Suppression of Mile-a-Minute Weed, CHAPTER Persicaria perfoliata, in the Eastern United States

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# NON-TECHNICAL SUMMARY

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Mile-a-minute weed, Persicaria perfoliata (Polygonaceae), was accidentally introduced into eastern North America with nursery stock in the 1930s. The vine spread slowly at first, but by the 1990s it was widely distributed in the Mid-Atlantic region, spreading rapidly, and causing considerable concern because of its ability to cover other vegetation, preventing forest regeneration and suppressing native plants. The biological control program against P. perfoliata began in 1996, and a permit for release of the host-specific mile-aminute weevil, Rhinoncomimus latipes (Coleoptera: Curculionidae), was obtained eight years later, in 2004. The weevil shows all the characteristics of a desirable biological control agent, including a high reproductive rate, three to four overlapping generations per year in the Mid-Atlantic United States, extreme host specificity, excellent dispersal capability, and the ability to suppress the target weed. No harmful non-target effects occurred from the weevil's introduction, and its present and projected benefits are high. Although mile-aminute weed is still present throughout the invaded area and can sometimes increase to noxious levels, the presence of the mile-a-minute weevil has reduced the weed's impact on native plants in many areas and, in areas where control of the weed is still needed, the weevil contributes substantially to integrated weed management.

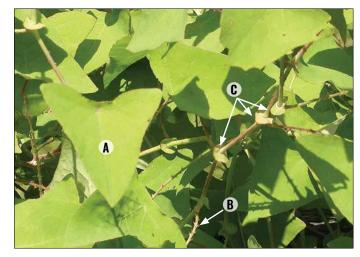
# HISTORY OF INVASION AND NATURE OF PROBLEM

#### The Species Invasion

Persicaria perfoliata (Polygonaceae) (Fig. 1), formerly Polygonum perfoliatum, is an annual vine that is widely distributed throughout Asia in its native range, including China, Korea, Japan, Indonesia, the Philippines, India, and parts of Russia (Liu et al., 2020). It was first introduced into eastern North America

Hough-Goldstein, J. and E. Lake. 2022. Suppression of mile-a-minute weed, Persicaria perfoliata, in the eastern United States, pp. 204–211. In: Van Driesche, R. G., R. L. Winston, T. M. Perring, and V. M. Lopez (eds.). Contributions of Classical Biological Control to the U.S. Food Security, Forestry, and Biodiversity. FHAAST-2019-05. USDA Forest Service, Morgantown, West Virginia, USA. https://bugwoodcloud.org/resource/files/23194.pdf

in the 1930s as a contaminant of holly seed sent from Japan to a nursery near York, Pennsylvania (Moul, 1948). Before 1980, the plant's range was confined to five counties in Pennsylvania (Hill et al., 1981) and six counties in Maryland (Riefner and Windler, 1979). By the mid-1990s, however, it had spread further in those two states and was also reported in Virginia, Delaware, West Virginia, Ohio, New York, New Jersey, and the District of Columbia, with dramatic increases in the size of many populations (Oliver, 1996). Since then, it has spread north to New Hampshire, south to North Carolina, and west to Ohio, with isolated infestations found in Indiana and Iowa (EDDMapS, 2021). Additional range expansion in North America is likely to occur.



**Figure 1.** *Persicaria perfoliata,* mile-a-minute weed. Note triangular leaves (A), backward-projecting spines (B), and the flared sheath (ocreae) surrounding the stems (C). (J. Hough-Goldstein, University of Delaware)

#### Nature of the Problem

The vines of *P. perfoliata* (mile-a-minute weed or devil's tearthumb) can grow rapidly, overtopping other plants and producing masses of intertwining foliage (**Fig. 2**). Although the negative impacts of *P. perfoliata* in North America have long been recognized, there are no specific studies of its effects. Observed impacts include inhibition of reforestation and natural forest regeneration by smothering tree seedlings, interference with recreational use of natural areas, reduction in quality wildlife habitat, and likely negative effects on native flora (McCormick and Hartwig, 1995; Oliver, 1996; Wu et al., 2002). Mile-a-minute weed can quickly overrun utility rights-of-way where herbicides have been used to control unwanted woody vegetation. Isolated individual plants can produce thousands of seeds (called achenes) during the summer and fall (Hough-Goldstein et al., 2008), which can survive for up to six years in the seed bank (Hough-Goldstein et al., 2015). Many seeds are shed and germinate under the previous year's plants, leading to seedling densities averaging as high as 200–500 per 0.5 m<sup>2</sup> (37–93/ft<sup>2</sup>) in the introduced range (Hough-Goldstein et al., 2009). Long-distance dispersal of seeds



**Figure 2.** Landscape infested with mile-a-minute weed, *Persicaria perfoliata.* (J. Hough-Goldstein, University of Delaware)

can occur by birds, deer, and water, in addition to accidental human-caused dispersal, for example through movement of nursery stock (Hough-Goldstein et al., 2015).

# WHY CONTROL THIS INVASIVE SPECIES?

The goal for suppression of mile-a-minute weed is to reduce its impact on native plants and allow for normal forest regeneration in disturbed areas. As an herbaceous annual, mile-a-minute plants die each fall, with new plants growing from seeds that germinate in the spring. A key aspect of long-term control is to deplete the existing seed bank and minimize additional seed production. Mile-a-minute plants have weak root systems, and the small seedlings are relatively easy to remove manually. Vines quickly grow over and through other vegetation, however, making mechanical control (through hand pulling or mowing) difficult to achieve without damaging desirable vegetation. The vining growth habit of this plant causes it to become draped over native or otherwise desirable plants, which makes control with broad-spectrum foliar herbicides difficult and potentially damaging to native plants. Pre-emergence herbicides kill new seedlings soon after germination, and these can be used effectively in early spring to control the weed without damaging most perennial plants; however, such treatments are incompatible with annual native plants, which may be killed (Templeton et al., 2020, but see Lake et al., 2014).

Given the ability of this invasive weed to spread and degrade native forest and edge plant biodiversity, and the difficulties in controlling the invader through either mechanical or chemical means, the classical biocontrol approach was selected to complement other management techniques. Biological control of milea-minute weed was intended to reduce the observed impacts of the plant on native plant communities and reduce herbicide use in areas such as rights-of-way, where the weed had to be controlled.

# THE ECOLOGY OF THE PROBLEM

As with all weed biological control projects, whether the target is annual, biennial, or perennial, and regardless of the growth habit of the target, the goal is not to eradicate the target weed but to reduce its competitive ability relative to the surrounding vegetation. Insects can exert stress on plants in a variety of ways, through stem or root boring, defoliation, seed predation, or sucking on phloem or xylem. Thus, any sufficiently host-specific herbivore can potentially have a positive effect toward controlling an invasive weed. Our first step, then, was to find host-specific insects in the weed's area of origin in Asia.

Mile-a-minute weed is primarily a pest of natural ecosystems rather than commercial crops or rangelands, and therefore reduced competitive ability may be sufficient to allow the native plant community to increase. Long-term success, however, may require a combination of mechanical, cultural, biological, and chemical control techniques. Furthermore, because one successful colonization event can lead to a persistent seed bank (Turnbull et al., 2000), early detection and rapid response to new populations and management of the seed bank will be necessary.

# **PROJECT HISTORY THROUGH AGENT ESTABLISHMENT**

Although mile-a-minute weed in the eastern United States is thought to have been introduced from Japan, the center of its native range is most likely China, and therefore this was where host-specific herbivores were sought when the project began (Ding et al., 2004). In China, *P. perfoliata* rarely attains the densities found in North America, suggesting that herbivores may be holding it to lower levels in its native range. However, it should be noted that *P. perfoliata* is widely used in traditional Chinese folk medicine (Liu et al., 2020), and, therefore, collection by people may also affect its population in Asia.

A collaborative project was initiated in 1996 between the USDA Forest Service and the Chinese Academy of Agricultural Sciences Institute of Biological Control to survey for and screen potential biological control agents in China for release against mile-a-minute weed in the United States (Ding et al., 2004). One hundred and eleven insect species were found feeding on mile-a-minute weed in China, including leaf-feeders, stem-borers, and fruit- and seed-feeders. Both generalists and specialists were present, and they caused extensive damage to plants. In a similar survey conducted in the United States in the 1980s, Wheeler and Mengel (1984) found 45 insect species feeding on mile-a-minute weed. Most of these insects were sap or leaf-feeders, all were generalists, and together they caused minimal damage to the plant, except for Japanese beetles, *Popillia japonica* (Coleoptera: Scarabaeidae), which can cause extensive defoliation.

Although eleven of the insect species collected by Ding et al. (2004) were considered potentially important because of the damage they caused, their likely narrow host range, or both, only one, *Rhinoncomimus latipes* (Coleoptera: Curculionidae), was ultimately determined to be host-specific enough to introduce into North America. This small weevil was tested on more than 50 plant species from 17 families in China from 1999 to 2002 (Ding et al., unpublished data). Weevils were sent to the USDA-ARS quarantine facility in Newark, Delaware where they were further tested on 28 species, mostly in the family Polygonaceae and including representatives of different tribes and sections within the family (Price et al., 2003; Colpetzer et al., 2004a). *Rhinoncomimus latipes* did not feed at all on any plant species outside the Polygonaceae. The adult weevils fed slightly on a few species in the family Polygonaceae, but they laid no eggs, and their larvae did not survive on any host except mile-a-minute weed. Based on these results, the weevil was approved for release by the USDA-APHIS in 2004. Host-specificity was later confirmed in an open field experiment, where weevils abandoned all potential non-target host species other than mile-a-minute weed even when the preferred plant host was removed (Frye et al., 2010).

*Rhinoncomimus latipes*, the mile-a-minute weevil (**Fig. 3**), overwinters in the adult stage in leaf litter or soil, emerging in the spring soon after mile-a-minute seedlings develop. The weevil lays eggs on leaves, stems, or buds of mile-a-minute weed plants. Eggs hatch in 3–5 days, and newly emerged larvae bore into the stems, where they feed internally. Once mature, the larvae leave the stem and pupate in the soil. Adult weevils emerge about a week later and seek mile-a-minute plants for mating and egg-laying, initiating a new generation (Price et al., 2003; Colpetzer et al., 2004b). Three to four generations can develop each year in the Mid-Atlantic region (Lake et al., 2011; Hough-Goldstein et al., 2016).

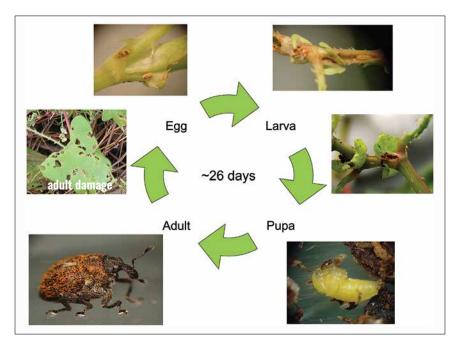


Figure 3. Rhinoncomimus latipes life cycle. (E. Lake, Mt. Cuba Center)

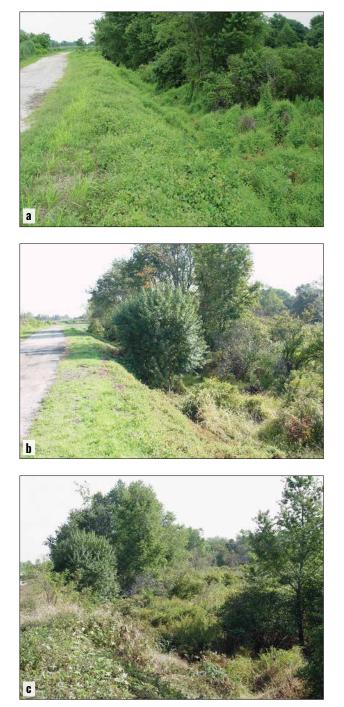
Mass rearing techniques were developed by the New Jersey Department of Agriculture Phillip Alampi Beneficial Insect Laboratory (Hough-Goldstein et al., 2015). Between 2004 and 2020, the efforts of this laboratory plus production by smaller rearing facilities resulted in the release of more than 800,000 weevils in eleven states. Weevils established at nearly every release site (Hough-Goldstein et al., 2009, 2015; C. Detweiler, pers. comm.).

# HOW WELL DID BIOLOGICAL CONTROL WORK?

Initial weevil releases were monitored using counts made inside standardized fixed quadrats (ten 1 x 0.5 m [3.3 x 1.6 ft] quadrats, approximately 10 m [33 ft] apart, at each site) at eight locations, with each release site paired with a non-release control site. Within 2–3 years, at three sites mile-a-minute weed densities dropped to <25% of weed levels before release of the weevils (Fig. 4), with no change in mile-a-minute weed at the non-release sites (Hough-Goldstein et al., 2009). At a fourth location, there was a similar level of reduction, but the noon-release control site was rapidly invaded by dispersing weevils, and therefore was not available for comparison. The other four locations were on islands in rivers, and mile-a-minute populations were reduced at both release and non-release sites, apparently due to environmental conditions such as late frost and extreme drought (Hough-Goldstein et al., 2009). Initial studies indicated weevils dispersed at a rate of 1.5-2.9 m (4.9-9.5 ft) per week after release in dense patches of mile-a-minute weed (Lake et al., 2011), while sampling on a broader scale showed weevils dispersed an average of 4.3 km (2.7 mi) per year (Hough-Goldstein et al., 2009).

In field cage experiments, weevils caused substantial plant mortality, delayed seed production, and reduced seed weight and viability (Hough-Goldstein et al., 2008; Smith and Hough-Goldstein, 2014). Surviving plants in field cages also showed loss of apical dominance, with damaged plants producing large numbers of lateral branches with small terminals and "stacked" nodes, close together on stems (Hough-Goldstein et al., 2008). This can be part of a compensatory response, in which a plant may produce more seeds (at the ends of the larger number of terminals). However, for a light-adapted vine such as *P. perfoliata*, numerous short terminals may not allow the plant to achieve needed sun exposure when in competition with other plants.

A replicated open-field study where weevils were released in the center of dense mile-a-minute populations showed significant reductions in milea-minute weed populations and higher weevil populations from 2005 to 2008 (Lake et al., 2011). In 2009, however, substantial spring rainfall and



**Figure 4.** Mile-a-minute weed, *Persicaria perfoliata*, (a) at the Floodgate Road, New Jersey release site in July 2004, (b) October 2006, and (c) October 2007 after *Rhinoncomimus latipes* feeding. Note the *Prunus* sp. bush in the foreground (middle) was not visible before weevil release in 2004 (a), because it was covered by mile-a-minute weed. The *Prunus* sp. grew once mile-a-minute was reduced. (a–c: Mark A. Mayer, New Jersey Department of Agriculture)

relatively cool temperatures likely slowed the development of the weevils while allowing rapid growth of mile-a-minute weed, resulting in a higher mile-a-minute weed population and a reduced number of the weevils. In 2010, however, weevil density again increased, and mile-a-minute weed cover declined, likely due to the opposite climate conditions (low rainfall and high temperatures) (Hough-Goldstein et al., 2016).

Laboratory and greenhouse experiments confirmed that, where water is limited, mile-a-minute weed produces fewer seeds with lower viability and plant biomass is reduced compared to plants that are well-watered (Berg et al., 2015). Both mile-a-minute weed and its associated weevil perform better in sun than in shade. Weevils are attracted to sunny areas and develop best on sun-grown plants (Hough-Goldstein and LaCoss, 2012; Smith and Hough-Goldstein, 2013). Mile-a-minute weed can persist at shady sites, near locations where it is suppressed by weevils in sunny spots, but plants in the shade are less vigorous and produce fewer seeds.

The amount of time required for development of mile-a-minute weevils at different temperatures was determined and used to develop a model for weevil population growth (Hough-Goldstein et al., 2016). As with all insects, mile-a-minute weevils develop more quickly at warmer temperatures, and because this weevil has the potential for multiple generations each year, much larger weevil populations can develop during a warm year compared to one with a cool spring and summer.

When abiotic conditions are not favorable for the weevil, additional use of herbicides and/or mechanical controls may be advisable to reduce the likelihood of a large pulse of seeds being added to the seed bank and extending the timeline for management efforts. Furthermore, increased applications of preemergent herbicides may be necessary the following spring (Hough-Goldstein et al., 2015, 2016).

Another important factor affecting weevil impacts on mile-a-minute weed populations is the composition of the surrounding plant community. Mile-a-minute weed populations can increase explosively if seeds are present in the soil and the surrounding plant community is disturbed, for example where trees have fallen naturally or been harvested, where power line rights-of-ways have been mowed or treated with herbicide, or where a site has been cleared in preparation for future construction. Mile-a-minute weed, however, is less likely to invade a well-established plant community, where other vegetation can outcompete it for light resources, particularly if the weevil is simultaneously attacking the weed. If the surrounding plant community consists primarily of other invasive, non-native plants, it may be beneficial to replant with desirable native plants at the same time that weevils are released (Cutting and Hough-Goldstein, 2013; Lake et al., 2014). Integrating the weevil, herbicide applications, and plantings of competitive native vegetation can, at least temporarily, limit mile-a-minute weed populations, prevent the invasive species treadmill, and increase the abundance of native plants (Lake et al., 2014). Due to different site histories, conditions, and plant communities, adaptive management may be needed over the long-term.

#### BENEFITS OF BIOLOGICAL CONTROL OF MILE-A-MINUTE WEED

Although mile-a-minute weed is still present throughout the invaded area and can sometimes increase to noxious levels, the presence of the mile-a-minute weevil has made this much less likely, and biocontrol contributes substantially to integrated weed management where control of the weed is still needed (Hough-Goldstein et al., 2015).

Mile-a-minute weed is still expanding its range, with recent populations developing in northern Ohio, Indiana, Iowa, and New Hampshire (EDDMapS, 2021). Long-range spread probably occurs with seeds in pots or in soil around the roots of nursery stock. An important component of control of this weed is education and prevention, including efforts to increase public awareness of potential mechanisms of spread (e.g., Rathfon, 2016). Mile-a-minute weed can rapidly form large infestations after establishing in a new area where the biocontrol weevil is not present (Hough-Goldstein et al., 2015). However, in small weed infestations, if seedlings are removed and plants are prevented from going to seed for several consecutive

years, eradication may be possible (Miller et al., 2018; Templeton et al., 2020). Early detection and rapid response to new patches of mile-a-minute weed, both within and outside the generally infested area, may prevent the development of a seed bank and the need for long-term management. Efforts should be made to release the weevil along the invasion front of mile-a-minute weed, where the weed has established populations that can no longer be eradicated.

Mile-a-minute weed will continue to expand its range, assisted by long-distance dispersal events by animals consuming the seed and accidental spread by humans. It is critical to continue to manage new populations of the weed both at the invasion front as well as in regions already invaded. States where new mile-a-minute weed populations are found should carefully monitor infestations and make new weevil releases unless new mile-a-minute weed patches can be eradicated. Weevils can be obtained from the New Jersey Department of Agriculture Phillip Alampi Beneficial Insect Laboratory or collected and moved from sites where they are abundant.

#### **ACKNOWLEDGMENTS**

We would like to thank the many land managers, conservation organizations, state parks, and private landowners in Delaware and southeastern Pennsylvania for their assistance and cooperation by 'donating their mile-a-minute patches to science' while we implemented and studied the impacts of biological control. Skilled and dedicated insect rearers at the Phillip Alampi Beneficial Insect Laboratory in New Jersey were key in developing the program, as were collaborators throughout the Northeast who assisted with the release and monitoring of the mile-a-minute weevil. We also thank the undergraduates, graduate students, and technicians who assisted with mile-a-minute research at the University of Delaware. Finally, we would like to thank Richard Reardon, USDA Forest Service, Forest Health Technology Enterprise Team (FHTET, retired), for financial support.

# REFERENCES

- Berg, S. A., J. A. Hough-Goldstein, E. C. Lake, and V. D'Amico. 2015. Mile-a-minute weed (*Persicaria perfoliata*) and weevil (*Rhinoncomimus latipes*) response to varying moisture and temperature conditions. *Biological Control* 83: 68–74.
- Colpetzer K., W. Fu, J. Ding, and J. Hough-Goldstein. 2004a. Host specificity of the Asian weevil, *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae), a biological control agent of mile-a-minute weed, *Polygonum perfoliatum* L. (Polygonales: Polygonaceae). *Biological Control* 30: 511–522.
- Colpetzer K., J. Hough-Goldstein, and K. R. Harkins. 2004b. 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). *Environmental Entomology* 33: 990–996.
- Cutting, K. and J. Hough-Goldstein. 2013. Integration of biological control and native seeding to restore invaded plant communities. *Restoration Ecology* 21: 648–655.
- 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. *Biological Control* 30: 487–495.
- EDDMapS. 2021. Early Detection & Distribution Mapping System. The University of Georgia Center for Invasive Species and Ecosystem Health. https://www.eddmaps.org/ [Accessed 22 March 2021].
- Frye, M. J., E. C. Lake, and J. Hough-Goldstein. 2010. Field host specificity of the mile-a-minute weevil, *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae). *Biological Control* 55: 234–240.
- Hill, R. J., G. Springer, and L. B. Forer. 1981. Mile-a-minute, *Polygonum perfoliatum* L. (Polygonaceae), a new potential orchard and nursery weed. *Regulatory Horticulture* 7: 25–28.
- Hough-Goldstein, J., and S.J. LaCoss. 2012. Interactive effects of light environment and herbivory on growth and productivity of an invasive vine, *Persicaria perfoliata*. *Arthropod-Plant Interactions* 6: 103–112.

- Hough-Goldstein, J., B. Butterworth, E. Lake, and M. Schiff. 2008. Impact of the biological control agent *Rhinoncomimus latipes* (Coleoptera: Curculionidae) on mile-a-minute weed, *Persicaria perfoliata*, in field cages. *Biological Control* 46: 417–423.
- Hough-Goldstein J., P. Morrison, R. Reardon, G. Robbins, M. A. Mayer, and W. Hudson. 2009. Monitored releases of *Rhinoncomimus latipes* (Coleoptera: Curculionidae), a biological control agent of mile-a-minute weed (*Persicaria perfoliata*), 2004–2008. *Biological Control* 51: 450–457.
- Hough-Goldstein, J., E. Lake, R. Reardon, and Y. Wu. 2015. *Biology and Biological Control of Mile-a-Minute Weed*. FHTET-2008-10, revised July 2015. USDA Forest Service, Morgantown, West Virginia, USA.
- Hough-Goldstein, J., E.C. Lake, K.J. Shropshire, R.E. Moore, and V. D'Amico. 2016. Laboratory and field-based temperature-dependent development of a monophagous weevil: implications for integrated weed management. *Biological Control* 92: 120–127.
- Lake, E., J. Hough-Goldstein, K. Shropshire, and V. D'Amico. 2011. Establishment and dispersal of the biological control weevil *Rhinoncomimus latipes* on mile-a-minute weed, *Persicaria perfoliata*. *Biological Control* 58: 294– 301.
- Lake, E., J. Hough-Goldstein, and V. D'Amico. 2014. Integrating management techniques to restore sites invaded by mile-a-minute weed, *Persicaria perfoliata. Restoration Ecology* 22: 127–133.
- Liu, J., Y. Zeng, G. Sun, S. Yu, Y. Xu, C. He, Z. Li, S. Jin, and X. Qin. 2020. *Polygonum perfoliatum* L., an excellent herbal medicine widely used in China: a review. *Frontiers in Pharmacology* 11: 581266.
- McCormick, L. H. and N. L. Hartwig. 1995. Control of the noxious weed mile-a-minute (*Polygonum perfoliatum*) in reforestation. *Northern Journal of Applied Forestry* 12: 127–132.
- Miller, W. R., B. A. Connolly, and D. Cygan. 2018. A new record of invasive mile-a-minute vine *Persicaria perfoliata* (Polygonaceae) in New Hampshire. *Rhodora* 120: 179–180.
- Moul, E. T. 1948. A dangerous weedy Polygonum in Pennsylvania. Rhodora 50: 64-66.
- Oliver, J. D. 1996. Mile-a-minute weed, (*Polygonum perfoliatum* L.), an invasive vine in natural and disturbed sites. *Castanea* 61: 244–251.
- Price, D. L., M. T. Smith, and J. Hough-Goldstein. 2003. Biology, rearing, and preliminary evaluation of host range of two potential biological control agents for mile-a-minute weed, *Polygonum perfoliatum L. Environmental Entomology* 32: 229–236.
- Rathfon, R. 2016. Mile-a-Minute Vine, *Persicaria perfoliata* (L.) H. Gross. Purdue Extension, Southern Indiana Cooperative Invasives Management, Invasive Plant Series Fact Sheet FNR-481-W.
- Riefner, R. E., Jr. and D. R. Windler. 1979. Polygonum perfoliatum L. established in Maryland. Castanea 44: 91-93.
- Smith, J. R. and J. Hough-Goldstein. 2013. Phototaxis, host cues, and host-plant finding in a monophagous weevil, *Rhinoncomimus latipes. Journal of Insect Behavior* 26: 109–119.
- Smith, J. R., and J. Hough-Goldstein. 2014. Impact of herbivory on mile-a-minute weed (*Persicaria perfoliata*) seed production and viability. *Biological Control* 76: 60–64.
- Templeton, S., A. Gover, D. Jackson, and S. Wurzbacher. 2020. Mile-a-Minute (*Persicaria perfoliata*). Penn State Extension Invasive Plant Fact Sheet, State College, Pennsylvania.
- Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88: 225–238.
- Wheeler, A. J. and S. A. Mengel. 1984. Phytophagous insect fauna of *Polygonum perfoliatum*, an Asiatic weed recently introduced to Pennsylvania. *Annals of the Entomological Society of America* 77: 197–202.
- Wu, Y., R. C. Reardon, and J. Ding. 2002. Mile-a-minute weed, pp. 331–341. In: Van Driesche, R., B. Blossey, M. Hoddle, S. Lyon, and R. Reardon (eds.). Biological Control of Invasive Plants in the Eastern United States. FHTET-2002–04. USDA Forest Service, Morgantown, West Virginia, USA.