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## Developing Biological Control of *Alliaria petiolata* (M. Bieb.) Cavara and Grande (Garlic Mustard)

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**ABSTRACT:** Invasive nonindigenous plants are a primary threat to native species and the integrity of natural areas by causing changes in species composition and ecosystem processes. For many of the most invasive species, natural area managers lack species-specific and successful long-term management options. Moreover, repeated use of fire, herbicides, flooding, mowing, and other management options may have negative impacts on native species. Increasingly, land managers are considering biological weed control—the introduction of host-specific natural enemies from the native range of a nonindigenous plant species. The spread of garlic mustard (*Alliaria petiolata* [M. Bieb.] Cavara and Grande), a European biennial herb, through forests of the eastern and midwestern United States and Canada has caused great concern. In 1998 a biological control program for garlic mustard was initiated and the search for potential biological control agents began in western Europe. Garlic mustard is under little herbivore pressure in North America, whereas 70 insect herbivores and 7 fungi are associated with this plant in Europe. While most of these species are not sufficiently host-specific to be considered for introduction into North America, five monophagous weevils and an oligophagous flea beetle that attack seeds, stems, and roots of garlic mustard were selected for further study, based on the assumption that simultaneous attack of different plant parts will provide superior control. Although literature records and preliminary investigations suggest that these herbivores have a very restricted host range, extensive experimental investigations will assess whether these insects are safe for introduction to North America. Development of successful biological control for garlic mustard will allow natural area managers to incorporate release of host-specific herbivores into their management strategy.

### Desarrollo de Control Biológico para *Alliaria petiolata* (M. Bieb.) Cavara y Grande (Garlic Mustard)

**RESUMEN:** Las plantas invasoras alóctonas son el problema principal de las especies nativas y la causa de los cambios de composición de especies y procesos de los ecosistemas. Para la mayoría de las especies de mayor poder invasor, los encargados de las áreas naturales carecen de opciones de manejo a largo plazo específicas para cada especie. Más aún, el uso repetido del fuego, herbicidas, inundación, cosecha, y otras opciones pueden tener un impacto negativo en las especies nativas. Cada vez más los encargados de las áreas naturales están considerando el control biológico de las semillas – la introducción de un huésped específico original del área de distribución de la planta alóctona. La distribución de *Alliaria petiolata* [M. Bieb.] Cavara y Grande, una hierba europea bianual, en los bosques del este y del ‘midwest’ de los E.E.U.U. y Canadá ha causado una gran preocupación. En 1998 se inició un programa de control biológico de *A. petiolata* y se comenzó la búsqueda de un potencial agente de control biológico en el oeste de Europa. *A. petiolata* tiene muy poca herbivoría en norte América, mientras que en Europa se encuentran 70 insectos y 7 hongos asociados a esta planta. La mayoría de esas especies no son huéspedes específicos para considerar su introducción en norte América, pero cinco gorgojos monófagos y un escarabajo pulga oligófago que ataca las semillas, tallos y raíces de *A. petiolata* han sido seleccionados para más estudios, basándose en la asunción que el ataque simultáneo de las diferentes partes de la planta proveerá un mejor control. Aunque las publicaciones previas sugieren que estos herbívoros tienen un rango muy restringido de huéspedes, la investigación experimental dirá si esos insectos son seguros para su introducción en norte América. El desarrollo exitoso del control de *A. petiolata* permitirá a los encargados de las áreas naturales incorporar la liberación de huéspedes herbívoros específicos como estrategia de manejo.

*Index terms:* biological control, *Ceutorhynchus*, ground-layer vegetation, nonindigenous invasive species, *Phyllotreta*

### INTRODUCTION

Invasive nonindigenous plants in natural areas alter species composition by preventing recruitment or reproduction of native species, change ecosystem processes such as fire regimes and nutrient cycling, and are considered one of the primary threats to rare and endangered species (Usher 1988, MacDonald et al. 1989, Ran-

dall 1996, Wilcove et al. 1998, Mack et al. 2000). At present, over 5000 plants have been identified as naturalized in the United States, of which at least 10% are invasive (U.S. Congress Office of Technology Assessment 1993). Reasons for differences among species in invasiveness are poorly understood (Williamson 1996), but lack of natural enemies, benign climates (Crawley 1989), shifts in resource allocation from

antiherbivore defenses to vegetative growth and reproduction (Blossey and Nötzold 1995, Willis and Blossey 1999), and hybridization (Ellstrand and Schierenbeck 2000) have been implicated as factors contributing to the success of nonindigenous species. We have little power to predict which species will be successful invaders or which ecosystems may be particularly vulnerable to invasions (Williamson 1996, Lonsdale 1999). However, maintaining the diversity of native species and the uniqueness of natural areas requires management of invasive species.

Ideally, long-term management of invasive plants should be self sustaining and economically feasible. Repeated use of fire, herbicides, flooding, or mowing may threaten species or communities of concern, and is often prohibitively expensive. Chemical treatment of purple loosestrife (*Lythrum salicaria* L.) often results in short-term reductions, but the species reinvades within a few years, often in higher abundances than in untreated areas (Skinner et al. 1994). A coordinated effort (at a cost of about \$200,000/year) targeting purple loosestrife on a watershed basis did not stop the spread of the species in Minnesota, although efforts were successful in controlling small and isolated populations without established seed banks (Blossey et al. 2001). The failure to control purple loosestrife resulted in the development of a biological control program and the introduction of four host-specific insect herbivores (Malecki et al. 1993, Hight et al. 1995).

Classical biological weed control (e.g., the introduction of host-specific herbivores from the native range of a nonindigenous plant) can be an ecologically sound, cost-effective, long-term management strategy to protect native species and their habitats. Successful weed biocontrol programs can reduce biomass of target plants to very low levels (McEvoy et al. 1991, McFadyen 1998, Blossey and Skinner 2000), allowing other previously suppressed plant species to increase. Worldwide, more than 1200 programs have released over 350 species of insects and pathogens targeting 133 plant species (Julien and Griffiths 1998). Appropriately funded and managed,

complete or partial control was achieved in over 80% of programs in New Zealand and South Africa (Hoffmann 1995, Fowler et al. 2000). Biological control, similar to chemical, mechanical, and physical control, may affect nontarget species (Howarth 1991, Simberloff and Stiling 1996, Louda et al. 1997, Follett and Duan 2000, Pemberton 2000, Wajnberg et al. 2001). Current regulations (U.S. Department of Agriculture 1999) incorporate measures to greatly improve decision-making processes and avoid release of nonspecific herbivores (Gassmann and Louda 2001). Yet risks to nontarget species must be weighed against risks of allowing invasive species to remain unchecked.

Garlic mustard, *Alliaria petiolata* (M. Bieb.) Cavara and Grande, a cool-season, shade-tolerant, obligate biennial herb, is an important invader in forests of the eastern and midwestern United States and Canada. Garlic mustard is one of the few nonindigenous herbaceous species able to invade and dominate the understory of North American forests. Although little long-term research has been conducted to document the impact of garlic mustard on native ground-layer vegetation, sites invaded by garlic mustard frequently have low native herbaceous species richness. Garlic mustard has been implicated as the cause of this low diversity (White et al. 1993, Anderson et al. 1996, McCarthy 1997). Herbicide, fire, cutting, and hand pulling may occasionally control small incipient infestations, but none of these methods has provided effective long-term control. At present, natural area managers have no species-specific, successful long-term tool to manage garlic mustard (Nuzzo et al. 1996, Drayton and Primack 1999). The purpose of this paper is to (1) summarize distribution, habitat, and spread of garlic mustard in North America; (2) provide a brief overview of the biology and impact of garlic mustard on native North American taxa; (3) summarize the effectiveness of available conventional control methods; and (4) summarize the status of the development of biological control for garlic mustard.

## DISTRIBUTION AND SPREAD OF GARLIC MUSTARD IN NORTH AMERICA

Garlic mustard is native to northern Europe, ranging from England to Sweden to the western regions of the former USSR (Turkistan, NW-Himalayas), India and Sri Lanka, and south to Italy and the Mediterranean basin (Tutin et al. 1964, Cavers et al. 1979, Hegi 1986). The species has been introduced to New Zealand (Bangerter 1985) and North America, where it was first recorded on Long Island in 1868 (Nuzzo 1993). Like many invasive European species in North America, garlic mustard spread from the northeastern seaboard westward (Figure 1) at a rate of approximately 366 km<sup>2</sup> year<sup>-1</sup> between 1868 and 1929 (Nuzzo 1993). Rate of spread increased to 1950 km<sup>2</sup> year<sup>-1</sup> between 1930 and 1949, and to 6400 km<sup>2</sup> year<sup>-1</sup> between 1950 and 1991 (Nuzzo 1993). By 2000, garlic mustard was most abundant in the northeastern and midwestern states, ranging from southern Ontario south to Georgia and Arkansas (Figure 1). Isolated occurrences are known from Utah and Colorado, and populations are established in the Pacific Northwest (Figure 1) and appear to be spreading. Typically, garlic mustard spreads in an "advance-retreat" pattern. Within Illinois forests, rate of spread averaged 5.4 m year<sup>-1</sup>; however, annual fluctuations ranged from advancing as much as 36 m to retreating by 18 m (Nuzzo 1999). This advance-retreat habit, combined with the biennial life cycle, explains the "sudden" appearance of a dense stand of garlic mustard in a forest where few plants were seen the year before. The general pattern of local spread is a ragged advancing front, supplemented by establishment of satellite populations 6–30 m ahead of the front. Garlic mustard spreads exclusively by seed (Cavers et al. 1979), which is dispersed 1–2 m from the mother plant by ballistic action. Long-distance dispersal is primarily through floodwaters (Cavers et al. 1979) and human transport (Lhotska 1975; Nuzzo 1992, 1993). In addition, it is likely that deer, mice, and other small mammals passively transport seeds in their fur. Although garlic mustard takes advantage of disturbances, the species is also able to invade relatively undis-

turbed and isolated forests independent of presence or cover of native species (Brothers and Spingarn 1992, Nuzzo 1999). Once established, garlic mustard becomes a permanent member of the community, steadily increasing in presence but with large annual fluctuations in cover and density (Byers and Quinn 1998, Nuzzo 1999, Meekens 2000).

Garlic mustard occurs in similar habitats in both its native European range and North America. It is most frequently found in deciduous forests, and also occurs in partial shade characteristic of open woods, forest edges, roadsides, urban areas, and occasionally in full sun (Trimbur 1973; Fitter et al. 1974; Cavers et al. 1979; Hegi 1986; Wilmanns and Bogenrieder 1988; Nuzzo 1991, 1993; Byers and Quinn 1998). Garlic mustard grows on sand, loam, and clay soils, and on both limestone and sandstone substrates, but rarely occurs on peat or muck soils. Although garlic mustard is widespread in Europe, populations are scattered and small, often restricted to road edges. Of 25 sites with "large" garlic mustard populations investigated for associated herbivores in Germany, Switzerland, and Austria, stand size was  $225 \pm 119 \text{ m}^2$  (mean  $\pm$ SE, range 10–3000  $\text{m}^2$ ) (Hinz and

Gerber 2001), whereas extensive populations of several hectares ( $>10,000 \text{ m}^2$ ) are common in North America.

### BIOLOGY

Garlic mustard is an obligate biennial; all plants overwintering as rosettes will flower, regardless of size, and subsequently die (Cavers et al. 1979, Bloom et al. 1990, Byers and Quinn 1998, Meekens 2000). The phenology is typical of cool-season European plants, and garlic mustard grows rapidly in late fall and early spring when native species are dormant (Cavers et al. 1979, Anderson et al. 1996). Flower stalks begin to elongate from the rosette in March or April. Flowers open as early as April and are insect pollinated. Pollination primarily occurs on the first day that flowers open; flowers that are not insect pollinated automatically self-pollinate (Cruden et al. 1996), allowing garlic mustard to establish and expand at sites from single colonizing individuals.

Seed production varies with habitat conditions and averages 66–356 seeds per plant (Byers and Quinn 1998, Nuzzo 1999, Susko and Lovett-Doust 2000), but can be as high as 7900 seeds for robust plants (Nuz-

zo 1993). In dense patches, seed production ranges from 3600 to 45000 seeds  $\text{m}^{-2}$  (Trimbur 1973, Anderson et al. 1996, Byers and Quinn 1998). Seeds require 50 to 105 days of cold stratification ( $1\text{--}10^\circ\text{C}$ ; Baskin and Baskin 1992, Meekins and McCarthy 1999), resulting in a dormancy period of 8 months in southern, and 8–22 months in northern, locales (Cavers et al. 1979, Baskin and Baskin 1992, Solis 1998). Simultaneous germination of the majority of seeds occurs after stratification requirements are met, and purportedly only a small proportion of seeds remain viable, forming a short-lived seed bank (Roberts and Boddrell 1983, Baskin and Baskin 1992). However, experiments demonstrate large geographic differences in germination rates ranging from as little as 3% to as much as 60% germination after 3 years (B. Blossey and V. Nuzzo, unpubl. data). In North America, seeds germinate in early spring, usually from late February to mid-May, depending on latitude (Cavers et al. 1979, Baskin and Baskin 1992). Reported seedling densities range from 830 to 1800 seedlings  $\text{m}^{-2}$  in central Illinois (Anderson et al. 1996) to as high as 20,000 seedlings  $\text{m}^{-2}$  in Ohio (Trimbur 1973). By June, seedlings develop into the characteristic rosette of first year plants and are 4–15 cm in diameter by early fall. First-year rosettes are sensitive to summer drought (Byers and Quinn 1998, Meekens 2000) and 60–90% die by fall (Anderson et al. 1996, Byers and Quinn 1998). New leaves produce a distinct garlic odor when crushed, but the fragrance fades as leaves age.

### IMPACT OF GARLIC MUSTARD ON NATIVE TAXA

It is generally assumed (but we have little quantitative evidence) that garlic mustard outcompetes the native ground-layer flora because invaded sites frequently have low diversity (White et al. 1993, Anderson et al. 1996, McCarthy 1997). Chestnut oak (*Quercus prinus* L.) seedlings had reduced growth in the laboratory when competing with garlic mustard, whereas jewelweed (*Impatiens capensis* Meerb.) and boxelder (*Acer negundo* L.) were competitively superior (Meekins and McCarthy 1999). Removing garlic mustard resulted in an increase in relative cover of annual plants

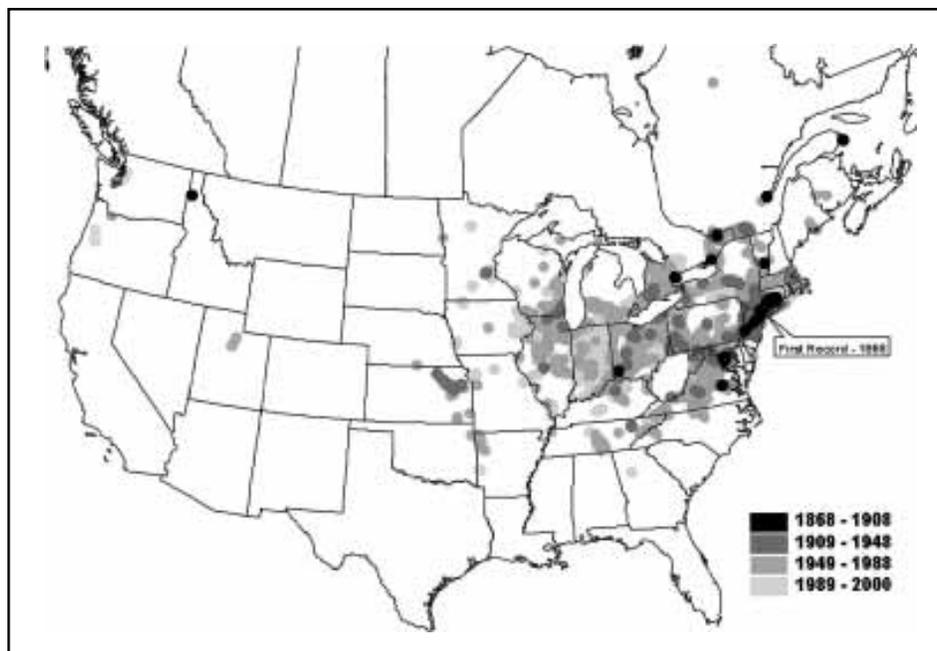


Figure 1. Spread of garlic mustard in 40-year intervals from 1868 to 1988 and from 1989 to 2000.

(primarily jewelweed), although actual percent cover of annuals was similar or higher in plots with garlic mustard (McCarthy 1997).

Garlic mustard produces several phytotoxic chemicals that may interfere with growth of native species, potentially through inhibition of mycorrhizal activity (Vaughn and Berhow 1999). About 75% of native North American ground-layer plants are mycorrhizal (Harley 1969), whereas garlic mustard, like other members of the Brassicaceae, is nonmycorrhizal.

Although quantitative evidence for ecosystem impacts of garlic mustard is anecdotal, garlic mustard appears to alter habitat suitability for several species of salamanders, molluscs, earthworms, and insect communities (J. Maerz and B. Blossey, unpubl. data). Garlic mustard interferes with oviposition of the native butterflies *Pieris napi oleracea* Harris and *P. virginensis* W.H. Edwards (Lepidoptera, Pieridae), whose native hosts are toothworts—*Cardamine concatenata* [*Dentaria laciniata*] (Michx.) O. Schwarz and *Cardamine* [*Dentaria*] *diphylla* (Michx.) A. Wood. Females of these butterflies lay eggs on garlic mustard because it contains sinigrin, a strong attractant that females use to identify the appropriate host plant (Huang et al. 1995). In mixed populations of garlic mustard and toothwort, garlic mustard is taller and often more abundant than toothwort, and female butterflies can have difficulty locating the native host plant. Confused females oviposit on garlic mustard, but larvae are unable to complete development there (Porter 1994, Huang et al. 1995). Garlic mustard is a population sink for these species (Porter 1994, Haribal and Renwick 1998). Invasion by garlic mustard reduces populations of the native host plants of *P. napi oleracea* and *P. virginensis* (Nuzzo 1993), and eggs laid on garlic mustard do not contribute to recruitment of adults, further reducing populations and potentially leading to endangerment of the species.

Literature and limited field surveys revealed little information on North American herbivores associated with garlic mus-

tard with potential as indigenous biocontrol agents. Species most commonly associated with garlic mustard are stem-mining weevils, a stem-mining fly, a leaf-mining fly, and pierid butterflies (Table 1). Widespread but uncommon attack by slugs, snails, aphids, leafhoppers, and several fungal pathogens has been recorded (Table 1). However, attack by these species has not been able to prevent further range expansion of garlic mustard (Figure 1).

## CONVENTIONAL CONTROL

Anticipated negative ecosystem impacts have prompted natural area managers to experiment with various techniques to stop the spread or control abundance of garlic mustard. The most effective method is to prevent initial establishment (Nuzzo 1991, Drayton and Primack 1999). Control efforts can occasionally be successful if infestations are recognized early, but successful long-term control is unlikely even with considerable expenditures of labor and money (Drayton and Primack 1999). Treatments have to be repeated over an extended period, potentially 4–10 years, to prevent local seed production until the seed bank is depleted (Drayton and Primack 1999). Eradication and control attempts using herbicides, fire, hand pulling, or combinations of these treatments have been successful in reducing but not eliminating populations (Nuzzo 1991, Nuzzo et al. 1996, Schwartz and Heim 1996). Established populations forming extensive monocultures are virtually impossible to control and repeated control treatments may themselves pose a threat to native species.

Cutting flowering stems at ground level provides effective control with minimal side effects, but is very labor intensive. Cutting is most effective when plants are in full bloom or have developed siliques (Nuzzo 1991); plants cut earlier in the flowering period may produce new flowering stems. Viable seed may form on cut stems (Solis 1998), and all stems need to be removed from the site, adding to the labor costs. Pulling is very labor intensive but effective if the upper half of the root is removed. Garlic mustard frequently snaps off at or above the root crown when pulled,

leaving adventitious buds that send up new flower stalks.

Burning and herbicide application both provide control at a lower labor cost, but each treatment has potential drawbacks: fire may increase presence of garlic mustard; and herbicides may negatively impact some native ground-layer species. Prescribed burning can maintain garlic mustard cover at a low level (Nuzzo et al. 1996) or have no effect (Luken and Shea 2000), but fire does not automatically reduce abundance of garlic mustard (Nuzzo 1991, Schwartz and Heim 1996, Luken and Shea 2000). Burning kills adult plants only if the root crown is sufficiently heated; a quick fire, or an incomplete fire, may remove rosette leaves, but undamaged root crowns will subsequently produce flower stalks from adventitious buds (Nuzzo et al. 1996). Burning may also enhance growth of seedlings that germinate after fire removes leaf litter (Nuzzo et al. 1996). Fire management is only feasible in fire-tolerant plant communities with sufficient fuel to carry burns, and fire may alter composition of native herbaceous vegetation (Nuzzo et al. 1996, Luken and Shea 2000).

Chemical treatment using Round-up (glyphosate) applied at 1%, 2%, and 3% concentrations to dormant rosettes in late fall or early spring can reduce cover of adult plants by as much as 95%. However, non-selective herbicide treatments also reduce cover of both sedges and grasses, and even repeated application does not sufficiently reduce garlic mustard infestations (Nuzzo 1991, 1996). In addition, large-scale repeated herbicide treatments are prohibitively expensive and time-consuming.

In summary, although conventional control methods have been experimentally shown to provide temporary, local reductions in garlic mustard populations, none have provided effective long-term control over large areas. In addition, abundance of garlic mustard in nearby unmanaged sites is a continued source for reintroduction of seeds. At present, natural area managers have no species-specific, successful long-term tool to manage garlic mustard. All available information indicates that the only viable long-term option for successful

**Table 1. Herbivores, pathogens, and pollinators associated with garlic mustard (*Alliaria petiolata*) in North America.**

Species	Order, Family	Status <sup>a</sup>	Reference	Remarks
<b>Herbivore</b>				
<i>Pieris virginiensis</i>	Lepidoptera, Pieridae	N S	Porter 1994, Courant et al. 1994	Native host <i>Dentaria</i> spp., larvae unable to complete development
<i>P. napi oleracea</i>	Lepidoptera, Pieridae	N G	Courant et al. 1994, Haribal and Renwick 1998	Native host incl. <i>Dentaria</i> spp., larvae usually unable to complete development
<i>P. n. marginata</i>	Lepidoptera, Pieridae	N ?	Courant et al. 1994	Larvae unable to complete development
<i>P. rapae</i>	Lepidoptera, Pieridae	I G	Renwick and Lopez 1999,	
Stem-mining fly	Diptera	? ?	B. Blossey and V. Nuzzo, unpubl. data	New York, Pennsylvania, Illinois
Stem-mining weevils	Coleoptera, Curculionidae	? ?	B. Blossey and V. Nuzzo, unpubl. data	New York, Pennsylvania, Illinois
Aphids	Homoptera, Aphididae	? ?	Cavers et al. 1979	
Leafhoppers	Homoptera	? ?	Cavers et al. 1979	
Flea beetles	Coleoptera, Chrysomelidae	? ?	Cavers et al. 1979; R. Root, Cornell University, pers. obs.	Widespread but uncommon
Slugs	?	? ?	Blossey, Nuzzo, pers. obs.	Widespread
Leaf miner	Diptera	? ?	Blossey, Nuzzo, pers. obs.	Illinois, New York, Pennsylvania
<b>Pathogens</b>				
<i>Alternaria</i> spp.		? G	B. Blossey, unpubl. data	New York
<i>Fusarium solani</i> (root rot)		? ?	Chen and Schwegman 1996	
Turnip mosaic virus		? ?	Stobbs & van Schagen 1987	
<i>Erysiphe cruciferarum</i>		I G	M. Scholler, Purdue University (pers. com.)	Indiana (widespread?)
<b>Pollinators</b>				
<i>Apis mellifera</i>	Hymenoptera, Apidae	I G	Cruden et al. 1996	
<i>Bombus</i> sp.	Hymenoptera, Apidae	? G	Cruden et al. 1996	
<i>Ceratina calcarata</i>	Hymenoptera, Apidae	? ?	Cruden et al. 1996	
<i>Andrena</i> cf. <i>milwaukeensis</i>	Hymenoptera, Andrenidae	? ?	Cruden et al. 1996	
<i>A.</i> cf. <i>cressonii</i>	Hymenoptera, Andrenidae	? ?	Cruden et al. 1996	
<i>A. forbesii</i>	Hymenoptera, Andrenidae	? ?	Cruden et al. 1996	
<i>A. vicina</i>	Hymenoptera, Andrenidae	? ?	Cruden et al. 1996	
<i>Lasioglossum forbesii</i>	Hymenoptera, Halictidae	? ?	Cruden et al. 1996	
<i>Augochlorella striata</i>	Hymenoptera, Halictidae	? ?	Cruden et al. 1996	
cf. <i>Augochloropsis</i> <i>metallica fulgida</i>	Hymenoptera, Halictidae	? ?	Cruden et al. 1996	
<i>Heliophilus</i> cf. <i>fasciatus</i>	Diptera, Syrphidae	? ?	Cruden et al. 1996	
<i>Eristalis</i> cf. <i>flavipes</i>	Diptera, Syrphidae	? ?	Cruden et al. 1996	
<i>E. dimidiatus</i>	Diptera, Syrphidae	? ?	Cruden et al. 1996	
<i>E. transversus</i>	Diptera, Syrphidae	? ?	Cruden et al. 1996	
<i>E.</i> cf. <i>bastardii</i>	Diptera, Syrphidae	? ?	Cruden et al. 1996	
<i>Eristalis</i> sp.	Diptera, Syrphidae	? ?	Cruden et al. 1996	
<i>Eupeodes</i> sp.	Diptera, Syrphidae	? ?	Cruden et al. 1996	
<i>Mallota</i> cf. <i>cimiciformis</i>	Diptera, Syrphidae	? ?	Cruden et al. 1996	
<i>Celastrina ladon</i>	Lepidoptera, Lycaenidae	? ?	Yahner 1998	

<sup>a</sup> N = Native, I = Introduced, S = Specialist, G = Generalist, ? = Unknown

management of garlic mustard is the development of a classical biological weed control program.

### GARLIC MUSTARD BIOLOGICAL CONTROL PROGRAM

In classical biological weed control, host-specific natural enemies from the native range of a nonindigenous plant are introduced in an attempt to reduce populations of invasive plants. Successful programs are species-specific, require low resource inputs, are self-sustaining, and are often compatible with other management strategies. In practice, weed biocontrol programs often suffer from lack of funding and lack of scientific rigor. Releases are seldom replicated or randomized, and objective measures of the depression in weed abundance are rarely provided (Crawley 1989, Lawton 1990). The emphasis on finding, screening, releasing, and distributing control organisms with little effort on post-release monitoring (McEvoy and Coombs 1999) has prevented improvements in the scientific basis and predictive ability of biological weed control (Lawton 1990, McEvoy and Coombs 1999, Blossey and Skinner 2000). This lack of data on long-term effects of control organisms on target host plants and their associated fauna and flora, and on factors that enhance or reduce effectiveness of biocontrol agents, is a severe handicap to moving beyond the biological control "lottery" (McEvoy and Coombs 2000). Merging basic research and experimentation during pre- and post-release evaluations, as planned for the garlic mustard biocontrol program, will produce significant advances in management of biological weed control programs.

Literature and field surveys revealed 70 insect herbivores and 7 fungi associated with garlic mustard in Europe (Hinz and Gerber 1998, 2001). The most important groups of natural enemies associated with garlic mustard were weevils (Curculionidae), particularly the genus *Ceutorhynchus*; leaf beetles (Chrysomelidae); and butterflies and moths (Lepidoptera). Most of these species are not sufficiently host-specific to consider introduction to North America. Five weevils and one flea beetle were selected as potential biological con-

trol agents based on their restricted host-range, feeding niches, and impact on garlic mustard (data on life histories and biology summarized from Hinz and Gerber 1998, 2001).

#### *Ceutorhynchus alliariae* and *C. roberti* (Coleoptera: Curculionidae)

Adults of *Ceutorhynchus alliariae* Brisout and *C. roberti* Gyllenhal feed on leaves; larvae mine stems and leaf petioles. Both

weevils are univoltine (one generation/year), share the same feeding niche, and have very similar life histories. Adults can be distinguished morphologically using coloration of their tarsi (feet), but no reliable features distinguish their immature stages. Both species show widely overlapping distributions in Europe, although *C. roberti* is the only species reported from Italy (Abazzi and Osella 1992). Adults overwinter in soil and leaf litter, and become active in early spring. Oviposition

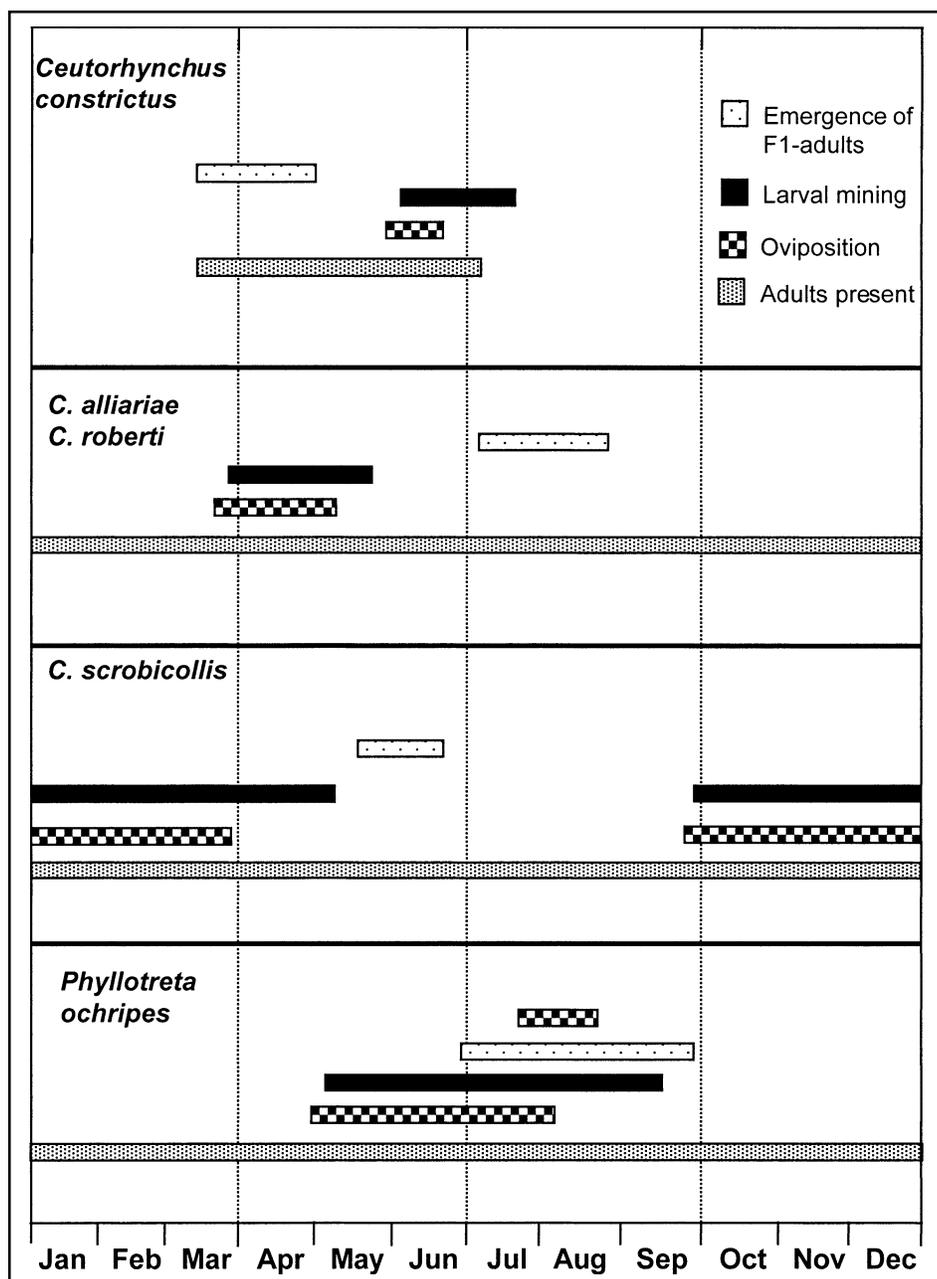


Figure 2. Phenogram of potential biological control agents of garlic mustard (life histories based on data from central Europe).

begins shortly after emergence; eggs are laid individually (*C. alliariae*) or in clusters of up to nine (*C. roberti*) into elongating stems and leaf petioles of garlic mustard. Larvae hatch after 1–3 weeks and feed internally. Development from egg to mature larva takes about 7 weeks, and third instars leave the host plant to pupate in the soil. New generation adults begin to emerge in June (Figure 2). Attack rates on garlic mustard in Europe ranged from 48–100% of shoots at various field sites investigated during 1998 and 1999, with an average of 2–11 larvae/shoot. High attack rates reduce seed production of garlic mustard, and at densities of 20–30 larvae/shoot premature wilting occurs. Experiments in the next 3 years will evaluate the impact and possible competitive interactions between these two stem feeders.

#### ***Ceutorhynchus scrobicollis*** (Coleoptera: Curculionidae)

*Ceutorhynchus scrobicollis* Nerensheimer & Wagner is a univoltine root-mining weevil. Little information about biology and ecology of this species was available when investigations began in 1998. The species is reported from Eastern and East-central Europe and Italy (Dieckmann 1972, Abazzi and Osella 1992). During field surveys the species was only found in eastern Austria and eastern Germany but was absent from field sites in southern Germany and Switzerland. Adults emerge in May and June and, after feeding on leaves for a brief period, aestivate during summer. In Europe, oviposition starts in mid-September and continues until spring (Figure 2). Eggs are laid mainly into leaf petioles and surfaces of rosette-leaves. Early larvae mine petioles and rosette meristems, but the majority of mature larvae feed in root crowns. Larvae overwinter but continue feeding and leave the host plant in spring to pupate in the soil. Within the European distribution of *C. scrobicollis*, attack rates ranged from 50% to 100% of plants, and usually four to eight larvae completed development within a single plant. Larvae feeding over winter often kill developing shoots. In spring and early summer, attacked plants appear water-stressed, and desiccate prematurely at high infestations.

#### ***Ceutorhynchus constrictus*** (Coleoptera: Curculionidae)

*Ceutorhynchus constrictus* (Marsham) is a univoltine weevil. Adults feed on leaves and larvae consume developing seeds. Of all *Ceutorhynchus* species associated with garlic mustard, *C. constrictus* is the most widespread and is common throughout Western and Central Europe (Dieckmann 1972). Adults emerge in April to feed and mate. Oviposition starts once garlic mustard begins to produce siliques in May and June (Figure 2). Eggs are laid in developing seeds and a single female may produce well over 150 eggs during a season. Larvae feed on developing seeds during June and July (Figure 2). Each larva consumes one or two seeds before leaving the silique to pupate in the soil. Mature larvae form an earthen cocoon and pupate, and fully developed adults overwinter in the soil until the following spring. Although the species was found at all field sites, attack rates were generally low, with only 0.3–6.4% of seeds attacked in southern Germany and Switzerland.

#### ***Ceutorhynchus theonae*** (Coleoptera: Curculionidae)

*Ceutorhynchus theona* Korotyaev is a newly described species collected in Dagh-estan, Russia, in spring 2000 and shipped into quarantine in Switzerland. Preliminary investigations conducted in Switzerland confirm that the species attacks seeds of garlic mustard. The biology of *C. theonae* appears similar to that of *C. constrictus*, but feeding by *C. theonae* appears more damaging. This new species will be included in the host-specificity testing procedure if sufficient adults can be obtained and rearing methods developed.

#### ***Phyllotreta ochripes*** (Coleoptera: Chrysomelidae)

Adults of the flea beetle *Phyllotreta ochripes* (Curtis) feed on leaves; larvae feed on roots of both bolting garlic mustard plants and rosettes. The species ranges widely over most of Europe and parts of Northwestern Asia (Gruev and Döberl 1997), appears to have a partial second generation (Figure 2), and was common in

field surveys in Switzerland, Germany, and Austria. Adults overwinter in leaf litter and can be found feeding on garlic mustard rosettes in early March. Females lay an average of 280 eggs in soil close to the root crown over a period of about 3 months (Figure 2). Larvae usually mine just beneath the epidermis of the root or root crown of bolting plants and rosettes as well as leaf petiole bases (Figure 2). Mature larvae pupate in the soil, and the first adults emerge by the end of June (Figure 2). Development from first instar to adult takes 30–65 days. Early emerging females may lay eggs in summer, indicative of a partial second generation. Little is known about the impact of *P. ochripes* on plant performance. Larvae are difficult to detect because of larval feeding habits on the outer parts of the root, and attack rates therefore are difficult to quantify. We will need to conduct controlled, common garden experiments to assess the impact of this flea beetle.

#### **Host-specificity Testing**

Host-specificity screening studies have been widely standardized (Wapshere 1989, USDA 1999) and provide reliable information on safety of introduced control agents (McFadyen 1998, Pemberton 2000). Host-specificity of all six species considered potential biological control agents for garlic mustard will be evaluated in Europe before any introductions are proposed. A sequence of different testing procedures is used involving about 50 different test plant species. For garlic mustard, special attention will be given to native North American crucifers (especially *Dentaria* and *Rorippa* spp.), cultivated crucifers (e.g., cabbages, *Brassica* spp.), as well as native plant species growing in the same habitats (e.g., forest spring ephemerals such as *Trillium* spp.). First, adults and larvae will be offered a single test plant in no-choice tests. Next, adults and larvae will be offered several plant species simultaneously in multiple-choice tests using plants that were attacked in no-choice tests. No-choice starvation tests are used to determine the physiological host range of a species, but tests often show a wider host range than later realized in the field. More realistic multiple-choice tests in the field will be

utilized using plants that are accepted for oviposition under no-choice conditions (Clement and Cristofaro 1995). All five *Ceutorhynchus* species selected as potential biocontrol agents for garlic mustard are reported to be monophagous—that is, they develop exclusively on garlic mustard (Dieckmann 1972)—and this will be tested in detail. Only *P. ochripes* was reported to complete larval development on species other than garlic mustard (Doguet 1994). Preliminary investigations confirmed these reports and documented successful larval development on *Rorippa amphibia* (L.) Besser and on eight additional species including several *Rorippa* spp. and *Brassica* spp. (Hinze and Gerber 2001). Although additional field tests will follow, these early results are strong indication that *P. ochripes* is not sufficiently host-specific to warrant introduction to North America because several North American native *Rorippa* species occur within the North American range of *A. petiolata*, including *Rorippa sinuata* (Nutt.) A. S. Hitchc., *Rorippa sessiliflora* (Nutt.) A. S. Hitchc., *Rorippa palustris fernaldiana* (Butters and Abbe) Stuckey, *Rorippa palustris hispida* (Desv.) Rydb., *Rorippa curvipes* Greene, and *Rorippa obtusa* (Nutt.) Britt. (Fernald 1970, Voss 1985, Gleason and Cronquist 1991).

### Selection of Most Promising Control Agents

Weed biocontrol programs continue to operate under the lottery model assuming that the introduction of numerous host-specific control agents will include the “silver bullet” or “tip the balance” due to accumulating impacts by multiple herbivores (McEvoy and Coombs 1999). However, criteria proposed for prioritizing potential biocontrol agents have little predictive power and produce contradictory rankings (Blossey 1995). Final selection of control agents for garlic mustard will be based on pre-release studies of their host-specificity, effectiveness in reducing plant performance, and their potential competitive interactions. Denno et al. (1995) reviewed 193 pairwise interactions among phytophagous species and found competitive interactions in 73% of the studies. Although few studies exam-

ined the interactions between above- and below-ground herbivores, all interactions adversely affected root-feeders (Masters et al. 1993, Denno et al. 1995). The potential for competitive interactions among herbivores on garlic mustard exists for stem miners, seed feeders, and for plant-mediated interactions of root- and stem-feeders. However, it is unclear how these interactions may influence the success or failure of biological weed control. All potential biocontrol agents for garlic mustard must first pass the host-specificity screening tests. Experiments over the next few years will analyze impact of single and multiple species on performance of garlic mustard, as well as resulting interactions among different herbivores to avoid antagonistic interactions among control agents.

### Monitoring: Pre- and Post-release Studies

The invasion of nonindigenous plants may affect native taxa and ecosystem processes in natural areas set aside to protect native species and ecosystem processes. Management of garlic mustard or other invasive plants aims to protect or restore ecosystems. However, quantitative evidence for ecosystem impacts of individual invasive species in general, and of garlic mustard in particular, are anecdotal (Blossey 1999). An important aspect of the biocontrol program against garlic mustard is collection of baseline data before introduction of control agents. We are developing a standardized monitoring protocol that will provide baseline data and assess the impact on native organisms after introduction of biocontrol agents. We are incorporating measures of (1) garlic mustard abundance, (2) abundance and impact of biological control agents, and (3) changes in native plant communities. We anticipate developing a protocol sophisticated enough to allow rigorous statistical analysis, yet simple enough to allow widespread use by natural area managers. We will compare garlic mustard population dynamics in Europe (in the presence of specialized herbivores) and in North America (in the absence of specialized herbivores) to help develop a better understanding of the factors that allow garlic mustard to be a successful invader. We anticipate such inves-

tigations to help predict which plant stages constitute “Achilles heels” and should be targeted for control.

The monitoring protocol and long-term evaluations will help us assess how ecosystems respond to changes in abundance of individual invasive species. Combining long-term monitoring with field evaluations of the impact of different biological control agents in various habitats throughout the range of garlic mustard in North America will help us improve management of garlic mustard. This research will help close the “monitoring and evaluation gap” (Blossey 1999, McEvoy and Coombs 2000) commonly observed in biological weed control. The development of standardized monitoring protocols will also help build partnerships and cooperation across disciplines and agencies and provide for the necessary replication and a more powerful analysis of the impact of a biological control program. In addition, following changes of floral and faunal communities through time will allow us to assess “quality” of replacement communities.

### CONCLUSIONS

Negative ecological impacts of garlic mustard in North America, in combination with the inability to control the species by conventional means, makes development of biological control an attractive alternative. Development of a successful garlic mustard biocontrol program will depend upon (1) experimentally verifying the host-specificity and effectiveness of potential control agents, (2) obtaining U.S. Department of Agriculture approval for introduction of tested organisms, (3) implementing a release program at selected sites in North America, (4) incorporating biological control into the management strategy of land managers, and (5) utilizing standardized protocols to monitor biocontrol agents, garlic mustard populations, and the response of native plant and animal communities. Combining long-term monitoring, experimental research, and evaluation will provide a framework for improving management of invasive plants using biological control. In addition, such investigations will continue to improve the scientific

basis and predictive ability of biological weed control.

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