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):
  - $S.\ alterniflora \times S.\ maritima \Rightarrow S.\ townsendii$
- 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

- Willapa BayDoubling Time
  - Allee: 6.3 yrs
  - No Allee: 1 yr.

- San Francisco Bay Doubling Time
  - Hybrid: 2 yrs
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)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>S. alterniflora</th>
<th>Hybrids</th>
<th>S. foliosa</th>
</tr>
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<tbody>
<tr>
<td>excluded</td>
<td>a</td>
<td>c</td>
<td>a</td>
</tr>
<tr>
<td>ambient</td>
<td>b</td>
<td>c</td>
<td>ad</td>
</tr>
<tr>
<td>added</td>
<td>b</td>
<td>c</td>
<td>d</td>
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</table>

Seed Set (# seeds / # florets)
No Inbreeding Depression

Treatment: progeny of *enclosed* vs. *ambient* inflorescences

<table>
<thead>
<tr>
<th>Trait</th>
<th>P-value</th>
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<tbody>
<tr>
<td>Germination</td>
<td>0.57</td>
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<tr>
<td>Survival</td>
<td>0.96</td>
</tr>
<tr>
<td>Growth (Shoot height &amp; Shoot number @ 6 mos.)</td>
<td>0.10</td>
</tr>
</tbody>
</table>
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)

<table>
<thead>
<tr>
<th>Locus</th>
<th>No. of alleles</th>
<th>Allele size range</th>
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<tr>
<td>SPAR.01</td>
<td>11</td>
<td>198 - 235</td>
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<td>SPAR.08</td>
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<td>178 - 205</td>
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<tr>
<td>SPAR.09</td>
<td>11</td>
<td>273 - 302</td>
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<tr>
<td>SPAR.10</td>
<td>8</td>
<td>336 - 350</td>
</tr>
<tr>
<td>SPAR.11</td>
<td>8</td>
<td>230 - 247</td>
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<tr>
<td>SPAR.15</td>
<td>9</td>
<td>263 - 283</td>
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<td>SPAR.16</td>
<td>7</td>
<td>372 - 386</td>
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<td>374 - 382</td>
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<td>SPAR.20</td>
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<td>SPAR.21</td>
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<td>204 - 273</td>
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<td>SPAR.23</td>
<td>20</td>
<td>248 - 291</td>
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<td>SPAR.26</td>
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<tr>
<td>SPAR.27</td>
<td>11</td>
<td>304 - 340</td>
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<td>SPAR.28</td>
<td>4</td>
<td>416 - 476</td>
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<td>SPAR.29</td>
<td>6</td>
<td>353 - 366</td>
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<tr>
<td>SPAR.33</td>
<td>6</td>
<td>250 - 260</td>
</tr>
<tr>
<td>SPAR.34</td>
<td>6</td>
<td>366 - 378</td>
</tr>
</tbody>
</table>
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)

  - Alameda (33, 67)
  - Robert’s Landing (42, 54)
  - Hayward (32, 69)
Results: Spatial Genetic Analysis

Distogram using mean Genetic Distance (Gregorius 1978)

<table>
<thead>
<tr>
<th>Spatial distance</th>
<th>Reference/ Mean</th>
<th>95% CI</th>
<th>95% CI</th>
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<td>0.50</td>
<td>0.55</td>
<td>0.60</td>
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<tr>
<td>152</td>
<td>0.65</td>
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<td>227</td>
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<tr>
<td>303</td>
<td>0.76</td>
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<tr>
<td>379</td>
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<td>455</td>
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<tr>
<td>530</td>
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<td>682</td>
<td></td>
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<tr>
<td>758</td>
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## Results: Seedling Abundance Parentage Analysis

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<tbody>
<tr>
<td><strong>Total No. Seedlings in GPS survey</strong></td>
<td>532</td>
<td>2707</td>
<td>137</td>
<td>1244</td>
<td>319</td>
<td>862</td>
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<tr>
<td><strong>Genotyped Seedlings (n)</strong></td>
<td>42</td>
<td>54</td>
<td>32</td>
<td>69</td>
<td>33</td>
<td>67</td>
</tr>
<tr>
<td><strong>a) Self-fertilized seedlings</strong></td>
<td>19 (45%)</td>
<td>32 (59%)</td>
<td>12 (38%)</td>
<td>34 (49%)</td>
<td>3 (9%)</td>
<td>5 (7%)</td>
</tr>
<tr>
<td><strong>b) Out-crossed seedlings with tidal flat parent</strong></td>
<td>21 (50%)</td>
<td>13 (24%)</td>
<td>16 (50%)</td>
<td>22 (32%)</td>
<td>6 (18%)</td>
<td>20 (30%)</td>
</tr>
<tr>
<td><strong>c) Out-crossed seedlings without tidal flat parent</strong></td>
<td>2 (5%)</td>
<td>9 (17%)</td>
<td>4 (13%)</td>
<td>13 (19%)</td>
<td>24 (73%)</td>
<td>42 (63%)</td>
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</table>
# Parentage Analysis:

## Robert's Landing Tidal Flats

<table>
<thead>
<tr>
<th>Parent Plant ID</th>
<th>RL11</th>
<th>RL9</th>
<th>RL7</th>
<th>RL108</th>
<th>RL1</th>
<th>RL14</th>
<th>RL12</th>
<th>RL16</th>
<th>RL10</th>
<th>RL8</th>
<th>RL106</th>
<th>RL107</th>
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<tbody>
<tr>
<td><strong>Self-fertilizing parent 2003 (n)</strong></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>16</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>% of RL selfed seedlings</td>
<td>5%</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>85%</td>
<td>5%</td>
<td>5%</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>% of all seedlings</td>
<td>2%</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>38%</td>
<td>2%</td>
<td>2%</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Out-crossing parent 2003 (n)</td>
<td>-</td>
<td>-</td>
<td>4</td>
<td>4</td>
<td>-</td>
<td>3</td>
<td>5</td>
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<td>1</td>
<td>2</td>
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<td>-</td>
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<tr>
<td><strong>Total Parentage 2003 (n)</strong></td>
<td>1</td>
<td>-</td>
<td>4</td>
<td>4</td>
<td>16</td>
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<td>4</td>
<td>5</td>
<td>1</td>
<td>2</td>
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<tr>
<td><strong>Self-fertilizing parent 2004 (n)</strong></td>
<td>2</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>24</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>-</td>
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<tr>
<td>% of RL selfed seedlings</td>
<td>6%</td>
<td>6%</td>
<td>-</td>
<td>-</td>
<td>3%</td>
<td>78%</td>
<td>3%</td>
<td>3%</td>
<td>3%</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>% of all seedlings</td>
<td>4%</td>
<td>4%</td>
<td>-</td>
<td>-</td>
<td>2%</td>
<td>46%</td>
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<td>2%</td>
<td>2%</td>
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<td>-</td>
<td>-</td>
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<tr>
<td>Out-crossing parent 2004 (n)</td>
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<td>-</td>
<td>2</td>
<td>1</td>
<td>-</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Total Parentage 2004 (n)</strong></td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>-</td>
<td>26</td>
<td>1</td>
<td>5</td>
<td>2</td>
<td>2</td>
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</table>

## Hayward Tidal Flats

<table>
<thead>
<tr>
<th>Parent Plant ID</th>
<th>HayM1</th>
<th>Hay31</th>
<th>Hay22M5</th>
<th>Hay47</th>
<th>HayCL29</th>
<th>HayM2</th>
<th>HayM2B</th>
<th>Hay49</th>
<th>Hay21</th>
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<tbody>
<tr>
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<td>4</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>% of HAY selfed seedlings</td>
<td>33%</td>
<td>8%</td>
<td>8%</td>
<td>-</td>
<td>17%</td>
<td>8%</td>
<td>17%</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>% of all seedlings</td>
<td>13%</td>
<td>3%</td>
<td>3%</td>
<td>-</td>
<td>6%</td>
<td>3%</td>
<td>6%</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Out-crossing parent 2003 (n)</td>
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<td>-</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1</td>
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<td>2</td>
</tr>
<tr>
<td><strong>Total Parentage 2003 (n)</strong></td>
<td>7</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td><strong>Self-fertilizing parent 2004 (n)</strong></td>
<td>20</td>
<td>-</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>-</td>
<td>4</td>
<td>3</td>
<td>-</td>
</tr>
<tr>
<td>% of HAY selfed seedlings</td>
<td>59%</td>
<td>-</td>
<td>12%</td>
<td>6%</td>
<td>12%</td>
<td>-</td>
<td>12%</td>
<td>9%</td>
<td>-</td>
</tr>
<tr>
<td>% of all seedlings</td>
<td>29%</td>
<td>-</td>
<td>6%</td>
<td>3%</td>
<td>6%</td>
<td>-</td>
<td>6%</td>
<td>4%</td>
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<tr>
<td>Out-crossing parent 2004 (n)</td>
<td>5</td>
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<td>3</td>
<td>2</td>
<td>2</td>
<td>1</td>
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<td>-</td>
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<tr>
<td><strong>Total Parentage 2004 (n)</strong></td>
<td>25</td>
<td>0</td>
<td>7</td>
<td>4</td>
<td>6</td>
<td>1</td>
<td>8</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>
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 ERADICATION

Invasive Spartina Project

http://www.spartina.org/

Photo: Drew W. Kerr, ISP
Acknowledgements

- California Sea Grant
- California Coastal Conservancy
- CalFed
- NSF Biocomplexity
- TEAM SPARTINA
  - Heather McGary, John Lambrinos, Heather Davis, Richard Hall, Mary Pakenham, Jun Bando, Janie Civille, Alex Lee.