

COMMENTARY

Potential for Biological Control of *Phragmites australis* in North AmericaLisa Tewksbury,* Richard Casagrande,* Bernd Blossey,† Patrick Häfliger,‡ and Mark Schwarzländer‡¹

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Phragmites australis is a cosmopolitan plant that is undergoing a population explosion in freshwater and tidal wetlands on the east coast of North America. The rapid spread of *P. australis* in recent years and the virtual absence of native herbivores feeding on *P. australis* have led wetland ecologists to believe that either the species or more aggressive genotypes were introduced. The historical record of the occurrence of *P. australis* in North America and the scarcity of indigenous herbivores provide conflicting evidence for the status of the species as native or introduced. A comparison of *P. australis* populations from North America and other continents using advanced genetic techniques is underway to help determine the status of current and historic North American genotypes. Literature and field surveys reveal that of the 26 herbivores currently known to feed on *P. australis* in North America (many accidentally introduced during the last decade), only 5 are native. In Europe, over 170 herbivore species have been reported feeding on *P. australis*, some causing significant damage. Of these herbivores, rhizome-feeding species with considerable negative impact on *P. australis* performance include the lepidopterans *Rhizodra lutosus* (already present in North America), *Phragmataecia castaneae*, *Chilo phragmitella*, and *Schoenobius gigantella*. Stem-boring moths in the genera *Archanara* and *Arenostola* and the chloropid fly *Platycephala planifrons* can have large detrimental impacts on *P. australis* in Europe and should be evaluated for their potential as biological control agents. In addition, the interaction of potential control agents with accidentally introduced *P. australis* herbivores needs to be evaluated in North America. Regardless of the results of the genetic analyses, any decision to introduce additional host-specific herbivores in an attempt to control *P. aust-*

lis will require considerable dialogue. This decision needs to weigh the current negative ecological and economic impacts of *P. australis* and the benefits and risks of a biological control program. © 2001 Elsevier Science

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INTRODUCTION

Common reed, *Phragmites australis* (Cav.) Trin. ex Steudel, is a cosmopolitan angiosperm believed by many to be the most widely distributed reed species in the world, ranging all over Europe, Asia, Africa, America, and Australia (Holm *et al.*, 1977). A native of the Old World, *P. australis* is able to grow in a wide range of habitats and displays high phenotypic and genotypic plasticity (Haslam, 1972a; van der Putten, 1997). Typically, *P. australis* grows in open wet areas and marshes, along riverbanks and roadsides, and in ditches and other watercourses. Low nitrogen or phosphorous availability, high salinity, extensive tidal flooding, and anaerobic soils may limit the growth of this clonal species (Chambers, 1997). *P. australis* is wind pollinated but self-incompatible, and its seeds are dispersed by wind and water (Haslam, 1972a). Recruitment from seed is thought to be low but may be quite variable and important in the spread to new sites (Haslam, 1972a; Fournier *et al.*, 1995; McKee and Richards, 1996; Meyerson *et al.*, 2000). Vegetative propagation through dispersal of rhizome fragments by water currents, animals, and construction equipment is another important means of colonization of new areas. Once established, expansion of a stand occurs primarily through vegetative growth of the extensive be-

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lowground rhizome system. Approximately two thirds of the biomass is allocated to the rhizome, which can reach a depth of 2 m (Szczepansky, 1969; Haslam, 1972b). This growth pattern produces homogenous clones with up to 200 culms/m² that can reach 4 m in height.

Throughout its large distribution, *P. australis* plays quite different roles within the ecosystem. Extensive reed beds are a highly valued (even considered endangered) ecosystem in Europe (Tscharntke, 1992c) and are protected because of their important ecological functions. In contrast, the rapid expansion of *P. australis* in North America during the past decades is considered a threat to biodiversity in natural areas and has resulted in aggressive control attempts (Marks *et al.*, 1994). The purpose of this paper is to summarize European literature focusing on *P. australis* protection, herbivores, and food-web communities and contrast it with research in North America focusing on control and negative ecological impacts of *P. australis*. We present summary information on life history and distributions of herbivores associated with *P. australis* in Europe and North America and discuss the status and evidence of *P. australis* as a native or introduced species in North America. Finally, we use this information to evaluate the benefits and potential risks of developing a biological control program for *P. australis* in North America.

ECOLOGICAL AND ECONOMIC IMPACTS OF *P. AUSTRALIS*

Many cultures, past and present, have found *P. australis* useful for various purposes. In the former Soviet Union, *P. australis* is used for fodder and cellulose; in Romania, where reeds have become an important part of the economy, they are turned into pulp for paper, cardboard, cellophane, synthetic fibers, alcohol, insulation materials, wood substitute for heating purposes, and fertilizer (Rodewald-Rodescu, 1974; Holm *et al.*, 1977; Graneli, 1984). In Egypt and throughout Europe, common reed is used for matting (Holm *et al.*, 1977) and thatching of roofs (Haslam, 1972b). In the United Kingdom, wetlands have been constructed to treat point-source pollution, the majority using pure reed bed treatment systems (Hawk and Jose, 1996). In the Netherlands, *P. australis* plays an important role in land reclamation, where it serves as a soil binder, preventing erosion and washouts. Polders (arable land reclaimed from the sea), which have been constructed by draining marshes, are often stabilized by seeding with *P. australis*. After the land is tiled and drained, *P. australis* is eliminated (Bakker, 1960). *P. australis* is also considered a serious weed of cotton, corn, and rice in the former Soviet Union, sugar beets in Zimbabwe and the Netherlands, and sugarcane in Australia (Holm *et al.*, 1977). Once established, it is very difficult

to eradicate, can obstruct views, and block canals, streams, and drainage ditches (Holm *et al.*, 1977).

The abundance of herbivores in European reed beds (Tscharntke, 1990, 1992a,b,c) forms the base of a multilayered food web. *P. australis* stands are important as staging and feeding grounds for many bird species during their annual migrations between Africa and Eurasia (Ormerod, 1990; Berthold *et al.*, 1993). A group of European warblers (reed warblers) has evolved a close association with *P. australis* as an exclusive breeding habitat (Berthold *et al.*, 1993). Management of reed beds is important to maintain the quality of the habitat for the conservation of 13 bird species that nest in common reed (Tscharntke, 1992c). Recent declines of *P. australis* in Europe have caused great concern and prompted the formation of EUREED, a European research program on reed dieback (van der Putten, 1997; Brix, 1999). Ironically, habitat destruction and manipulation of hydrologic regimes, eutrophication, pollution, and increased disturbance, often believed responsible for the population explosion of *P. australis* in North America, are considered key contributing factors for reed declines in Europe (Ostendorp, 1989; van der Putten, 1997).

Over the past several decades, *P. australis* populations in North America have dramatically increased in both freshwater and brackish wetlands, particularly along the Atlantic Coast (Marks *et al.*, 1994). Although 3500-year-old fossil *Phragmites* rhizomes were found in some North American peat cores (Niering *et al.*, 1977; Clark, 1986; Orson *et al.*, 1987), many wetland ecologists, seeing the rapid spread of *P. australis* in recent years, believe that it is an introduced species (Mikkola and Lafontaine, 1994). The replacement of diverse wetland vegetation by *P. australis* monocultures has caused declines in water birds and other wetland wildlife (Thompson and Shay, 1989; Jamison, 1994; Meyerson *et al.*, 2000) and decreases in plant diversity and alterations in nutrient cycling and hydrologic regimes (Marks *et al.*, 1994; Chambers, 1997). A wide variety of control measures are used to slow the invasion of *P. australis* (Marks *et al.*, 1994). The U.S. Fish and Wildlife Service recommendations include the use of herbicides, mowing, disking, dredging, flooding, draining, burning, and grazing (Cross and Fleming, 1989). According to Howard *et al.* (1978), the most effective control methods are cutting, draining, saltwater flushing, herbicides, and various combinations of these methods. Summer burning of *P. australis* can decrease its dominance and increase species diversity in marshes (Thompson and Shay, 1989). Dense *P. australis* stands can make mosquito larvicide application very difficult. Management of tidal gates and open marsh water has been used to control *P. australis* and to eliminate mosquito breeding areas in Connecticut (Capotosto, 1990). All methods produce partial or

short-term control; however, at present there is no long-term species-specific control measure.

***P. AUSTRALIS*: INDIGENOUS OR INTRODUCED TO NORTH AMERICA?**

The most commonly used definition for an indigenous species in North America is the presence of the species pre-Columbian or pre-European settlement (Schwartz, 1996). However, numerous species were introduced as crops by indigenous peoples long before European colonization (Williams, 1989). Criteria to help in the assessment of a species' status were put forward by Webb (1985) and Preston (1986) and combined by Schwartz (1996). They include fossil evidence, known introduction routes or dates, information on growing habitats, genetic diversity, and reproductive patterns, and occurrence of specialized herbivores. Fossil evidence for *P. australis* indicates the presence of the species 3500 years ago in peat samples (Orson *et al.*, 1987) and 40,000 to 11,000 years ago in Shasta ground sloth dung (Hansen, 1978), suggesting that the species is native to North America. However, only 5 native North American herbivores (only a single species appears to be a specialist) are known to feed on *P. australis* compared to over 140 in Europe (Tables 1 and 2). Further evidence for the introduced status of *P. australis* is the difference in bird use. While American and Least Bitterns in North America (*Botaurus lentiginosus* and *Ixobrychus exilis*) avoid nesting in *P. australis* (Lor, 2000), their sibling species in Eurasia (*Botaurus stellaris* and *Ixobrychus minutus*) show a strong preference for extensive reed beds (Snow and Perrins, 1998).

P. australis was used by indigenous cultures in the southwestern United States. The Anasazi at Mesa Verde in southwestern Colorado used stems as part of woven mats and fencing and as thatch for roofs (Kane and Gross, 1986). They were also used to make reed grass cigarettes for smoking of tobacco (Adams, 1990) and as arrow shafts (Allen, 1999). In native cultures elaborate networks existed for trading tools and agricultural and medicinal plants (Pringle, 1997), which stretched over hundreds of kilometers. The peopling of the Americas began over 14,000 years ago and perhaps as far back as 20,000–40,000 years (Dillehay, 1997). At present, competing hypotheses contend that the earliest Americans either came from Asia over the Bering Strait or came from Europe and arrived by sea rather than by land (Gibbons, 1996; Morell, 1998; Wright, 1999). Although speculative, it is at least conceivable that *P. australis* had sufficient importance for the earliest Americans that they carried seeds or rhizomes during their migrations. This could explain the scarcity of specialized North American herbivores and the relatively recent fossil record, including the occurrence of *P. australis* fragments in sloth dung. The low abun-

dance of specialized herbivores could also be a result of large-scale population fluctuations (potentially extinctions and recolonization) of *P. australis* in North America.

Alternatively, the recent noticeable increase in *P. australis* populations along the east coast of North America has been attributed to the introduction of more aggressive European genotypes (Metzler and Rosza, 1987; Tucker, 1990; Mikkola and Lafontaine, 1994; Besitka, 1996). *P. australis* was considered an uncommon species in New England by Eaton (1952), until he noticed an expanding population along the Sudbury River in Massachusetts from 1949 to 1952. Two marshes in South Carolina where *P. australis* was absent in 1968 had extensive monodominant stands in 1994, with the threat of *P. australis* eliminating other plant species (Stalter and Baden, 1994). Besitka (1996) compared guard-cell lengths of historic and present day populations of *P. australis* from the same locations in the northeast. She concluded that historical hexaploid North American specimens were replaced by tetraploid plants (which are more common in Europe) in the middle of the 19th century, most likely introduced via trans-Atlantic shipping (Burk, 1877). Isozyme studies of *P. australis* from the Mississippi delta have identified two different strains, with the dominant tetraploid covering most of the delta (Hauber *et al.*, 1991; Chambers, 1997). However, a recent comparison of genotypes from rapidly expanding "invasive" populations and those from noninvasive populations detected similarities of invasive and noninvasive populations in the same geographic region (Pellegrin and Hauber, 1999).

Even under the assumption that "more aggressive" European genotypes were introduced, it remains difficult to explain the population explosion of *P. australis* through anthropogenic alterations of nutrient inputs, pollution, or changes in hydrologic regimes (Stuckey, 1988; Marks *et al.*, 1994; Chambers, 1997). It remains unclear why European genotypes would be able to take advantage of these changes in North America, but decline under similar circumstances in Europe (Ostendorp, 1989; van der Putten, 1997; Brix, 1999).

One distinct difference between Europe and North America is the presence of herbivores (Tables 1 and 2). Recently, Blossey and Nötzold (1995) attributed the increased competitive ability of nonindigenous plants to the absence of their specialized natural enemies. According to this hypothesis, plants in their indigenous environments invest significant resources into herbivore defense. These resources become available to increase vegetative growth and competitive ability once a plant invades herbivore-free space. This shift in resource allocation could potentially explain the relatively recent population explosion of *P. australis* in North America. Research in Europe and North America using advanced molecular techniques is currently

TABLE 1

Phytophagous Insects, Mites, and Pathogens Recorded on *Phragmites australis* in North America

Species	Larval feeding habit ^a	Native	Specificity ^b	References
Acari				
Tarsonemidae				
<i>Steneotarsonemus phragmitidis</i> (Schlechtendal)	Leaf sheaths, growing meristem	No	M	B. Blossey and F. Eichiner (unpublished data)
Diptera				
Agromyzidae				
<i>Cerodontha incisa</i> (Meigen) Syn: <i>Poemyza incisa</i>	Leaf mines	U	P	Spencer, 1969, 1990
Cecidomyiidae				
<i>Calamomyia phragmites</i> Felt Syn: <i>Asteromyia phragmites</i> (Felt)	Stem galls	Yes	M	Gagné, 1989; Frohne, 1938
<i>Giraudiella inclusa</i> (Frauenfeld) Syn: <i>Perrisia incurvans</i> Nijveldt	Stems	No	M	B. Balme and R. Casagrande (in preparation); B. Blossey and M. Schwarzländer (unpublished data)
<i>Lasioptera hungarica</i> (Möhn)	Stem galls	No	M	B. Balme and R. Casagrande (in preparation); B. Blossey and M. Schwarzländer (unpublished data)
Chloropidae				
<i>Oscinella frit</i> (Linnaeus)	Leaves, inquiline of galls	No	P	Sabrosky, 1987
<i>Lipara similis</i> Schiner	Stems	No	M	Sabrosky, 1958; B. Balme and R. Casagrande (in preparation)
<i>Lipara rufitarsis</i> Loew	Stem galls	No	M	B. Balme and R. Casagrande (in preparation)
<i>Lipara pullitarsis</i> Dorskocil & Chvála	Stem galls	No	M	B. Blossey and F. Eichiner (unpublished data)
<i>Lipara lucens</i> Meigen	Stem galls	No	M	Sabrosky, 1958
Dolichopodidae				
<i>Thrypticus</i> sp. Loew	Stems	No	M	B. Blossey and F. Eichiner (unpublished data)
Homoptera				
Aphididae				
<i>Hyalopterus pruni</i> (Geoffr.) Syn: <i>Hyalopterus arundinis</i> (Fabricius)	Leaves	No	O	Frohne, 1938; Krause, 1996
Coccidae				
<i>Eriopeltis festucae</i> (Fonscolombe)	Leaves	No	P	Kosztarab, 1996; Miller <i>et al.</i> , 1999
Pseudococcidae				
<i>Chaetococcus phragmitis</i> (Marchal)	Stems, leaf sheaths	No	O	Kosztarab, 1996; Krause, 1996; B. Balme and R. Casagrande (in preparation)
Hymenoptera				
Eurytomidae				
<i>Tetramesa phragmitis</i> (Erdös) Syn: <i>Gahaniola phragmitis</i> (Erdös)	Stems	No	M	Krombein <i>et al.</i> , 1979; B. Balme and R. Casagrande (in preparation)
Lepidoptera				
Elachistidae				
<i>Dicranoctetes saccharella</i> (Busch)	Leaf blotch mines	Yes	P	Braun, 1948; Wagner, 1987; B. Balme and R. Casagrande (in preparation)
Hesperiidae				
<i>Ochlodes yuma</i> (Edwards)	Leaves	Yes	M	Pyle, 1981; Opler <i>et al.</i> , 1995
<i>Poanes viator</i> (Edwards)	Leaves	Yes	O	Beutenmüller, 1902; Gochfeld and Burger, 1997; Royer and Marone, 1992; Shapiro, 1970
Crambidae				
<i>Sclerocona acutellus</i> (Eversmann)	Stems	No	U	B. Balme and R. Casagrande (in preparation)

TABLE 1—Continued

Species	Larval feeding habit ^a	Native	Specificity ^b	References
Noctuidae				
<i>Apamea ophiogramma</i> (Esper)	Stems	No	P	Troubridge <i>et al.</i> , 1992; Mikkola and Lafontaine, 1994
<i>Apamea unanimitis</i> (Hübner)	Leaves	No	P	Mikkola and Lafontaine, 1994
<i>Rhizedra lutosa</i> (Hübner)	Stems, rhizomes	No	M	McCabe and Schweitzer, 1991; Mikkola and Lafontaine, 1994
<i>Hydraecia micacea</i> (Esper)	Stems	No	P	Mikkola and Lafontaine, 1994
<i>Leucania linita</i> Guenée	Stems	U	U	Ferguson <i>et al.</i> , 1999
<i>Simyra henrici</i> Grote	Stems	Yes	P	B. Blossey (unpublished data)
Thysanoptera				
Phlaeothripidae				
Unidentified thrips	U	U	U	Frohne, 1938
Fungi				
<i>Alternaria</i> sp.	Leaves, stems	U	U	B. Blossey (unpublished data)

^a U, unknown.

^b Specificity as recorded in the literature (M, monophagous; O, oligophagous; P, polyphagous; U, unknown).

underway to provide a comparison of present-day and historical *P. australis* populations from different continents and test their competitive ability (K. Saltonstall, Yale University, personal communication). The genetic comparison of present-day and historic genotypes from North America and overseas will allow an assessment of the status of North American *P. australis* populations as (1) native and distinct from overseas populations, (2) a mix of native and introduced genotypes, or (3) identical to overseas populations. We will also gain information about the distribution and origin of any distinct genotypes and whether native genotypes are potentially excluded by the more aggressive invasive genotypes (which could influence management decisions). Once this research is completed we will have a better understanding of the underlying genetic and environmental factors of the *P. australis* population explosion in North America.

HERBIVORES ON *P. AUSTRALIS* IN NORTH AMERICA

Our extensive literature and limited field surveys revealed that only 26 herbivore species are known to feed on *P. australis* in North America; 16 are recent introductions, 5 are of unknown status, and only 5 are native (Table 1). Only the Yuma skipper, *Ochlodes yuma* (Edwards), a species distributed through the western United States, and a gall midge, *Calamomyia phragmites*, are considered native and monophagous on *P. australis* (Gagné, 1989; Opler *et al.*, 1995). The native broad-winged skipper, *Poanes viator* (Edwards), may provide additional evidence for a relatively recent North American introduction of *P. australis*. This species has recently increased its range by including *P. australis* in its diet (Gochfeld and Burger, 1997). A century ago this skipper was uncommon in the New York City area (Beutenmüller, 1902) and was still considered scarce in New Jersey in 1965 (Muller, 1965).

Shapiro (1970) proposed two subspecies of *Poanes viator*: *P. v. viator*, localized in the Great Lakes Region and feeding on sedges, and *P. v. zizaniae*, a Coastal Plain subspecies feeding on *Zizania aquatica* L., wild rice. He reported preoviposition behavior of *P. v. zizaniae* females toward *P. australis*, but no oviposition or larval development occurred. However, large larvae collected from wild rice would feed on *P. australis*. The subspecies *zizaniae* is now locally abundant along the east coast, increasing its population as *P. australis* has increased its range (Gochfeld and Burger, 1997). The range of *P. v. zizaniae* extends from New England southward along the Atlantic coast and westward along the Gulf coast to Texas (Royer and Marrone, 1992). We readily find *P. viator* larvae feeding on *P. australis* in Rhode Island (at night) and we have reared them to adult on common reed.

In addition to some older records of European species in North America (Frohne, 1938), more accidental introductions were recently reported (Table 1). Our continuing but limited field surveys in the northeast have added substantially to the list of introduced herbivores, and more extensive surveys are expected to reveal the occurrence of even more introduced species.

The European rhizome-feeding noctuid moth *Rhizedra lutosa* was first reported in 1988 from New Jersey (McCabe and Schweitzer, 1991) and was subsequently collected in Albany County and the Catskill mountains of New York in 1991 (Mikkola and Lafontaine, 1994). We have found *R. lutosa* in blacklight traps in Rhode Island since 1995. Since then we have found it in Connecticut, in Massachusetts, in the Fingerlakes and the western Adirondacks regions in upstate New York, and as far west as eastern Ohio (B. Blossey, personal observation). According to Bretherton *et al.* (1983), moths fly from August until the end of October. Moths are caught in blacklight traps as late as November in Rhode Island. Eggs are laid on leaves near the base of

TABLE 2

Phytophagous Arthropods and Fungi Associated with *Phragmites australis* in Europe, Asia, Africa, and North America

Species	Larval feeding habit ^a	Distribution ^b	Specificity ^c	References
Acari				
Pyemotidae				
<i>Siteroptes avenae</i> (Müller)	Leaves/leaf sheaths	E	P	Rack and Carstensen, 1981; Vogel, 1984
Syn: <i>Siteroptes graminum</i> Reuter, <i>Pediculoides graminum</i>				
<i>Siteroptes reniformis</i> Krantz	In <i>Lipara</i> galls	E	U	Rack and Carstensen, 1981
<i>Therismoptes arundinis</i> Schlechtendal	Galls	E	M	Van der Toorn and Mook, 1982
Tarsonemidae				
<i>Steneotarsonemus phragmitidis</i> (Schlechtendal)	Leaf sheaths, growing points	E, NA	M	Durska, 1970; Skuhrový <i>et al.</i> , 1975; Skuhrový, 1981; Rack and Carstensen, 1981
<i>Steneotarsonemus gibber</i> Suski	U	E	U	Rack and Carstensen, 1981
<i>Tarsonemus pilliger</i> (Schlechtendal)	U	E	U	Waitzbauer, 1969; Skuhrový, 1981
<i>Tarsonemus lacustris</i> Schaarschmidt	In <i>Lipara</i> galls	U	U	Rack and Carstensen, 1981; Abraham and Carstensen, 1982
Coleoptera				
Chrysomelidae				
<i>Acmenychnus inermis</i> (Zoubkoff)	Leaves	E	M	Krivosheina and Nikulina, 1991; Narchuk and Kanmiya, 1996
<i>Donacia cinerea</i> Herbst	Rhizomes	E, As	P	Mohr, 1966; Joy, 1976; Lopatin, 1984; Cooter, 1991
<i>Donacia clavipes</i> Fabricius	Rhizomes	E, As	O	Mohr, 1966; Joy, 1976; Lopatin, 1984; Cooter, 1991; Bienkowski, 1996; Menzies and Cox, 1996
<i>Macrolea mutica</i> (Fabricius)	Rhizomes	E, As	O	Hawk and José, 1996
<i>Plateumaris braccata</i> (Scopoli)	Rhizomes	E, As	M	Mohr, 1966; Haslam, 1972a; Joy, 1976; Lopatin, 1984; Cooter, 1991; Menzies and Cox, 1996
<i>Psylliodes reitteri</i> Weise	Stems	E	O	Mohr, 1966
Curculionidae				
<i>Dicranthus elegans</i> (Fabricius)	Stems, rhizomes	E	M	Lohse, 1983
Malachiidae				
<i>Anthocomus coccineus</i> (Schaller)	Flowers	E	U	Vogel, 1984
Diptera				
Agromyzidae				
<i>Agromyza albipennis</i> Meigen	Leaf mines	E, As, NA	P	Hering, 1957
<i>Agromyza baetica</i> Griffiths	Leaf mines	E	M	Spencer, 1990
<i>Agromyza graminicola</i> Hendel	Leaf mines	E, Af	M	Griffiths, 1963; Spencer, 1976, 1990
<i>Agromyza hendeli</i> Griffiths	Leaf mines	E	M	Griffiths, 1963; Spencer, 1976; Tschirnaus, 1981; Spencer, 1990; Scheirs and DeBruyn, 1992; Scheirs <i>et al.</i> , 1993
<i>Agromyza phragmitidis</i> Hendel	Leaf mines	E, As	M	Griffiths, 1963; Spencer, 1976; Tschirnaus, 1981; Spencer, 1990; Scheirs <i>et al.</i> , 1993, 1997
<i>Agromyza spenceri</i> Griffiths	Leaf mines	E	M	Griffiths, 1963; Spencer, 1990
<i>Cerodontha denticornis</i> (Panzer)	Leaf mines	E, As, Af, NA	P	Hering, 1957
<i>Cerodontha incisa</i> (Meigen)	Leaf mines	E, As, NA	P	Spencer, 1969, 1990; Scheirs and De Bruyn, 1992; Scheirs <i>et al.</i> , 1993
Syn: <i>Poemyza incisa</i> Meigen				
<i>Cerodontha lateralis</i> (Macquart)	Leaf mines	E, Af, NA, As	P	Hering, 1957; Vogel, 1984
Syn: <i>Poemyza (Phytobia) lateralis</i> Macquart				
<i>Cerodontha phragmitidis</i> Nowakowski	Leaf mines	E	M	Spencer, 1990; Scheirs and De Bruyn, 1992; Scheirs <i>et al.</i> , 1993
Syn: <i>Poemyza phragmitidis</i> Nowakowski				
<i>Cerodontha phragmitophila</i> Hering	Leaf mines	E	O	Hering, 1957; Spencer, 1990

TABLE 2—Continued

Species	Larval feeding habit ^a	Distribution ^b	Specificity ^c	References
Anthomyzidae				
<i>Anthomyza collini</i> Andersson	Inquiline in <i>Lipara</i> galls	E	M	DeBruyn, 1985; Tscharnatke, 1993
<i>Anthomyza gracilis</i> (Fallén)	Inquiline in <i>Lipara</i> galls, leaf sheaths	E	O	Haslam, 1972a; DeBruyn, 1985
Syn: <i>Anthomyza sordidella</i> (Zetterstedt)				
Asteiidae				
<i>Leiomyza scatophagina</i> (Fallén)	U	E	U	Haslam, 1972a
Cecidomyiidae				
<i>Asynapta phragmitis</i> (Giraud)	Wilted leaves	E	U	Tscharnatke, 1999
<i>Asynapta thuraii</i> Kieffer	Under leaf sheath	E	O	Grabo, 1991
<i>Calamomyia phragmites</i> Felt	Stem galls	NA	M	Frohne, 1938; Gagné, 1989
Syn: <i>Asteromyia phragmites</i> (Felt)				
<i>Giraudiella inclusa</i> (Frauenfeld)	Stem galls	E, NA, Af	M	Mook, 1971; Haslam, 1972a; Mesbah <i>et al.</i> , 1976; Skuhrový, 1981; Tscharnatke, 1988, 1989a, 1992a
Syn: <i>Perrisia incurvans</i> Nijveldt				
<i>Lasioptera arundinis</i> (Schiner)	Stem galls on sideshoots	E, As	M	Skuhrový, 1981; Rohfritsch, 1992, 1997; Tscharnatke, 1992c
Syn: <i>Thomasiella arundinis</i> (Schiner)				
<i>Microlasioptera flexuosa</i> (Winnertz)	Stems	E	M	Skuhrový, 1981; Tscharnatke, 1993, 1994
Syn: <i>Thomasiella flexuosa</i> Winnertz				
<i>Lasioptera hungarica</i> Möhn	Stems	E	M	Skuhrový, 1981; Tscharnatke, 1993, 1994
Syn: <i>Thomasiella massa</i> (Erdős)				
<i>Mayetiola destructor</i> (Say)	U	E	P	Rodewald-Rudescu, 1974
Chloropidae				
<i>Calamoncosis aprica</i> (Meigen)	Stem, inquiline in galls	E	M	Tschirnhaus, 1981; Grabo, 1991
<i>Calamoncosis duinensis</i> (Strobl)	U	E, As	M	Kanmiya, 1981; Tschirnhaus, 1981
<i>Calamoncosis minima</i> (Strobl)	Stem	E, As, Af	M	Haslam, 1972a; Tschirnhaus, 1981; Vogel, 1984; DeBruyn, 1985; Grabo, 1991; Narchuk, 1994
<i>Chlorops pumilionis</i> (Bjerkander)	Leaves, leaf-sheath	E, As	P	Vogel, 1984
<i>Cryptonevra diadema</i> (Meigen)	Stem	E, As, Af	M	DeBruyn, 1985; Grabo, 1991; Narchuk, 1994
<i>Cryptonevra flavitarsis</i> (Meigen)	Inquiline in <i>Lipara</i> galls	E, As, Af	M	Tschirnhaus, 1981; DeBruyn, 1985; Grabo, 1991; Narchuk, 1994
Syn: <i>Haplegis consimilis</i> Collin, <i>H. nigratarsis</i> Duda				
<i>Cryptonevra tarsata</i> (Fallén)	Inquiline in <i>Lipara</i> galls	E	M	Wendt, 1968
Syn: <i>Haplegis tarsata</i> (Fallén)				
<i>Elachiptera breviscutellata</i> Nartshuk	U	E, As	U	Tschirnhaus, 1981
<i>Elachiptera cornuta</i> (Fallén)	Stems, inquiline in galls, saprothag	E	P	Vogel, 1984; Grabo, 1991
Syn: <i>Crassiseta cornuta</i>				
<i>Elachiptera scrobiculata</i> (Strobl)	Saprothag?	E, As	P	Wendt, 1968; Vogel, 1984
<i>Elachiptera tuberculifera</i> (Corti)	U	E, As	P	Vogel, 1984
<i>Eribolus hungaricus</i> Becker	Stems, inquiline in galls	E	M	Tschirnhaus, 1981; Vogel, 1984; Grabo, 1991
<i>Eurina lurida</i> Meigen	U	E, As, Af	U	Séguy, 1934; Tschirnhaus, 1981
<i>Homalura dumonti</i> Séguy	U	E	U	Séguy, 1934
<i>Lasiosina albipila</i> (Loew)	Wilted leaves	E	U	Tscharnatke, 1999
<i>Lipara baltica</i> Karpis	Stem galls	E	M	Beschovski, 1984
<i>Lipara brevopilosa</i> Nartshuk	Stem galls	As	M	Beschovski, 1984
<i>Lipara frigida</i> Kanmiya	Stem galls	As	M	Beschovski, 1984
<i>Lipara japonica</i> Kanmiya	Stem galls	As	M	Beschovski, 1984

TABLE 2—Continued

Species	Larval feeding habit ^a	Distribution ^b	Specificity ^c	References
<i>Lipara lucens</i> Meigen	Stem galls	E, As, NA	M	Durska, 1970; Doskocil and Chvala, 1971; Mook, 1971; Haslam, 1972a,b; Chvala <i>et al.</i> , 1974; Skuhrový <i>et al.</i> , 1975; Skuhrový, 1981; Abraham and Carstensen, 1982; Van der Toorn and Mook, 1982; Stone <i>et al.</i> , 1983; DeBruyn, 1992; Tschardtke, 1992c, 1993, 1994; Dely-Draskovits <i>et al.</i> , 1994; Narchuk, 1994
<i>Lipara pullitarsis</i> Doskocil & Chvála	Stem galls	E	M	Doskocil and Chvala, 1971; Chvala <i>et al.</i> , 1974; Skuhrový <i>et al.</i> , 1975; Abraham and Carstensen, 1982; DeBruyn, 1985; Tschardtke, 1992c, 1993; Dely-Draskovits <i>et al.</i> , 1994; Narchuk, 1994; Gromysz-Kalkowska and Grochowska, 1996
<i>Lipara rufitarsis</i> Loew	Stem galls	E, As	M	Doskocil and Chvala, 1971; Chvala <i>et al.</i> , 1974; Skuhrový <i>et al.</i> , 1975; Skuhrový, 1981; DeBruyn, 1985; Dely-Draskovits <i>et al.</i> , 1994; Narchuk, 1994
Syn: <i>Calamoncosis tomentosa</i> (Macquart)				
<i>Lipara salina</i> sp. n.	Stem galls	As	M	Narchuk and Kanmiya, 1996
<i>Lipara similis</i> Schiner	Stems	E, As	M	Durska, 1970; Haslam, 1972a; Chvala <i>et al.</i> , 1974; Skuhrový <i>et al.</i> , 1975; Skuhrový, 1981; DeBruyn, 1985, 1988; Gromysz-Kalkowska and Hubicka, 1988; Tschardtke, 1992c, 1993, 1994; Dely-Draskovits <i>et al.</i> , 1994; Narchuk, 1994
<i>Lipara vallicola</i> Kanmiya	Stem galls	As	M	Beschovski, 1984
<i>Oscinella angustipennis</i> Duda	Leaf sheaths	E	M	DeBruyn, 1985
<i>Oscinella frit</i> (Linnaeus)	Leaves, inquiline of galls	E, As, NA	P	DeBruyn, 1985; Sabrosky, 1987; CAB International, 1999
<i>Oscinella nitidissima</i> (Meigen)	Inquiline of galls	E, As, NA	U	Seguy, 1934; Wendt, 1968
Syn: <i>Oscinosoma nitidissima</i> (Seguy)				
<i>Platycephala planifrons</i> (Fabricius)	Stem	E	M	Skuhrový <i>et al.</i> , 1978; Skuhrový, 1981; Tschardtke, 1993, 1994; Narchuk, 1994
<i>Platycephala subelongata</i> Kanmiya	Stem	As	M	Kanmiya, 1983
<i>Platycephala umbraculata</i> (Fabricius)	Stem	E, As	M	Séguy, 1934; Wendt, 1968
<i>Tropidoscinis zuercheri</i> Duda	Stem, inquiline in <i>Lipara</i> galls	E, As	O	Haslam, 1972a; Vogel, 1984; Grabo, 1991; Narchuk, 1994
Syn: <i>Incertella zuercheri</i> (Duda)				
Dolichopodidae				
<i>Thrypticus bellus</i> Loew	Stems	E	M	Waitzbauer <i>et al.</i> , 1973
<i>Thrypticus smaragdinus</i> Gerstaecker	Stems, rhizomes	E	M	Lübben, 1908
Opomyzidae				
<i>Opomyza florum</i> (Fabricius)	Mines between leaf sheaths and stems	E	P	Vogel, 1984
Syn: <i>Agromyza florum</i> , <i>Musca florum</i>				
Scathophagidae				
<i>Cleigastra apicalis</i> (Meigen)	Inquiline	E	P,C	Waitzbauer, 1969; Vogel, 1984; DeBruyn, 1985
Syn: <i>Cnemopogon apicalis</i> Meigen				

TABLE 2—Continued

Species	Larval feeding habit ^a	Distribution ^b	Specificity ^c	References
Heteroptera				
Miridae				
<i>Stenodema calcaratum</i> (Fallén)	Leaves	E	P	Grabo, 1991
<i>Stenodema laevigatum</i> (Linnaeus)	Leaves	E	P	Grabo, 1991
Lygaeidae				
<i>Dimorphopterus spinolae</i> (Signoret)	U	As	U	Li, 1982
Homoptera				
Aclerididae				
<i>Aclerda wiltshirei</i> Bodenheimer	U	As	M	Miller <i>et al.</i> , 1999
<i>Nipponaclerda biwakoensis</i> McConnell	U	As	P	Miller <i>et al.</i> , 1999
<i>Nipponaclerda turicana</i> Borchsenius	U	As	P	Miller <i>et al.</i> , 1999
Aphididae				
<i>Hyalopterus amygdali</i> (Blanchard)	Leaves	E, As	O	Haslam, 1972a; Huang <i>et al.</i> , 1986
<i>Hyalopterus pruni</i> (Geoffroy)	Leaves	E, NA, As, Af, Aus	O	Frohne, 1938; Stary, 1965; Mook, 1971; Pintera, 1971; Haslam, 1972a; Skuhřavý, 1981; Tschardtke, 1992c; Krause, 1996; CAB International, 1999
Syn: <i>Hyalopterus arundinis</i> (Fabricius)				
Cercopidae				
<i>Philaenus spumarius</i> (Linnaeus)	Leaves, stems	E	P	Grabo, 1991
Cicadellidae				
<i>Paralimnus phragmitis</i> (Boheman)	Leaves	E	M	Grabo, 1991
Delphacidae				
<i>Chloriona dorsata</i> (Edwards)	Leaves	E	M	Haslam, 1972a; Grabo, 1991
<i>Chloriona glaucescens</i> (Fieber)	Leaves	E	M	Haslam, 1972a; Grabo, 1991
<i>Chloriona smaragdula</i> (Stål)	Leaves	E	M	Strübing, 1960; Haslam, 1972a; Grabo, 1991
<i>Chloriona unicolor</i> (H.-S.)	Leaves	E	M	Haslam, 1972a
<i>Chloriona vasconica</i> Ribaut	Leaves	E	M	Grabo, 1991
<i>Delphax crassicornis</i> (Panzer)	Leaves	E	M	Stresemann, 1986
<i>Delphax pulchellus</i> (Curtis)	Leaves	E	M	Haslam, 1972a; Stresemann, 1986
Syn: <i>Araeopus pulchellus</i> (Curtis)				
<i>Euidella (Euides) speciosa</i> (Boheman)	Leaves	E	M	Strübing, 1960; Haslam, 1972a
Pseudococcidae				
<i>Adelosoma phragmitidis</i> Borchsenius	Leaf sheaths	As	O	Miller <i>et al.</i> , 1999
<i>Antonina crawi</i> Cockerell	Leaf bases	E, NA, As, Aus	P	Miller <i>et al.</i> , 1999
<i>Chaetococcus phragmitis</i> (Marchal)	Leaf sheaths	E, NA, Af, As	O	Kosztarab and Kozár, 1988; Tschardtke, 1993; Kosztarab, 1996; Krause, 1996; Miller <i>et al.</i> , 1999
<i>Chaetococcus turanicus</i> Borchsenius	U	As	O	Miller <i>et al.</i> , 1999
<i>Chorizococcus halli</i> McKenzie & Williams	Leaf sheaths	Af	P	Miller <i>et al.</i> , 1999
<i>Dysmicoccus glandularis</i> Bazarov	U	As	M	Miller <i>et al.</i> , 1999
<i>Dysmicoccus walkeri</i> (Newstead)	U	E, As	P	Miller <i>et al.</i> , 1999
<i>Kiritshenkella sacchari</i> (Green)	Leaf sheaths	As	P	Miller <i>et al.</i> , 1999
<i>Miscanthicoccus miscanthi</i> (Takahashi)	U	NA, As	O	Miller <i>et al.</i> , 1999
<i>Neotrionymus monstata monstata</i> Borchsenius	U	As	O	Miller <i>et al.</i> , 1999
<i>Trionymus copiosus</i> (Borchsenius)	U	As	M	Miller <i>et al.</i> , 1999
<i>Trionymus kurilensis</i> Danzig	U	As	P	Miller <i>et al.</i> , 1999
<i>Trionymus hamberdi</i> (Borchsenius)	Leaves, leaf sheaths	E	P	Kosztarab and Kozár, 1988
<i>Trionymus isfarensis</i> (Borchsenius)	Stems	E, As	O	Kosztarab and Kozár, 1988
<i>Trionymus phragmitis</i> (Hall)	In leaf sheaths	E, Af	P	Kosztarab and Kozár, 1988
<i>Trionymus subterraneus</i> (Newstead)	U	E, As	P	Miller <i>et al.</i> , 1999
<i>Trionymus thulensis</i> Green	Stems, leaf sheath, roots	E	P	Kosztarab and Kozár, 1988

TABLE 2—Continued

Species	Larval feeding habit ^a	Distribution ^b	Specificity ^c	References
Coccidae				
<i>Eriopeltis festucae</i> (Fonscolombe)	Leaves	E, NA, As	P	Kosztarab and Kozár, 1988; Kosztarab, 1996; Miller <i>et al.</i> , 1999
<i>Eriopeltis lichtensteini</i> Signoret	Leaves	E, As	P	Kosztarab and Kozár, 1988; Miller <i>et al.</i> , 1999
<i>Poaspis jahandiezi</i> (Balachowsky)	Leaves	E	P	Kosztarab and Kozár, 1988; Miller <i>et al.</i> , 1999
<i>Rhizococcus pseudinsignis</i> (Green)	Leaves	E	P	Kosztarab and Kozár, 1988
Eriococcidae				
<i>Eriococcus trispinatus</i> (Wang)	Leaves	As	P	Miller <i>et al.</i> , 1999
Hymenoptera				
Eurytomidae				
<i>Tetramesa phragmitis</i> (Erdős)	Stems	E, NA	M	Buhr, 1965; Krombein <i>et al.</i> , 1979; Dely-Draskovits <i>et al.</i> , 1994
Syn: <i>Gahaniola phragmitis</i> Erdős, <i>Harmolita (Isthomosoma)</i> <i>phragmitidis</i> (Schlechtendal)				
Cephidae				
<i>Calameuta filiformis</i> (Eversmann)	Stems	E	P	Cameron, 1890; Taeger and Blank, 1998
Syn: <i>Cephus arundinis</i> Giraud				
Lepidoptera				
Cosmopterigidae				
<i>Cosmopterix coryphaea</i> Wlsgl.	Leaf mines	E	U	Hering, 1957
<i>Cosmopterix lienigiella</i> Lienig & Zeller	Leaf blotch mines	E	M	Grünberg, 1909; Hering, 1957; Haslam, 1972a
<i>Cosmopterix orichalcea</i> Stainton	Leaf mines	E	P	Hering, 1957
Syn: <i>Cosmopterix druryella</i> Zeller				
<i>Cosmopterix phragmitidis</i> Amsel	Leaf mines	As	U	Salem and Al ahmadi, 1993
<i>Cosmopterix scribaiella</i> Zeller	Leaf blotch mines	E	M	Grünberg, 1909; Hering, 1957; Sterling, 1997
Cossidae				
<i>Phragmataecia castaneae</i> (Hübner)	Stems	E, As	M	Grünberg, 1909; Scorer, 1913; Haslam, 1972a; Pruscha, 1972; Skuhrový, 1981; Hawk and José, 1996
Elachistidae				
<i>Dicranoctetes saccharella</i> (Busch)	Leaf blotch mines	NA	P	Braun, 1948; Wagner, 1987
<i>Elachista maculicerusella</i> Bruand	Leaf blotch mines	E, As	P	Haslam, 1972a; Savela, 1999; Bland, 1996
Syn: <i>Elachista cerusella</i> (Hübner) <i>Elachista monosemiella</i> Roessler				
Gelechiidae				
<i>Brachmia inornatella</i> (Douglas)	Stems	E	M	Haslam, 1972a
<i>Chrysoesthia drurella</i> (Fabricius)	Leaf mines	U	P	Haslam, 1972a; Stresemann, 1986
<i>Monochroa arundinetella</i> (Stainton)	Leaf mines	E	O	Hering, 1957
Hesperiidae				
<i>Ochlodes faunus</i> (Turati)	Leaves	E, As	P	Pyle, 1981; Opler <i>et al.</i> , 1995
<i>Ochlodes yuma</i> (Edwards)	Leaves	NA	M	Pyle, 1981; Opler <i>et al.</i> , 1995
<i>Poanes viator</i> (Edwards)	Leaves	NA	O	Beutenmüller, 1902; Shapiro, 1970; Royer and Marone, 1992; Gochfeld and Burger, 1997
<i>Polytremis pellucida</i> (Murray)	Leaves	As	M	Opler <i>et al.</i> , 1995; Tuzov <i>et al.</i> , 1997
Lasiocampidae				
<i>Euthrix potatoaria</i> (Linnaeus)	Leaves	E	P	Scorer, 1913; Vogel, 1984
Syn: <i>Philudoria (Cosmotriche)</i> <i>potatoria</i> (L.)				
Noctuidae				
<i>Apamea ophiogramma</i> (Esper)	Stems	E, NA	P	Forster and Wohlfahrt, 1971; Mikkola and Jalas, 1977; Troubridge <i>et al.</i> , 1992; Mikkola and Lafontaine, 1994

TABLE 2—Continued

Species	Larval feeding habit ^a	Distribution ^b	Specificity ^c	References
<i>Apamea unanimitis</i> (Hübner)	Leaves	E, NA	P	Mikkola and Jalas, 1977; Mikkola and Lafontaine, 1994
<i>Archanara aerata</i> (Butter)	U	As	U	Wang, 1992
<i>Archanara algae</i> (Esper)	Stems	E	P	Forster and Wohlfahrt, 1971
<i>Archanara dissoluta</i> (Treitschke)	Stems	E, As	M	Grünberg, 1909; L'homme, 1935; Allan, 1936; Durska, 1970; Forster and Wohlfahrt, 1971; Haslam, 1972a; Mikkola and Jalas, 1977; Bretherton <i>et al.</i> , 1983; Michel and Tschardtke, 1993
Syn: <i>Nonagria dissoluta</i> Treitschke				
<i>Archanara geminipuncta</i> (Haworth)	Stems	E, As	M	Grünberg, 1909; Brombacher, 1931; Allan, 1936; Wyniger, 1963; Forster and Wohlfahrt, 1971; Haslam, 1972a; Skuhrový, 1981; Tschardtke, 1989a, 1990; Hawk and José, 1996
Syn: <i>Nonagria (Noctua) geminipuncta</i> Haworth				
<i>Archanara neurica</i> (Hübner)	Stems	E, As	M	Grünberg, 1909; Forster and Wohlfahrt, 1971; Bretherton <i>et al.</i> , 1983
<i>Archanara sparganii</i> (Esper)	Stems and leaves	E	P	Grünberg, 1909; L'homme, 1935
Syn: <i>Nonagria (Noctua) sparganii</i> Esper				
<i>Arenostola phragmitidis</i> (Hübner)	Stems	E, As	M	Grünberg, 1909; Allan, 1936; Stokoe and Stovin, 1948; Forster and Wohlfahrt, 1971; Savela, 1999
Syn: <i>Arenostola semicana</i> (Esper)				
<i>Arenostola unicolor</i> Warren	U	As	U	Krivosheina and Nikulina, 1991
<i>Chilodes maritimus</i> (Tauscher)	Old stems	E	O,C	Stokoe and Stovin, 1948
Syn: <i>Senta maritima</i> , <i>Nonagria maritima</i>				
<i>Hydraecia micacea</i> (Esper)	Stems	E, NA	P	Bergmann, 1954; Mikkola and Jalas, 1977; Mikkola and Lafontaine, 1994
<i>Leucania linita</i> Guenée	Stems	NA	U	Ferguson <i>et al.</i> , 1999
<i>Leucania obsoleta</i> (Hübner)	Leaves	E, As	M	Grünberg, 1909; Scorer, 1913; Stokoe and Stovin, 1948; Haslam, 1972a; Marek, 1977; Mikkola and Jalas, 1977; Van der Toorn and Mook, 1982; Bretherton <i>et al.</i> , 1983
Syn: <i>Mythimna obsoleta</i> (Hübner)				
<i>Mythimna conigera</i> (Denis & Schiffermüller)	U	E	P	Bergmann, 1954; Vogel, 1984
Syn: <i>Cirphis conigera</i> , <i>Leucania conigera</i> , <i>Sideritis conigera</i>				
<i>Mythimna impura</i> (Hübner)	Leaves	E	P	Grünberg, 1909; Stokoe and Stovin, 1948; Mikkola and Jalas, 1977; Heath and Emmett, 1983
<i>Mythimna pudorina</i> (Denis & Schiffermüller)	Leaves	E, As	P	Grünberg, 1909; Scorer, 1913; Stokoe and Stovin, 1948; Mikkola and Jalas, 1977
<i>Mythimna straminea</i> (Treitschke)	Leaves	E, As	P	Grünberg, 1909; Scorer, 1913; Stokoe and Stovin, 1948; Agassiz, 1977; Mikkola and Jalas, 1977
<i>Nonagria typhae</i> (Thunberg)	Stems	E	O	Boldt, 1932
Syn: <i>Phragmatiphila typhae</i> Thunberg				

TABLE 2—Continued

Species	Larval feeding habit ^a	Distribution ^b	Specificity ^c	References
<i>Photedes brevilinea</i> (Fenn)	Stems, leaves	E	P	Allan, 1936; Forster and Wohlfahrt, 1971; Haslam, 1972a,b; Hawk and José, 1996
<i>Plusia festucae</i> (L.)	U	E	P	Grünberg, 1909; Bergmann, 1954
<i>Rhizdra lutosus</i> (Hübner)	Stems, rhizomes	E, As, NA	M	Grünberg, 1909; Allan, 1936; Blair, 1950; Baynes, 1964; Forster and Wohlfahrt, 1971; Mikkola and Lafontaine, 1994
<i>Senta flamma</i> (Curtis)	Leaves	E, As	P	Grünberg, 1909; Allan, 1936; Bergmann, 1954; Haslam, 1972a; Mikkola and Jalas, 1977; Bretherton <i>et al.</i> , 1983
<i>Simyra albovenosa</i> (Goeze)	Leaves	E, As	P	Haslam, 1972a; Mikkola and Jalas, 1977
Syn: <i>Arsilonche (Pharetra) albovenosa</i> Goeze				
<i>Simyra henrici</i> Grote	Stems	NA	P	B. Blossey (unpublished data)
<i>Xylena vetusta</i> (Hübner)	U	E	P	Savela, 1999
Crambidae				
<i>Chilo niponella</i> (Thunberg)	Stems	As	O	Li, 1987; CAB International, 1999
Syn: <i>Chilo hyrax</i> Bleszynski				
<i>Chilo phragmitella</i> (Hübner)	Stems, rhizomes	E, As	O	Grünberg, 1909; Raebel, 1925; Haslam, 1972a; Skuhravý, 1981; Van der Toorn and Mook, 1982; Tschardtke, 1993
<i>Donacaula forficella</i> (Thunberg)	Rolled leaves	E	P	Goater, 1986
<i>Donacaula mucronellus</i> (Denis & Schiffermüller)	Stems	E	O	Grünberg, 1909; Goater, 1986
<i>Pseudobissetia terrestrellus</i> Christoph	Stems	As	U	Liu, 1987
Syn: <i>Pseudobissetia terrestila</i>				
<i>Schoenobius gigantella</i> (Denis & Schiffermüller)	Stems, rhizomes	E	M	Grünberg, 1909; Haslam, 1972a; Pruscha, 1972
<i>Sclerocona acutellus</i> (von Eversmann)	U	E, NA	U	Tschardtke, 1999
Syn: <i>Calamochrous acutellus</i> von Eversmann				
Lymantriidae				
<i>Laelia coenosa</i> (Hübner)	Stems	E, As	P	Scorer, 1913; DeWorms, 1979; Li, 1987
Tortricidae				
<i>Clepsis spectrana</i> (Treitschke)	Leaves	E	P	Hannemann, 1961
Thysanoptera				
Phlaeothripidae				
<i>Haplothrips aculeatus</i> (Fabricius)	Flowers	E, NA, As, Af	P	Rodewald-Rudescu, 1974; Vogel, 1984; CAB International, 1999
<i>Haplothrips hukkineni</i> (Priesner)	Flowers	E, Af	U	Rodewald-Rudescu, 1974; Grabo, 1991
<i>Haplothrips tritici</i> (Kurdjumov)	Leaves	E, As, Af	P	Rodewald-Rudescu, 1974; CAB International, 1999
Thripidae				
<i>Chriothrips manicatus</i> (Haliday)	Flowers	E	P	Vogel, 1984
<i>Limothrips denticornis</i> (Haliday)	Leaves	E	P	Grabo, 1991
Fungi				
<i>Alternaria tenuissima</i> (Kunze ex Pers.)	Leaves, stems	Cosmopol.	P	Kanaujia <i>et al.</i> , 1978
<i>Claviceps microcephala</i> Wallr.	Seeds	E	U	Hürlimann, 1951; Björk, 1962
<i>Claviceps purpurea</i> (Fr.)	U	U	P	Haslam, 1972a
<i>Coniosporium arundinia</i> (Corda) Saccardo	U	E	U	Rodewald-Rudescu, 1974
<i>Deightoniella arundinacea</i> (Corda) Hughes	Leaves, stems, rhizomes	U	M	Durska, 1970; Haslam, 1972a
<i>Deightoniella roumeguerei</i> (Cav.)	U	E	U	Ban <i>et al.</i> , 1998
<i>Hendersonia epicalamia</i> Cooke	Leaves, leaf sheaths	E	U	Haslam, 1972a
<i>Hendersonia graminicola</i> Lev.	Leaves, leaf sheaths	E	U	Haslam, 1972a
<i>Leptosphaeria arundinacea</i> Sow.	U	E	U	Haslam, 1972a

TABLE 2—Continued

Species	Larval feeding habit ^a	Distribution ^b	Specificity ^c	References
<i>Leptosphaeria graminis</i> (Fick.) Saccardo	U	E	U	Haslam, 1972a
<i>Leptosphaeria graminicola</i> Gr.	U	E	U	Haslam, 1972a
<i>Lophiostoma arundinis</i> (Pers.: Fr.) Ces. & de Not.	U	E	U	Rodewald-Rudescu, 1974
<i>Neovossia danubialis</i> Savulescu	Ovaries	E, As	U	Rodewald-Rudescu, 1974; Terui and Harada, 1974
<i>Phoma rimosa</i> West	Leaves	E	U	Haslam, 1972a
<i>Pleospora rubicunda</i> Niessl.	U	E	U	Haslam, 1972a
<i>Polythrinciopsis phragmitis</i>	U	E	U	Fischl <i>et al.</i> , 1998
<i>Puccinia alnetorum</i> Gäumann	U	E	P	Gäumann, 1959
<i>Puccinia arundinacea</i> Hedw.	U	E	U	Rodewald-Rudescu, 1974
<i>Puccinia coronata</i> Corda	Whole plant	Cosmopol.	P	Gäumann, 1959
<i>Puccinia graminis</i> Person	Leaves, stems, inflorescence, seeds	Cosmopol.	P	Gäumann, 1959
<i>Puccinia magnusiana</i> (Korn)	Leaves	U	U	Haslam, 1972a
<i>Puccinia obtusata</i> Otth	Leaves, leaf sheaths	E	O	Gäumann, 1959
<i>Puccinia okatamaensis</i> Ito	U	As	U	Harada and Hasegawa, 1975
<i>Puccinia phragmitis</i> (Schum.) Koern.	U	E, As, NA	P	Haslam, 1972a; Harada, 1987
<i>Puccinia trabutii</i> Roumeguere & Saccardo	Leaves, leaf sheaths	E, As, Af	P	Gäumann, 1959; Rodewald-Rudescu, 1974; Baka and Gjaerum, 1996
Syn: <i>Puccinia isiacae</i> (Thuemen)				
<i>Puccinia trailii</i> Plowright	Leaves	E	P	Gäumann, 1959; Rodewald-Rudescu, 1974
<i>Scirrhia nischke</i>	U	E	U	Rodewald-Rudescu, 1974
<i>Scirrhia rimosa</i> (Alb. Et Schw.)	U	U	U	Haslam, 1972a
<i>Torula graminicola</i>	U	E	P	Rodewald-Rudescu, 1974
<i>Ustilago grandis</i> Fries	Young shoots	E	U	Durska, 1970; Haslam, 1972a

^a U, unknown.

^b Distribution on continents (NA, North America; E, Europe; As, Asia; Af, Africa; Aus, Australia; U, unknown; Cosmopol., cosmopolitan).

^c Specificity as recorded in the literature (M, monophagous; O, oligophagous; P, polyphagous; C, carnivorous; U, unknown).

the reed shoots or in the litter. Larvae hatch in late April or early May and burrow into emerging shoots where they feed on the growing meristems. After consuming the inner parts of the basal internodes, they mine the rhizomes. Attacked rhizomes are packed with frass, leaving only the membranous outer layer intact. Infested shoots dry out, causing blanching of the leaves, which break easily. In June and July larvae are found in wide horizontal rhizomes, which they leave to pupate in the soil. The requirement for pupation in the soil limits *R. lutosa* to drier reed stands.

The moth *Apamea unanimitis* was first collected near Ottawa, Canada in June of 1991 (Mikkola and Lafontaine, 1994). Larvae feed on leaves of *P. australis*, *Phalaris* sp., and *Glyceria* sp., overwinter fully grown, and pupate in the spring within broken stems. Adults fly in June and July. *Apamea ophiogramma* was first reported in 1989 from British Columbia, Canada (Troubridge *et al.*, 1992) and has since been found in New York, Vermont, Quebec, and New Brunswick (Mikkola and Lafontaine, 1994). Larvae feed in stems of *Phragmites*, *Phalaris*, and *Glyceria* species, overwinter in the soil, and complete development in the stems

in spring. Pupation occurs in the soil, and moths fly in July and August (Mikkola and Lafontaine, 1994).

The legless reed mealybug, *Chaetococcus phragmitis*, has recently been found in Delaware, Maryland, New Jersey, and New York (Kosztarab, 1996). Native to Central Europe, Armenia, Azerbaijan, and the Mediterranean region (Ben-Dov, 1994), the only known host plants of this mealybug are *Phragmites* and *Arundo* spp. (Kosztarab, 1996). *Chaetococcus phragmitis* can represent 60–99% of the insect biomass on *P. australis* in New York (Krause, 1996).

Four species of chloropid gall-inducing flies in the genus *Lipara* have been found in the Northeast. Sabrosky (1958) reported *L. similis* as an import interception and identified *L. lucens* from a 1931 collection. *L. rufitarsis* was collected in Rhode Island and Connecticut in 1998. We recently found *L. pullitarsis* along the coast of New Jersey, and there are no previous records of these species in North America. Regional surveys in the northeast (B. Blossey and F. Eichner, unpublished data) reveal a widespread distribution and abundance of *L. similis*, *L. rufitarsis*, and *L. pullitarsis*; however, *L. lucens* has not been found after the

TABLE 3

Host Specificity of Herbivores Associated with *P. australis* Outside North America

Host specificity ^a	Number of species (n = 171)	Percentage
Monophagous	66	38.6
Oligophagous	22	12.9
Polyphagous	62	36.3
Unknown	21	12.3

^a Specificity defined according to the number of host records in the literature (monophagous: exclusively reported from *P. australis*; oligophagous: maximum of five host plant records within the tribes Arundineae, Glycerieae, and Phalarideae and within family Typhaceae or two host plant records in family Poaceae; polyphagous: species that do not fulfill requirement for previous two categories).

initial record in 1931 and may not be established in North America.

At one site in Rhode Island *L. similis* larvae were found in 80% of the *P. australis* stems; similar high attack rates of *Lipara* spp. are frequently observed throughout southern New York state and in the Finger Lakes region (Balme and R. Casagrande, unpublished data). These high attack rates are very different from data collected in Europe, where attack rates usually remain <5% (Skuhrový, 1981; Schwarzländer and Häfliger, 1999). However, although the attack of *Lipara* spp. reduces stem length in North America (B. Blossey, unpublished data), differences in height and shoot biomass of attacked and unattacked stems were reported to be not significantly different (Tschardt, 1999). The reasons for the differences in attack rates and response of *P. australis* to attack are unclear.

Additional species such as the gall midge *Lasioptera hungarica*, a dolichopodidae *Thrypticus* sp., the aphid *Hyalopterus pruni*, and the wasp *Tetramesa phragmitis* appear widespread. The mite *Steneotarsonemus phragmitidis* was recently discovered in the Finger Lakes region of New York and the rice grain gall midge *Giraudiella inclusa* in Massachusetts, Connecticut, New York, and New Jersey (B. Blossey and M. Schwarzländer, unpublished data).

POTENTIAL FOR DEVELOPING BIOLOGICAL CONTROL FOR *P. AUSTRALIS*

The literature reveals an abundance of herbivores on *P. australis* outside North America, particularly in Europe (Table 2). The low number of herbivores found in Asia and Africa is probably on underestimation because that fauna is less well known than the fauna in Europe. We identified 201 species (164 insects, 7 mites, and 30 fungi) that are associated with *P. australis* outside North America (Table 2). We excluded predators or parasitoids attacking species living on *P. aust-*

TABLE 4

Feeding Niche of Herbivores Associated with *P. australis* Outside North America

Feeding niche	Number of species ^a (n = 171)	Percentage
Flowers	4	2.3
Leaves and leaf sheaths	75	43.9
Stems	55	32.2
Roots	9	5.3
Unknown	26	15.2

^a Excluding inquilines; multiple entries possible.

ralis but included species that may be inquilines, saprophytic, or both. Over 60% of the species listed in Table 2 are monophagous (Table 3), and the most represented orders are Lepidoptera (46 species) and Diptera (58 species). Over 70% of all herbivores attack leaves and stems of *P. australis* (Tables 4 and 5) and only 4 of the monophagous species feed in rhizomes (Table 5). Of the 201 species known from outside North America, 21 (10.4%) have already been accidentally introduced (Table 1).

Our literature and field surveys demonstrated that an abundance of monophagous species that could have potential as biological control agents exist outside North America (Table 2). However, deciding which of them are best suited for a biological control program could prove difficult (Blossey, 1995). Criteria for prioritizing potential control agents include host specificity, distribution, impact on target plant, phenology, fecundity, and mortality factors of potential control agents (Harris, 1973, 1991; Goeden, 1983; Wapshere, 1985). Relative importance of these criteria is subject to debate, and the different approaches provided contradictory rankings when applied to selection of control agents for purple loosestrife (Blossey, 1995).

Many of the insects recorded from *P. australis* have been studied extensively in Europe where they are considered pests of reed beds (Mook and van der Toorn, 1982). Generally these studies lack information on the impact of herbivores on plant population dynamics, so

TABLE 5

Feeding Niche of all Monophagous Herbivore Species on *P. australis* Outside North America

Feeding niche	Number of species ^a (n = 66)	Percentage
Flowers	0	0
Leaves and leaf sheaths	23	34.8
Stems	34	51.5
Roots	5	7.6
Unknown	3	4.5

^a Excluding inquilines; multiple entries possible.

we are unable to predict their impact in North America. The fact that 21 insect species have already been accidentally introduced to North America does not make the selection any easier, since new introductions may need to compete with already established species. Denno *et al.* (1995) reviewed 193 pairwise interactions among phytophagous species and found competitive interactions in 73% of the studies, with the majority involving asymmetric competition. Although few studies examined the interactions between aboveground and belowground herbivores, all interactions adversely affected root-feeders (Denno *et al.*, 1995). This confirms predictions of a model of interactions of spatially separated herbivores proposed by Masters and Brown (1995). It is unclear how these interactions may influence the success or failure of biological weed control. There is no known example where a less successful species displaced a more successful control agent (McFadyen, 1998); however, this conclusion is largely based on simple observations and not on experimental or quantitative evidence. Any predictions are further complicated by potential differences in secondary plant chemistry (Rhoades, 1985), influence of different genotypes (Fritz *et al.*, 1987; Whitham *et al.*, 1991; Underwood, 1994), and cumulative herbivore impacts (Root, 1996), which may interact with biotic factors to shape population dynamics of herbivores and *P. australis*. The different population densities, attack rates, and responses of *P. australis* to gall induction by *Lipara* spp. in North America compared to Europe is further indication that predictions based on studies in the native range may have limitations.

We favor an approach outlined by Malecki *et al.* (1993) for the purple loosestrife biological control program, which assumes that simultaneous attack of different plant structures will enhance plant suppression. This will involve the simultaneous introduction of several host-specific herbivores. Establishing a follow-up monitoring protocol to evaluate the impact of single and multiple herbivores after the release will be critical to help guide management decisions and to advance our understanding of the effects of herbivory on plant population dynamics (Crawley, 1989). One of the guiding principles in our selection of promising biological control agents is provided by Gaudet and Keddy (1988) who showed that competitive hierarchies within wetland plant communities are determined by plant biomass, height, and canopy diameter. Plant species that grow taller and produce higher amounts of biomass are competitively superior. Accordingly, we should select control agents that directly (or indirectly) influence these parameters.

P. australis is able to grow under a wide range of environmental conditions, and two distinct phenotypes, "water reed" and "dry reed," have been recognized. Water reed has larger shoot diameters and taller growth than dry reed. Any successful control program

needs to target *P. australis* growing under a variety of conditions. The bulk of *P. australis*' biomass is located below ground, and root:shoot ratios of 2:1 to 4:1 have been described (Vogel, 1984; Schieferstein, 1996), with starch as the main storage component (Vogel, 1984). Rhizomes can be found as deep as 1.5 m under optimal conditions (Schieferstein, 1996). However, Kudo and Ito (1988) did not detect a direct relationship of belowground to aboveground biomass. Instead, ratios varied from center to edge of a clone. Clonal integration appears higher for *P. australis* than for clonal grasses; colonies of connected shoots showed an integrated response to herbivore attack (Tscharntke, 1990).

Based on the biology and ecology of *P. australis* in North America, we propose to give highest priority to European rhizome feeders as biological control agents, followed by stem and leaf feeders. From the list of potentially available monophagous candidates (Tables 2 and 5), we propose as a first step to study the root feeders *Rhizodra lutosus* (already established in North America), *Phragmataecia castaneae*, *Chilo phragmitella*, and *Schoenobius gigantella* for their host specificity and potential as biological control agents. Simultaneously, the shoot-feeding moths in the genera *Archanara* and *Arenostola* and the chloropid fly *Platycephala planifrons* should be evaluated for their potential as biological control agents. In addition, the interaction of accidentally introduced herbivores (*R. lutosus*, *Lipara* spp., *G. inclusa*, etc.) and their impact on plant performance needs to be evaluated. Overall, we anticipate that attack of belowground rhizomes will kill aboveground shoots, reduce storage reserves and recovery potential, and sever and disconnect rhizomes, further reducing the competitive ability of *P. australis*.

In Europe, van der Toorn and Mook (1982) report the destructive potential of *R. lutosus*, particularly in drier sites. In New York and Rhode Island we see typical signs of attack at the edge of *P. australis* clones where *R. lutosus* may reduce shoot density and prevent clone expansion. Further survey work is needed to determine the distribution of *R. lutosus*, and long-term monitoring will evaluate the impact of the species on *P. australis* in different habitat types. Larvae of *C. phragmitella* were reported feeding at the shoot base and in the rhizome (van der Toorn and Mook, 1982; Schwarzländer and Häfliger, 1998). The species colonized more mature reed stands and is found in shoots and rhizomes of water reed (Pruscha, 1972; Schwarzländer and Häfliger, 1998, 1999), but little is known about the biology and ecology of the species. Similar to *C. phragmitella*, larvae of *P. castaneae* mine the basal parts of shoots and upper rhizome parts of common reed. The species is believed to be widespread throughout Europe and reported locally common (Pruscha, 1972). Larval development takes 1–2 years and mature larvae reach 45 mm in size. A similar life history is described for *S. gigantella*, and this species is only found in water reed,

which would nicely complement other rhizome feeders that are restricted to drier areas (Pruscha, 1972; Schwarzländer and Häfliger, 1999). In early spring, larval feeding of *S. gigantella* causes premature shoot death; later in the season larvae mine deeper parts of the rhizome where they also overwinter (Schwarzländer and Häfliger, 1999). *S. gigantella* larvae destroy several shoots during their development; to change stems, they cut a 3-cm-long section out of the old shoot and use this "boat" to move to a new shoot (Häfliger *et al.*, 2001).

Four species of Donaciinae are reported to attack *P. australis* (Table 2). However, only *P. braccata* (and potentially *Donacia clavipes*) appear to be host specific (Menzies and Cox, 1996). Larvae are suspected to feed on submersed rhizomes and roots of *P. australis* and obtain oxygen through a pair of hollow caudal spines, which are inserted into host plant tissues (Cooter, 1991). Pupation occurs in hard brown cocoons attached to the roots of the host plant and larval development may take 2–3 years (Cooter, 1991; Bienkowski, 1996). In addition, the aquatic weevil *Dicranthus elegans* is listed as monophagous (Lohse, 1983). Eggs are laid through the shoot cortex of water reed, and larvae mine the internodes. However, it is uncertain whether larval feeding by these beetles impairs performance of common reed (Schwarzländer and Häfliger, 1999; Häfliger *et al.*, 2001).

Except for the work of van der Toorn and Mook (1982) on *R. lutosa*, we have little information on the impact of these belowground herbivores on population dynamics and performance of *P. australis*. In contrast, shoot-attacking species have been studied extensively in Europe because of their visible impacts and concerns for reed management (van der Toorn and Mook, 1982). The best-studied and most important species is the univoltine moth *Archanara geminipuncta*. Adults fly in mid-summer and lay eggs on green reed shoots where they overwinter under the leaf sheaths. Hatching larvae enter newly emerging shoots in spring. Larvae prefer large-diameter stems (>5 mm) and need at least three shoots to complete their development (Tscharntke, 1990, 1992b), which causes the tips of attacked shoots to wilt. Larvae pupate in lower internodes of damaged or undamaged shoots. While attack by *A. geminipuncta* kills young shoots, older stems of *P. australis* produce side shoots in the year of attack. Attack rates of >90% of stems are possible and shoot height is reduced up to 45% (Tscharntke, 1990). Narrower shoots are formed by *P. australis* in the spring following extensive *A. geminipuncta* damage (Tscharntke, 1990; Mook and Van der Toorn, 1985). Outbreak and crash cycles are reported with 3- or 4-year intervals, with food shortage and larval competition driving local population dynamics of *A. geminipuncta* and other *Archanara* species (Tscharntke, 1990). In a study in southern Germany, egg parasitoids

accounted for 28–50% and predatory mites for 15% mortality of *A. dissoluta* and *A. geminipuncta*; larval mortality (parasitoids, predators, and diseases) was 74% and pupal mortality 76% (Michel and Tscharntke, 1993). The highest mortality occurred at highest first instar larval densities, supposedly through competition for suitable shoots, extended foraging times, and exposure to predators (Michel and Tscharntke, 1993). The two sibling species *A. dissoluta* and *A. neurica* occur in much lower densities than *A. geminipuncta*.

Galls of *G. inclusa*, called "rice grain" galls because of their size and shape, protrude inward from the internode wall and are crowded in basal parts of internodes. Adults of the first generation emerge synchronously from galls within 2 weeks at the end of May (Tscharntke, 1988, 1989a, 1992a). The first generation attacks the 9 lower internodes; second to fourth generations attack the 10th internode or higher and side shoots induced by shoot damage. Gall abundance is negatively correlated with the diameter of shoots and positively with the number of side shoots (Tscharntke, 1988, 1989b, 1992a). Damage to main shoots by *A. geminipuncta* triggers growth of numerous narrower shoots which are highly susceptible to attack of the second to fourth generations of *G. inclusa*. Attacked shoots show elongation of 7–11%, which potentially enhances survival and productivity of attacked shoots. However, internodes attacked by gall midges also break more easily (Tscharntke, 1992b), and galls appeared to function as a partial block to the normal flow of resources (Tscharntke, 1989b). At high densities (>2000 galls/m²) and stressed by brackish water, shoots were shorter and distorted, dried up apically, and split open (Tscharntke, 1989b). It is difficult to predict how the potential introduction of this species without its specialized parasitoid community (at least 14 species are known in Europe (Tscharntke, 1992b)) and abundance of bird predation (Tscharntke, 1992b) will affect the population dynamics of the gall maker and its impact on *P. australis*. Its ability to colonize stressed thin shoots in brackish water may make it a suitable candidate along the Atlantic coast. However, *G. inclusa* was also reported to cause considerable damage to reed in Hungary (Erdös, 1957), and high attack rates of the species apparently caused shoot death (Schwarzländer and Häfliger, 1999).

Initial studies in Europe demonstrated that the early season attack of the fly *Platycephala planifrons*, family Chloropidae, results in dramatic reductions in shoot growth and biomass production of *P. australis*, often similar to the attack of *A. geminipuncta* (Schwarzländer and Häfliger, 1998). This species is abundant and one of the most damaging herbivores in European surveys for potential biological control agents. Life history and ecology are poorly known but larvae were found overwintering in dormant buds that are formed

in the fall for growth in the following spring (Schwarzländer and Häfliger, 1998, 1999).

CONCLUSION

P. australis has been established in North America for at least several thousand years and thus appears a questionable candidate for classical biological control. However, the negative ecological and economic impacts of *P. australis* in North America, in combination with the inability to control the species with conventional means, makes the development of biological control a worthwhile alternative. Clearly, land managers in most regions of North America consider the range expansion and population explosion of *P. australis* undesirable and have made a commitment to control of the species (Marks *et al.*, 1994). When evaluating benefits, potential risks, and costs of implementing a biological control program targeting *P. australis*, we have to consider the potential health risks and ecosystem-wide effects associated with continued aerial application of herbicides, mechanical harvesting, flooding, or any other control method.

The ability to utilize the currently established insect herbivores as biological control agents is limited. *P. australis* populations have continued to expand despite arrival and spread of these herbivores. However, there appear to be at least several promising candidate species in Europe. The introduction of host-specific herbivores after extensive host-range testing is not entirely risk free, and there is no guarantee that herbivores will significantly reduce *P. australis* populations. The goal of biological control is to reduce (not eradicate) populations of an invasive plant to an acceptable level.

Considering the realized negative impacts of *P. australis* on the functioning and integrity of North American fresh and saltwater wetlands, the potential risks associated with the development of biological control appear small in comparison. We favor the further development of a biological control program and the eventual release of host-specific agents. However, any decision to go ahead with this program has to involve extensive dialogue among agencies, organizations, and individuals who are concerned with management of *P. australis*. We encourage this dialogue and hope that this paper will provide a framework for the discussions to follow.

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