BIOLOGICAL CONTROL 5, 47–53 (1995)

Host Specificity of Three Potential Biological Weed Control Agents Attacking Flowers and Seeds of *Lythrum salicaria* (Purple Loosestrife)

BERND BLOSSEY[1] AND DIETER SCHROEDER

International Institute of Biological Control, European Station 1, Chemin des Grillons, CH-2800 Delémont, Switzerland

Received November 18, 1993; accepted June 22, 1994

Lythrum salicaria **is a Eurasian herbaceous perennial that has become a serious invader of wetlands in the United States and Canada. Dense monospecific stands replace a diverse native flora resulting in the degradation of these wetland habitats. There are presently no satisfactory means of control. Biological control offers the most promising method of resolving this problem. A root-mining weevil and two leaf-feeding chrysomelids from Europe were released in North America in 1992. The host specificity of three additional flower- and seed-feeding species was investigated. The two weevils, *Nanophyes marmoratus* and *N. brevis*, have a wide geographic and ecological range. Both develop exclusively on *Lythrum salicaria* within its native European range and were found to be highly host specific during screening tests. Minor adult feeding was observed in no-choice tests on a few other species within the Lythraceae. Successful larval development was restricted to purple loosestrife. The only known field host of the third species, the gall midge *Bayeriola salicariae*, is purple loosestrife. Oviposition and successful larval development of *B. salicariae* in cages and the open field occurred on potted test plants of another three *Lythrum* species. The introduction of *N. marmoratus* and *N. brevis* into North America is expected to further reduce seed output and lessen the competitive ability of purple loosestrife. Their introduction was approved in 1994.**

KEY WORDS: ***Nanophyes marmoratus; Nanophyes brevis; Bayeriola salicariae; Lythrum salicaria;*** **purple loosestrife; biological weed control; host specificity.**

INTRODUCTION

Purple loosestrife (*Lythrum salicaria* L., Lythraceae) is a herbaceous perennial of European origin that has become naturalized in North America. It arrived during the early 1800s in ship ballast and was also introduced as a herb and ornamental (Stuckey, 1980). The plant has since become a serious weed in marshes and alluvial wetlands (Thompson *et al.*, 1987; Malecki *et al.*, 1993b). The main problem areas occur in the northeast and north-central United States and in parts of southern Canada. Recently its spread into the arid Midwest and West along major rivers and irrigation systems is causing concern. Where thoroughly established, *L. salicaria* tends to form dense monospecific stands that displace the more diversified native flora (Malecki and Rawinski, 1985).

Profuse seed production, a high germination rate, and large rootstocks make purple loosestrife an aggressive invasive species. There is currently no satisfactory means of control (Thompson *et al.*, 1987). Herbicides used most often against purple loosestrife are glyphosate [Rodeo, *N*-(phosphonomethyl)glycine], 2,4-D [(2,4-dichlorophenoxy)acetic acid], and, on an experimental basis, triclopyr [Garlon 3A, (3,5,6-trichloro-2-pyridinyl)-acetic acid]. These are nonspecific, disruptive to sensitive aquatic or semiaquatic habitats, expensive, and do not provide control over a prolonged period of time (Skinner *et al.*, 1994).

Purple loosestrife is not attacked to any noticeable degree by native North American phytophagous insects or plant pathogens (Hight, 1990). This gives it a competitive advantage over native wetland plants. The aim of this biological control program is to counterbalance the present competitive advantage of purple loosestrife by establishing effective host-specific herbivores attacking roots, leaves, and reproductive organs.

Following identification and host-range screening of three biological control agents of purple loosestrife (Blossey *et al.*, 1994a,b), the weevil *Hylobius transversovittatus* (Goeze) and the two chrysomelids *Galerucella calmariensis* (L.), and *G. pusilla* (Duft.) were released in North America in summer 1992. Their attack is expected to reduce plant vigor and survival considerably. This will also affect flowering and seed output (Blossey, 1993, 1994). However, even at high insect population levels surviving plants will still produce seeds (Blossey, 1994). These seeds will build up the existing seed bank

[1] Present address: New York Cooperative Fish and Wildlife Research Unit, Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, New York 14853.

1049-9644/95 $6.00

and provide a continuous source for new recruitment. Release and establishment of control agents attacking reproductive organs is expected to minimize this additional source of seed. Therefore, the biology and host specificity of three potential control agents, the two weevils *Nanophyes marmoratus* Goeze and *N. brevis* Boh. and the gall midge *Bayeriola salicariae* Gagné, were studied in Europe.

THE ORGANISMS

L. salicaria (Myrtales: Lythraceae)

L. salicaria has European and Asian distribution centers. The European segment extends from Great Britain across Europe into central Russia. Its northern limit is near the 65th parallel (Tutin *et al.*, 1968). *L. salicaria* is common throughout central and southern Europe and along the coastal fringe of the Mediterranean basin. In Asia, the main islands of Japan are the core of the species' native range, with outlying populations extending from the Amur River south across the lowlands of Manchuria and China to southeast Asia and India (Hultén and Fries, 1986). As an invading species, *L. salicaria* is found in eastern Africa (Ethiopia), Australia, Tasmania, New Zealand, Peru, the United States, and southern Canada (Thompson *et al.*, 1987; Kutschera *et al.*, 1992).

Depending on site conditions, mature plants of *L. salicaria* are between 0.5 and 3 m high, with a maximum of 30–50 shoots emerging from a common rootstock. Large plants produce more than 2.5 million seeds which remain viable for many years (Thompson *et al.*, 1987; Welling and Becker, 1990). Germination can occur on a variety of substrates with a wide range of pH. However, successful seedling establishment only occurs on moist soil, mainly in late spring or early summer when temperatures are high (Shamsi and Whitehead, 1974). Both in Europe and North America, *L. salicaria* is found in a great variety of sites, from rock crevasses to gravel, sand, clay, and organic soils. Moisture is the most important factor for growth and reproduction, but well established plants can persist at dry sites for many years.

Nanophyes marmoratus (Coleoptera: Curculionidae)

The subfamily Nanophyinae presently includes 18 genera and some 276 species of beetles, all associated with Lythraceae and distributed in all regions, but poorly represented in the New World (4 species). In the Palearctic region it is represented by 4 genera, 1 subgenus, and 87 species (Alonso-Zarazaga, 1989). According to Dieckmann (1963), in Europe the genus *Nanophyes* consists of 13 species.

In northwestern Germany overwintered adults appear on *L. salicaria* during the second half of May. The beetles start feeding on the youngest leaves at shoot tips. As soon as flower buds develop, beetles move to upper parts of flower spikes where they copulate and feed on receptacles and ovaries within closed flower buds. Oviposition starts at the end of June and extends into September. Eggs are laid into tips of young flower buds before petals are fully developed. Generally, only a single egg is deposited per bud. Attacked buds remain closed, do not flower, and are later aborted. The larvae first consume the stamens, and, in most cases, the petals; they then eat the ovary. Only a single larva can complete its development per flower bud. Mature larvae form a pupation chamber from their frass at the bottom of the bud. The new-generation beetles appear mainly in August and feed on the remaining green leaves of purple loosestrife before overwintering. Complete development from egg to adult takes about 1 month. There is one generation per year.

N. marmoratus occurs throughout Europe and western Siberia (Dieckmann, 1963). With a few exceptions, *N. marmoratus* was abundant and found at all sites visited in northern and central Europe. The species tolerates a wide range of environmental conditions and adults generally were present at isolated sites with only a few host plants.

N. brevis (Coleoptera: Curculionidae)

After overwintering, adults appear together with those of *N. marmoratus* on young shoots of *L. salicaria* and feed on the youngest leaves. The two species separate as soon as flower spikes develop. *N. marmoratus* occupies the upper part of the flower spike with unopened flower buds, while *N. brevis* concentrates on the lower part with opened flowers. Here *N. brevis* feeds exclusively on the receptacles. Oviposition is restricted to fertilized flowers, and eggs are laid directly into the ovary. The larvae feed on developing seeds and pupate within inflated ovaries. Normally, only a single larva is found per ovary. Complete larval development takes about 7 weeks. The main emergence period is in August and September, but beetles can still be found on their host plant in late October. *N. brevis* is univoltine.

N. brevis occurs throughout central and southern Europe including the entire European Mediterranean and Asia Minor. The species is also recorded from Egypt (Dieckmann, 1963).

B. (Bayeria) salicariae (Diptera: Cecidomyiidae)

B. salicariae adults emerge and reproduce continually between April/May and September. Adults are short-lived and emerging females have well-developed ovaries containing between 80 and 120 eggs. Eggs are laid in varying numbers per batch into leaf or flower buds. Hatching larvae move to meristematic tissues where galls are induced. The pea-sized leaf–bud galls contain up to 11 larvae; the much smaller flower–bud galls normally have only a single larva. Development from egg to adult during the summer takes about 1 month. During

late spring and summer the full-grown larvae pupate within the gall from which the adults emerge. From August onward an increasing proportion of full-grown larvae leave the gall. They move into the top soil layer where they form a cocoon and overwinter. All larvae completing development in September or later leave the galls and overwinter in the soil.

B. salicariae occurs from southern Scandinavia throughout the European distribution of purple loosestrife (Buhr, 1964). This gall midge has been found, with increasing abundance from April to September, at over 100 sites checked for its presence in north and central Europe.

MATERIALS AND METHODS

A list of plant species (Table 1) was approved for host-specificity screening by the Technical Advisory Group (TAG) for the Introduction of Biological Control Agents of Weeds, U.S. Department of Agriculture, Animal and Plant Health Inspection Service (Coulson, 1992). Plants belonged to one of three groups: (A) taxonomically associated plants, (B) associated wetland plants of wildlife importance, and (C) important agricultural plants. The phylogenetically related plants of group A are based on the system of Cronquist (1981). The order Myrtales has 12 families, and 4 of these families are native to much of North America (Lythraceae, Thymelaceae, Onagraceae, and Melastomataceae). Of the remaining 8 families, 5 are strictly tropical in their distribution and lack important introductions into North America. Only *Punica granatum* (pomegranate) is included in the test list because it is an introduced semitropical agricultural fruit that is grown in the United States. Plants that make up group B are not taxonomically related to purple loosestrife, but occur in the same habitat and are therefore likely to be exposed to any introduced biological control agent. Group C contains a selection of crop plants which were tested for additional safety.

Screening tests were conducted at the Christian-Albrechts University, Kiel, Germany. Test plant species were either shipped from the United States or obtained from European field populations. Plants were grown in 10-cm-diam clay pots from seeds, roots, or tubers in commercial potting soil (natural soil, nutrients added by the manufacturer). Most plants were grown outdoors to ensure healthy specimens.

Adults of *N. marmoratus* used in host specificity tests were collected at sites in northern Germany in the vicinity of Kiel. Adults of *N. brevis* were field collected in the Rhine Valley in southwestern Germany. Galls of *B. salicariae* were collected in the vicinity of Hamburg, northern Germany. Fall-collected galls were stored in plastic bags and emerging larvae were transferred daily into vials filled with fresh sphagnum moss and overwintered outdoors. The emerging adults were used in experiments the following spring. Additional adults were obtained from galls collected in spring.

Identification of the two *Nanophyes* species was confirmed by the late Dr. L. Dieckmann, Department of Insect Taxonomy, Institute for Plant Protection, Eberswalde, Germany. Identification of *B. salicariae* was verified by Dr. R. J. Gagné, USDA-ARS, Beltsville, Maryland. Voucher specimens of this species are located in the U.S. National Museum of Natural History, Washington, DC.

No-Choice Adult Feeding Tests

Adult feeding tests were only conducted for the two weevil species since adults of *B. salicariae* do not feed after emergence. In May/June 1991 and 1992 adults of *N. marmoratus* and *N. brevis* were field collected from purple loosestrife plants using an aspirator. Adult feeding tests were conducted before oviposition started in late June and early July. Experiments were conducted in a glasshouse under ambient temperatures (range 15–30°C) and photoperiod (16–18 h). Two pairs of adults were caged in glass tubes (5.5 cm high, 3 cm in diameter) on cut leaves and buds. Moistened florist foam at the bottom of the tube kept the plant material fresh for several days. Tubes were arranged in a completely randomized design and tests were run for 3 days. For *N. marmoratus* the number of feeding holes was counted. For *N. brevis* feeding damage was less conspicuous; therefore, the damage was classified in one of four damage classes: no feeding (0 points), nibbling (1 point) was the presence of a few feeding marks; moderate feeding (2 points) was the removal of an obvious amount of plant tissue, and normal feeding (3 points) was the removal of tissue similar in amount observed on the control, purple loosestrife. The maximum possible score was 15 points. For each plant and weevil species, the tests were replicated five times.

Oviposition and Larval Development Tests

Well-developed potted test plants were offered in a multiple-choice design including purple loosestrife in outdoor walk-in cages ($3 \times 2 \times 2$ m, fine insect netting). Since *N. marmoratus* and *N. brevis* are flower- and seed-feeders it was crucial to offer plants at the right phenological stage. To match flowering periods of test plants and oviposition periods of *N. marmoratus* and *N. brevis*, plants were seeded at varying times or planted under different growing conditions (photoperiod, temperature, moisture, and nutrients), depending on experience in earlier experiments. Tests were staggered and experiments run in July and August 1991 and 1992. However, some test plant species did not flower at all or did not flower at the right time (see Table 1). Test plants reaching the right phenological stage were arranged at random and in varying numbers and combinations in the walk-

TABLE 1

List of Test Plant Species for Host-Specificity Screening with Biological Control Agents Against Purple Loosestrife

	A. Taxonomically associated plants	
Lythraceae	1. *Lythrum salicaria* L.[a]	2. *L. lineare* L.
	3. *L. alatum* Pursh.	4. *L. californicum* Torr. & Gray
	5. *L. hyssopifolia* L.[a]	6. *Decodon verticillatus* (L.) Ell.
	7. *Rotala ramosior* (L.) Koehne	8. *Ammannia coccinea* Rottb.
	9. *A. robusta* Heer & Regel	10. *Cuphea viscosissima* Jacq.
	11. *C. wrightii* Gray[b]	12. *C. laminuligera* Koehne[b]
	13. *C. lanceolata* Alton[b]	14. *C. lutea* Rose[b]
	15. *Lagerstroemia indica* L.[a,c,d]	
Punicaceae	16. *Punica granatum* L.[a,c,d]	
Melastomataceae	17. *Rhexia mariana* L.[b,d]	
Onagraceae	18. *Ludwigia alternifolia* L.	19. *Epilobium angustifolium* L.
	20. *Oenothera biennis* L.	21. *Gaura parviflora* Dougl.
	22. *G. biennis* L.	23. *Circaea quadrisulcata* (L.) Hara
	B. Associated wetland plants of wildlife importance	
Typhaceae	24. *Typha latifolia* L.	
Sparganiaceae	25. *Sparganium eurycarpum* Engelm.[d]	
Alismataceae	26. *Sagittaria latifolia* Willd.[d]	
Poaceae	27. *Zizania aquatica* L.[d]	
Cyperaceae	28. *Scirpus americanus* Pers.	29. *S. acutus* Muhl.
	30. *Carex comosa* Bostt.	
Salicaceae	31. *Salix interior* Rowlee[d]	
Polygonaceae	32. *Rumex crispus* L.[a]	33. *Polygonum coccineum* Muhl.[d]
Chenopodiaceae	34. *Chenopodium album* L.[a]	
Ranunculaceae	35. *Ranunculus sceleratus* L.	36. *R. bulbosus* L.[a,d]
	C. Important agricultural plants	
Poaceae	37. *Triticum aestivum* L.[a]	38. *Oryza sativa* L.[a]
	39. *Zea mays* L.	
Chenopodiaceae	40. *Beta vulgaris* L.[a,d]	
Fabaceae	41. *Glycine max* L.[a]	
Malvaceae	42. *Gossypium hirsutum* L.[d]	
Asteraceae	43. *Helianthus annuus* L.	

[a] Species not native to North America.
[b] *Nanophyes brevis* not tested on this species.
[c] *Bayeriola salicariae* not tested on this species.
[d] Plants did not flower at all or did not flower at the right time. No oviposition tests were performed for *N. brevis* and *N. marmoratus*.

in cages. In the cage with *N. brevis* 10–20 bumble bees and honey bees were added every 2–3 days. This has proven successful to insure pollination and the availability of the appropriate phenological stage for oviposition (B. Blossey, personal observation). Test plants were exposed to 50–100 pairs of adult *N. marmoratus* or *N. brevis* in each test (1 cage for each species). Test plants were replaced after 2 weeks and flower buds dissected to determine attack rates. Tests were replicated five times for each weevil and plant species.

Experiments with *B. salicariae* were conducted outdoors from 5 July to 15 August 1990 and from 1 May to 15 September 1991. Test plants (including the original host purple loosestrife) were arranged at random in varying combinations in two walk-in cages. Throughout 1990 and 1991 emerging adults (0–20 per day, 420 total,

TABLE 2

Results of Host-Specificity Screening of *Nanophyes marmoratus*

Test plant species[a]	No-choice adult feeding (No. holes[b])	Multiple-choice oviposition (No. attacked flowers[c])
Lythrum salicaria	45.6 ± 3.6	Several 100
L. lineare	2.2 ± 1	0
L. alatum	3.4 ± 2.7	0
L. californicum	0.2 ± 0.2	0
L. hyssopifolia	12.4 ± 3.4	0
Cuphea wrightii	0.2 ± 0.2	0
Rhexia mariana	0.2 ± 0.2	0
Epilobium angustifolium	1.8 ± 0.7	0
Polygonum coccineum	0.2 ± 0.2	0

[a] All other species remained unattacked.
[b] Means ± SE of five replicates.
[c] Total of five replicates in field cage.

1:1 sex ratio) were released daily into the cages. After termination of the experiment in the fall of each year, plants were checked under a dissecting microscope. The number of galls was counted, and whether successful larval development (to the adult stage) had occurred was recorded. The latter could be determined by the presence of pupation cocoons in dissected galls.

Field Tests

Caged *B. salicariae* oviposited on some species in the Lythraceae. To test oviposition in the field, five potted test plants of each of the 15 species in the Lythraceae (see Table 1) were exposed to *B. salicariae* during the 1992 oviposition period at a field site close to Hamburg. Plants were arranged at random along a ditch. After 3 weeks, the plants were collected, kept in a common garden for another 6 weeks to allow for gall development, and examined under a dissecting microscope. The presence or absence of galls was noted and it was determined whether larvae had developed successfully.

RESULTS

N. marmoratus

Normal adult feeding was restricted to *L. salicaria* but a moderate amount of feeding was observed on *L. hyssopifolia* (Table 2). Few feeding marks were found on seven other test plant species (Table 2), whereas all others were refused (compare Tables 1 and 2). Oviposition followed by successful larval development was restricted to *L. salicaria* (Table 2). In none of the other test plant species were eggs or developing larvae found during dissections. New-generation beetles in the walk-in cages fed on *L. hyssopifolia* at the end of the season after purple loosestrife plants had dried up, but oviposition never occurred on this test plant.

TABLE 3

Results of Host-Specificity Screening of *Nanophyes brevis*

Test plant species[a]	No-choice adult feeding[b]	Multiple-choice oviposition (No. attacked flowers[c])
Lythrum salicaria	15	>200
L. alatum	2	0
L. hyssopifolia	10	0
Decodon verticillatus	5	0
Ludwigia alternifolia	3	0

[a] All other species remained unattacked.
[b] Sum of scores of five replicates/test plant species according to feeding damage (no feeding = 0, nibbling = 1, moderate feeding = 2, normal feeding = 3 points).
[c] Total of five replicates in field cage.

N. brevis

Normal feeding of *N. brevis* was restricted to the control *L. salicaria* (Table 3). Some moderate feeding occurred on *L. hyssopifolia* and some nibbling on *L. alatum*, *D. verticillatus*, and *L. alternifolia* (Table 3). All other test plant species were refused (compare Tables 1 and 3). Oviposition followed by successful larval development was restricted to purple loosestrife (Table 3). Neither eggs nor developing larvae were found during dissections of any of the other test plant species.

B. salicariae

In both the field-cage and open-field tests, galls formed exclusively on *L. salicaria*. A limited number of successful ovipositions occurred in both test series on *L. hyssopifolia*, *L. alatum*, and *L. californicum* (Table 4). However, no normally shaped galls developed. The plants produced swellings and callus tissue, resulting in

TABLE 4

Results of Host-Specificity Screening of *Bayeriola salicariae*

	Oviposition and gall development[b]	
Test plant species[a]	Cage[c]	Field
Lythrum salicaria	>60	Numerous
L. alatum	2 ± 1	Few
L. californicum	1.8 ± 0.8	Few
L. hyssopifolia	20.4 ± 4.2	Normal

[a] All other species remained unattacked.
[b] Number of galls produced.
[c] Data are means ± SE of five replicates/test plant species.

stunted and abnormal shoot growth. Larvae of *B. salicariae* successfully completed development on all three species. All other test plant species remained free from attack (compare Tables 1 and 4).

DISCUSSION

Both *N. marmoratus* and *N. brevis* are highly host specific, and oviposition followed by successful larval development is restricted to the target plant purple loosestrife. The nibbling by *N. marmoratus* and *N. brevis* on few other test species is of no significance to these plants. Moreover, *L. hyssopifolia,* which was moderately attacked, is an introduced invasive plant in North America. No adverse effects to any plant other than *L. salicaria* are expected from the introduction of these two species.

The two *Nanophyes* species occupy a well-defined niche in the inflorescences of purple loosestrife. Their attack of different phenological stages will therefore be additive. Based on field observations in Europe (Blossey and Schroeder, 1992) the combined action of these two control agents is expected to reduce seed production of *L. salicaria* by 50–70%. Since both species are highly parasitized in Europe (attack rates can reach 90%), their introduction in the absence of natural enemies could result in an even higher degree of seed destruction. Their ability to spread over a wide geographic range should allow their establishment throughout the current distribution of purple loosestrife in North America.

The attack of the gall midge *B. salicariae* should further reduce the seed output of *L. salicaria.* In Europe, the midge reaches higher attack rates only toward the end of the season. A possible reason is the high parasitization rate (attaining 90%) in early generations (Blossey and Schroeder, 1992). In the screening tests with *B. salicariae,* successful development was observed on three *Lythrum* species besides *L. salicaria.* However, not all *Lythrum* species were susceptible to attack by *B. salicariae* (no gall formation on *L. lineare;* compare Tables 1 and 4). The somewhat wider host range, even though not considered a threat to field populations of *L. alatum* and *L. californicum,* gives *B. salicariae* a lower priority for introduction. In addition, gall midges have been found to be vulnerable to attack by native parasitoids, significantly reducing their impact on the target weed populations (Julien, 1989). *N. marmoratus* and *N. brevis* are highly host specific and able to destroy a large percentage of the annual seed production of purple loosestrife. *B. salicariae* should only be considered for introduction if the attack of the two weevils needs to be complemented by an additional flower feeder.

Environmental Consequences of Release

There are at present no satisfactory means of effective long-term control of *L. salicaria.* The measures presently in use to lessen competition from *L. salicaria* in selected areas are expensive and disruptive for the flora and fauna of the treated areas, and their effect is not persistent. Therefore, all state and federal agencies involved in the control program [USDA, U.S. Department of the Interior (USDI), the Army Corps of Engineers, etc.] set a high priority on biological control of *L. salicaria* (Malecki *et al.,* 1993a,b; Blossey *et al.,* 1994a,b).

All *Lythrum* species have attractive flowers, and several species, including the target species, are grown as ornamentals. The establishment of *N. marmoratus* and *N. brevis* is expected to further increase the destruction of flower buds and seeds by primarily attacking those that have escaped attack by the *Galerucella* species (Malecki *et al.,* 1993b). No adverse effects are seen from their introduction except for the further reduction in the abundance of attractive purple loosestrife flowers. This is a consequence of any purple loosestrife control and not peculiar to these control agents. The expected end result is restoration of the natural floral diversity within areas presently dominated by *L. salicaria.* The introduction of *N. marmoratus* and *N. brevis* was approved by TAG in 1994.

ACKNOWLEDGMENTS

This work was funded by USDI, Fish and Wildlife Service, through Cornell University (Ithaca, NY), and the Departments of Agriculture and Wildlife, State of Washington. We thank G. Petersen and R. Lietz for technical assistance. H. Pschorn-Walcher, retired Director of the Institute for Ecology, Christian-Albrechts University, provided greenhouse and garden space for the experiments. Special thanks to S. D. Hight, USDA-ARS (Beltsville, MD), who guaranteed the provision of plant material of native North American species for the tests in Europe. Comments by R. Malecki and two anonymous reviewers on the earlier versions improved this paper.

REFERENCES

Alonso-Zarazaga, M. A. 1989. Revision of the supraspecific taxa in the Palaearctic Apionidae Schoenherr, 1823. 1. Introduction and subfamily Nanophyinae Seidlitz, 1891. *Fragm. Entomol. Roma* **21,** 205–262.

Blossey, B. 1993. Herbivory below ground and biological weed control: Life history of a root-boring weevil on purple loosestrife. *Oecologia* **94,** 380–387.

Blossey, B. 1994. Impact of *Galerucella pusilla* Duft. and *G. calmariensis* L. (Coleoptera: Chrysomelidae) on field populations of purple loosestrife (*Lythrum salicaria* L.). *In* "Proceedings of the VIII International Symposium on Biological Control of Weeds, Canterbury, New Zealand." (E. S. Delfosse and R. R. Scott, Eds.). DSIR/CSIRO, Melbourne, in press.

Blossey, B., and Schroeder, D. 1992. "Biocontrol of *Lythrum salicaria* in the United States: Final Report." International Institute of Biological Control, European Station, Delémont, Switzerland.

Blossey, B., Schroeder, D. Hight, S. D., and Malecki, R. A. 1994a. Host specificity and environmental impact of two leaf beetles (*Galerucella calmariensis* and *G. pusilla*) for the biological control of purple loosestrife (*Lythrum salicaria*). *Weed Sci.* **42,** 134–140.

Blossey, B., Schroeder, D. Hight, S. D., and Malecki, R. A. 1994b. Host

specificity and environmental impact of the weevil *Hylobius transversovittatus*, a biological control agent of purple loosestrife (*Lythrum salicaria*). *Weed Sci.* **42,** 128–133.

Buhr, H. 1964. "Bestimmungstabellen der Gallen (Zoo- und Phytocecidien) an Pflanzen Mittel- und Nordeuropas," pp. 708–710. Fischer, Jena.

Coulson, J. R. 1992. The TAG: development, functions, procedures, and problems. *In* "Regulations and Guidelines: Critical Issues in Biological Control." Proceedings of a USDA/CSRS National Workshop, June 10–12, 1991, Vienna, VA. (Charudattan, R. and Browning, H. W., Eds.), pp 53–60. Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL.

Cronquist, A. 1981. "An Integrated System of Classification of Flowering Plants." Columbia Univ. Press, New York.

Dieckmann, L. 1963. Die mitteleuropäischen Arten der Gattung *Nanophyes* Schönh. nebst einer neuen Art aus Bulgarien. *Reichenbachia Dresden* **1,** 169–194.

Hight, S. D. 1990. Available feeding niches in populations of *Lythrum salicaria* L. (purple loosestrife) in the Northeastern United States. *In* "Proceedings of the VII International Symposium on Biological Control of Weeds, Rome, Italy," (E. S. Delfosse, Ed.), pp. 269–278. Ist. Sper. Patol. Veg. (MAF), Rome, Italy.

Hultén, E., and Fries, M. 1986. "Atlas of North European Vascular Plants," Vol. 2. Koeltz Scientific Books, Königstein, Germany.

Julien, M. H. 1992. "Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds," 3rd ed. CAB International, Wallingford, UK.

Kutschera, L., Lichtenegger, E., and Sobotik, M. 1992. "Wurzelatlas mitteleuropäischer Grünlandpflanzen." Gustav Fischer Verlag, Stuttgart.

Malecki, R. A., and Rawinski, T. J. 1985. New methods for controlling purple loosestrife. *NY Fish Wildlife J.* **32,** 9–19.

Malecki, R. A., Blossey, B., Hight, S. D., and Schroeder, D. 1993a. "Introduction and Field Release of *Nanophyes marmoratus* and *N. brevis*, Two Additional Control Agents of Purple Loosestrife: Petition for Approval to Technical Advisory Group for the Introduction of Biological Weed Control Agents. USDA, Animal and Plant Health Inspection Service. Available from the authors.

Malecki, R. A., Blossey, B., Hight, S. D., Schroeder, D., Kok, L. T., and Coulson, J. R. 1993b. Biological control of purple loosestrife. *BioSci.* **43,** 680–686.

Shamsi, S. R. A., and Whitehead, F. H. 1974. Comparative ecophysiology of *Epilobium hirsutum* L. and *Lythrum salicaria* L. I. General biology, distribution and germination. *J. Ecol.* **62,** 279–290.

Skinner, L. C., Rendall, W. J., and Fuge, E. L. 1994. "Minnesota's Purple Loosestrife Program: History, Findings and Management Recommendations." Special Publication 145. Minnesota Department of Natural Resources, St. Paul, MN.

Stuckey, R. L. 1980. Distributional history of *Lythrum salicaria* (Purple loosestrife) in North America. *Bartonia* **47,** 3–20.

Thompson, D. Q., Stuckey, R. L., and Thompson, E. B. 1987. Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. *Fish Wildlife Res.* **2,** 55.

Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M., and Webb, D. A. (Eds.). 1968. "FLORA EUROPAEA," Vol. 2. University Press, Cambridge.

Welling, C. H., and Becker, R. L. 1990. Seed bank dynamics of *Lythrum salicaria* L.: Implications for control of this species in North America. *Aquat. Bot.* **38,** 303–309.