

Laboratory Performance of Two Polyphagous Invasive Weevils on the Predominant Woody Plant Species of a Northern Hardwood Community

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ABSTRACT A complex of invasive weevils that consume roots as larvae and foliage as adults have become established in northern hardwood forests in North America. We evaluated adults of the two most prominent species, *Phyllobius oblongus* and *Polydrusus sericeus*, for longevity, foliage consumption, and egg production on several putative hosts commonly found in this ecosystem. Adult pairs were monitored in no-choice laboratory assays for the duration of their lifespans on basswood, *Tilia americana*, ironwood, *Ostrya virginiana*, sugar maple, *Acer saccharum*, raspberry, *Rubus* spp., or leatherwood, *Dirca palustris*. Overall, *P. sericeus* lived more than twice as long as *P. oblongus* and lived longer on all hosts. *P. sericeus* consumed more total leaf area than *P. oblongus* on basswood, ironwood, and raspberry, but *P. oblongus* had a higher leaf consumption rate on sugar maple. Basswood was a very good host for *P. sericeus*. Leatherwood was not a suitable host for either weevil species. The higher longevity and fecundity of *P. sericeus* than *P. oblongus* did not agree with that expected from population data, in that the latter species is substantially more abundant. This likely reflects *P. oblongus*' superior performance on sugar maple, the dominant flora in the study area. These data provide a basis for estimating the broader impacts of adult weevil feeding.

KEY WORDS Curculionidae, exotic species, *Phyllobius oblongus*, *Polydrusus sericeus*, root herbivores

Invasive species pose significant threats to the functioning and biodiversity of native ecosystems (Gurevitch and Padilla 2004, Hendrix et al. 2008). They are partially or fully responsible for nearly 50% of the extinct or imperiled status of indigenous species in the United States (Wilcove et al. 1998), and cost the U.S. economy an estimated \$138 billion annually (Pimentel et al. 2000). Forests are particularly susceptible to exotic insect invasions because of their vast area and diverse biomes (Liebhold et al. 1995, Niemelä and Mattson 1996, Mattson et al. 2007, Langor et al. 2009). More than 400 documented invasive forest insect species are established in North America (Mattson et al. 1994, 2007; Langor et al. 2009). Invasive species have altered forest ecosystems by selectively killing plants, altering competition hierarchies, reducing ecosystem productivity, and altering ecosystem biogeochemical cycles (Mattson 1998, Lovett et al. 2006).

A complex of nine invasive weevils (Coleoptera: Curculionidae) is established in North American

northern hardwood forests (Coyle et al. 2008), of which two species are particularly abundant: *Phyllobius oblongus* L. and *Polydrusus sericeus* (Schaller) (Witter and Fields 1977, Pinski et al. 2005a). The folivorous adults and rhizophagous larvae threaten natural forest functioning in the Great Lakes and northeastern regions of North America, where northern hardwood forests predominate. *P. oblongus* feeds on many fruit and forest trees, especially sugar maple (Simmons and Knight 1973, Witter and Fields 1977). In addition to foliar feeding, adult feeding on sugar maple buds can cause bud mortality or loss of apical dominance the following spring (Simmons and Knight 1973). *P. sericeus* is also polyphagous, feeding on many forest tree species, including alder, linden, maple, and birch (Pinski et al. 2005b).

The life histories of these univoltine weevils are similar. Adults emerge from the soil in late May to early June and begin foliar feeding and mating almost immediately. Oviposition occurs ~2 wk later, and eggs are inserted into the soil. Larvae hatch in ~1 mo and begin feeding on fine root tissue. Larvae overwinter in the soil and resume feeding the following spring until pupation. Adults are fast walkers, and both species fly as adults, although *P. sericeus* is a much stronger flier than *P. oblongus*.

Our knowledge regarding this complex of invasive herbivores is increasing. Adult and larval abundance

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of *P. oblongus* is substantially higher than that of *P. sericeus* in northern hardwood stands of Minnesota, Wisconsin, and the Upper Peninsula of Michigan (Pinski et al. 2005a, Coyle et al. 2008). Adult weevil host preference and performance have been partially characterized (Pinski et al. 2005b); however, no studies have examined weevil responses to hosts over the entire lifespan of adults. Additionally, no studies have evaluated responses of these weevils on raspberry or leatherwood, two plants that are common in northern hardwood forests. Our objective was to characterize *P. oblongus* and *P. sericeus* longevity, leaf area consumption, and oviposition over their adult lifespans on several common northern hardwood forest woody plant species.

Materials and Methods

Plant Material. Foliage was collected in a northern hardwood forest stand near Taylor Lake in the Ottawa National Forest (Gogebic Co., MI). This ecosystem is a temperate deciduous community characterized by sandy loam soils (Bockheim 1997). Sugar maple (*Acer saccharum* Marsh.), ironwood [*Ostrya virginiana* (Mill.) K. Koch], yellow birch (*Betula alleghaniensis* Britton), eastern hemlock (*Tsuga canadensis* Carr.), and basswood (*Tilia americana* L.) are the dominant tree species (Goodburn 1996). The regional climate is characterized by a mean annual air temperature of 4–5°C, 850-mm annual rainfall, and a frost-free period of 100 d (Goodburn 1996).

We tested *P. oblongus* performance on sugar maple, ironwood, leatherwood (*Dirca palustris* L.), and raspberry (*Rubus* spp.) in 2007 and on basswood in 2008. We tested *P. sericeus* performance on sugar maple, ironwood, and raspberry in 2007, basswood in 2008, and leatherwood in 2009. Foliage collections for *P. oblongus* assays occurred on Julian date (JD) 151 (sugar maple, ironwood, leatherwood, raspberry) in 2007 and JD 156 (basswood) in 2008. Foliage for *P. sericeus* was collected on JD 166 (sugar maple, ironwood, raspberry) in 2007, JD 178 (basswood) in 2008, and JD 185 (leatherwood) in 2009. For each putative host plant species, a group of that species (occupying ≤ 30 m²) was identified in the field, and all foliage was taken from plants in this area. Shoots (at least 30 cm in length) from all plants were clipped and transported to the laboratory with the excised ends submerged in water. Shoots were standardized for sun exposure, and leaves were standardized for position. We standardized leaves between leaf plastochron index (Larson and Isebrands 1971) 2 and 6.

Insects. *Phyllobius oblongus* or *P. sericeus* pairs were collected in the same area as the foliage. Weevil pairs were captured from a diverse assemblage of putative hosts, including woody and herbaceous species. Collections were timed to coincide with the onset of weevil emergence to ensure that weevils had little previous feeding experience; this was also the time mating began. This collection method has been shown to be effective in previous studies (Pinski et al. 2005b, Hillstrom et al. 2010). Individual pairs were kept in

vials, transported to the laboratory, and starved for 24 h before starting each assay. Voucher specimens are deposited in the Department of Entomology Insect Research Collection at the University of Wisconsin.

Experimental Design. No-choice assays were conducted in petri dishes to measure weevil performance ($n = 25$ for sugar maple, ironwood, raspberry, and basswood; $n = 10$ for leatherwood). For each dish, one leaf was cut from the stem at the base of the petiole, and the end of the petiole was wrapped in a wet cotton ball to provide moisture. Leaves were placed in a petri dish (2 cm tall by 15 cm diameter) with a piece of moistened Whatman filter paper on the bottom. Cotton balls were remoistened every other day or as needed. One half of a Kimwipe tissue was placed in the dish to provide an oviposition site (Pinski et al. 2005b). One apparently healthy (based on appearance, movement, and behavior) pair of weevils was placed in the dish, and the dishes were housed in growth chambers with a 16:8 L:D photoperiod and a day:night temperature regimen of 24:18°C. Mortality was recorded daily.

The total number of days each weevil lived within a single dish was summed. The male was always smaller than the female, allowing us to determine which weevil had died and thereby calculate longevity of each sex. Females can lay multiple fertile egg clutches after mating. Dead weevils were removed from the dishes, and the assays were continued until both weevils had died. Leaves were changed every 4–5 d regardless of how much feeding had occurred and were changed earlier if deemed necessary because of consumption, spoilage, or desiccation.

Leaves were photocopied immediately before initiation of the assay and again after removal from dishes. The difference between the two measurements was the amount of leaf area eaten and was measured digitally using WinFOLIA Pro software (Régent Instruments, Quebec, Canada). We recorded both total leaf area consumed per dish and the amount of leaf area consumed per weevil per day alive. We tested whether leaf area is a suitable surrogate for leaf mass on these plant species by quantifying their relationship. On JD 155 in 2009, we clipped 20 branches in the field from each plant species used in the assays and transported them to the laboratory in water. One leaf, similar to what was used in the assays, was selected from each of these branches, and fresh leaf area and fresh leaf weight were measured. Leaves were dried at 60°C to a constant weight and reweighed. Simple regression analyses (Proc REG; SAS, Cary, NC) were conducted to determine the relationships between fresh leaf area and fresh and dry leaf weight. Relationships between fresh leaf area and leaf mass were highly correlated (Table 1). Therefore, we report fresh leaf area consumed hereafter. We also examined whether size of the adults varied among species to determine whether one species might consume more foliage or lay more eggs, because of larger size alone. We weighed 25 adults of each species to the nearest milligram on an analytical balance (Mettler-Toledo, Columbus, OH) and analyzed these data using a one-

Table 1. Relationship of leaf area (cm²) with fresh and dry weight for five woody plant species

Host	Weight (g)	<i>a</i>	<i>b</i>	<i>R</i> ²	<i>F</i> _{1,19}	<i>P</i>
Basswood	Fresh	102.55	2.5882	0.9127	188.18	<0.0001
	Dry	449.37	-0.0620	0.8580	108.73	<0.0001
Ironwood	Fresh	110.03	1.6384	0.7562	55.83	<0.0001
	Dry	449.34	-5.9543	0.8832	136.13	<0.0001
Leatherwood	Fresh	89.02	-0.0560	0.9826	1015.09	<0.0001
	Dry	383.79	-1.3772	0.9091	180.04	<0.0001
Raspberry	Fresh	70.44	4.7950	0.8393	94.04	<0.0001
	Dry	248.22	1.1582	0.8282	86.79	<0.0001
Sugar maple	Fresh	106.24	5.4837	0.9887	1568.65	<0.0001
	Dry	320.38	8.3600	0.9810	929.40	<0.0001

All relationships were linear in the form $y = ax + b$. Data were analyzed using simple linear regression (Proc Reg; SAS, Cary, NC).

way analysis of variance (ANOVA; Proc ANOVA; SAS, Cary, NC). We found no significant difference ($F = 0.32$; $df = 1,49$; $P = 0.5741$) between mean \pm SE adult weight of *P. oblongus* (2.49 ± 0.06 mg) and *P. sericeus* (2.57 ± 0.13 mg). Therefore, the data from our assays do not seem to be affected by relative size differences between weevil species.

Kimwipes in the assay dishes were changed every other day, and any eggs on them were counted. Eggs were not found anywhere else in the dishes. We recorded the total number of eggs produced by the female in each dish and the rate of egg production. To minimize potential effects of prior feeding in the field, we also analyzed these data with eggs laid on the first day of the assay omitted.

Statistical Analyses. Total weevil days alive and female and male longevity data did not require transformation to achieve normality. Total leaf area consumed and leaf area consumption rate data were log transformed. The total number of eggs and egg production rate, both with and without oviposition on the first day of the assay, were square-root transformed. All data were analyzed using a two-way ANOVA (Proc MIXED; SAS) with weevil species and host as fixed factors. Data were also analyzed separately within a species. Means were compared using the Student's *t*-test, with an α level of 0.05 considered significant.

Results

Longevity. Longevity of adult weevils was affected by weevil species, host, and their interaction (Table

2). Overall, *P. sericeus* lived more than twice as long as *P. oblongus* (Table 3). This trend held for all hosts except leatherwood, on which neither species thrived. *P. oblongus* survived the longest on basswood and raspberry (total weevil days: $F = 13.53$, $df = 4,96$, $P < 0.0001$, Fig. 1A; female longevity: $F = 8.98$, $df = 4,96$, $P < 0.0001$, Fig. 1B; male longevity: $F = 10.07$, $df = 4,96$, $P < 0.0001$, data not presented). *P. sericeus* total weevil days ($F = 20.51$, $df = 4,104$, $P < 0.0001$) were highest on basswood, ironwood, and raspberry (Fig. 1A), whereas female ($F = 11.51$, $df = 4,104$, $P < 0.0001$, Fig. 1B) and male ($F = 11.63$, $df = 4,104$, $P < 0.0001$, data not presented) longevity was highest on basswood and raspberry.

Leaf Consumption. Total leaf area consumption was affected by weevil species, host, and their interaction (Table 2). Overall, *P. sericeus* consumed 123% more leaf area than *P. oblongus* (Table 3). Weevils consumed the most ironwood, followed by basswood, raspberry, and sugar maple. These trends were true for *P. oblongus* ($F = 378.04$, $df = 4,96$, $P < 0.0001$) and *P. sericeus* ($F = 637.04$, $df = 4,104$, $P < 0.0001$; Fig. 1C). Leatherwood was not consumed by either weevil species. *P. sericeus* consumed more total leaf area than *P. oblongus* on basswood, ironwood, and raspberry, but consumption was equal between weevil species on sugar maple and leatherwood (Fig. 1C). Both *P. oblongus* ($F = 378.04$, $df = 4,96$, $P < 0.0001$) and *P. sericeus* ($F = 637.04$, $df = 4,104$, $P < 0.0001$) consumed the most total leaf area on ironwood.

Leaf area consumption rate was affected by host and the species \times host interaction (Table 2). Leaf

Table 2. Statistical values for two invasive weevil species, *P. oblongus* and *P. sericeus*, on five woody hosts from a northern hardwood forest community in Gogebic Co, MI, and their interaction

Performance parameter	Weevil species		Host		Weevil \times host interaction	
	<i>F</i> _{1,200}	<i>P</i>	<i>F</i> _{4,200}	<i>P</i>	<i>F</i> _{4,200}	<i>P</i>
Total longevity (d)	236.43	<0.0001	30.99	<0.0001	6.05	<0.0001
Female longevity (d)	112.39	<0.0001	18.05	<0.0001	3.54	0.0081
Male longevity (d)	144.21	<0.0001	17.00	<0.0001	5.13	0.0006
Total leaf area consumed (cm ²)	70.14	<0.0001	969.02	<0.0001	13.37	<0.0001
Leaf area consumption rate (cm ² /weevil/d)	3.49	0.0633	1233.28	<0.0001	17.16	<0.0001
Total egg production (eggs)	90.68	<0.0001	13.16	<0.0001	12.95	<0.0001
Egg production rate (eggs/weevil/d)	33.22	<0.0001	2.54	0.0030	9.50	<0.0001
Total egg production (first day eggs omitted)	64.23	<0.0001	16.82	<0.0001	9.94	<0.0001
Egg production rate (first day eggs omitted)	21.55	<0.0001	10.43	<0.0001	6.59	<0.0001

Table 3. Performance in laboratory assays of two species of invasive polyphagous root-feeding weevils established in northern hardwood forest ecosystems

Performance parameter	<i>Phyllobius oblongus</i>	<i>Polydrusus sericeus</i>
Total longevity (d)	11.41 ± 0.57b	26.42 ± 1.09a
Female longevity (d)	5.86 ± 0.34b	13.40 ± 0.74a
Male longevity (d)	5.55 ± 0.31b	13.02 ± 0.64a
Total leaf area consumed (cm ²)	6.40 ± 0.49b	14.30 ± 1.02a
Leaf area consumption rate (cm ² /weevil/d)	0.54 ± 0.04a	0.49 ± 0.03a
Total egg production (eggs)	23.03 ± 3.20b	100.43 ± 10.62a
Egg production rate (eggs/weevil/d)	3.68 ± 0.45b	7.28 ± 0.60a
Total egg production (first day eggs omitted)	22.01 ± 3.21b	87.77 ± 9.80a
Egg production rate (first day eggs omitted)	3.17 ± 0.39b	5.80 ± 0.57a

Means ± SE within a performance parameter sharing a letter are not significantly different at $\alpha = 0.05$.

consumption rate for *P. sericeus* was 90% that of *P. oblongus*, indicating that the increased total leaf area consumed by *P. sericeus* was mostly a function of a longer lifespan. *P. oblongus* leaf consumption rate on sugar maple was over twice that of *P. sericeus*, but *P. sericeus* feeding rate was >25% greater on raspberry (Fig. 1D). Both *P. oblongus* ($F = 550.28$, $df = 4,96$, $P < 0.0001$) and *P. sericeus* ($F = 705.20$, $df = 4,104$, $P < 0.0001$) preferred ironwood over all other host species (Fig. 1D).

Egg Production. Total egg production and egg production rate were significantly affected by weevil species, host, and their interaction (Table 2). Overall, *P. sericeus* had higher fecundity than *P. oblongus* over their lifetime, ovipositing five times as many total eggs, and more than four times as many eggs when oviposition on day 1 was omitted (Table 3). Weevils produced more eggs on basswood than on sugar maple and leatherwood, with and without oviposition on the first day included. *P. sericeus* laid more total eggs than *P. oblongus* on all hosts except sugar maple ($F = 12.95$, $df = 4,209$, $P < 0.0001$; Fig. 1E). However, when eggs laid on the first day of the assay were omitted, *P. sericeus* and *P. oblongus* egg production no longer differed on leatherwood (Fig. 1G). *P. oblongus* egg production ($F = 2.01$, $df = 4,96$, $P = 0.0998$) did not differ among hosts (Fig. 1E). However, when oviposition on the first day was omitted, egg production was significantly lower on leatherwood than all other hosts ($F = 3.58$, $df = 4,96$, $P = 0.0091$; Fig. 1G). *P. sericeus* total egg production ($F = 20.06$, $df = 4,104$, $P < 0.0001$) was lowest on sugar maple and leatherwood (Fig. 1E). When oviposition on the first day was omitted, leatherwood was shown to be an unusable host ($F = 18.99$, $df = 4,104$, $P < 0.0001$; Fig. 1G).

Egg production rate was significantly affected by weevil species, host, and their interaction (Table 2). *P. sericeus* egg production rate was nearly twice that of *P. oblongus* (Table 3). Egg production rate was lowest on sugar maple, unless oviposition on the first day was omitted. When oviposition on the first day was omit-

ted, leatherwood was a significantly poorer host. *P. sericeus* had a higher oviposition rate than *P. oblongus* on basswood, raspberry, and leatherwood (Fig. 1F). When oviposition on the first day was omitted, *P. sericeus* and *P. oblongus* egg production rate no longer differed on leatherwood (Fig. 1H) because they were both extremely low. *P. oblongus* egg production rate ($F = 2.25$, $df = 4,96$, $P = 0.0691$) did not differ among hosts. However, when oviposition on the first day of the assay was omitted, oviposition rate varied greatly ($F = 5.00$, $df = 4,96$, $P = 0.0011$) among host species (Fig. 1H). *P. sericeus* egg production rate ($F = 11.12$, $df = 4,104$, $P < 0.0001$) was lowest on sugar maple (Fig. 1F). When oviposition on the first day was omitted, leatherwood was shown to be a very poor host ($F = 12.24$, $df = 4,104$, $P < 0.0001$; Fig. 1H).

Discussion

Polydrusus sericeus survived longer, ate more, and oviposited more than *P. oblongus* over their adult lifespans (Table 1), which agrees with previous short-term assays (Pinski et al. 2005b). Similarly, field studies indicate that *P. sericeus* is present for ≈ 10 wk compared with 5 wk for *P. oblongus* (Witter and Fields 1977, Pinski et al. 2005a). *P. sericeus* and *P. oblongus* preferred ironwood, followed by basswood and then sugar maple in our study and in that by Pinski et al. (2005b).

Although both *P. sericeus* and *P. oblongus* have been observed on leatherwood (Petrice et al. 2000), neither consumed any foliage in our study, even when faced with the prospect of starving to death. Leatherwood twigs are known to contain highly unique phenolic compounds (Ramsewak et al. 1999), and the fruits have compounds with insecticidal properties (Ramsewak et al. 2001). This suggests the possible presence of antifeedant properties in leatherwood foliage, although to our knowledge, this has not been tested. Leatherwood leaves have high levels of antioxidants (McCune and Johns 2007), which may negatively affect fitness of some herbivores (Barbehenn et al. 2003). Likewise, neither species oviposited when leatherwood was its only source of foliage. From a methodological standpoint, recording oviposition both throughout the full adult lifespan and with the first day of oviposition removed proved a useful means of separating effects of prior feeding from host-specific assays in field-collected insects.

Despite a longer lifespan and higher oviposition rate, *P. sericeus* is only 17% as abundant as *P. oblongus* in this area of the Ottawa National Forest (Pinski et al. 2005a). This might suggest that community composition could eventually shift from dominance by *P. oblongus* to *P. sericeus*. However, *P. sericeus* has been established in this area for several decades (Witter and Fields 1977). A possible explanation for the continued numerical domination by *P. oblongus* is that sugar maple, a host on which *P. oblongus* has a higher leaf area consumption rate and slightly higher oviposition rate, comprises >96% of the for-

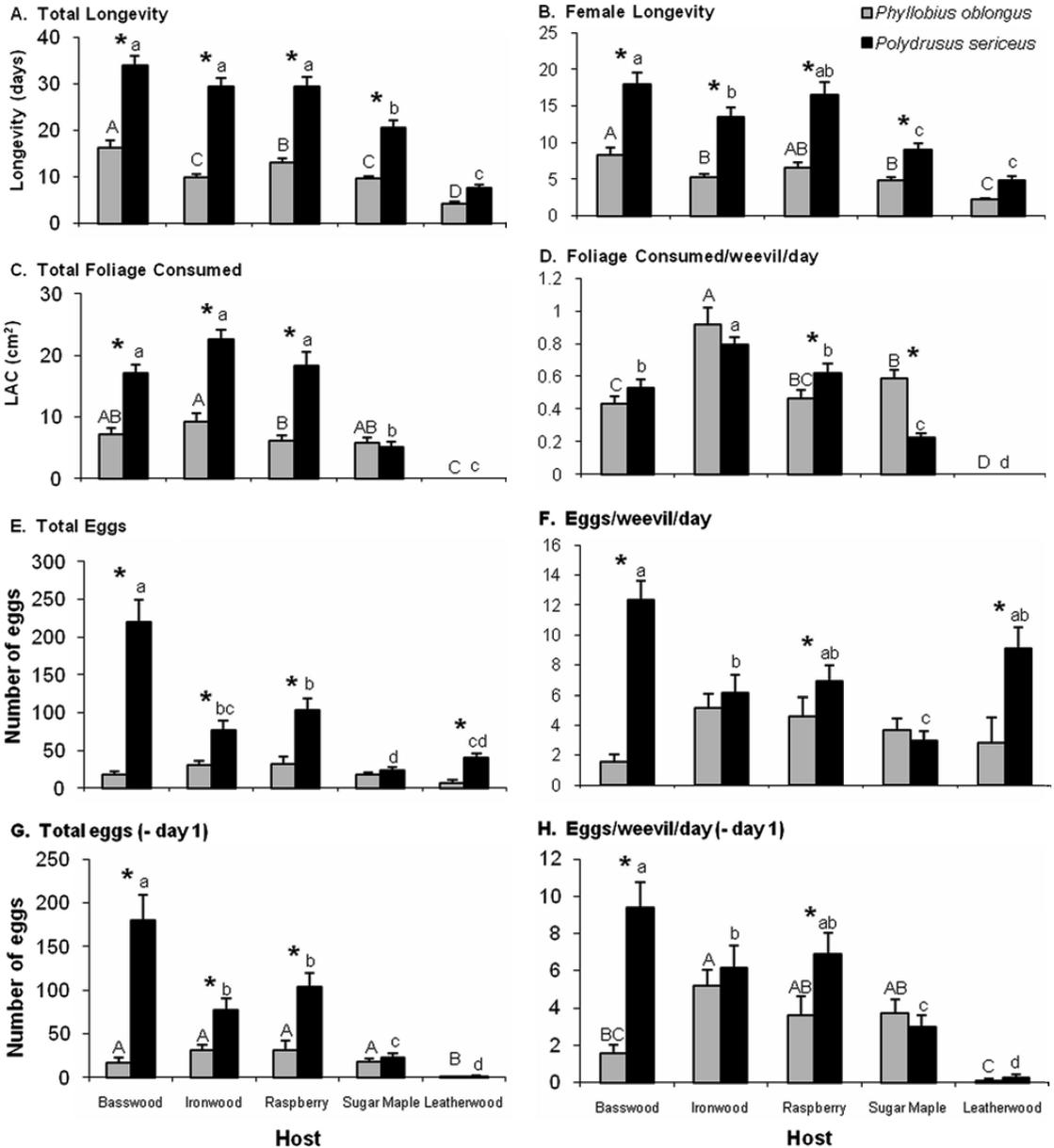


Fig. 1. Effect of host tree on species performance of *P. oblongus* and *P. sericeus* performance in no-choice assays (A) total longevity, (B) female longevity, (C) total foliage consumption, (D) foliage consumption rate, (E) total egg production, (F) egg production rate, (G) total egg production with eggs oviposited on the first day of the assay omitted, and (H) egg production rate with eggs oviposited on the first day of the assay omitted. Male longevity data mirrored that of females and are not presented. Within a performance parameter, *P. oblongus* means sharing the same uppercase letter and *P. sericeus* means sharing the same lowercase letter are not significantly different at $\alpha = 0.05$. Within a performance parameter, hosts having an asterisk (*) indicate significant differences at $\alpha = 0.05$ between the two weevil species.

est understory (Pinski et al. 2005a). Because *P. oblongus* emerges earlier in the spring than *P. sericeus* (Pinski et al. 2005a), it has an immediate abundance of a host plant on which it outperforms *P. sericeus*. This supports the view that both laboratory and field assays are needed to evaluate the potential impacts of invasive insects, and conversely, for planned in-

roductions of insects feeding on invasive plants (McClay and Balcunas 2005).

We currently have little information on the extent to which these invasive insects may affect trees at the individual or stand level. These laboratory assays allow us to make a coarse first approximation of total leaf consumption, although more directed field

studies are needed to incorporate complex ecological interactions that would modulate feeding under natural conditions. Larval densities can reach nearly 1,000/m² (Coyle et al. 2008), and weevil composition is ≈80% *P. oblongus* and 20% *P. sericeus* (Pinski et al. 2005a, Coyle 2010). Sugar maple seedlings have leaves averaging 67.2 cm² in these stands (Coyle 2010), which is a mean of four leaves per seedling (Morrison and Mauck 2007), and stand density averages 35 sugar maple seedlings/m² (Coyle 2010). Using these estimates, the data in Fig. 1, and assuming 25% larval survival to adulthood, >10% of total seedling leaf area could be removed. The ecological impacts of this defoliation have not been studied, but it seems reasonable to speculate that it could influence patterns of growth, nutrient cycling, and competitive interactions among understory species that are struggling in the shade on a marginal carbon budget even without weevil defoliation and root feeding.

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