Self-fertility in invasive cordgrass hybrids (*Spartina alterniflora* x *S. foliosa*) overcomes pollen limitation and generates rapid spread

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Background: Invasive *Spartina*

S. alterniflora

Native to US East & Gulf Coasts

- Invasive range:
  - Britain, China
  - US Pacific Estuaries (Willapa Bay, WA)

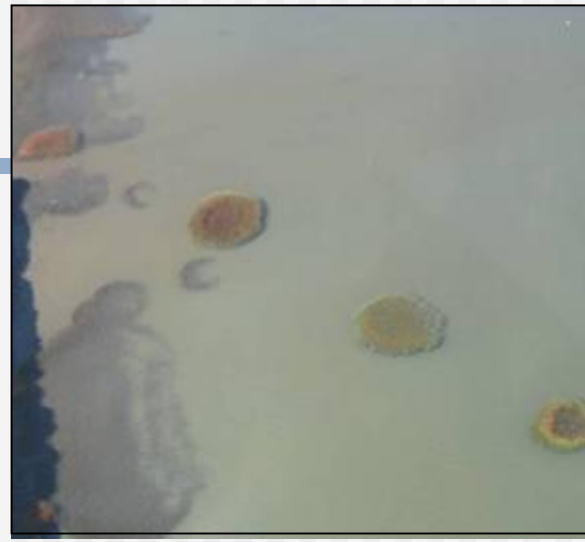
S. anglica

Allopolyploid speciation in Britain (late 1800s):

S. alterniflora x *S. maritima* => *S. townsendii*

- Invasive range:
  - Britain, New Zealand, Tasmania
  - US Pacific Estuaries (Puget Sound, WA)

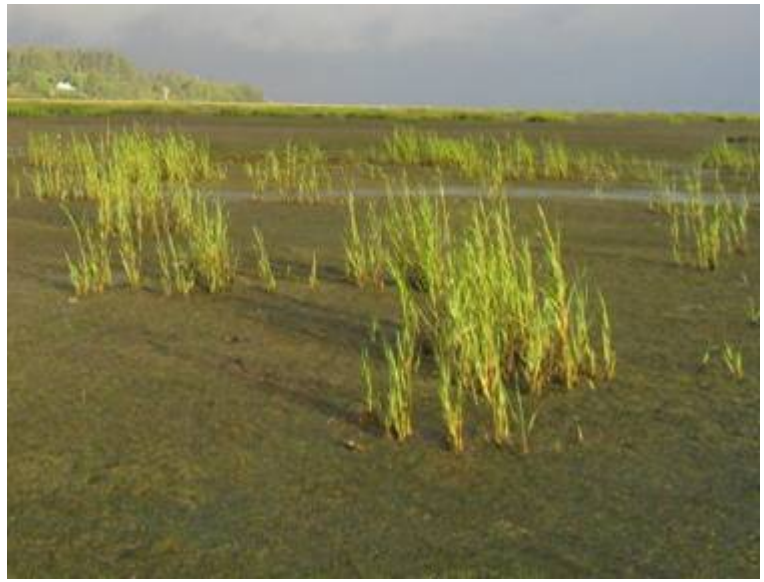
Spartina Reproductive System



Clonal, vegetative growth

Sexual reproduction

- Wind pollinated
- Seeds spread on the tide
  - Viable for up to 8 months
- No seed bank
- Mainly out-crossing in native ranges



Successful colonization of open habitat

Pacific Invasions: Willapa Bay, WA

S. alterniflora invasion

~ 100 yrs.

No native *Spartina*

Constant growth rate

Weak Allee effect: no seed at low density.

Spread is slowed: Infertile young colonists; Fertile old meadows.

Pacific Invasions: SF Bay

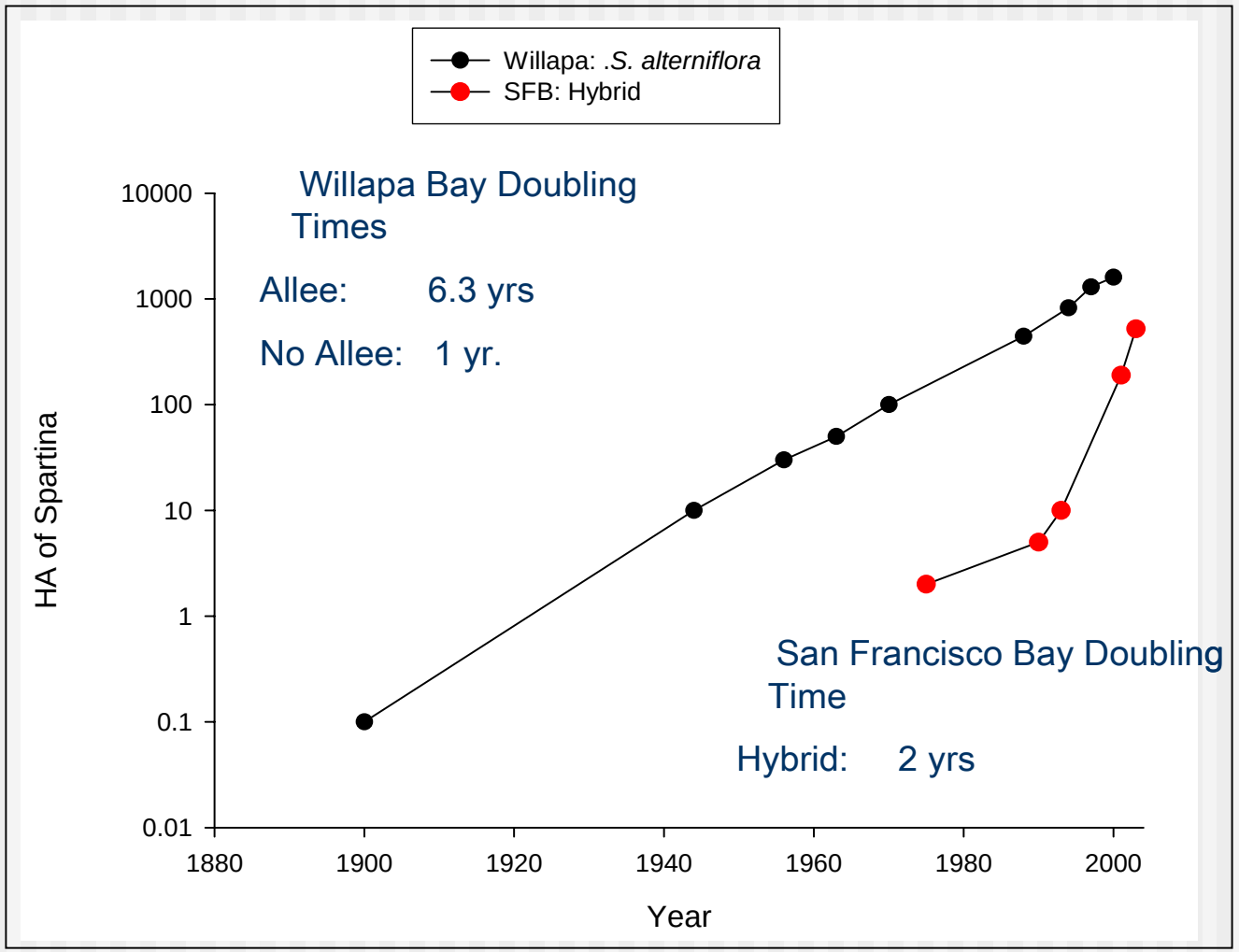
Hybrid *Spartina* swarm in SF Bay

- *S. alterniflora* x *S. foliosa* (native)
- ~ 30 years
- High genetic variability of individuals in hybrid swarm
  - => F1s are rare in nature
  - Transgressive segregation

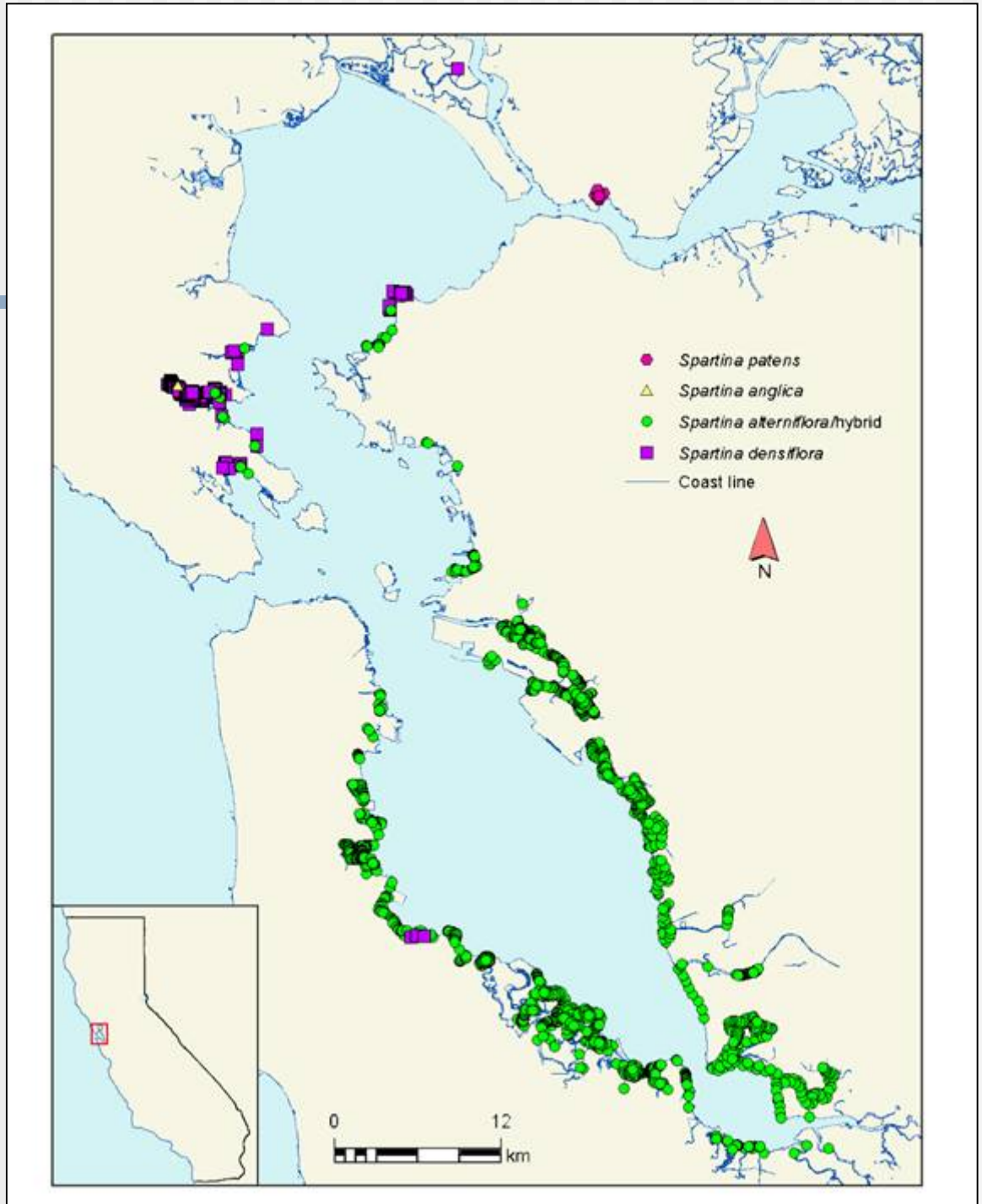
Parent species non-invasive in SF Bay

- Only a small number of extant SF Bay *S. alterniflora*
- Native *S. foliosa* also threatened by invasion

Hybrids highly invasive



Hybrid Distribution



Invasive Spread - Front 1

Native marshes

- Direct competition (Pakenham-Walsh 2004)
- Pollen swamping (Anttila et al. 1998)

Invasive Spread: Front 2

Vast open tidal flats

- Harsh environmental conditions
  - Tidal inundation

- Pollen limitation (Davis et al. 2004)

Rationale

SF Bay tidal flat colonization

- High reproductive fitness
  - Mixed mating system to avoid Allee effect
    - Cross-fertilization within marshes (main foci)
    - Self-fertilization during colonization in tidal flats (nascent foci)
  - No inbreeding depression

- Natural selection
  - Certain hybrid individuals lead tidal flat invasion
    - High fitness
    - Lead colonization by dominating seedling recruitment via self-fertilization

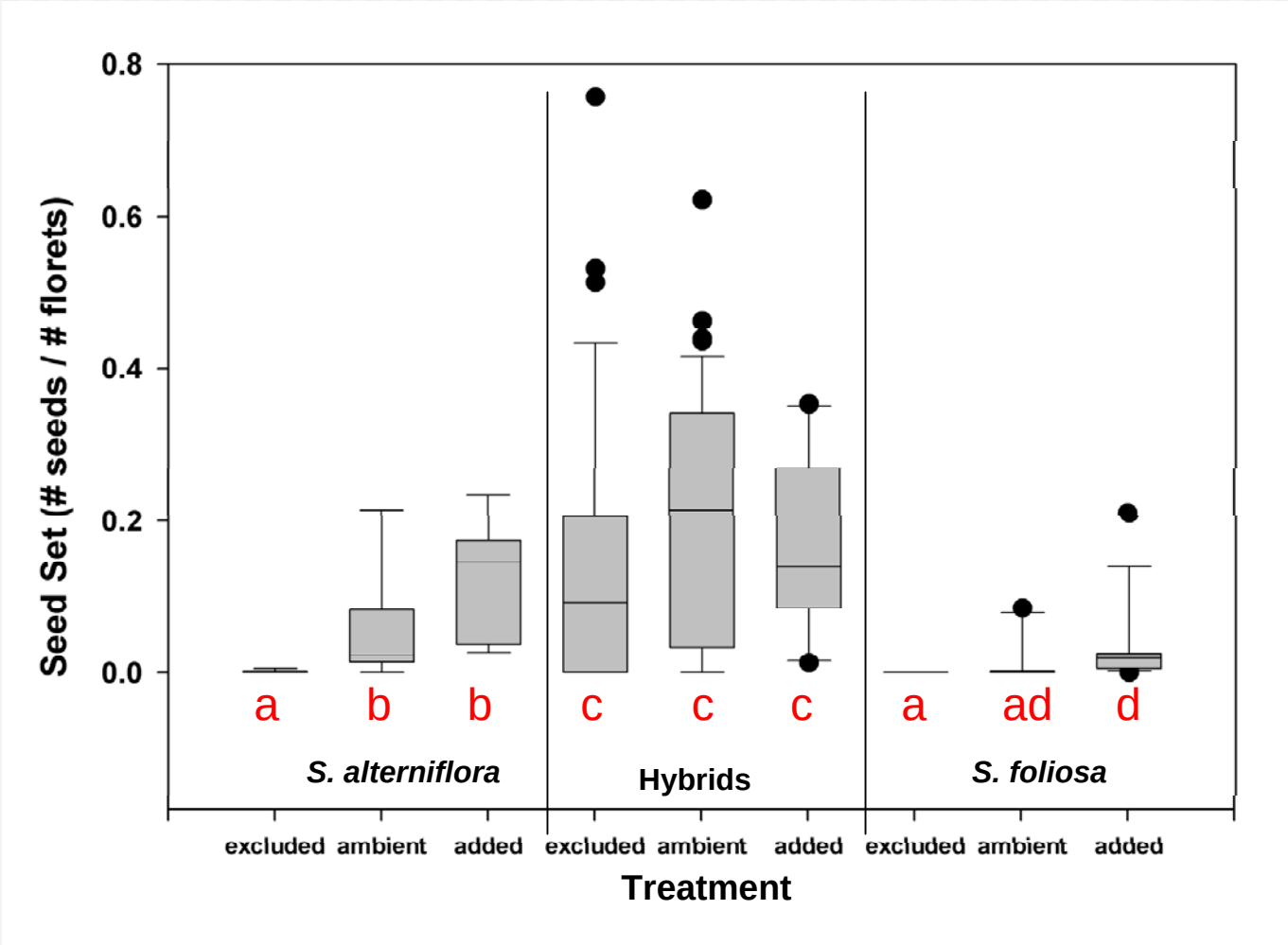
Objectives

1. Self-fertilization in nature
   - SFB hybrids
     - Inbreeding depression
   - Parent species
     - Selfing only when forced in greenhouse
       - Willapa Bay *S. alterniflora* (Davis 2005)
2. Tidal Flat seedling recruitment dynamics
   - Spatial genetic structure
     - Local vs regional recruitment
   - Determine drivers of recruitment
   - Seedling survival

Methods: Hybrid self-fertilization

- SF Bay parent species & hybrids
  - Pollen manipulations *in situ*
    - Treatments: excluded, ambient, added
      - SF Bay *S. foliosa*: n = 9
      - SF Bay *S. alterniflora*: n = 5
      - SF Bay *Spartina* hybrids: n = 33
- Inbreeding depression
  - Treatments: ambient vs. excluded
    - Field collected seed germination
      - Seed mothers: n = 15
      - Inflorescences/plant/treatment: n = 5
    - Seedling greenhouse survival

Results: Self-fertilization ($P < 0.05$)



No Inbreeding Depression

Treatment: progeny of enclosed vs. ambient inflorescences

Germination	P = 0.57
Survival	P = 0.96
Growth (Shoot height & Shoot number @ 6 mos.)	P = 0.10

Conclusions 1

- Hybrids are highly self-fertile in SFB
- Parent species are not self-fertile in SFB
- No inbreeding depression for self-fertilized progeny

Rationale

Adaptation for hybrid self-fertility: Nascent foci of invasion in tidal flats

- Open tidal mudflats
  - Isolated plants surrounded by uninfested area
    - Most seeds fall in open habitat
    - => fast expansion potential
- Shoreline marshes
  - adjacent plants in meadows
    - Most seeds fall inside meadow boundary
    - => slower expansion potential

Methods

Tidal Flat seedling recruitment dynamics 2003/2004

- GPS/GIS & molecular marker analysis
  - Spatial genetic analysis (SGS; Degen 2001)
    - Local vs. regional recruitment
  - Seedling abundance
  - Parentage analysis (FAMOZ; Gerber et al. 2003)
  - Seedling survival

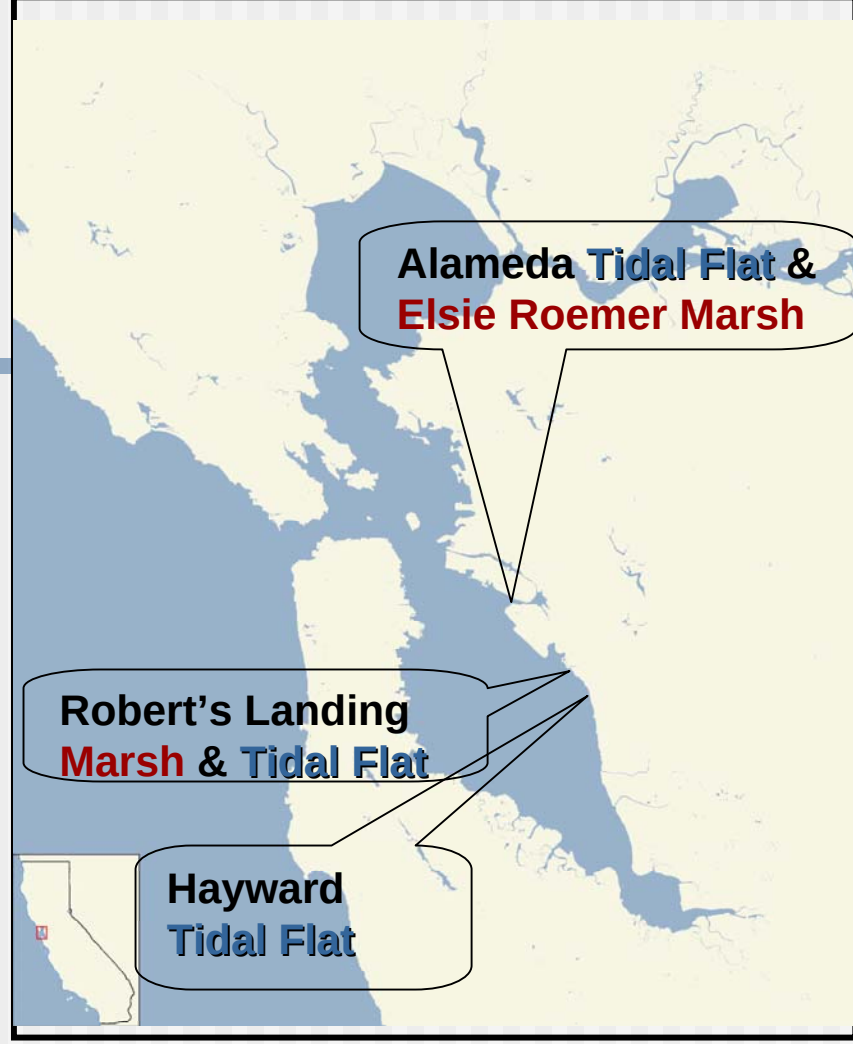
17 SSR loci (Blum et al. 2004, Sloop et al. 2005)

Locus	No. of alleles	Allele size range
SPAR.01	11	198 - 235
SPAR.08	10	178 - 205
SPAR.09	11	273 - 302
SPAR.10	8	336 - 350
SPAR.11	8	230 - 247
SPAR.15	9	263 - 283
SPAR.16	7	372 - 386
SPAR.17	5	374 - 382
SPAR.20	6	172 - 182
SPAR.21	13	204 - 273
SPAR.23	20	248 - 291
SPAR.26	13	263 - 300
SPAR.27	11	304 - 340
SPAR.28	4	416 - 476
SPAR.29	6	353 - 366
SPAR.33	6	250 - 260
SPAR.34	6	366 - 378

Methods: Genetic Sampling

SF Bay hybrids:

- Shoreline hybrid marsh
  - Adults
    - Alameda (25)
    - Robert's Landing (30)
- Tidal flat
  - Adults
    - Alameda (9)
    - Robert's Landing (19)
    - Hayward (24)

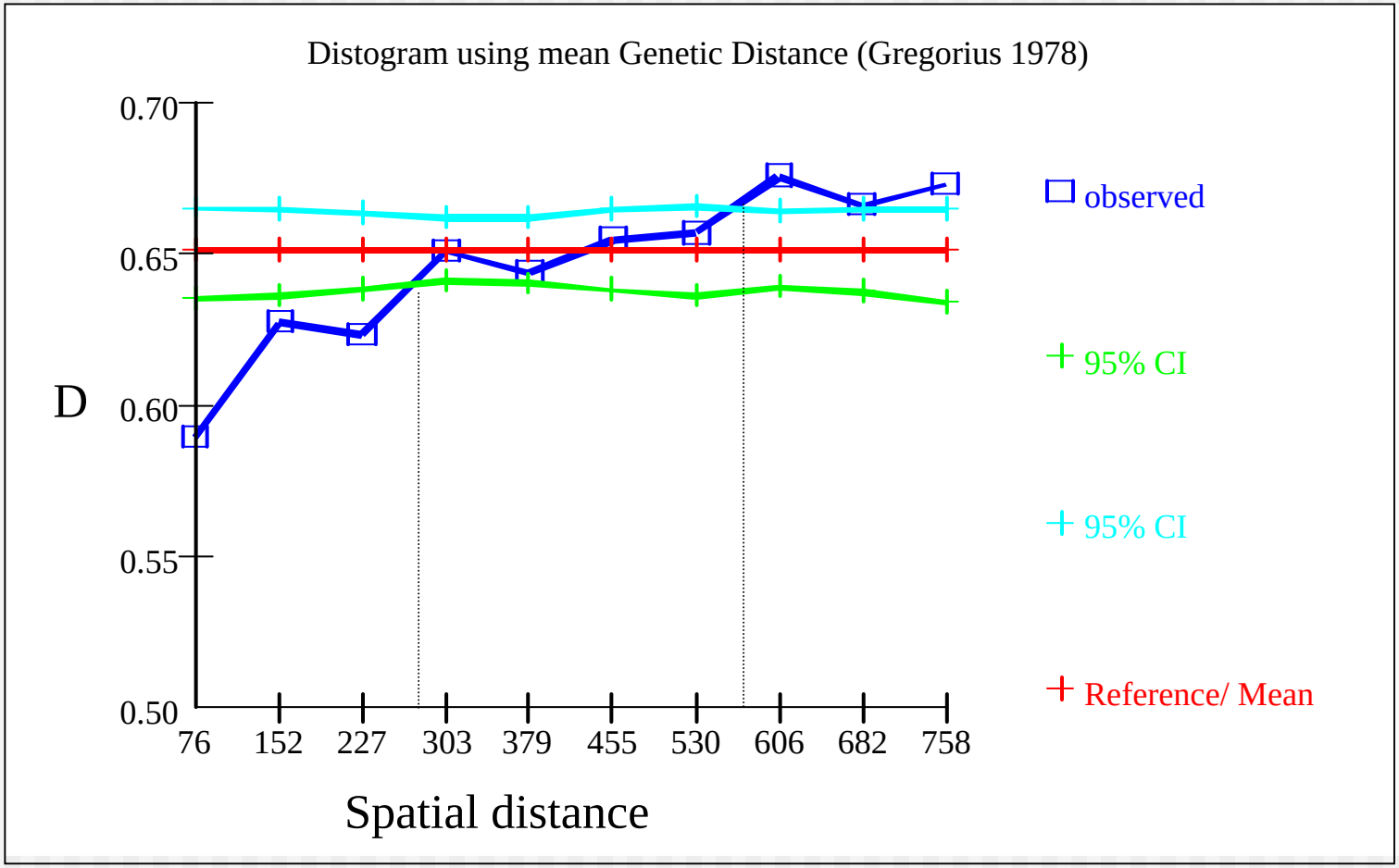


- Seedlings (2003, 2004)
  - Alameda (33, 67)
  - Robert's Landing (42, 54)
  - Hayward (32, 69)

Alameda

Hayward

Results: Spatial Genetic Analysis



Results: Seedling Abundance Parentage Analysis

A) Seedlings	RL2003	RL 2004	HAY 2003	HAY 2004	ALA 2003	ALA2004
Total No. Seedlings in GPS survey	**532**	**2707**	**137**	**1244**	**319**	**862**
Genotyped Seedlings (n)	**42**	**54**	**32**	**69**	**33**	**67**
a) Self-fertilized seedlings	**19 (45%)**	**32 (59%)**	**12 (38%)**	**34 (49%)**	**3 (9%)**	**5 (7%)**
b) Out-crossed seedlings with tidal flat parent	21 (50%)	13 (24%)	16 (50%)	22 (32%)	6 (18%)	20 (30%)
c) Out-crossed seedlings without tidal flat parent	2 (5%)	9 (17%)	4 (13%)	13 (19%)	24 (73%)	42 (63%)

Parentage Analysis:

Robert's Landing Tidal flats	Parent Plant ID RL11	RL9	RL7	RL108	RL1	RL14	RL12	RL16	RL10	RL8	RL106	RL107
Self-fertilizing parent 2003 (n)	1	-	-	-	-	**16**	1	1	-	-	-	-
% of RL selfed seedlings	5%	-	-	-	-	**85%**	5%	5%	-	-	-	-
% of all seedlings	2%	-	-	-	-	**38%**	2%	2%	-	-	-	-
Out-crossing parent 2003 (n)	-	-	-	4	4	**-**	-	3	5	-	1	2
Total Parentage 2003 (n)	**1**	**-**	**-**	**4**	**4**	**16**	**1**	**4**	**5**	**-**	**1**	**2**
Self-fertilizing parent 2004 (n)	2	2	-	-	1	**24**	1	1	1	-	-	-
% of RLselfed seedlings	6%	6%	-	-	3%	**78%**	3%	3%	3%	-	-	-
% of all seedlings	4%	4%	-	-	2%	**46%**	2%	2%	2%	-	-	-
Out-crossing parent 2004 (n)	-	-	2	-	1	**2**	-	4	1	2	-	-
Total Parentage 2004 (n)	**2**	**2**	**2**	**-**	**2**	**26**	**1**	**5**	**2**	**2**	**-**	**-**

Hayward Tidal flats	Parent Plant ID Hay M1	Hay31	Hay22M5	Hay47	HayCL29	HayM2	HayM2B	Hay49	Hay21
Self-fertilizing parent 2003 (n)	**4**	**1**	**1**	**-**	**2**	**1**	**2**	**-**	**-**
%of HAY selfed seedlings	**33%**	8%	8%	-	17%	8%	17%	-	-
% of all seedlings	**13%**	3%	3%	-	6%	3%	6%	-	-
Out-crossing parent 2003 (n)	**3**	-	1	-	-	-	1	-	2
Tot. Parentage 2003 (n)	**7**	**1**	**2**	**0**	**2**	**1**	**3**	**0**	**2**
Self-fertilizing parent 2004 (n)	**20**	**-**	**4**	**2**	**4**	**-**	**4**	**3**	**-**
% of HAY selfed seedlings	**59%**	-	12%	6%	12%	-	12%	9%	-
% of all seedlings	**29%**	-	6%	3%	6%	-	6%	4%	-
Out-crossing parent 2004 (n)	**5**	-	3	2	2	1	4	-	-
Tot. Parentage 2004 (n)	**25**	**0**	**7**	**4**	**6**	**1**	**8**	**3**	**0**

Parentage Analysis

- Tidal flat vs. meadow parents
  - RL tidal flat parents:
    - 2003: 95%
    - 2004: 83%
  - HAY tidal flat parents:
    - 2003: 87%
    - 2004: 81%
  - ALA tidal flat parents:
    - 2003: 38%
    - 2004: 27%

Seedling survival from 2003 to 2004

Alameda: 45% (~150 seedlings)

Robert's Landing: 12% (~ 65 seedlings)

Hayward: 9% (~ 15 seedlings)

Conclusions 2

- All genetically surveyed seedlings were hybrids
- Spatial genetic structure in seedling recruitment
  - Distribution of genotypes spatially non-random up to ~200 meters
  - Local tidal flat plants involved in recruitment
- About half of the surveyed seedlings were self-fertilized at RL & HAY
  - Tidal flat plants dominate as most-likely parents
  - Two plants dominate parentage of seedlings in both years
- Some seedling survival from ‘03 to ’04
- Seedling recruitment is episodic
  - Substantial increase from ‘03 to ‘04, bust in ‘05

Implications

Hybridization is a highly effective way to produce invasiveness

- High genetic variation in hybrid swarm
  - Raw material to select for high reproductive fitness
    - Transgressive genotypes exceeding parent traits
    - Adaptation for self-fertilization in isolation
    - No inbreeding depression
- Hybrid individuals with high fitness will drive the invasion at nascent foci in the tidal flat
- Episodic seedling recruitment
  - Small number of seedling survivors will steadily increase
  - SFB tidal flats will turn into *Spartina* hybrid meadows

HYBRID SPARTINA ERDADICATION

Invasive *Spartina* Project

http://www.spartina.org/

Photo: Drew W. Kerr, ISP

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