



Invasive hybrid cordgrass (*Spartina alterniflora* x *S. foliosa*) recruitment dynamics in open mudflats of San Francisco Bay



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Abstract

Hybrid *Spartina* currently spread at a rate exceeding exponential growth in the San Francisco Bay (SFB).

We predict:

- A subset of transgressive hybrid *Spartina* plants (competitively and reproductively superior to both parents and other hybrids) likely drive the invasion.
- In order to colonize the vast open SFB mudflats and found new populations hybrid cordgrass plants have to
 - evolve self-compatibility and
 - exhibit fast vegetative and rapid lateral growth.
- New seedlings have to be robust and fast growing to survive and establish, since the mudflat tidal cycle covers or exposes plants for up to six hours.

We investigated mudflat seedling recruitment dynamics:

- A small number of hybrid and native *Spartina* have colonized the open mudflats along the eastern shore of SFB.
 - We identified the numbers and locations of recruiting seedlings at three SFB sites in 2003 and 2004 via GPS/GIS.
 - We determined the relationship of all established adult plants and parentage of seedlings using microsatellite markers¹ and FAMOZ software².

Our results show:

- All sampled seedlings as hybrids
 - A dramatic increase in seedling recruitment in 2004
 - Distinct family groups with inter-related adult clones as sires for most seedlings
 - Isolated plants on the outer edge of the mudflat produced more self-fertilized seedlings than more aggregated plants.
- These results support transgressive hybrid plants as the likely drivers of the invasion.

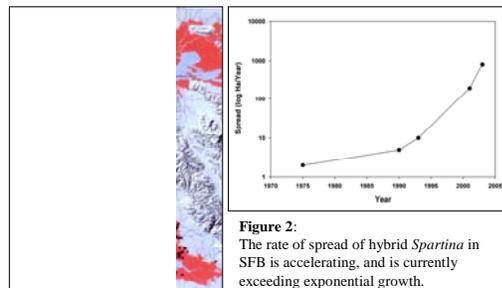


Figure 1: Open mudflats of SFB and potential spread of *Spartina* hybrids (red areas).

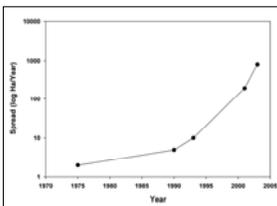


Figure 2: The rate of spread of hybrid *Spartina* in SFB is accelerating, and is currently exceeding exponential growth.

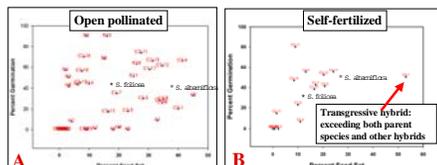


Figure 3: A & B) Percent seed set vs. % germination of hybrid seedlings from four locations (C = Cogswell Marsh; R = Robert's Landing¹; H = Hayward¹; A = Alameda¹; 'open mudflat sites'). *Average percent values of parent species^{3,4}. C) Average greenhouse seedling survivorship (log₁₀) of 2001 progeny of 16 hybrid mothers at Cogswell Marsh.

Prediction:

Hybrid individuals with the highest reproductive fitness will drive the invasion of open mudflats in SFB

MOST IMPORTANT FITNESS TRAITS ARE:

- Self-compatibility
- High reproductive output (seed set/germination rate)
- Seedling vigor
- Fast growth rate (Lateral & vertical)

These traits cause SELECTIVE SUPERIORITY of those individuals that possess all/most of them with regard to other hybrids and both parent species.



Figure 4: Stages in cordgrass recruitment: a) First-year seedling; b) Second/third year cluster; c) Fourth/fifth year clone; d) Adult clone; e) Flowering clone with hundreds of inflorescences with ripening seeds (~100-400 potential seeds per hybrid inflorescence)

Evidence:

Isolated mudflat hybrids show increased self-compatibility

Both hybrid parent species (*S. alterniflora* and *S. foliosa*) are marginally self-compatibility (Figure 3). Hybrids are greatly variable in their ability to successfully set self-fertilized seed; certain hybrids are transgressive and exceed both parent species and other hybrids (Figure 3).

GENETIC/PARENTAGE ANALYSIS*

- 38% of establishing seedlings are likely self-fertilized (Hayward Shoreline) (Figure 5).
- The majority of 2003 seeds per parent from isolated hybrid plants are self-fertilized (Robert's Landing).
- Isolated hybrid plants (Fig. 5: plants 1-3) set more self-fertilized seeds than all other plants in closer proximity to each other.

*Parentage Analysis via maximum likelihood method² of assigning parentage according to microsatellite marker analysis using eight genetic loci¹

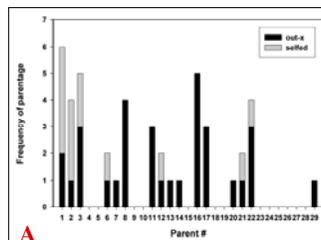


Figure 5: Parentage analysis of 2003 seedlings at Hayward shoreline (HAY).

A (above): Number of self-fertilized versus out-crossed seedlings per most likely parent; Parent numbers correspond to map B; 38 % of surveyed seedlings are likely self-fertilized.

B (right): Distribution of parent plants at HAY in 2003; Seedlings are depicted as green stars. Half/Full-sibship analysis of adult plants shows three major family groups:
F1 [1 6 11 12 26 27 28 29],
F2 [4 7 9 10 16 18 20 21 23 24 25] (*S.foliosa*)
F3 [3 8 19 22],
 1 sibling pair: [13 17],
 No relation: 2 5 14 15.

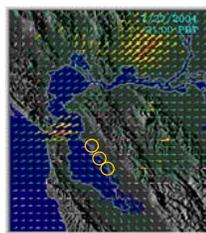


Figure 4 (left): Prevailing winds during the summer/*Spartina* pollination season. Isolated clones in the open mudflats have no access to pollen from on-shore *Spartina*. In order to set seed these plants have to be able to self-fertilize. Circles depict the three study sites (North to South: Alameda island, Robert's Landing, Hayward shoreline).

¹ Blum et al 2004, *Molecular Ecology Notes* 4: 39-42;

Sloop et al 2004, *Molecular Ecology Notes*, submitted.

² FAMOZ software: Geibert et al 2003, *Molecular Ecology Notes* 3: 479-481.

³ H. G. Davis et al., 2004. *Proc. Nat. Acad. Sci.* 101: 13804-13807.

⁴ D. R. Ayres, unpublished data.

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Evidence:

Hybrid seedling recruitment is accelerating in open mudflats of SF Bay

DRAMATIC INCREASE IN SEEDLING RECRUITMENT FROM 2003-2004 AT ALL THREE GPS/GIS SURVEY SITES

Hayward Shoreline (Figure 6):

- ALL surveyed recruiting seedlings are HYBRIDS
 - Evidence for seedling survival from 2003 to 2004
 - Recruitment is most likely from local sources
- Establishing seedlings are the likely progeny of the surrounding clones, with three major families as the most likely colonizers (Figure 5).



Figure 6: Temporal variation in seedling recruitment at Hayward shoreline. Distribution of seedlings in Spring 2004 (red stars) increased >500-fold from Spring 2003 (green triangles). Overlap of stars and triangles suggests survival of 2003 seedlings. (Adult plants are shown in purple)

Conclusion

- Spartina* hybrid seedling recruitment is increasing at previously invaded mudflat sites.
- While recruitment is mainly local, seed exportation on the tide will likely intensify.
- We predict that transgressive hybrid plants, with the greatest reproductive fitness (self-compatible, high seed set, robust seedlings etc.), will drive the spread, colonizing new open mudflat sites all around SFB at an ever increasing rate.
- This will not only further threaten the persistence of the native California cordgrass *S. foliosa*, but will likely irreversibly change the character of the SFB ecosystem.
- Open mudflats will turn into hybrid *Spartina* meadows, which over time, after the accretion of sediment, will change from intertidal to terrestrial.