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Physiological Ecology

Effects of dietary moisture content and cut wood of different species on survival and weight of Asian longhorned beetle larvae (Coleoptera: Cerambycidae)

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The wood-boring cerambycid *Anoplophora glabripennis* (Motschulsky), Asian longhorned beetle, is a highly destructive invasive pest that feeds on healthy hardwoods by tunneling under the bark and then within the sapwood as larvae mature. Larval weight gain and survival can be affected by the nutritional content, moisture content, and physical traits of the available food source. In this study, we experimentally manipulated the larval resource quality by controlling the moisture content of artificial diet (70% and 40% moisture) and by inserting larvae into cut wood of 2 different hosts (sugar maple [*Acer saccharum* Marshall] and gray birch [*Betula populifolia* Marshall]). First and/or fifth instars from a Chicago, Illinois laboratory colony were used to follow larval survival, weight, and pupation. Artificial diet moisture content did not affect larvae survival; however, larvae reared on a diet containing 70% moisture weighed more on average than those reared on a diet containing 40% moisture for all time intervals weights were taken. First instars reared in cut gray birch were more likely to survive, grow larger, and molt than first instars reared on cut sugar maple (only one larva survived). The species of cut wood did not have a significant impact on the survival, weight gain, or adult emergence of fifth instars. Our findings suggest that this insect's tolerance of highly variable host quality provides it with ample capacity to survive, disperse, and reproduce even when dietary moisture content is low or declining, as might be expected in trees in the late stages of infestation.

Keywords: Anoplophora glabripennis, host wood moisture, pupation, survival, pupation

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Graphical Abstract

Introduction

The wood-boring cerambycid beetle *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), referred to as the Asian longhorned beetle, is native to China and Korea and occurs across a broad geographic range (21° to 43°N and 100° to 127°E), where it is commonly a serious pest in deciduous forests and city trees (Lingafelter and Hoebeke 2002). Established populations have been discovered in and around urban centers in the eastern United States, eastern Canada, and several countries in Europe where costly programs have been implemented to eradicate these infestations (Javal et al. 2019a, 2019b, Coyle et al. 2021). The insect has moved internationally in the larval form within solid wood packing material originating in its native range (US Department of Agriculture and Health Inspection Service [USDA-APHIS-MRP] 2015). Molecular data have also confirmed that this insect has also moved within countries, likely in cut wood, over longer distances than it is capable of flying (Javal et al. 2019a, 2019b, Cui et al. 2024). This species threatens forest ecosystems, recreation, and the availability of natural resources (USDA-APHIS-MRP 2015). Potential tree loss due to *A. glabripennis* infestations could impact native species as well as huge numbers of trees in both urban and rural settings (Nowak et al. 2001).

In the United States, *A. glabripennis* adults emerge from host trees between early summer and early autumn. After 9 to 15 d of maturation feeding (Keena 2002), adults mate and females oviposit eggs, singly, beneath the bark of apparently healthy and already-infested host trees. When oviposition occurs early in the season, larvae hatch after 1 to 2 wk. First instars through the late third or early fourth instars feed on the inner bark, cambium, and outer sapwood, which tend to have a higher moisture and nutrient content than the heartwood; thus, larvae utilize the best tissues first. However, later instar larvae tunnel deeper into the xylem, which tends to have a lower moisture content and higher density than the phloem and cambium. Therefore, larger larvae may be less sensitive to the moisture and nutritional content of their diet. The extensive tunneling and girdling caused by larvae within the sapwood and heartwood also disrupts sap flow, creating drier conditions in heavily infested trees, which could also impact the larvae growing within them. Little research has been conducted to determine the effects of a lower moisture content on *A. glabripennis* larvae.

Larvae stop developing late in the season and remain within the xylem through the winter, with pupation delayed until the following spring (Haack et al. 2010, Schmitt et al. 2025). Some larvae, however, may reach a minimum pupation size during one growing season and could proceed to pupation if the right thermal conditions exist, allowing them to complete development in less than a year. This regularly occurs in the laboratory and has been suggested by phenology modeling (Keena and Moore 2010, Trotter and Keena 2016, Schmitt et al. 2025). Prior to pupation, larvae excavate a pupal chamber near the outer bark. The duration of the pupal stage is temperature dependent (Keena and Moore 2010) and may range from 2 to 3+ wk. Metamorphosis is complete when adults are fully sclerotized and chew their way out of the host tree. Generally, *A. glabripennis* adults disperse only short distances from their natal host trees and may remain there to mate and oviposit as long as the host remains alive (Smith et al. 2001, Trotter and Hull-Sanders 2015, Trotter et al. 2019). The fact that this species spends most of its developmental period within the host tree makes detection and eradication challenging, but its lower propensity to fly makes locating and destroying infested trees to eliminate the infestation possible.

This beetle's acceptance of a broad range of host tree species and climate conditions are factors conducive to its establishment outside its native range (Nowak et al. 2001, MacLeod et al. 2002). In Asia, the primary host species of *A. glabripennis*

include *Acer* spp., *Salix* spp., *Populus*, and *Ulmus*, although they will also feed on several other genera (Wu and Jiang 1998). In North America, *A. glabripennis* has primarily attacked species of maple, including Norway maple (*Acer platanoides* L.), sugar maple (*Acer saccharum* Marshall), silver maple (*Acer saccharinum* L.), red maple (*Acer rubrum* L.), sycamore maple (*Acer pseudoplatanus* L.), and boxelder (*Acer negundo* L.) (Haack et al. 1997, Turgeon et al. 2022). It has also infested species of birch (*Betula* spp. L.), poplar (*Populus* spp. L.), willow (*Salix* spp. L.), horsechestnut (*Aesculus hippocastanum* L.), and elm (*Ulmus* spp. L.) (Meng et al. 2015). Ninety percent or more of the first trees infested in both North American and European invaded sites have been *Acer* species, followed by *Salix*, *Ulmus*, *Aesculus*, and *Betula* species in descending order by percentage (Branco et al. 2022). Successful completion of development from egg to adult within a genus does vary substantially. In Massachusetts, USA, 53% to 64% of the infested trees were red maple, 11% to 18% were Norway maple, and 9% to 14% were sugar maple (Dodds et al. 2013). Similarly, a study on the survival of *A. glabripennis* eggs laid under the bark of cut *Acer* bolts showed that larvae that hatched survived longer and weighed more in the wood of less dense species (boxelder and red maple) than in the wood of denser *Acer* species (sugar and silver maple) (Keena et al. 2001).

As larvae, *A. glabripennis* are incapable of escaping hosts with declining or poor host quality. Host quality may be a critical determinant of both survival and the timing of various life history traits. For example, time to pupation, number and duration of instars, stage weights, survival, and fecundity are all traits that can vary in cerambycids in response to variability in temperature and the quality of the food resource (Haack and Slansky 1987, Hanks et al. 2005, Walczyńska 2009, Keena and Moore 2010). In heavily infested trees, the extensive larval tunneling can disrupt water transport within the xylem, resulting in lower available moisture in the affected branches and trunk sections (Boddy and Rayner 1983). Firewood and solid wood packing material also represent potential host wood with low and declining moisture content that can prolong time to pupation. The exact impact of reduced available moisture content in host tissues on *A. glabripennis* larvae is not known. A lower available moisture content could act as a cue to pupate faster to escape declining resources, or it could conversely cause slower weight gain, reducing the probability of reaching adulthood. The tree species that larvae feed on can also have a huge impact on their survival, weight gain, and time to pupation, even within the same host genus, as already mentioned. Many characteristics (nutritional content, secondary compounds, wood density, moisture content, etc.) of the host species wood likely lead to these impacts both in live trees and cut wood. Little is known about host species effects on survival and larval weight gain in cut wood.

To improve understanding of the effects of host moisture content on larval weight gain, pupation, and survival, we experimentally manipulated the moisture content of an artificial diet and reared *A. glabripennis* larvae on both a wet and dry diet. We then used cut wood (a larval food source that was declining in available moisture content) from 2 tree species that differed in wood density to observe the effects of larval host wood with a decreasing moisture content on survival, larval weight gain, and pupation. We also discuss the impacts of our findings on eradication programs aimed at this exotic pest.

Methods

Insect Strain

To conduct these studies, we used larvae from the Illinois laboratory strain maintained at the USDA Forest Service Quarantine Facility in Ansonia, Connecticut. The study beetles were in their 35th (diet trials) and 36th (cut wood trials) generations that have been continuously reared on artificial diet (Keena 2005). The colony was founded using beetles reared from infested branches obtained during the initial eradication program in Chicago, Illinois in February 1999 (1,450 adults, 41.58°N and 87.42°W.). The infested branches were transported under permit to the USDA Forest Service quarantine facility in Ansonia, Connecticut. Voucher specimens of adult *A. glabripennis* from this strain were deposited at the Entomology Division, Yale Peabody Museum of Natural History, New Haven, CT. Every generation, 200 to –300 larvae have been reared, and sibling and first cousin matings have not been allowed to help maintain the genetic diversity of the colony over time.

Rearing on Artificial Diet With Different Moisture Contents

Pourable, high-moisture AG2 diet (Keena 2005), a standard used in rearing continuous laboratory colonies of *A. glabripennis*, served as our wet treatment and contained 70 ± 0.6% moisture as measured using a moisture meter (A&D Company Limited, Tokyo, Japan, MF-50 Moisture Analyzer). After mixing, we poured this diet into 118 ml clear plastic cups used for small larvae and for simulated overwintering periods and 228 ml clear plastic cups used for larger larvae. The cups were covered, and the diet was allowed to set at room temperature for 24 h. It was then placed in plastic bags and held at 5 °C until used. The average moisture content of Norway maple (a highly preferred *Acer* host species) wood varies with the season, exceeding 70% in the spring and dropping to around 60% during summer (Schill et al. 1996). Therefore, to simulate conditions in heavily infested host trees or in wood cut for firewood, we manipulated the moisture content of the artificial diet to average 40 ± 1.1% moisture content. To accomplish this, we made the artificial diet with 50% less water than the wet diet and transferred the diet to 23 × 33 × 5 cm trays instead of cups. After drying for approximately 24 h at room temperature, the diet was then cut into rectangular cubes that would fit into the cups and tested with a moisture meter to obtain initial measurements. The diet was then dried under a hood for approximately 15 h, which reduced the moisture content to approximately 40%. Outer surfaces were drier than the centers of each cube. After this drying period, the diet sample, which included both dry exterior and moister middle, was tested with the moisture meter to ensure it had reached the proper moisture content. The pieces of dry diet were placed into 4 or 8 oz cups, placed in plastic bags, and held at 5 °C until used.

The first instars were tested in 3 separate trials (from the same generation) as larvae became available until there was a total of 120 larvae (60 larvae in both the dry diet group and wet diet group, respectively). Larvae from 19 different female parents were evenly distributed between the 2 diets. Filter paper was used in the lids of all the diet cups to prevent cheese mites from getting into the diet and potentially affecting the results. Larvae were individually weighed and randomly placed into

treatments. We established first instars in this artificial diet by using a flamed metal spatula to cut a keel-shaped wedge from the diet and then transferred a single larva into this cavity. We removed the base of each wedge, a volume corresponding roughly to the size of first instars, and then replaced the wedge to provide sufficient contact for the newly hatched larvae to burrow into the diet. Larvae were kept at the optimal rearing temperature of 25 °C (Keena and Moore 2010) and 60% RH for the duration of the study in a walk-in temperature chamber. After 4 wk on the diet, larvae were removed from their diet cups and weighed individually; deaths were recorded. Larvae were then placed into 0.5 cm diameter holes cut into the diet in a 228 ml diet cup with fresh artificial diet matching their respective treatment. After 8 wk on the new diet, the larvae were removed, weighed, and placed into fresh diet, with larger diameter holes made in the diet for the larger larvae. Larvae were checked for prepupation and pupation twice a week until week 12. Prepupae and pupae were removed from the diet cups and placed in 50 ml tubes with a 1-inch-wide piece of paper towel to simulate pupation chambers. Prepupae were checked daily for pupation. Pupae were weighed to determine pupal weights, and sex was assessed. Pupae were also checked daily for adult emergence. New adults were weighed 4 d after discovery, which allowed them time to harden off.

After 12 wk in the artificial diet, the larvae were again removed and weighed. Any larvae that had not become prepupae by this time were placed in 118 ml diet cups and held at 5 °C for 84 d to simulate a winter chill. After chilling, they were moved to 228 ml cups again and held at 25 °C and 60% RH, where they were checked regularly until they became adults or died.

Following Larval Survival and Weight Gain in Cut Wood

Selection of Hosts to Use

Acer species are the most often used hosts by *A. glabripennis* in North American infestations and were therefore the most desirable to use for the cut wood study, but sugar maple was the only species available for this study. *Anoplophora glabripennis* is not as successful at completing development on living sugar maple or other denser *Acer* species (Dodds et al. 2013). Higher density wood has a higher moisture content than less dense wood, but a higher percentage of that water is bound in the denser cell wall structure and not free between the cells in the wood (Glass and Zelinka 2021). Wood density is a measure of weight per volume, allowing it to change with the moisture content of the wood. Green wood (ie fresh cut wood) moisture content varies both between species in a genus and between genera. The average moisture content of green sugar maple wood is 72% in the sapwood and 65% in the heart wood (Glass and Zelinka 2021). The other host species that was chosen was gray birch (*Betula populifolia* Marshall) because it has less dense wood, and the average moisture content of green wood of this species is higher than that of sugar maple. The closely related *Betula* species, paper birch (*Betula papyrifera* Marshall), has an average moisture content of 72% in the sapwood and 89% in the heart wood, which is similar to that of the wet artificial diet used in the other experiment (Glass and Zelinka 2021). These 2 hosts, although potentially different in phytochemistry and nutritive value, represent 2 different green wood densities (see Jenkins et al. 2003 for specific gravity of the 2 species: 0.45 for gray birch and 0.56 for sugar maple) and 2 different green wood moisture contents. During the study, the moisture content of the wood would decline, and it has been estimated that green *Acer* wood will lose about 25% of the moisture in the first 60 d when exposed to ambient temperatures (Ruiz-Villanueva et al. 2016). Therefore, moisture content in the cut wood would change over time instead of remaining constant like in the first experiment.

First-Instar Trials

Ten sugar maple bolts and 10 gray birch bolts were cut on US Forest Service, Northern Research Station property in Ansonia and Hamden, Connecticut. The bolts were cut (May for first instars and June for fifth instars) from 3 to 4 trees per area, which received plenty of sun and were located along the edge of wooded areas. Sugar maple bolts were cut from the lower lateral branches, while the gray birch bolts were cut from the trunks of smaller diameter trees. On average, the sugar maple bolts measured 72.4 ± 1.8 cm in length and 6.0 ± 0.3 cm in diameter, while the gray birch bolts measured approximately 75.3 ± 1.1 cm in length and 6.1 ± 0.3 cm in diameter. The ends of the bolts were sealed with melted paraffin wax to slow moisture loss from the cut ends. Bolts were used 12 to 14 d after being collected. Six holes were drilled into each bolt with a 2.8 mm (7/64 inch) wide drill bit. The holes were placed approximately 12.7 cm apart and were 1.5 cm deep. Additionally, holes were drilled at an angle, so they were just below the bark in the sapwood. Holes were alternated between the sides of each bolt to provide more space between the larvae and were labeled A to F to mark the position of each larva.

A total of 120 first instars (60 per host) were set up in bolts. The 120 larvae were set up in 3 trials (from the same generation), with all 3 trials initiated during a 2-wk period. Structuring the samples this way allowed us to take advantage of pulses of newly hatched larvae emerging in the quarantine colony. Each larva was weighed and randomly assigned to a bolt. We alternated between host species as we set up the bolts. Each larva was placed headfirst into its hole, and wood shavings from its respective host species were loosely packed over it. Self-adhering gauze tape (2-cm-wide SAF-T-Tape) was wrapped around the holes as an additional measure to hold the larvae in the bolts while allowing air flow. Bolts were placed upright in bins and held at 25 °C and 60% RH for the duration of the study. Bolts were checked every 1 to 2 wk for frass or other signs of survival or tunneling. If frass was discovered in a particular hole, the mesh tape covering it was removed to allow the larva to continue pushing frass out more easily. If a larva was found dead in its hole, its instar was determined.

The bark thickness was measured, and then the bark was peeled off the 20 bolts 53 to 55 d after setup. Surviving larvae were weighed, and the widths of their head capsules were measured at their widest points using a digital micrometer (Qfun, Guangdong, China, Vernier Digital Caliper Stainless Steel 150 mm Accuracy: 0.02 mm). Instars were also determined for both live and dead larvae by comparing both weights and head capsule widths to published means for larvae reared at 25 °C (Keena and Moore 2010).

Additional data on the bolts used were taken, after the data on larval weight gain and survival were collected, to provide more information on what may have contributed to the apparent differences in the survival of the 2 species of trees. The bolts used for the first instars were allowed to dry inside the quarantine, autoclaved, and then allowed to dry again. A chop saw

was then used to cut 3.5 to 4.0 cm cookies from each bolt. The ends of each chunk were sanded, and the growth rings were counted (both the total number and the number in the outer 1 cm). The cookie diameter (cm) was measured at both ends using a diameter tape, and the maximum and minimum height (cm) was measured using a ruler. An average radius (average diameter/2) and an average height were calculated for each cookie, and they were weighed (g). A volume was calculated for each cookie (cm^3), and the weight was divided by the calculated volume to determine a dry wood density (g/cm^3).

Fifth-Instar Trials

To obtain fifth instars to insert into the bolts, a total of 80 newly hatched larvae were weighed and then placed into 50 × 15 mm petri dishes filled with artificial diet as described in Keena and Moore (2010). Larvae were checked weekly to monitor their instars, and the diet was replaced when they reached the third instar. Instars were determined by finding and counting shed head capsules. Starting at the fifth week, we checked for fifth instars 3 times a week. Over the course of a week, a total of 53 fifth instars and 7 late fourth instars (not all larvae had reached the fifth instar when needed) were set up in 3 trials. Ten sugar maple bolts and 10 gray birch bolts were cut, and the ends were waxed 9 d before the first bolts were set up. The bolts had the same average dimensions as those used for the first instars. Three 2.5-cm-deep holes were drilled per bolt using a 6.7-mm-wide (3/8 inch) drill bit. The top and bottom holes were on one side of the bolt, and the third hole was in the middle on the reverse side to provide the larvae more space to tunnel and thereby reduce the chances of contact. Larvae were inserted headfirst; sawdust from the corresponding host species was packed behind them, and the holes were secured with the gauze tape, as was done with the larvae in the first-instar trials. Bolts were placed upright in bins and held at 25 °C and 60% RH for the duration of the study. Bolts were checked every 1 to 2 wk for frass or other signs of survival or tunneling. If frass was discovered in a particular hole, the mesh tape covering it was removed to allow the larva to continue pushing frass out more easily. If a larva was found dead in its hole, its instar was determined.

The 20 bolts were dissected 63 d after setup. Because the bolts had to be split to find the larvae, no bolt characteristics were measured and calculated as was done for the first-instar bolts. Surviving larvae were weighed, and their head capsules were measured at their widest points using a digital micrometer. Final instars were determined for both live and dead larvae by comparing both weights and head capsule widths to published means for larvae reared at 25 °C (Keena and Moore 2010).

Statistical Methods

Statistical analyses were performed using SAS 9.4 (SAS Institute 2015). Data were evaluated to determine if they were normally distributed using Shapiro–Wilk and Anderson–Darling tests. In the artificial diet study, PROC GLIMMIX was used to evaluate the fixed effects of treatment, sex, and the interaction between the 2 on body mass at each stage and days to pupation (with and without chill). Larval maternal family was treated as a random effect. Each model was fitted to a normal distribution with an identity link function because the response variables were normally distributed. A chi-square test for homogeneity was used to assess whether the frequency counts for live and dead larvae after 4 wk, larvae and pupae at 12 wk, and pupae with and without chill were identical for the wet and dry diet treatments. In the cut bolt study, PROC GLIMMIX was used to evaluate the fixed effects of tree species, instar inserted, and the interaction between the 2 for percentage survival using a beta distribution and logit link function. When fifth instars were inserted into bolts, the fixed effect of tree species was evaluated on larval weights and head capsule widths. The bolt was treated as a random effect, and a gamma distribution with a log link function was used. When first instars were inserted, only the birch bolt results were analyzed (only 1 larva survived on maple out of 60 larvae). The fixed effect of final instar (with bolt treated as a random effect) on final larval weight was evaluated with a gamma distribution and log link function because that data were not normally distributed. PROC GLIMMIX was used to evaluate the fixed effects of tree species on bolt density, age, and bark thickness, and the model was fitted to a normal distribution with an identity link function. Differences among means for all models were determined using the Tukey–Kramer post hoc analysis and $\alpha = 0.05$.

Results

Artificial Diet With Different Moisture Contents

Sixty-five percent (39/60) of *A. glabripennis* larvae on the wet diet survived the feeding period. A total of 16 larvae on the wet diet died, 2 were lost due to handling, and 3 died during the simulated winter chill period. Eleven out of the 16 larvae died in the first 4 wk, which was 61% of all larvae on the wet diet that died. A total of 14 larvae on dry diet died, and 5 died during the chill period. Eight out of the 14 died in the first 4 wk, which was 57% of all larvae on dry diet that died. Table 1 summarizes the percentage of larval survival, pupation (before and after chill), and percentage of adult emergence. The percentages of individuals surviving at each time interval were not statistically different between the 2 diets. The percentages

Table 1. Comparison of larval survival, pupation, and adult survival as percentages of initial *Anoplophora glabripennis* reared on 2 artificial diets differing in moisture content

Diet treatment	Initial *n*	% Live larvae		% Pupation		Total % adult emergence
		4 wk	12 wk	12 wk	Post-chill	
Wet	60	82	50	25	42	67
Dry	60	87	48	33	35	68
Statistics: chi-square test for homogeneity using counts		$\chi^2 = 0.563$, df =1, $P = 0.4531$ live: dead	$\chi^2 = 0.562$, df =1, $P = 0.4534$ larvae: pupae		$\chi^2 = 1.050$, df =1, $P = 0.3055$ no-chill: chill	

Diet treatments: The wet diet contained 70% moisture by weight. The dry diet contained 40% moisture by weight. Percent live larva at 12 wk only includes those that went to chill. Larvae in the pre-pupal stage at 12 wk did not undergo a chill period so are counted with those that pupated by that time.

of larvae pupating with and without a chill were also not significantly different at 12 wk. However, there was a trend toward more pupation without chill on the dry diet. This may have increased the differences in pupation if we had allowed the larvae longer before a chill was imposed, since more larvae on the dry diet were still actively feeding at 12 wk (as evidenced by fresh frass).

The average weights of larvae when first placed into the 2 diets did not differ significantly ($F = 0.02$, df = 118, 1, $P = 0.898$) and averaged 5.4 ± 0.1 mg. Both treatment and sex had a significant effect on the weights of larvae and adults reared on the 2 diets, but the interaction terms were not significant (Table 2). Both females and males reared on the wet diet consistently weighed more than their counterparts reared on the dry diet (Fig. 1). By 4 wk, larvae on the wet diet averaged more than the minimum required for pupation (500 mg), and by 8 wk, all but 5 larvae (2 wet and 3 dry) had reached the minimum weight for pupation. By 8 wk, there were also clear differences in larval weight by sex, with females weighing more than the males on the same diet (Fig. 1).

The first pupation after setup on both diets occurred at 62 d (both males) and the last pupation on both diets occurred at 212 d (both females, which includes 84 d of chill). The average number of days from setup to pupation, both with and without chill, are given in Table 3. Treatment had a significant effect on days to pupation when there was no simulated winter chill but not when a chill was needed. On average, individuals on the wet diet pupated earlier than those reared on the dry diet. Sex had a significant effect regardless of chill, and males pupated sooner than females on average (Table 3). The interaction between treatment and sex was not significant.

Larval Survival and Weight Gain in Cut Wood

The percentage of larvae that survived in the cut wood varied significantly as a function of initial instar used ($F = 44.9$; df 1, 36; $P < 0.0001$), host tree species ($F = 14.5$; df 1, 36; $P = 0.0005$), and the interaction term ($F = 13.6$; df 1, 36; $P = 0.0007$) (Fig. 2). Overall, 59 of the original 60 first instars inserted into sugar maple died during the 53 to 55 d feeding period (1.7% survival). The one surviving larva had become a second instar but was damaged during bolt dissection. In the gray birch bolts, 29 of the first instars that were inserted died during the feeding period, while 31 survived (51.7% survival), including 2 larvae that were damaged during bolt dissection. There was a significant difference between the percentage survival of first instars inserted into the 2 host species (Fig. 2). Of the fifth instars inserted in sugar maple, 8 larvae died during the feeding period while 22 survived (73.3% survival), including 2 that were damaged during bolt dissections and one later as a pupa. In gray birch, 11 fifth instars died during the feeding period while 19

Table 2. Statistics for comparison of body mass of larvae and adults of *Anoplophora glabripennis* from the Illinois strain for 2 sexes and 2 artificial diets that differed in moisture content

	Larvae at 4 wk	Larvae at 8 wk	Larvae at 12 wk	Adult
Diet treatment	$F = 75.4$, df = 60, 1, $P < 0.0001$	$F = 26.3$, df = 60, 1, $P < 0.0001$	$F = 21.2$, df = 28, 1, $P < 0.0001$	$F = 27.5$, df = 60, 1, $P < 0.0001$
Sex	$F = 7.1$, df =60, 1, $P = 0.0099$	$F = 34.4$, df = 60, 1, $P < 0.0001$	$F = 23.1$, df = 28, 1, $P < 0.0001$	$F = 100.1$, df = 60, 1, $P < 0.0001$
Diet treatment × Sex	$F = 0.0$, df = 60, 1, $P = 0.9494$	$F = 0.1$, df = 60, 1, $P = 0.7839$	$F = 0.1$, df = 28, 1, $P = 0.8202$	$F = 0.3$, df = 60, 1, $P = 0.5759$

Diet treatments: The wet diet contained 70% moisture by weight. The dry diet contained 40% moisture by weight. Means followed by the same letter are not significantly different, based on the least squares means separation test with $\alpha = 0.05$ and with a Bonferroni correction (SAS Institute, Inc. 1999).

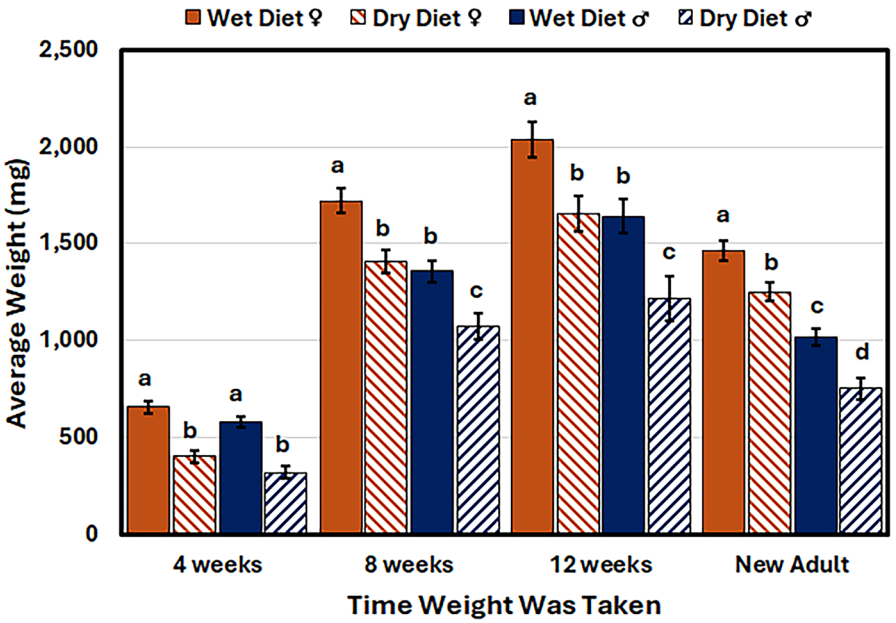

Fig. 1. Average weights (±SE, g) of *Anoplophora glabripennis* individuals, by sex, from the Illinois strain on 2 artificial diets differing in moisture content. Different letters within each timeframe the weights were taken indicate that the means are significantly different. Statistics are given in Table 2.

Table 3. Comparison of mean (±SE) time to pupation, with and without a chill period, for *Anoplophora glabripennis* larvae on 2 artificial diets differing in moisture content

Diet treatment	Sex	*n* without chill	Time to pupation (d) without chill	*n* with chill	Time to pupation (d) with chill
Wet	♂	9	68.8 ± 3.0 b	13	190.2 ± 2.4 b
Wet	♀	6	82.0 ± 3.7 ab	12	200.6 ± 2.6 a
Dry	♂	9	79.3 ± 3.2 ab	7	183.1 ± 4.1 b
Dry	♀	11	89.2 ± 2.9 a	14	196.7 ± 2.4 ab
Statistics: Treatment			$F = 8.8$, df = 18, 1, $P = 0.0083$		$F = 0.7$, df = 25, 1, $P = 0.3969$
Sex			$F = 7.9$, df = 18, 1, $P = 0.0118$		$F = 13.1$, df = 25, 1, $P = 0.0013$
Treatment × Sex			$F = 0.7$, df = 18, 1, $P = 0.4145$		$F = 1.0$, df = 25, 1, $P = 0.3112$

Diet treatments: The wet diet contained 70% moisture by weight. The dry diet contained 40% moisture by weight. Means within a column followed by the same letter are not significantly different, based on the least squares means separation test, with $\alpha = 0.05$ and with a Bonferroni correction (SAS Institute, Inc. 1999).

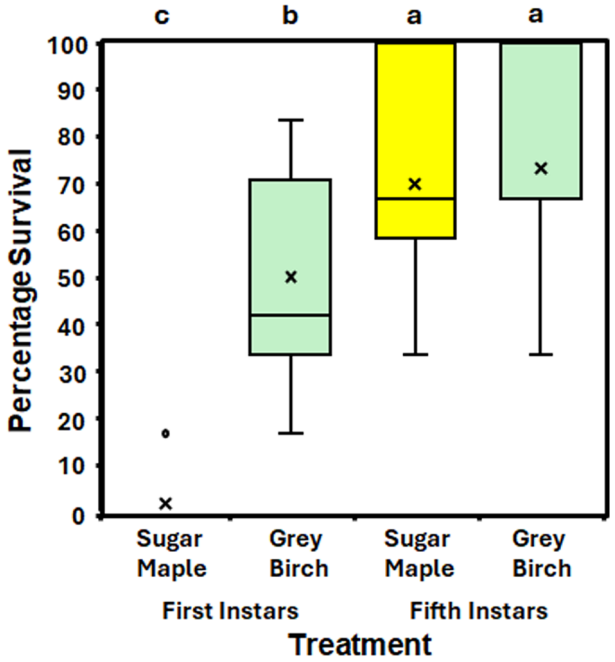

Fig. 2. Percentage survival of *Anoplophora glabripennis* larvae inserted into cut wood of gray birch and sugar maple. The x indicates the mean and the bar is the median. Different letters indicate that the means are significantly different (Instar × Tree Species interaction $F = 13.6$, df = 36, 1, $P = 0.0007$).

survived (63.3% survival), including 7 larvae that were damaged during bolt dissections. The percentage survival of fifth instars was statistically similar on the 2 hosts (Fig. 2).

There was no statistical difference in the setup weights of the first instars ($F = 13.6$; df 1, 36; $P = 0.7861$) or fifth instars ($F = 13.6$; df 1, 36; $P = 0.9619$) used in the study (Table 4). No final weights were obtained for the sugar maple first-instar group because the only surviving larva was damaged. For gray birch, the average final weight for larvae in the first-instar group was 98.0 ± 10 mg. Within this group, the final weights of the larvae differed significantly between the bolts in which they were reared ($F = 3.74$; df 9, 20; $P = 0.0068$) and their final instar ($F = 21.06$; df 2, 24; $P < 0.0001$) (Fig. 3). First instars reared in gray birch gained on average 32, 72, and 145 mg depending on if their final instar was second, third, or fourth, respectively (Fig. 3 and Table 4). Final fifth-instar weights did not differ significantly between tree species ($F = 0.01$; df 1, 15.91; $P = 0.9101$) (Fig. 4 and Table 4) but were on average 186 and 191 mg lower than the setup weights for the gray birch and sugar maple fifth instars, respectively. Only 4 larvae gained weight, 2 on each tree species. As the photos within Figure 4 indicate, the larvae deeply scored the sapwood as they tunneled under the bark.

Table 4. Comparison of initial larval mass, final head capsule width, and estimated instar for *Anoplophora glabripennis* inserted and reared in cut wood of 2 species

Tree species	Initial instar	Mean setup body mass ± SE in mg (*n*)	Live larvae after dissection	
			Mean head capsule width ± SE in mm (*n*)	Mean instar ± SE (*n*)
Gray Birch	First	5.8 ± 0.1 a (60)	2.35 ± 0.08 (31)	3.2 ± 0.1 (31)
Sugar maple	First	5.9 ± 0.1 a (60)	1.79 (1)	2 (1)
Gray Birch	Fifth	628 ± 33 a (30)	3.80 ± 0.07 a (17)	5.1 ± 0.1 a (18)
Sugar maple	Fifth	630 ± 32 a (30)	3.87 ± 0.07 a (18)	5.2 ± 0.1 a (20)

Means followed by the same letter within initial instar group are not significantly different, based on the least squares means separation test with $\alpha = 0.05$ and with a Bonferroni correction (SAS Institute, Inc. 1999). Some individuals were damaged during dissection or were pupae or adults so not all data was collected.

The final instars when first instars were inserted could not be compared between sugar maple and gray birch, but final instar did differ by gray birch bolt ($F = 2.64$; df 9, 21; $P = 0.0321$). By the end of the feeding period, 12.90% of larvae in gray birch were in the second instar, 54.84% were in the third instar, and 32.26% were in the fourth instar (Fig. 3). For fifth instars, host species did not have a statistically significant effect on final head capsule widths ($F = 0.57$; df 1, 18.79; $P = 0.4578$) (Table 4). Since head capsule widths vary by instar, host species also did not have a significant effect on final instar ($F = 0.3$; df 1, 16.13; $P = 0.5914$) (Table 4). When the fifth instars were inserted, they molted no more than once.

Table 5 provides data on the characteristics of the bolts used for first-instar rearing. The sugar maple bolts that were used were older and had higher dry weights, higher densities, and thicker bark than the gray birch bolts used. Also, they had a denser cell structure in the outer cm, which was where the larvae mainly fed.

Discussion

The moisture content of the larval diet did not affect larval survival or percentage pupation but did affect larval weight. Larvae reared on a diet with a higher moisture content

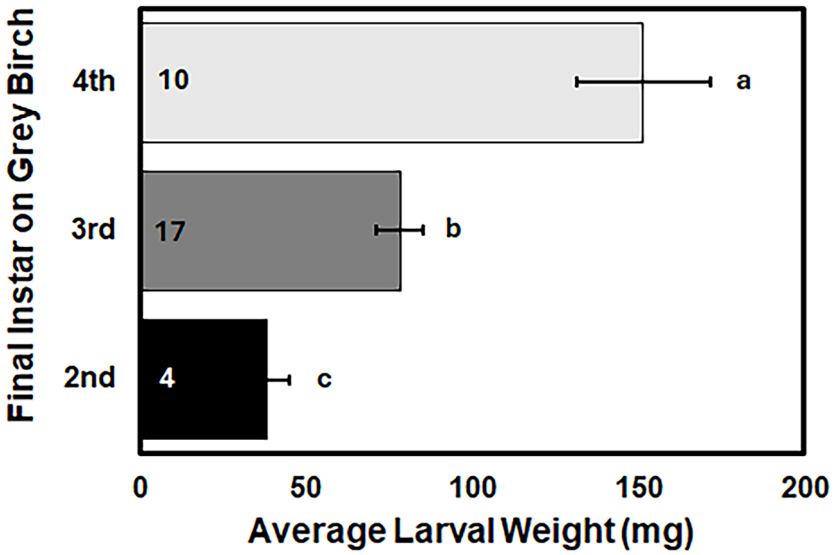

Fig. 3. Average final weights (±SE, g) of *Anoplophora glabripennis* larvae, by instar, inserted as first instars into bolts of cut gray birch. Different letters indicate that the means are significantly different ($F = 21.1$, df = 24, 2, $P < 0.0001$).

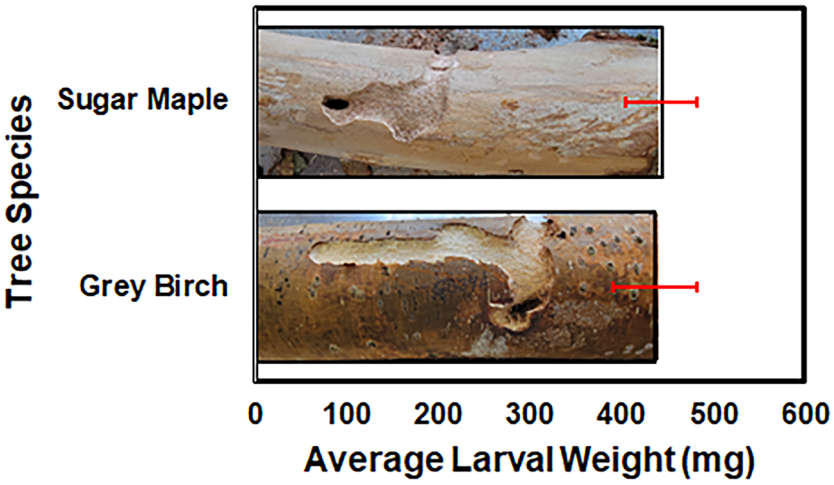

Fig. 4. Average final weights (±SE, cm^2) of *Anoplophora glabripennis* larvae inserted as fourth or fifth instars into cut bolts of 2 species of trees. The means were not significantly different ($F = 0.01$, df = 16, 1, $P = 0.9101$).

Table 5. Comparison of wood species bolt characteristics used for inserting first-instar *Anoplophora glabripennis* larvae

Tree species	Mean wood density ± SE in g/cm^3	Mean total growth rings ± SE	Mean growth rings in first cm beneath the bark ± SE	Mean bark thickness ± SE in mm
Gray Birch	0.54 ± 0.01 b	11.6 ± 1.2 b	5.7 ± 0.8 b	1.1 ± 0.1 b
Sugar maple	0.67 ± 0.01 a	20.3 ± 1.2 a	8 ± 0.8 a	1.9 ± 0.1 a
Statistics:	$F = 48.0$, df = 18, 1, $P < 0.0001$	$F = 24.8$, df = 18, 1, $P < 0.0001$	$F = 6.2$, df = 18, 1, $P = 0.0232$	$F = 35.5$, df =18, 1, $P < 0.0001$

Means followed by the same letter in a column are not significantly different, based on the least squares means separation test with $\alpha = 0.05$ and with a Bonferroni correction (SAS Institute, Inc. 1999).

weighed more at every time interval (4, 8, and 12 wk) and as adults than those reared on the dry diet. The host species of cut wood affected the survival of first instars but not fifth instars when they were inserted in cut bolts. When fifth instars were inserted, the tree species of the cut wood had no significant impact on the average final weights or final instars of larvae. First instars that survived when inserted into cut wood gained weight on average, while fifth instars on average lost weight.

Insects must obtain enough moisture either from their environment or the food they eat to prevent desiccation and loss of their stored water reserves, which are required for survival. Some larvae of *A. glabripennis* will die if they lose 26% of their bodily moisture by weight, and all will be dead at 40% moisture loss (Chen et al. 2008). Therefore, insects have ranges of permissible dietary moisture that they select for, and moisture contents above and below that have deleterious effects on both their survival and weight gain (Reese and Beck 1978). For

example, some cerambycids (eg *Phoracuntha semipunctata* F. and *Callidiellum rufipenne* Motschulsky) require stressed hosts for their survival and development, so the females selectively lay on hosts with particular bark moisture contents (Hanks et al. 1999, Ueda and Shibata 2007). The acceptable dietary moisture content that *A. glabripennis* requires remains to be determined; however, the wet and dry artificial diets evaluated in this study were apparently within the permissible range for the larvae since there was no statistically significant difference in survival between them. It is possible, though, that larvae in the dry diet were able to select the moistest part of the diet since the exterior of the chucks that were used were drier than the interior and the measured moisture content was an average. In addition, these results may not translate well to a natural setting since moisture in an artificial diet is suspended in an agar matrix instead of being either free between cells or bound in cell walls. Therefore, moisture may be more available in an artificial diet than it would be in wood.

Although there was no impact on larval survival between the 2 artificial diets, there was an apparent effect on larval weight gain. Larval weight gain in the first 4 wk was significantly slower on the dry diet than on the wet diet, and the larvae were never able to reach the same weights as those on the wet diet. Efficiency of conversion of nutrients in artificial diets has been shown to be negatively correlated with the percentage of dry matter by weight present in the diet, and the same studies show there is a concomitant decrease in diet consumption when diets contain more dry matter (less water by weight, Reese and Beck 1978). The decreased consumption and conversion of nutrients results in lower-weight individuals. Although we did not measure the dry matter in the 2 artificial diets, the dry matter in the dry diet had to be higher than in the wet diet since we started with 50% less water and then dried the diet further effectively increasing the dry matter to water ratio. The largest *P. semipunctata* adults emerge from wood with the most ideal moisture content when other factors that can affect cerambycid adult size (crowding, bolt size, host species, etc.) were kept constant (Hanks et al. 2005); similarly, the larger adults of *A. glabripennis* emerged from larvae grown on the wet diet. This suggests that the wet diet represented a higher quality food resource since the adults reared on the wet diet weighed more than those reared on the dry diet, which would confer higher fitness since larger *A. glabripennis* females live longer and can lay more eggs (Keena 2002). In addition, although the adults that emerged from the dry diet were smaller, they did not pupate sooner (within a sex) than those on the wet diet, and more did not pupate without a chill. Therefore, there was no indication that the less optimal moisture content led to quicker pupation to escape a poorer food resource.

In a larval food source that has declining moisture content, like the cut logs, desiccation is a major issue that insects must deal with. Insects' ability to resist desiccation is impacted by how much stored water they have, how fast they lose water, and what percentage of water loss is lethal (Hoffmann and Harshman 1999). Desiccation increases as the surface area to volume ratio increases, so smaller larvae would be more prone to water loss than larger larvae. Smaller larvae may also have lower water reserves. This may explain why the inserted first instars had lower survival rates than the fifth instars, but it does not explain the host differences in first instars survival. First instars likely also experience greater exposure to secondary compounds since they are concentrated in the cambial layer, so there could be host differences that affected larval survival. The fact that on average 70% of the fifth instars on both hosts survived, fed extensively (as evidenced by their tunneling), and even pupated in some cases suggests that both hosts were acceptable hosts of similar nutritional quality. The starting moisture content of the wood of the 2 species would likely have been lower in the gray birch ($62 \pm 1.1\%$ moisture on average in live wood, Tomczak et al. 2021) than in sugar maple (65% moisture on average in live heartwood and 72% on average in sap wood, Glass and Zelinka 2021). However, the water would be held differently in the 2 species because gray birch is a less dense wood than sugar maple. In dense wood, more water is bound in the densely packed cell structure than free between the cells. So, it may be less available to the insect once the free water, which is lost first, is gone. Lower-density trees also utilize higher concentrations of cations, like potassium, in their water storage, which could change how moisture is lost after trees are cut (Lira-Martins et al. 2022). There may have been differences in the rate at which the 2 tree species of cut wood dried as a result. The moisture content at the time of bolt cutting may also play a factor in larval survival, since more first instars inserted into gray birch in week 1 survived than those inserted in week 2. The bolts used in both weeks were about the same number of days post-cutting when used, but they were cut at different times. There was rain just before the first cut and not the second. However, neither of these factors seemed to have an impact on the survival of fifth instars, which were inserted into the cut wood.

The more densely packed annual rings of cells in the sugar maple compared to the gray birch would also have impacted the hardness (ability to be penetrated by a solid object) of the wood. As moisture content drops, the hardness of the wood increases, which can affect the ability of the larvae to utilize it (Green et al. 2004). Because smaller larvae have smaller mandibles and weaker muscles than larger larvae, the first instars inserted into the sugar maple bolts may not have been able to feed on the harder wood and would have faced both starvation and desiccation. Our findings are also in agreement with earlier findings that when *A. glabripennis* females were allowed to lay eggs under the bark of cut wood of 4 maple species (sugar, red, silver, and boxelder), the larvae that hatched survived longer and grew faster on the 2 softer, less dense maple species (boxelder and red maple) than on the harder, denser maple species (sugar and silver maple) (Keena et al. 2001). Cerambycids have been found to be more abundant in lower-density wood in dry tropical forests (Vargas-Cardoso et al. 2023), but there is no trend data for temperate forests. Wood density has also been shown to be the best predictive factor for where cerambycid larvae that utilize dead wood will be located (Saint-Germain et al. 2007).

The adults that emerged from the cut wood of both species were extremely small males that were estimated to have pupated in the fifth instar, which is the earliest it is estimated to occur. The timing of pupation is linked to larvae attaining a critical threshold weight necessary for pupation (Davidowitz and Nijhout 2004); in *A. glabripennis*, this is estimated to be 500 mg (Keena and Moore 2010). Almost all the fifth instars that were inserted into the wood were ≥500 mg in weight but none of the first instars that survived on gray birch had reached that weight when extracted from the bolts; the maximum weight of a few fourth instars was approximately400 mg. However, the adults that emerged from the cut wood were much lighter than they were when inserted as larvae, meaning they had lost considerable weight as most of the fifth instars had.

So, these larvae were unable to gain weight despite extensive feeding (they were not starving), which is in line with the lower weight gain expected when dealing with a drier diet. However, the larvae that survived after being inserted as first instars in gray birch seemed to be able to gain weight and develop. So, larvae that have been developing in a higher moisture diet may not do as well in a drier diet, especially if the moisture content drops quickly as it did in the cut bolts. Also, the larvae that pupated and emerge from cut infested wood from North American infestations in the laboratory are heavier and later instars since the adults weigh on average >800 mg (Keena 2002). This suggests that larvae that are larger than those we used may be better equipped to survive in cut wood as is evident from their repeated invasions into Europe and North America (Javal et al. 2019a, 2019b, Coyle et al. 2021). Still, care should be taken in extrapolating laboratory data to real-world conditions where temperature and humidity can vary greatly from what we used in our studies. Also, cerambycid time to pupation can be greatly prolonged in other species when larvae are growing in dry wood (Haack 2017), so a longer study comparing more species of cut wood should be done to assess the true ability of this species to survive to pupation under these conditions.

From a management perspective, the findings of these studies suggest first that *A. glabripennis* may not be able to complete development from first instar to adult in cut wood. On sugar maple, the first instars die quickly, but about 50% survive for about 8 wk on gray birch. In addition, if the gray birch did not have sufficient moisture present at the time of cutting, larval mortality would likely be higher, and larvae might not be able to gain enough weight to enter the sapwood and pupate, so even less dense wood may not remain a viable food resource long enough for larvae to reach pupation. Also, *A. glabripennis* larvae in wood when it is cut that are >500 mg (the minimum weight for pupation) can survive. Some percentage of larvae that have successfully entered the xylem with the minimum weight will likely survive to emerge as adults. Therefore, the timing of when wood is cut likely will influence the success of *A. glabripennis* in reaching pupation and subsequently emerging as adults. If infested trees need to be cut and then stored for long periods of time before chipping, cutting early in the summer when many *A. glabripennis* individuals are eggs or young larvae will reduce their chances of survival to adults.

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Author Contributions

Sabrina Osowiecki (Conceptualization [equal], Data curation [lead], Formal analysis [equal], Investigation [lead], Methodology [equal], Visualization [equal], Writing—original draft [lead], Writing—review & editing [supporting]) and Melody Keena (Conceptualization [equal], Formal analysis [equal], Funding acquisition [lead], Methodology [equal], Project administration [lead], Resources [lead], Supervision [lead], Visualization [equal], Writing—original draft [supporting], Writing—review & editing [lead])

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Conflicts of Interest

None declared.

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