

Habitat trade-offs in the summer and winter performance of the planthopper *Prokelisia marginata* introduced against the intertidal grass *Spartina alterniflora* in Willapa Bay, Washington

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Summary

Spartina alterniflora is invasive in estuaries of the Pacific coast of North America, as well as in Europe, Asia, Australia, and New Zealand. Willapa Bay, located along the southern coast of Washington state, has the largest infestation of invasive *S. alterniflora* and is the site of the first biocontrol program against this grass. The recently introduced biocontrol agent, *Prokelisia marginata* (Delphacidae), has exhibited explosive growth during the summer months, followed by severe declines over the winter. Correlations of quantifiable site characteristics with the growth and decline of 12 released populations reveal the habitat favouring *P. marginata*. Factors favouring population growth during the summer include high host leaf nitrogen and low spider abundance. Winter survival was greatly improved by the presence of intact dead *S. alterniflora* culms throughout the winter. Interestingly, sites favouring *P. marginata* population growth in the summer had the lowest survival over the winter. These correlations and trade-offs suggest possible future strategies for enhancing biocontrol through habitat manipulation.

Keywords: biological control, population growth, *Prokelisia marginata*, *Spartina alterniflora*, winter survival.

Introduction

In the three years since its first introduction for biological control of *Spartina alterniflora* in Willapa Bay, Washington State, the planthopper *Prokelisia marginata* (Delphacidae) has exhibited explosive population growth, demonstrated impacts on the target plant in field cages, and attained local field densities approaching those known to kill the target weed (Grevstad et al. 2003). However, in spite of these encouraging early signs, the long-term persistence and impact of the agent population has been uncertain, due largely to low overwinter survival. The intertidal environment that *Spartina* invades is particularly harsh

during the winter months, with frequent storms and a 2.3 to 3.4 m mean tidal range (Sayce 1988). After two of three initial released populations failed to survive the winter of 2001–02, and the third population only barely persisted, 12 additional release sites were selected, based on their relatively protected locations. By using a larger number of release sites, we hoped to find at least some sites where *P. marginata* populations would expand rapidly and persist year to year. Additionally, by performing periodic population surveys at these sites and quantifying habitat characteristics, we sought to identify habitat factors associated with improved *P. marginata* performance during both the summer and winter months. After one year of following these populations, we have gained important clues as to how to give this biocontrol program the best chance of succeeding.

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Invasive *Spartina*

Spartina alterniflora, commonly called smooth cordgrass or Spartina, is native and ecologically valued on the Atlantic coast of North America, but it is introduced and a serious environmental threat on the Pacific coast of North America. *S. alterniflora* and the closely related *S. anglica* and *S. townsendii* are also invasive in Europe, China, Australia, and New Zealand (Aberle 1993). This perennial grass invades estuarine intertidal mudflats, which are normally devoid of emergent vegetation, dramatically transforming them into expansive swards of tall dense vegetation. The invasion brings threats to a wide variety of birds, fish, and commercially harvested clams and oysters that rely on the mudflat habitat.

Willapa Bay, a 23,000 hectare estuary along the southern Washington coast, has the most advanced infestation of invasive *S. alterniflora*. The plant was accidentally introduced as early as the 1890s during a period when it was used as packing material for oysters shipped from the Atlantic coast (Frenkle and Kunze 1984). The plant was slow to spread until the mid 1900s when an apparent increase in seed production launched the population into a phase of rapid expansion (Sayce 1988; Feist and Simenstad 2000). Aerial photos document a 60% increase in Spartina cover throughout the bay between 1994 and 1997 (Reeves 1999). In 2002, an estimated 2400 solid hectares of *S. alterniflora* plus 2200 hectares of scattered patches were present in Willapa Bay (Wecker et al. this volume).

Novel aspects of the *Spartina* biocontrol program

Several aspects of the *Spartina* biocontrol program are unique. First, this is the first use of classical biocontrol against a grass. A lack of projects targeting grasses (Julien and Griffiths 1998) may reflect the fact that weedy grasses often have relatives of economic or ecological importance and tend to be risky targets. This is not the case for *S. alterniflora* in Willapa Bay. As a member of the tribe Chlorideae, *S. alterniflora* has few close relatives in North America and none in coastal areas north of the San Francisco Bay area. Second, the biocontrol program is the first in a marine intertidal environment. This environment has created unique challenges for the biological control program as described in this paper. Third, the use of a planthopper agent is unusual. The only other documented planthopper agent is *Stobaera concinna* (Stål), used against *Parthenium hysterophorus* (L.) and *Ambrosia artemisiifolia* (L.) in Australia (McFadyen 1985; Julien and Griffiths 1998). Finally, this project differs from most classical biocontrol projects in that the targeted weed is invasive in the same country where it is native and the biocontrol agent has likewise been transferred between states rather than between countries. The host specificity testing was nonetheless as rigorous as that used in

foreign introductions (Grevstad et al. 2003), including a full review by the Technical Advisory Group on Biological Control of Weeds. In the past, interstate introductions of biocontrol agents have been made without a formal technical review, including one that has been harmful to native plants (Louda and O'Brien 2002).

Prokelisia marginata life history

Prokelisia marginata is native to the Atlantic and Gulf coasts of North America. It also occurs in California, where it may have been introduced in recent decades. *P. marginata* is highly host specific, using only a small number of closely related *Spartina* spp. as hosts (Grevstad et al 2003). In addition to *S. alterniflora*, it can complete development on *S. anglica* and *S. foliosa* (native to California and Mexico). It may also be capable of using the European *S. maritima* and *S. townsendii*, although these species were not included in host range tests. *P. marginata* weakens the plant by ingesting sap from the phloem and also by laying eggs under the leaf surface, causing structural damage and scarring to the leaf. *P. marginata* is known to have three generations per year in its native range and in California (Denno et al. 1996, Roderick 1987) but so far has produced no more than two generations in per year in Willapa Bay. Nymphs pass through five instars before moulting into adults. Overwintering occurs in the nymphal stages. The majority of nymphs pass the winter inside leaf curls of senesced plants (thatch). Some can also be found on short green shoots, which are sparse in winter.

Materials and Methods

Releases of approximately 9000 mixed stage *P. marginata* were made at 12 sites throughout Willapa Bay in late May and early June of 2002. The sites were specifically selected for their perceived winter habitat quality. We selected sites in which at least some of the senesced *S. alterniflora* culms remained intact over the winter. Such sites tended to be in the upper tidal zones, in small backwater sloughs, or otherwise protected from winter storms and wave action. In unprotected and lower tidal zone sites, the *Spartina* culms typically break off and drift away or become waterlogged and decompose.

Insects used for releases were reared on *S. alterniflora* in a greenhouse during the winter and spring of 2002. The parent stock was collected from Willapa field populations in late fall. In mid-to-late May, the planthoppers were released into field sites by nestling infested rearing plants into a designated 5 × 5 m area of a much larger sward. Most of the planthoppers moved onto nearby field plants within a few days.

The planthopper populations were surveyed at three times: (1) in early July, before any new eggs had hatched; (2) in late September, after one full generation; and (3) in April of the following spring. A gas-powered

insect vacuum converted from a hand-held leaf blower (see Grevstad et al. 2003) was used to sample *P. marginata*. At each release site, insects were vacuumed from the vegetation at 12 sample points in July and September, and at 24 sampling points in the following spring (April). At each sample point an area the size of the intake tube (0.0346 m^2) was thoroughly vacuumed. Sample points were evenly spaced in a grid arrangement within 5 m radius of the release centre. The vacuum bags were brought back to the laboratory, where the numbers of *P. marginata* nymphs and adults from each sample were counted.

During the September and April surveys, the number of spiders in each sample was also noted. To assess the possible influence of variation in plant nitrogen on the *P. marginata* populations, 20 randomly selected leaves (2nd from top) were collected from each site in mid-September. The leaves were dried in a drying oven, ground to a fine powder, and analyzed for nitrogen content. In April, we quantified characteristics of the wintering habitat inside eight 0.25 m^2 quadrats spaced 2 m apart along two transects bisecting the releases area. In each quadrat, we counted the number of new green shoots, measured the height of the tallest shoot, and assessed the percentage of dead culms from the previous year's growth that were still intact and in good condition.

Results

Summer increase

At most sites, population densities increased substantially between the first and the second census (Fig. 1). The average population increase was by a factor of 2.84 ± 0.90 . Change in density ranged from a 50% decline to a nearly 12-fold increase. The change in density is an underestimate of the actual reproduction rate because many insects disperse from the initial release area. (In an earlier study, roughly two thirds of the population was found to disperse beyond the immediate release area by the end of the first summer (Grevstad et al. 2003).) The average population density at the end of the summer was 4270 ± 1570 planthoppers per m^2 with a range of 947 to just over 20,000 per m^2 . The one site that attained 20,000 per m^2 had nearly four times the density of the next most populous site.

Winter decline

Survival over the winter was low, but better than in previous years. The average fraction surviving from October 2002 to April 2003 was 0.043 ± 0.019 . At five sites, no *P. marginata* were recovered in April. The highest level of survival at a site was 0.18. At all but one site, the density of *P. marginata* recovered in the spring was lower than densities measured soon after release in the previous summer. Because some insects dispersed,

the decline in density does not necessarily mean a decline in population size.

A striking pattern to arise from these results is that sites where *P. marginata* performed well during the summer had lowest survival during the winter (Fig. 2). Five of the six populations attaining greater than median density appear to have gone extinct, with the extant population surviving at a rate of only 0.43%. In contrast, all of the six populations that attained lower than median fall densities persisted through the winter and the average survival rate was 8.4%.

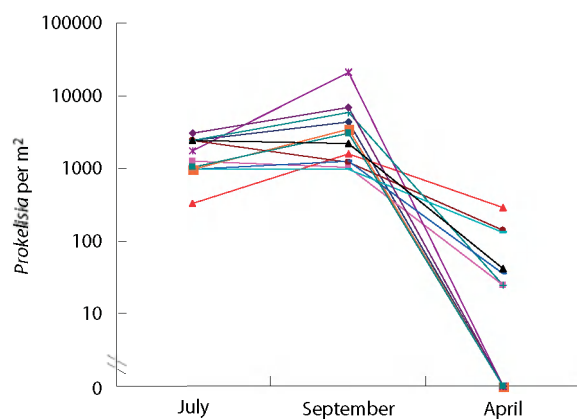


Figure 1. Densities of *Prokelisia marginata* at 12 release sites in July, September, and April after approximately 9000 individuals were released at each site in early June.

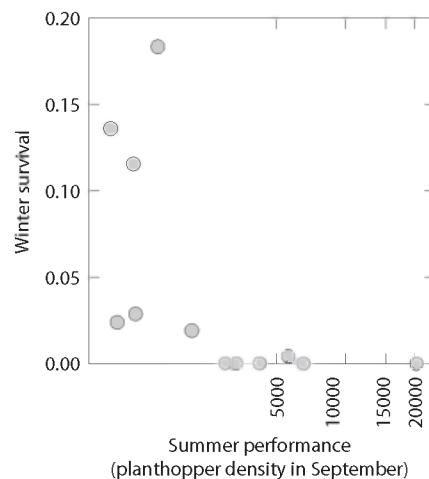


Figure 2. Relationship between winter and summer performance of *Prokelisia marginata* at 12 release sites in Willapa Bay. Winter survival was measured as the ratio of spring to fall *P. marginata* densities. Summer performance was measured as the planthopper density attained by September after release of 9000 individuals at each site in early June.

Site influences

We found clear correlations between *P. marginata* performance and measurable site characteristics. During the summer months, *P. marginata* performance, measured as the density attained by the end of the summer, was positively correlated with leaf nitrogen content ($F = 16.5$, $P = 0.002$, Fig. 3a). Leaf nitrogen content at release sites ranged from a low of 1.09% to a high 2.09%. Summer performance was also strongly negatively correlated with spider density ($F = 11.8$, $P = 0.006$). Spider densities among sites varied by two orders of magnitude with a range of 22 to 2218 per m² in September and a range of 2.4 to 176 per m² in April. The outbreak site mentioned above was the site with the highest leaf nitrogen content. It also had the second lowest spider density.

During the winter, increased survival was strongly associated with the presence of intact thatch over the winter ($R^2 = 0.62$; $P = 0.002$; Fig. 4a). The level of thatch in the quadrats varied among sites from 0 to 90%, even though all sites had moderate to high levels of thatch in the previous spring when the sites were chosen. Thus, there is variation from year to year in the condition of thatch at particular locations. There appears to be a threshold level of *Spartina* thatch needed to support *P. marginata* through the winter. Survival was reasonably high at levels of 70% intact thatch or above, but was low or zero at lower levels.

Interestingly, during the winter, the relationship with spider density was reversed from that in the summer ($R^2 = 0.45$; $P = 0.017$; Fig. 4b). *P. marginata* survived better at sites where spider densities were high. The likely explanation is that the same conditions that promote *P. marginata* survival also promote spider survival. Predation by spiders does not appear to be a significant mortality factor during the winter. The two other habitat characteristics measured during the spring survey, shoot density and culm height, were not significantly correlated with *P. marginata* survival (Fig. 4c,d).

When only the net result of combined summer population growth and winter declines is considered, i.e. the density of *P. marginata* emerging in the spring, the level of intact thatch was the only factor that significantly influenced *P. marginata* performance ($R^2 = 0.62$, $P = 0.003$).

Discussion

Following analyses of the performance of *Prokelisia marginata* at 12 new release sites, the initial challenges imposed by the harsh Willapa Bay environment now appear surmountable. The careful selection of sites that were better protected from wind and wave action, as well as the use of a larger number of varied release locations, provided improved overall performance compared to the first years releases at only three sites. We now also have three easily quantified habitat factors—high leaf nitrogen, low spider density, and the presence of intact thatch over the winter—that can be used to select future release sites for even greater improvement in *P. marginata* performance.

Our results suggest that *P. marginata* should ideally be released into sites that have high nitrogen and low spiders in summer *and* have thatch that remains intact over the winter. But such sites may be hard to come by, as none of our 12 sites had that combination. Instead nitrogen was negatively correlated with thatch condition and spiders were positively correlated with thatch condition. High nitrogen plants and low spider abundance are often found in lower tidal areas and channel banks, where there is greater water flow and better access to nutrients, but where the currents and wave action are likely to break off dead culms during the fall and winter. Also, the taller growth of high nitrogen plants makes them more susceptible to breakage during the fall and winter. As a result of these correlations, populations that had explosive growth during the summer, reaching sampled densities of 20,000 per m², went extinct or nearly so during the winter. In the end, the presence of intact thatch was the only single factor

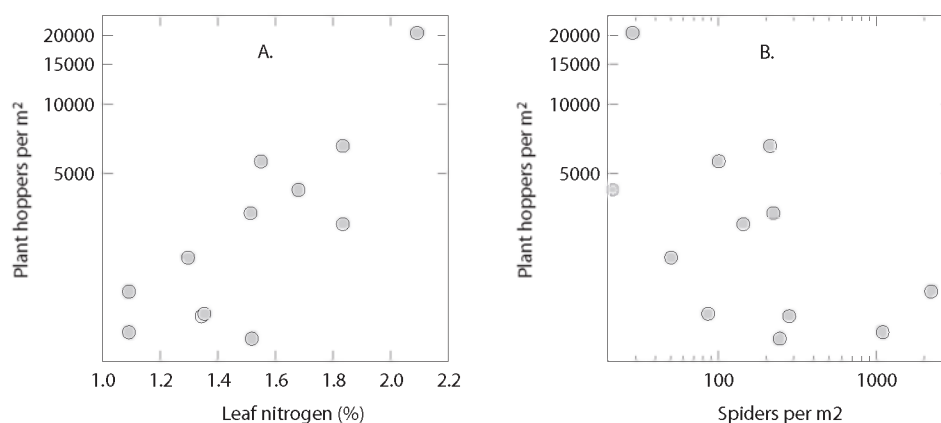


Figure 3. Relationship between *Prokelisia marginata* performance and (A) percent nitrogen content of *S. alterniflora* leaves and (B) spider density.

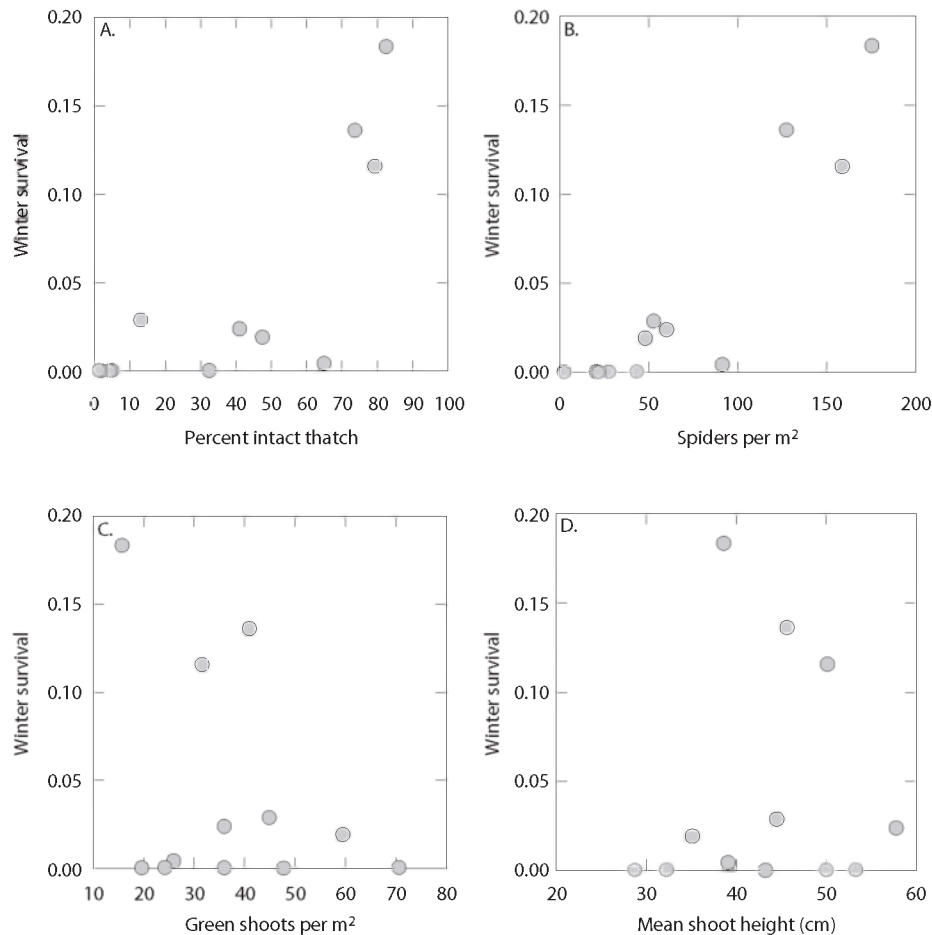


Figure 4. *Prokelisia marginata* winter survival as a function of (A) percentage of *Spartina* thatch remaining intact, (B) spring spider densities, (C) density of green shoots, and (D) mean tallest shoot height.

that adequately predicted *P. marginata* performance over the full year period.

Newly released populations of *P. marginata* in Willapa Bay seem to be foiled by the spatial separation of superior winter and summer habitat. However, *P. marginata* in its native range has a life history strategy adapted to it. In New Jersey saltmarshes, *P. marginata* reproduces in tall, nitrogen rich plants along channel edges during the summer and then disperses in fall to nearby high marsh *Spartina* that is more favourable for winter survival (Denno and Grissell 1979). This dispersal also allows *P. marginata* to elude predation by spiders (Denno and Peterson 2000). Such seasonal migration between upper and lower tidal zones has not been observed in Willapa Bay. Instead any dispersal that occurs is not directed toward upper tide zones, and the majority of the planthoppers remain within a few metres of the release area at the onset of winter (Grevstad et al. 2003).

An important difference between east coast and invasive west coast *Spartina* marshes is that, on the east coast, there are two forms of *S. alterniflora*; a tall form that grows in lower tide zones and near channel edges, and a short stiff form, 10–15 cm tall, that grows in

expansive swards in the high marsh. In Willapa Bay, only the tall form of *S. alterniflora* is found and, in all but the most protected areas, it breaks off during winter. Given that there are very large expanses of *Spartina* in Willapa Bay in areas where *P. marginata* cannot survive the winter and only scattered small areas where it can, it is reasonable to question the potential of *P. marginata* to have widespread impact on the target plant over its full distribution. Perhaps a more likely outcome is that the planthopper will have impacts in some areas but not others.

The results suggest opportunities for habitat manipulation and conservation biocontrol practices to enhance the effectiveness of the biocontrol program. One possibility is to improve *P. marginata* population growth or even create outbreaks through fertilization of *Spartina* plants in the vicinity of releases. This could be done in sites that had good winter habitat and relatively low spider densities. Fertilization experiments with *P. marginata* have been tried on the east coast with mixed results. Bowdish and Stiling (1998) and Denno et al. (1996) found that fertilizing increased *P. marginata* densities by factors of roughly two and four respectively, while Silvanima and Strong (1991) found initial

increases in abundance that did not persist, and Vince et al. (1981) found no effect of fertilization. Vince et al. (1981) noted higher numbers of spiders in fertilized plots that may have suppressed the planthoppers. Another approach to enhancing biocontrol is to move large numbers of planthoppers from the high reproduction sites when they are abundant in the fall and move them to protected locations to spend the winter. Experiments are needed to determine what kind of sheltering will provide the best winter survival with the least effort. The possibility for doing this on a large scale is not prohibitive. The state and federal agencies currently involved in the *Spartina* control work have large machines capable mowing and transporting *Spartina* stems in large quantities.

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