Host Plant Phenology Affects Performance of an Invasive Weevil, *Phyllobius oblongus* (Coleoptera: Curculionidae), in a Northern Hardwood Forest

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ABSTRACT   We investigated how host plant phenology and plant species affected longevity, reproduction, and feeding behavior of an invasive weevil. *Phyllobius oblongus* L. (Coleoptera: Curculionidae) is common in northern hardwood forests of the Great Lakes Region. Adults emerge in spring, feed on foliage of woody understory plants, and oviposit in the soil. Preliminary data indicate that adults often feed on sugar maple, *Acer saccharum* Marshall, foliage early in the season, then feed on other species such as raspberry, *Rubus* spp. Whether this behavior reflects temporal changes in the quality of *A. saccharum* tissue or merely subsequent availability of later-season plants is unknown. We tested adult *P. oblongus* in laboratory assays using young (newly flushed) sugar maple foliage, old (2–3 wk postflush) sugar maple foliage, and raspberry foliage. Raspberry has indeterminate growth, thus always has young foliage available for herbivores. Survival, oviposition, and leaf consumption were recorded. In performance assays under no-choice conditions, mated pairs were provided one type of host foliage for the duration of their lives. In behavioral choice tests, all three host plants were provided simultaneously and leaf area consumption was compared. Adults survived longer on and consumed greater amounts of young maple and raspberry foliage than old maple foliage. *P. oblongus* preferred young maple foliage to old maple foliage early in the season, however, later in the growing season weevils showed less pronounced feeding preferences. These results suggest how leaf phenology, plant species composition, and feeding plasticity in host utilization may interact to affect *P. oblongus* population dynamics.

KEY WORDS   *Acer saccaharum*, exotic species, folivore, plant-insect interactions, *Rubus*

Invasive species pose significant economic and ecological hazards, such as the loss of native species, altered plant-insect relationships, and increased pest management costs (Mooney and Cleeland 2001, Pimentel et al. 2005). One particularly pervasive and damaging group is nonindigenous forest insects (Brockerhoff et al. 2006), which cost the U.S. ≈2.1 billion dollars annually (Pimentel et al. 2005). A more thorough understanding of the ecology of specific invasive insects is needed to develop appropriate strategies to protect economic and environmental resources. For example, host plant quality and availability can strongly affect the performance of various invasive species (Potter and Held 2002, Mannion et al. 2003, van Tol et al. 2004, Fisher 2006, McEwan et al. 2009).

A complex of exotic root-feeding weevils has become established in North American deciduous forests, including the Great Lakes Region (Pinski et al. 2005a, Coyle et al. 2008). *Phyllobius oblongus* L. (Coleoptera: Curculionidae) appears to be the most abundant species in this complex (Pinski et al. 2005a). Adults emerge in early summer, feed on the foliage of understory woody plants, mate, and oviposit in the soil. Adults are present in the field for about 8 wk, and females can lay multiple fertile egg clutches after mating. Larvae feed on roots and overwinter belowground. Adults are polyphagous, but show strong preference for certain plant species (Witter and Fields 1977, Pinski et al. 2005b, Coyle et al. 2010). While no direct field impact studies have been conducted, *P. oblongus* has been associated with damaged sugar maple buds (Simmons and Knight 1973).

The seasonal distribution of these weevils suggests that host utilization patterns may be more complex than suggested by simple laboratory assays based on single time points. Adults initially feed on sugar maple, *Acer saccharum* Marshall, or raspberry, *Rubus* spp., in some years, but become more abundant on raspberry as the growing season progresses (Coyle 2010). Previous work (Coyle et al. 2010) suggested that change in hosts might extend *P. oblongus*' adult lifespan and ovipositional period, thereby influencing population dynamics. If so, forest management practices that fa-

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vor disturbance-adapted raspberry plants could foster eruptions of, and provide corridors for, these invasive insects. However, an underlying element of this model has not been examined, i.e., whether raspberry is inherently preferable to sugar maple, or whether phenological shifts in host quality drive behavioral responses of *P. oblongus.*

Phenological changes strongly affect the nutritional quality and defensive chemistry of foliage to many insect herbivores (Scheirs et al. 2002, Egusa et al. 2006). Temporal changes in host quality can affect insect population dynamics, emergence patterns, and feeding preference (Feeny 1970, Chen and Poland 2009, Fry et al. 2009). An understanding of how *P. oblongus* responds to phenological changes in sugar maple and raspberry could facilitate population sampling, and suggest forest management strategies that may reduce the impact of this exotic species. Under natural conditions, plant phenological changes are typically accompanied with insect aging, so this factor also needs to be considered when evaluating underlying mechanisms (Smith et al. 2002, Li et al. 2009).

Because sugar maple is the most abundant tree species in these stands (Goodburn 1996), interactions between *P. oblongus* and sugar maple are of particular interest. We investigated how the longevity, oviposition rate, and feeding intensity (i.e., the amount of leaf area consumed) of *P. oblongus* varied with the phenology of sugar maple and raspberry foliage.

Methods and Materials

Plant Material. Three types of foliage were evaluated concurrently: newly flushed sugar maple (young maple foliage), 2–3 wk postflush sugar maple (old maple foliage), and newly-flushed raspberry (raspberry foliage). Raspberry has indeterminate growth, that is, young foliage is always available, so there is no "old" raspberry foliage for the purpose of this study.

Two maple leaf age classes were made available for simultaneous testing by transporting one group of saplings to a slightly lower latitude (see below). Young maple and raspberry foliage were collected from the Ottawa National Forest near Taylor Lake in Gogebic Co., MI, (46.2399°N, 89.0462°W; elevation 1749′) in a northern hardwood forest ecosystem. The soil is sandy loam (Bockheim 1997) to a depth of 30 cm, below which it has a high composition of clay and rocks. The region has a mean annual air temperature of 4–5°C, a frost-free period of 100 d, and averages 850 mm of rainfall annually (Goodburn 1996). The dominant tree species in this area is sugar maple, with basswood (*Tilia americana* L.), ironwood (*Ostrya virginiana* (Miller) K. Koch), and leatherwood (*Dirca palustris* L.) also present (Goodburn 1996). Raspberry and gooseberry (*Ribes* spp.) are common understory shrubs. Twenty sugar maple saplings and raspberry plants were marked in the field, and from each of these plants one maple branch or raspberry shoot was collected on four and 18 June 2008. Plant material was transported to the laboratory in water.

Old maple foliage was obtained by transplanting 20 sugar maple saplings with field soil from the Ottawa National Forest into pots and transporting them to the University of Wisconsin-Madison campus (43.0758°N, 89.4239°W; elevation 850′) in the spring of 2007. The UW-Madison campus is characterized by a mean annual temperature of 7–8°C, a frost free period of 160 d, and 928 mm of average annual rainfall. The UW-Madison campus is ≈400 km south of the collection site; thus, these plants experienced budbreak ≈3-wk earlier than those in the Ottawa National Forest. Potted saplings were kept outside in mostly sunny conditions, and were allowed to senesce in 2007 and reflush naturally in 2008. Leaves were clipped at the base of the petiole and transported to the laboratory in individual plastic bags in a cooler on ice on 5 and 19 June 2007.

Insects. Adult mating pairs were hand-collected from a mixture of woody plant species in the Ottawa National Forest near the same location where foliage was collected. Single mating pairs were placed in individual vials, transported to the laboratory, and starved for 24 h before use in assays. Although we cannot know the mating or feeding history of weevils collected under natural conditions, this method appears to have little effect on subsequent ability to show host-specific preference and performance in laboratory assays (Pinski et al. 2005b, Coyle et al. 2010, Hillstrom et al. 2010).

Weevils were collected on 4 June and 18 June 2008. *Phyllobius oblongus* has a very narrow emergence period (Coyle 2010). For example, in 2007 we sampled emergence traps weekly for 5 wk, and observed that over 94% of all *P. oblongus* were caught within a 1-wk period (Coyle 2010). Likewise, in 2008, adult *P. oblongus* first appeared between 29 May and 5 June, and by 19 June their emergence period was nearly complete (Coyle 2010). Because of this synchronous emergence pattern, weevils collected on the two dates likely represented differently aged, rather than differently emerged, individuals. We termed them putatively "young" and "old" weevils, respectively, with collection date as a proxy for age. Voucher specimens were deposited in the Department of Entomology Insect Research Collection at the University of Wisconsin-Madison (Coyle et al. 2010).

Performance Assays Under No-Choice Conditions. We conducted two no-choice assays following previously described methods (Pinski et al. 2005b, Coyle et al. 2010). Assays were initiated one day after each weevil collection, and evaluated young maple, raspberry, and old maple foliage, with putatively young and old weevils, respectively. For each assay ($n = 20$ per foliage type) we used one leaf from each plant. We used LPI (Larson and Isebrands 1971) 3 or 4 for maple saplings, and LPI 4 or 5 for raspberry plants.

Leaves were clipped at the petiole near the stem and immediately digitally scanned to determine leaf area before initiation of each assay. One whole leaf, with the petiole wrapped in moist cotton, was placed in a plastic petri dish (2 cm tall × 15 cm diameter) with a piece of moistened Whatman filter paper on the bottom, along with a dry Kimwipe tissue. Kimwipe

tissues were used to monitor oviposition, as previous work has shown that Kimwipe tissue provides a good ovipositional surface for *P. oblongus* in petri dish assays (Pinski et al. 2005b).

One apparently healthy pair of *P. oblongus* was added to each petri dish. Dishes were kept in growth chambers with a 16:8 liters:day photoperiod and a day:night temperature regime of 24°:18°C. Dishes were monitored daily, and cotton balls were remoistened every other day or whenever they began to desiccate. The total number of days that each weevil lived within a dish was summed and termed total longevity. The male was always smaller than the female, allowing determination of the longevity of each sex. Dead weevils were removed from the dishes, and assays were continued until both weevils had died. Kimwipe tissues were changed daily and total number of eggs was counted. Leaves were changed every 5 d or as needed, and were scanned after removal from assays to determine leaf area consumed.

Behavioral Choice Assays. Three-way choice tests were conducted using young maple, old maple, and raspberry foliage. Assays were conducted 1 d after each weevil collection, with putatively young and old weevils, respectively. Two 2.8 cm^2 discs were punched from one leaf of each host plant, and placed together in a plastic petri dish configured as before. Leaves were collected from the same plant stem and in the same manner as in no-choice assays. One pair of apparently healthy *P. oblongus* was placed in the center of each dish. Dishes ($n = 20$ per foliage type) were kept in growth chambers with a 16:8 liters:day photoperiod and a day:night temperature regime of 24°:18°C, and were maintained for 48 h. Leaf disks were digitally scanned to determine leaf area consumed.

Statistical Analyses. Total egg production and oviposition rate data were log transformed, and leaf area consumption and consumption rate data were square root transformed to achieve normality. There is a strong relationship between leaf area and leaf mass of sugar maple and raspberry, with r^2 values ranging from 0.83 to 0.99 (Coyle et al. 2010). Therefore, leaf area consumption is a reliable surrogate for leaf mass consumption.

We analyzed each trial separately to avoid the confounding the factor of weevil and foliar ages. No-choice data from each weevil age category trial were analyzed separately as a randomized complete block design using Proc GLM (SAS Institute, version 9.0, Cary, NC) with host foliage type as the fixed factor. All means were compared using Fisher least significant difference (LSD) with an α level of 0.05. One petri dish was excluded from the first trial and three were excluded from the second trial because of missing or accidental human-induced mortality of insects.

Behavioral choice data from each weevil age category trial were analyzed separately as a randomized complete block design using Proc analysis of variance (ANOVA) (SAS Institute, version 9.0, Cary, NC) with host foliage type as the fixed factor. All means were compared using Fisher LSD with an α level of 0.05.

Table 1. Effects of three foliage types on performance of *P. oblongus* adults in no-choice assays

Performance parameter	Young weevils		Old weevils	
	F (2, 58)	P value	F (2, 56)	P value
Total longevity (d)	2.61	0.0825	1.16	0.3219
Female longevity (d)	1.07	0.3484	0.76	0.4715
Male longevity (d)	4.11	**0.0216**	0.89	0.4158
Total eggs	2.31	0.1087	0.56	0.5750
Eggs/female/d	1.97	0.1484	0.50	0.6118
Total leaf area consumed (cm^2)	27.67	**<0.0001**	1.13	0.3293
Leaf area consumed/weevil/d (cm^2)	41.72	**<0.0001**	0.99	0.3788

Performance parameter statistics are shown separately for putatively young and old adult *P. oblongus*. Where significant differences occurred, *P* values are shown in boldface type.

Results

Performance Assays Under No-Choice Conditions. Host foliage type phenology affected several performance parameters of adult *P. oblongus* (Table 1). Host foliage type did not affect total adult longevity (Fig. 1A) or female longevity (Fig. 1B), but longevity of putatively young males (Fig. 1C) was greater on young than old maple. Host plant did not affect total egg production (Fig. 1D) or egg production rate (Fig. 1E). Putatively young weevils produced over twice as many eggs on young maple than on old maple. In contrast, egg production was not affected by host foliage type in putatively older weevils. Total leaf area consumption and consumption rate by young weevils were greater on young maple and raspberry foliage than old maple foliage (Fig. 1 F). As with egg production, feeding did not differ among host plants for older weevils (Fig. 1G).

Behavioral Choice Assays. Host foliage type phenology influenced adult *P. oblongus* feeding preference from both putative age categories (Fig. 2). Young maple and raspberry foliage were preferred by younger adults ($F = 35.53$; df = 2, 59; $P < 0.0001$), and were consumed over three times more than old maple foliage. Older weevils preferred young maple foliage over raspberry foliage, and both young maple and raspberry foliage over old maple foliage ($F = 11.01$; df = 2, 59; $P < 0.0001$).

Discussion

Seasonal changes that are known to occur in maple foliage could potentially contribute to the effects we observed of leaf age on adult *P. oblongus*. In particular, increased leaf toughness, decreased water content, and decreased nitrogen content can reduce herbivore performance (Feeny 1970, Schultz et al. 1982, Čížek 2005, Sanson 2006). Only a 2–3 wk difference, which is a relatively small proportion of maple's total growing season, had a sevenfold difference in weevil feeding (Fig. 1F and G).

Putatively young weevils showed higher performance than older weevils, which is consistent with results from many insect species (Fox 1993, Makee and
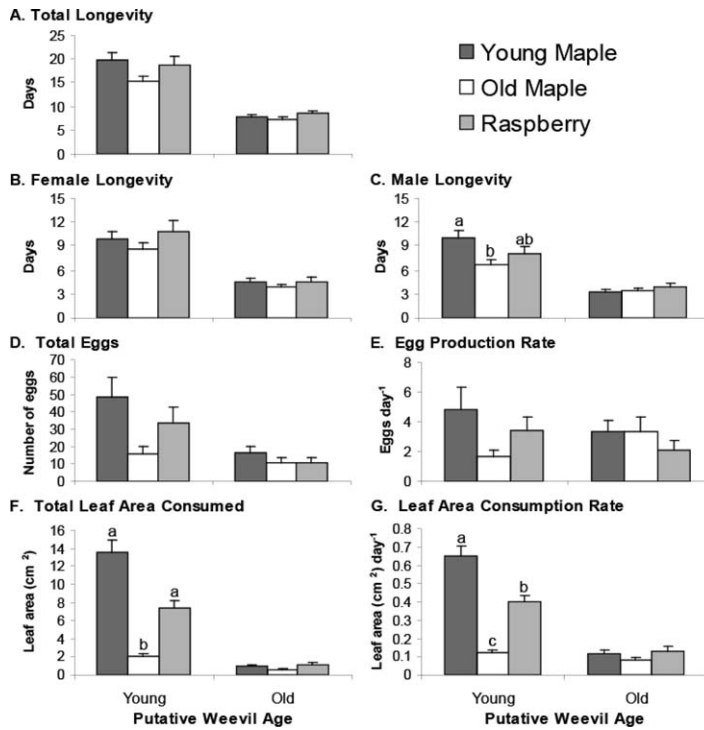
Fig. 1. Effects of foliage type on performance of *P. oblongus* adults in no-choice assays. Performance parameters shown separately for putatively young and old adult *P. oblongus* (age estimated based on time of collection): (A) total longevity, (B) female longevity, (C) male longevity, (D) total egg production, (E) egg production rate, (F) total leaf area consumed, (G) leaf area consumption rate. For each parameter, means within a weevil age category sharing a letter are not significantly different at $\alpha = 0.05$.

Saour 2001, Smith et al. 2002, Ridgel et al. 2003, Li et al. 2009). However, despite their lower vigor, older *P. oblongus* seemed better able to exploit old host foliage. For example, older weevils consumed more old maple foliage, the least preferred tissue, than did young weevils in choice tests (Fig. 2). In addition, older *P. oblongus*, showed no significant difference in any per-

Fig. 2. Feeding preferences of *P. oblongus* adults in behavioral choice assays. Leaf area consumption rate (mean ± SE) shown separately for putatively young and old adult *P. oblongus* (age estimated based on time of collection). Within a weevil age category, means sharing a letter are not significantly different at $\alpha = 0.05$.

formance parameter between old maple foliage and either young maple or raspberry foliage under no-choice conditions (Fig. 1). Likewise, the trend for higher oviposition on young than old maple foliage by young weevils was absent in putatively older weevils. Under natural conditions, older *P. oblongus* no longer have access to young sugar maple foliage, and raspberry is far less abundant in these stands (Kraft et al. 2004). Therefore, the ability to use older maple may be advantageous. Plasticity in host utilization can broaden the range of plants on which polyphagous herbivores successfully feed and reproduce (Renwick 2001). In addition, for sexually reproducing species such as *P. oblongus*, the ability of males to survive equally well on old maple, young maple, or raspberry could indirectly contribute to elevated population levels (Rankin and Kokko 2007, Schmickl and Karsai 2010).

We cannot relate differences in putatively young versus old weevil performance to a precise difference in age. Similarly, potential differences in feeding and ovipositional experience could contribute variance to our laboratory assays of wild individuals. Future studies using laboratory-reared individuals could control for these variables, and thereby complement studies using field-collected individuals that developed under more realistic conditions.
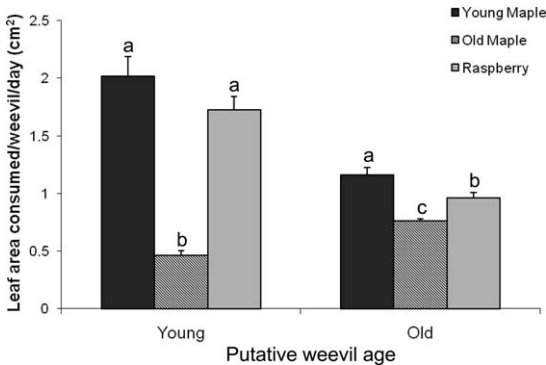
The ability of *P. oblongus* to exploit raspberry, a plant that continually produces young foliage, appears to increase their feeding and ovipositional potential. Raspberry shows the same foliar quality as young maple for weevil longevity, oviposition, and feeding. Therefore, forest management practices, such as logging, road construction, and clear cutting, which favor this disturbance-adapted plant (Ricard and Messier 1996, Kraft et al. 2004) may contribute to the success of *P. oblongus* and other invasive insects with similar behavior.

Acknowledgments

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