

Host Breadth and Ovipositional Behavior of Adult *Polydrusus sericeus* and *Phyllobius oblongus* (Coleoptera: Curculionidae), Nonindigenous Inhabitants of Northern Hardwood Forests

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Environ. Entomol. 34(1): 148–157 (2005)

ABSTRACT *Polydrusus sericeus* (Schaller) and *Phyllobius oblongus* (L.) are nonindigenous root-feeding weevils in northern hardwood forests of Wisconsin and Michigan. Detailed studies of adult host range, tree species preferences, and effects of food source on fecundity and longevity have not been conducted in North America. *P. sericeus* and *P. oblongus* adults fed on leaves of all 11 deciduous tree species offered in no-choice assays, but amount of consumption varied among species. *P. sericeus* consumed more yellow birch (*Betula alleghaniensis* Britton), basswood (*Tilia americana* L.), and ironwood [*Ostrya virginiana* (Miller) K. Koch] than maple (*Acer* spp.). Conversely, *P. oblongus* consumed more ironwood than poplar (*Populus* spp.) and yellow birch, with maple being intermediate. Females ate 2.5 times as much as males. Mean frass production by *P. sericeus* was strongly correlated with foliage consumption among host tree species. In feeding choice assays, *P. sericeus* preferred yellow birch over ironwood, basswood, and aspen (*Populus tremuloides* Michaux). *P. sericeus* produced 29.93 ± 1.43 eggs/d when feeding on yellow birch compared with 2.04 ± 0.36 eggs/d on sugar maple (*Acer saccharum* Marshall). *P. oblongus* produced 4.32 ± 1.45 eggs/d when feeding on sugar maple compared with just 0.2 ± 0.1 eggs/d on yellow birch. Overall, total egg production for *P. sericeus* and *P. oblongus* averaged 830.1 ± 154.8 and 23.8 ± 11.8 eggs, respectively, when feeding on their optimal host plants. *P. sericeus* survived approximately five times longer in assays than *P. oblongus*, and it oviposited a total of 25.8 ± 4.0 d, whereas *P. oblongus* oviposited 1.9 ± 0.9 d. Egg size among *P. sericeus* and *P. oblongus* was 0.53 ± 0.008 by 0.32 ± 0.003 and 0.56 ± 0.005 by 0.29 ± 0.004 mm, respectively. In laboratory rearing of *P. sericeus* on yellow birch seedlings, 18% of the initial 500 larvae completed development to adults.

KEY WORDS host range, *Phyllobius*, *Polydrusus*, oviposition, rearing

A COMPLEX OF NONINDIGENOUS root-feeding weevils has become widely established throughout the northern hardwood forests of the Great Lakes region. These European species include *Phyllobius oblongus* (L.), *Polydrusus sericeus* (Schaller), and *Sciaphilus asperatus* (Bonsdorff), of which the first two are predominant (Pinski et al. 2005). Adults are particularly abundant on understory seedlings, where they have been apparent in Michigan and Wisconsin since 1969 (Simmons 1972). The life histories and seasonal phenologies of these univoltine weevils are reported in Vollman (1954), Witter and Fields (1977), Levesque and Levesque (1994), and Pinski et al. (2005). However, the host range and species preferences are poorly understood.

The adults of each species are typically found feeding on the foliage of just a few forest tree species in Wisconsin and Michigan, including sugar maple (*Acer saccharum* Marshall), mountain maple (*Acer spicatum* Lamark), American elm (*Ulmus americana* L.), yellow birch (*Betula alleghaniensis* Britton), black cherry (*Prunus serotina* Ehrhart), and speckled alder [*Alnus rugosa* Du Roi (Spreng)] (Witter and Fields 1977). However, they are described in the European literature as polyphagous, feeding on a wide variety of tree and shrub species (Henshaw 1888, Fryer 1919, Masee 1941, Morris 1978, Jarfas et al. 1985, Casteels and De Clercq 1988, Helsen and Blommers 1988, Marko et al. 1995, Gharadjedaghi 1997, Czerniakowski 1998). Despite such generalist feeding habits, their food choice can be quite specific, because Rousi et al. (1997) found significant differences in the palatability of white birch clones (*Betula pendula* Roth and *B. pubescens* Ehrhart) to *P. oblongus* in Europe. Our understanding of the host range and feeding preferences of this nonindigenous weevil complex is further complicated by field sampling data in the Great Lakes region, which have shown no consistent relationships between wee-

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vil species and stand composition (Pinski 2004). Furthermore, we have no information on how various food sources can affect the longevity and fecundity of these weevils, despite the pronounced effects host plants are known to have on species with similar life histories, such as the black vine weevil (*Otiorhynchus sulcatus* [F.]) and the strawberry root weevil (*Otiorhynchus ovatus* [L.]) (Penman and Scott 1976, Nielsen and Dunlap 1981, Shanks et al. 1984).

Detailed information of the host ranges and feeding preferences of larvae is likewise not available. Vollman (1954) made general observations of larvae feeding in the upper soil layers (5–25 cm deep) on roots of tree species on which adults feed. The impacts of below-ground feeding by this complex are not known. Below-ground herbivores can exert subtle effects that may go unnoticed for substantial periods, including reduced plant diversity, altered successional processes, altered patterns of carbon and nitrogen allocation, increased susceptibility to other herbivores and pathogens, and reduced total yield (Syvertsen and McCoy 1985, Brown and Gange 1991, 1992, Hunter 2001). Moreover, detailed feeding and impact studies cannot be conducted until appropriate rearing and bioassay conditions are established.

The purpose of this research is to (1) characterize the host breadth of adult *P. sericeus* and *P. oblongus* in the Great Lakes region, (2) determine the relative feeding preferences among suitable hosts of *P. sericeus*, (3) determine how adult feeding on various species of suitable hosts affects fecundity, and (4) develop a rearing system for subsequent larval feeding and impact assays.

Materials and Methods

Host Breadth of Adult Weevils. Foliage was collected 14 July 2002 and 17 July 2003 in the Ottawa National Forest, Upper Peninsula, MI, from 11 northern hardwood tree species. Host tree selection focused on the species most commonly found in study sites. These included sugar maple, red maple (*Acer rubrum* L.), mountain maple, yellow birch, paper birch (*Betula papyrifera* Marshall), ironwood [*Ostrya virginiana* (Miller) K. Koch], American basswood (*Tilia americana* L.), quaking aspen (*Populus tremuloides* Michaux), hybrid poplar (*Populus* spp.), speckled alder, and northern red oak (*Quercus rubra* L.). No-choice laboratory feeding assays were conducted with *P. sericeus* in 2002 and 2003, with the only difference being that mountain maple was tested in 2002 only.

One leaf from each of 10 trees per species was removed at the petiole. All test leaves were fully expanded, located within the first six positions from the branch tip inward, at least partially shaded from direct sunlight, and without any visible signs of insect herbivory or pathogens. Leaves were placed in 10-ml tubes filled with distilled water and stored in plastic bags in a cooler until the start of the assay. Weevils were field collected from sites near those used for foliage collection. Weevils were collected by sweep-

netting understory plants of multiple species. They were stored in a plastic box (30 by 20 by 10 cm) lined with damp filter paper and containing crumpled tissue paper. Insects were starved for 24 h before assays.

Initial leaf area was determined by digital scanning (WinFolia 2001a; Regent Instruments 2001). Whole leaves were used because these weevils feed at the perimeters and because damaging tissue can potentially induce changes in leaf chemistry (Risch 1985, Jones and Coleman 1988). Arenas consisted of 15-cm-diameter petri dishes lined with damp filter paper containing one leaf in a water tube and one weevil. Weevils were randomly arranged across treatments and replicates ($n = 10$). Assay units were randomly positioned in growth chambers (1–35L; Percival, Boone, IA) at a 15:9-h (L:D) photoperiod and a 24:18°C (L:D) temperature regimen. Weevils were allowed to feed for 72 h, and additional distilled water was added to the filter paper at 36 h.

After the assay, weevil sex (2003 only) and survivorship were recorded. Sex was determined based on the anterior edge of the hind tibia, which has a brush of long prominent, erect setae in males but is sparsely pilose in females, and the last abdominal sternite, which has an emarginate apical margin in males (Fowler 1891, Sleeper 1957). The number of frass pellets was recorded, and a subsample was photographed with a Nikon digital camera (E995; Nikon, Melville, NY). Leaves were removed from the assay unit, wiped clean, and rescanned to obtain postfeeding area and leaf area consumed. Foliage was dried at 70°C, and dry mass consumed was calculated by multiplying the post assay specific leaf mass (mg/cm^2) by the area consumed.

Three different feeding measurements, leaf area, dry mass, and frass pellet production, were analyzed, because each has limitations. Leaf area consumption does not account for differences in leaf thickness among tree species, and can be difficult to measure for species such as alder, whose architecture resists complete leaf flattening for scanning. Dry mass accounts for leaf thickness, but includes veins, which comprise a substantial proportion of a leaf's mass, are inedible by these weevils, and vary among tree species. Frass production is an indirect measure of weevil consumption because it also reflects digestion, but it is a significant predictor of both leaf area and mass consumed (see Results).

The host breadth of *P. oblongus* was assayed using similar methods. Weevils and foliage were field collected 19 June 2003, and the same 11 tree species ($n = 10$) were tested. Because of equipment malfunction, some assays were repeated on 7 July 2003 ($n = 7$). Leaf area, leaf mass, and weevil survival were recorded.

The effects of tree species on leaf area consumed, dry mass consumed, and frass production were analyzed by one-way analysis of variance (ANOVA; PROC GLM; SAS Institute 1999). Units in which weevils died were omitted from analysis. For *P. sericeus*, square root transformations of leaf area and mass consumption in 2002 and 2003 and a \log_e transformation of frass production in 2002 were applied to correct

unequal variances. Frass production data in 2003 did not require transformation. Leaf area and mass consumption by *P. oblongus* were transformed by square root. If *F* was significant ($P < 0.05$), means were separated using Fisher protected least significant difference (LSD) test with a Bonferroni correction. A two-way ANOVA (PROC GLM; SAS Institute 1999) was used to analyze the effect of *P. sericeus* sex, host species, and their interaction on leaf area and mass consumed and frass produced during 2003 assays. Relationships between leaf area and mass consumption with frass production were assessed using simple linear regressions with Minitab statistical software (Release 13; Minitab 1999).

Feeding Preferences of *P. sericeus*. Host species preference was evaluated in a four-way choice test in 2003. Conditions were similar to no-choice assays, except where noted. Weevils and foliage were collected on 3 August 2003. Test species included yellow birch, ironwood, basswood, and aspen, based on their palatability in no-choice assays. The assay units were plastic boxes (30 by 20 by 10 cm) containing one leaf from each species. Leaves were randomly positioned in each corner, with the foliage facing the center. One weevil was placed in the center of each box, and boxes were randomly positioned in growth chambers as above. Assays were for 72 h. Experimental design was a randomized complete block with four treatments and 20 replicates, i.e., trees.

The effects of host species on leaf area and mass consumption were analyzed using one-way ANOVA (PROC GLM; SAS Institute 1999). Replicates in which weevils died during the assay were excluded. Data were transformed by square root to correct unequal variances. If *F* was significant ($P < 0.05$), means were separated using Fisher protected LSD test with a Bonferroni correction.

Ovipositional Behavior. Preliminary assays were conducted during Summer 2002 to develop methods for studying oviposition in the laboratory. We modified the methods of van Emden (1950), Vollman (1954), and Fields (1974). One hundred thirty field-collected (12 June) *P. sericeus* were held in a plastic box with a screen lid. We covered the bottom of the container with moistened filter paper and crumpled Kimwipes (EX-L; Kimberly-Clark, Mississauga, Ontario, Canada). Distilled water and a mixture of yellow birch, linden (*Tilia cordata* Miller), Norway maple (*Acer platanoides* L.), and sugar maple foliage from the University of Wisconsin–Madison campus were provided continually. Kimwipes were replaced every 3–10 d. On each collection date, the number of egg masses and number of eggs per mass were recorded. The change in oviposition throughout the life spans of females in captivity was analyzed with a one-way ANOVA (PROC GLM; SAS Institute 1999). A \log_e transformation of the number of eggs per mass was applied.

We standardized larval feeding history for subsequent oviposition assays in 2003. Eggs from the 2002 assays were left on Kimwipes, placed in 15-cm petri

dishes, and stored in a growth chamber (1–30BL; Percival) at 24 h dark and 24°C. Distilled water was replenished to keep Kimwipes damp. Newly eclosed larvae were placed in the soil of potted yellow birch seedlings, on which they were reared to adult.

The effect of adult feeding substrate on *P. sericeus* fecundity was tested. As adults emerged from potted seedlings, one male–female pair was randomly provided either sugar maple ($n = 15$) or yellow birch ($n = 16$) foliage. Yellow birch foliage was collected from potted seedlings not used in the larval rearing assay, and sugar maple foliage was collected from the University of Wisconsin–Madison campus. The assay unit was a 15-cm petri dish lined with damp filter paper, a crumpled Kimwipe, and two leaves in a water tube. Ovipositional assays began 22 May 2003 and continued until the last weevil pair died on 13 July 2003. Assay units were stored in a growth chamber at a 15:9-h (L:D) photoperiod and a 24:18°C (L:D) temperature regimen. Foliage was replaced approximately every 3 d, and distilled water was added to the filter paper every 2 d. Kimwipes were replaced daily, at which time the number of egg masses and eggs per mass were recorded. Replicates were removed, and data were no longer recorded once either sex of the weevil pair died. We adjusted fecundity data for mortality by continuing basing the mean on the number of surviving pairs.

The effect of adult host plant on *P. oblongus* fecundity was studied using similar methods. As before, adult feeding substrates were sugar maple ($n = 12$) and yellow birch ($n = 12$) foliage. Assays were conducted 5–26 June 2003. Adult *P. oblongus* were field collected, so larval and prior adult feeding histories were unknown. Male and female *P. oblongus* were paired for ovipositional assays by removing weevils observed copulating in captivity, because sex is difficult to determine by exterior characters. Sex was confirmed by dissection after the assays were completed (Vollman 1954).

The effects of adult feeding substrate on *P. sericeus* and *P. oblongus* fecundity were tested separately by one-way ANOVA (PROC GLM; SAS Institute 1999). Data were omitted from *P. oblongus* replicates where dissection indicated the pair was not one of each sex. A square-root transformation was applied to the number of eggs per weevil per day to correct for unequal variance. The fecundities of *P. sericeus* and *P. oblongus* feeding on their respective optimal hosts were compared using one-way ANOVA (PROC GLM; SAS Institute 1999). A square-root transformation was applied to the number of eggs per weevil per day.

Observations on *P. sericeus* and *P. oblongus* egg size and appearance were made to help with future identifications in the field. Egg size was measured using an ocular micrometer at 25 \times . Additional observations included physical changes during egg maturation and the longevity of starved larvae. Observations of *P. sericeus* and *P. oblongus* eggs were conducted during ovipositional assays in 2003.

Laboratory Rearing of *P. sericeus*. Yellow birch seedlings were inoculated 26–31 July 2002 by placing

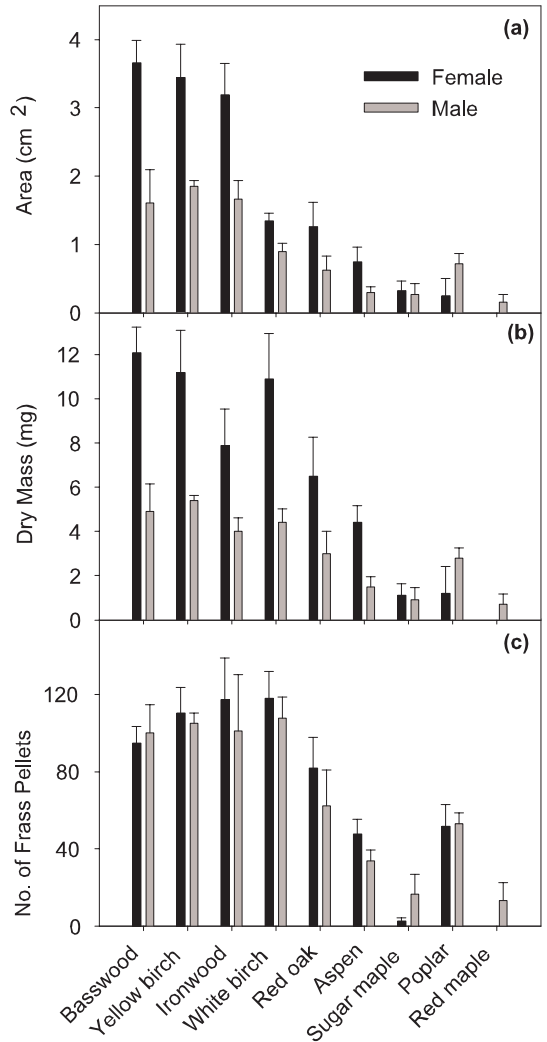
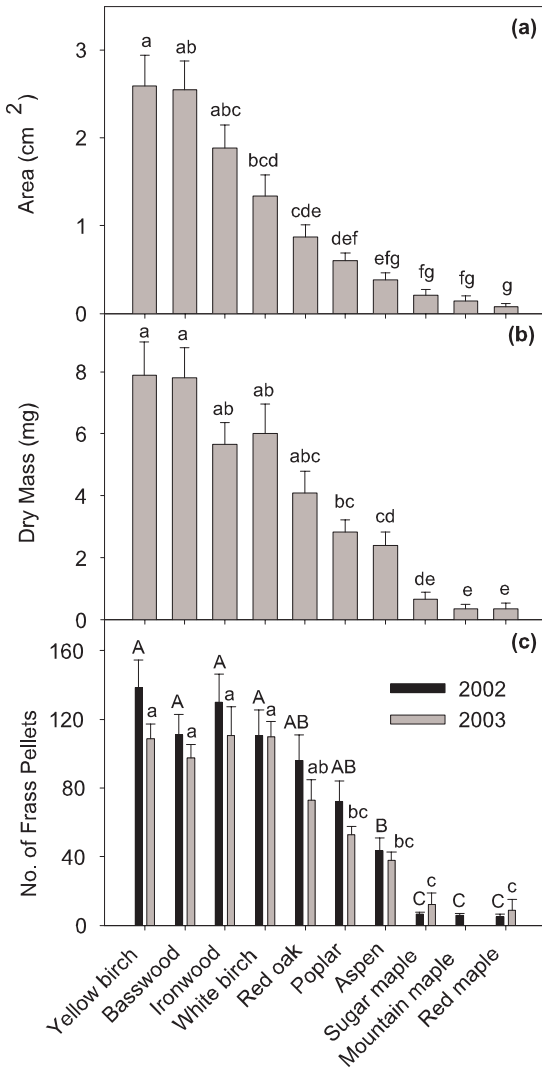


Fig. 1. Effect of host plant species on (a) leaf area consumption, (b) dry mass consumption, and (c) frass pellet production by *P. sericeus* during no-choice feeding assays. Data are means + SE. Bars with the same letter do not differ at $P > 0.05$. Bars with capital and lowercase letters distinguish between 2002 and 2003 results, respectively. See text for statistics.

Fig. 2. Effects of *P. sericeus* sex and host plant species on (a) leaf area consumption, (b) dry mass consumption, and (c) frass production during no-choice feeding assays. Data are means + SE. See text for statistics.

newly eclosed larvae in a 1-cm-deep trench encircling the stem. Three treatments (0, 20, or 30 larvae) with 10 replicates each were randomly assigned. Twenty and 30 larvae/pot correspond to 274 and 411 larvae/m². Larval densities in the field are highly variable, being as high as 2,800 larvae/m² (W.J.M., unpublished data), with means of 10–252 larvae/m², including local densities up to 1,894 at four study sites (Pinski 2004).

Yellow birch seed source was the Flambeau River State Forest, Sawyer County, WI, and seedlings were grown in outdoor beds at the Wisconsin Department of Natural Resources Hayward nursery. On delivery,

bare-root 2-yr-old seedlings top-pruned to 36 cm were planted in 18.9-liter pots with a mix of 2:1 field soil to torpedo sand. Field soil was collected from the University of Wisconsin West Madison Agricultural Research Station. Seedlings were grown outside under shade cloth (50% shade) and were watered approximately every 3 d during the summer. A plastic tarp was placed under pots to prevent root growth into the ground. Seedlings were overwintered in a cold frame filled with compost 15 cm above the soil surface. Compost was removed the following April, and emergence traps were erected. Emergence traps consisted of white screen netting placed over a stake and secured to the pot. The number of adults collected from each trap was recorded daily and then less frequently as emergence declined.

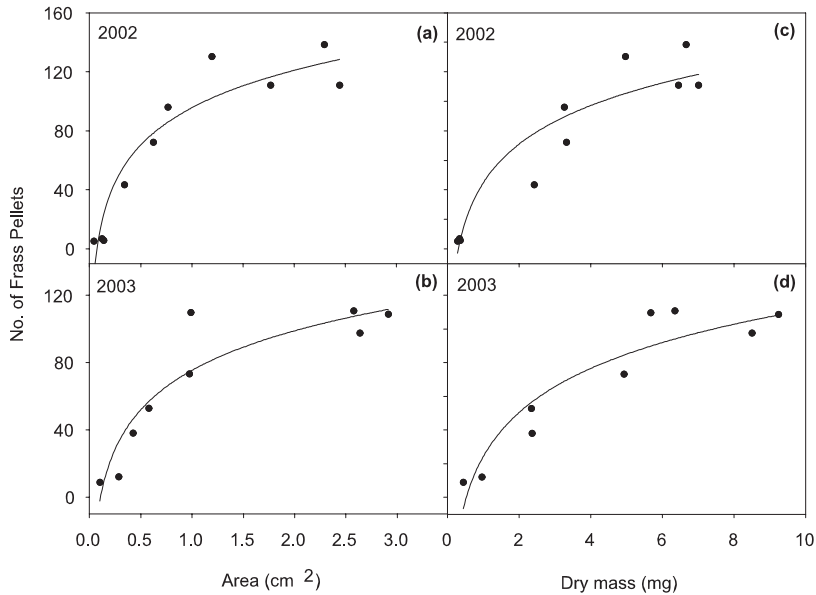


Fig. 3. Relationships between the mean foliage consumption and mean number of frass pellets produced by *P. sericeus* feeding on various host species: (a and b) leaf area, (c and d) leaf mass. (a) $y = 95.63 + 36.596\log_e(x)$; $df = 1,8$; $R^2 = 0.90$; $P < 0.0001$. (b) $y = 75.406 + 33.853\log_e(x)$; $df = 1,7$; $R^2 = 0.86$; $P = 0.0003$. (c) $y = 305.29 + 37.693\log_e(x)$; $df = 1,8$; $R^2 = 0.89$; $P < 0.0001$. (d) $y = 285.74 + 37.884\log_e(x)$; $df = 1,7$; $R^2 = 0.89$; $P = 0.0002$.

Results

Host Breadth of Adult Weevils. Leaf area and leaf mass consumption by *P. sericeus* did not vary between 2002 and 2003 ($P > 0.05$), so data were pooled for analysis. Sample sizes used in analyses were $n = 17$ – 20 , with the exception of mountain maple ($n = 5$). The alder leaf measurements were removed from analyses because of difficulties in obtaining accurate digital scans. *P. sericeus* fed on all tree species offered in no-choice feeding assays. On aspen, they also ate petioles. The leaf area consumed per weevil varied significantly among tree species ($F_{9,163} = 32.47$; $P < 0.0001$). They consumed more yellow birch, basswood, and ironwood than poplar, aspen, sugar maple, mountain maple, and red maple (Fig. 1a). The leaf dry mass consumed per weevil also varied among tree species ($F_{9,163} = 26.58$; $P < 0.0001$). More yellow birch, basswood, ironwood, white birch, and red oak mass were consumed than sugar maple, mountain maple, and red maple (Fig. 1b). The number of frass pellets produced differed between years ($F_{1,163} = 5.15$; $P = 0.0246$), so these data were analyzed separately. Sample sizes used in analyses were $n = 8$ – 10 during 2002 and 2003, with the exception of mountain maple in 2002 ($n = 5$). The number of frass pellets produced per weevil varied among tree species in both 2002 ($F_{9,77} = 41.58$; $P < 0.0001$) and 2003 ($F_{8,77} = 19.42$; $P < 0.0001$). In both years, more frass was produced by *P. sericeus* feeding on yellow birch, ironwood, basswood, white birch, and red oak than sugar maple, mountain maple, and red maple (Fig. 1c). The mean number of frass pellets produced by *P. sericeus* feeding on alder was 85.9 ± 6.2 and 75.0 ± 6.7 in 2002 and 2003, respectively.

Weevil sex had a significant effect on overall mean leaf area ($F_{1,68} = 10.17$; $P = 0.0022$) and dry mass ($F_{1,68} = 15.11$; $P = 0.0002$) consumed by *P. sericeus*. Females ($N = 36$) consumed more foliage (mean leaf area = 1.97 ± 0.27 cm², dry mass = 6.9 ± 0.9 mg) than males ($N = 50$; mean leaf area = 0.79 ± 0.1 cm², dry mass = 2.9 ± 0.3 mg; Fig. 2a and b). However, weevil sex did not affect frass pellet production ($F_{1,68} = 0.00$; $P = 0.9762$). Females and males produced on average 77.53 ± 8.35 and 62.36 ± 6.47 frass pellets, respectively (Fig. 2c). There was also a significant tree species by weevil sex interaction for leaf area ($F_{8,68} = 3.25$; $P = 0.0034$) and dry mass consumption ($F_{8,68} = 3.37$; $P = 0.0026$), but not frass production ($F_{8,68} = 0.72$; $P = 0.6760$).

Mean frass production by *P. sericeus* was strongly correlated with foliage consumption among host tree species. Leaf area consumption and frass production were strongly related in logarithmic fashion during no-choice feeding assays both in 2002 (Fig. 3a) and 2003 (Fig. 3b). Similar relationships between frass production and leaf mass consumption were observed in both 2002 (Fig. 3c) and 2003 (Fig. 3d). Frass resulting from sugar maple, red maple, and red oak consumption appeared less dense, smaller, and less dark than that from aspen, poplar, and basswood (Pinski 2004). Consumption of alder, white birch, ironwood, and yellow birch yielded frass pellets intermediate between these groups.

Phyllobius oblongus fed on all tree species tested during no-choice assays. Red oak foliage desiccated during this assay and could not be scanned. Sample sizes used in analyses varied ($n = 5$ – 9). The mean leaf

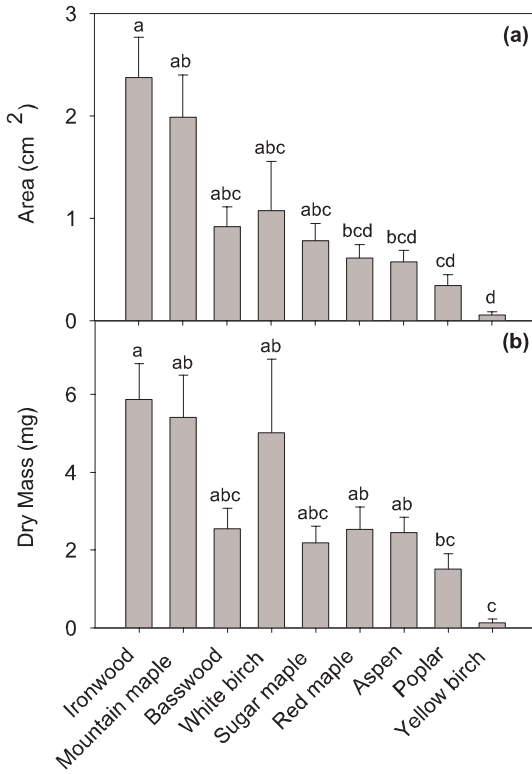


Fig. 4. Effect of host plant species on (a) leaf area consumption and (b) dry mass consumption by *P. oblongus* in no-choice feeding assays. Data are means + SE. Bars with the same letter do not differ at $P > 0.05$. See text for statistics.

area consumed per weevil varied significantly among tree species ($F_{8,52} = 6.78$; $P < 0.0001$). *P. oblongus* consumed more ironwood than red maple, aspen, poplar, and yellow birch (Fig. 4a). The mean leaf dry mass consumed per weevil also varied significantly among tree species ($F_{8,52} = 5.07$; $P = 0.0001$). More ironwood was consumed than poplar and yellow birch (Fig. 4b).

Feeding Preferences of *P. sericeus*. The leaf area and leaf mass consumed by *P. sericeus* in four-way choice tests did not vary among replicates ($P > 0.05$), so they were pooled before analysis ($n = 14$). Mean leaf area consumed varied significantly among tree species ($F_{3,52} = 8.13$; $P = 0.0002$). Weevils ate more yellow birch than ironwood, basswood, or aspen (Fig. 5a). The mean leaf mass consumed also varied among tree species ($F_{3,52} = 4.45$; $P = 0.0074$). More yellow birch was consumed than basswood and aspen, with ironwood being intermediate (Fig. 5b). The difference in leaf mass of yellow birch versus ironwood consumed was not statistically significant when the conservative Bonferroni correction was used, but was significant using the LSD test ($P < 0.05$). There was no preference for ironwood or basswood over aspen despite such differences in the no-choice assays.

Ovipositional Behavior. *Polydrusus sericeus* and *P. oblongus* oviposited in masses. Within a mass, eggs were glued to each other and the ovipositional surface

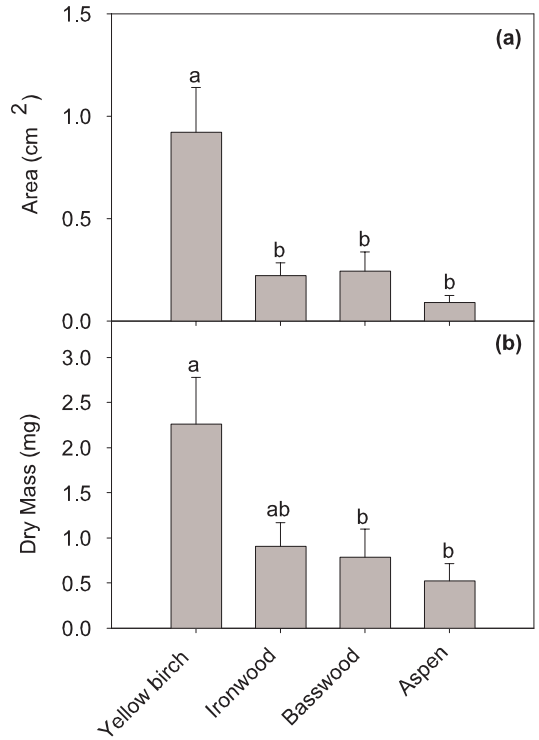


Fig. 5. Feeding by *P. sericeus* during behavioral choice tests. (a) Leaf area consumption. (b) Dry mass consumption. Data are means + SE. Bars with the same letter do not differ at $P > 0.05$. See text for statistics.

by an off-white secretion. Eggs were oblong to oblong-ovate. *P. sericeus* eggs were 0.53 ± 0.008 by 0.32 ± 0.003 mm ($N = 14$) and bright yellow immediately on oviposition. Eggs faded to white at 4 d, except where yolk reserves remained near their center. *P. oblongus* eggs were 0.56 ± 0.005 by 0.29 ± 0.004 mm ($N = 10$) and pale yellow on oviposition, before darkening to brown after 48 h. Egg eclosion of *P. sericeus* and *P. oblongus* occurred at ≈ 9 –10 and 12–13 d, respectively, under conditions of 15:9 h (L:D) and 24:18°C (L:D). Approximately 2 d before egg eclosion, stemmata and mandibles were easily apparent through the chorion, and movement was pronounced. On eclosion, larvae did not consume the chorion. Nearly all eggs successfully completed eclosion. Newly eclosed *P. sericeus* larvae lived up to 10 d without food, but were very sluggish after 6 d. *P. oblongus* larvae lived up to 3 d without food.

The temporal distribution of *P. sericeus* oviposition under laboratory conditions is presented in Fig. 6a. Overall, 1,894 eggs were deposited from 16 July to 12 August 2002 in an asymptotic fashion. The number of eggs per mass also varied with time. There were fewer eggs per mass 12 August (10.8 ± 0.7) than on 18 July (17.7 ± 2.4) or 2 August (18.1 ± 2.1 ; $F_{3,78} = 4.55$; $P = 0.0054$; Fig. 6b).

The host plant species on which adult *P. sericeus* fed strongly affected fecundity. Overall, the total number

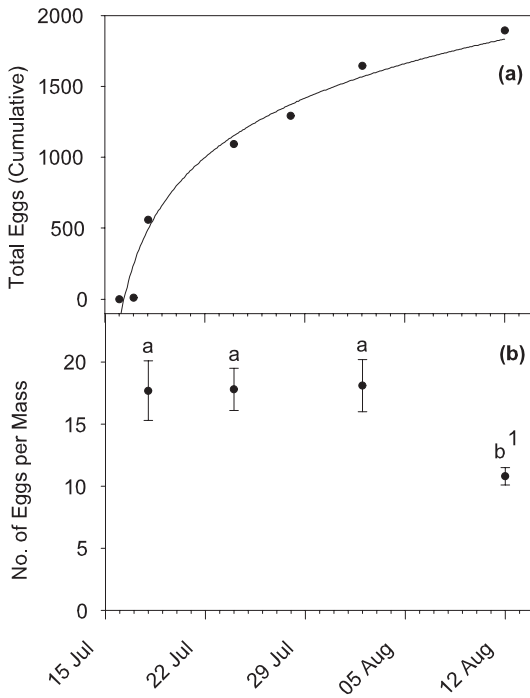


Fig. 6. Ovipositional pattern of *P. sericeus*. (a) Total egg production. 130 adults started assay 16 July. The equation of the trend line is $y = -170 + 601.3 \log_e(x)$, $df = 1, 5$; $R^2 = 0.96$; $P < 0.0001$. (b) Eggs per mass. Data are means \pm SE. Sample size of egg masses from 18 July, 24 July, 2 August, and 12 August were $n = 15, 30, 14,$ and 23 , respectively. Data points with the same letter do not differ at $P > 0.05$. See text for statistics. *Raw means are shown, although means comparison on $\log_e(y)$ transformed data did not indicate a statistically significant difference between 24 July and 12 August at $P > 0.05$.

of eggs per female averaged 830.1 ± 154.8 ($n = 16$; range, 0–2,117) when fed yellow birch compared with only 42.5 ± 11.4 ($n = 15$; range 0–159) when fed sugar maple. When adjusted for mortality, there were 1,488.7 eggs per surviving *P. sericeus* when fed yellow birch compared with just 60.5 eggs when fed sugar maple (Fig. 7a). Females oviposited nearly 15 times more eggs per day on a neutral surface (Kimwipes) when fed yellow birch (29.93 ± 1.43) than sugar maple (2.04 ± 0.36 ; $F_{1,754} = 337.54$; $P < 0.0001$). The number of egg masses per female per day averaged 1.49 ± 0.07 ($n = 443$) and 0.18 ± 0.03 ($n = 313$) when fed yellow birch and sugar maple, respectively. The mean number of eggs per mass was 20.1 ± 0.5 ($n = 661$; range, 1–96) and 11.6 ± 1.23 ($n = 55$; range, 2–28) when feeding on yellow birch and sugar maple, respectively.

Host plant consumption also affected *P. oblongus* fecundity, but in the opposite pattern. Overall, the total number of eggs per female averaged 23.8 ± 11.8 ($n = 8$; range 0–101) when fed sugar maple compared with only 2.0 ± 2.0 ($n = 9$; range 0–18) when fed yellow birch. When adjusted for mortality, there were 40.3 eggs per surviving *P. oblongus* when fed sugar

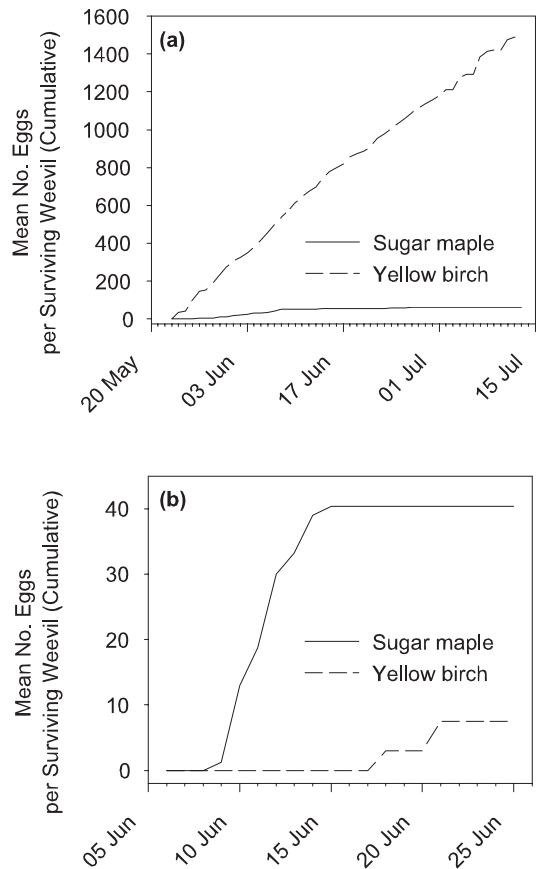


Fig. 7. Effect of adult feeding on yellow birch and sugar maple on (a) *P. sericeus* and (b) *P. oblongus* fecundity. See text for statistics.

maple compared with just 7.5 eggs when fed yellow birch (Fig. 7b). *P. oblongus* oviposited nearly 22 times more eggs per day on the neutral surface when fed sugar maple (4.32 ± 1.45) than yellow birch (0.2 ± 0.1 ; $F_{1,131} = 18.93$; $P < 0.0001$). The number of egg masses per female per day averaged 0.34 ± 0.10 ($n = 44$) and 0.022 ± 0.016 ($n = 89$) when fed sugar maple and yellow birch, respectively. The number of eggs per mass averaged 12.7 ± 1.7 ($n = 15$; range, 2–28) and 9.0 ± 0.0 ($n = 2$) when feeding on sugar maple and yellow birch, respectively.

Overall, the mean number of eggs produced per day by *P. sericeus* feeding on its optimal host plant, yellow birch, was significantly greater than *P. oblongus* feeding on its optimal host plant, sugar maple ($F_{1,485} = 39.18$; $P < 0.0001$). In addition, *P. sericeus* lived five times longer when feeding on yellow birch (27.7 ± 3.8 d), than did *P. oblongus* feeding on sugar maple (5.8 ± 1.1 d). The number of days to first oviposition was just 2.7 ± 0.3 for *P. sericeus*, and the mean total number of days during which oviposition occurred was 25.8 ± 4.0 . For *P. oblongus*, the number of days to first oviposition while in the laboratory averaged $4.6 \pm$

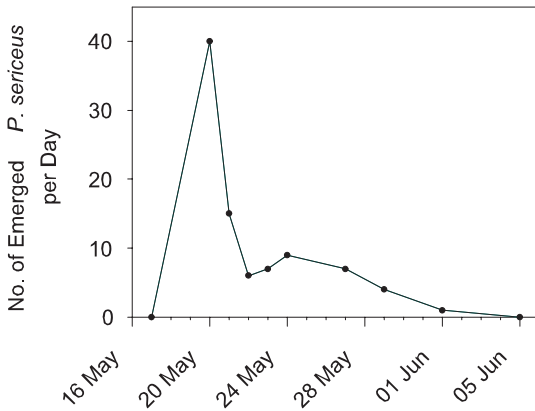


Fig. 8. Number of *P. sericeus* adults emerging per day from potted yellow birch seedlings in Madison, WI, during 2003. Seedlings ($n = 10$) were inoculated August 2002 with 0, 20, or 30 newly eclosed larvae per tree.

2.1, and the total number of days during which oviposition occurred averaged just 1.9 ± 0.9 .

Laboratory Rearing of *P. sericeus*. *Polydrusus sericeus* adults began emerging from outdoor potted yellow birch seedlings on 20 May 2003 (Fig. 8). Of the original 500 newly eclosed larvae used to inoculate the yellow birch seedlings, 17.8% completed development and emerged as adults: 44.9% of these were collected on 20 May and all were collected by 4 June. Adults were observed copulating immediately on emergence, and the first oviposition was observed just 2 d later. Copulation occurred frequently, resulting in multiple ovipositions every 1–2 d when adults fed on preferred host species.

Discussion

Polydrusus sericeus and *P. oblongus* adults fed on the foliage of all hardwood tree species tested under no-choice conditions (Figs. 1 and 4). These results provide the first host breadth data on *P. sericeus*, and this broad host range supports observations on *P. oblongus* by Witter and Fields (1977). Additionally, this feeding breadth agrees with descriptions in the European literature as polyphagous (Masse 1941, Witter and Fields 1977, Morris 1978).

Despite this polyphagy, leaf consumption by *P. sericeus* and *P. oblongus* varied greatly among host tree species. *P. sericeus* consumed more yellow birch, basswood, and ironwood than aspen or maple (Fig. 1a and b). In contrast, *P. oblongus* consumed more ironwood than poplar or yellow birch, with maple consumption intermediate between these groups (Fig. 4a and b). Although Simmons and Knight (1973) and Witter and Fields (1977) found *P. oblongus* to be prevalent in stands dominated by sugar maple regeneration, controlled laboratory assays indicate this is not a preferred host (Fig. 4). Most likely this association reflects the dominance, and hence high availability, of sugar maple

in northern hardwood forest understories (Goodburn 1996), rather than a compositional response to *P. oblongus* feeding. Feeding trends were similar between the sexes, although female *P. sericeus* consumed twice as much foliage as males (Fig. 2a and b).

Frass counts closely reflected both leaf area and leaf mass consumption (Fig. 3). Counting frass pellets is less time intensive than scanning leaves and may be more accurate for tree species on which foliage consumption is very small or difficult to measure. Strong relationships have been likewise observed between frass dry mass and percent defoliation for estimating pest populations of larval lepidopterans (Miller et al. 1991, Coffelt and Schultz 1993). Because frass production can be confounded by palatability, digestion, and compensatory feeding (Dethier 1982), it should complement rather than replace consumption data where possible.

These results reinforce the view that both no-choice and behavioral choice tests are needed to characterize an herbivore's host breadth and preference. For example, *P. sericeus* showed a pronounced preference for yellow birch over ironwood, basswood, and aspen during choice tests (Fig. 5). However, feeding on ironwood and basswood was not significantly different from yellow birch in no-choice assays (Fig. 1). Likewise, feeding on aspen was significantly less than on basswood or ironwood compared with yellow birch in no-choice assays but showed no separation from these in behavioral choice tests (Fig. 5). Such distinctions can also depend on the number of choices provided (Raffa et al. 2002).

Adult host plant has a pronounced effect on fecundity. *P. sericeus* fecundity was substantially higher when they fed on yellow birch compared with sugar maple, whereas the opposite was true for *P. oblongus* (Fig. 7). Overall, *P. sericeus* had greater longevity and fecundity when feeding on its optimal host plant than did *P. oblongus*. *P. oblongus* males were short-lived in the laboratory, with 80% of the ovipositional assays ending with a male death. Egg survivorship was always high. Egg size varied little among these two weevil species. These eggs were generally smaller, darker, and more spherical than those of a third invasive weevil species, *S. asperatus* (Pinski 2004). Additionally, there were distinct differences in appearance throughout egg maturation among *P. sericeus*, *P. oblongus*, and *S. asperatus*. This information can be applied to differentiate these species in the field.

A rearing system for *P. sericeus* was successfully established. A large number of eggs can be obtained in a relatively short time with minimal effort. In contrast, maintaining larval development was more time intensive and yielded lower returns. Overall, larval to adult survivorship was relatively high considering the uncertainties of working with below-ground herbivores. This system seems adequate for studies on larval feeding and impacts. Currently, only one generation per year can be produced by these methods.

Future research should emphasize how these feeding preferences relate to prior experience, population dynamics, the host range, feeding preferences, im-

pacts of larvae, and linkages between below- and above-ground processes. In addition, interactions among these weevils at both the within-tree and within-site scales, and interactions with other recently determined members of this nonindigenous root-feeding complex (Pinski et al. 2005), should be investigated. We cannot yet relate our findings to natural forest systems. There is a particular need for long-term information on how invasive, root-feeding insects affect forest dynamics such as recruitment, succession, and stand conversion and on native arthropod compositions.

Acknowledgments

We thank J. Ludden for conducting preliminary feeding assays. Field and laboratory assistance by A. Boyd, E. Lewandowski, K. Kieler, J. Frie, and R. Hoffman, Department of Entomology, University of Wisconsin (UW)-Madison and aid in specimen dissections by S. Krauth, Insect Research Collection, Department of Entomology, UW-Madison is greatly appreciated. We thank T. Marty and the Wisconsin Department of Natural Resources for providing test seedlings and L. Hummel for gracious help and support at the UW-Madison Walnut St. Greenhouses. B. Aukema, Department of Entomology, UW-Madison, helped with statistical analyses. We thank personnel from the Ottawa National Forest and UW-Madison for providing lands for insect and foliage collections. The USDA Forest Service and the UW-Madison College of Agricultural and Life Sciences funded these studies. The critical reviews of D. Young, D. Mahr (Department of Entomology), E. Kruger (Department of Forest Ecology and Management, UW-Madison), and two anonymous reviewers are greatly appreciated.

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Received 25 June 2004; accepted 11 November 2004.
