Rooted in Hell:
Predicting Invasion Rates of *Phragmites Australis*

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BACKGROUND

Jake demonstrates the difficulties of living with phragmites!

Across the estuaries of the east coast and wetlands of the Great Lakes, the invasive grass *Phragmites australis* outcompetes other vegetation and destroys local ecosystems. Because its roots are tolerant to salinity that other plants find hellish, *Phragmites* invasions begin with vegetative spread of genetic clones in brackish marshlands. This plant can grow over three meters tall at densities of 50 stems/m^2, provides poor wildlife habitat, and is very difficult to eradicate.

A discrete life stage model on a yearly time step captures seed survivorship in a seed bank, sexual and asexual recruitment into a juvenile age class, and differential competition among all classes with adults. Small patches are often a single genetic individual, spreading asexually via stolons and rhizomes. When patches become genetically diverse, viable seeds are produced and invasion rates increase by an order of magnitude.

To aid in the management of *Phragmites*, we obtain invasion rates with and without genetic variation. These invasion speeds suggest prioritizing eradication of genetically diverse stands and simulations provide guidance on the scale of interventions.

Current management techniques include burning, grazing seedlings, and large scale herbicide spray.

THE MODEL

Parameters	Description	Estimated Values/Units
a	$\sigma_1(1-g_1)$	0.5 per year
b	$\sigma_1 g_1 \sigma_3 \sigma_4$	0.001 per year
c	$\sigma_2 g_2 \sigma_3 \sigma_4$	0.0005 per year
σ_6, σ_7	Survivorship of adults and rhizomes resp.	0.95, 0.5 per year
β_1, β_2	Competition (seedlings vs. adults), (rhizomes vs. adults)	0.2, 0.1 per stem
f_s	Adult fecundity (seed production)	5000 seeds/stem
$f_v(A)$	Density-dependent adult fecundity (rhizome production)	16 stems/m^2 for steady state density of adults
l	Maximum yearly horizontal rhizome growth	5 m
α	Mean seed dispersal distance	100 m

$$S_{n+1} = aS_{new}$$

Seeds in the seed bank — Newly dispersed seeds

$$J_{n+1} = (bS_{new} + cS_n)e^{-\beta_1 A_n} + \sigma_7 J_{new} e^{-\beta_2 A_n}$$

Juvenile stems — Germinated seeds from seed bank — New juvenile clones (vegetative spread) — Competition terms

$$A_{n+1} = \sigma_5 J_n + \sigma_6 A_n$$

Adult stems

Seed dispersal via Laplace redistribution kernel

$$S_{new}(x) \equiv \int_{-\infty}^{\infty} k_s(x-y) f_s A_n(y)\,dy \qquad k_s(x) = \frac{1}{2\alpha} e^{-\frac{|x|}{\alpha}}$$

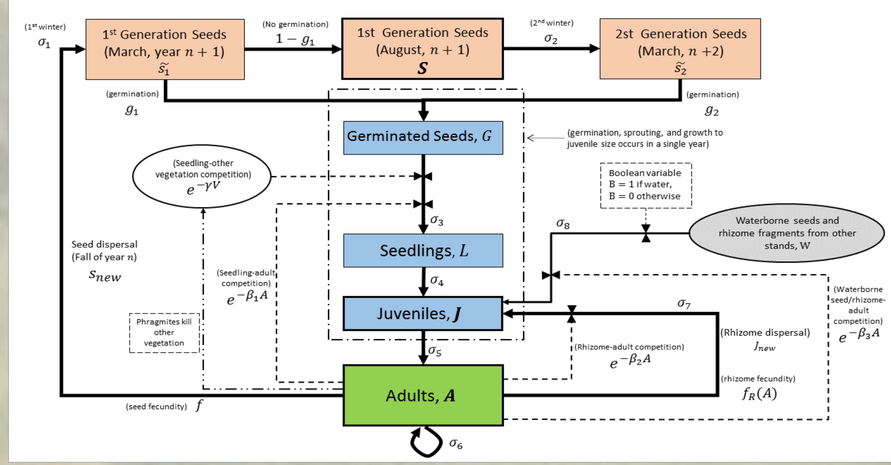
Vegetative spread via Uniform redistribution kernel

$$J_{new}(x) \equiv \int_{-\infty}^{\infty} k_v(x-y) f_v[A_n(y)]\,dy \qquad k_v(x) = \begin{cases} \frac{1}{2l} & |x| \le l \\ 0 & |x| > l \end{cases}$$

Type II functional response for rhizome production

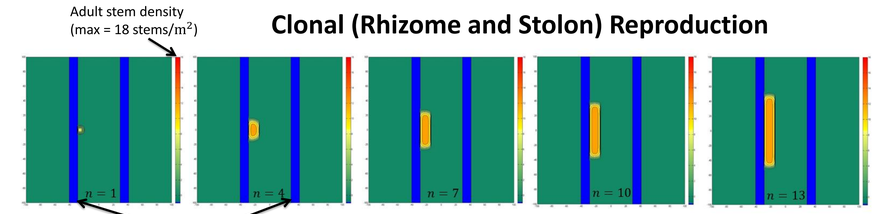
$$f_v[A_n(x)] = \frac{\phi A_n(x)}{r + A_n(x)}$$

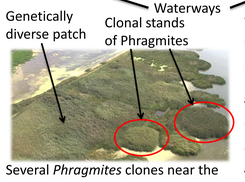
LIFE CYCLE DIAGRAM



SIMULATIONS

Clonal (Rhizome and Stolon) Reproduction

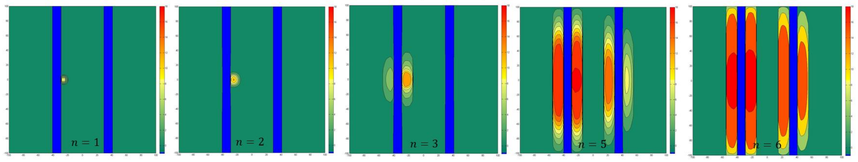




Several *Phragmites* clones near the Great Salt Lake. Where clones meet rapid spread by seed dispersal begins.

Simulation of the model for a single clone over 13 years, including only vegetative reproduction (above). *Phragmites* does not grow in deep water but also cannot grow on arid ground (modeled above as distances over 10 m from water). Individual clones therefore spread slowly along wet borders, and are unable to jump over barriers.

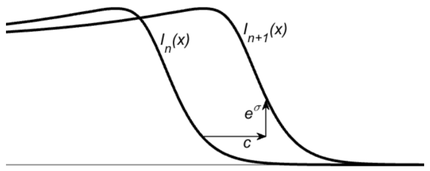
Clonal and Sexual (seed) Reproduction



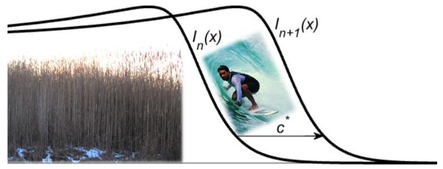
Simulation of invasion by a genetically diverse stand of *Phragmites* over six years (above). With multiple genetic individuals in a stand, sexual reproduction is possible. Seeds are wind-borne and can easily travel hundreds of meters. Each adult stem has a large inflorescence, capable of producing 1-5,000 viable seeds (right). While asexual propagation is necessary for stands to fill in and reach peak density, long distance spread via seeds allows a genetically diverse stand to jump over barriers that would be impermeable to individual clones. Diverse stands should be prioritized for control actions.

INVASION SPEED CALCULATION

- Linearize the (matrix) model and assume exponential form for solutions:
  $\mathbf{Y}_{n+1}(x) = \int_{-\infty}^{\infty} \mathbf{A}(y)\mathbf{Y}_n(x-y)\,dy$ where $\mathbf{Y}_n(x) = e^{-\tau x}\mathbf{v}$
- Assume a point on next year's front is a horizontal translation and vertical multiple of some point on the current front:
  $\mathbf{Y}_{n+1}(x) = \mathbf{Y}_n(x-c)e^{\sigma}$



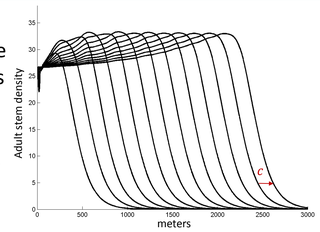
- Max growth, σ, appearing at speed c, relates to the eigenvalues, $\lambda(\tau)$, of the linearized operator and shape parameter, τ, via
  $e^{\tau c + \sigma} = \max_{\lambda} [\lambda(\tau)] \equiv \rho(\tau)$
- Choose speed c^*, such that the maximum value of σ gives zero growth in the surfer's frame of reference:
  $c^* = \min_{0<\tau} \left(\frac{1}{\tau} \ln \rho(\tau) \right)$



RESULTS

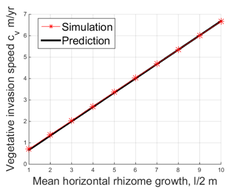
Analytic speed predictions are in good agreement with simulation speeds for a wide range of parameter values. With parameters provided by the Kettenring Wetland Ecology Lab, we predict invasion speeds of

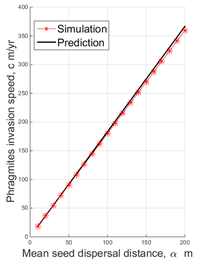
- 1.7 m/yr for spread of an individual clone
- 180 m/yr for a genetically diverse stand



Axial spread of a genetically diverse *Phragmites* stand over thirteen years. Stand density peaks when vegetative dispersal fills in a stand and subsequently declines due to internal competition.

- ❖ Invasion speed of a genetically diverse stand is nearly 3 times that of an individual clone with the same mean dispersal distance (10 m).
- ❖ Invasion speed of a genetically diverse stand is over 100 times that of an individual clone for realistic mean dispersal distances.





Our invasion speed analysis underscores the need to prioritize control of genetically diverse stands. Future versions of the model will allow managers to test eradication strategies *in silico*.

REFERENCES

- Kettenring, K. and K. Mock, 2012. Genetic diversity, reproductive mode, and dispersal differ between the cryptic invader, *Phragmites australis*, and its native conspecific. Biological Invasions 14: 2489-2504.
- Kettenring, K. M., McCormick, M. K., Baron, H. M. and Whigham, D. F., 2011. Mechanisms of *Phragmites australis* invasion: feedbacks among genetic diversity, nutrients, and sexual reproduction. Journal of Applied Ecology 48(5): 1305-1313.
- Neubert, M. G., Caswell, H., 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. Ecology 81(6), 1613-1628.

- We wish to thank Karin Kettenring's lab for help with parameters, field excursions, and many discussions on *Phragmites* dynamics. Portions of this work were supported by NSF grant #1245421 and the Western Wildlands Environmental Threat Assessment Center.

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