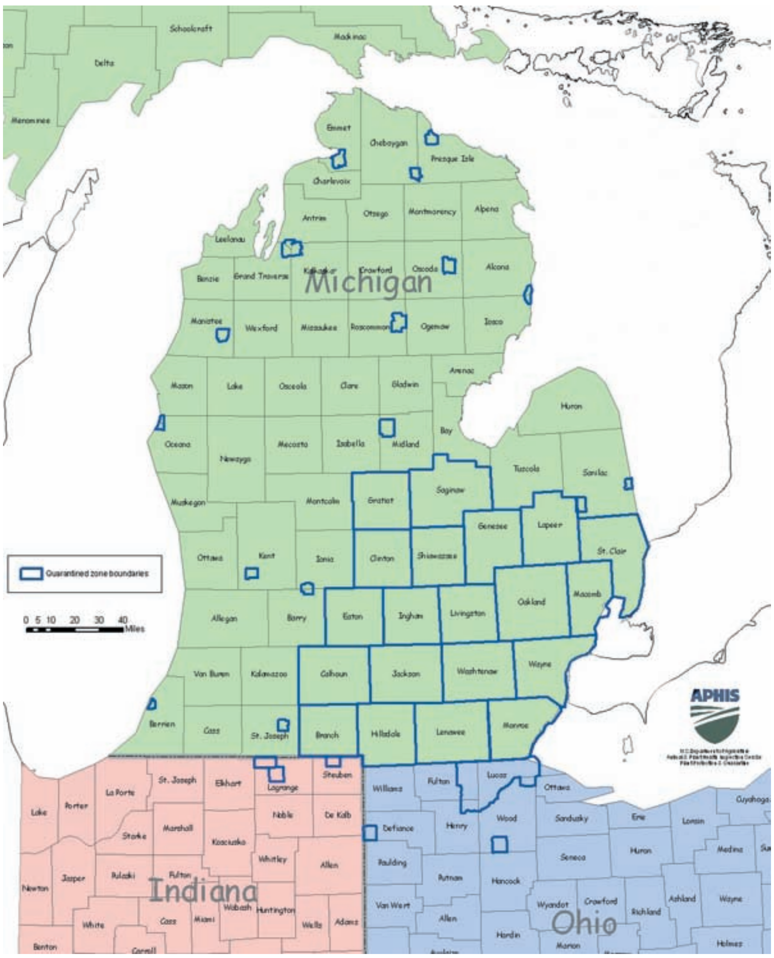


Fig. 3. Borders of current *A. planipennis* quarantine (14 Feb. 2005). Source: USDA APHIS.

A. planipennis has the potential to cause economic and ecological damage to ash on a scale similar to the impacts of invasive pests on American chestnut and American elm (Burns and Honkala 1990, Liebhold et al. 1995, NRC 2002). The area known to be infested by *A. planipennis* in North America has been expanded, largely because of improved detection methods. As of March 2005, *A. planipennis* infestations were present in 20 southeastern Michigan counties included in the federal quarantine. In addition, at least 25 localized "outlier" populations were discovered in 2003–2004 in western and northern Michigan, northern Indiana, and Ohio (Fig. 3). Efforts to contain the spread of *A. planipennis* and to manage populations in the infested area will require a broad understanding of its biology and host relations. When *A. planipennis* was first discovered in Michigan, the available information was limited to taxonomic descriptions (Jendek 1994) and several paragraphs published in Chinese references (Chinese Academy of Science 1986, Yu 1992). During the past four years, scientists have begun to characterize the life history and ecology of *A. planipennis* and to develop the tools that will facilitate monitoring and detection,

Fig. 4. Typical leaf feeding damage. A. planipennis beetles consume foliage before mating and flight.

population management, and our ability to mitigate the impact of *A. planipennis*.

Research Needs: Life Cycle

Defining the life cycle of *A. planipennis* was an early priority for applied research. Basic information on phenological events (e.g., initial adult emergence, peak adult activity, larval development, and overwintering behavior) was needed for detection and survey efforts, development of control options, and understanding of population dynamics, dispersal, and interactions with natural enemies.

Adult emergence, monitored in 2003 and 2004, begins as early as mid- to late May or early June, depending on local conditions. In both years, the first observance of adult *A. planipennis* coincided with the accumulation of 230–260 degree days, calculated on a base 10 ºC threshold (Brown-Rytlewski and Wilson 2004). Upon emergence, adult beetles feed on ash foliage (Fig. 4) for 5–7 d before mating, and females feed for another 5–7 d before beginning to oviposit. Beetles continue to feed during the remainder of their life span and multiple matings can occur (Bauer et al. 2004a, Lyons et al. 2004).

Most females lay 60–90 eggs in laboratory settings, although one female reared in captivity in Ontario laid 258 eggs over a 6-wk span (Lyons et al. 2004). Eggs, laid individually in bark crevices or sometimes under bark flaps, are initially cream-colored but turn reddish brown within a few days (Bauer et al. 2004a).

Weekly monitoring of *A. planipennis* beetles captured on sticky bands on host trees in six of our study sites showed that adult activity peaked from late June to early July in southeastern Michigan (Fig. 5). Beetles, each of which can live for 3–6 wk, were rarely observed after early August. Biweekly dissection of trees with moderate-to-heavy *A. planipennis* infestations in southeastern Michigan showed that larval eclosion in late July or early August is followed by rapid growth as larvae feed, excising serpentine galleries through phloem and scoring the outer xylem (Fig. 6). Most larvae complete feeding in October or November and then excavate a cell ~1-cm deep in the sapwood or outer bark, where they overwinter as prepupal larvae (Fig. 7). Dissections of heavily infested trees in December showed >80% of larvae in prepupal cells. Pupation begins in mid-April and continues into May, followed by adult emergence ~3 wk later.

Our field observations indicated that *A. planipennis* larvae pass through four instars, but we confirmed this in 2004 by measuring width and height of the sclerotized epicranium, as viewed anteriorly, of 200 larvae collected from green ash trees in autumn 2004 or reared from ash logs in the laboratory. Head capsule dimensions were measured using a dissecting microscope and a Unislide Measuring System equipped with an Acu-Rite sliding scale and a linear encoder (Velmex, East Bloomfield, NJ), which was interfaced with a Quick-check QC-100 digital measuring device that recorded dimensions (0.01 mm precision).

Although *Agrilus* instars also can be distinguished based on the length of the urogomphi, our results indicated that simply measuring the exposed epicranium was a reliable method for distinguishing developmental stadia (Fig. 8a). [**Fig. 8 near here**] Width and height of head capsules were highly correlated ($r^2 = 0.991$), indicating that either measurement could be used to distinguish among instars. Head capsule size became more variable within instars as larvae matured. The range in head capsule sizes for fourth instars was especially broad (Fig. 8a), presumably reflecting sexual dimorphism in adult body size between the larger females and generally smaller males. To verify this, 37 fourth instars were reared to adults, which were then sexed and the exuvial head capsules were measured

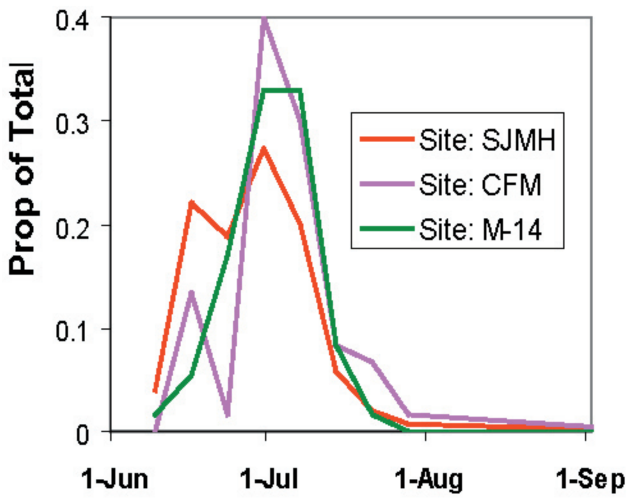


Fig. 5. A. planipennis flight phenology, mean catch (n = 24) at three sites in Michigan.

Fig. 6. Larval gallery of *A. planipennis*. Fourth instar is excavating prepupal cell into sapwood (r).

as described earlier. Head capsules of female *A. planipennis* were mostly in the upper portion of the range; male *A. planipennis* tended to have smaller head capsules (Fig. 8b).

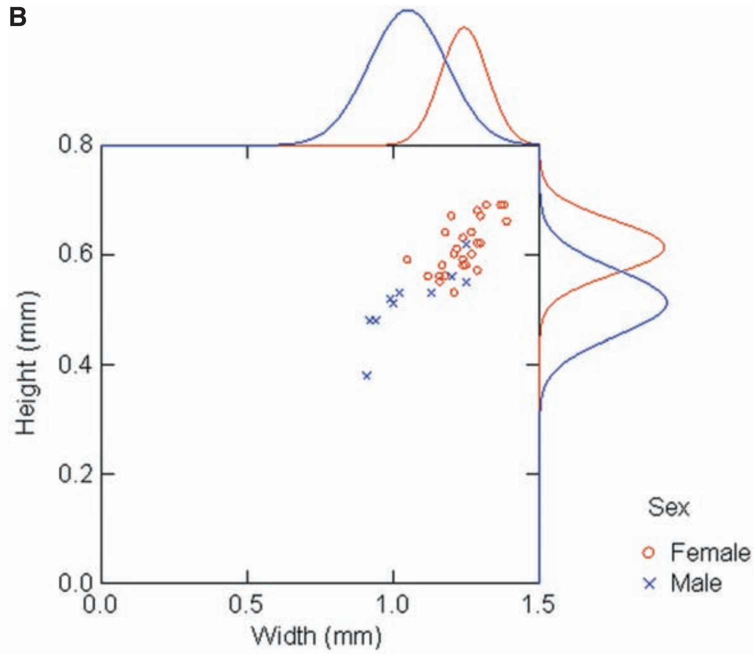
The initial characterization of a 1-yr life cycle was consistent with early field observations and with the life cycle of well-known native *Agrilus* spp. such as the bronze birch borer, *A. anxius* Gory, and the twolined chestnut borer, *A. bilineatus* (Weber). However, several observations led us to reevaluate voltinism of *A. planipennis*. Most significantly, winter dissections of vigorous but lightly infested trees at "outlier" sites with low densities of *A. planipennis* revealed a preponderance of small larvae, rather than the prepupal larvae expected. At two sites, for example, only 18% of the 282 *A. planipennis* larvae were prepupae; most were second and third instars (DGM, unpublished data). Spring dissections of infested trees, even in the heavily infested areas of southeastern Michigan, showed that when larvae failed to reach the fourth instar before winter, pupation appeared to be delayed until the second spring (Fig. 9). We also noted instances of callus tissue overlaying the initial portions of larval feeding galleries that continued into current-year xylem tissue. Galleries extending from year-old tissue into current-year tissue are indicative of 2-yr larval development (Fig. 10). **[Fig. 10 near here]**

It is not yet clear why delayed larval development occurs or what proportion of *A. planipennis* larvae require 2 yr for development. Although delayed development appears to be more common in low-density *A. planipennis* populations, we also have found that 2-yr development occurs occasionally in moderately to heavily infested trees in the core area of the infestation. It is possible that a second year of development is required when oviposition occurs late in the summer and larvae do not reach the prepupal stage before winter. Alternatively, a chemical or mechanical defensive response by newly infested trees may slow larval development, but other factors, such as cold temperatures or low nutrient levels, may also be involved. Additional studies are planned to address this phenomenon because it has important implications for survey activities and dynamics of *A. planipennis* populations.

Interactions between *A. planipennis* and its Hosts

Host Range. Observations and survey results from affected areas of southeastern Michigan clearly showed that *A. planipennis* could attack and successfully develop on *F. pennsylvanica* and *F. americana*, the most common species in forested and landscape settings. In China, ash species, including *F. mandshurica* Rupr. and *F. chinensis* Roxb., are the only reported hosts of *A. planipennis* (Chinese Academy of Science 1986, Yu 1992). Observations and collections of *A. planipennis* in China since 2002 all have been associated with *Fraxinus* spp. trees (Liu et al. 2003, Wei et al. 2004, Bauer et al. 2005, Gould et. al 2005). There was concern, however, that as ash trees died in the

Fig. 7. First and second instar *A. planipennis*. Inset: prepupal stage larvae overwinter in sapwood cell.



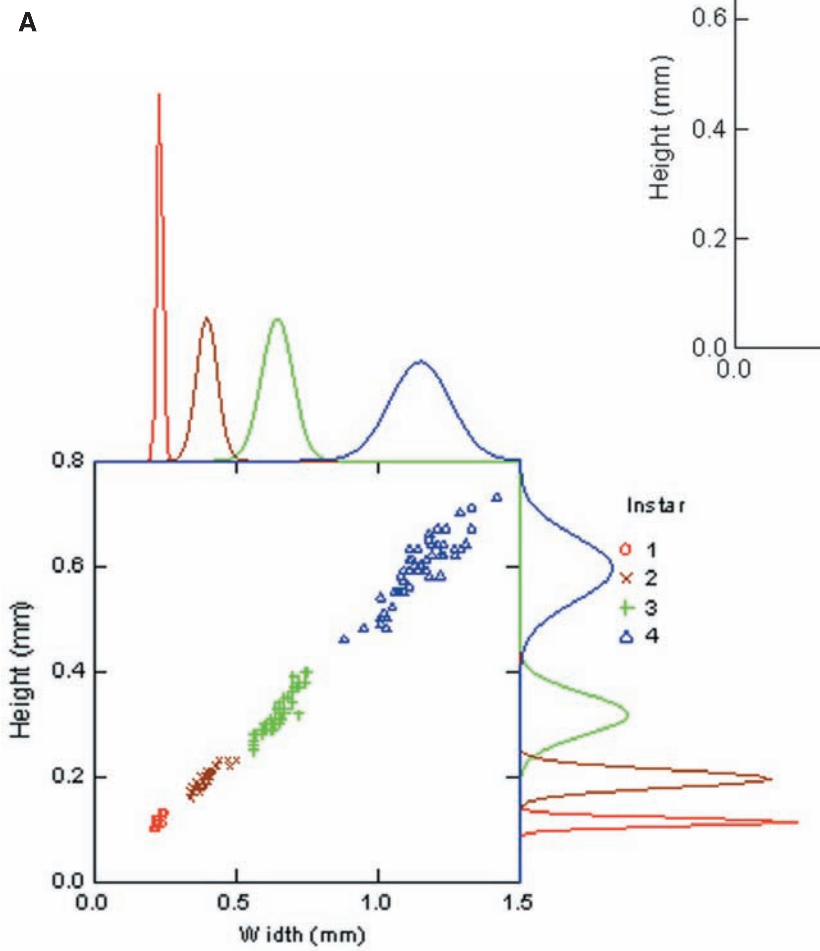


Fig. 8. Width and height dimensions (mm) of *A. planipennis* head capsules. Left: Characterization of instars for 200 larvae (*n* = 50 specimens per larval stage). Right: Comparison of sexes for 37 larvae (*n* = 26 females; *n* = 11 males) that were reared to adulthood in the laboratory. Scatterplots are bordered by normal curves fit to the density distribution of each larval stage or sex for each dimension.

United States, *A. planipennis* might shift to other genera. This concern arose from literature reporting that in Japan, the host range of *A. planipennis ulmi* included *Juglans mandshurica* Maxim., *Pterocarya rhoifolia* Sieb. & Zucc. (wingnut), and *Ulmus davidiana* var. *japonica* Planch. (Akiyama and Ohmomo 1997, Haack et al. 2002). Close relatives of these Asian trees, including black walnut, *Juglans major* (Torr.) Heller; American elm, *Ulmus americana* L.; and hickory, *Carya* spp., are abundant and important in much of North America. If *A. planipennis* were able to use additional hosts successfully, the impacts and management issues associated with this pest in North America could change dramatically.

Intensive studies were initiated in 2003–2004 to assess A. *planipennis* host range by comparing oviposition and larval development on *Fraxinus* spp. with that on other North American species in the family Oleaceae [e.g., privet, *Ligustrum* spp. and Japanese tree lilac, *Syringa reticulata* (Blume) Hara], and other genera of concern including black walnut, American elm, and shagbark hickory [*C. ovata* (P. Mill) K. Koch].

No-choice, two-choice, and field tests are in progress (McCullough et al. 2004, Agius et al. 2005). Preliminary results indicated that female *A. planipennis* will oviposit on species other than *Fraxinus* in no-choice laboratory tests and occasionally in the field. Careful dissection of small log sections and trees used in these trials has shown that *A. planipennis* excavate galleries and appear to develop normally on *Fraxinus* logs and trees. First instars sometimes attempt to feed on phloem of species such as black walnut and Japanese tree lilac, but these efforts invariably fail (Agius et al. 2005).

Privet is one potential alternative host that remains a concern. In no-choice tests, larvae were able to develop to the second instar before sections of host material became too dry. Galleries on privet sections were fairly similar in appearance and density to galleries in sections of *Fraxinus* used in the same test. Haack and Petrice (2005) also deter-

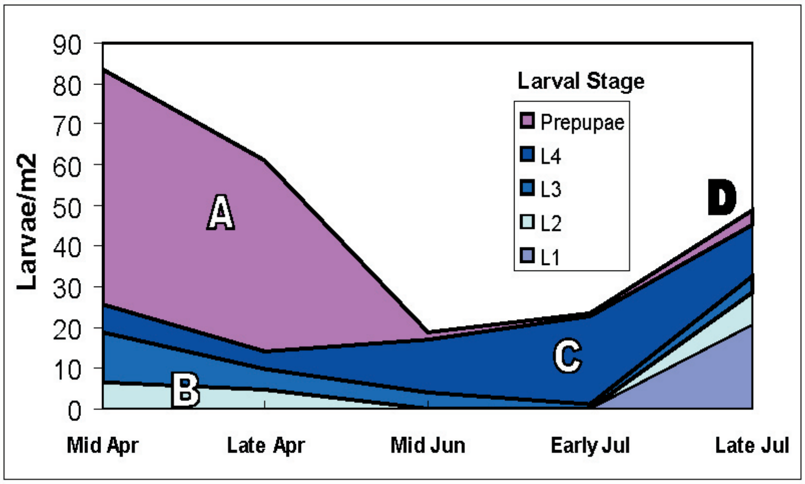


Fig. 9. *A. planipennis* life stage distribution, 2004. The majority of larvae are prepupal in spring (A); these individuals complete pupation and emerge in late June. Second and third instars present in spring (B) become mature in early July (C) and excavate prepupal cells beginning in late July (D); these larvae remain in cells until the following summer.

mined that adult beetles would feed on leaf disks cut from members of the ash family (Oleaceae), including privet. However, the possibility that *A. planipennis* could complete development on privet remains to be determined through ongoing studies. We also continue to monitor large privet shrubs growing near woodlots or in parks with a high density of ash, almost all of which were killed by *A. planipennis* in 2003 or 2004. To date, no evidence of *A. planipennis* colonization of privet in such situations has been observed (A. C. Agius and DGM, unpublished data).

Host Preference. All native *Fraxinus* spp. that occur in Michigan, including all cultivars used in landscapes, have been attacked and killed by *A. planipennis*. Tree size does not appear to greatly influence *A. planipennis* host selection, at least when populations are at moderate-to-high densities. We have observed larval development in stems or branches that range in size from 2 cm to 1.5 m in diameter. There appears to be considerable variation, however, in the preference of ovipositing females and perhaps in the response of ash species to *A. planipennis* colonization. Observations and data collected from neighborhoods and woodlots where green ash and white ash occur at similar densities show that green ash trees are consistently attacked sooner than white ash trees. For example, pair-wise comparisons from several sites reveal that densities of *A. planipennis* on white ash trees do not begin to increase until green ash trees have been heavily attacked and start to decline. Similar comparisons in woodlots where white ash and the relatively rare blue ash, *F. quadrangulata* Michx., cooccur indicate that infestations are initially higher on white ash, but blue ash trees become infested as white ash trees succumb (Agius et al. 2005).

Preliminary data from laboratory and field tests suggest that black ash, which is not commonly mixed with other ash species, also is highly attractive and suitable for *A. planipennis*. Even in forested areas made up of a single ash species, the distribution of *A. planipennis* among trees within stands is often heterogeneous. Heavily infested trees with abundant exit holes and almost complete dieback can be found adjacent to similar trees that remain healthy with little or no evidence of colonization by *A. planipennis*.

The underlying mechanisms for the apparent patterns in *A. planipennis* host preference are not understood. Volatiles may be involved in selection by female beetles of hosts for oviposition. Studies are currently underway to determine whether larval conditioning affects adult host selection of species for oviposition (Barron 2001). Physical traits of potential hosts may also be involved. Female beetles demonstrate a strong preference for oviposition on hosts with rough bark and abundant crevices. Green ash trees often have rougher bark than white ash trees of similar age and size.

In addition, it is not yet clear whether North American ash species vary in their response to larval feeding by *A. planipennis*. Preliminary data indicate that the density of *A. planipennis* appears to increase at a similar rate among all ash species, so variation in inducible responses may be quickly overwhelmed. Additional research is needed to further assess what factors mediate between-tree differences in infestation and whether defensive mechanisms of ash trees could be enhanced or exploited through selective propagation.

Detection/Monitoring

Effective means for early detection of low-density *A. planipennis* infestations, evaluating success

Fig. 10. Two-year gallery of *A. planipennis*. First year of larval development in callused, dark area (r); second year gallery ascending on (l) through current-year phloem.

of control or eradication activities, and monitoring spread of populations are critical components of the overall *A. planipennis* program. Initial delimiting surveys conducted by regulatory and natural resource personnel relied on visual assessments of trees in a systematic pattern, progressing outwardly from the edge of the known infested core area. It became evident, however, that visual surveys were inadequate, especially for locating recent or low-density *A. planipennis* infestations. External symptoms on ash trees, such as crown dieback, bark splits, woodpecker attacks, and epicormic shoots, are rarely visible during the early stages of infestation. Characteristic D-shaped exit holes left by emerging adults are often difficult to find on large trees with thick, rough bark. Moreover, there was a clear tendency—across habitat types and for white and green ash—for early attacks to occur in the canopy, with colonization of the lower stem occurring only after tree decline and external symptoms are evident. For example, intensive sampling of green ash trees 13–15 m tall and 30 cm diam with a low-to-moderate *A. planipennis* infestation showed that essentially all of the early attacks (exit holes) and most current-year larvae occurred above 2 m (Fig. 11).

Although traps and lures are available for many species of bark beetles (Coleoptera: Scolytidae) and defoliating moths (Lepidoptera), relatively little is known about attracting and trapping buprestids. Two common native *Agrilus* spp. preferentially colonize stressed host trees. The bronze birch borer primarily attacks birches weakened or stressed by drought, old age, insect defoliation, soil compaction, or stem or root injury (Anderson 1944) and is presumably attracted to stressed-tree volatiles. Haack and Benjamin (1982) found that girdling oaks (*Quercus* spp.) significantly increased colonization by the twolined chestnut borer. In addition, male twolined chestnut borers were attracted to logs on which females were caged (Dunn and Potter 1988), suggesting that a female-produced short-range attraction pheromone could also be involved.

We observed that the susceptibility of ash trees to *A. planipennis* is highly heterogeneous within stands—some trees appeared much more attractive than their immediate neighbors. Furthermore, attack densities were typically higher and development more rapid on previously infested hosts, suggesting that selection may have favored adult attraction to stress volatiles. To investigate stress-mediated attraction, during 2003 and 2004, we compared the number of *A. planipennis* adults captured on sticky bands attached to healthy ash trees and trees that were physically or chemically wounded (i.e., girdled or treated with herbicide). We found a marked increase in attraction of emerald ash borer to stressed trees, as evidenced by significantly higher numbers of captured adults and/or higher densities of larval galleries.

As a result, girdled trap trees were incorporated into detection surveys implemented by regulatory agencies in 2004 (Fig. 12). The MDA conducted a statewide survey with >10,000 trap trees deployed at densities that increased with proximity to the core or to areas of concern such as campgrounds,

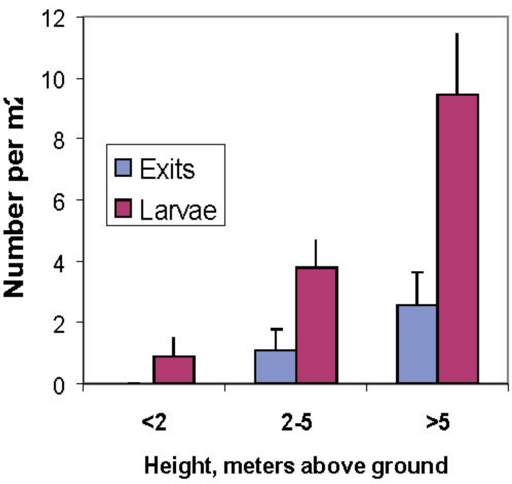


Fig. 11. Density of *A. planipennis* in relation to height. A typical dataset for 12–15m tall green ash (n = 48) in final year of EAB infestation. Exits representing EAB from all previous years (blue bars) and larvae of the current year (red bars) are all >2 m; larvae from final year occur at all levels.

Fig. 12. Girdled trap tree, one of 10,000 used in a regionwide effort to identify the scope of *A. planipennis* infestation.

sawmills, developments with recently planted ash nursery trees, and along state borders. The trap trees were visually inspected during the summer to collect suspect adults captured on the sticky bands and to check trees for exit holes or other external symptoms. Trees were felled during winter and fall 2004, and sections of bark were removed on the upper trunk and in the canopy to locate *A. planipennis* larvae. Although bark removal was time-consuming and expensive, it was a key aspect of the survey. More than half of the trap trees on which *A. planipennis* was detected had larvae but no adult beetles or external symptoms of infestation. Results from the 2004 trap tree survey led to the detection of several new outlier infestations and the expansion of the regulated area to include seven additional counties in Michigan (MDA 2004). Girdled trap trees are proving to be more effective detection tools where *A. planipennis* densities are low, for example, at the leading edge of an infestation or in outlier populations where surrounding trees are relatively healthy and less attractive.

Although the use of girdled trap trees significantly improved the effectiveness of the survey and detection program in Michigan, the technique is labor intensive and destructive. There is great interest in developing effective traps and attractive lures that could be used more efficiently to detect and survey *A. planipennis* populations. Early observations suggested that *A. planipennis* adults may use visual and olfactory cues in locating optimal hosts. Scientists from USDA APHIS and Tennessee State explored different trap shapes and colors, and preliminary results indicate that large silhouettes and purple hues were most attractive to *A. planipennis* adults (Francese et al. 2005a, b, c).

To identify olfactory cues, we collected volatiles from ash trees and prepared extracts from ash leaves, bark, and phloem (Poland et al. 2004, 2005). Volatile extracts were analyzed by coupled gas chromatography-electroantennal detection (GC-EAD) to determine whether *A. planipennis* antennae respond to any of the compounds emitted by their hosts. At least 13 volatile compounds emitted by ash trees consistently elicited antennal responses and were subsequently tested in a walking olfactometer bioassay. Beetles were released in a central chamber with two side chambers connected by 2.5-cm-diam tubing. Air was drawn through the system by a vacuum pump and passed through the side chambers into the central chamber. Volatile stimuli were tested by placing a sample compound in one of the side chambers and a solvent control in the other. Attractive responses of *A. planipennis* were measured by comparing the number of beetles that oriented toward the test compound and away from the control solvent.

Preliminary results suggest that several of the ash compounds are attractive to *A. planipennis* adults in laboratory bioassays. Field experiments suggested that baiting purple traps of various shapes with a blend of ash volatiles significantly increased attraction of *A. planipennis* compared with unbaited traps or traps baited with individual compounds; but even the most effective blends were not as attractive as girdled trees (Poland et al. 2005). Additional research is underway to identify stress-induced volatiles and determine the optimal attractive blend for potential use in *A. planipennis* trapping programs.

Dispersal

Spread of *A. planipennis* can occur at two levels: long-range transport via movement of infested materials and short-range spread as beetles fly to new hosts. An overriding concern for the successful containment of *A. planipennis* is the potential for human-assisted movement of infested firewood, nursery stock, logs, and related material. Such movement is prohibited by quarantine regulations and is subject to severe penalties. Nevertheless, localized outlying infestations detected in Ohio, Indiana, and Maryland, as well as several outliers in Michigan, resulted from movement of infested firewood or nursery stock. In most cases, infested material was transported before the quarantine was established. However, unintentional movement may still occur because of lack of awareness of the quarantine regulations. Current outreach and education programs in Michigan, Ohio, and Indiana are especially focused on preventing movement of potentially infested firewood (e.g., www.emeraldashborer.info).

Understanding short-range natural dispersal is important for predicting the gradual outward expansion of the core and outlier infestations and for establishing survey and management protocols. Many factors are involved in natural dispersal of insects, including flight capability, density and distribution of hosts, wind and other meteorological conditions, and physical barriers. Currently, research using several approaches is underway to investigate *A. planipennis* dispersal.

Flight capability is being evaluated in the laboratory by using insects tethered in computer-monitored flight mills (Bauer et al. 2004b, Taylor et al. 2005). Recorded variables include flight speed, maximum distance, and periodicity for males and females of different status (age, feeding, and mating status) and under varying light and temperature conditions. Under some circumstances, individual beetles have flown several kilometers. Flight data under artificial laboratory conditions, however, must be validated by field observations of dispersal.

Preliminary data have been gathered at three outlier sites in Michigan. At each site, the date and point location for the introduction of infested host material were determined based on trace-back surveys of nursery stock or firewood. At each site, systematic sampling for larval galleries in 147–220 ash trees, located at increasing intervals from the introduction point out to a 0.8-km radius, allowed us to estimate the distance and direction of dispersing *A. planipennis* females. In each case, very few galleries were found >0.5 km from the origin. Further analyses are underway to model the rate and pattern of spread based on the distribution of infested trees relative to the host distribution at each site.

Another approach to investigate dispersal in the field is based on dendrochronological analysis using cross-sections or increment cores collected from infested trees. Infestation by *A. planipennis* can be determined by using indirect evidence, such as reduced radial growth, or direct evidence if the sample intersects a larval gallery or pupal cell. Ash samples can be cross-dated with known events such as major droughts to determine the year of infestation. Based on the year of first infestation at various locations throughout the core infested area, the leading edge, and outlier sites, the rate and pattern of spread can be estimated and modeled. Early results suggest that dispersal in low-density outlier sites in Michigan has been <1 km/yr.

Attempts at mark–release–recapture studies have not been successful because of the lack of effective means for recapturing released beetles (Haack and Petrice 2004). Potential use of harmonic radar to follow the movement of individual beetles in the field is currently under investigation.

Insecticides for *A. planipennis* Control

Faced with the eventual lethality of *A. planipennis* infestation, the logical first alternative for homeowners and landscape managers in southeastern Michigan was to seek a conventional insecticide that could be used to save high-value shade and ornamental ash trees. Regulatory officials also needed information on insecticide effectiveness as a potential option that might be used to suppress *A. planipennis* populations as part of containment efforts. Conventional approaches to control native pests such as bronze birch borer include soil drenches or injections with imidacloprid-based products, trunk injection of compounds (e.g., imidacloprid, acephate, or dicrotophos), and cover sprays with conventional insecticide products. Soil and trunk injections are generally preferred in many urban settings because these systemic applications minimize applicator exposure, impacts on nontarget organisms, drift, and environmental contamination. Injections can be problematic, however, because uptake and within-tree distribution of systemic compounds can vary depending on tree vigor, growing conditions, and extent of previous *A. planipennis* injury.

Our studies have focused on identifying optimal timing for injections and sprays, monitoring persistence and within-tree translocation of imidacloprid products applied with different methods, and determining the relative toxicity of imidacloprid to adult and larval *A. planipennis* (McCullough et al. 2003, 2005b,c). Results to date indicate that insecticide treatments can substantially reduce *A. planipennis* larval density compared with untreated trees, but effectiveness varies among injection methods and products.

No treatment has yet provided 100% control of *A. planipennis*, which has so far prohibited the use of insecticides for regulatory activities outside of the quarantined area in southeastern Michigan. However, our results, along with other reports, suggest that several currently registered insecticide products can be used to protect valuable shade trees from *A. planipennis*, at least in the short term (McCullough et al. 2003, 2005b,c). Annual treatment appears to be necessary, at least until *A. planipennis* densities drop substantially. Costs and potential injury associated with repeated trunk injections must also be considered.

Whether insecticides can suppress *A. planipennis* sufficiently to permit the continued survival of landscape ash over the long term will depend on the efficacy of a given control method, the *A. planipennis* density that trees can tolerate without losing vigor or value, and the duration and intensity of pest pressure in the vicinity of the tree. Long-term studies will focus on a better understanding of these variables.

Biological Control

Effective natural enemies could potentially be useful in suppressing high density *A. planipennis* populations in southeastern Michigan and Windsor. Scientists from federal agencies, working with Chinese collaborators, began searching for natural enemies in China and elsewhere in 2002. Explorations have not yet presented a clear picture. Extensive surveys in Japan and Korea in 2003 and 2004 located abundant stands of *Fraxinus* spp., but no evidence of *A. planipennis* infestation (Schaefer 2005, Williams et al. 2005). Schaefer (2005) reported that *A. planipennis* is, in fact, listed as an endangered species in parts of Japan. Explorations in China found locally abundant populations of *A. planipennis* associated with plantations of North American ash species, Asian ash species growing outside of a natural forest setting (Liu et al. 2003), and girdled ash trees in forested areas (Gould et al. 2005).

In China, parasitism by a braconid, *Spathius* sp., and a eulophid, *Tetrastichus* sp., affected up to 50% of larvae in individual trees in a *F. mandshurica* plantation (Liu et al. 2003, Gould et al. 2005). An encyrtid parasitoid was also reared from *A. planipennis* eggs collected in 2004 (Bauer et al. 2005). Efforts are ongoing to evaluate the potential use of Chinese parasitoids for classical biological control in North America and to identify additional species of natural enemies in Asia (Gould et al. 2005). Additional research will be necessary to gauge the relative contributions of natural enemies, host resistance, and *Fraxinus* distribution in regulating *A. planipennis* in China and to determine how those interactions function in North America.

Meanwhile, researchers are continuing to investigate the potential value of indigenous natural enemies for controlling *A. planipennis* populations in Michigan. Clerid beetles and other native insect predators have been observed attacking *A. planipennis* larvae. Several hymenopteran parasitoids have been reared from *A. planipennis* larvae and eggs in Michigan; however, parasitism rates were only 0.05 and 0.3%, respectively (Bauer et al. 2005).

Predation by North American woodpeckers so far appears to be the most important source of mortality in *A. planipennis* populations. The rate of woodpecker predation can be readily documented by comparing the count of the distinctive, ragged holes left by woodpeckers foraging on large larvae or prepupae with the number of exit holes representing successful emergence of *A. planipennis* adults (Fig. 13). In data collected from 24 southeastern Michigan sites, we found woodpecker mortality ranged from 9 to 95% (Fig. 14) (Cappaert et al. 2005). Clearly, woodpeckers may play an important role in the population dynamics of *A. planipennis*; further study is needed to determine how woodpecker abundance, behavior, and habitat use interact with *A. planipennis* to affect predation rates.

Five species of pathogens, collectively causing ~2% infection of larvae, also were isolated from *A. planipennis* collected from trees in southeastern Michigan (Bauer et al. 2004c). The most common, *Beauveria bassiana*, is of particular interest because it can be formulated as a microbial pesticide. A commercial *B. bassiana* product, Botanigard (Emerald Bio, Lansing, MI), is highly virulent against *A. planipennis*, and field trials with preemergent treatment demonstrated >80% control of adults. Lower levels of larval control also were achieved with sprays on bark surface (Bauer et al. 2004d). Future work with *B. bassiana* will focus on additives to improve UV stability and increase penetration through bark surfaces.

Plans for *A. planipennis* Containment

Effectively containing *A. planipennis* in North America will require additional research, a strong regulatory effort, and cooperation from residents in affected areas. Much has been learned about *A. planipennis* since July 2002, but many critical research needs remain. Improved methods for detecting *A. planipennis* and suppressing populations, as well as a better understanding of *A. planipennis* dispersal, population dynamics, and possible host resistance are key areas for ongoing and future studies. Containment will be especially challenging for regulatory personnel, given the extent of the currently affected area and the difficulties inherent in working with a phloem-feeding insect.

The national EAB SAP estimates that a successful *A. planipennis* program would likely require a sustained effort over a 12- to 15-yr period. Funding for the survey, suppression, and regulatory activities integral to such an effort is not ensured, despite widespread recognition of the potentially severe economic and ecological impacts of this exotic pest.

Budget limitations, coupled with the detection of multiple outlier populations in lower Michigan in 2004, have led regulatory officials to focus on protecting "gateways" to minimize the risk of spread of *A. planipennis* through the United States and Canada (EAB SAP 2005). This strategy is predicated upon the barriers to natural dispersal imposed by Lake Michigan and Lake Huron for the United States and Lake Erie for Ontario. Areas

Fig. 13. Downy woodpecker (left) nesting in dead ash. Woodpecker predation (right) inflicts up to 95% mortality on *A. planipennis* prepupa.

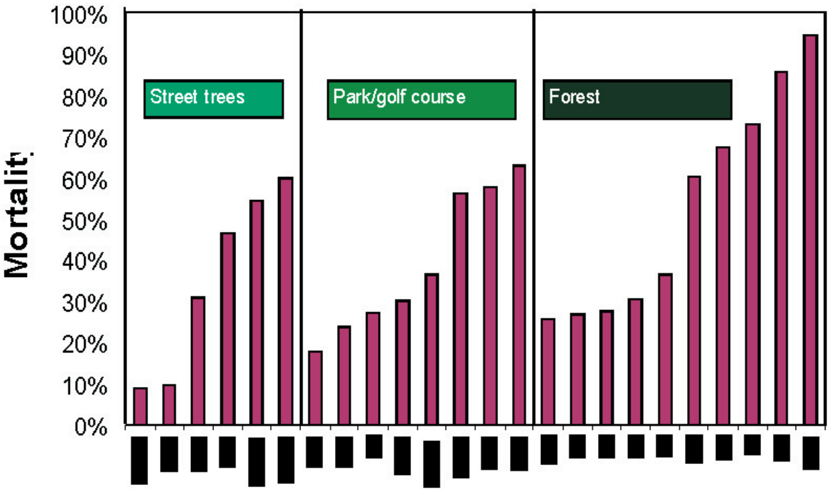


Fig. 14. Mean *A. planipennis* mortality attributable to woodpecker predation at 24 Michigan sites, grouped by habitat type.

designated as high-priority gateways include northeastern Ohio and the southern border of Michigan, areas of northern lower Michigan approaching the Straits of Mackinac, and an area centered on the St. Clair River between southeastern Michigan and Ontario. Surveys, eradication, and regulatory activities will be especially intensive in these gateway areas.

Artificial movement of *A. planipennis* remains an ongoing concern. Sales and movement of ash nursery trees, logs, and related products out of quarantined areas have been tightly regulated and largely controlled. Inadvertent transport of infested ash firewood out of quarantined areas, primarily by people headed to recreation areas, campgrounds, hunting cabins, and recreational cottages, however, is much more difficult to curtail. Continued education and outreach activities, along with regulatory action, will be required to increase awareness of the risks posed by infested firewood and to elicit cooperation from residents of affected areas.

Acknowledgment

We thank Andrea Agius for leading field work on emerald ash borer host range; Peter de Groot, Gary Grant, and Linda McDonald for assisting with GC-EAD analysis and field trapping experiments; and Robert Haack and Cesar Rodriguez for commenting on an earlier version of the manuscript. Funding to support studies discussed here was provided by the U.S. Dept. of Agriculture Forest Service, Project GREEEN at Michigan State University, and the U.S. Dept. of Agriculture Agricultural Research Service.

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David Cappaert, Deborah G. McCullough, Therese M. Poland, and Nathan W. Siegert [AU: Please add a sentence or two about each of you, with contact information for yourself.]