

Performance and Host Association of Spotted Lanternfly (*Lycorma Delicatula*) among Common Woody Ornamentals

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1 **Performance and host association of spotted lanternfly (*Lycorma delicatula*) among common**
2 **woody ornamentals**

3

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15 **Running title:** Performance of spotted lanternfly among woody ornamentals

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18 interactions

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27 **Abstract**

28 Despite the broad host range of *Lycorma delicatula*, the performance of this invasive pest on
29 non-*Ailanthus* host plant species is difficult to document realistically without using field
30 conditions given this pest's requirements for vast amounts of phloem. In spring 2020, we
31 examined the performance of *L. delicatula* with and without access to *Ailanthus altissima* by
32 tracking development, survival, host tree association and oviposition in large enclosures planted
33 with one each of *Juglans nigra*, *Salix babylonica* and *Acer saccharinum* along with either one *A.*
34 *altissima* or one *Betula nigra*. We reared nymphs with and without access to *A. altissima*,
35 released them into the corresponding large enclosures as third instars, and monitored them from
36 early July 2020 through November 2020. Insect survival was higher and development faster with
37 access to *A. altissima*. Third and fourth instar nymphs were most frequently observed on *A.*
38 *altissima* when it was present, while adults were equally associated with *A. saccharinum* and *A.*
39 *altissima*. In the absence of *A. altissima*, nymphs were most frequently found on *S. babylonica*,
40 while adults were most often on *A. saccharinum*. Females with access to *A. altissima* deposited
41 nearly 7-fold more egg masses than those without access to *A. altissima*. In another experiment,
42 the offspring of parents that had been reared without access to *A. altissima* showed similar
43 survival and development time from egg to adult as offspring from parents that never had access
44 to *A. altissima*. These findings suggest that managers need to be aware that even in the absence
45 of *A. altissima* in the landscape, several hardwood host trees can be utilized by *L. delicatula* to
46 develop and reproduce.

47

48 **Keywords:** performance, preference, offspring, *Lycorma delicatula*, *Ailanthus altissima*, insect-
49 plant interaction

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52 **Introduction**

53 Since 2014, the spotted lanternfly (SLF), *Lycorma delicatula* (White) (Hemiptera: Fulgoridae),
54 an exotic planthopper, has invaded nine states in the Northeast, mid-West, and mid-Atlantic
55 regions of the U.S. Native to China, Taiwan and Vietnam, *L. delicatula* has also expanded its
56 range to include South Korea and Japan [1-4]. Following its initial detection in Berks County,
57 Pennsylvania (Barringer et al. 2015), *L. delicatula* has spread to New Jersey, New York,
58 Virginia, Maryland, Delaware, West Virginia, Connecticut, and Ohio [4-5]. The invasion success
59 of this pest may be partly due to its apparent capacity for dispersal [6-7] and its potential to
60 occupy a wide range of climatic conditions and ecosystems, especially disturbed habitats where
61 the preferred host *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae) (tree-of-heaven) is
62 abundant [3, 8, 9].

63

64 As a generalist phloem feeder, *L. delicatula* has proven to be a prominent pest in forest and
65 agricultural ecosystems and a nuisance pest in suburban landscapes, causing significant
66 economic losses to vineyards, nurseries, and sawmills in the invaded regions [4, 10]. For the
67 ornamentals and forest products industries, the major economic impacts are primarily due to the
68 cost of best management practices to comply with quarantine restrictions, and in some cases,
69 reduced sales [10-11]. *Lycorma delicatula* is projected to cause \$42.6 million in damages
70 annually if it spreads across Pennsylvania [11]. Although studies on the impacts of feeding by *L.*
71 *delicatula* on host plant health are in their infancy, phloem feeding by nymphs and adults is
72 known to cause physiological stress in young stems that may in turn cause infested branches to
73 wilt, lose vigor or die following heavy infestations [10, 12]. Feeding by *L. delicatula* results in

74 the production of copious amounts of honeydew, which promotes the growth of sooty mold on
75 plants below feeding sites, impeding photosynthesis of affected plants [13-16]. Damage caused
76 by *L. delicatula* decreases grapevine growth, reducing crop yield by up to 90% and sometimes
77 killing the vines (*Vitis* spp. L. [Vitales: Vitaceae]) [10, 12]. Additionally, *L. delicatula* poses a
78 threat to the growth of several hardwood trees, including silver maple (*Acer saccharinum* L.
79 [Sapindaceae]), red maple (*A. rubrum* L. [Sapindaceae]), black walnut (*Juglans nigra* L.
80 [Juglandaceae]), weeping willow (*Salix babylonica* L. [Salicaceae]), river birch (*Betula nigra* L.
81 [Betulaceae]) and tulip tree (*Liriodendron tulipifera* L. [Magnoliaceae]) [1, 2, 17-19].
82
83 *Lycorma delicatula* prefers *A. altissima* in both its native and invasive ranges, though it can
84 utilize over 103 plant species across 33 families [4, 17, 18]. In North America, feeding by *L.*
85 *delicatula* has been observed on 56 plant species, which include native, cultivated, and nonnative
86 species [18]. The rapid spread of this pest is likely facilitated by the prevalence of *A. altissima*, in
87 addition to other suitable host plant species [18]. Despite the broad host range of *L. delicatula*,
88 basic information is lacking on its host preferences and relative performance when feeding on
89 common woody ornamentals (but see [19-20]). Our previous study in 2019 [19] found that it can
90 complete development and reproduce on young weeping willow (*S. babylonica*), silver maple (*A.*
91 *saccharinum* L) and river birch (*B. nigra*) without access to *A. altissima*. Development to adult
92 was delayed by one week and the number of egg masses laid by females were significantly fewer
93 in enclosures with no access to *A. altissima*. It is, however, unclear whether *L. delicatula* without
94 access to *A. altissima* can perform as well as those with *A. altissima* if provided larger trees to
95 provide a greater quantity of phloem. Thus, in 2020, we investigated the performance and host
96 association of *L. delicatula* among planted common woody ornamentals that were larger in 2020

97 than in 2019. A further objective of this study was to determine whether offspring (F₁
98 generation) from parents that were reared from egg to adult without access to *A. altissima* suffer
99 any lingering fitness effects as they develop into adults.

100

101 **Materials and methods**

102 **Origin and maintenance of trees and insect cultures.**

103 In Macungie, Berks County, PA, we set up ten 5.76 m² plots in mid-September 2018; five plots
104 each were randomly allocated to two treatments: ‘with *Ailanthus*’ and ‘without *Ailanthus*’ [19].
105 All plots contained one *S. babylonica*, one *A. saccharinum*, and one *J. nigra* spaced 1 m apart; in
106 addition, the ‘with *Ailanthus*’ plots were also planted with one *A. altissima*, while the ‘without
107 *Ailanthus*’ plots contained one river birch (*B. nigra*) in place of *A. altissima*. We purchased the
108 *Salix babylonica* and *B. nigra* as 15-gallon potted trees at New Hanover Gardens
109 (Perkiomenville, PA), and *A. saccharinum* as 7-gallon and *J. nigra* as 2-gallon trees from
110 Octoraro Native Plant Nursery (Kirk, PA). Since *A. altissima* is a ubiquitous invasive plant,
111 small trees were dug up and transplanted from a local property with the owner’s permission. We
112 selected these species because they common in this region of the U.S. and are often used as hosts
113 trees by *L. delicatula* in Pennsylvania. *L. delicatula* were confined to each plot using a
114 rectangular screen enclosure made of PAK25 Anti-Insect Mesh (Hummert International, MO)
115 attached to a frame (3 × 2.4 × 2.4 m) made of galvanized steel tubes (38 mm diameter) at each
116 corner to prevent collapse during windy thunderstorm. To obtain access to each enclosure we
117 instaleed a 1.8 m zipper on one side. To prevent *L. delicatula* nymphs or adults from escaping
118 from the enclosures, sandbags (7.6 × 99 cm) were sewn into the bottom edge of the enclosure to

119 weigh down the sides. We installed drip irrigation connected to the well on the property. In the
120 early spring, trees were pruned to minimize crowding.

121

122 In January 2020, egg masses of *L. delicatula* were field collected in Allentown, PA and kept in
123 two pop-up cages (90 × 60 × 60 cm) under ambient environmental conditions in an unheated
124 greenhouse in Macungie, PA. In early May, egg masses were transferred to 20 pop-up cages (90
125 × 60 × 60 cm) containing potted host plants and housed under a canopy at the experimental site.
126 In this way, all plants received direct sunlight for part, but not all, of the day. These pop-up cages
127 were divided between two treatments: ‘with *Ailanthus*’ (10 cages) and ‘without *Ailanthus*’ (10
128 cages). Pop-up cages ‘with *Ailanthus*’ contained one potted ~60 cm tall *A. altissima* (planted
129 from field-collected seeds), one potted ~45 cm tall *V. vinifera* (cv. Cabernet-Franc; Hermann J.
130 Wiemer Vineyard, Dundee, NY), one potted ~45 cm tall strawberry and one potted ~45 cm tall
131 sunflower, while pop-up cages ‘without *Ailanthus*’ contained one potted ~45 cm tall *V. vinifera*,
132 strawberry and sunflower. Neonates in both treatments were reared to third instar until release
133 into each multi-tree enclosure.

134

135 **Experiment I: *Lycorma delicatula* survival, development and host plant associations.**

136 Between July 7 and July 10, 2020, 120 third instars were released into each multi-tree enclosure.
137 Enclosures ‘with *Ailanthus*’ received nymphs with prior access to *A. altissima* from the pop-up
138 cages with potted *A. altissima* (see details above) and vice versa [19]. Each week we monitored
139 plots for survival, life stage, and which host tree the insects were found on by counting the
140 numbers of nymphs (from July 15, 2020 to September 2, 2020) and adults (August 12, 2020 to
141 November 4, 2020) present on each host tree species and on other surfaces in each enclosure.

142 After reaching adulthood, we began monitoring and recording for oviposition weekly from
143 through November 4, 2020 when a hard freeze killed all remaining adults.

144

145 To determine how *L. delicatula* feeding affected tree growth, we measured trunk diameters at 10
146 cm above the soil line using a caliper on July 8, 2020 before releasing *L. delicatula* into the
147 enclosures and on November 3, 2020 at the end of the experiment. To document growth between
148 2019 and 2020, we compared trunk diameter of trees by species between 2019 and 2020 on June
149 4 and October 31. Trunk diameter measurements for *J. nigra* were not available because most of
150 these trees had died during the 2019 studies and were replaced in spring of 2020.

151

152 **Experiment II: Performance of *L. delicatula* offspring.**

153 To compare fitness of offspring from parents that did or did not have access to *A. altissima* trees
154 during development from egg to adult, we collected egg masses from the prior experiment (as
155 above) conducted in 2019 [19]. In early-June of 2020 these egg masses were carefully collected
156 from the trees in each multi-tree plot, placed in Petri dishes and held in pop-up cages (90 × 60 ×
157 60 cm) containing two potted *A. altissima* trees, with 4 replicates per treatment. The pop-up
158 cages were placed in open field conditions in the same location but were sheltered from direct
159 rainfall. Trees were watered thrice per week and replaced once per month with fresh potted *A.*
160 *altissima* trees. Weekly, we recorded survival and development of *L. delicatula* by counting the
161 numbers of nymphs and adults present in each cage.

162 **Statistical analysis.**

163 To evaluate the effect of the presence or absence of *A. altissima* on the survival of *L. delicatula*
164 in Experiments I and II, we fit a generalized linear mixed model with a binomial error

165 distribution and logit link function using the *glmmTMB* function [19] in R [21-22]. Our model
166 included treatment, date of observation, and the interaction between these two factors as
167 predictors, and cage as a random effect to account for repeated observations. Similarly, to assess
168 the effect of *A. altissima* presence on the timing at which individuals reached the fourth instar
169 and adulthood in Experiments I and II, we fit a GLM mixed effects model with a binomial error
170 distribution and a logit link function. We predicted the proportion of individuals in each cage that
171 had reached the fourth instar and adult stages based on the date, treatment (with or without *A.*
172 *altissima*) and interaction of these two factors. We again included cage as a random effect in the
173 model to account for repeated observations. We assessed the significance of the treatment by
174 conducting a likelihood ratio test to compare the full model against a reduced model, excluding
175 treatment as a predictor. Repeated measures GLM ANOVA was used to compare the host plant
176 association (i.e., the proportion of nymphs and adults of *L. delicatula* on a given tree species) of
177 *L. delicatula* in the presence or absence of *A. altissima* using SPSS version 20.0 (IBM, SPSS Inc.
178 Chicago, IL). If the overall model was significant, differences between trees was determined
179 using the Bonferroni *post hoc* test. The Mann Whitney U test was used to compare the number of
180 eggs masses between treatments using SPSS version 20.0. The impact of *L. delicatula* feeding on
181 trunk diameter and trunk diameter growth of tree species between 2019 and 2020 was evaluated
182 with a GLM ANOVA using SPSS version 20.0. If the overall model was significant, differences
183 between trees was determined using the Bonferroni *post hoc* test. *Juglans nigra* trees were not
184 included in the analysis because most died during the 2019 studies and had to be replaced in
185 spring of 2020.

186

187 **Results**

188 **Survival, development time, host association and egg mass count.**

189 Following release into multi-tree enclosures, the proportion of individuals of *L. delicatula* (from
190 third instar nymph to adult) that survived was approximately 10% higher in enclosures with *A.*
191 *altissima* compared to the non-*Ailanthus* enclosures throughout the season ($\chi^2 = 16.29$, $df = 1$, $P =$
192 0.001 ; Fig. 1). Third instar nymphs in *A. altissima* enclosures developed slightly faster to fourth
193 instar ($\chi^2 = 56.26$, $df = 1$, $P = 0.001$; Fig. 2); fitted logistic regression curves showed that 50% of
194 third instars with *Ailanthus* reached the fourth instar 2.1 days earlier than those without *Ailanthus*.
195 In cages containing *A. altissima* 50% of fourth instars reached adulthood 8.4 days earlier than those
196 in enclosures without *A. altissima* ($\chi^2 = 9.67$; $P = 0.001$; Fig. 3).

197

198 Host plant association of third and fourth instar nymphs as well as adults in *A. altissima*
199 enclosures were influenced by the available tree species but did not differ over time (Table 1;
200 Fig. 4a-c). In enclosures with *A. altissima*, third instars were most frequently observed on *A.*
201 *altissima* (Fig. 4a), while fourth instars were found with equal frequency on *A. altissima*, *S.*
202 *babylonica* and *A. saccharinum* (Fig. 4b). Adults were mostly observed on *A. saccharinum*
203 despite the presence of *A. altissima* (Fig. 4c). In enclosures without *A. altissima*, host plant
204 association of nymphs and adults differed as a function of tree species but did not differ over
205 time (Table 2; Fig. 5a-c). In enclosures without *A. altissima*, third instars were most frequently
206 observed on *S. babylonica* (Fig. 5a), while fourth instars were found with equal frequency on *S.*
207 *babylonica* and *B. nigra* (Fig. 5b). Again, adults were most commonly associated with *A.*
208 *saccharinum* (Fig. 5c).

209

210 **Table 1.** Repeated measures binomial GLM ANOVA for data on the effect of tree species and
 211 time on the proportion of *Lycorma delicatula* nymphs and adults present on individual trees in
 212 cages where they had access to *Ailanthus altissima*.

Variable	Source of variation	df	MS	F-value	P-value
Third instars	Tree species	3	3495	11.20	0.001
	Time	16	0.023	0.001	0.999
	Tree species × Time	9	388.3	1.24	0.301
	Error	59			
Fourth instars	Tree species	4	5218	20.68	0.001
	Time	5	0.067	0.011	0.967
	Tree species × Time	20	414.2	1.84	0.061
	Error	100			
Adults	Tree species	3	14347	13.45	0.001
	Time	11	1.03	0.009	0.991
	Tree species × Time	33	358.9	2.98	0.063
	Error	176			

213 df: degrees of freedom; MS: mean squares.
 214 Statistically significant values are indicated in bold.

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232 **Table 2.** Repeated measures binomial GLM ANOVA for analysis of data on the effect of tree
 233 species and time on the proportion of *Lycorma delicatula* nymphs and adults present on
 234 individual trees in cages without *Ailanthus altissima*.

Variable	Source of variation	df	MS	F-value	P-value
Third instars	Tree species	3	1241	10.42	0.001
	Time	3	0.09	0.05	0.970
	Tree species × Time	9	292.3	2.45	0.057

	Error	59			
Fourth instars	Tree species	4	4071	8.22	0.001
	Time	5	0.021	0.001	0.999
	Tree species × Time	20	342.5	1.42	0.129
	Error	100			
Adults	Tree species	3	14352	13.05	0.001
	Time	11	0.32	0.003	0.993
	Tree species × Time	33	3231	2.11	0.071
	Error	176			

235 DF: degrees of freedom; MS: mean squares.

236 Statistically significant values are indicated in bold.

237

238

239 The number of egg masses laid by females was 6.8-fold higher in enclosures with *A. altissima*
240 ('with *Ailanthus*': 19.20 ± 2.13 (mean \pm SE) than 'without *Ailanthus*' 2.80 ± 0.42 ; $U = 20.0$, $P =$
241 0.040). Egg masses were first observed on September 30, 2020 in the presence of *A. altissima*
242 and oviposition continued until November 4 when field temperature dropped below 0 °C, killing
243 the remaining adults in both treatments. Of these egg masses, 23 were laid on *A. altissima*, 21 on
244 *A. saccharinum*, 30 on *S. babylonica*, 1 on *J. nigra*, and 14 and 7 on wooden planks and red
245 maple logs placed in the enclosures, respectively. Oviposition occurred in all five of these
246 enclosures for a total of 96 egg masses. In enclosures without *A. altissima*, 14 egg masses were
247 recorded, with at least one egg mass in each of the 5 enclosures. Oviposition in these cages
248 occurred between October 14 and November 4, 2020. Of these 14 egg masses, one was on *B.*
249 *nigra*, 2 on *S. babylonica*, 6 on *A. saccharinum*, 2 on planks and 3 on red maple logs.

250

251 **Impact of *Lycorma delicatula* feeding on tree species.**

252 For both treatments, trunk diameter differed significantly by year ('with *Ailanthus*': $F_{1,29}=79.27$;
253 $P = 0.0001$; 'without *Ailanthus*': $F_{1,29}=40.84$; $P = 0.0001$) and tree species ('with *Ailanthus*':
254 $F_{2,29}=45.47$; $P = 0.0001$; 'without *Ailanthus*': $F_{2,29}=101.87$; $P = 0.0001$). There were no

255 significant tree species \times year interactions ('with *Ailanthus*': $F_{2,29}=1.15$; $P = 0.334$; 'without
256 *Ailanthus*': $F_{2,29}=2.25$; $P = 0.070$). Trees used in 2020 were on average $26.0\pm 2.3\%$ larger than
257 the same trees were in 2019 (Fig. 6a and b). Trunk diameter increase differed significantly by
258 year ('with *Ailanthus*': $F_{1,29}=14.47$; $P = 0.0001$; 'without *Ailanthus*': $F_{1,29}=13.25$; $P = 0.0001$)
259 but not by tree species ('with *Ailanthus*': $F_{2,29}=1.51$; $P = 0.252$; 'without *Ailanthus*': $F_{2,29}=0.10$;
260 $P = 0.903$). There were no significant tree species \times year interactions ('with *Ailanthus*':
261 $F_{2,29}=0.11$; $P = 0.899$; 'without *Ailanthus*': $F_{2,29}=3.10$; $P = 0.057$). Trees in both treatments and
262 of every species except river birch grew ≥ 2 -times more in diameter in 2019 on average than the
263 same trees grew in 2020; river birch grew 1.2-times more in 2019 than in 2020 (Figs. 7a and b).
264

265 **Offspring performance.**

266 After being released in popup cages with access to healthy *A. altissima*, the proportion of
267 hatched offspring from eggs laid the previous fall did not differ as a function of parental diet (χ^2
268 $= 0.70$, $df = 1$, $P = 0.401$). Development time (hatch to adults) also did not differ between
269 offspring from parents with or without access to *A. altissima* ($\chi^2 = 0.13$, $df = 1$, $P = 0.722$).
270

271 **Discussion**

272 *Lycorma delicatula* can complete development and reproduce without access to *A. altissima*,
273 confirming our findings from the previous year [19], and providing additional insight into host
274 association and the impact of *L. delicatula* on diameter growth of common woody ornamental
275 trees in response to feeding pressure from *L. delicatula*. Fitness of the insect was greater in the
276 presence of *A. altissima*. Survival was higher, development time was faster, and the number of
277 egg masses was 6.8-fold higher than for insects that lacked access to *A. altissima*. This study

278 also showed that offspring from parents that had been reared without access to *A. altissima* did
279 not suffer fitness effects into the next generation. We hypothesize that reduced egg mass
280 production in cages without *Ailanthus* was caused by slower development resulting in a shorter
281 time span between adult emergence and freezing-induced mortality during which adults can mate
282 and lay eggs. However, in southern climates where freezing temperatures appear several months
283 later in the year or not at all, lack of access to *A. altissima* may have less impact on fitness since
284 there could be time for slower developing adults to continue oviposition into the early winter.

285

286 In this study, survival to adult was high for both treatments (with and without *Ailanthus*),
287 although survival was slightly higher (10% difference) in the presence of *A. altissima*. By early
288 September 2020, approximately 63% of the individuals released in *A. altissima* enclosures and
289 non-*Ailanthus* enclosures were still alive. This is in contrast to our 2019 study where survival on
290 younger, smaller trees was less than 20% for both treatments (with and without *Ailanthus*) by
291 September 2 when most lanternflies were adults [19]; however, the previous study started with
292 the release of newly hatched first instars. Lower survival in 2019 could have been due to early
293 mortality of first and second instar nymphs and/or having access to smaller trees in 2019 than in
294 2020 in that larger and vigorous trees may provide a greater volume of phloem and nutrients over
295 time.

296

297 The faster development time of *L. delicatula* in enclosures with *A. altissima* suggests that adults
298 could reach sexual maturity faster in areas where *A. altissima* is abundant. Development time
299 remains one of the most crucial fitness indicators of host plant nutritional quality and can
300 influence insect survival, behavior and physiology [23]. For example, several studies have found

301 that slow development in phytophagous insects can cause high mortality of immature stages in
302 the field by exposing them to unfavorable environmental conditions for a longer time period [24-
303 25]. A key fitness cost caused by prolonged development in *L. delicatula* was narrowing of the
304 reproductive window for adults, which was reflected in markedly fewer eggs being laid before
305 freezing temperatures killed the remaining adults [19].

306

307 Third and fourth instar nymphs were mostly associated with *A. altissima* when it was present,
308 however, more adults were found on *A. saccharinum* than on *A. altissima* when both tree species
309 were present. This may occur when the pest has exhausted the ability of *A. altissima* to provide
310 sufficient sap flow, which also coincides with the onset of senescence of this tree species in mid-
311 September. In the absence of *A. altissima*, *B. nigra*, *A. saccharinum*, *J. nigra* and *S. babylonica*
312 together appeared to provide sufficient nutrition for growth and reproduction, but sap flow may
313 be lower in these species, which could explain the delayed development time in the absence of *A.*
314 *altissima*. However, we cannot rule out that if given access to mature and vigorous suitable hosts
315 such as *A. saccharinum* or *A. rubrum*, sexual maturity could have occurred at the same rate as
316 those with access to *A. altissima*. These two maple species are heavily utilized by *L. delicatula*
317 adults in the field in the fall (D.D. Calvin et al. unpublished data). Although the trees in our study
318 were significantly larger than they were the previous year, they were still smaller than trees that
319 are selected by wild populations of *L. delicatula* adults in the field where profuse feeding is
320 associated with reproductive maturation (pers. observations).

321

322 Several factors ranging from sap flux to host-tree bark characteristics and the presence or
323 absence of defensive chemicals may influence feeding preference in *L. delicatula* [26-27]. For

324 example, *L. delicatula* has been reported to survive longer on, and prefer, host trees with a high
325 concentration of sugars similar to those produced by *A. altissima* and *V. vinifera* [28]. In prior
326 work by Lee and colleagues [19], the authors reasoned that the improved performance on and
327 preference for *A. altissima* and *V. vinifera* is related to high concentrations of sucrose and
328 glucose in *A. altissima* phloem, and high proportions of sucrose and fructose in *V. vinifera*
329 phloem. Several authors have also noted that *L. delicatula* seems to prefer hosts with trunks and
330 branches that do not have thick bark but have high sap turgor pressure, allowing for ingestion of
331 phloem at a greater rate [17, 18, 20]. The trees used in our study were chosen because they are
332 frequently infested in the field and do not have the thick bark that occurs on oak trees, for
333 example, which are infrequent hosts [29].

334

335 Although egg masses were laid on all host trees as well as planks and logs, *S. babylonica*, *A.*
336 *saccharinum*, and *A. altissima* were generally preferred for oviposition. Oviposition substrate
337 selection can be vital to the reproductive success of insect herbivores. The preference-
338 performance hypothesis (a.k.a. mother knows best hypothesis) predicts correlation between
339 oviposition preference by the female parent and host suitability for offspring development [30-
340 31]. However, it does not translate well to species like *L. delicatula* with immature stages that
341 are highly mobile or instances where the adults and immature life stages feed on different hosts
342 [32]. Although tree species and branch structure may play a role in the selection of sites for
343 oviposition [17], why *L. delicatula* oviposits on non-living materials remains to be explained.
344 The basis for oviposition preferences is not always easy to empirically verify [31]. Some *L.*
345 *delicatula* researchers think that females lay most of their eggs in the vicinity of where they fed
346 to fatten up and become reproductively mature because it's harder for them to fly once they've

347 gained so much weight [33]. Alternatively, as is evident in some insects and mite species [31,
348 34], *L. delicatula* may be following a strategy where females do not necessarily oviposit on
349 suitable hosts in order to make it harder for predators to find their eggs and early instars.

350

351 The ability of *L. delicatula* to survive, develop and produce egg masses with or without *A.*
352 *altissima* may be due to the presence of multiple, suitable host plant species in the enclosures. It
353 is not uncommon for generalist feeders to require diet mixing to acquire the necessary nutrients
354 for development and reproduction [35-36], and *L. delicatula* appears to demonstrate better fitness
355 when provided multiple suitable host plants. While they can be reared from nymphs to adults on
356 a single species such as *V. vinifera* or *A. altissima*, without diet mixing, adults may not produce
357 eggs. For example, *L. delicatula* that were reared exclusively on *A. altissima* or *V. vinifera* failed
358 to produce egg masses, whereas their counterparts that received a combination of both did (Tracy
359 Leskey, USDA/ARS, personal communication).

360

361 The fact that trunk diameter growth of trees was significantly greater (by 3 mm) in 2019
362 compared to 2020 suggests that exposure of host trees to *L. delicatula* feeding pressure for two
363 seasons in a row may have limited the growth of these trees, although abiotic factors such as
364 climate could play a role. Our results also suggest that economically important ornamentals trees
365 and other indigenous host tree species may be significantly impacted when exposed to feeding
366 pressure for more than one season. Feeding by nymphs and adults of *L. delicatula* can reduce
367 photosynthesis and carbon storage (Lavelly et al. unpublished data; Centinari et al. unpublished
368 data), potentially causing stunted growth and/or mortality of host plants [37-38]. Although
369 feeding by *L. delicatula* can result in oozing trunk wounds, wilting, branch death, and sooty

370 mold [15], the extent of damage and effects of herbivory on woody ornamental trees in North
371 America are only beginning to be investigated. Our results on the impact of *L. delicatula* feeding
372 should be considered preliminary and need to be interpreted with caution as our study lacked the
373 adequate control (trunk diameter growth) data to make a definitive statement on the impact of *L.*
374 *delicatula* feeding on host tree species.

375

376 Although *L. delicatula* developed more slowly without access to *A. altissima*, the offspring from
377 eggs produced by these adults did not suffer ongoing fitness effects, which could have
378 implications for the spread of this pest in the United States. While range expansion of *L.*
379 *delicatula* is likely facilitated by the prevalence of *A. altissima*, it is clear that other hardwood
380 tree species can serve as suitable hosts to support development and reproduction. It's possible
381 that in a warmer southern climate, adults that develop more slowly in a region without *A.*
382 *altissima* may have time to catch up and lay as many egg masses as they would have if there was
383 access to *A. altissima*. Overall, our findings suggest that managers need to be aware that even in
384 the absence of *A. altissima* in the landscape, several hardwood host trees can be utilized by *L.*
385 *delicatula* to develop and reproduce.

386

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397

398 **Competing interests**

399 The author declares no competing interests.

400

401 **Data Availability Statement**

402 All relevant data are within the paper

403

404 **Author contributions**

405 KH and OU conceptualized and designed the study; OU performed the field experiments; OU
406 and JK performed the statistical analysis; OU wrote the manuscript; KH and JK critically
407 reviewed and amended the manuscript.

408

409 **IUCN Policy Statement**

410 Collection of plant material was done in compliance with relevant institutional, national,
411 and international guidelines and legislation.

412

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546 **Figure legends**

547 **Figure 1.** Proportion of *Lycorma delicatula* (nymphs and adults combined) that survived in
548 enclosures with planted *Ailanthus altissima*, *Acer saccharinum*, *Juglans nigra* and *Salix*
549 *babylonica* ('*Ailanthus*,' $n = 5$ enclosures) or enclosures with the same tree species except for the
550 presence of *Betula nigra* in place of *A. altissima* ('without *Ailanthus*,' $n = 5$ enclosures) from
551 July 15 to November 4, 2020. Fitted binomial regression lines are shown, with shaded areas
552 indicating 95% confidence intervals for predicted regression means. In total, 120 third-instar
553 nymphs were released in each enclosure and their numbers and host tree associations were
554 recorded weekly.

555

556 **Figure 2.** Proportion of *L. delicatula* that developed from the third to the fourth instar over time,
557 with fitted logistic regression lines, in enclosures with and without *Ailanthus altissima*.

558

559 **Figure 3.** Proportion of *L. delicatula* that emerged as adults over time, with fitted logistic
560 regression lines, for enclosures with and without *Ailanthus altissima*.

561

562 **Figure 4.** Mean (\pm SE) proportion of *Lycorma delicatula* third instars (A) fourth instars (B) and
563 adults (C) present on each tree species in enclosures with *Ailanthus* (*Ailanthus altissima*), silver
564 maple (*Acer saccharinum*), black walnut (*Juglans nigra*) and willow (*Salix babylonica*) ($n = 5$
565 enclosures) from July 15 to November 4, 2020. Nymphs and adults found on annual plants (2%)
566 within the enclosure or on enclosure walls (98%) are included as ‘Others.’ Means within a
567 column followed by different letters are significantly different (Bonferroni post hoc test: $P <$
568 0.05). No adults were found on black walnut and no third instar nymphs were found on other
569 surfaces.

570

571 **Figure 5.** Mean (\pm SE) proportion of *Lycorma delicatula* third instars (A), fourth instars (B) and
572 adults (C) present on each tree species in enclosures with silver maple (*Acer saccharinum*), black
573 walnut (*Juglans nigra*), willow (*Salix babylonica*) and river birch (*Betula nigra*) (without
574 *Ailanthus altissima*, $n = 5$ enclosures) from July 15 to November 4, 2020. Nymphs and adults
575 found on other plants (2%) within the enclosure or on enclosure walls (98%) are included as
576 ‘Others.’ Means within a column followed by different letters are significantly different
577 (Bonferroni post hoc test: $P < 0.05$). No adults were found on black walnut and no third instar
578 nymphs were found on other surfaces.

579

580 **Figure 6.** Mean (\pm SE) trunk diameter (mm) of tree species in enclosures with *Ailanthus* (A) and
581 without *Ailanthus* (B) ($n = 5$ enclosures) in 2019 and 2020. Measurements were made on
582 October 31, 2019 and November 3, 2020. Means within a column followed by different letters
583 are significantly different (Bonferroni post hoc test: $P < 0.05$). Black walnut trees were not
584 included in the analysis because most died during the 2019 studies and had to be replaced in
585 spring of 2020.

586

587 **Figure 7.** Mean (\pm SE) increase in trunk diameter (mm) of tree species in enclosures with
588 *Ailanthus* (A) and without *Ailanthus* (B) ($n = 5$ enclosures) in 2019 and 2020. Measurements
589 were made on June 4 and October 31, 2019, and July 8 and November 3, 2020. Increase in trunk
590 diameter was obtained by subtracting trunk diameter data collected at the start of the experiment
591 from those collected at the end of the experiment. Diameter increase did not differ ($P > 0.05$)
592 between species in 2019 and 2020 but differed ($P < 0.05$) between 2019 and 2020 in both sets of
593 cages (in ‘with *Ailanthus* cages’: $F_{1,29}=14.47$; $P = 0.0001$; in ‘without *Ailanthus*’ cages:
594 $F_{1,29}=13.25$; $P = 0.0001$). Means within a column followed by asterisks are significantly different
595 (Bonferroni post hoc test: $P < 0.05$). Black walnut trees were not included in the analysis because
596 most died during the 2019 studies and had to be replaced in spring of 2020.

Figures

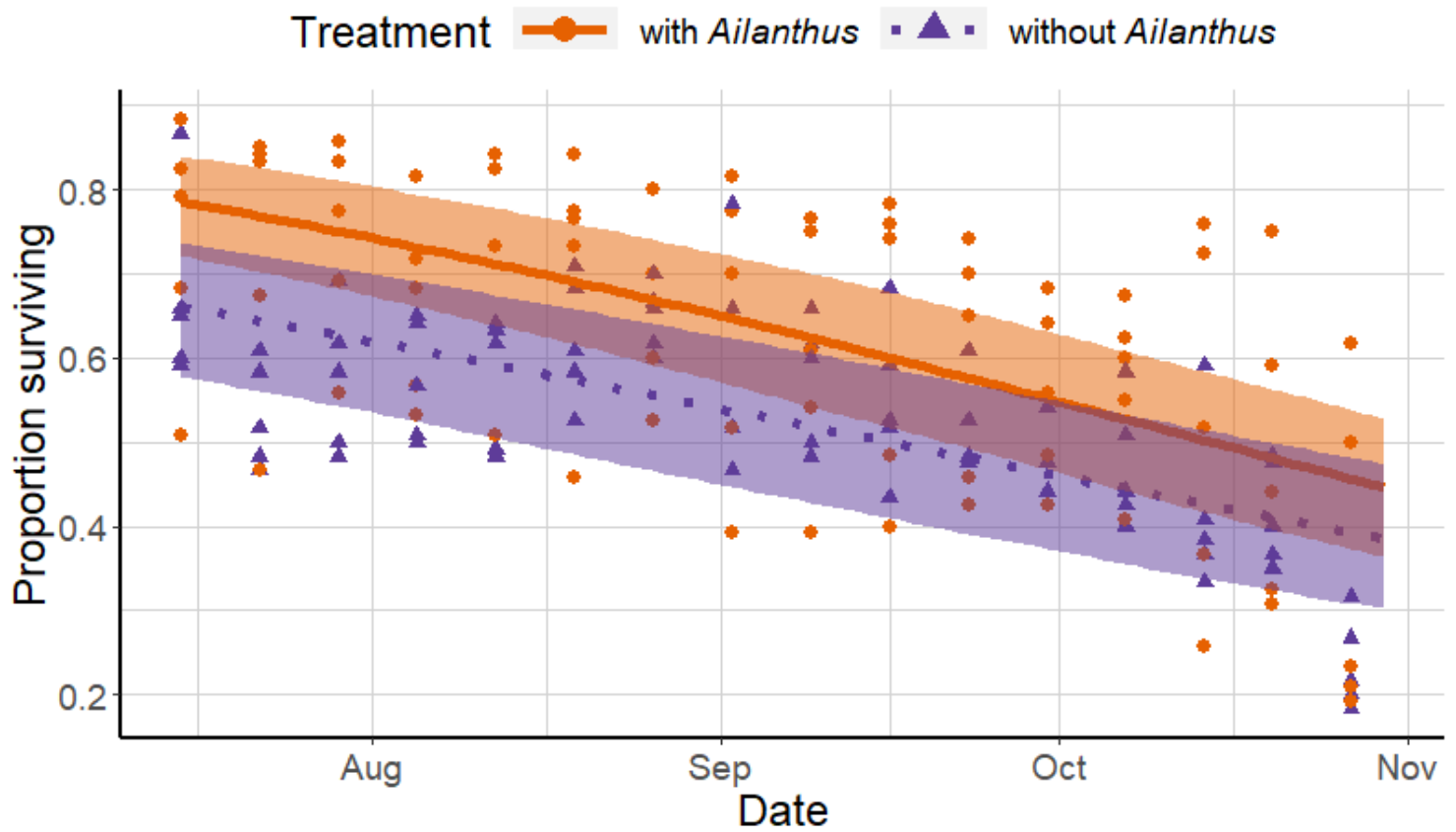


Figure 1

Proportion of *Lycorma delicatula* (nymphs and adults combined) that survived in enclosures with planted *Ailanthus altissima*, *Acer saccharinum*, *Juglans nigra* and *Salix babylonica* ('Ailanthus,' n = 5 enclosures) or enclosures with the same tree species except for the presence of *Betula nigra* in place of *A. altissima* ('without Ailanthus,' n = 5 enclosures) from July 15 to November 4, 2020. Fitted binomial regression lines are shown, with shaded areas indicating 95% confidence intervals for predicted regression means. In total, 120 third-insta nymphs were released in each enclosure and their numbers and host tree associations were recorded weekly.

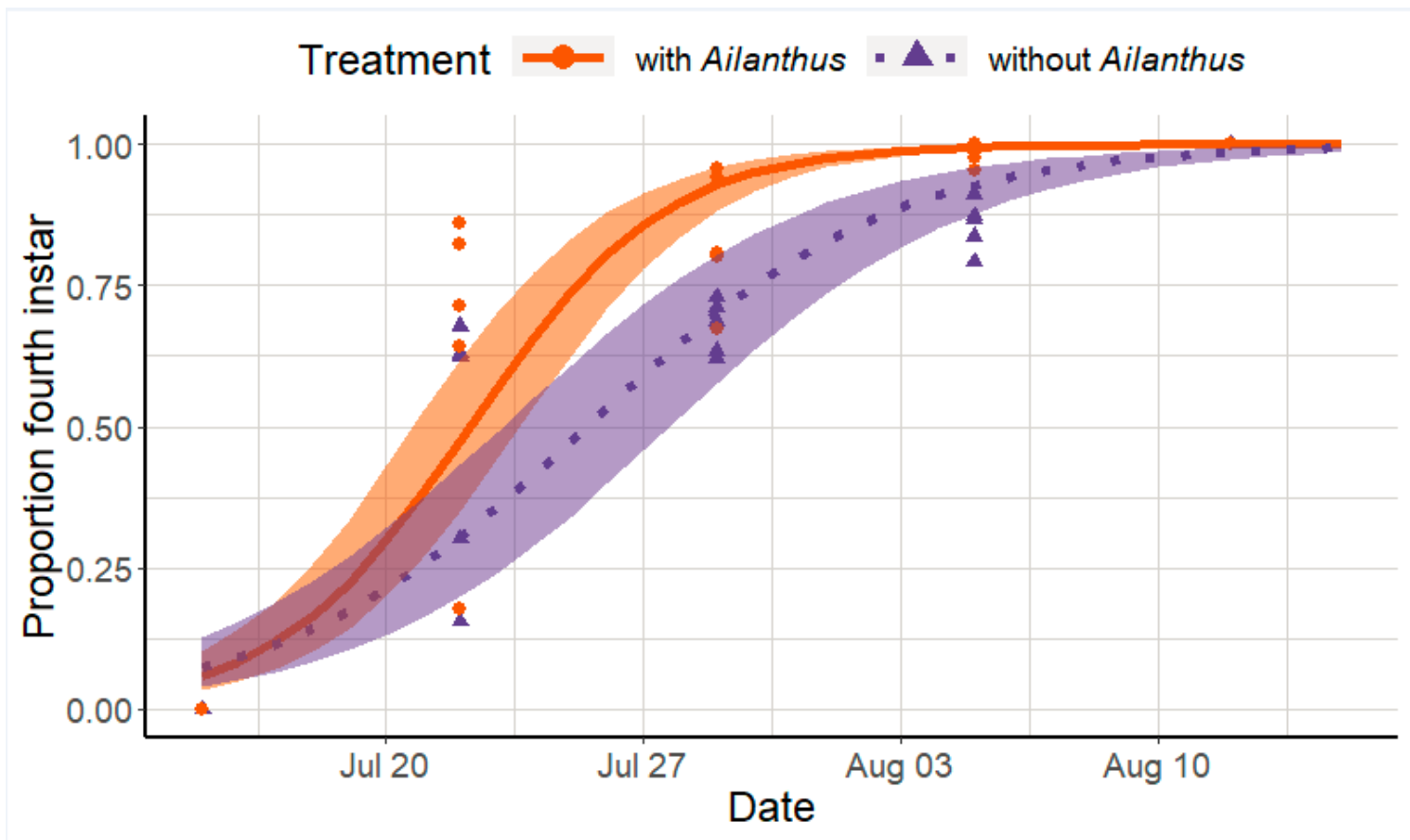


Figure 2

Proportion of *L. delicatula* that developed from the third to the fourth instar over time, with fitted logistic regression lines, in enclosures with and without *Ailanthus altissima*.

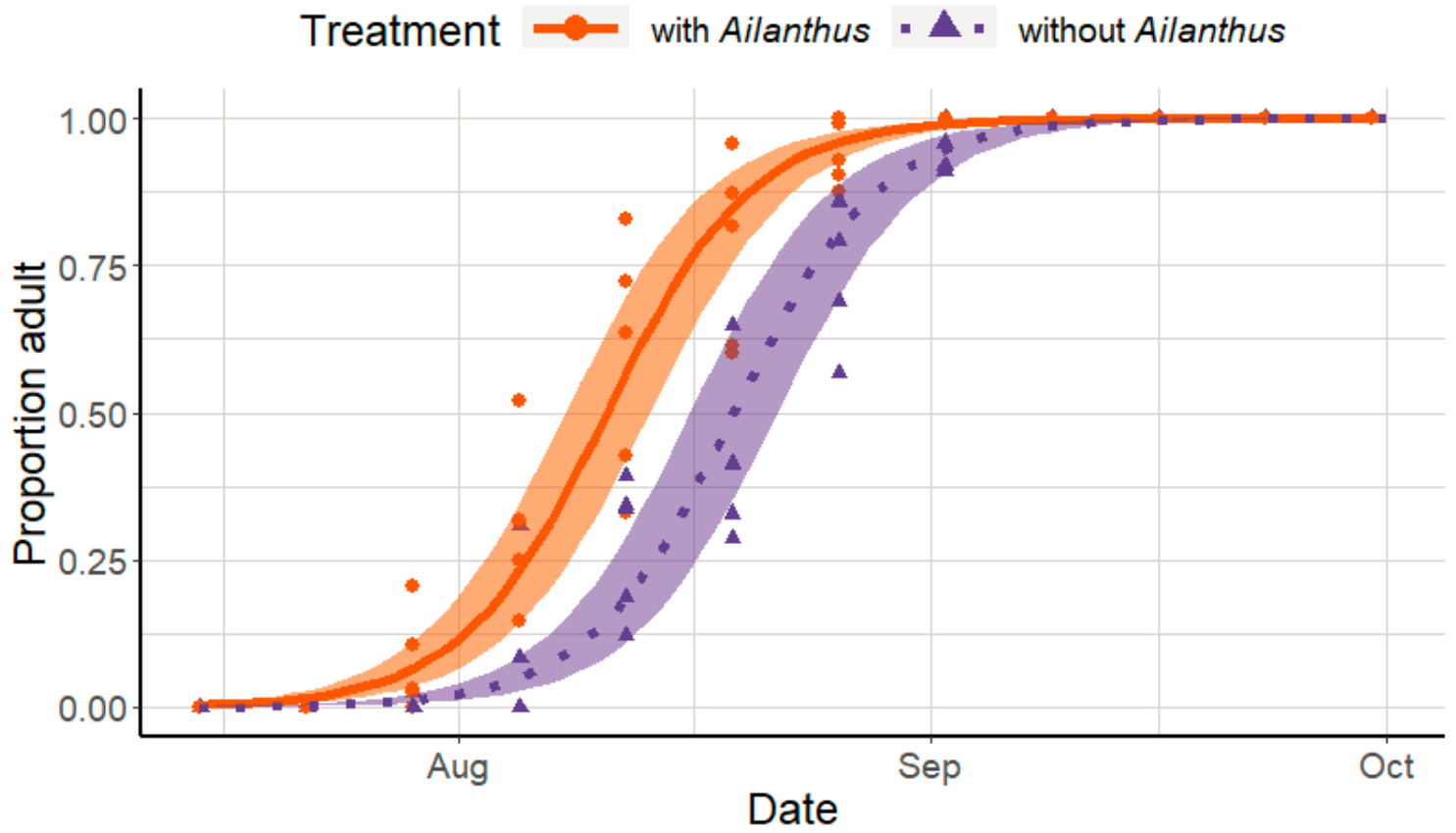


Figure 3

Proportion of *L. delicatula* that emerged as adults over time, with fitted logistic regression lines, for enclosures with and without *Ailanthus altissima*.

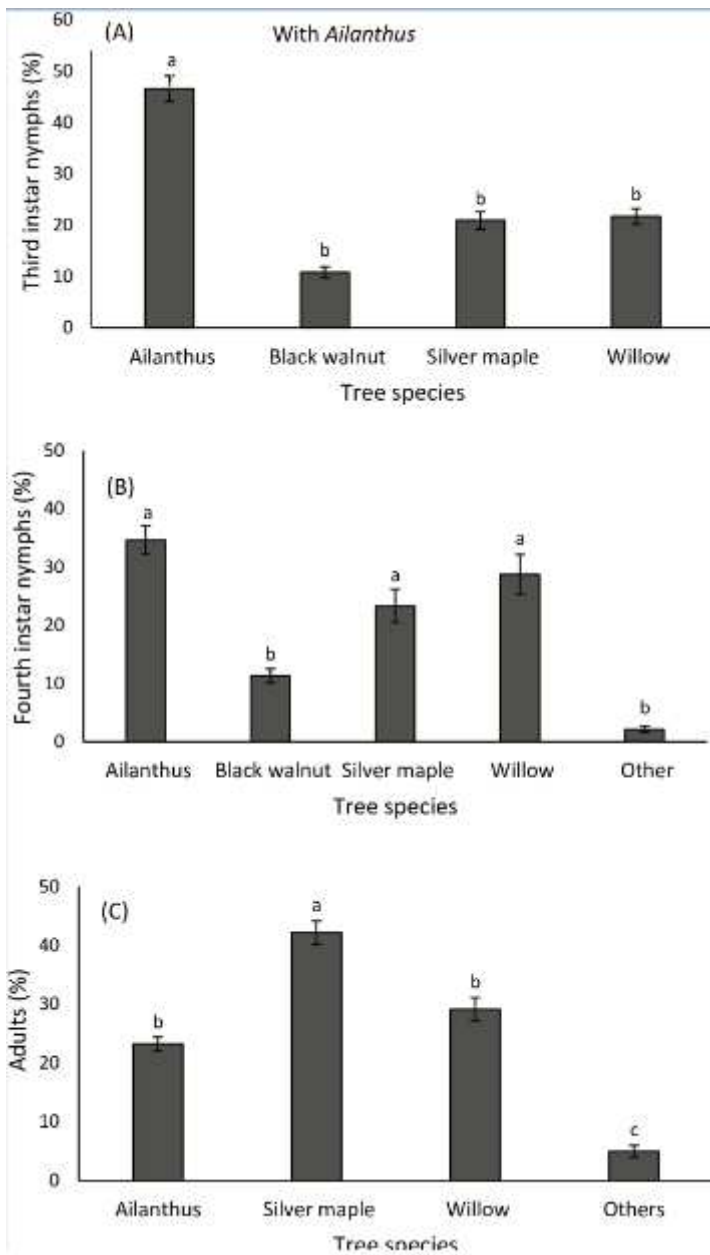


Figure 4

Mean (\pm SE) proportion of *Lycorma delicatula* third instars (A) fourth instars (B) and adults (C) present on each tree species in enclosures with *Ailanthus* (*Ailanthus altissima*), silver maple (*Acer saccharinum*), black walnut (*Juglans nigra*) and willow (*Salix babylonica*) ($n = 5$ enclosures) from July 15 to November 4, 2020. Nymphs and adults found on annual plants (2%) within the enclosure or on enclosure walls (98%) are included as 'Others.' Means within a column followed by different letters are significantly different (Bonferroni post hoc test: $P < 0.05$). No adults were found on black walnut and no third instar nymphs were found on other surfaces.

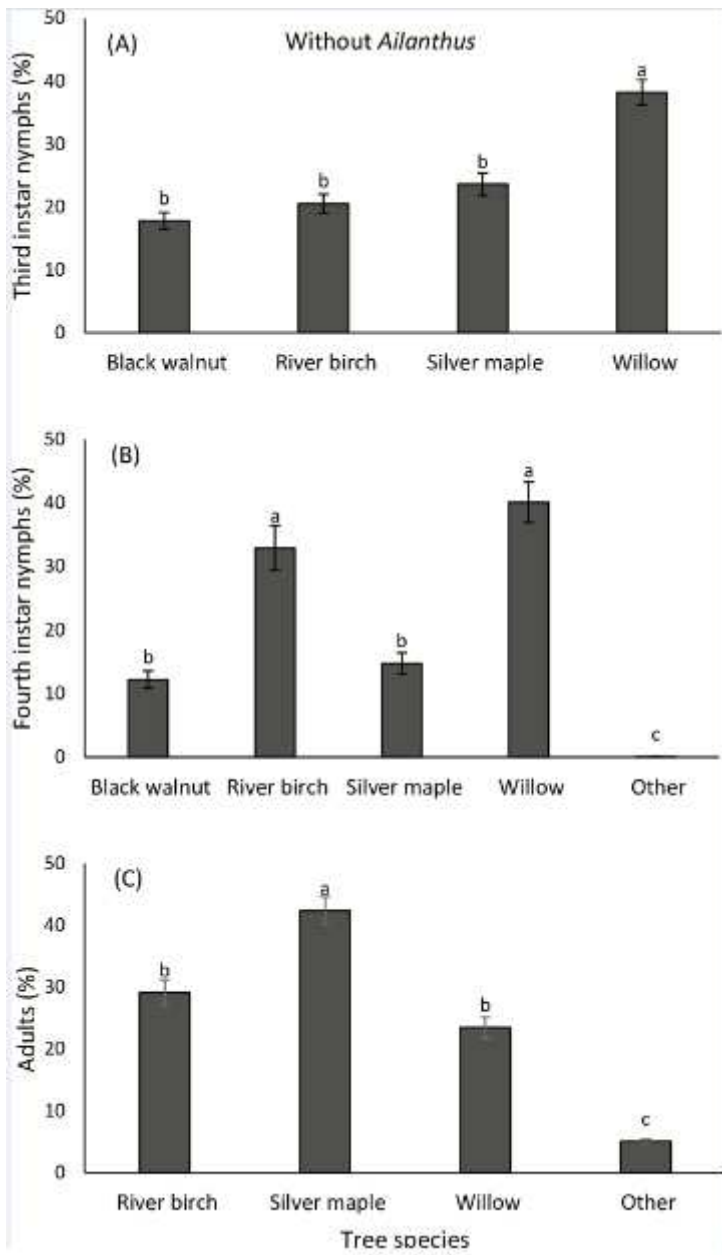


Figure 5

Mean (\pm SE) proportion of *Lycorma delicatula* third instars (A), fourth instars (B) and adults (C) present on each tree species in enclosures with silver maple (*Acer saccharinum*), black walnut (*Juglans nigra*), willow (*Salix babylonica*) and river birch (*Betula nigra*) (without *Ailanthus altissima*, $n = 5$ enclosures) from July 15 to November 4, 2020. Nymphs and adults found on other plants (2%) within the enclosure or on enclosure walls (98%) are included as 'Others.' Means within a column followed by different letters are significantly different (Bonferroni post hoc test: $P < 0.05$). No adults were found on black walnut and no third instar nymphs were found on other surfaces.

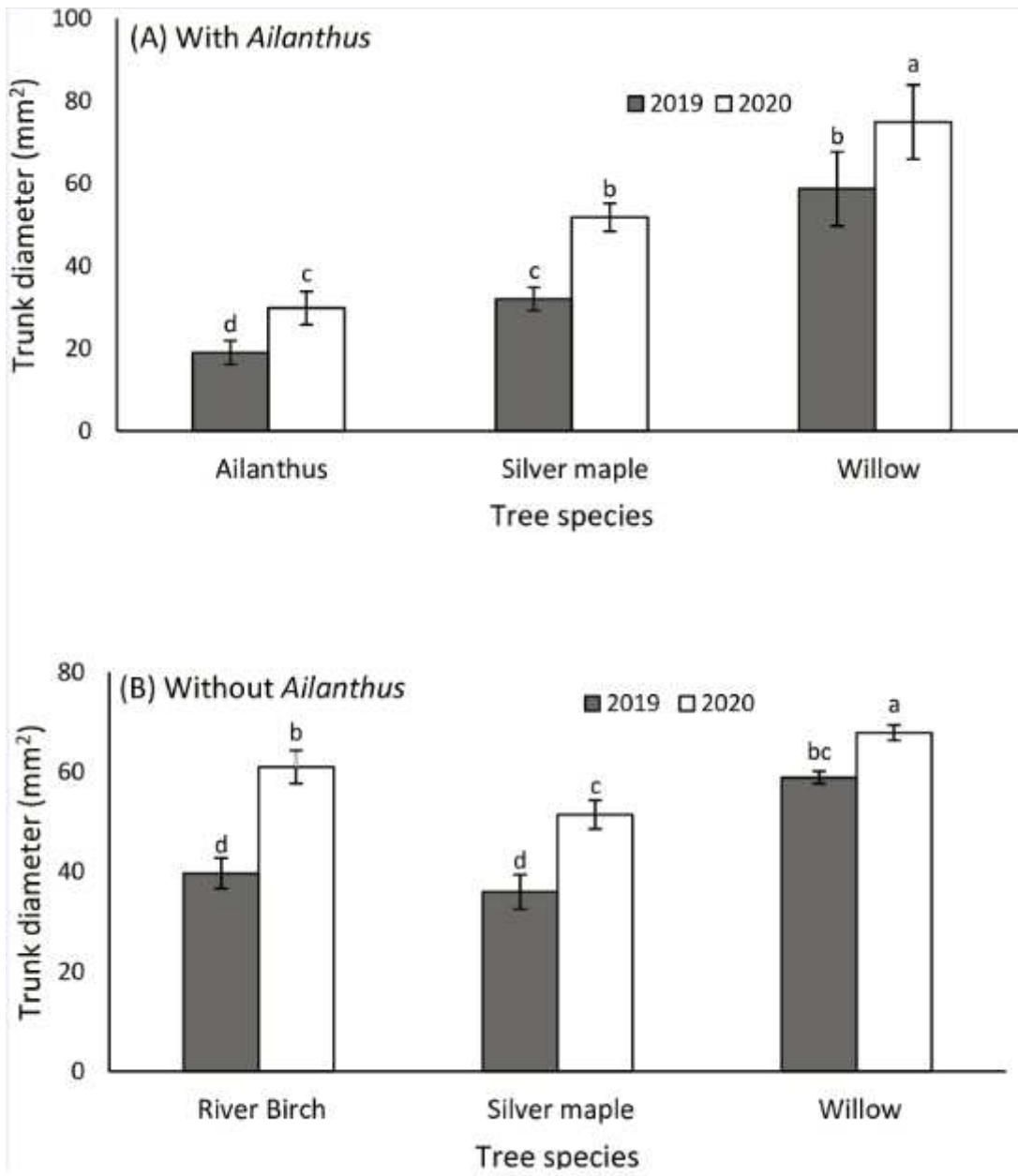


Figure 6

Mean (\pm SE) trunk diameter (mm) of tree species in enclosures with *Ailanthus* (A) and without *Ailanthus* (B) ($n = 5$ enclosures) in 2019 and 2020. Measurements were made on October 31, 2019 and November 3, 2020. Means within a column followed by different letters are significantly different (Bonferroni post hoc test: $P < 0.05$). Black walnut trees were not included in the analysis because most died during the 2019 studies and had to be replaced in spring of 2020.

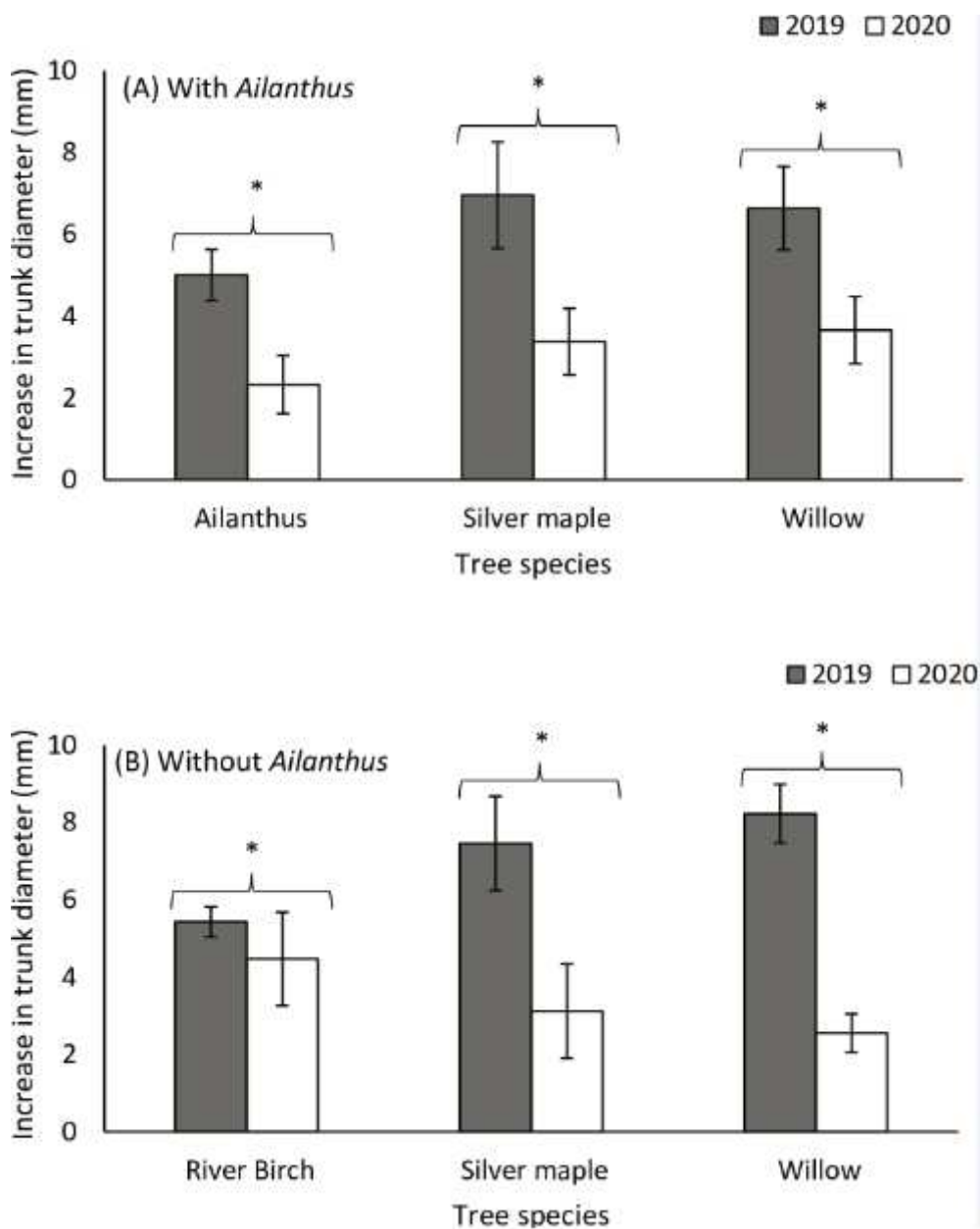


Figure 7

Mean (\pm SE) increase in trunk diameter (mm) of tree species in enclosures with Ailanthus (A) and without Ailanthus (B) ($n = 5$ enclosures) in 2019 and 2020. Measurements were made on June 4 and October 31, 2019, and July 8 and November 3, 2020. Increase in trunk diameter was obtained by subtracting trunk diameter data collected at the start of the experiment from those collected at the end of the experiment. Diameter increase did not differ ($P > 0.05$) between species in 2019 and 2020 but differed ($P < 0.05$) between 2019 and 2020 in both sets of cages (in 'with Ailanthus cages': $F_{1,29}=14.47$; $P = 0.0001$; in 'without Ailanthus' cages: $F_{1,29}=13.25$; $P = 0.0001$). Means within a column followed by asterisks are significantly different (Bonferroni post hoc test: $P < 0.05$). Black walnut trees were not included in the analysis because most died during the 2019 studies and had to be replaced in spring of 2020.