

Distribution and impact of exotic gall flies (*Lipara* sp.) on native and exotic *Phragmites australis*

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Received 27 February 2006; received in revised form 13 September 2006; accepted 18 September 2006

Abstract

Two exotic gall fly species infest stems of native and exotic *Phragmites australis* (Cav.) Trin. ex Steudel in northeastern North America. In this study, we determined the distribution of *Lipara similis* Schiner and *L. rufitarsis* Loew in native and exotic *P. australis* in Rhode Island. We also studied the within-stand distributions of each fly species and their effects on flowering of native and exotic *P. australis*. We collected stems from populations throughout southern Rhode Island and measured stem length and diameter, and percent flowering. Stems were then dissected to determine *Lipara* infestation. *L. similis* and *L. rufitarsis* were found throughout Rhode Island infesting both native and exotic *P. australis*, but their presence and abundance varied among sites. Within stands, *L. similis* infests the taller, thicker interior stems and *L. rufitarsis* infests the shorter, thinner exterior stems. *Lipara similis* reduces stem length by 6%; *L. rufitarsis* infestation reduces stem length by 37%. The flowering rate of uninfested stems is significantly lower in native *P. australis* stems than in exotic stems. Both *Lipara* species prevent infested stems from flowering. In adjacent stands of native and exotic *P. australis*, *L. rufitarsis* infests significantly more native stems than exotic stems, possibly further reducing the reproductive potential of the native plants relative to the exotic. *Lipara* species may play a role in facilitating the displacement of native *P. australis* by the exotic genotype.

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Keywords: *Phragmites australis*; *Lipara similis*; *Lipara rufitarsis*; Haplotype; Invasive species; Native species displacement; Gall fly

1. Introduction

In North America, a non-native haplotype of common reed, *Phragmites australis* (Cav.) Trin. ex Steudel, is rapidly invading ecosystems formerly occupied by native haplotypes (Saltonstall, 2002), forming monocultures in wetlands and changing ecosystem structure and function (Meyerson et al., 2000). Sixteen known European herbivores have been found in the United States associated with the exotic haplotype of *P. australis* (Tewksbury et al., 2002), but the distribution and effects of many of these insects on native and exotic haplotypes is unknown.

P. australis (Poaceae) is a perennial rhizomatous grass with a cosmopolitan distribution (Tucker, 1990). In North America, *P. australis* subsp. *americanus* Saltonstall, P.M. Peterson & Soreng (Saltonstall et al., 2004) consists of 11 native haplotypes (Saltonstall, 2002). However, Saltonstall (2002) identified one exotic haplotype in North America, which is replacing native haplotypes across the east. The native subspecies was absent

from southern New England in this initial investigation and Saltonstall (2003) hypothesized that local extinctions in these areas may have been caused by the invasion of exotic *P. australis*. However, we recently found a new native haplotype (type AB, Lambert and Casagrande, in press) on Block Island, Rhode Island.

Shoot flies in the genus *Lipara* Meigen (Diptera: Chloropidae) are specialists on *P. australis* throughout the Palaearctic region (Beschovski, 1984). Sabrosky (1958) reported the accidental introduction of *L. similis* into the United States in a shipment containing *P. australis* as packing material. Several species are now widespread and abundant in northeastern North America (Blossey et al., 2002; Tewksbury et al., 2002). Balme (2000) found *L. similis* Schiner infesting stems of exotic *P. australis* in stands throughout Rhode Island, but did not note any significant damage to the plants. We recently found two shoot fly species infesting native and exotic *P. australis* in Rhode Island.

Distribution of *Lipara* species in *P. australis* stands is highly influenced by shoot diameter (Chvála et al., 1974; De Bruyn, 1994), which, in turn, is strongly affected by environmental factors (De Bruyn, 1995). *Lipara lucens* Meigen and *L. rufitarsis* Loew prefer thin shoots; *L. similis* Schiner and *L. pullitarsis* Doskocil & Chvála accept shoots of all sizes

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(De Bruyn, 1993, 1994; Tschardtke, 1993). Larval feeding causes an apical gall to form in infested shoots, which stunts stems and prevents panicle formation (Chvála et al., 1974). In Europe, stem attack rates vary among sites (2–40%), with little resulting loss of plant biomass (Schwarzländer and Häfliger, 2000), but in the United States infestation rates can reach 80% (Balme, 2000; Blossey et al., 2002.)

Lipara species are common in the stems of *P. australis* in Europe where their galls prevent plants from flowering (Chvála et al., 1974). Adults lay eggs on the outside of stems and the larvae bore into the tip of the shoot in late spring or early summer, killing the apical meristem and altering stem structure (De Bruyn, 1994). The larvae feed between the newest leaves at the top of the stem and destroy the panicle soon after it begins development (Chvála et al., 1974). *Lipara rufitarsis* infestation causes a noticeable gall in which the larvae complete development. *Lipara similis* completes development in the upper leaves of the stem and does not cause a noticeable gall. Before winter, the larvae of both species shift upward in the stem and the leaf sheath hardens, protecting the overwintering larvae (Chvála et al., 1974). Larvae pupate in the spring and emerge as adults and lay eggs in the summer (Schwarzländer and Häfliger, 1998).

In this study, we determined (1) the abundance and distribution of *Lipara* species within and among *P. australis* stands throughout coastal Rhode Island, (2) if *Lipara* species infestation differs between native and exotic haplotypes of *P. australis*, and (3) if *Lipara* species have a differential effect on the growth and reproduction of native and exotic genotypes.

2. Methods

2.1. Study sites

In 2003, 17 sites were surveyed across southern Rhode Island, representing wet, dry, and brackish habitats (Table 1). Fourteen sites were selected on the mainland and three sites

were selected on Block Island. Stands were selected to represent *P. australis* populations throughout the state (but was limited to publicly accessible sites), with most stands selected in southern RI where *P. australis* is most abundant. No stands on the mainland were within 5 km of each other. On Block Island, no stands were within 1 km of each other, except at the Block Island Conservancy where native and exotic *P. australis* stands are growing within 5 m of each other, and the exotic stand is expanding toward the native stand. These two Block Island stands were used to determine if *Lipara* densities are greater in native stands with adjacent exotic stands. All stands on the mainland were the non-native haplotype (type M, following the designation of Saltonstall, 2002). Stands on Block Island were haplotype M and native type AB. Stems were also collected in August 2002 from the only other known native (type E) stand in Arrowsic, Maine where the closest exotic *P. australis* stand was approximately 13 km distant. At all sites, coordinates were determined with a Garmin etrex[®] GPS and the approximate areas were found by measuring each stand at its greatest length and width. All stands were at least 5 years old, >15 m², and had a growth form characteristic of a mature stand with relatively tall, thick stems in the middle of the stand and short, thin stems at the expanding edges. Stands over 0.25 ha were not measured, but were categorized as large.

2.2. *Lipara* distribution among and within stands/effects on stems

Stem collection for the Rhode Island sites began in mid-August 2003 when galls on *P. australis* became apparent and was completed within 6 weeks. By August, larvae in dissected stems are visible by eye. We took stem samples from both the edge and the interior of stands. Within 5 m of the edge, 2-m transects ($N = 5$) were run parallel to the edge of the stand. The first transect line was placed at the center of the stand and subsequent transects were placed parallel to the initial transect

Table 1
Stem collection sites in Rhode Island and Maine

Location	Habitat	Latitude, longitude	Haplotype
Coventry	Wet	71°41'40", 41°41'33"	M
Charlestown	Dry	71°37'35", 41°21'49"	M
Mosquito Beach (Block Island)	Brackish	71°34'08", 41°11'19"	M
Town Beach (Block Island) ^a	Brackish	71°34'12", 41°11'03"	AD
Worden Pond, South Kingstown	Wet	71°34'04", 41°25'96"	M
Sprague Park, Narragansett	Wet	71°28'07", 41°26'03"	M
Galilee salt marsh, Narragansett	Brackish	71°30'11", 41°22'47"	M
Newton Avenue, Narragansett	Dry	71°27'13", 41°24'45"	M
Ryan Park, North Kingstown	Wet	71°28'32", 41°33'27"	M
Jamestown	Brackish	71°23'24", 41°27'49"	M
Calf Pasture Point, North Kingstown	Dry	71°24'11", 41°37'53"	M
Prudence Island	Dry	71°20'43", 41°37'57"	M
Portsmouth	Dry	71°14'00", 41°38'05"	M
Sachuest Pt., Tiverton	Dry	71°14'50", 41°28'59"	M
Little Compton	Wet	71°11'21", 41°31'21"	M
Block Island Conservancy native ^a	Brackish	71°34'04", 41°10'46"	AD
Block Island Conservancy exotic	Dry	71°34'04", 41°10'45"	M
Arrowsic, Maine ^a	Brackish	69°46'15", 43°52'33"	E

^a Denotes native populations.

and spaced 5 m apart. Along each transect, six stems intersecting the transect line were randomly chosen and cut at their base. This method was also used to collect stems from 2-m transects ($N = 5$) in the center of the stand. All stems from each transect were bundled together for transport and kept at 7 °C until dissection.

In a previous study, stems from the Maine site were collected in September 2002 (unpublished data). We included these data to increase our sample size for native *P. australis* stands – this was the only other known native stand in New England. Two transects were run through the *P. australis* stand, with four 1-m² plots randomly set along each transect. All stems within each plot were cut at the base and bundled together for transport back to the lab where they were kept at 7 °C until dissection.

In the lab, stem length (cm) was measured from the base of the cut stem to the last node on the stem. Presence or absence of a panicle on each stem was recorded and the panicle length was measured from the last node to the top of the panicle. We measured the basal diameter of each stem 1 cm below the bottom node to the nearest 0.1 mm with a digital caliper. Plants without panicles were dissected by splitting the stem lengthwise. Presence or absence of *Lipara* was recorded and species determination was made by gall morphology and larval markings (Chvála et al., 1974).

A two-way ANOVA was used to analyze differences in infestation rates among sites and within stands (interior versus exterior) for the dependent variables percent stems with *L. similis* and percent stems with *L. rufitarsis*. The two stands at the Block Island Conservancy were excluded from this analysis and analyzed separately (see below). To determine baseline estimates of differences in basal diameter between uninfested stems in the stand interior and exterior, basal diameter was analyzed using a *t*-test. Differences in stem basal diameter of uninfested stems, *L. similis* infested stems, and *L. rufitarsis*

infested stems were analyzed using a one-way ANOVA. Tukey's test was used for multiple comparisons. Reductions in shoot length caused by infestation were evaluated for *L. similis* and *L. rufitarsis* by comparing the lengths of uninfested stems with stems infested by each species. For each species, only populations with flies present were used in the analysis (nine plant populations for each species). Stem length was analyzed with a nested ANOVA using location of stems within stand (interior versus exterior) nested inside level of infestation (infested versus not infested). Basal stem diameter is constant throughout the growing season and highly correlated with growth rate, stem and flower lengths, and shoot and rhizome biomass (Mook, 1967; Tschardtke, 1988; Thursby et al., 2002), and was used as a covariate in the analysis. To evaluate differences in stem length and flowering rate among native and exotic *P. australis* populations, each of these factors was compared using a *t*-test. To assess flowering, only stands in full bloom at the time of collection were analyzed for flowering rate, which included Town Beach, Block Island Conservancy native, and Maine for the native group, and Ryan Park, Portsmouth, Sachuest, Jamestown, Mosquito Beach, and BI Conservancy exotic for the exotic group.

2.3. *Lipara* distribution and effects in adjacent native and exotic stands

Stems collected from plots at the Block Island Conservancy site were used to look at *Lipara* distribution, infestation rates, and effects on flowering between native and exotic haplotypes growing in the same habitat. These permanent plots were part of a different observational study, and were analyzed separately from the above study. One square meter permanent plots were placed 5 m apart in adjacent native (16 plots) and exotic (11 plots) *P. australis* stands in a grid covering the entire stands.

Table 2

Lipara similis and *L. rufitarsis* infestation rates for interior and exterior of stands, and total infestation rates for stems collected in Rhode Island and Maine

Location	Percent infested stems				Total <i>Lipara</i>
	<i>L. similis</i>		<i>L. rufitarsis</i>		
	Interior	Exterior	Interior	Exterior	
Coventry	34.0 ± 7.0	14.0 ± 5.0	0	0	24.0 ± 6.9
Charlestown	0	0	3.4 ± 2.7	13.4 ± 4.9	8.4 ± 4.1
Mosquito Beach (Block Island)	10.0 ± 5.2	0	0	3.4 ± 2.7	6.7 ± 4.0
Town Beach (Block Island)	14.0 ± 5.0	6.6 ± 5.2	0	6.8 ± 3.3	13.7 ± 4.7
Worden Pond, South Kingstown	0	0	0	0	0
Sprague Park, Narragansett	50.2 ± 7.7	37.8 ± 7.1	4.0 ± 3.2	14.8 ± 5.8	53.4 ± 8.0
Galilee Salt marsh, Narragansett	4.0 ± 3.2	0	3.4 ± 2.7	7.4 ± 3.6	7.4 ± 3.4
Newton Avenue, Narragansett	0	6.8 ± 3.3	0	0	3.4 ± 2.5
Ryan Park, North Kingstown	6.6 ± 5.2	11.6 ± 5.7	3.4 ± 2.7	15.8 ± 3.3	18.7 ± 7.1
Jamestown	10.0 ± 5.1	0	0	26.6 ± 6.7	18.3 ± 6.5
Calf Pasture Point, North Kingstown	0	0	0	7.4 ± 3.6	3.7 ± 2.8
Prudence Island	0	0	0	0	0
Portsmouth	16.8 ± 7.3	10.0 ± 5.2	0	13.4 ± 7.7	20.0 ± 7.2
Sachuest Pt., Tiverton	0	0	0	0	0
Little Compton	0	0	0	0	0
Arrowsic, Maine	0	0	0	0	0
Total	9.7 ± 6.3	5.8 ± 4.6	0.9 ± 1.4	7.2 ± 4.4	11.9 ± 6.6

Mean percentages ± S.E. are given. $N = 60$ stems for each site.

An unequal number of plots was used between stands because the native stand is much larger than the exotic stand. Stems were harvested 11 September 2003 by cutting every stem from each plot at its base. Stems from each plot were bundled together with duct tape for transport and stored at 7 °C until dissection.

The native and exotic BI Conservancy stand data were used to determine if infestation rates differ when native and exotic stands are adjacent. Percent stem infestation by *L. rufitarsis* and *L. similis* in the native and exotic stands was analyzed using the Mann–Whitney Test because of extreme variation in percentage data from the two stands.

In 2005, we resampled three stands from this study (Town Beach, Block Island Conservancy native and exotic) using the methods described in Section 2.2. For each *Lipara* species, differences in percent of stems infested among sites were analyzed using a one-way ANOVA. Tukey's test was used for post-hoc comparisons. All data analyses were conducted using SPSS 11.0 (LEAD technologies, Inc.)

3. Results

3.1. *Lipara* distribution among and within stands

Eleven out of 15 stands had some level of *Lipara* infestation, with a mean of $11.9 \pm 1.5\%$ (mean \pm S.E.) stems infested (Table 2). Sprague Park had the highest infestation rate ($53.4 \pm 7.2\%$), and four sites had no *Lipara* (Worden Pond, Prudence Island, Sachuest Point, and Little Compton). Infestation rates of *L. similis* and *L. rufitarsis* differed significantly among sites (Table 3). Charlestown and Calf Pasture Point had only *L. rufitarsis* and Newton Avenue had only *L. similis*. The native Maine stand did not have any *Lipara*. There was no significant difference in infestation between the Town Beach native stand and exotic stands in 2003.

Often the two species occurred together in the stand, but *Lipara similis* infested significantly more interior stems ($9.7 \pm 1.3\%$) than exterior stems ($5.8 \pm 1.3\%$) (Table 3) and

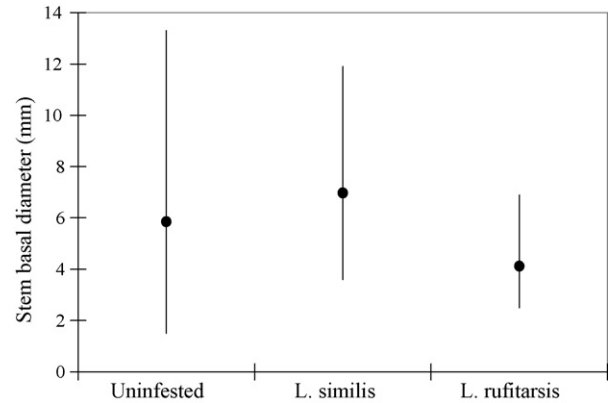


Fig. 1. Basal stem diameter (mm) of *P. australis* stems that are uninfested, infested by *L. similis*, or infested by *L. rufitarsis*. Circles show the mean of each group and bars represent the maximum and minimum values of stem diameters observed in each group. All groups were significantly different from each other (Tukey's test, $p < 0.001$).

L. rufitarsis infested significantly more exterior stems ($7.2 \pm 0.9\%$) than interior stems ($0.9 \pm 0.9\%$) (Tables 2 and 3).

3.2. *Lipara* effects on stems

Uninfested stems in the stand interior had significantly greater basal diameters than stems in the stand exterior ($t = 9.385$, d.f. = 828, $p < 0.001$). Mean stem diameter was 6.2 ± 0.3 mm for interior stems and 5.1 ± 0.2 mm for exterior stems. Stem diameter differed significantly among uninfested stems, *L. similis*-infested stems, and *L. rufitarsis*-infested stems (Table 3, Fig. 1), with all three groups significantly differing from each other (Tukey's test, $p < 0.001$). In *P. australis* populations with *L. similis*, infestation caused a significant reduction in stem length (Table 3, Fig. 2a), averaging 6.4% and 1.9% reductions in interior and exterior stem lengths, respectively. *Lipara rufitarsis* infestation also caused a

Table 3

ANOVA statistics for infestation rates, stem heights, and basal diameters for stems collected from 16 sites in 2003 and a resampling of three collection sites in 2005

	N	d.f.	F	p
Lipara abundance among stands				
<i>L. similis</i> infestation rate	150	14, 120	12.2	<0.001
<i>L. rufitarsis</i> infestation rate	150	14, 120	3.0	<0.001
Lipara distribution and effects within stands				
Stem location (interior vs. exterior)				
<i>L. similis</i>	75	1, 120	4.8	0.030
<i>L. rufitarsis</i>	75	1, 120	22.6	<0.001
Basal diameter				
Uninfested, <i>L. similis</i> infested, <i>L. rufitarsis</i> infested	865	6, 859	42.3	<0.001
<i>L. similis</i> infestation (infested vs. uninfested)				
Stem height	484	3, 480	93.9	<0.001
<i>L. rufitarsis</i> infestation (infested vs. uninfested)				
Stem height	465	3, 461	165.6	<0.001
2005 survey—Lipara abundance among stands				
<i>L. similis</i> infestation rate	90	2, 89	8.9	<0.001
<i>L. rufitarsis</i> infestation rate	90	2, 89	4.2	0.017

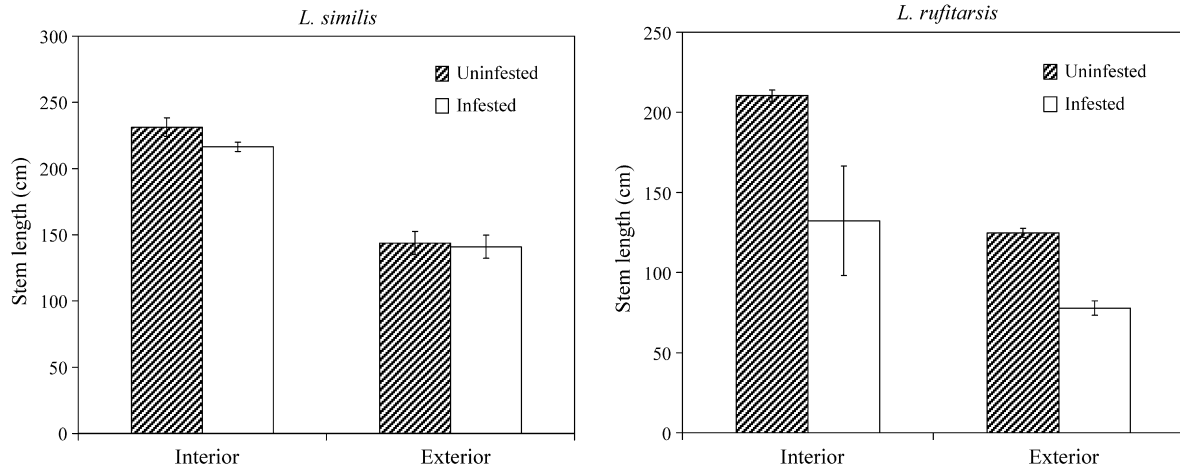


Fig. 2. Differences in length of uninfested stems and stems infested with *L. similis* (left) and *L. rufitarsis* (right) in the interior and exterior of *P. australis* stands. Standard error bars are shown.

significant reduction in stem length (Table 3, Fig. 2b), averaging 37.1% and 37.6% reductions in interior and exterior stem lengths, respectively.

In uninfested stems, flowering rates of exotic *P. australis* were significantly different from the native haplotypes ($t = 4.012$, d.f. = 1, 7, $p = 0.005$). Exotic stands averaged $72.2 \pm 4.0\%$ flowering stems and native stands averaged $38.8 \pm 15.7\%$ flowering stems. No stems infested with either *Lipara* species flowered.

3.3. *Lipara* distribution and effects in adjacent native and exotic stands

Where the native population was growing adjacent to the exotic haplotype, *L. rufitarsis* infested significantly more

native stems ($37.0 \pm 18.5\%$) than exotic stems (0%) ($p = 0.046$). However, there was no difference in the abundance of *L. similis* between these stands (mean infestation rate of $20 \pm 11.8\%$ for the exotic haplotype and $19.3 \pm 0.8\%$ for the native haplotype).

In 2005, we found significant differences in infestation rates of both *L. similis* and *L. rufitarsis* among the native and exotic populations on Block Island (Table 3). *L. similis* infestation was greater in the Block Island Conservancy native stand than the Block Island Conservancy exotic stand or Town Beach native stand (Fig. 3). Unlike 2003, *L. rufitarsis* was present in both the native and exotic stands at the Block Island Conservancy. Furthermore, *L. rufitarsis* infestation was greater in both Block Island native stands compared to the exotic stand (Fig. 3).

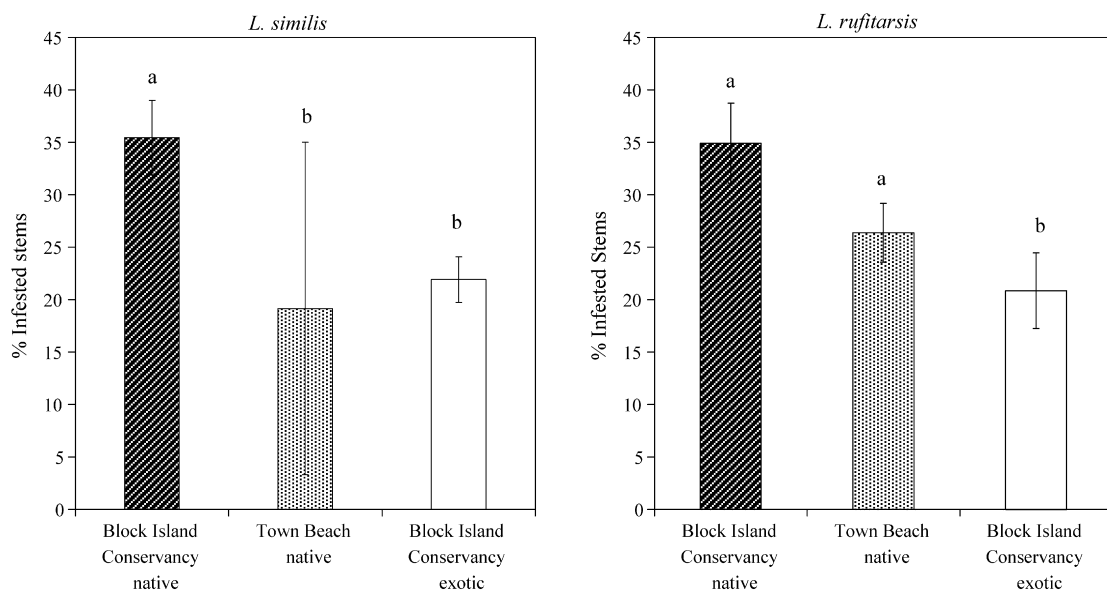


Fig. 3. Difference in *L. similis* infestations (left) and *L. rufitarsis* infestations (right) in three *P. australis* stands on Block Island, Rhode Island. The data are from August 2005 when the stands were resampled. Standard error bars are shown. Groups with different letters above them are significantly different from each other (Tukey's test).

4. Discussion

Lipara infestation varies greatly among sites. Some stands had no *Lipara*; other stands had over 50% of stems infested. *Lipara* species distributions among *P. australis* stands are highly dependent on stem diameter (Chvála et al., 1974; De Bruyn, 1993, 1994; Tschardtke, 1988, 1992). In turn, intraspecific variation in *P. australis* stem diameter is caused by varying soil moisture and nutrient supply (Gorham and Pearsall, 1956; Haslam, 1971; Van der Toorn, 1972). For example, stands growing in wet habitats are taller and thicker than stands in dry habitats (Tschardtke, 1988, 1999), and typically have lower stem densities and growth rates than stands growing in shallow water or dry areas (Vretare et al., 2001). Therefore, habitat type indirectly influences *Lipara* presence and abundance among stands (De Bruyn, 1993, 1995; Tschardtke, 1993). Habitats in our study were quite variable, including dry, freshwater, and brackish environments. This variability most likely influenced *P. australis* stem morphology, and in turn, caused site-specific differences in *L. similis* and *L. rufitarsis* populations.

In 2003, both *Lipara* species indiscriminately attacked both native and exotic *P. australis*, and in one instance had significantly greater populations in native stands (see below). We found the strongest differences in our resampling efforts in 2005, where both native stands on Block Island had significantly higher *L. similis* infestation rates than the exotic stand. We do not know what caused the inter-annual variation in *Lipara* populations between native and exotic stands, but our findings do provide evidence that *Lipara* populations can be substantially higher on native populations.

Within stands, the distribution of each species is consistent. *Lipara similis* is most abundant in the thicker stems in the stand interior, infesting stems with an average diameter of 6.9 mm. However, they are also common in exterior stems. Adult *L. similis* emerge in late June (Chvála et al., 1974), when most stems have already emerged and are rapidly growing, so flies most likely select the larger stems as suitable sites for oviposition. Conversely, *L. rufitarsis* is found almost exclusively in thinner stems (mean diameter = 4.5 mm) on the edge of stands (Table 2). This is also true for *L. rufitarsis* in European stands (De Bruyn, 1993, 1994; Tschardtke, 1993, 1999). De Bruyn (1993) reports *L. rufitarsis* infesting stems with a mean diameter of 2.9 mm. Tschardtke (1992) found that *L. rufitarsis* only survives on stems with a mean basal diameter up to 4.5 mm. As we found in this study, stem diameter influences host plant choice by *Lipara*. It may also influence *L. rufitarsis* colonization of native *P. australis* populations, which generally have shorter and thinner stems than exotic stands. We did find evidence of this with our 2005 resampling on Block Island where both native stands had significantly higher *L. rufitarsis* populations than the exotic stand.

Both *Lipara* species significantly reduced shoot length, although *L. rufitarsis* had a much greater impact on growth. Pokorný (1971) found that *L. similis* reduced stem length by 27% in European *P. australis* populations. Currently, we do not

know if the reduction in stem growth caused by flies affects the competitive potential of native or exotic genotypes.

Larval feeding damage prevents flowering in native and exotic haplotypes. Because native haplotypes have significantly lower flowering rates than the exotic haplotype (data from this study and unpublished data), further reduction in flowering caused by fly infestation may be more detrimental to the native haplotypes. Whereas clonal expansion in *P. australis* occurs primarily through rhizomes and vegetative reproduction (Chambers et al., 1999), seed dispersal may be an important means by which *P. australis* colonizes new habitats (Gervais et al., 1993). Thus, *Lipara* species may be reducing the ability of native *P. australis* to colonize relative to the exotic haplotype. Still, the relative importance of asexual versus sexual reproduction in this clonal grass is poorly understood and controlled experimental studies are needed to better determine the relative importance of sexual and asexual reproduction in recruitment and the effects of insect damage on plant reproduction.

At the Block Island conservancy, where native and exotic stands grow within 3 m of each other, *Lipara* populations differed between stands. Although the exotic stand was small, it was very robust, with tall, thick stems unsuitable for *L. rufitarsis*, but appropriate for *L. similis*. The native BI Conservancy stand morphology was typical of other native stands in the northeast (Lambert, 2005), having relatively short stems and a low stem density compared to exotic populations. Although this native stand is the same haplotype as the Town Beach site, its *Lipara* infestation rate was much higher. We partially attribute this to its thin stems and close proximity to the exotic stand. Infestation also had a negative effect on flowering of the native stand, significantly decreasing its already low flowering rate compared to the exotic haplotype. Because of our small sample size, these results need to be accepted with caution. Currently, we do not know of any other sites in New England where native and exotic haplotypes are growing together. In 2005, we found significantly greater populations of *L. similis* and *L. rufitarsis* in both native Block Island stands. We do not know if differences in fly populations between years were caused by inter-annual population variation or increasing dispersal and population growth.

P. australis growth is enhanced in saturated soils because it transports oxygen to its roots and rhizomes through pressurized ventilation (Armstrong and Armstrong, 1991). Bore holes and infestation by insects can disrupt this gas flow in *P. australis*, reducing the ability of the rhizosphere to obtain oxygen, leading to dieback, in studies from Europe (Armstrong et al., 1996). Pressurized ventilation inhibition also decreases allocation to root biomass, affecting growth rate, and rhizome length, and density (Vretare and Weisner, 2000). Native and exotic haplotypes differ in stem architecture, with the native plants having, on average, shorter, thinner stems than the exotic (Lambert, unpublished data). Further research is needed to determine what effect *Lipara* infestation has on pressurized ventilation among haplotypes.

Over the past century, the exotic *P. australis* haplotype has replaced native haplotypes in most of the eastern United States (Saltonstall, 2002). Current theory attributes this explosion of *P. australis* to the introduction of a more aggressive (competitive) haplotype (Tucker, 1990; Besitka, 1996). In addition to the aggressiveness of exotic *P. australis*, 16 non-native insect herbivores of *P. australis* have been accidentally introduced into North America, including both *Lipara* species surveyed in this study (Tewksbury et al., 2002). Although these non-native herbivores do not appear to hinder the growth or dispersal of the exotic haplotype, they may be contributing to the loss of native populations. For example, the exotic aphid, *Hyalopterus prunii* (Geoffroy), shows a clear preference for native *P. australis* haplotypes, killing new shoots and whole clones grown in pots (Lambert, 2005). *Lipara* infest other native stands in the northeastern United States, including one site in the Montezuma National Wildlife Refuge in New York where Blossey (2003) found higher *L. similis* and *L. rufitarsis* infestation rates in a native stand (type E) than in an adjacent exotic stand. The current abundance and widespread distribution of exotic *P. australis* may be facilitating the spread of *Lipara* to native stands, providing yet another way in which this exotic plant adversely impacts native populations of *P. australis*.

Acknowledgments

We thank H. Faubert, L. Tewksbury, R. Thomas, and J. Winiarski for help with fieldwork and T. Dudley, H. Ginsberg, K. Killingbeck, P. Logan, B. Maynard, and two anonymous reviewers for comments on earlier versions of this manuscript. Access to native stands on Block Island was kindly provided by The Block Island Conservancy. Funding was provided by Rhode Island Sea Grant and the RI Agricultural Experiment Station.

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