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Controlling Invasive Cordgrass: A Tale of Two Estuaries

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ABSTRACT: Open intertidal mud is a hallmark of Pacific estuaries. Shore birds, marine life, and the traditional fishing and oystering in these habitats depend upon openness. Alien cordgrasses of the genus *Spartina* threaten these estuaries. Growing further down the intertidal gradient than any other land plant, *Spartina alterniflora* (Smooth Cordgrass, introduced from the Atlantic coast) and *Spartina anglica* (English Cordgrass, introduced from the United Kingdom) form swards of dense stems and thick root-mats that exclude both wildlife and traditional human activities.

San Francisco Bay has been invaded by Smooth Cordgrass brought from Maryland in the mid 1970s. This alien species competes and hybridizes with the closely-related native California cordgrass, *S. foliosa*. The native species produces mostly hybrid seed where it grows with the alien. Without control, the alien could cause the extinction of California cordgrass. Owing to concern for the native cordgrass, biological control is not an option for San Francisco Bay. Alien and hybrid cordgrass are vulnerable to the herbicide Rodeo, which is licensed for use in aquatic systems.

Willapa Bay and Puget Sound, Washington have been invaded by Smooth Cordgrass and English Cordgrass, respectively. Research has shown that both of these populations are unusually susceptible to a highly-specialized insect that feeds upon cordgrass in its native range; this insect does not occur in Washington, and no native cordgrasses occur there either. This circumstance suggests that biological control of the alien populations of cordgrass in the estuaries of Washington State is a sensible control option.

CORDGRASSES IN AMERICAN PACIFIC ESTUARIES

Open mud without vegetation is a hallmark of middle and lower intertidal zones in Pacific estuaries. The high intertidal region is occupied by low-growing species, with *Distichlis spicata* and *Salicornia virginica* often holding the lion's share of space; the remainder is shared by various combinations of such species as *Triglochin maritima, Jaumea carnosa,* and *Deschampsia caespitosa*. From 20 to 30 additional species complete the list of Pacific salt marsh plants (Chapman 1977). California Cordgrass, *Spartina foliosa,* frequently forms a modest lower boundary to the marsh vegetation, southward from Sonoma County, north of San Francisco Bay, through Baja California. No native cordgrasses are found north of Sonoma County on the Pacific coast. California Cordgrass is not an aggressive species, rarely invading stands of other plant species. It is a relatively short cordgrass; most plants are less than 0.75 m tall. With a culm density that is low for cordgrasses, *S. foliosa* does not cause appreciable accretion of sediment.

Smooth Cordgrass, *Spartina alterniflora,* native to Atlantic and Gulf coast marshes, occupies much lower intertidal habitats and is distinctly more aggressive than California Cordgrass. Smooth Cordgrass regularly invades patches of other saltmarsh species, grows to more than a meter tall, and forms dense monospecific swards (Adam 1990). English Cordgrass, *Spartina anglica*, is as aggressive as Smooth Cordgrass (Gray *et al.* 1991). Both species have spread widely in some of the Pacific estuaries to which they have been introduced. Both present substantial threats to Pacific saltmarsh species, including plants, fishes, marine invertebrates, and even marine mammals. A particularly conspicuous menace is to shorebirds, which forage upon open mud. Pacific estuaries have been greatly reduced by human activities over the past century (Macdonald 1977), and invasive Smooth and English cordgrasses threaten to accelerate this loss of habitat. Alien cordgrasses also threaten traditional human uses of Pacific estuaries, hindering access to the shore, interfering with mariculture and navigation, and blocking flood control channels (Daehler and Strong 1996).

Mindful of the uniqueness of the open mud vulnerable to invasion by *S. alterniflora* in Pacific estuaries, Adam (1990) remarked in his global overview of salt marshes that "...should [Smooth Cordgrass be introduced] it may cause profound change to western marshes." Little did he appreciate the degree to which his prediction has been realized. Smooth Cordgrass was introduced to Willapa Bay at least 60 years ago (Scheffer 1945; Sayce 1988) and has spread widely, reducing habitat for migratory birds, promoting siltation of mud and sand flats, and overgrowing oyster culture beds (Boyle 1991). English Cordgrass was introduced into Puget Sound in 1961 and has also spread widely, causing similar impacts to the environment (Parker and Aberle 1979). In the past few years the State of Washington has mounted a large-scale, expensive effort to control these cordgrasses with a combination of cutting and glyphosate herbicide treatments (J. Civille, pers. comm.).

Smooth Cordgrass was introduced to San Francisco Bay about twenty years ago (Daehler and Strong 1995) and has spread widely. It now competes (Callaway and Josselyn 1992) and hybridizes (Ayres *et al.* 1999) with California Cordgrass throughout the south portion of the Bay. San Francisco Bay supports the largest remaining stand of California Cordgrass in the United States. The habitat of the alien Smooth Cordgrass completely overlaps that of California Cordgrass, and the spread of the aggressive alien threatens the very existence of this important native species.

POSSIBILITIES FOR CONTROL

The complementary touchstones of safety in biological control are (a) choice of enemy species with very narrow diets and (b) target species with no close relatives. These reduce the chance of collateral damage to species other than the intended target. Therefore, classical biological control is not an option in San Francisco Bay because any introduced organism that would harm alien cordgrass would probably also harm the closely related native California Cordgrass. Thus, only chemical and physical controls are options in San Francisco Bay. Cutting the plant and applying the herbicide Rodeo™ have shown promise in preliminary trials in San Francisco Bay (Chamberlain 1995).

One complicating factor is the hybridization that occurs between the introduced Smooth Cordgrass and the native California Cordgrass in San Francisco Bay. The hybrids are not morphologically distinct from either parent, and RAPDs (randomly amplified polymorphic DNA) are used for determining hybrid status (Daehler and Strong 1997a). Current work (Ayres *et al.* 1999) shows that hybrids are widespread throughout the south end of the Bay, and that the hybrid swarm consists of backcrossed as well as F_1 individuals. These hybrids are fertile and are reproducing by seed. Morphologically, hybrids appear to be as fit as either parent, and they will probably become more common as seed disperses ever more widely in the Bay. Eradication efforts must be well informed about the distribution of these hybrids.

In contrast to the situation in San Francisco Bay, the alien cordgrasses in Washington State are prime candidates for biological control. No close relatives of cordgrass live in estuaries or near the coast north of the San Francisco Bay region, so Willapa Bay and Puget Sound are safe places to introduce highly specialized insect herbivores of cordgrass. These insects are restricted to areas where cordgrasses are native (Strong *et al.* 1984: Daehler and Strong 1997b) so the populations of alien cordgrasses in Willapa Bay and Puget Sound have not been exposed to these insects during their stay in the Pacific. Our experiments have concentrated upon the planthopper *Prokelisia marginata*, which is native to California where it feeds upon California Cordgrass, and to Atlantic and Gulf coast marshes where it feeds upon Smooth Cordgrass.

Smooth Cordgrass from Willapa Bay is quite vulnerable to the planthopper *Prokelisia marginata* (Daehler and Strong 1995). We discovered this in the greenhouse at the Bodega Marine Laboratory in Bodega Bay, California, where many Willapa Bay clones fed upon by *P. marginata* were severely harmed, and some were killed. High densities of the planthopper led to the deaths of about 1/3 of the Willapa Bay plants after the second summer of feeding by the planthopper. The control plants with very-low (but not zero) densities of the hopper grew normally and suffered very low mortality. This suggests that *Prokelisia marginata* could harm Smooth Cordgrass in Willapa Bay, were it introduced. Similarly, we have recently found in the greenhouse that both *Prokelisia marginata* and *Prokelisia dolus*, a sibling species to *P. marginata* that feeds upon Smooth Cordgrass on the Atlantic and Gulf coasts and upon California Cordgrass in Southern California (Denno *et al.* 1996), feeds upon and kills *Spartina anglica* clones from Puget Sound (Wu *et al.* 1999).

LOST RESISTANCE

The low resistance of the exiled cordgrass populations to feeding by *Prokelisia* species is unusual. In contrast, Smooth Cordgrass from both native areas and San Francisco Bay, and California Cordgrass are quite resistant to feeding by these insects (Daehler and Strong 1997b). These plants suffered little even at high densities of the planthopper.

While Smooth Cordgrass in San Francisco Bay was never exiled from specialist *Spartina*-feeding herbivores, the Washington populations of cordgrass have grown through a number of generations in the absence of specialist insect herbivores. Smooth Cordgrass has been in Willapa Bay for at least 60 years (Scheffer 1945; Sayce 1988). This species can set seed within three years, so this amounts to perhaps twenty or more generations of isolation from these insects in Willapa Bay. English Cordgrass has never been subjected to herbivory by *Prokelisia* spp. This plant species arose in England during the 19th century from a cross between European *Spartina maritima* and *S. alterniflora* from North America that was probably introduced with cast-off ships' ballast (Ferris *et al.*1997). This produced the sterile *Spartina* x *townsendii*, which subsequently gave rise to the fertile amphiploid *Spartina anglica*.

Why are these exiled cordgrass populations less resistant to *Prokelisia* than populations that have not been isolated from specialist herbivores? Three general ideas suggest themselves. Genes for herbivore resistance could have been absent by chance from the founding population resulting in a lack of resistance in contemporary populations. Second, the founding population could have gone through a deleterious genetic bottleneck in which inbreeding led to a loss of vigor resulting in erosion of herbivore defense and reduced competitive ability (Barrett 1982). However, sexual reproduction and rapid population growth can sometimes staunch such a loss of genetic diversity (Slatkin 1996), so it is not surprising that weed populations established by a few founders can be genetically diverse (Colosi and Schaal 1992).

The final hypothesis is based upon the premise that resistance or tolerance to herbivores represents a significant metabolic and developmental cost to a plant. The plant maintains resistance at a cost of slower growth or otherwise diminished capacities reducing its competitive ability, a major component of fitness in weeds (McEvoy 1993). Thus, resistance should be selected against in plant populations that have been exiled from their specialist herbivores where resistance has no value. For example, Blossey and Kamil (1996) have found such a correlation in purple loosestrife; lower resistance is coupled with greater competitive ability in weedy North America and Australian populations relative to native European populations of this plant. In a test of his trade-off hypothesis, Dino Garcia-Rossi (1998) of our laboratory performed a greenhouse experiment in which Smooth Cordgrass clones from Willapa Bay were placed in competition with clones from San Francisco Bay, in the presence of very low or very high densities of the planthopper. Confirming the susceptibility-resistance patterns found earlier (Daehler and Strong 1997b), the San Francisco Bay clones thrived while the clones from Willapa Bay were all killed in the treatment combinations that included high densities of the planthopper. However, the trade-off hypothesis was not confirmed as there was no difference in competitive ability between the two populations.

A practical question remaining is, will the planthoppers harm alien cordgrasses in the field? Questions for basic science are, what is (are) the mechanism(s) that cause these phloem-feeding insects to harm vulnerable cordgrass populations, and why are some populations vulnerable?

LITERATURE CITED

Adam, P. (1990) Saltmarsh Ecology. Cambridge University Press, New York.

Ayres, D. R., D. Garcia-Rossi, H. G. Davis, and D. R. Strong (1999) Extent and degree of hybridization between exotic (*Spartina alterniflora*) and native (*S. foliosa*) cordgrass (Poaceae) in California, USA determined by random amplified polymorphic DNA (RAPDs). *Molecular Ecology* 8: 1179-1186.

Barrett, S. C. B. (1982) Genetic variation in weeds. Pages 78-112 in: Charudattan, R. and H. L. Walker (eds.), Biological Control of Weeds with Plant Pathogens, John Wiley & Sons, New York.

Blossey, B. and J. Kamil (1996) Is the superior competitive ability of invasive plants a result of changes in biomass allocation patterns? *Bulletin of the Ecological Society of America* 77: 41.

Boyle, B. J. (1991) Policy considerations. Pages 7-8 in: Mumford, T.F., Jr., P. Peyton, J.R. Sayce and S. Harbell (eds.), Spartina Workshop Record (November 14-15, 1990, Seattle, Washington), Washington Sea Grant Program, University of Washington, Seattle, Washington.

Callaway, J. C. and M. N. Josselyn (1992) The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in South San Francisco Bay. *Estuaries* 15: 218-226.

Chamberlain, S. (1995) Comparison of methods to control *Spartina alterniflora* in San Francisco Bay. M. A. thesis, San Francisco State University, San Francisco.

Chapman, V. J. (ed.) (1977) Wet Coastal Ecosystems. Elsevier Scientific Publishing Co., New York.

Colosi, J. C. and B. A. Schaal (1992) Genetic variation in wild proso millet. *Proceedings of the North Central Weed Science Society* 47: 21-22.

Daehler, C. C. and D. R. Strong (1995) Impact of high herbivore densities on introduced smooth cordgrass, *Spartina alterniflora*, invading San Francisco Bay, California. *Estuaries* 18: 409-417.

Daehler, C. C. and D. R. Strong (1996) Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. *Biological Conservation* 78: 51-58.

Daehler, C. C. and D. R. Strong (1997a) Hybridization between introduced smooth cordgrass (*Spartina alterniflora*; Poaceae) and native California cordgrass (*S. foliosa*) in San Francisco Bay, California, USA. *American Journal of Botany* 84(5): 607-611.

Daehler, C. C. and D. R. Strong (1997b) Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivore-free growth. *Oecologia* 110: 99-108.

Denno, R. F., G. K. Roderick, M. A. Peterson, A. F. Huberty, H. G. Dobel, M. D. Eubanks, J. E. Losey and G. A. Langellotto (1996) Habitat persistance underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecological Monographs* 66: 389-408.

Ferris, C., R. A. King and A. J. Grey (1997) Molecular evidence for the maternal parentage in the hybrid origin of *Spartina anglica* C. E. Hubbard. *Molecular Ecology* 6: 185-187.

Garcia-Rossi, D. (1998) Consequences of the loss of herbivore resistance for invasive cordgrass *Spartina alterniflora*. M. S. thesis, Sonoma State University, California.

Gray, A. J., D. F. Marshall and A. F. Raybould (1991) A century of evolution in *Spartina anglica*. *Advances in Ecological Research* 21: 1-62.

Macdonald, K. B. (1977) Coastal salt marsh. Pages 264-294 in: Barbour, M. G. and J. Major (eds.), Terrestrial Vegetation in California, John Wiley & Sons, New York.

McEvoy, P. B. R., Cox, C. S. and M. Huso (1993) Disturbance competition and herbivory effects on Ragwort *Senecio-Jacobaea* populations. *Ecological Monographs* 63(1): 55-75.

Parker, R. C. and B. Aberle (1979) A Situation Report on the Spartina Infestation in Northwest Washington. Washington State Department of Game, Olympia, Washington.

Sayce, K. (1988) Introduced Cordgrass, *Spartina alterniflora* Loisel. in Saltmarshes and Tidelands of Willapa Bay, Washington. U. S. Fish and Wildlife Service, Ilwaco, Washington.

Sheffer, T. H. (1945) The introduction of *Spartina alterniflora* to Washington with oyster culture. *Leaflets of Western Botany* 4(6): 163-164.

Slatkin, M. (1996) In defense of founder-flush theories of speciation. *American Naturalist* 147: 493-505.

Strong, D. R., J. H. Lawton and T. R. E. Southwood (1984) Insects on Plants: Community Patterns and Mechanisms. Harvard University Press, Cambridge, Massachusetts.

Wu, M.-Y., S. Hacker, D. Ayres, and D.R. Strong (1999) Potential of *Prokelisia* spp. as biological control agents of English cordgrass, *Spartina anglica*. *Biological Control* 16:267-273.