Applications: Examples from the Everglades and Elsewhere

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Approach: Look at some of the ecological issues of a specific locale see how they can translate into mathematically interesting problems

Currently of interest in Everglades

- Ecotone dynamics of competing halophytic and freshwater vegetation types under rising sea level, changing groundwater salinity and storm surges.

- Dynamics of small fish populations and food webs in a seasonally flooding and drying marsh. Effects of canals on these.

- Landscape patterns, ridge and slough, tree islands (Larsen, others)

- Population dynamics, especially of small populations

- Spread of many invading species, and biocontrol (Carol Horvitz)
Forecasting Coastal Ecotone Dynamics

Photo: jasoncdukes.files.wordpress.com
Co-workers

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Tom J. Smith, U.S. Geological Survey
Sea level is rising at an increasing rate...

Sea Level at Key West, Florida, has been rising 3.27 mm/year in recent decades...

23 cm since 1930
... which is causing a gradual shift in the boundary zone between salt-tolerant mangrove vegetation and freshwater sawgrass vegetation is moving inland at about 50 meters per year on this flat elevation gradient (3 cm per kilometer).

Low productivity ‘White zone’ between advancing mangroves and retreating sawgrass

Slide from Michael Ross et al.
... and it is possible that discrete salinity inundation events are damaging forests in Florida, possibly leading to vegetation shifts.
So we want to see if we can understand and forecast the types of changes that we see occurring along the coastline; e.g.

Encroachment of mangroves into hardwood hammock habitat is one example.
Mangrove and tropical hardwood hammocks are two types of Everglades vegetation that overlap in geographic area, though generally hardwoods occupy slightly higher elevation.
Mangrove-Hardwood Hammock Boundary – Key Largo

This sharp boundary is maintained despite only a tiny elevation gradient
Both mangroves and hammock species obtain their water from the vadose zone (unsaturated soil zone). In coastal areas this vadose zone is underlain by highly brackish ground water, so that evapotranspiration, by depleting water in the vadose zone during the dry season, can lead to infiltration by more saline ground water.

Although hardwood hammock trees tend to decrease their evapotranspiration when vadose zone salinities begin to increase, thus limiting the salinization of the vadose zone, mangroves can continue to transpire at relatively high salinities.
The model, MANHAM, simulates competition between mangroves and tropical hardwood hammock trees on a landscape, including hydrologic and salinity processes in the vadose zone (unsaturated zone, roughly the rooting zone).
Model overview

- Vegetation dynamics is simulated in a two-dimensional continuous coordinate system.

- Hydrodynamics was modeled in a grid-based three-dimensional soil space using several stacked layers.
Submodels
---Soil water and salinity dynamics

- Soil water fluxes were simulated by Darcy’s equation

\[ \theta \frac{\partial S_v}{\partial t} = TS_v - F \frac{\partial S_v}{\partial z} \]

- Salinity increase due to uptake of water by roots
- Salinity change due to water fluxes

Plans are to replace our water and salinity modeling by SUTRA, by C. I. Voss and A. M. Provost
Fields of Neighborhood (Berger, 2000)
Results: If we start with an initially random distribution of mangroves and hammock trees, we always get boundary formation of trees...

Hardwood hammock (blue) and mangrove (red), with random initial distribution (left) and 50 years’ simulation (right). After 50 years hammock retreat to inland side. The boundary is self-reinforcing and leads to a sharp salinity gradient in the vadose zone.
We would like to be able to forecast whether storm surges or series of storm surges can lead to vegetation regime shifts…

Typical record of storm surge

Sometimes the monitoring stations don’t survive the storm surge

Slides from Tom Smith and Dennis Krohn
The direct effects have been estimated by reconstructing the wind field of the hurricane...

Wind speed = 60 meters/second
... and created a storm surge
....and we have simulations that tend to show this can happen

This all tends to require detailed simulations… but

Darker magenta is higher mangrove density
We can also study a very simplified of two-species Lotka-Volterra (LV) competition with the effects of a growth inhibitor, salinity. This occurs along a one-dimensional gradient.

\[
\frac{\partial N_1}{\partial t} = N_1 (\rho_1 h(S) - \alpha_{11} N_1 - \alpha_{12} N_2) + D_1 \frac{\partial^2 N_1}{\partial z^2}
\]

\[
\frac{\partial N_2}{\partial t} = N_2 (\rho_2 m(S) - \alpha_{21} N_1 - \alpha_{22} N_2) + D_2 \frac{\partial^2 N_2}{\partial z^2}
\]

\[
\frac{dS}{dt} = \beta_0 g(z) + \frac{\beta_1 N_2}{k + N_2} g(z) - \varepsilon S + D_s \frac{\partial^2 S}{\partial z^2}
\]

where \( D \) is the diffusion coefficient, \( z \) is distance from the seaward edge of the landscape. The groundwater salinity, \( g \), was arbitrarily chosen to represent the spatial heterogeneity of the system. It is assumed that \( g \) is 30 ppt at the seaward edge and 0 at the landward edge.
Ignoring diffusion for the moment, one can find the separatrix for the trajectories for any initial conditions.

This is a useful first step and effects of diffusion will be examined next.

Comparisons are being made with the complex model.
Modeling the Fish Community of the Freshwater Everglades

Donald L. DeAngelis, USGS/FISC
Joel E. Trexler, Florida International University
Fred Jopp, Frei Universität Berlin and University of Miami
Doug Donalson, U.S Army Corps of Engineers
Develop dynamic models of fish in Everglades landscapes with hydrologic scenarios. Study the effects on fish biomass dynamics of:

- Canals and other waterbodies as drought refuges for small fishes but also piscivorous fish habitats.
- Range of marsh water level fluctuations within years and over multi-year time periods.
- Piscivores that can move from permanent waterbodies into marsh.
- Different topographic configurations.
We are considering the aggregation of small native fishes that are prey for wading birds.

- **Bluegill**
  *Lepomis macrochirus*

- **Coastal Shiner**
  *Notropis petersoni*

- **Least killifish**
  *Heterandria formosa*

- **Pygmy Sunfish**
  *Elassoma evergladii*

- **Sailfin molly**
  *Poecilia latipinna*

- **Striped Mullet**
  *Mugil cephalus*

- **Swamo Darter**
  *Etheostoma fusiforme*
Model Structure

- Classical food web model
- Part 1: ODE describe structure and the fluxes between spatial cells
  - Functional responses, recycling
- Part 2: rules for movement of migratory species between cells
- Spatially explicit, grid-based \((n \times 10k)\)
GEFISH: Movement Rules for Fish

White: movement from low water to high water areas during drydowns. This reverses during reflooding.

Red: net diffusional movement from high fish density to low density areas.
We are currently performing simulations on artificial landscapes. This allows studying competition and trophic cascades in temporally and spatially varying landscapes.
...and then will examine small areas within the overall landscape where field studies are being conducted.

This is all pretty complex, but... we can also simplify things and consider only a one generic species and its interaction with a generic prey. We have done this first to investigate how these small fishes are able to spread rapidly up the elevation gradient as water level increases.

Source: USGS: Thomas J. Smith
If we assume that the fish can follow a resource gradient, where the resource emerges immediately as an area becomes wetted. We have the equations:

\[
\frac{\partial R}{\partial t} = r \left( 1 - \frac{R(s,t)}{K} \right) R(s,t) - \frac{fR(s,t)F(s,t)}{1 + hfR(s,t) + wfF(s,t)}
\]

\[
\frac{\partial F(s,t)}{\partial t} = \frac{\gamma fR(s,t)F(s,t)}{1 + hfR(s,t) + wfF(s,t)} - mF(s,t) - \frac{\partial}{\partial s} \left[ \varepsilon \frac{\partial G(s,t)}{\partial s} F(s,t) \right]
\]

We call this the ‘dynamic IFD hypothesis’.

We can model the landscape in a very simple way

- Varying water level
- Lowest water level
- Permanent water
- Elevation gradient
We also used an alternative pure diffusion model, in which we used estimates of the diffusion rate, D,

\[
\frac{dR(s,t)}{dt} = r \left( 1 - \frac{R(s,t)}{K} \right) I(s,t) - \frac{fR(s,t)F(s,t)}{1 + hfR(s,t) + wfF(s,t)}
\]

\[
\frac{\partial F(s,t)}{\partial t} = \frac{\gamma fR(s,t)F(s,t)}{1 + hfR(s,t) + wfF(s,t)} - mF(s,t) + D \frac{\partial^2 F(s,t)}{\partial s^2}
\]

where \( D = 0.001 \text{ m}^2 \text{ sec}^{-1} \).

This compares the movement of the fish up the elevation gradient in relation to the moving flooding front after 100 days.

Top. Diffusion alone, with our best estimate of the diffusion coefficient.

Bottom. Advection, with an estimate (unfortunately very uncertain), of the advection coefficient.
Landscape Pattern Example: Everglades Ridge and Slough Pattern

- The Everglades is characterized by large areas of ‘ridge and slough’ landscape.

  [see Larsen et al., Ecological Monographs 77:591-614, 2007; Ross et al., Hydrobiologia 569:37-59, 2006]
Example: Everglades Ridge and Slough Pattern

Changes in flow of water are leading to a degradation of that pattern in some places (e.g., Chris McVoy, South Florida Water Management District).

Degraded former ridge and slough habitat
To address this problem, the processes that create and maintain patterns must be understood.

Geologist/ecologists addressed this using hypothesized mechanisms in a detailed process model; e.g., Laurel Larsen et al. (2007), Larsen and Harvey (2011).
• Hypothesis of Larsen et al. (2007):

  • During wetter periods flood pulses deposited sediment in random locations on the stream bed or around preexisting patches of emergent vegetation (a couple of millennia ago).

  • During the low-flow season or periods of drought, sawgrass, which requires an exposed peat surface for germination, colonized the deposits.

  • The sawgrass or other emergent vegetation would have provided stability during subsequent high-water periods, trapped suspended particles, and slowed local flow velocity, promoting additional sedimentation.
• Under the differential peat accretion hypothesis, these sawgrass patches may have also accreted peat more rapidly than sloughs, causing further topographic differentiation to an equilibrium elevation difference between ridge and slough.

• Once the incipient proto-ridges were initiated, current shadows behind the deposits, ridge coalescence, and/or the development of roughness-induced secondary circulation cells would have promoted elongation and eventual channelization of the flow.
The gravity erosion is a diffusional process.

\[
\frac{\partial (\text{peat elevation})}{\partial t} = \frac{\partial^2 (\text{peat elevation})}{\partial x^2} + \text{Net Peat Accretion}(x)
\]
Everglades population models for species with small populations are spatial.

Many are individual- or agent-based; for example the snail kite model.
EVERKITE: A spatially explicit individual-based snail kite model

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Program website:  atlss.org

Why model the snail kite?

– There is solid empirical evidence that snail kites are very sensitive to hydrological conditions.

– There is a great amount of empirical data available for the snail kite as well as ongoing empirical research.

– Snail kites are limited in their range to southern and central Florida and are therefore a good indicator for the integrity of the network of wetlands in this area.

– Being an endangered bird of prey found in the Everglades, there is great public interest in the snail kite.
The model incorporates field data on the snail kite to allow examination of its population dynamics under different hydrologic scenarios.
Movement patterns of individuals – memory of discrete habitat sites (i.e., ‘landscape map’), gained by exploration, plays a role.
Local Drying Event – response is movement to another site.
Widespread Drying Event

Spatially correlated droughts pose a threat
Main Components and Mechanisms of EVERKITE

- Individual-based (or agent-based)
- Spatial resolution currently limited to the wetland level (14 wetlands plus peripheral habitat)
- Weekly time steps
- Includes four major processes: aging, breeding, movement and mortality
- Breeding, movement and mortality are modeled in relation to hydrological conditions
- Density dependence currently not included
- Produces all demographic parameters of the kite populations (lambda, densities per wetland, etc).
Opportunities for mathematics

– Investigation of formation of cognitive landscape map by the birds. Exploratory movements take time and energy. What level of exploration is optimal? Agent-based models (ABM) such as Folse et al. 1989, have been doing this for a long time.)

– Evolution of responses to drying events. When is it optimal to give up on the current habitat site? Does high level of spatial autocorrelation of droughts lead to tendency for longer movements in response to unfavorable conditions?

– Integrating agent-based approaches into mathematical ecology. For example, agent-based models can be represented by Markov matrix models (very large matrices). This may allow certain types of calculations; e.g., $\lambda$ under long-term conditions.

Opportunities for mathematics

Following up on the last remarks, a lot of progress may be made in all of the theme areas here by supplementing rigorous mathematics with less rigorous, but more flexible agent-based modeling.

The Everglades tree islands raise some questions that bear on basic ecological theory.
Tree islands, energy flow and nutrients

Some peculiarities of the Everglades tree islands raise some questions that bear on basic ecological theory.
Collaborators

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It is interesting first to go back to Alfred J. Lotka’s principle of maximum energy flux – that a selection operates to maximize the total energy flux of a system ... and to ask...

Is this consistent with the $R^*$ law of Tilman (1977, 1982) - when consumers exert top-down control on resources, the species that can survive at the lowest levels of a limiting resource will be the best competitor for that resource and will displace all other species?
Getting back to tree islands.

There are hypotheses on how the tree islands came to be.

They seem to exist through self-organizing processes.

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They maintain themselves through acquiring nutrients from the surrounding oligotrophic marsh due, perhaps, to their higher levels of evapotranspiration. They have levels of available phosphorus about 100 times higher than the surrounding marsh.


These vegetation types are modeled as competing.
Correlation of high productivity with higher nutrient levels may seem reasonable in some sense.

Still, it would not seem consistent with the R* rule that the better competitor should reduce nutrient to a lower level than the poorer competitor.

A more landscape orientation of the R* rule is needed.

The first goal is to establish the relationship between Maximum Power Principle and the R* rule.

The basic idea in the model is that the plant can allocate primary production (carbon, energy) among foliage, roots, and wood.

Under given circumstances (e.g., external nutrient input, whether or not the tree is competing with other trees with other strategies), what is the best way to allocate the energy; that is, for greatest primary production.
Schematic of carbon fixation and the cycling of a limiting nutrient. It is a modified version of the G’DAY* model, with the details of litter decomposition and soil processes omitted, but a soil nutrient pool added. The foliage, roots, and wood compartments have variables for both carbon and nutrient.

\[ \eta_f G + \eta_r G + \eta_w G = 1 \]

More schematically...

- **Foliage**: \( C_f, N_f \)
- **Roots**: \( C_r, N_r \)
- **Wood**: \( C_w, N_w \)

**Litter**

**Net Mineralization**

\[ (1 - \lambda) U \]

Loss to Storage in Recalcitrant Forms

\[ \lambda U \]

**Mineral Nutrient in Soil Pore Water** \( N_{pore} \)

**Leaching**, \( Q*N_{pore} \)

\[ Q*N_{input} \]
Basic Model Equations

\[ G = \text{net carbon production, or growth per unit time (g C m}^{-2} \text{ day}^{-1}) \]

\[ G = G_0 I(C_f)E(v_f) = G_0 \left[ 1 - e^{-k_f b_f C_f} \right] \frac{v_f}{v_0 + v_f}. \quad v_f = N:C \text{ ratio in foliage} = N_f/C_f \]

\[ U = \text{nutrient uptake rate of plant-available nutrient (g N m}^{-2} \text{ day}^{-1}) \]

\[ U = \left( \frac{g_N N_{\text{pore}}}{k_N + N_{\text{pore}}} \right) \left( 1 - e^{-k_r b_r C_r} \right) \]
Equations for Carbon Dynamics

\[ \frac{dC_r}{dt} = \eta_r G - \gamma_r C_r \]

\[ \frac{dC_f}{dt} = \eta_f G - \gamma_f C_f \]

\[ \frac{dC_w}{dt} = \eta_w G - \gamma_w C_w \]

Carbon allocation from primary production

Senescence
Equations for Nutrient Dynamics

\[
\frac{dN_f}{dt} = (U - \eta_w v_w G) \frac{\eta_f}{\eta_f + \rho \eta_r} - \gamma_f N_f
\]

\[
\frac{dN_r}{dt} = (U - \eta_w v_w G) \frac{\rho \eta_r}{\eta_f + \rho \eta_r} - \gamma_r N_r
\]

\[
\frac{dN_w}{dt} = \eta_w v_w G - \gamma_w v_w C_w
\]

The \(- \eta_w v_w G\) represents fixed N:C allocation to wood.
Equations for Nutrient Uptake and Pore Water Nutrient Dynamics

\[ U = \left( \frac{g_N N_{\text{pore}}}{k_N + N_{\text{pore}}} \right) \left( 1 - e^{-k_r b_r C_r} \right) \]

Uptake rate

\[ \frac{dN_{\text{pore}}}{dt} = Q(N_{\text{input}} - N_{\text{pore}}) - U + \lambda(\gamma_f N_f + \gamma_r N_r + \gamma_w v_w C_w) \]

Input and Leaching  Uptake  Mineralization
Methods

We want to determine if maximum rate of production (maximum power), or \( \max(G^*) \) (where * means steady state) corresponds to minimum \( R^* \), or \( \min(R^*) \), or \( \min(N_{pore}^*) \).

So our strategy is to solve the above equations for \( G^* \) (steady state).

Then we find the set of \( \eta_f, \eta_r, \eta_w \) that maximizes \( G^* \).

(Actually, we fix allocation to wood, \( \eta_w \))

Does this also minimize \( N_{pore}^* \)?
Assume the system is at steady state (*), so that each of the right hand sides of the differential equations is set to zero. Define a strategy set as \( S = (\eta_f, \eta_r, \eta_w) \). Using the 7 equations to eliminate all other variables, an implicit function for \( G^* \) can be derived.

\[
F(S, G^*, N^*_\text{pore}) = \frac{G^*}{G_0} \left( \frac{g_N N^*_\text{pore}}{k_N + N^*_\text{pore}} \right) \left( 1 - e^{-k_b \eta_b G^*/\gamma_r} \right) - \eta_w v_w G^* \left[ \frac{1 - e^{-k_{bf} \eta_f G^*/\gamma_f}}{G^* v_0 (\eta_f + \rho \eta_r)} \right] = 0 \quad (1)
\]
In the expression $F(S, G^*, N_{pore}^*)$, $N_{pore}^*$ can be expressed simply in terms of $G^*$ in the second order equation.

$$Q N_{pore}^{*2} + BN_{pore}^* - Q N_{input} k_N = 0 \quad (2)$$

and where

$$B = g_N (1 - \lambda) \left(1 - e^{-k_r b_r n_r G^*/\gamma_r} \right) + Q \left(k_N - N_{input} \right)$$

Solving eqn (2) for $N_{pore}^*$ yields,

$$N_{pore}^* = \frac{-B + \sqrt{B^2 + 4(Q^2 N_{input} k_N)}}{2Q}$$

This can be plugged into eqn (1) to obtain the final implicit equation for $G^*$ in terms of the allocation strategy set $S$. We cannot solve this…
\[ B = g_N \left( 1 - \lambda \right) \left( 1 - e^{-k_r B r \eta_r G^* / \gamma} \right) + Q \left( k_N - N_{\text{input}} \right) \]

...but, It can be shown that \( B \) increases monotonically as \( \eta_r G^* \) increases...

\[ N_{\text{pore}}^* = \frac{-B + \sqrt{B^2 + 4 \left( Q^2 N_{\text{input}} k_N \right)}}{2Q} \]

...and, it can be shown that \( N_{\text{pore}}^* \) decreases monotonically as \( B \) increases.

That implies that when \( \eta_r G^* \) reaches a maximum, \( N_{\text{pore}}^* \) will reach a minimum.
Analytic Results

We found \textit{analytically} that the strategy that minimizes the nutrient level at equilibrium, Min($R^*$) [or Min($N_{pore}$) in our model], is not the same as that which maximizes the rate of primary production, or total power, $G^*$. Instead, the strategy for Min($R^*$) was proven to be mathematically identical with one that maximizes rate of energy allocation to roots, Max($\eta_r G^*$). 

Our simulations confirmed that.
Further Results

Second, surprisingly, analysis and simulations show that the allocation strategies of model plants that are able to out-compete the other plants differ from strategies that produce either Min($R^*$) or Max($G^*$).
Figure 3a. Net carbon production, $G^*$, energy flux to roots, $\eta_r G^*$, energy flux to foliage, $\eta_f G^*$, and soil pore water nitrogen, $N_{pore}$, as functions of allocation fraction of carbon to foliage, $\eta_f$, for fixed $\eta_w$. Nutrient input, $N_{input} = 2.0 \times 10^{-8}$; best competitor has strategies in range $\eta_f = 0.35-0.4$. $\lambda = 0.99$, $Q = 5.0$, $\eta_w = 0.2$. 

Range of $\eta_d$ over which species can mutually invade each other. No species with $\eta_d$ outside of this range can invade.
Figure 3b. Net carbon production, $G^*$, energy flux to roots, $\eta_r G^*$, energy flux to foliage, $\eta_f G^*$, and soil pore water nitrogen, $N_{\text{pore}}$, as functions of allocation fraction of carbon to foliage, $\eta_f$, for fixed $\eta_w$. $N_{\text{input}} = 10.0 \times 10^{-8}$; best competitor has strategies in range $\eta_f = 0.33-0.37$. $\lambda = 0.99$, $Q = 5.0$, $\eta_w = 0.2$. 

Allocation strategy, $\eta_f$
Figure 3c. Net carbon production, $G^*$, energy flux to roots, $\eta_r^* G^*$, energy flux to foliage, $\eta_f^* G^*$, and soil pore water nitrogen, $N_{pore}$, as functions of allocation fraction of carbon to foliage, $\eta_f$, for fixed $\eta_w$. $N_{input} = 12.5 \times 10^{-8}$; best competitor has strategies in range $\eta_f = 0.2-0.26$. $\lambda = 0.99$, $Q = 5.0$, $\eta_w = 0.2$. 

Max($\eta_f G$) Min($N_{pore}$)
Conclusions

Maximum energy flux is somewhat consistent with the $R^*$ rule in this model.

The vascular plants that are the best competitors are neither those that minimize $R^*$ (soil pore water nutrient concentration, $N_{pore}^*$, here) nor those that maximize power (net rate of carbon production, $G^*$, here).

But we would like to get more analytic results for these.
Nutrient cycling in terrestrial ecosystems involves not only the vertical recycling of nutrients at specific locations in space, but also biologically driven horizontal fluxes between different areas of the landscape.

This latter process can result in net accumulation of nutrients in some places and net losses in others. We examined the effects of such nutrient-concentrating fluxes on the $R^*$ rule, which predicts that the species that can survive in steady state at the lowest level of limiting resource, $R^*$, can exclude all competing species.
Basic Assumption

We assumed that tree island processes draw nutrients from outside the zone of local recycling at a rate proportional to the local biomass density.

- Evapotranspiration
- Import by nesting birds
- Dry deposition from air currents
The Everglades landscape shows accumulation of nutrients (P) in tree islands that is high relative to the surrounding marsh (100-fold relative differences in concentration in soil solution between marsh and tree islands). Why are the plants in the marsh so much more effective at reducing the concentration of soil nutrients, when the tree islands are pumping more energy?
Fig. 1. Schematic of model used in this paper. It is a modified version of the G'DAY model (Comins and McMurtrie, 1993), with the details of litter decomposition and soil processes omitted, but an available soil pore water nutrient pool added. The foliage and root compartments have separate variables for carbon and nutrient. Nutrient fluxes are represented by solid lines and carbon fluxes by dashed lines.
As a function of the magnitude of external input, the relationship between $\max( \eta_r G^*)$ and $N_{pore}^*$ could switch from the traditional $R^*$-rule to the opposite, where $N_{pore}^*$ is maximized at the point of $\max( \eta_r G^*)$.

This could be shown analytically by an extension of the preceding analysis. But again, we cannot solve explicitly for $G^*$. 
**Fig. 2c.** Tree growth rate (carbon fixed per unit time), $G^*$, carbon flux to roots, $\eta_r G^*$, carbon flux to foliage, $\eta_f G^*$ and soil pore water nutrient, $N_{pore}^*$ ($\times 10^4$), as functions of allocation fraction of carbon to foliage, $f$, for four different values of the biomass-dependent external nutrient input, $\Psi$. (c) $\Psi = 0.000035$. Other parameters are $q = 0.005 \text{ kgm}^{-2} \text{ yr}^{-1}$, $\nu r = 0.008$, $\gamma_f = 0.10 \text{ yr}^{-1}$, $\gamma_r = 0.30 \text{ yr}^{-1}$, $G_0 = 7.56 \text{ kg Cm}^{-2} \text{ yr}^{-1}$, $\gamma_0 = 0.06$, $g_N = 3.00$, $k_N = 0.01$, $br = 1.0 \text{ m}^2 \text{ kg}^{-1}$, $bf = 2.5 \text{ m}^2 \text{ kg}^{-1}$, $kf = 0.50$, $kr = 0.01$, and $N_{input} = 0.0025 \text{ kg kg}^{-1}$. 

Primary production allocated to roots

Available nutrient concentration
Primary production allocated to roots

Available nutrient concentration

**Fig. 2d.** Tree growth rate (carbon fixed per unit time), $G^*$, carbon flux to roots, $\eta_r G^*$ carbon flux to foliage, $\eta_f G^*$ and soil pore water nutrient, $N_{\text{pore}}^*$ ($\times 10^4$), as functions of allocation fraction of carbon to foliage, $f$, for four different values of the biomass-dependent external nutrient input, $\Psi$. (d) $\Psi = 0.00005$. Other parameters are $\Psi = 0.9993$, $q = 0.005 \text{ kg m}^{-2} \text{ yr}^{-1}$, $\nu r = 0.008$, $\gamma_f = 0.10 \text{ yr}^{-1}$, $\gamma_r = 0.30 \text{ yr}^{-1}$, $G_0 = 7.56 \text{ kg C m}^{-2} \text{ yr}^{-1}$, $g_N = 0.06$, $k_N = 0.01$, $br = 1.0 \text{ m}^2 \text{ kg}^{-1}$, $bf = 2.5 \text{ m}^2 \text{ kg}^{-1}$, $k_f = 0.50$, $kr = 0.01$, and $N_{\text{input}} = 0.0025 \text{ kg kg}^{-1}$. 
Conclusions

The minimization of $R^*$ for the same strategy that maximizes the flux of carbon to fine roots holds only for the special case that there are no inputs of nutrient to the plant that are positively related to plant biomass.

Nutrient fluxes across the landscape may result from various factors dependent on biomass, so that the $R^*$ rule is replaced by more complex relationships.

But these results are again somewhat limited.
Thank you

Questions?

Slide from Hal Wanless