

Reproductive Biology of the Bronze Birch Borer (Coleoptera: Buprestidae) on Selected Trees^{1,2}

Rodney C. Akers³ and David G. Nielsen

Department of Entomology, The Ohio State University
Ohio Agricultural Research and Development Center
Wooster, OH 44691

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ABSTRACT Reproductive biology of the bronze birch borer, *Agrilus anxius* Gory, was examined by measuring the influence of host on maturation feeding period, fecundity, incubation period, egg viability, and longevity. Initially, females fed *Betula pendula* Roth leaves had the highest fecundity and egg hatchability. However, when large numbers of beetles were caged on an individual *B. pendula* in 1982, females did not oviposit. Fecundity and egg hatch varied on *Populus deltoides* Bartr. ex March between years but was consistently high, and the percentage of females ovipositing when fed this host was usually highest. Some beetles fed *Quercus palustris* Muenchh. or *Salix elaeagnos* Scop. produced eggs; no reproduction occurred on *Acer saccharinum* L. Host species and environmental variables influenced the beetle's reproductive biology, but some of the observed differences may be explained by reduced foliage quality resulting from inducible plant defense or spacing pheromones produced by beetles at high densities.

KEY WORDS *Agrilus anxius*, bronze birch borer, Buprestidae, reproductive biology.

The bronze birch borer, *Agrilus anxius* Gory, was first recognized as a serious pest of ornamental birches in the late 1800's (Chittendon 1898). Larval feeding scars the cambium, restricts phloem translocation, interferes with movement of water, and ultimately contributes to tree death. Consequently, most studies have examined the larval stage and its impact on the host (Balch and Prebble 1940, Anderson 1944, Barter 1957, Ball 1979, Loerch 1983).

The limited research that has been conducted with adults is dominated by host foliage preference tests. Britton (1923) observed adults feeding naturally on willow, *Salix* sp., poplar, *Populus* sp., and birch, *Betula* sp. Field observations by Hutchings (1923) indicated beetle preference for poplar and willow foliage over birch. Carlson and Knight (1969) maintained adults in the laboratory on apple pieces, but concluded that tree foliage was the probable food source. In laboratory preference tests, beetles consumed more poplar and willow than birch foliage and preferred

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³ Current address: BASF Corporation, 1401 Brookhaven Drive, Wilson, NC 27893.

quaking aspen, *Populus tremuloides* Michx., over willow, birch and other poplar species (Barter 1957, Nash et al. 1951).

Information about the influence of host on reproductive biology of bronze birch borer adults is lacking. To manipulate beetles for future research, it is imperative to quantify parameters of *A. anxius* reproductive biology on potential adult hosts. This study was conducted to investigate host influence on beetle maturation feeding period (preoviposition period), fecundity, longevity, incubation period, and egg viability.

Materials and Methods

Infested birch were felled in the Wooster vicinity and placed in an insectary at The Ohio State University, Ohio Agricultural Research and Development Center (OARDC), Wooster, Ohio. Newly emerged, unmated *A. anxius* beetles were collected daily and separated by sex. Host influence on adult biology was investigated by caging virgin beetle pairs on leaves of selected trees on the OARDC campus. Beetles 1- to 2-d-old were caged on attached leaves (1 pair/leaf) in 19.2 cm³ transparent plastic petri dishes with tops and bottoms partially replaced with nylon mesh to provide ventilation. Cages were examined every other day for eggs and dead beetles and moved to fresh leaves at this time. When eggs were found, adults were removed and caged on a new leaf. Cages with eggs were positioned in the interior of a tree canopy and examined daily for egg eclosion.

In 1980, 25 beetle pairs, 5 prs/each of 5 30-cm-tall rooted cuttings (poplars) or seedlings (birch), were placed on *Populus generosa* A. Henry, *P. deltoides* Bartr. ex. March (cottonwood), and *Betula* sp. in a polyhouse. In 1981, 10 beetle pairs were placed on separate leaves of single, mature *P. deltoides* and *Betula pendula* Roth (European white birch). In 1982, 15 beetle pairs were placed on a single, mature *Quercus palustris* Muenchh. (pin oak), *Salix elaeagnos* Scop., and *Acer saccharinum* L. (silver maple); 5 pairs were placed on each of 3 cottonwoods. Also in 1982, 15 beetle pairs were monitored from a high population of beetles (100 pairs) maintained on a single European white birch (ca. 42 m tall, 8.5 cm DBH). In 1983, 15 beetle pairs were placed on a single, mature pin oak and *S. elaeagnos*, and 5 pairs were placed on each of 3 cottonwoods and European white birch. In addition, 15 beetle pairs were again monitored from a high population of beetles (100 pairs) maintained on a single European white birch, as above).

Comparisons of adult maturation feeding, fecundity, longevity, incubation period, and egg viability on different hosts were analyzed by Student's t-test or one way analysis of variance. In 1980, 1982, and 1983 comparisons of the aforementioned beetle biological parameters were conducted within each tree species. Only female longevity when fed *P. generosa* in 1980, and male and female longevity when fed cottonwood in 1982 were significantly different ($P = 0.05$). All other parameters in all years were nonsignificant between plants of the same species. Consequently, each beetle pair was considered an experimental unit to allow greater flexibility in analysis and interpretation. Means were separated with Duncan's (1955) new multiple range test ($P = 0.05$).

Results and Discussion

Longevity. Beetle longevity varied with host and between years, in some cases. In 1980 and '81 when beetles were caged on rooted seedlings, cuttings, or on

mature leaves of mature trees, longevity was higher on birch than poplar (Table 1). Females fed birch foliage lived 26 days, while those fed poplar lived 19 days. In similar studies, beetle longevity was 23 days on poplar and birch (Balch and Prebble 1940) and 24 days on quaking aspen (Barter 1957).

When high numbers of beetles were caged on European white birch in 1982 and '83, longevity was significantly reduced, in comparison to other hosts evaluated (Table 1). In those years, cottonwood was the nominal host, and adults lived next longest when fed foliage of pin oak or willow.

Agrius anxius adults can survive on a number of non-larval hosts. Larvae are only able to colonize trees in a weakened condition (Anderson 1944, Barter 1957), and suitable larval hosts are not distributed regularly. Since females apparently must find weakened trees for reproduction, it is adaptive for them to utilize hosts other than birches to provide energy when searching for oviposition sites.

On nearly all hosts evaluated and in all years, females lived longer than males (Tables 1). This is not surprising, since males are only necessary for mating, and females need mate only once for nominal oviposition (Akers and Nielsen, unpublished). Barter (1957) reported no difference in life span of males and females when adults were fed detached aspen leaves.

Overall, longevity was highest in 1982 when unseasonably warm temperatures in May stimulated early adult emergence, followed by cool weather in June that delayed reproduction.

Fecundity. Egg production and viability varied with adult host (Table 2). Significantly more eggs were produced by beetles fed birch or cottonwood rather than *P. generosa* in 1980. In terms of overall egg production, data from 1980 and '81 suggested that birch was a nominal host for the birch borer.

When comparisons were made for only ovipositing females on a host, there was no significant host influence on fecundity (Table 2). However, the propensity to oviposit was significantly higher on birch ($X^2 = 7.0$, $P = 0.05$) and cottonwood ($X^2 = 12.89$) than on *P. generosa*. On the latter, 7% of the females oviposited, whereas 71% and 50% of those fed birch or cottonwood, respectively, oviposited in 1980. In 1982 and '83, propensity to oviposit remained high on cottonwood (92 and 93%, respectively), versus 53 and 14% on oak and 15 and 0% on willow. These differences are significant ($P = 0.01$, $X^2 = 39.1$ in '82, $X^2 = 40.1$ in 1983). Beetles were more likely to oviposit when at low versus high density on attached leaves of field-planted *B. pendula* ($P = 0.05$, $X^2 = 4.62$).

Barter (1957) reported that a caged, mated *A. anxius* female produced 25 larvae. Through dissection, he found an average of 50 oocytes per gravid female before oviposition and predicted that the reproductive potential was even higher. In 1981, fecundity of ovipositing beetles on *B. pendula* approached that observed by Barter. Low fecundity in our study in 1980 may be attributed to feeding beetles on first year rooted seedlings or cuttings or high greenhouse temperatures that may have stressed beetles, thereby reducing egg production. Although we do not know if caging beetles altered fecundity, females oviposited within cages on a variety of hosts during all years of the study and throughout their lifetime. Non-ovipositing females in our studies were observed mating and feeding on all hosts except silver maple.

Although only 15 of the 100 beetle pairs on the single European white birch were monitored routinely for longevity and fecundity in 1982, none of the 100

Table 1. Longevity and maturation feeding period of *Agrilus anxius* on selected trees near Wooster, OH.

Study date	Plant* host	\bar{X} ♂ Longevity + S.D. (Days) †	\bar{X} ♀ (Days) †	\bar{X} Days to 1st ‡ oviposition ± S.D.
June, 1980	<i>Betula</i> sp.	19.1 ± 3.6 a	22.2 ± 5.4§ a	15.4 ± 1.5 a
	<i>Populus deltoides</i>	15.4 ± 3.1 b	19.2 ± 2.3¶ a	15.2 ± 1.2 a
	<i>P. generosa</i>	15.6 ± 3.8 b	17.3 ± 3.1 b	15.0 ± 1.4 a
June, 1981	<i>B. pendula</i>	—	26.5 ± 13.7 a	12.1 ± 5.8 a
	<i>P. deltoides</i>	—	18.8 ± 9.4 b	13.7 ± 5.0 a
May, 1982	<i>B. pendula</i> (100 prs)	14.2 ± 2.9 d	22.0 ± 6.9¶ c	—
	<i>P. deltoides</i>	38.1 ± 9.6 a	46.4 ± 9.7§ a	24.6 ± 4.5 a
	<i>Quercus palustris</i>	19.8 ± 4.6 b	35.8 ± 7.1¶ b	20.1 ± 4.6 a
	<i>Salix elaeagnos</i>	18.8 ± 4.9 bc	34.6 ± 12.3¶ b	24.0 ± 0.0 a
	<i>Acer saccharinum</i>	14.9 ± 2.9 cd	20.4 ± 3.4¶ c	—
June, 1983	<i>B. pendula</i>	10.7 ± 2.2 b	14.7 ± 3.8¶ c	9.5 ± 1.0 a
	<i>P. deltoides</i>	16.6 ± 6.9 a	27.6 ± 9.3¶ a	15.8 ± 6.3 a
	<i>Q. palustris</i>	14.8 ± 4.2 a	19.1 ± 6.3¶ b	14.0 ± 0.0 a
	<i>S. elaeagnos</i>	10.0 ± 2.3 b	14.5 ± 4.6¶ bc	—

* In 1980, *A. anxius* adults were fed on attached leaves of *Betula* seedlings and *Populus* spp. clonal cuttings; in 1981-1983, adults were fed on attached leaves of mature trees.

† Means/sex/year followed by the same letter are not significantly different at the $P = 0.05$ level according to Duncan's (1955) new multiple range test for 1980, 1982, and 1983 data; Student's *t*-test for 1981. ¶ or § indicate significant differences between sexes per host at $P = 0.05$ or $P = 0.10$, respectively, according to Student's *t*-test.

‡ Means/year followed by the same letter are not significantly different at the $P = 0.05$ level according to Duncan's (1955) new multiple range test.

Table 2. Host Influence on *A. anxius* fecundity, egg incubation period, and hatchability near Wooster, OH.

Study date	Plant* host	\bar{X} Fecundity \dagger \pm S.D. (No. ♀'s)	\bar{X} Fecundity \pm S.D. \ddagger of ovipositing ♀'s (No. ♀'s)	\bar{X} No. eggs § hatched \pm S.D./ ♀ ovipositing	\bar{X} Days to \uparrow 1st hatch \pm S.D.
June, 1980	<i>Betula</i> sp.	4.4 \pm 5.6 (17) a	6.2 \pm 5.8 (12) a	---	---
	<i>Populus deltoides</i>	3.5 \pm 4.7 (24) a	7.1 \pm 4.2 (12) a	---	---
	<i>P. generosa</i>	1.1 \pm 3.3 (18) b	9.5 \pm 5.0 (2) a	---	---
June, 1981	<i>B. pendula</i>	18.6 \pm 16.7 (12) a	24.8 \pm 14.5 (9) a	11.3 \pm 9.4 a	---
	<i>P. deltoides</i>	6.2 \pm 10.6 (16) b	9.9 \pm 12.1 (10) b	2.4 \pm 5.6 b	---
May, 1982	<i>B. pendula</i> (100 prs)	0.0	---	---	---
	<i>P. deltoides</i>	11.0 \pm 7.6 (12) a	12.0 \pm 7.1 (11) a	2.9 \pm 2.8 a	15.2 \pm 2.1 b
	<i>Quercus palustris</i>	4.3 \pm 5.8 (13) b	8.0 \pm 5.8 (7) a	3.6 \pm 3.8 a	24.8 \pm 1.3 a
	<i>Salix elaeagnos</i>	1.7 \pm 4.6 (13) bc	11.0 \pm 7.1 (2) a	4.0 \pm 1.41 a	14.0 \pm 2.8 b
	<i>Acer Saccharinum</i>	0.0	(14)	---	---
June, 1983	<i>B. pendula</i> (100 prs)	0.0	(15)	---	---
	<i>B. pendula</i>	2.1 \pm 5.5 (15) b	7.8 \pm 9.1 (4) a	3.8 \pm 6.8 a	13.0 \pm 4.2 a
	<i>P. deltoides</i>	15.5 \pm 10.1 (13) a	16.8 \pm 9.3 (12) a	6.8 \pm 6.9 a	15.3 \pm 4.6 a
	<i>Q. palustris</i>	1.4 \pm 3.5 (14) b	9.5 \pm 2.1 (2) a	3.0 \pm 1.4 a	18.0 \pm 4.2 a
	<i>S. elaeagnos</i>	0.0	(12)	---	---

* In 1980, *A. anxius* adults were fed on attached leaves of *Betula* seedlings and *Populus* spp. clonal cuttings; In 1981-1983, adults were fed on attached leaves of mature trees.

\dagger \pm § \uparrow Means/year followed by the same letter are not significantly different at the $P = 0.05$ level according to Duncan's (1955) new multiple range test for 1980, 1982, and 1983; Student's t -test for 1981. Data for 1980 transformed to $\text{Log}_{10}(X + 1)$ for analysis. Numbers of females vary from text due to insects escaping from cages.

females oviposited (Table 2). This treatment was repeated in 1983 with the same result. Mature eggs were not found in dead females, but internal decomposition was rapid, perhaps precluding their detection.

Based on our unpublished observations of beetle density in infested birch plantations and landscapes, we would not expect to find as many as 200 beetles feeding on an individual tree of the size used in our study. This population density of birch borer adults may have stimulated a defensive response within the host. Partial defoliation by herbivores has been demonstrated to reduce leaf quality in *Alnus rubra* and *Salix sitchensis* (Rhoades 1983), *Quercus rubrum* L. (Schultz and Baldwin 1982), and *Betula pubescens* spp. *Tortuosa* Ledeb. (Haukioja and Niemela 1977).

It is also possible that artificially high feeding density by adults on leaves caused the tree to produce volatiles that inhibit either egg maturation or oviposition. This phenomenon has been found in Lepidoptera (Schurr and Holdaway 1970, Renwick and Radke 1980, 1981), in response to larval feeding.

It is possible that birch borer adults produce a spacing pheromone that tends to minimize over-utilization of oviposition sites (*sensu* Prokopy et al. 1984). This behavior would be especially adaptive to an insect that is a K-strategist that kills its host.

Barter (1957) found that a single, mated, female bronze birch borer in a cage produced as many or more eggs than did several mated females in a cage. He also found that as cage size increased, oviposition increased dramatically. These results, combined with ours, suggest that a spacing pheromone produced by beetles is the most likely explanation for reduced fecundity associated with high beetle density. If this occurs, it is not known if gametogenesis is retarded or if gravid females simply refrain from oviposition in the presence of a spacing pheromone.

Maturation Feeding. Within all test years, mean days to first oviposition did not vary significantly between hosts (ANOVA, $P = 0.05$) (Table 1). The shortest maturation feeding period for an individual female was 7 days (1981). In similar studies, oviposition did not occur until at least 6 days after adult emergence (Barter 1957, Williams and Neiswander 1959). The range in average days to first oviposition between years for a particular host indicated that environmental conditions influence the length of the preoviposition feeding period.

Egg Viability. Host influence on hatchability was significant only in 1981. Hatch was higher for eggs from females fed birch than cottonwood foliage (Table 2).

Average days to first egg hatch was influenced by host only in 1982. Eggs produced by females fed pin oak required significantly longer to hatch (Table 2).

Summary and Conclusions

In our preliminary studies (1980 & '81), reproductive potential of the birch borer was high when adults were fed birch foliage under laboratory and greenhouse conditions. Since birches are the only known larval host for this species, it seemed that adults had also specialized on birch. However, subsequent experimentation under field conditions indicated that egg production and other reproductive parameters were nominal on cottonwood. Carlson and Knight (1969) suggested that

this beetle evolved from an ancestor that fed on willow and poplar. Many species of *Agrilus* are still in a high state of evolutionary flux in regard to host plants (Fisher 1920).

The European white birch on which adults were caged out-of-doors were growing in an experimental block of *Betula* species that were becoming heavily infested by borer larvae. The endemic beetle population was increasing dramatically, and tree mortality was common (unpublished). Perhaps this high background level of beetles in the experimental birch planting resulted in a threshold level of a spacing pheromone that retarded gametogenesis or reduced propensity to oviposit.

Factors that drive maturation feeding and reproductive behavior of birch borer adults are still mostly unknown. We do not know if females select stressed trees for oviposition or if eggs are laid on both vital and non-vital trees. However, moderate beetle longevity and low fecundity would indicate that females may differentially oviposit on weakened hosts as suggested by previous investigators (Anderson 1944, Barter 1957). This question is currently under investigation in Michigan (D. A. Herms, pers. comm.).

It appears that the best way to obtain bronze birch borer eggs or larvae for experimentation is to cage individual pairs at low density, if trees growing out-of-doors are used as adult hosts. Caging mated females or mating pairs individually on attached or detached leaves in the greenhouse may also be most productive if beetle density is minimized. Indoor rearing should probably be done where air exchange is constant, in case spacing pheromone is produced. Choice of adult diet is still unclear, but both cottonwood and European white birch may be good choices.

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