

Susceptibility of Native and Non-Native Common Reed to the Non-Native Mealy Plum Aphid (Homoptera: Aphididae) in North America

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ABSTRACT An aggressive, non-native haplotype (distinct genetic lineage within a species) of *Phragmites australis* is invading brackish and freshwater systems in the eastern United States, potentially displacing native haplotypes. We studied the differential susceptibility of native and non-native populations collected from sites throughout North America to the non-native aphid, *Hyalopterus pruni*. In a greenhouse study, we found significantly higher aphid populations on native haplotypes than on the non-native haplotype 2 mo after infestation. Aphid feeding caused chlorosis and death of native stems, and in some cases, killed whole native genets. The non-native plants remained relatively undamaged. In a field study, non-native plants had significantly lower aphid densities than native plants or remained aphid free. There was an interactive effect in which aphid populations increased on the native plants over the 1-mo study period but remained low on non-native plants over the same period. The susceptibility of native North American populations of *P. australis* to non-native aphid infestation may indirectly affect the ability of these native plants to compete with non-native plant populations, ultimately contributing to the decline of native haplotypes.

KEY WORDS genetic resistance, *Hyalopterus pruni*, invasive species, indirect interactions, *Phragmites australis*

The mechanisms determining plant invasion success are often poorly understood and confound attempts to reduce the environmental and economic impacts of biological invasions (Keane and Crawley 2002, Levine et al. 2003). Many theories have been generated to explain why some invaders are successful, including absence of population regulators (predators, parasitoids, pathogens, etc.) common in their home range (Elton 1958, Keane and Crawley 2002), anthropogenic facilitation (Bertness et al. 2002, Mack et al. 2000), allelopathy (Callaway and Aschehoug 2000, Hierro and Callaway 2003), and higher dispersal ability than natives (Seabloom et al. 2003, MacDougall and Turkington 2005). The evolution of increased competitive ability (EICA) hypothesis states that plants are often introduced into novel environments without their herbivores, and in turn, reallocate resources from defense to competition (Blossey and Notzöld 1995). Much recent work has focused on the potential for invasive plants to lose resistance traits in their non-native range in favor of enhanced resource acquisition (Blossey and Notzöld 1995, Maron and Vilà 2001, Maron et al. 2004, Müller-Schärer et al. 2004). In North America, an introduced, invasive haplotype (genetically distinct strain) of common reed (*Phragmites australis* Cav. Trin. ex Steudel) is now abundant where

native haplotypes once occurred (Saltonstall 2002) and researchers speculate that the greater competitive ability of the invasive haplotype is responsible for this displacement (Besitka 1996, Chambers et al. 1999). Can differential herbivory among native and exotic haplotypes be responsible for this? Here, we report on the varied abilities of native and non-native haplotypes of common reed to resist attack by the non-native mealy plum aphid, *Hyalopterus pruni* Geoffr.

Host plant genotype strongly influences a plants ability to resist herbivores (Denno and McClure 1983, Karban 1992) and may be instrumental in regulating long-term herbivore population dynamics (Underwood and Rausher 2000). Many studies have documented the effect of genotype on interspecific differences in plant resistance (Berenbaum et al. 1986, Agrawal et al. 1999, Mutikainen et al. 2000). However, information on the importance of differential plant resistance among native and exotic genotypes in the context of plant invasions is lacking.

In a University of Rhode Island greenhouse, where native and non-native *P. australis* are growing in a common garden, we observed *H. pruni* heavily infesting native haplotypes AB, B, E, and S, whereas only lightly infesting the non-native haplotype M (haplotype designations follow Saltonstall 2002). Our objectives were to determine if non-native and native populations have differential susceptibility to *H. pruni*, and what effect the aphids have on survival of the

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Table 1. Collection locations, haplotypes used, origin, and no. of aphids per gram for greenhouse-grown *P. australis*

| Location | Haplotype | Origin | Aphids per gram | SE | Tukey test results |
|-----------------------------------|-----------|------------|-----------------|-------|--------------------|
| Bear Lake, ID ^a | B | Native | 3,239 | 552 | ab |
| Quirvia NWR, KS ^a | B | Native | 3,533 | 1,014 | ab |
| Dieppie, New Brunswick, Canada | E | Native | 5,528 | 1,007 | a |
| Germentown, New Brunswick, Canada | E | Native | 2,957 | 630 | ab |
| Memramcook, New Brunswick, Canada | S | Native | 3,382 | 823 | ab |
| Block Island, RI ^a | AB | Native | 3,460 | 285 | ab |
| Zellwood, FL | I | Unknown | 924 | 332 | bc |
| Galilee, RI | M | Non-native | 352 | 135 | c |
| Moncton, New Brunswick, Canada | M | Non-native | 320 | 137 | c |
| Montezuma NWR, NY | M | Non-native | 311 | 181 | c |
| Moses Lake, WA | M | Non-native | 513 | 290 | c |

Rows with different letters are significantly different using Tukey's test. $N = 6$ stems analyzed for each location.

^a Haplotypes died before the start of the field experiment, and thus, were not used for that experiment.

various haplotypes. Because the non-native haplotype of *P. australis* is a natural host of *H. pruni* in Europe (Pintera 1971, Carver 1989, Tschamtkke 1992), we predicted that the non-native haplotype M would have lower aphid populations than the native haplotypes and that the aphids would have a greater negative impact on the native populations than on the invasive form.

Materials and Methods

Study Organisms. *Hyalopterus pruni* is a pest of plums and peaches worldwide (Hill 1987). This palaeartic species is most likely from Eurasia, home to its host plants in the genus *Prunus* (Smith 1935, Mosco et al. 1997). *Hyalopterus pruni* was first reported as a fruit tree pest in the United States in 1881 (Smith 1935) and now occurs throughout the United States (Krause 1996, Balme 2000, unpublished data). These aphids overwinter in the egg stage on trees and migrate to their secondary host, *P. australis*, in the late spring and summer (Smith 1935). In Rhode Island, we observed that aphids migrate to non-native *P. australis* in mid-July and persist at low levels until mid-September, when populations disappear. Pintera (1971) found that, although *H. pruni* heavily infests *P. australis* in Europe, feeding does not significantly damage stands.

Phragmites australis is a cosmopolitan grass with high phenotypic plasticity (Clevering and Lissner 1999, Paucă-Comănescu et al. 1999) and a high degree of genetic variability worldwide (reported in Clevering and Lissner 1999, Koppitz 1999). Haplotype M is widespread in Asia, Europe, and the United States (where it is invasive); it is genetically similar to other Eurasian haplotypes and is the most likely ancestral strain of all modern haplotypes (Saltonstall 2002). There are at least 16 native haplotypes throughout North America (Saltonstall 2002, Lambert and Casagrande 2006). The native haplotypes, recently designated collectively as *P. australis* subspecies *americanus* Saltonstall, P. M. Peterson and Soreng, can be distinguished from the non-native haplotype based on morphological and genetic characteristics (Saltonstall et al. 2004). Population decline and local extinctions of the native subspecies may be a result of competitive

displacement by the non-native haplotype (reviewed in Chambers et al. 1999, Saltonstall 2003a).

Greenhouse Experiment. Plants used in this study were collected by collaborators throughout North America (Table 1) from the same populations genetically evaluated for haplotype by Saltonstall (2002, 2003a). We tested additional populations that we collected in Rhode Island for native/non-native status using the restriction fragment-length polymorphism analysis methods of Saltonstall (2003b). Native Rhode Island plants were sent to K. Saltonstall for confirmation of haplotype. All plants were labeled and maintained in a common garden at the University of Rhode Island.

On 28 August 2002, we planted rhizomes of six haplotypes of *P. australis* collected from 11 locations (six pots per location, total 66 pots; Table 1). Two rhizomes with four to five nodes were planted in 3.8-liter nursery pots in a 50/50 sand/peat mix. One gram of Osmocote timed release fertilizer (14 N:14 P:14 K) was used as a top dressing, and soil was saturated daily with tap water. Pots were evenly spaced in a randomized design on greenhouse benches so that no plants came in contact with each other. Plants were grown under a 16 L: 8 D photoperiod supplemented with high intensity sodium vapor lamps (Sylvania metalarc M58 R, M/250U bulbs, Osram Sylvania, Ltd., Danvers, MA). Plants were allowed to grow for ~2 mo, during which time aphids naturally colonized plants. We maintain all *P. australis* haplotypes in the greenhouse, and they are commonly infested with aphids—this is the most likely source of aphids on the plants in this study. However, there are non-native *P. australis* stands and *Prunus* spp. trees within 2 km of the greenhouse that may also have contributed to the aphid populations. On 11 November 2002, one stem was randomly selected from each pot and cut beneath the fifth leaf from the top of each stem ($n = 6$ stems for each location). The top of the stem, with attached leaves, was selected because we determined in a preliminary study that most aphids were found on the new growth on the upper portion of the stem, regardless of haplotype. These stems with aphids were placed in plastic bags and frozen at -10°C until aphids were counted. The number of aphids on each stem was

recorded. The aphids were washed off the stem with tap water, and the stems were dried at 60°C for 5 d. Stems were weighed, and number of aphids/g was calculated. This was done to standardize measurements because the non-native stems were always larger and weighed more than the native stems.

At the end of the experiment, aphid damage and stem survival in each potted plant were recorded. Aphid damage was quantified by the color of leaves on each stem after the 8-wk experiment. Leaves for each stem were classified as either damaged (leaves with any degree of yellowing characteristic with aphid feeding) or undamaged (leaves completely green). Percentage of damaged leaves for each haplotype and percentage of dead stems (stems that were brown and dry with no green tissue) in each pot were recorded.

Number of aphids per gram was analyzed using a single factor analysis of variance (ANOVA) with population location (six stems per location) as the grouping variable. Tukey's honestly significant difference (HSD) test was used for multiple comparisons to determine differences among locations (i.e., populations).

Field Experiment. We conducted a field study to determine aphid feeding effects on native and exotic *P. australis* haplotypes using plants that have been growing in a common garden in Kingston, RI, since 2001. In June 2001, five haplotypes from 11 locations throughout North America (Table 1) were planted using a randomized design. Three rhizome fragments with four to five nodes each were planted together in a plastic pot (27 cm diameter by 44 cm high) in a 50/50 (volume) sand/peat mix. There was a total of 14 pots for each haplotype. Pots were placed in 1.5-m-diameter by 0.15-m-deep plastic pools filled with fresh water. Pools were refilled with water as needed to maintain a constant water level of 0.15 m. All plants were sprayed periodically with Safer's Insecticidal Soap during the 2001–2003 growing seasons to control aphid populations but were not sprayed in 2004 before the initiation of the experiment.

Before the beginning of the experiment, two of the native haplotypes (AB and B) had died from aphid feeding damage from the previous year and were not used. All plants used in this experiment appeared healthy (new *P. australis* shoots emerge each spring and are not infested with aphids until July) and included three haplotypes (native types E and S and non-native type M) from eight locations (Table 1). There were 7 replicate pots for type E, 9 for type S, and 20 for type M. We began recording aphid densities 29 July 2004 when aphid colonization was first observed. Stems were checked for aphids twice per week, and total number of stems, number of stems with aphids, and aphid density were recorded for each pot. Because of high aphid populations (>5,000 aphids for some native plants) and aphid movement producing inaccurate counts of individuals in preliminary trials, aphid density for each pot was recorded using the following categories: 0, no aphids; 1, 1–5% of leaf surfaces covered; 2, 6–25% of leaf surfaces covered; 3, 26–50% of leaf surfaces covered; 4, 51–75% of leaf

surfaces covered; 5, >75% of leaf surfaces covered. The final data set was collected on 30 August 2004.

Data from populations with the same haplotype were grouped for analysis. The dependent variables (number of stems and number of aphid infested stems) were analyzed using a mixed factorial (repeated-measures) ANOVA with sampling date as the within-subjects factor and haplotype as the between-subjects factor. The data did not meet the assumption of sphericity. We used the Geisser-Greenhouse correction to evaluate the critical value for the *F* statistic. Tukey's HSD test was used for multiple comparisons for the main effect of haplotype. Aphid density between haplotypes was analyzed using χ^2 tests. Family-wise error rate was corrected to $P = 0.017$ using the Bonferroni correction.

Results

Greenhouse Experiment. There was a significant difference in the number of aphids/g among plants from different locations ($F_{10,54} = 9.49, P < 0.001$). Plants from native populations had significantly higher aphid densities compared with plants from exotic populations (Tukey's test, $P = 0.037$; Table 1). The native populations had a mean of $3,683 \pm 718$ (SE) aphids/g compared with the non-native populations (mean, 374 ± 186 aphids/g). The number of aphids per gram did not significantly differ among the locations with native haplotypes (B, E, S, AB), nor did it significantly differ among locations with haplotype M or I. The Florida population (I) was significantly different from only Dieppie (E), which had the highest number of aphids (Tukey's test, $P < 0.001$; Table 1). By the end of the experiment, aphids caused yellowing and wilting of 100% of the leaves of all the native plants. Aphid damage killed >50% of the native stems, with Memramcook and Germantown plants suffering 100% mortality. No non-native stems yellowed or died as a result of aphid damage. The honeydew created by the aphids caused a black sooty fungus to develop on the leaves of the native plants. The fungus did not grow on the non-native or type I haplotypes.

Field Experiment. There was a significant interaction between haplotype and date for number of aphid-infested stems ($F_{1,9,3} = 3.28, P < 0.001$). For the native haplotypes E and S, the number of infested stems increased over the observation period, but the non-native stems (M) experienced no such increase (Fig. 1). There was no difference among haplotypes in total number of stems, but there was a significant main effect for number of aphid-infested stems ($F_{2,35} = 14.48, P < 0.001$) where the non-native haplotype had significantly fewer infested stems than the natives (Tukey's test, $P = 0.014$). Stem infestation did not differ among native haplotypes; haplotype E had 7.3 ± 1.2 infested stems, haplotype S had 9.5 ± 1.0 infested stems, and haplotype M had only 3.3 ± 0.7 infested stems.

Aphid densities differed significantly among the three haplotypes, with haplotype S experiencing the highest densities, haplotype E having intermediate

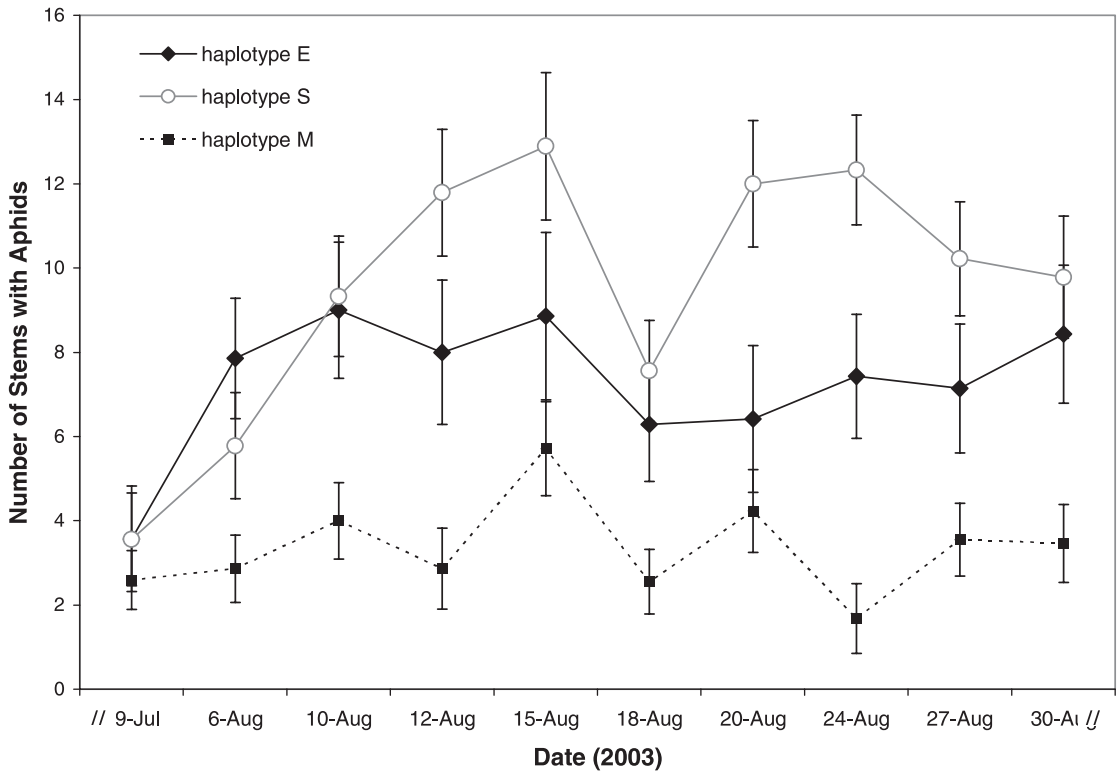


Fig. 1. Number of stems infested with aphids for native *P. australis* haplotypes E and S and non-native haplotype M grown outdoors in pots in a common garden. SE bars are shown.

densities, and haplotype M having the lowest (Table 2; Fig. 2).

Discussion

Native and non-native haplotypes of *P. australis* differed in their susceptibility and response to aphid attack, both in the greenhouse and in the field. Aphid populations grew rapidly on the native populations, causing yellowing and death of stems. In contrast, aphid populations were low on the non-native haplotype, and there was little evidence of feeding damage on these plants. It remains to be seen if differential attack from aphids has a greater negative effect on the success of native populations, and indirectly, alters competition among native and exotic haplotypes. Indirect effects occur when a shared predator has differential effects on the outcome of competition between competing species (Strauss 1991) and may be the most important determinant of species distribu-

tions and diversity (Strauss 1991, Wooten 1994). A logical next step is studying the outcome of competition among native and exotic haplotypes in the presence and absence of herbivores.

We found evidence for genetically based differences among the haplotypes in their tolerance to aphids. In the greenhouse experiment, native plants from Dieppie had the highest aphid populations, although native plants from Memramcook and German-town were most affected by aphid damage, with all stems killed. Haplotype I had an intermediate susceptibility to aphids compared with the native and exotic haplotypes. We cannot explain the basis for this result because previous genetic analysis could not definitively determine the ancestral origin of haplotype I (Saltonstall 2002). In the field, haplotype S was the most susceptible with the highest number of infested stems and highest aphid densities, and by the end of the experiment, most of these stems had yellow and withered leaves. In contrast, infestation rates on the non-native haplotype were low throughout August, with almost 50% of the pots having few or no aphids and no noticeable stem or leaf damage was observed on any non-native plants. Other studies have shown that native and non-native plant populations can display marked differences in tolerance to herbivory (Daehler and Strong 1997, Bossdorf et al. 2004). Daehler and Strong (1997) found differences in resistance to planthoppers between *Spartina alterniflora*

Table 2. χ^2 analysis of aphid density on three haplotypes of *P. australis* grown in a common garden field experiment

| Comparison | χ^2 | df | P |
|----------------------------------|----------|----|--------|
| Haplotype E \times haplotype S | 30.12 | 5 | <0.001 |
| Haplotype E \times haplotype M | 97.56 | 5 | <0.001 |
| Haplotype S \times haplotype M | 192.38 | 5 | <0.001 |

The Bonferroni correction adjusted familywise error rate.

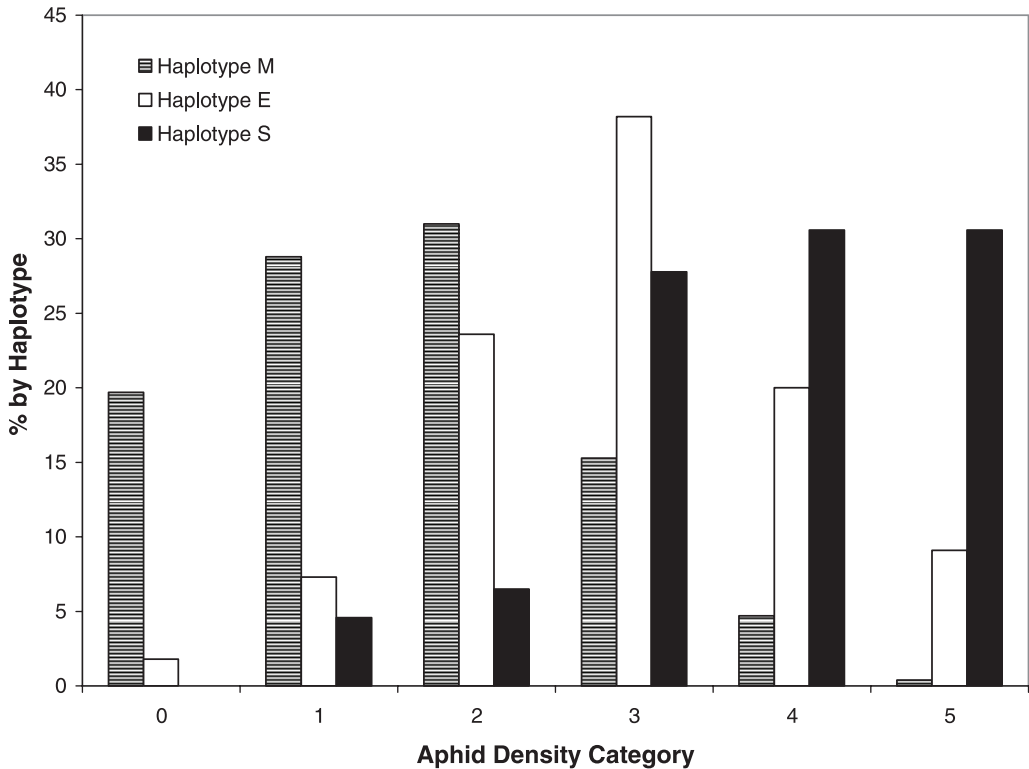


Fig. 2. Percentage of potted plants, grown outdoors in a common garden, that experienced various categories of aphid density. Haplotypes E and S are native; M is non-native. Categories were defined as follows: 0, no aphids; 1, 1–5% of plant surface covered; 2, 6–25% of plant surface covered; 3, 26–50% of plant surface covered; 4, 51–75% of plant surface covered; 5, >75% of plant surface covered.

Lois populations growing in the presence of planthoppers and in the absence of plant hoppers for a century. Herbivore-free populations experienced high mortality when reacquainted with herbivores, whereas populations with a previous history of planthopper feeding were relatively unaffected. Daehler and Strong (1997) attributed the reduced planthopper resistance to multiple factors, including a loss in herbivore tolerance in the absence of planthoppers either by drift or selection. Native North American *P. australis* haplotypes exhibit geographic structuring (Saltonstall 2002, 2003a) and are probably influenced by different selection forces, possibly contributing to differences in susceptibility that we observed. As a whole, the North American *P. australis* subspecies has been isolated from European populations for possibly as long as 40,000 yr (Hansen 1978), during which time they may have lost traits that once conferred resistance to these herbivores (Blossey and Nötzold 1995).

The native haplotypes were damaged and killed directly by aphid feeding and indirectly by the black sooty fungus that grew on the honeydew deposited by aphids. Aphid feeding can cause curling, wilting, and premature loss of leaves (Pollard 1973, Hill 1987), as well as chlorosis (Xinzhi et al. 2002). In both the greenhouse and field experiments, chlorosis of leaves was severe on the native haplotypes, and eventually,

these leaves withered and fell off the stem, leading to stem death. In previous years, several native haplotypes in our collection were lost because of aphid damage. As *H. pruni* feeds, it produces honeydew, which is colonized by a black sooty fungus (Smith 1935, Starý 1965, Blackman and Eastop 1984). This fungus can impair photosynthesis (Gullan and Cranston 1994).

We observed aphids feeding on native (E) and non-native *P. australis* stands in Maine and native (AB) and non-native Block Island stands. Native *P. australis* stands consistently had higher aphid populations than non-native stands. However, only one native population in Maine had aphid populations that reached the levels found in native plants in our greenhouse and mesocosm experiments (unpublished data). This discrepancy between aphid levels in natural populations and on plants in our study may be related to the colonization behavior of *H. pruni* (Mook and Wiegiers 1999). Tschardtke (1989) found that attack and damage by *H. pruni* was most severe on the edges of stands and in small stands. Although our experiments showed real differences among haplotypes, it is possible that our plot layout may have aggravated aphid numbers. Aphid predation and parasitism by natural enemies was minimal in the greenhouse test, but we observed aphid predators (ladybird beetle

larvae, lacewing larvae, and syrphid fly larvae) feeding on aphids on both native and non-native *P. australis* stems in the field experiment with no obvious preference for specific haplotypes. In natural areas, predators may be important in reducing aphid populations; however, native populations can experience high aphid densities in these settings (unpublished data).

Theories explaining the success of non-native plants in novel, enemy-free environments predict that selection will favor allocation of resources to growth/reproduction rather than defenses (Blossey and Nötzold 1995, Williamson 1996, Crawley 1997). In the case of *P. australis*, researchers suggest that the non-native haplotype is more aggressive and outcompetes native haplotypes (Besitka 1996, Saltonstall 2002), but the reasons for increased competitive ability are not known. Native North American *P. australis* populations apparently share a common ancestry with European populations including those of haplotype M, which arrived in North America relatively recently (Saltonstall 2002). The susceptibility of native North American haplotypes to *H. pruni* is consistent with hypotheses concerning plant invasion success (although on a much longer time scale than previous examples), except they are still (presumably) inferior competitors. However, non-native *P. australis* populations in North America seem to have resistance levels comparable with or perhaps even greater than European populations (Tewksbury et al. 2002). Similarly, Lambert et al. (2006) found that non-native gall flies (*Lipara* sp.) can have significantly higher infestation rates in native *P. australis*. At least 26 non-native herbivores have been unintentionally introduced with non-native *P. australis* (Tewksbury et al. 2002) and may be contributing to the decline of native plant populations by reducing their survival and shifting competitive interactions in the favor of the non-native plants.

The effects of *H. pruni* on natural populations of *P. australis* and the ability of natural enemies to control them still must be determined, but it seems from this study that *H. pruni* has the ability to directly kill native haplotypes and indirectly reduce their ability to compete with non-native haplotypes. Greater understanding of these multitrophic level interactions can contribute to our understanding of multispecies invasions and enhance efforts to manage non-native plants.

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