BIOLOGICAL CONTROL OF SPARTINA

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Biological control using introduced natural enemies can be an effective approach to the long term control of widespread weeds. A biological control program against *Spartina* spp. is underway in Washington State, where more than 10,000 hectares (ha) of intertidal mudflat are affected by *Spartina alterniflora* and *Spartina anglica*. Releases of the planthopper *Prokelisia marginata* have been made into Willapa Bay each year since 2000 and into Puget Sound since 2003. Prior to introducing this insect, rigorous host specificity testing and a review by the Technical Advisory Group on Biological Control of Weeds confirmed that the risk to non-target plants was minute. Populations of the biocontrol agent were initially slow to establish and grow. However, early problems with high winter mortality have been remedied through a combination of improved release site selection and the use of cold-hardy east coast biotypes. At least two populations in Willapa Bay are well established and expanding. At a localized scale, we have measured 50 percent reductions of *Spartina* biomass and 90 percent reduction in viable seed set due to *P. marginata*. The full extent of the impact will only be known with time.

While the use of biological control in California may pose a risk to the closely related native *Spartina foliosa*, it would be an excellent option in other other parts of the world where *Spartina* has invaded and where there are no closely related native *Spartina* species. In addition to *P. marginata*, other candidate biocontrol agents from the Atlantic Coast are currently being investigated.

Keywords: Biological control, *Spartina alterniflora*, *Spartina anglica*, *Prokelisia marginata*, Willapa Bay, Puget Sound

INTRODUCTION

Classical biological control of a pest or weed involves the introduction of a natural enemy (biocontrol agent) from another geographic region. The goal is to establish a permanent population of the biocontrol agent that will provide long-term control. During the last century, close to 1,000 biological control introductions for weeds were made throughout the world (Julien and Griffiths 1998). Modern weed biocontrol projects in the United States proceed only after extensive testing of the natural enemy followed by a review by the federal Technical Advisory Group on Biological Control of Weeds to ensure that it will not harm other organisms. Weed biocontrol has proven to be a safe and often very effective method of long term control of widespread invasive plants (Cruttwell-McFadyen 1998).

Biological control has both advantages and disadvantages over traditional control. Unlike most chemical and mechanical approaches, biological control is highly specific to the target weed. Since biological control agents have been chosen for their host specificity, they will not harm other plant species intermixed with the weed. Biological control is economical over large areas. Once established, the biological control agent will reproduce, spread to new sites, and continue to damage the plant with little or no additional input. Biological controls have no toxic residues or health hazards as do some herbicides. When it is successful, biological control can provide a permanent solution to a weed problem, although it usually maintains a very low level of infestation rather than bringing about full eradication.

The disadvantages of biological control include the large amount of pre-release research that is required. Moreover, even with careful selection of host-specific agents, there will always be some small risk to non-target organisms from either direct or indirect interactions. Biological control is often slow in its action, taking several years and even up to a decade for an impact to be seen. Finally, the complexities of ecological interactions mean that the effectiveness of biological control is difficult to predict ahead of time. The probability of successful control increases when multiple biocontrol agents are used (Denoth et al. 2003).

A biological control program for *Spartina alterniflora* and *Spartina anglica* in Washington State was developed during the late 1990s. The biocontrol agent *Prokelisia marginata*, a sapsucking planthopper, was introduced beginning in 2000. In this paper, we provide background information about this biological control program. Then we present results of a comparison of the performance of four populations of *P. marginata* imported from different geographic locations. Finally, we present possible future directions for the biocontrol program including the screening of additional agents from *S. alterniflora*'s native range.

BACKGROUND ON *SPARTINA* BIOCONTROL IN WASHINGTON STATE

To date only one biological control agent has been introduced into Washington for control of *Spartina* spp. The delphacid planthopper, *Prokelisia marginata*, was introduced from California into Willapa Bay beginning in 2000 and into north Puget Sound in 2003. The introductions were made only after extensive testing demonstrated its high level of host specificity (Grevstad et al. 2003) and after ruling out the possibility that it could vector a disease (Davis et al. 2002). The project was reviewed and approved by the Technical Advisory Group on Biological Control of Weeds and permitted by the Washington State Department of Agriculture and the U.S. Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS).

P. marginata is native to the Atlantic and Gulf Coasts of North America and also occurs in San Francisco Bay, California. Genetic analyses (R. Denno and D. Hawthorne, University of Maryland, pers. comm.) indicate that *P. marginata* was probably introduced to California from the East Coast in recent decades. The absence of *Prokelisia* spp. in an early 1970's survey of insects on *Spartina foliosa* in San Francisco Bay also supports a recent introduction to the West Coast (Cameron 1972). *P. marginata* was selected as a promising biocontrol agent because of its narrow host range and its known potency against *S. alterniflora* and *S. anglica* (Daehler and Strong 1997; Wu et al. 1999). *P. marginata* adults and nymphs feed by sucking the sap from the plant, draining its energy supply. *Spartina* is also damaged by the scars that arise on the leaf surface where adult females insert eggs. If high enough densities of *P. marginata* are attained, feeding and oviposition scars cause the leaves to turn brown and eventually kill the plant.

The *Spartina* biocontrol program is unique in being the first classical biocontrol program to target a grass, although others are being considered (Tewksbury et al. 2002; Witt and McConnachie 2004). It is also the first application of classical weed biocontrol in a marine intertidal environment. This project differs from most classical biocontrol projects in that the targeted weed is invasive in the same country to which it is native (although a different region). The biocontrol agents are likewise transferred between states rather than between countries.

To the advantage of a biological control program, invasive *Spartina* in Washington appears to have lost resistance to herbivory since its introduction. In greenhouse experiments (Daehler and Strong 1997; Wu et al. 1999; Garcia-Rossi et al. 2003), plants from the invasive populations in Washington suffer much greater biomass reduction and mortality from *P. marginata* than plants from native locations. Herbivore exclusion and addition experiments in the field also demonstrate this difference in response (compare Daehler and Strong 1996 with Grevstad et al. 2003). The vulnerability of the Washington populations may be due to an evolved loss of resistance in the absence of herbivores (Garcia-Rossi et al. 2003). The mechanism of *Spartina* vulnerability is unknown, but it may be related to the structural breakdown of vascular cells as a result of piercing by the planthopper during feeding and oviposition (Wu et al. 1999). The possibility that the vulnerability is due to a disease vectored by the planthopper was ruled out by Davis et al. (2002).

Over the past few years, *P. marginata* has been released at 40 locations in Willapa Bay and Puget Sound. Results have been encouraging, but not without setbacks. Following release, *P. marginata* populations typically grow explosively during their first summer and cause visible damage to the plants by fall (Grevstad et al. 2003). Local densities in some sites have exceeded 50,000 insects per m^2. A 50% reduction in local biomass was measured in an early field cage experiment (Grevstad et al. 2003). A 90% reduction in field seed viability was found in localized areas where *P. marginata* density was greater than 30 per stem (Grevstad, unpublished data). However, low survival of nymphs over the winter has prevented these populations from building to the high densities over large areas required to have large-scale impacts on the *Spartina* population. In spite of the summer boom, *P. marginata* populations are typically much smaller the following spring than they were at the time of release. Some of these populations eventually build up densities, but many have gone extinct and others are dwindling or growing only slowly.

Determining the best geographic source of P. marginata

In selecting a geographic source of a biocontrol agent, it is important to consider the ways that herbivore populations may be locally adapted. Classical biological control programs often seek an agent source population from a location that has a climate similar to the region where it will be introduced. However, in the case of the *Spartina* biocontrol program, a close match to the Willapa Bay climate does not exist. The San Francisco Bay area has a similarly moderate climate but temperatures are approximately 5ºC warmer at all times of year. East Coast locations have more extreme seasonality and no location can match both winter and summer temperatures. A northeastern location such as Rhode Island has the best match during the summer months, but a mid-Atlantic location, such as Virginia, has the best match during the winter.

In addition to climate and host plant adaptations, seasonal adaptations affecting the phenology of the biocontrol agent are also likely to vary among potential agent source populations. Many insects use photoperiod as a cue for synchronizing life history events with seasonal change in environmental conditions. When an insect is moved from one geographic location to another, its phenology may not be synchronized to the new seasonal schedule. In Willapa Bay, the California population of *P. marginata* has been observed to emerge in late February, a time that may be too early for nymph survival in the cooler and longer winters of coastal Washington. Based on a match of the timing of arrival of warm temperatures, a Rhode Island source may be the best match. However, the possibility that late emergence could reduce the number of generations produced each year makes this outcome uncertain.

Another consideration in choosing a source is potential variation in ability to compensate for plant defenses. A population from a location farther south, such as Georgia, while poorly adapted climatically, could be better adapted for overcoming plant defenses to herbivory, which are known to be greater in southern *Spartina* plants (see Pennings et al. 2005 and Katz et al. 2005 in these proceedings). A "new association" between a southern herbivore and northern plant could make biocontrol more effective.

In the spring of 2004, after obtaining permits from USDA-APHIS and the Washington State Department of Agriculture, four populations *P. marginata* were introduced into Willapa Bay. The source populations were (1) Sausalito, San Francisco Bay, California, (2) Grayville, Rhode Island, (3) Quinby, Virginia, and (4) Jekyll Island, Georgia. All populations passed through a period of quarantine in a laboratory in Davis, California before being imported into Washington for rearing in a greenhouse.

At each of five sites in Willapa Bay, we set up four 4x4-meter (m) release plots located at similar tidal elevations within the same *Spartina* meadow, but separated by at least 100 m. Each plot was randomly assigned one of the four source populations. Five thousand insects of the assigned population were released into each plot by placing heavily infested *Spartina* stems clipped from five rearing plants uniformly throughout the plot. A 100 m distance between release plots ensures that populations will remain separate long enough to compare their phenology and performance. *P. marginata* were sampled in late September using an insect vacuum converted from a leaf blower. Eight uniformly spaced sample points 21-cm in diameter (corresponding to the vacuum tube's diameter) within each release area were vacuumed. Adults and nymphs were counted separately and adults were scored for wing form;

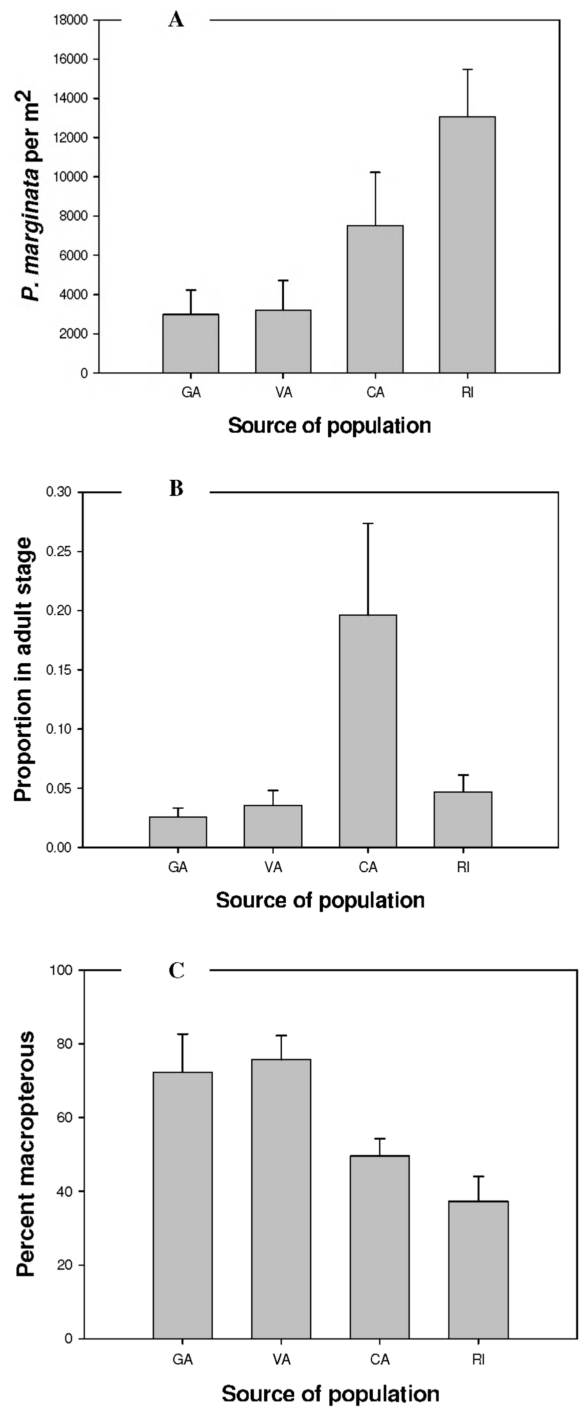

Fig. 1. (A) Densities of *Prokelisia marginata* measured at the end of September following introduction of 5,000 individuals from each of four geographic sources. (B) The proportion of each source population in the adult stage at the end of September. (C) The percentage of adults in each population that were macropterous (long-winged). Each bar represents the mean and standard error for five replicate populations from each source.

either brachypterous (rudimentary or abnormally small) or macropterous (long or large).

We found striking differences among the four populations in the densities attained by the end of summer (Fig. 1A; ANOVA F=9.227, P=0.002). The best performing geographic source, in terms of the densities of *P. marginata* obtained by end of summer, was Rhode Island, which is also the location with the best summer temperature match to Willapa Bay. In post-hoc tests, Rhode Island populations significantly differed from Georgia and Virginia, but did not significantly differ from California. California did not significantly differ from Georgia and Virginia.

The populations also differed in the proportion of the population that was in the adult stage at the end of September (Fig. 1B; ANOVA F=3.637, P=0.030). California populations had four to five times the proportion of adults found in the other populations. This may indicate differences in phenology although further data is needed.

Finally, we found differences among the four populations in the proportion of individuals that were macropterous (Fig. 4C; ANOVA F=8.71, P<0.001). Macroptery frequency in *P. marginata* is a plastic response that increases with unfavorable conditions (Denno et al. 1985). The low proportion of macropters in the Rhode Island populations could be an indication that the conditions in Willapa Bay are favorable for that ecotype. However, it could also reflect inherent genetic differences among populations.

So far, these results suggest that the Rhode Island population may be best suited to the Willapa environment, at least during the summer months. The timing of spring emergence, winter survival, and overall population growth from year to year will determine which population is most successful in the long term.

Potential future biocontrol agents

While we expect *P. marginata* to have an impact on *S. alterniflora* and *S. anglica* in at least some areas, it may not control these plants in all areas where they grow. In particular, the lowest tidal areas sustain high levels of disturbance during the winter and are unlikely to harbor dense populations of *P. marginata* because the insects will need to recolonize these sites each summer. The use of multiple biological control agent species can enhance biocontrol effectiveness by contributing to control in different habitats (Nowierski et al. 2002). It can also enhance control by imposing additive stress on the plants (Harris 1981) and by increasing the odds that at least one very effective agent will be established (Myers 1985). Denoth et al. (2003) found that the success rate of weed biocontrol programs increased from roughly 27% with one introduced agent to 50% with two agents, 70% with 3-4 agents, and it approached 100% for programs using five or more agents. Thus the addition of more agents would greatly enhance the likelihood of attaining long term biological control of *Spartina*.

Table 1. Natural enemies of *Spartina alterniflora* from the Atlantic Coast of North America. The list is a compilation from personal field surveys and the following literature: Davis and Gray (1966); Denno (1977); McCoy and Rey (1981); Montague et al. (1981); Vince et al. (1981); Stiling and Strong (1983); and Newton (1984).

Sap suckers	***Prokelisia marginata* (Homoptera: Delphacidae) **Prokelisia dolas* (Homoptera: Delphacidae) *Delphacodes penadetecta* (Homoptera: Delphacidae) **Trigonotylus uhleri* (Heteroptera: Miridae) **Haliaspis spartinae* (Homoptera: Coccidae) *Haliaspis peninsularis* (Homoptera: Coccidae) *Sanctanus aesuarium* (Homoptera: Cicadellidae) *Draeculacephala portola* (Homoptera: Cicadellidae) *Ischnodemus badius* (Heteroptera: Lygaeidae) *Rhytidolomia senilus* (Heteroptera: Pentatomidae)
Leaf chewers	*Orchelimum fulicinium (Orthoptera: Tettigoniidae)* *Orchelimum fidicinium*
Stem borers	*Chaetopsis aenea (Diptera: Otittidae)* *Chaetopsis apicalis* *Calamomyia alterniflorae (Diptera: Cecidomyiidae)* *Mordellistena spendens (Coleoptera: Mordellidae)* *Languria taedata (Coleoptera: Languriidae)* *Donacaula sordidella Zincken (Lepidoptera: Pyralidae)* *Thrypticus violaceus (Diptera: Dolichopidae)* *Chilo demotellus Walker (Lepidoptera: Pyralidae)*
Root borer	*Lissorhoptrus spp. (Coleoptera: Curculionidae)*
Seed feeders	*Oscinella carbonaria Loew (Diptera: Chloropidae)* *Contarinia sp. near sorghicola (Diptera: Cecidomyiidae)*
Leaf miner	*Hydrellia valida Loew (Diptera: Ephydridae)*
Snail	*Littoraria irrorata (Mesogastropoda: Littorinidae)*
Fungus	***Claviceps purpurea (maritime variety) (Ascomycetes)*

* Present in California

** Present in California and Washington

We completed a literature review and field surveys along the Atlantic Coast in 2001 and 2002. These investigations revealed at least 22 insect species plus a fungus and a snail with apparent specialization on *S. alterniflora* (Table 1).

Two promising species are the picture-wing flies (Ottitidae) *Chaetopsis aenea* and *Chaetopsis apicalis*. The larvae of these flies develop inside young *S. alterniflora* shoots, feeding on meristem tissue and developing leaves. The result is death of the shoot tip and no flower production in nearly 100% of the stems that are infested. Both species occur from Florida to Maine. The potency of these flies lies in the fact that a single larva can kill a shoot. By comparison, it takes approximately 200 planthoppers to kill a shoot (Daehler and Strong 1997). In our surveys, we found several sites where the rate of shoot death due to this insect was greater than 50%.

Other promising candidates include the sapsucking insects, *Trigonotylus uhleri*, *Haliaspis spartinae,* and *Prokelisia dolas*. All three of these species have the advantage that they already occur in California, where the native *Spartina foliosa* occurs. Thus, introduction of these insects to Washington does not pose a risk to *S. foliosa* if they were to disperse from Washington to California. *T. uhleri* is a mirid bug that feeds primarily on the tips of the leaves. *H. spartinae* is a scale insect that occurs in low densities on the Atlantic Coast but can be found at very high densities in San Francisco Bay. *P. dolas* is a close relative of our current biocontrol agent. *P. dolas* has been shown to be more tolerant of low host quality than *P. marginata* (Denno et al. 2000), which suggests that it could be a potent biocontrol agent. However, this species has been shown to outcompete *P. marginata* (Denno et al. 2000). This could be detrimental to the overall biocontrol program because unlike *P. marginata*, *P. dolas* is unable to exploit the majority of *Spartina* occuring in mid to lower tidal elevations.

UPDATE ON BIOCONTROL PROGRAM

Much has happened with regard to control of *Spartina* in Willapa Bay and Puget Sound since this report was originally prepared in 2004. In particular, the state and federal agencies involved in the control program increased capacity and improved the effectiveness of the herbicide control treatments and eventually sprayed all *Spartina*-infested areas in Washington including biocontrol sites in an effort to eradicate the plant. As of 2007, prior to herbicide treatment of the last remaining biocontrol site, the *P. marginata* population was increasing and spreading in the north end of Willapa Bay with measured densities of more than 10,000 per m^2, sufficient to cause browning of the plants over a two-acre area. The full impact of biological control may never be known. If *P. marginata* is capable of persisting on the sparse shoots that remain, it may help suppress any reinvasion of *Spartina* if traditional control methods are discontinued.

CONCLUSIONS

The biological control agent, *Prokelisia marginata*, has a demonstrated capacity for reducing *Spartina* biomass and seed set in Washington. In the first few years of the biocontrol program, poor overwintering survival of nymphs kept populations from growing from year to year. With the introduction of *P. marginata* ecotypes from the East Coast, we are confident that we have provided the best opportunity for *P. marginata* to be successful. *P. marginata* from Rhode Island outperformed *P. marginata* from other locations in the first summer after release. Impacts to *Spartina* in the lab (Daehler and Strong 1997) and in field cages (Grevstad et al. 2003) have been clearly demonstrated. Impacts on a much larger scale were beginning to be seen in 2007 prior to herbicide treatment of biocontol sites.

The success of a biological control program for *Spartina* could be further improved with the screening and introduction of additional biocontrol agents. Several promising candidate agents have been selected from a diverse community of insects and other organisms that use *S. alterniflora* as a host in their native range. Biological control could be a valuable tool in other parts of the world where *Spartina* has invaded, especially where complete eradication is too expensive or not feasible. Even where traditional control programs are underway, biological control can contribute to *Spartina* reduction in an integrated weed management approach, or it can serve as a backup in the case that complete eradication is not achieved. Unfortunately, San Francisco Bay is not a good target location for biological control because of the risk to the native *S. foliosa*. However, it would be an excellent option in China, New Zealand, and Australia where there are no native *Spartina* species.

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