

# Feeding and Oviposition Behavior of *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae) and Its Predicted Effectiveness as a Biological Control Agent for *Polygonum perfoliatum* L. (Polygonales: Polygonaceae)

K. COLPETZER, J. HOUGH-GOLDSTEIN,<sup>1</sup> K. R. HARKINS, AND M. T. SMITH<sup>2</sup>

Delaware Agricultural Experiment Station, Department of Entomology and Wildlife Ecology, College of Agriculture and Natural Resources, University of Delaware, Newark, DE 19716–2160

Environ. Entomol. 33(4): 990–996 (2004)

**ABSTRACT** Feeding and oviposition on different parts of mile-a-minute weed, *Polygonum perfoliatum* L. (Polygonales: Polygonaceae), by *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae), a potential biological control agent for the weed, were studied in quarantine. An additional experiment was conducted to test the effects of different levels of simulated damage by *R. latipes* on *P. perfoliatum* growth, survival, and reproduction. Female weevils consumed more *P. perfoliatum* overall than males and selectively fed on capitula more than on ocreae or leaves, whereas males fed more on ocreae than on leaves or capitula. More eggs were also laid on capitula than on other plant parts. Female feeding preference is probably because of the high protein content of the capitula, because protein is required for continued egg production, whereas males may maximize their reproductive success by feeding low and close to *P. perfoliatum* stems to intercept females as they emerge from pupation in the soil and ascend the plants to feed. The feeding and oviposition preferences of female *R. latipes* for plant capitula suggest that host specificity tests for this species should be conducted with plants that are flowering. Damage that simulated the effect of *R. latipes* larval feeding caused plant mortality when it was initiated on small *P. perfoliatum* plants and reduced biomass and seed production when it was initiated on larger plants. Thus *R. latipes* could have a substantial impact on *P. perfoliatum* if the weevil is released into the weed's introduced range in North America.

**KEY WORDS** *Rhinoncomimus latipes*, mile-a-minute weed, *Polygonum perfoliatum*, feeding, simulated herbivory

PRACTITIONERS OF CLASSICAL BIOLOGICAL control of weeds are increasingly challenged to show the safety of the organisms they propose to import and their predicted effectiveness (DeClerck-Floate and Bouchier 2000, Kluge 2000, McEvoy and Coombs 2000, Louda et al. 2003). Although various methods for prerelease assessment have been proposed, Blossey (1995) concluded that such methods did not effectively allow for selection of the most successful agents before release, even for insect species that had been extensively studied in their European home range before release in North America. For alien plants that originate in Asia, the lack of easily accessible literature and research infrastructure has often hampered such extensive field studies in the native range. Nevertheless, several approaches may help assess potential effectiveness of new agents before release in a new area.

Study in quarantine of the insect's feeding and oviposition behavior on the host plant can help predict its potential impact on the plant. For example, *Eustenopus villosus* Boheman (Coleoptera: Curculionidae) feed and oviposit on the capitulum (developing seed head) of yellow starthistle (*Centaurea solstitialis* L.; Fornasari et al. 1991). This insect is thought to be an effective control agent because its feeding and oviposition distorts *C. solstitialis* buds and reduces seed production (Fornasari et al. 1991, Fornasari and Sobhian 1993, Connett et al. 2001). Study of the herbivore's preferred feeding and oviposition site can also help with the design of an appropriate postrelease monitoring strategy by suggesting where the insect is most likely to be found and may also help ensure the proper evaluation of host specificity. For example, if an agent only oviposits on the flowers of its host or only oviposits when its host is flowering, host specificity tests should be conducted with plants that are flowering. Both egg maturation and oviposition behavior can vary substantially depending on host availability and quality (Papaj 2000).

<sup>1</sup> E-mail: jhough@udel.edu.

<sup>2</sup> United States Department of Agriculture—Agricultural Research Service Beneficial Insect Introduction Research Unit, Newark, DE 19716.

Experimental simulation of the agent's observed mode of damage to the host plant is another possible approach to assessing potential effectiveness. For example, McEvoy et al. (1991) used simulated herbivory as part of an assessment of the impact of cinnabar moth (*Tyria jacobaeae* L., Lepidoptera: Arctiidae) feeding on tansy ragwort (*Senecio jacobaeae* L.). Simulated damage can suggest the plant's sensitivity to the type of damage inflicted by the proposed agent, although the effects of mechanical damage may differ from actual herbivory (Baldwin 1990), and damage to individual plants may not translate directly to impacts on plant populations. Tiffin and Inouye (2000) compared estimates of plant damage from natural versus artificial or manipulated herbivory and concluded that estimates derived from simulated herbivory are likely to be unbiased, but less precise, than those from natural herbivory.

In this study, feeding and oviposition on different parts of mile-a-minute weed, *Polygonum perfoliatum* L. (Polygonales: Polygonaceae), by *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae) were studied in quarantine. In addition, an experiment was conducted to test the effect of different levels of simulated damage by *R. latipes* on *P. perfoliatum* growth, survival, and reproduction.

*Polygonum perfoliatum* is an annual vine indigenous to temperate regions of Bhutan, China, India, Indonesia, Japan, Korea, Nepal, the Philippines, Russia, and Vietnam (Wu and Raven 2003). It was introduced into a nursery in Stewartstown, PA, during the 1930s (Moul 1948, Riefner 1982), and has since spread to Delaware, the District of Columbia, Maryland, New Jersey, New York, Ohio, Virginia, and West Virginia (Oliver 1996), and more recently, Connecticut (Lamont and Fitzgerald 2001). It has been listed as a noxious weed in several states because it forms dense, prickly thickets that displace native vegetation, interfere with forest regeneration, and reduce the recreational value of natural areas (Mountain 1989, McCormick and Hartwig 1995, Oliver 1996).

The USDA Forest Service initiated a classical biological control program for *P. perfoliatum* in 1996. During 6 yr of field surveys in China, over 100 insect species were collected from *P. perfoliatum* (Ding et al. 2004). One of the most promising, both in terms of observed impact on the plant in China and host-specificity (Price et al. 2003, Colpetzer et al. 2004), was *Rhinoncomimus latipes* Korotyaev. This weevil was initially misidentified as *Homorosoma chinensis* (Wagner) (synonym: *Homorosoma chinense* Wagner). Specimens were later sent to B. A. Korotyaev of the Zoological Institute of the Russian Academy of Sciences, who identified them as *R. latipes* Korotyaev (Korotyaev 1997). Field release of this weevil in North America has been recommended by the Technical Advisory Group for Biological Control Agents of Weeds, and an application for a release permit is currently under consideration by the USDA APHIS-PPQ.

Adult *R. latipes* are  $\approx 2$  mm long, eat young leaves of *P. perfoliatum*, and lay eggs on leaves and stems. After hatching, larvae bore into the stem, where they com-

plete development, exit the stem, and drop to the soil for pupation. Damage to the plant occurs primarily from larval feeding, which kills the stem from the exit hole to the stem terminal (Price et al. 2003). In China, adult weevils overwinter in litter and emerge in the spring when *P. perfoliatum* is 30–50 cm tall. The weevil is thought to be univoltine in northern China, but may have multiple generations further south (D. Jianqing, personal communication).

## Materials and Methods

***Rhinoncomimus latipes* Feeding and Oviposition Behavior.** *Rhinoncomimus latipes* originating from adults collected in Changsha, Hunan province of China in 2000 and 2001 were reared on *P. perfoliatum* in a quarantine room kept at  $22 \pm 0.5^\circ\text{C}$  at the USDA-ARS Beneficial Insects Introduction Research Unit in Newark, DE, using the methods of Price et al. (2003). Voucher specimens of *R. latipes* have been deposited in the University of Delaware Department of Entomology and Wildlife Ecology Insect Reference Collection.

*Polygonum perfoliatum* plants were grown in a greenhouse from seeds collected locally and germinated using the methods of Colpetzer and Hough-Goldstein (2004). Plants were supplied with drip irrigation and supplemental light that provided a 16-h photophase and a minimum photosynthetic photon flux of  $200 \mu\text{mol}/\text{m}^2/\text{s}$ . They were fertilized every other week with 250 ml of a 0.4% solution of Miracle-Gro Professional (21% N; 5% P; 20% K).

Ten newly emerged male and 10 newly emerged female *R. latipes* adults were placed individually in plastic cylindrical cages (15 cm diameter by 20 cm high) with removable screen covers. The weevils were sexed by assessing the shape of the metasternum, which is more convex in the female than in the male (Price et al. 2003). Once oviposition began, females were marked with white-out (Sailor Corporation of America, Fayetteville, GA) on their elytra to facilitate sorting following mating.

Each container was supplied with a freshly cut *P. perfoliatum* stem in a 125-ml Erlenmeyer flask filled with water and stopped with cotton. All stems were 20 cm long, with a single capitulum (Fig. 1), and were taken from 1.5- to 2-mo-old plants. Stems were replaced every 3 d for 63 d. When plant material was changed, all 20 *R. latipes* were placed in a 9-cm petri dish and allowed to mate for  $\approx 2$  h.

Each time plant material was changed, feeding damage was measured on ocreae (saucer-shaped leafy structures that encircle the stem at each leaf node), leaves, and capitula (including the three terminal ocreae and two terminal leaves associated with flowers or fruits: Fig. 1). Although some feeding by females was observed on flowers and fruits, this was not quantified. Area consumed was measured by pressing the individual plant parts, photocopying them onto transparencies, and processing the transparencies through a portable leaf area meter (LI-3000A; LI-COR, Lincoln, NE) twice before and twice after filling in the

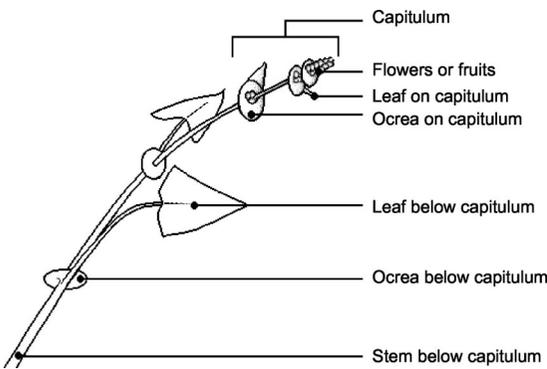


Fig. 1. Aerial structures of *P. perfoliatum*.

area eaten using a permanent marker. Eggs found on capitula, stems, leaves, and ocreae were also counted.

To determine whether male *R. latipes* emerged from pupation before females, three male and three female *R. latipes* adults were put in each of four plastic cylindrical cages containing 5 cm of moist vermiculite. Each cage was supplied with a 30-cm length of *P. perfoliatum* stem, still attached to a potted plant. After 24 h, and on 4 consecutive d, the weevils were moved to new cages with new stems. All containers were held without weevils to allow eggs that had been laid on the stems to hatch, larvae to develop, and pupation to occur in the vermiculite. After 20 d, *P. perfoliatum* stems were removed from the containers, which were then monitored daily for emerging adults. The sex of newly emerged adults was determined as described above.

The amount of *P. perfoliatum* consumed by *R. latipes* was  $\log(x + 1)$  transformed and analyzed using a repeated measures two-way analysis of variance (ANOVA) by sex and plant part, with cages as the repeated measure. The transformation did not completely normalize the data, but skewness and kurtosis moments (1.44 and 2.04, respectively) were within acceptable limits, and the mean was within the interquartile range. A one-way repeated measures ANOVA with sex and plant part combined and with nominated posterior contrasts was used for mean separation. Number of eggs deposited on *P. perfoliatum* during the period that females were ovipositing (days 9–63) was analyzed using PROC GENMOD with a negative binomial probability distribution, type III contrasts, log linkages, and cages as the repeated measure (SAS Institute 1999). The algorithm converged, and data were properly dispersed ( $\chi^2 = 656.4632$  and  $\chi^2/df = 0.8683$ ). This procedure produced a test similar to a one-way repeated measures ANOVA by plant part but did not require the errors to be independent, have equal variances, or be normally distributed (Orelien 2001). Nominated posterior contrasts were employed for mean separation. The relationships between feeding location and weevil age and oviposition location and weevil age were subjected to regression analysis (PROC REG; SAS Institute 1999). Mean emergence times of male and female adult *R. latipes* were compared using a two-sample *t*-test.

**Simulated Damage to *P. perfoliatum*.** *Polygonum perfoliatum* plants were grown from seed collected locally in September 2001 and germinated using the methods of Colpetzer and Hough-Goldstein (2004). Germinated seeds were planted in Promix in plastic pots on 12 April 2002, and placed in a greenhouse under drip irrigation as described above.

On 7 May, 52 *P. perfoliatum* plants, 30–50 cm tall, were transplanted into a 12 by 39 m untilled field (planted in corn the previous year) at the University of Delaware Experiment Station Farm, Newark, DE. The field was divided into 3 by 3-m plots, and a single plant was transplanted into the center of each plot. Plots were arranged in a randomized complete block design with four replications and 13 treatments, including the control. Several seedlings failed to establish and were replaced with plants from the greenhouse before treatments were applied.

Treatments consisted of clipping plants with dissection scissors, beginning when plants were small (15 leaves), medium-sized (60–90 leaves), or large (240 leaves). For each size class, damage by one to four female beetles per plant was simulated. In the laboratory, *R. latipes* eggs are laid singly or in small clusters at a rate of  $\approx 3$  eggs/d, and newly hatched larvae crawl down the stem and bore into the first unoccupied node. Larval feeding then causes death of the stem from that node apically to the stem terminal (Price et al. 2003). Therefore, damage by one beetle was simulated by clipping three nodes from a stem terminal each day, two beetles by clipping six nodes, etc. Only the shoot that had the greatest length from the base of the plant to the apex was clipped each day. Clipping continued for each plant until that plant died or until 6 August, when the experiment was terminated. All seeds produced before 6 August were collected into marked paper bags and left to dry in a ventilated greenhouse. On 6 August, all remaining *P. perfoliatum* seeds, stems, and leaves were collected, allowed to dry, and subsequently weighed.

Mean plant survival times from planting to a maximum of 91 d (when the experiment ended) were analyzed using a two-way ANOVA by block and treatment followed by Tukey's test for mean separation. Seed number and plant biomass data were not normally distributed and did not have homogeneous variances even when transformed; therefore, these data were analyzed using the nonparametric Kruskal-Wallis test (PROC GLM on ranks; SAS Institute 1999), with mean separation based on least significant difference (LSD). Untransformed means and SEs are shown in the figures.

## Results

***Rhinoncomimus latipes* Feeding and Oviposition Behavior.** The total amount of foliage consumed per weevil per 3 d averaged  $0.39 \pm 0.03$  cm<sup>2</sup> (SEM) for females and  $0.23 \pm 0.03$  cm<sup>2</sup> for males. Females consumed significantly more *P. perfoliatum* overall ( $N = 20$ ,  $df = 1$ ,  $F = 74.71$ ,  $P < 0.0001$ ) and significantly more capitula (Fig. 2) than males.

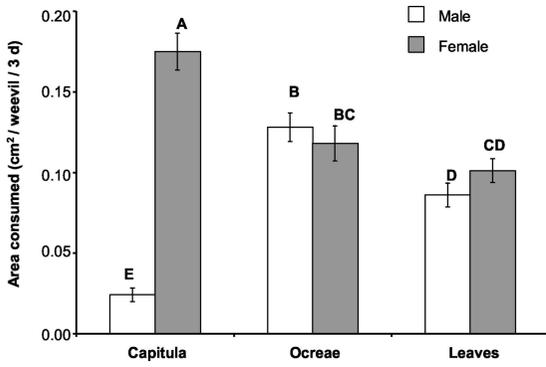


Fig. 2. *Rhinocomimus latipes* male and female consumption (mean  $\pm$  SEM) of different parts of *P. perfoliatum*. Means sharing the same letters are not significantly different (ANOVA, type III contrasts).

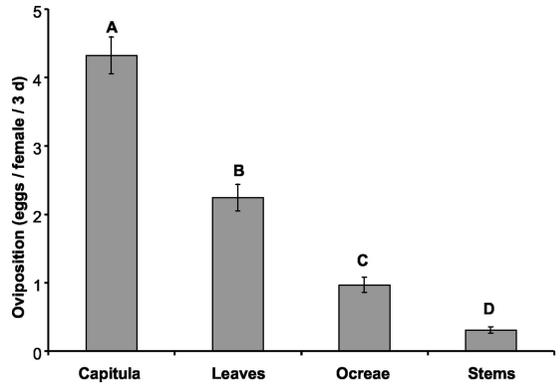


Fig. 4. *Rhinocomimus latipes* oviposition (mean  $\pm$  SEM) on different parts of *P. perfoliatum*. Means sharing the same letters are not significantly different (PROC GENMOD, type III contrasts).

Females consumed more capitula than ocreae or leaves (Fig. 2), and capitula consumption increased significantly with age, whereas leaf feeding declined (Fig. 3A). Males consumed more ocreae than leaves or capitula (Fig. 2). Male preference for feeding on ocreae increased with age, whereas leaf feeding

declined and capitula feeding increased slightly (Fig. 3B).

Females laid more eggs on *P. perfoliatum* capitula than on any other plant part ( $N = 10$ ,  $df = 3$ ,  $\chi^2 = 9.82$ ,  $P = 0.0202$ ; Fig. 4), and this preference became more pronounced as the weevils aged (Fig. 5). After the first 9 d, mean egg production fluctuated between 6 and 12 eggs per female per 3 d for the remainder of the experiment (Fig. 6).

Male *R. latipes* emerged from pupation  $\approx 2$  d before females, with time to emergence averaging  $25.1 \pm 0.1$  d ( $N = 28$ ) for males and  $26.8 \pm 0.1$  d ( $N = 30$ ) for females ( $t = 46.65$ ,  $P < 0.0001$ ).

Simulated Damage to *P. perfoliatum*. All plants that were clipped to simulate *R. latipes* damage beginning when they were small died by 6 August, whereas only one of the large clipped plants died before the experiment was terminated. Mortality of medium-sized plants ranged from 25% at the lowest level of damage to 100% at the highest level. Small clipped plants survived for an average of 15–21 d, whereas medium-sized

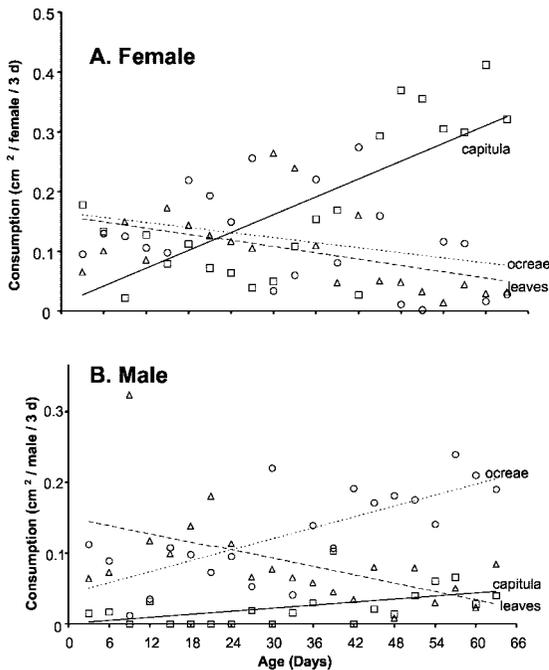


Fig. 3. Female (A) and male (B) *R. latipes* consumption of *P. perfoliatum* over time. For females on capitula,  $Y = 0.01160 + 0.00497X$  ( $R^2 = 0.5378$ ;  $F = 22.11$ ;  $P = 0.0002$ ); on ocreae,  $Y = 0.16495 - 0.00141X$  ( $R^2 = 0.1074$ ;  $F = 2.29$ ;  $P = 0.1470$ ); and on leaves,  $Y = 0.15953 - 0.00176X$  ( $R^2 = 0.2277$ ;  $F = 5.60$ ;  $P = 0.0287$ ). For males on capitula,  $Y = 0.00002 + 0.00072X$  ( $R^2 = 0.2528$ ;  $F = 6.43$ ;  $P = 0.0202$ ); on ocreae,  $Y = 0.04260 + 0.00258X$  ( $R^2 = 0.5385$ ;  $F = 22.17$ ;  $P = 0.0002$ ); and on leaves,  $Y = 0.15044 - 0.00195X$  ( $R^2 = 0.2908$ ;  $F = 7.79$ ;  $P = 0.0116$ ).  $\square$ , capitula;  $\circ$ , ocreae;  $\triangle$ , leaves.

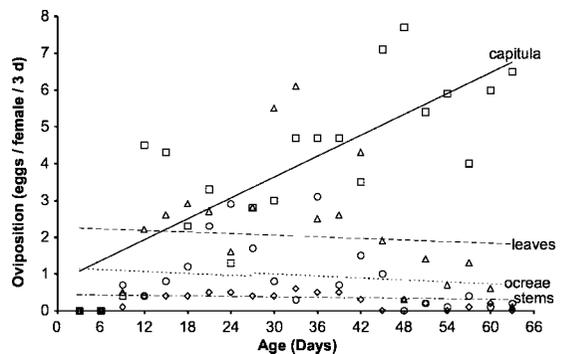


Fig. 5. *Rhinocomimus latipes* oviposition on *P. perfoliatum* over time. On capitula,  $Y = 0.78810 + 0.09459X$  ( $R^2 = 0.6258$ ;  $F = 31.77$ ;  $P < 0.0001$ ); on leaves,  $Y = 2.26286 - 0.00710X$  ( $R^2 = 0.0060$ ;  $F = 0.11$ ;  $P = 0.7396$ ); on ocreae,  $Y = 1.16619 - 0.00879X$  ( $R^2 = 0.0305$ ;  $F = 0.60$ ;  $P = 0.4488$ ); and on stems,  $Y = 0.34762 + 0.00216X$  ( $R^2 = 0.0387$ ;  $F = 0.77$ ;  $P = 0.3952$ ).  $\square$ , capitula;  $\triangle$ , leaves;  $\circ$ , ocreae;  $\diamond$ , stems.

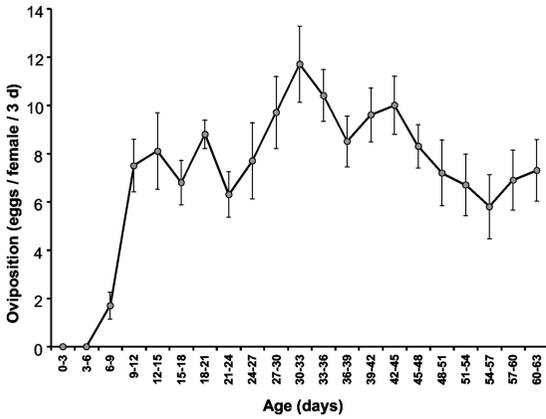


Fig. 6. *Rhinoncomimus latipes* age-specific fecundity (mean  $\pm$  SEM).

plants survived for 51–91 d, depending on level of damage (Fig. 7).

The mean amount of biomass produced by large plants clipped to simulate damage by one to four beetles, and medium-sized plants clipped to simulate damage by one beetle, did not differ from the control (Fig. 8A), but the medium-sized plants damaged at the two-, three-, and four-beetle levels produced significantly less biomass than the control plants. The number of seeds produced by large plants at any damage level did not differ significantly from the number produced by the control plants (Fig. 8B), but plants damaged at any level beginning when they were medium-sized produced significantly fewer seeds than the control. Small plants are not included in Fig. 8 because they all died before 6 August and produced no biomass or seed.

Discussion

The overall greater consumption of *P. perfoliatum* by female than by male *R. latipes* is predicted by anisogamy, the differential investment in gametes by the sexes. Because sperm are small and relatively

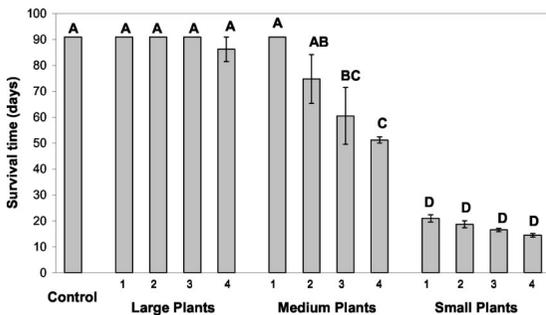


Fig. 7. Mean survival time of *P. perfoliatum* plants subjected to four levels of simulated *R. latipes* damage (1–4 beetles/plant) beginning when small, medium-sized, or large. Means sharing the same letters are not significantly different (ANOVA, Tukey’s test).

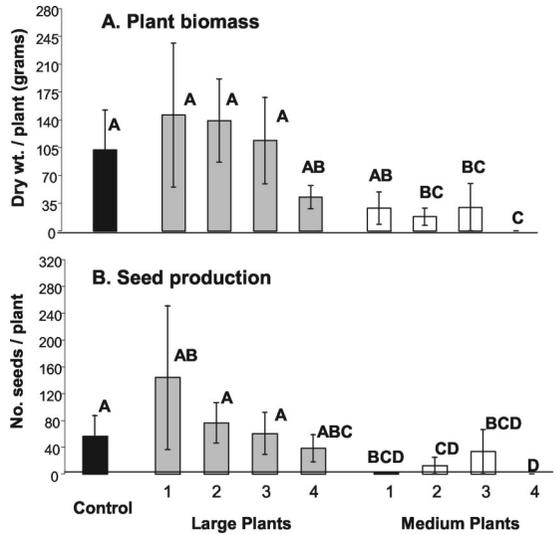


Fig. 8. Plant biomass (A) and seed production (B) on 6 August 2002 for undamaged (control) and *P. perfoliatum* plants subjected to four levels of simulated *R. latipes* damage (1–4 beetles/plant) beginning when medium-sized or large. Means sharing the same letters are not significantly different (Kruskal-Wallis test, LSD).

cheap to produce, whereas ova are large and relatively costly to produce, females are expected to consume more resources than males while attempting to maximize their fitness (Alcock 2001).

Males and females fed selectively on different plant parts, with females feeding more on capitula and males feeding more on ocreae and leaves. Female selective feeding on capitula, which increased with age, may be an attempt to acquire sufficient protein for oviposition, especially once initial stores have been depleted. Production of ova requires a substantial amount of protein (Nation 2002), and pollen is a good protein source (Roulston et al. 2000).

Male preference for ocreae and leaves may be a mechanism to increase mating opportunities. *R. latipes* pupate in the soil, and adults emerge and ascend *P. perfoliatum* stems to feed. Because males emerge from pupation  $\approx$ 2 d before females, they may maximize their reproductive success by feeding low on *P. perfoliatum* and close to the stems (i.e., on ocreae) while waiting for females to emerge. In our experiment, males and females were held individually on plants (but mixed together for mating every 3 d), and it is possible that their feeding site selections may differ when the sexes are present on plants together.

Oviposition primarily on *P. perfoliatum* capitula may result in part from the females’ preference for feeding on capitula, but probably also serves to increase larval survival. Apical portions of the stems are tenderer than basal portions, and numerous larvae were observed during rearing that seemed to have died because they were unable to penetrate the semiwoody lower portion of a *P. perfoliatum* stem.

The feeding and oviposition preferences of female *R. latipes* for plant capitula suggest that host specificity

tests should be conducted with plants that are flowering, at least for assessing maximum potential weevil success. Also, if the weevil is introduced into North America, postrelease monitoring for the insects could focus on plant terminals, where adult female feeding, eggs, and larval infestation will be concentrated.

The results of the simulated damage study suggest that *R. latipes* could cause substantial seedling mortality in *P. perfoliatum* if plants are attacked when small, and reduced seed production if somewhat larger plants are infested. The relative phenology of the plant and the insect in North America is difficult to predict before release, and thus, the extent to which such damage will occur is not known. Although the accuracy of plant clipping in simulating weevil damage has not been validated, plant mortality and reduced seed production were also observed on potted plants during weevil rearing. Attempts to rear *R. latipes* on potted plants without confining them to stem apices were unsuccessful, because as few as three pairs of adults and their progeny killed the plants before any larvae left the stems to pupate. When *R. latipes* were confined to stem apices for oviposition (and moved to new terminals and new plants as needed), an average of four pairs of weevils and their progeny did not kill plants, but the plants rarely developed seeds, whereas seeds were removed weekly from plants of similar size and age in the greenhouse.

*Polygonum perfoliatum* is an annual species with a persistent seed bank (Van Clef and Stiles 2001), and therefore reduction in *P. perfoliatum* populations solely through reduced seed production will be slow. Predicting the extent to which combined seedling mortality and reduced seed production will impact the weed's population will require additional study of the life history and ecology of *P. perfoliatum* in its introduced range. The results of this study suggest that *R. latipes* could have a substantial impact if introduced into North America for control of *P. perfoliatum*.

### Acknowledgments

We thank R. C. Reardon and D. W. Tallamy for valuable consultation and guidance throughout the study and P. Tobin for statistical advice. We also thank R. Fuester (director of the USDA-ARS Beneficial Insects Introduction Research Unit, Newark, DE) for finding space for us in their quarantine facility and D. Jianqing (Biological Control Institute, Chinese Academy of Agricultural Sciences, Beijing, China) for collecting and shipping *R. latipes* to Delaware. This study was supported in part by a Forest Health Technology Enterprise Team, USDA Forest Service, Cooperative Agreement with JHG, and a University of Delaware undergraduate research grant (Science and Engineering Scholars Program) to K.R.H.

### References Cited

- Alcock, J. 2001. The evolution of reproductive behavior, pp. 317–356. In *Animal behavior: an evolutionary approach*, 7th ed. Sinauer, Sunderland, MA.
- Baldwin, I. T. 1990. Herbivory simulations in ecological research. *Trends Ecol. Evol.* 5: 91–93.
- Blossey, B. 1995. A comparison of various approaches for evaluating potential biological control agents using insects on *Lythrum salicaria*. *Biol. Control.* 5: 113–122.
- Colpetzer, K., and J. Hough-Goldstein. 2004. A rapid germination protocol for mile-a-minute weed, *Polygonum perfoliatum* L. *Seed Sci. Technol.* (in press).
- Colpetzer, K., J. Hough-Goldstein, J. Ding, and W. Fu. 2004. Host specificity of the Asian weevil, *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae), a potential biological control agent of mile-a-minute weed, *Polygonum perfoliatum* L. (Polygonales: Polygonaceae). *Biol. Control.* 30: 511–522.
- Connett, J. F., L. M. Wilson, J. P. McCaffrey, and B. L. Harmon. 2001. Phenological synchrony of *Eustenopus villosus* (Coleoptera: Curculionidae) with *Centaurea solstitialis* in Idaho. *Environ. Entomol.* 30: 439–442.
- DeClerck-Floate, R., and R. S. Bouchier. 2000. Ecological principles of biological control: from population theory to weed biocontrol practice, pp. 517–520. In N. R. Spencer (ed.), *Proceedings X international symposium on biological control of weeds*. Montana State University, Bozeman, MT.
- Ding, J., W. Fu, R. Reardon, Y. Wu, and G. Zhang. 2004. Exploratory survey in China for potential insect biocontrol agents of mile-a-minute weed, *Polygonum perfoliatum* L., in eastern USA. *Biol. Control.* 30: 487–495.
- Fornasari, L., and R. Sobhian. 1993. Life history of *Eustenopus villosus* (Coleoptera: Curculionidae), a promising biological control agent for yellow starthistle. *Environ. Entomol.* 22: 684–692.
- Fornasari, L., C. E. Turner, and L. A. Andres. 1991. *Eustenopus villosus* (Coleoptera: Curculionidae) for biological control of yellow starthistle (Asteraceae: Cardueae) in North America. *Environ. Entomol.* 20: 1187–1194.
- Kluge, R. L. 2000. The future of biological control of weeds with insects: no more 'paranoia', no more 'honeymoon', pp. 459–467. In N. R. Spencer (ed.), *Proceedings X international symposium on biological control of weeds*. Montana State University, Bozeman, MT.
- Korotyaev, B. A. 1997. New and little known species of weevils from East Asia (Coleoptera: Apionidae, Curculionidae). *Zoosystematica Rossica.* 5: 285–288.
- Lamont, E. E., and J. M. Fitzgerald. 2001. Noteworthy plants reported from the Torrey Range—2000. *J. Torrey Bot. Soc.* 128: 409–414.
- Louda, S. M., R. W. Pemberton, M. T. Johnson, and P. A. Follett. 2003. Nontarget effects—the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. *Annu. Rev. Entomol.* 48: 365–396.
- McCormick, L., and N. Hartwig. 1995. Control of the noxious weed mile-a-minute (*Polygonum perfoliatum*) in reforestation. *Northern J. Appl. Forestry.* 12: 127–132.
- McEvoy, P. B., and E. M. Coombs. 2000. Why things bite back: unintended consequences of biological weed control, pp. 167–194. In P. A. Follett and J. J. Duan (eds.), *Nontarget effects of biological control*. Kluwer, Boston, MA.
- McEvoy, P., C. Cox, and E. Coombs. 1991. Successful biological control of ragwort, *Senecio jacobaea*, by introduced insects in Oregon. *Ecol. Appl.* 1: 430–442.
- Moul, E. 1948. A dangerous weedy *Polygonum* in Pennsylvania. *Rhodora.* 50: 64–66.
- Mountain, W. L. 1989. Mile-a-minute (*Polygonum perfoliatum* L.): update—distribution, biology, and control suggestions. *Regulatory Hortic.* 15: 21–24.

- Nation, J. L. 2002. Nutrients for oogenesis, pp. 429–430. *In* Insect physiology and biochemistry. CRC, Boca Raton, FL.
- Oliver, J. D. 1996. Mile-a-minute weed (*Polygonum perfoliatum* L.), an invasive vine in natural and disturbed sites. *Castanea*. 61: 244–251.
- Orelien, J. G. 2001. Model fitting in PROC GENMOD, Paper 264-26. *In* SUGI 26 proceedings. SAS Institute, Cary, NC. Available: [www2.sas.com/proceedings/sugi26/proceed.pdf](http://www2.sas.com/proceedings/sugi26/proceed.pdf).
- Papaj, D. R. 2000. Ovarian dynamics and host use. *Annu. Rev. Entomol.* 45: 423–448.
- Price, D. L., J. Hough-Goldstein, and M. T. Smith. 2003. Biology, rearing and preliminary evaluation of host range of two potential biological control agents of mile-a-minute weed, *Polygonum perfoliatum* L. *Environ. Entomol.* 32: 229–236.
- Riefner, R. 1982. Studies of the Maryland flora VIII: range extension of *Polygonum perfoliatum* L., with notes on introduction and dispersal in North America. *Phytologia*. 50: 152–159.
- Roulston, R. H., J. H. Cane, and S. L. Buchmann. 2000. What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecol. Monogr.* 70: 617–643.
- SAS Institute. 1999. SAS/STAT user's manual, version 8.0. SAS Institute, Cary, NC.
- Tiffin, P., and B. D. Inouye. 2000. Measuring tolerance to herbivory: accuracy and precision of estimates made using natural versus imposed damage. *Evolution*. 54: 1024–1029.
- Van Clef, M., and E. W. Stiles. 2001. Seed longevity in three pairs of native and non-native congeners: assessing invasive potential. *Northeastern Naturalist*. 8: 301–310.
- Wu, Z., and P. H. Raven (eds.). 2004. *Flora of China*, vol. 5 (Ulmaceae through Basellaceae). Science Press, Beijing, China.

*Received 9 July 2003; accepted 13 May 2004.*

---