Biology and damage traits of emerald ash borer (*Agrilus planipennis* Fairmaire) in China

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Abstract Emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) is a major stem borer of ash (*Fraxinus* spp.). It is univoltine in Tianjin, while it is semivoltine in Heilongjiang Province, and both univoltine and semivoltine in Changchun, Jilin Province, where the majority is univoltine. The longevity of emerald ash borer adults is 17.2 ± 4.6 days ($n = 45$), eggs 9.0 ± 1.1 days ($n = 103$), univoltine larvae 308 days, semivoltine larvae 673 days, and pupae 61.2 ± 1.6 days ($n = 45$). It takes about 100 days from the time larvae bore into the phloem to when they complete the pupal cell. In a 10-year-old velvet ash (*Fraxinus velutina* Torr.) plantation in Tianjin, emerald ash borer preferred to oviposit on the regions of boles from 50–150 cm above ground, accounting for 76.7% of the total girdling. Girdling on the south side of the tree boles accounted for 43.40% of the total girdling. The emerald ash borer population density is higher at the edge of the plantation compared with the center.

Key words biology, damage traits, emerald ash borer, life history
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Introduction

Emerald ash borer (*Agrilus planipennis* Fairmaire) (EAB) (Coleoptera: Buprestidae) is a major pest of ash (*Fraxinus* spp.) trees, distributed in Heilongjiang, Jilin, Liaoning, Tianjin, Hebei, Shandong Provinces and Inner Mongolia, Xinjiang Autonomous regions in China (Wei *et al*., 2004). Synonyms of *A. planipennis* include *A. marcopoli* Obenberger (in China), *A. marcopoli ulmi* Korosawa (in Korea and Japan), and *A. feretrius* Obenberger (in Taiwan, China) (Jendek, 1994). In the early 1960s, this pest threatened an introduced ash, *F. pennsylvanica* Marsh. var. *lanceolata* (Borkh.) Sarg, and a native ash, *F. mandshurica* Rupr., in Harbin and Shenyang; therefore, all of the introduced ash were removed from these areas (Liu, 1966; Yu, 1992). In the 1990s, EAB severely damaged ash trees that were mostly introduced from North America (e.g., *F. americana* L., *F. pennsylvanica* Marsh., *F. pennsylvanica* Marsh. var. *lanceolata* (Borkh.) Sarg, and *F. velutina* (Torr.) (Liu *et al*., 1996; Liu *et al*., 2003; Gao *et al*., 2004; Sun & Li, 2004; Wei *et al*., 2004; Zhao *et al*., 2004). EAB severely damaged the native ash, *F. mandshurica* Rupr., but it caused little damage to two widely distributed native ashes, *F. chinensis* Roxb and *F. rhynchophylla* L. in China (Yu, 1992; Wei *et al*., 2004; Zhao *et al*., 2004; Zhao *et al*., 2005).

Emerald ash borer is regarded as one of the most important invasive pests in North America (Haack *et al*., 2002; Cappaert *et al*., 2005; Poland & McCullough, 2006; Mastro *et al*., 2007). It was first discovered attacking ash trees in southeastern Michigan and neighboring Ontario, Canada, in 2002 (Haack *et al*., 2002). Over 20 million ash trees have been infested in Michigan alone (Poland & McCullough,

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2006). In 2007, additional infestations have been found in Illinois, Indiana, Ohio, Maryland and Virginia, primarily a result of inadvertent transport of infested ash nursery stock, firewood and logs. The potential economic, ecological and social impacts of this pest are tremendous given that ash is an important timber and landscape species throughout North America. It is estimated that there are more than 7 billion ash trees in the US, of which more than 700 million occur in Michigan, 280 million in Ohio, and 150 million in Indiana (Mastro *et al*., 2007). If *A. planipennis* becomes widely established in Michigan alone, it could result in a total loss of 307 million board feet of ash saw logs and veneer with a compensatory value as high as $18.9 billion in Michigan alone (Poland & McCullough, 2006; Mastro *et al*., 2007).

Although EAB has been recorded to be semivoltine in Heilongjiang Province (Yu, 1992), and univoltine both in Shenyang City, Liaoning Province and in Tianjin (Liu, 1966; Liu *et al*., 1996; Gao *et al*., 2004; Sun & Li, 2004; Wei *et al*., 2004; Zhao *et al*., 2004; Zhao *et al*., 2005), it is not clear where the transitional area is located and the type of life cycle EAB has in this area. In this paper we report on the life history of EAB in different geographical areas of China and provide biological characteristics as well as damage traits of EAB in that area based on 2 years of field survey combined with laboratory observations.

Materials and methods

Study sites

Three sites were selected for this study: Harbin Experimental Forest of Northeast Forest University, Harbin, Heilongjiang Province; Jingyuetan National Forest Park, Changchun, Jilin Province; and Guangang Forest Park, Dagang District, Tianjin, China.

A 42-year-old *F. mandshurica* plantation was selected at the Harbin Experimental Forest (45°43'N, 126° 37'E) at an elevation of 145 m. The plantation was 1.6 hm^2 with 0.6 canopy density. The row-spacing was 2.0 m, and the distance between trees within a row was 3.0 m. Diameter at breast height (DBH) of ash 27.4 $\pm$6.5 cm, and height 11.6 $\pm$ 4.2 m. The soil was a medium-thick chernozem. The annual average temperature is about 4.5°C, rainfall 480 mm, sunlight 2 500 hours, and frost-free period 120–130 days.

A 8-year-old *F. mandshurica* plantation in the Jingyuetan National Forest Park is located at 42° 46'N, 125° 27' E at an elevation of 220 m. The area of the plantation is 2.2 hm^2 with a south slope of 11°, 0.8 canopy density, and dark brown soil with medium thickness. The row spacing is 2.0 m, and the distance between trees within a row is 2.0 m. The average DBH of ash is 4.81 $\pm$ 2.18 cm, and average height 3.75 $\pm$ 0.94 m. The annual average temperature is about 4.8°C, rainfall 522–615 mm, sunlight 2 866 hours, and frost-free period approximately 160 days.

A 10-year-old *F. velutina* plantation in Guangang Forest Park is located at 38°55'N, 117°31'E at an elevation of 3 m. The area of the plantation is 2.2 hm^2. The row spacing is 1.5 m, and the distance between trees within a row is 1.0 m. The average DBH of ash is 7.64 $\pm$ 3.39 cm, and average height 5.87 $\pm$ 2.15 m. The plantation has halaquept soil with medium thickness and 2%–4% salt content. In Dagang area, the annual average temperature is 13°C rainfall 416 mm, sunlight 3 000 hours, and frost-free period is 238 days.

Biology

The surveys for EAB life stages were conducted from April 2004 to June 2005 in Tianjin, from April 2004 to June 2006 in Changchun, Jilin Province, and from April 2004 to June 2006 in Harbin, Heilongjiang Province. Five trees attacked by EAB were sampled every 5 days in order to observe the development of each larval instar and associated damage. Five trees attacked by EAB were randomly sampled daily in order to observe pupal development and record pupation. Both lab observations and field surveys were used to observe the daily change of pupae and eggs, emergence, mating, oviposition of adults, as well as their damage traits.

The number of each larval instar and pupae surveyed and the percentage of each larval instar and pupae were calculated. EAB adults were collected from infested ash in late April in 2004 that had been placed in a sleeve cage. The numbers of male and female EAB adults that emerged from the logs were recorded daily.

A total of 45 EAB adults were captured in late April over 4 days (10–15 adults/day) and placed in a sleeve cage (100 × 100 × 150 cm) in Guangang Forest Park. The EAB adults were fed fresh *F. mandshurica* leaves and twigs. Three *F. mandshurica* boles (length: 150 cm, diameter: 10 cm) were placed in the cage to allow mating. The time of mating was recorded, and oviposition and death were investigated every day. Eggs deposited on bark were placed in glass tubes and the changes in their development and hatch time were recorded. Ten EAB were collected during early pupation and placed in the tubes (one EAB per tube) then placed in a box with no light). The eclosion time was recorded.

Survey of damage traits

Surveys were conducted in the 10-year-old *F. velutina* plantation in Guangang Forest Park in Tianjin in July 2004 and April 2005. Five plots consisting of 50 trees each were established with four at the edges and one in the center of the plantation. One EAB-infested tree was randomly sampled per row; a total of 10 EA trees were randomly sampled and dissected on each plot. Both trunk and branches were investigated.

Vertical distribution of EAB larvae in the boles

The boles were dissected and the numbers of EAB larvae recorded based on four segments of the bole measured from above the soil line:, 0–50 cm, 51–100 cm, 101–150 cm, and 151 cm and over.

Relationship of the attacked position of boles and their orientation

The boles were dissected and the numbers of EAB larvae recorded based on four orientations (north, south, east, and west). This survey was conducted with the vertical distribution.

Horizontal distribution of EAB larvae in the plantation

This survey was conducted together with the vertical distribution in July 2004. In April 2005, ten out of 50 trees in each plot were sampled and examined again using the same sample method as 2004. In two years, a total of 100 trees with 20 on each plot were sampled and the numbers of larvae were recorded.

Results

Biology

Emerald ash borer was observed to have a 1-year life cycle in Tianjin (Table 1). Pupation of the overwintering larvae lasted for approximately 31.2 ± 1.6 days (n = 45) beginning in early April, and ending in mid-June. Adult emergence began in early May, peaked in mid- to late May, declined in early June, and ended in early July. Female adults began laying eggs in mid-May and ended in mid-July. In late May, the early-instar larvae were observed to feed in the cambial region, and this damage continued until early November. From late September to early November, the last-instar larvae bored into the xylem and built pupal cells (depth: 10.7 ± 1.6 mm, length: 18.5 ± 3.0 mm, width: 5.8 ± 1.0 mm, n = 33). In the pupal cell the larva doubled over with its head away from the emergence hole to prepare for overwintering. Before pupation in the following year, overwintering larvae shorten, straighten and thereby the head ends up pointed towards the emergence hole.

Emerald ash borer was observed to be semivoltine in Harbin, Heilongjiang Province (Table 2) and the majority of EAB were semivoltine in Changchun, Jilin Province. Pupation of the overwintered larvae for the second year began in late April, and ended in late June. Eclosion of EAB adults began in late May and ended in early July. The egg stage occurred from early June to late July. In mid-June, early-instar larvae bored between the phloem and the xylem and this damage continued until late September when they started overwintering in the gallery. The feeding damage of the overwintering larvae in the first year began in mid-April. In mid-August, the larva entered a pupal cell (depth: 11.06 ± 1.19 mm, length: 16.91 ± 2.15 mm, width: 5.80 ± 0.96 mm, n = 35), curled up with its head away from the emergence hole to prepare for the overwintering. In the following year, before pupation the second-time overwintering larvae straightened up and turned its head towards the emergence hole.

Adults After eclosion the EAB adult stayed in the pupal cell for 5.43 ± 1.24 days (n = 37), and then bored a D-shape emergence hole through the bark and exited the tree. Typically, the adults exit at 12:00 h on sunny and warm days. The newly emerged EAB adult climbs upwards on

Table 1 Univoltine life history of emerald ash borer (Tianjin, 2004–2005).

Jan.–Mar.			Apr.			May			Jun.			Jul.			Aug.			Sept.			Oct.			Nov.			Dec.		
E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L
			◎	◎	◎	◎	◎	◎	◎	◎																			
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■	■	■	■	■											■	■	■	■	■	■	■	■	■	■	■	■	■	■	■

E: The first 10 days; M: The second second 10 days; L: The third 10 days; ◎: Pupa; ●: adult; ○: egg; ◇: larva; ■: overwintering larva.

Table 2 Semivoltine life history of emerald ash borer (Harbin, Heilongjiang Province, 2004–2006).

Jan.–Mar.			Apr.			May			Jun.			Jul.			Aug.			Sept.			Oct.			Nov.			Dec.		
E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L
					◎	◎	◎	◎	◎	◎																			
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■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■												
■	■	■	■	■	■	■										■	■	■	■	■	■	■	■	■	■	■	■	■	■

E: The first 10 days; M: The second 10 days; The third 10 days; ◎: pupa ●: adult; ○: egg; ◇: larva; ■: overwintering.

the bole and vibrates its wings continuously without feeding. In general, an EAB adult crawls for about 3 m (n = 15) before its wings totally open and it is able to fly. EAB adults are active and have strong flight capability. They were observed to move around on the leaves and branches from 8:00 h to 18:00 h when it was warm and sunny. Adults sometimes feign death.

In 2005, we investigated the timing of adults emergence. In Tianjin (1-year life cycle area) peak eclosion appeared in mid-May, 80.6% of total adults emerged (Table 3). The eclosion period lasted 19 days. In Harbin (semivoltine area) peak eclosion appeared in early June (51.1%) (Table 3). Males eclosed earlier than females, while at peak and late emergence the number of female adults was higher than that of male adults. In Tianjin (univoltine area) the sex ratio of females to males was 1:1.57 (n = 216), and in Harbin (semivoltine area) the sex ratio was 1:1.81 (n = 45).

After initial flight, adults began to feed on leaves. EAB adults begin feeding on the edge of the leaves. On each occasion, the adult eats up to 1 cm^2 foliage. After feeding for 5.4 ± 1.2 days (n = 37) the adults start mating. Mating generally takes place on the branches and leaves and peaks from 14:00–15:00 h.

One female adult can lay 70.97 ± 14.38 eggs (n = 32). In general, a female adult slowly climbs upward on the southwestern side of a stem, finds a suitable location in the bark crevices, curves its abdomen downward, extends its ovipositor and lays eggs. In the field, one female adult laid 1.64 ± 0.83 eggs (n = 53) individually at one location, while in the laboratory one female laid a maximum of 21 eggs at one location. Longevity of the male adults was 16.75 ± 3.32 days (n = 28), and longevity of female adults was 18.75 ± 5.79 days (n = 17).

Eggs The eggs are flat and round, with a diameter of about 1 mm. The initial color was from milky white to maize, occasionally jade-green, and all colors turned to gray after 2 days. Developmental time of eggs was 9.03 ± 1.05 days (n = 103). Eggs deposited in direct sunlight were observed not to hatch due to dehydration.

Larvae Early larvae were achromatous and transparent, and turned to milky white after feeding. A larva was observed to bore through the bark, feed first on the phloem, and then feed on the cambium. In the cambial region, EAB larva fed in a zigzag pattern both downward (42.72 %, n = 44) and upward (57.28 %, n = 59). Larvae mainly fed and damaged the cambium layer in naturally infested trees. The damaged area was oval-shaped with an S-shaped gallery in vigorous trees; while the damaged area and galley were irregular in stressed trees. In the areas where EAB needs two years to complete one generation, dead larvae could be seen in severely damaged and dead trees with straight horizontal or vertical galleries. In most situations, late

Table 3 Number of emerald ash borer adults emerging from univoltine and semivoltine life cycles.

Location	Tianjin† (May 2005)			Harbin‡ (May–June 2004)		
Time	1st–10th	11–20th	21st–31st	21st–31st May	1st–10th June	11st–20th June
Adult after eclosion	3	174	39	13	23	9
Percentage (%)	1.39	80.56	18.06	28.89	51.11	20.00

†Sampling site: Guangang Forestry, Dagang District, Tianjin.
‡Sampling site: Harbin Experimental Forest, Harbin.

instar larvae turn in the other direction and bore into the xylem and build pupal cells that have an opposite direction to the galleries in the cambium layer.

In Tianjin, very few EAB were observed to overwinter as 2nd and 3rd instar larvae in their galleries between the phloem and xylem. Next year overwintering larvae continued to feed on the phloem and xylem and built pupal cells in late July or early August for overwintering. These EAB need 2 years to complete their life cycle, which accounted for 5%−7% of the total EAB population in Tianjin (univoltine area) (Table 4).

In Tianjin, the EAB with 1-year life cycle bored into the xylem and built the pupal cells starting in late September, peaking in mid-October, and ending in early November. It took approximately 100 days from the time larvae were found in the phloem in early June to they started building pupal cells in late September. Late-hatched larvae were still in early development when they stopped feeding when the tree stopped growing. These EAB need 2 years to complete one generation. This result indicated that EAB larvae have a slow development.

In Heilongjiang Province, although the majority of the EAB population had a semivoltine life history, a few EAB were univoltine that accounted for 8% of the total EAB population in Harbin (Table 4). These EAB were those larvae that hatched earliest and built pupal cells in mid- or late October; while semivoltine EAB larvae built pupal cells in mid-August of the second year of development. The frass in the gallery of univoltine EAB larvae was the same color and fresh; while the frass in the gallery of semivoltine EAB larvae had two distinctive colors, fresh (light brown) and old (dark brown). This phenomenon may be used to determine the type of life cycle of the larvae in the galleries.

In Changchun, Jilin Province, the majority of EAB were semivoltine, and the rest were univoltine. The adults were observed from May to July. During the surveys in April, 2004 to 2006, every larval instar was observed in the galleries. From August to October, the last-instar larva was observed to bore into xylem and build pupal cells. These 2-year life cycled larvae overwintered in the galleries, then pupated and emerged. In Changchun, EAB were also observed to damage the small branches (< 2 cm in diameter) of *F. mandshurica*. However, the larvae were smaller and they were unable to bore into the xylem and build pupal cells. Thus they were unable to complete their life cycle. No pupal cells or exit holes were found on these small branches.

Pupae EAB pupae are white exarate, 12.51 ± 1.19 mm ($n = 53$) in length, and about 4 mm in width. Compound eyes began to change color 10 days after pupation. Mouthparts turned to black 15 days after pupation. Eclosion occurred 30 days after pupation (Table 5). Pupation was from early April to mid-June in Tianjin.

Damage traits

Vertical distribution of larvae in boles EAB larvae mainly damaged the 51−150 cm region of the boles in which the number of larvae accounted for 76.73% of the total larvae (0−50 cm: 9.48%; 151 cm and above: 13.79%, n =116).

Table 4 Overwintering larvae of emerald ash borer. Parasitized larvae are not included.

Location	Time	No. of overwintering larvae in galleries	No. of overwintering larvae in pupal cells	No. of pupal cells for univoltinese	No. of pupal cells for mivoltine	Total	Percentage (%)
Tianjin	April 2004	7	93	–	–	100	7
Tianjin	April 2005	5	95	–	–	100	5
Harbin	April 2006	–	–	2	23	25	8

Table 5 Field and lab observation of emerald ash borer (EAB) pupation.

Description	Collection	Eye turns color	Wing bud occurs	Black ordinate	Mouthpart turns black	EAB turns black	EAB turns green hard	Wing becomes	Eclosion
Date†	7th Apr.	17th Apr.	18th Apr.	19th Apr.	20th Apr.	25th Apr.	27th Apr.	30th Apr.	6th May
Date‡	9th Apr.	17th−18th Apr.	18th−20th Apr.	19th−27th Apr.	20th−23th Apr.	25th−30th Apr.	28th Apr. −6th May	30th Apr. −8th May	6th−15th May

†Field survey of EAB pupation in Tianjin. Five pupae were collected and observed daily. Date of the changes began.

‡Lab observation of EAB pupation in Tianjin. Observed daily and the date recorded from the changes began to all adults emerged. The number of pupae observed is 30.

Relationship of the attacked positions and the degree of smoothness of bark Smooth bark at the attacked position accounted for 12.74% of the total bark, while coarse bark accounted for 87.26% (n = 102).

Relationship of attacked positions of boles and their orientation The attacked positions on the south side of the boles accounted for 43.40% of total attacked positions, while the attacked positions on other three sides (north: 21.70%, east: 16.98%, and west: 17.92%, n = 106) accounted for about 20% each.

Horizontal distribution of EAB in the plantation EAB density in the southern and western sampling plots in the plantation accounted for 51.82% (n = 301) of the total population surveyed, while the central sampling plot accounted for 13.62% (n = 301) of the total population. EAB caused more severe damage to the ash at the edges of the plantation than in the center.

Discussion

Life histories of EAB in Changchun, Jilin Province include semivoltine and univoltine, and some in between. This area is the transitional zone of EAB life history from semivoltine to univoltine. This is the first report of EAB life history in this transitional area. This research confirmed the previous research that EAB requires 2 years to complete one generation in Harbin, Heilongjiang Province (Yu, 1992), and 1 year in Tianjin and Shenyang, Liaoning Province (Liu, 1966; Liu *et al*., 1996; Gao *et al*., 2004; Sun & Li, 2004; Wei *et al*., 2004; Zhao *et al*., 2004; Zhao *et al*., 2005). In North America, EAB generally has a 1-year life cycle in southern Michigan but could require 2 years to complete a generation in colder regions (Mastro *et al*., 2007).

In branches < 2 cm in diameter and EAB are small and unable to enter the xylem, while they are successful on larger branches. One possible explanation for this phenomenon is that the small branches are not able to provide sufficient nutrition for the development of EAB. An alternative explanation is that the branches are physically too thin to build pupal cells. In Tianjin, EAB does not damage trunk and branches smaller than 3 cm in diameter (e.g., Yang, Z.Q., 2004, pers. com.). The difference could be due to different tree species or climatic factors, and needs further investigation.

Emerald ash borer prefers abundant sunlight for mating and oviposition. The 51–150 cm region of the boles has more bark crevices compared to the regions of 150 cm and above, which benefits oviposition, egg protection, and is suitable for feeding by early instar larvae. Smooth bark was less likely to be selected by females for oviposition, as it is not suitable for egg protection and hatching. Thus breeding ash with smooth bark can be a way of EAB resistance through reducing host trees.

The survey in Tianjin shows that the developmental rate of EAB larvae is slow compared to that in previous results, and it takes about 100 days from larvae boring into the xylem to complete the pupal cell. However, previous results indicate that in this stage larvae produce rapid development (45 days) (Liu *et al*., 1996; Zhao *et al*., 2005). The result in this study suggests that the larvae with rapid development are 5%–7% of the total EAB population, which need 2 years to complete their life cycle. The frost-free period in certain areas may be used to explain the biological characteristics of EAB (e.g., longevity, life cycle) in the same area. It takes at least 150 days for EAB to complete one generation. In Harbin the frost-free period is 120–130 days which is less than the 150-day requirement. So EAB is semivoltine in Harbin. However, in Changchun, the frost-free period is 160 days, so EAB produces a mixed population of semivoltine and univoltine. In Shenyang, the frost-free period is 183 days, and likewise, in Tianjin, the frost-free period is 210 days, so EAB produces univoltine populations both in Shenyang and in Tianjin. All Buprestidae overwinter in the larva stage. They basically have a 1-year life cycle and no two-generation per year life cycle; in cold northern areas, Buprestidae need 2 or 3 years to complete one generation (Yu, 1992). The result in this paper supports this previous research and indicates a slow development in EAB larval stage.

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