

Applications: Examples from the Everglades and Elsewhere

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U. S Geological Survey

*Meeting: Emerging Challenges at the Interface of
Mathematics, Environmental Science, and Spatial Ecology*

BIRS, Banff, July 2011

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

Leonel da Silveira Lobo Sternberg, University of Miami

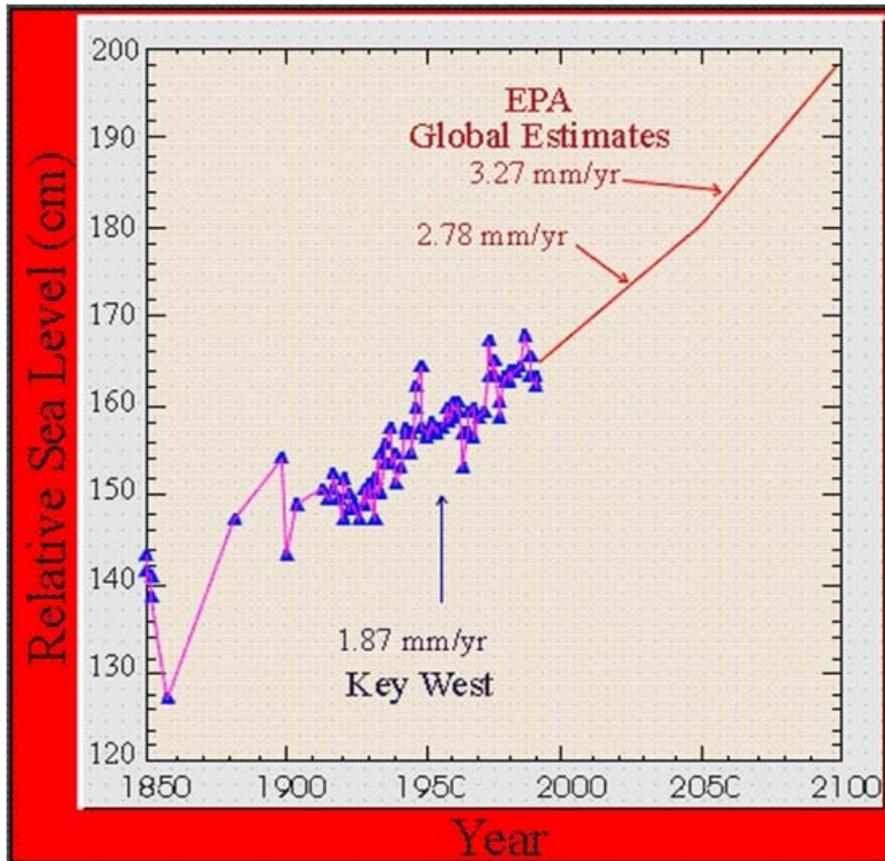
Jiang Jiang, University of Miami

Su Yean Teh, Universiti Sains Malaysia

Hock Lye Koh, Universiti Sains Malaysia

Tom J. Smith, U.S. Geological Survey

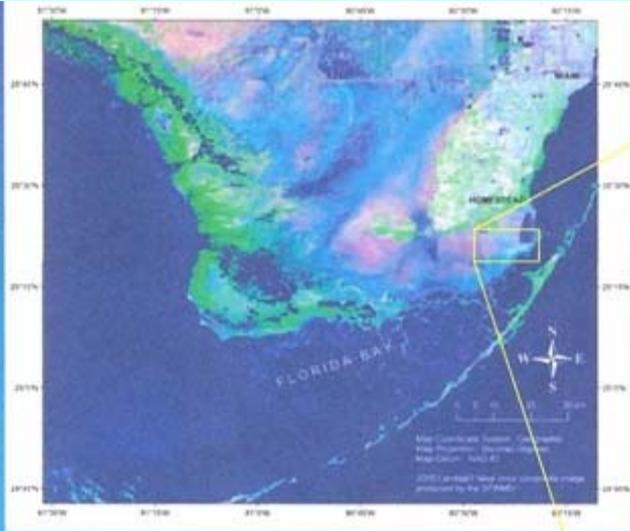
Sea level is rising at an increasing rate...



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

... and it is possible that discrete salinity inundation events are damaging forests in Florida, possibly leading to vegetation shifts.

Sea level rise and pine forest loss in the Florida Keys



MS Ross¹, K Zhang¹, JP Sah¹, JJ O'Brien² & RG Ford³

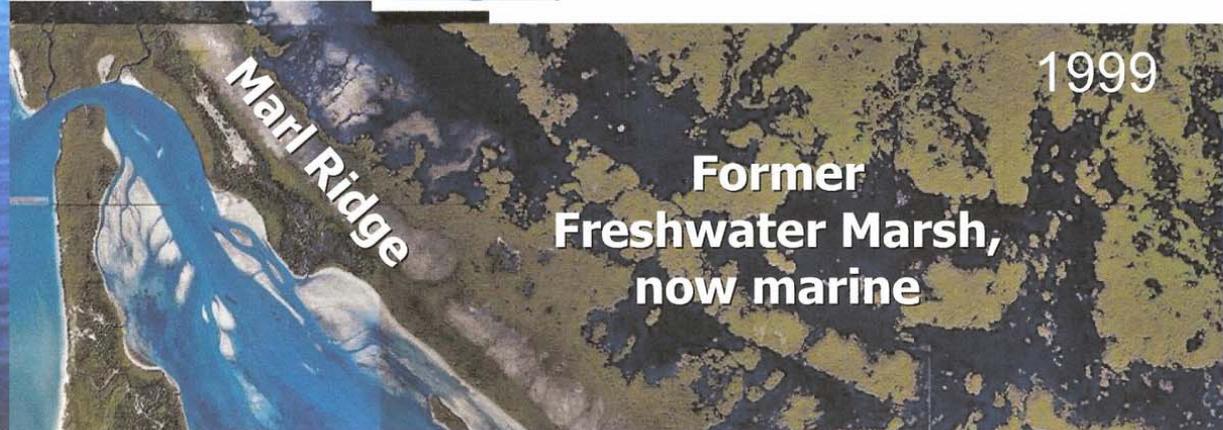
¹Florida International University, ²US Forest Service, ³UC Santa Cruz

Slide from Mike Ross

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.

The freshwater marsh is now a shallow marine lagoon



Mangrove and tropical hardwood hammocks are two types of Everglades vegetation that overlap in geographic area, though generally hardwoods occupy slightly higher elevation.



Mangroves (halophytic)



Hardwood Hammock (glychophytic)



Mangrove-Hardwood Hammock Boundary – Key Largo



This sharp boundary is maintained despite only a tiny elevation gradient

Image © 2008 DigitalGlobe

© 2008 Tele Atlas

Streaming ||||| 100%

Pointer 25°12'35.99" N 80°20'37.00" W

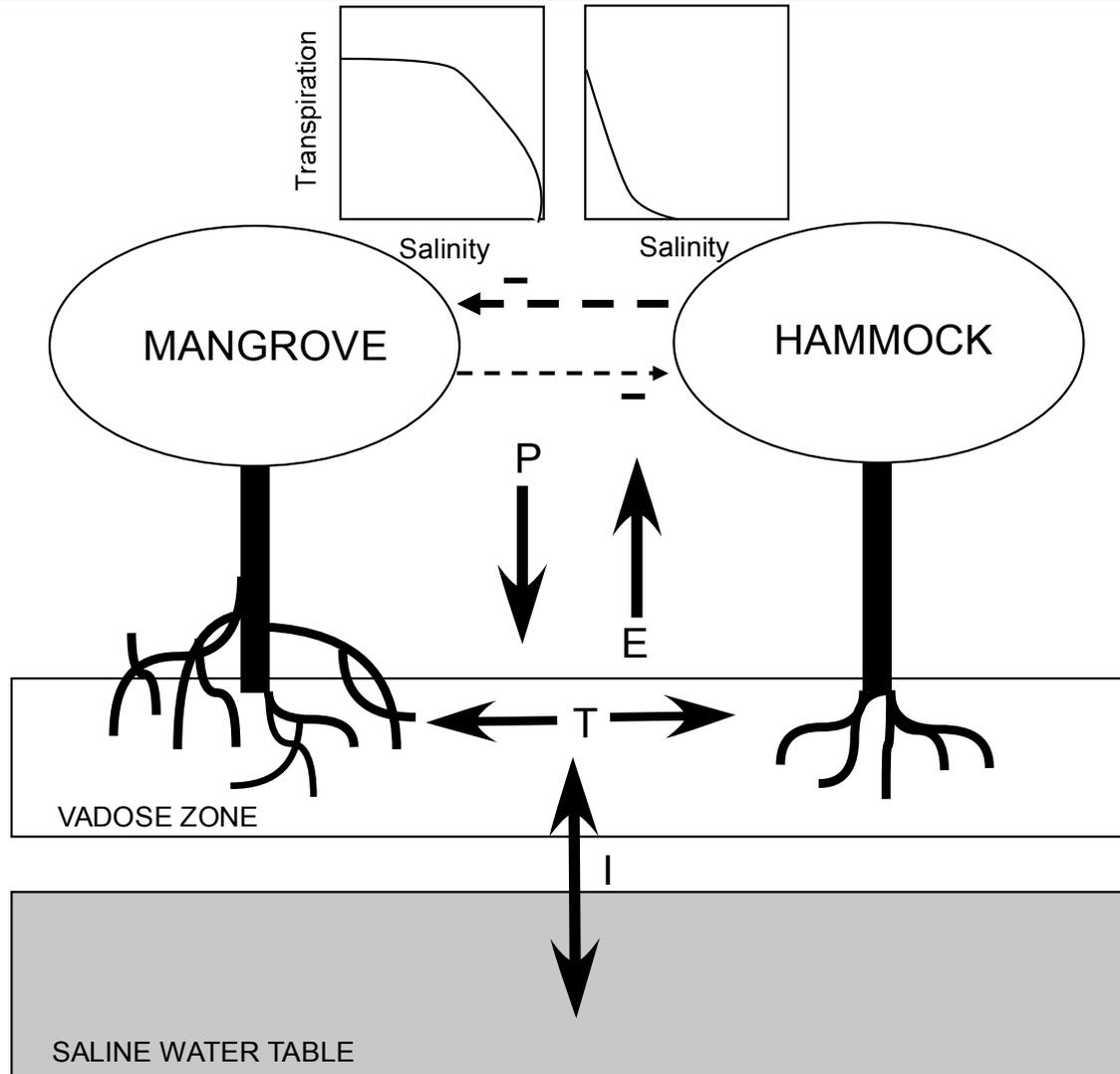


Mechanisms of Boundary Stability

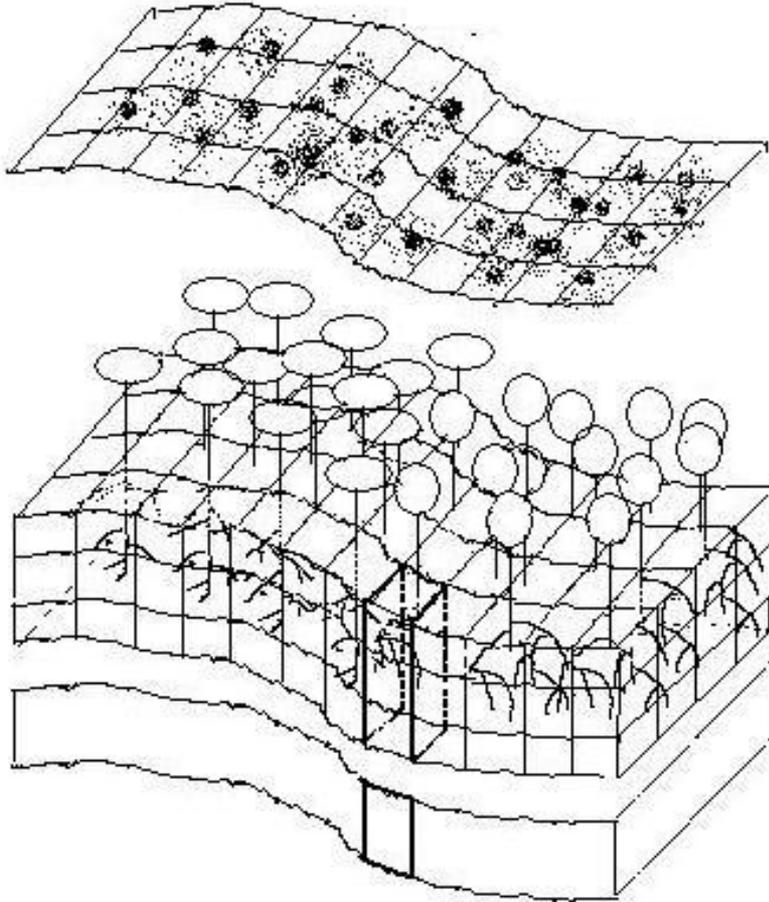
Both mangroves and hammock species obtain their water from the vadose zone (unsaturated soil zone). In coastal areas this vadose zone is underlain by highly brackish ground water, so that evapotranspiration, by depleting water in the vadose zone during the dry season, can lead to infiltration by more 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

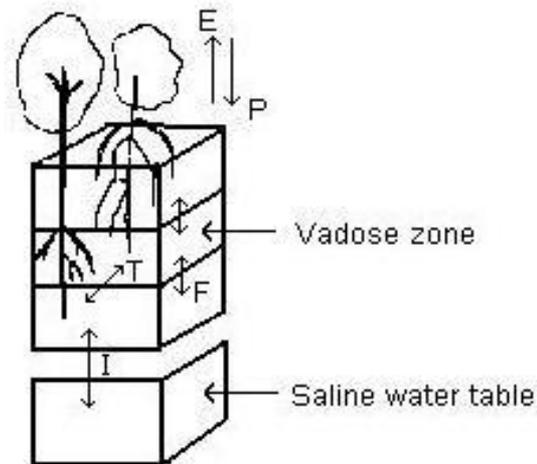
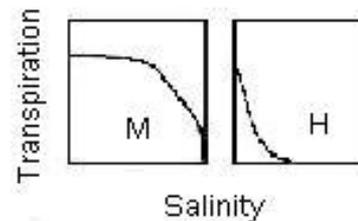
---Soil water and salinity dynamics

- Soil water fluxes were simulated by Darcy's equation

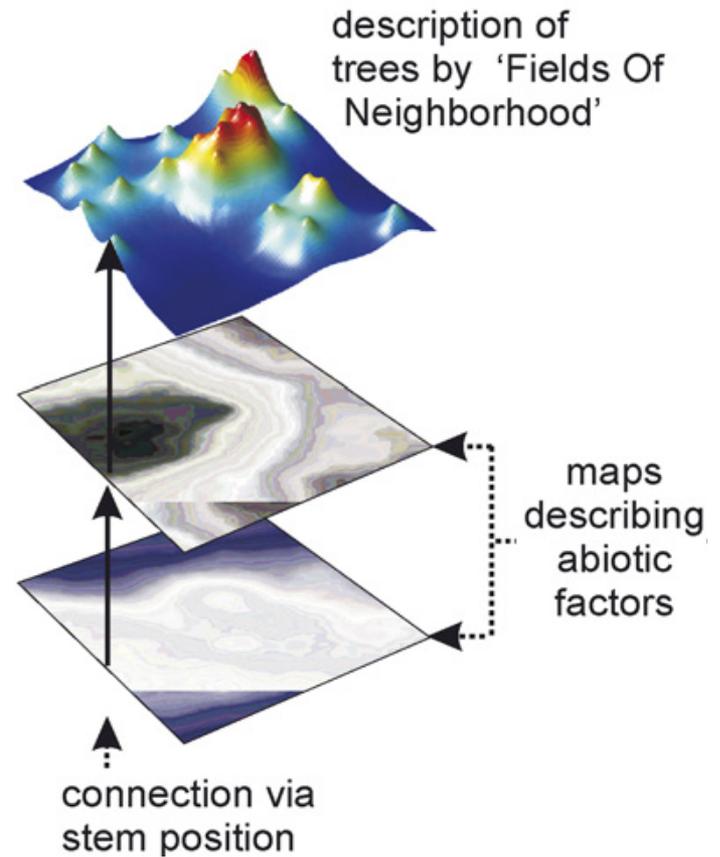
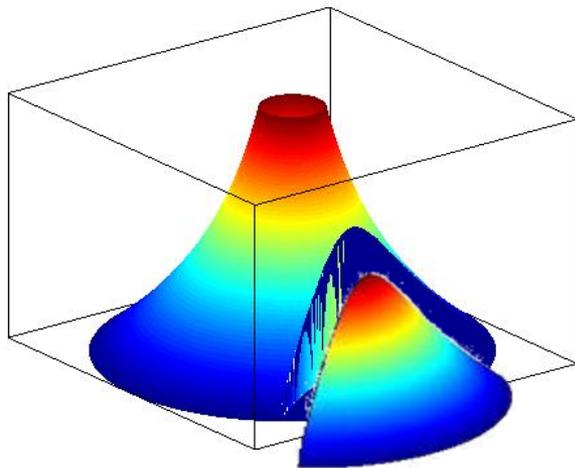
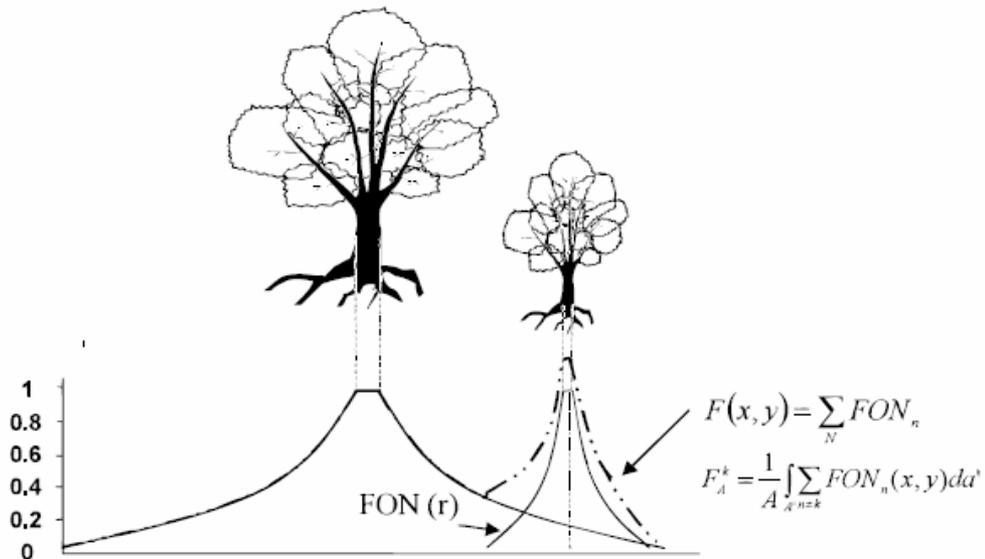
$$\theta \frac{\partial S_v}{\partial t} = T S_v - F \frac{\partial S_v}{\partial z}$$

salinity increase due to uptake of water by roots

salinity change due to water fluxes

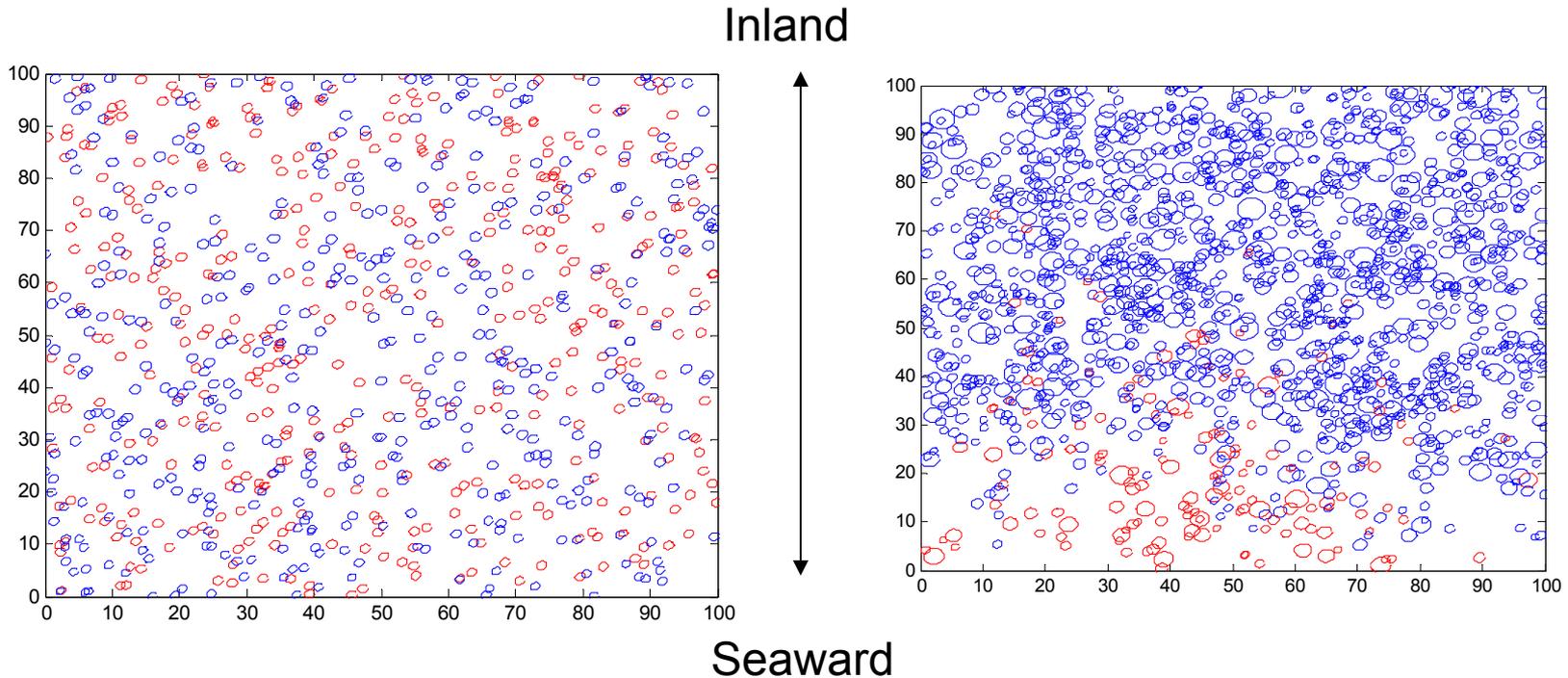


Plans are to replace our water and salinity modeling by SUTRA, by C. I. Voss and A. M. Provost



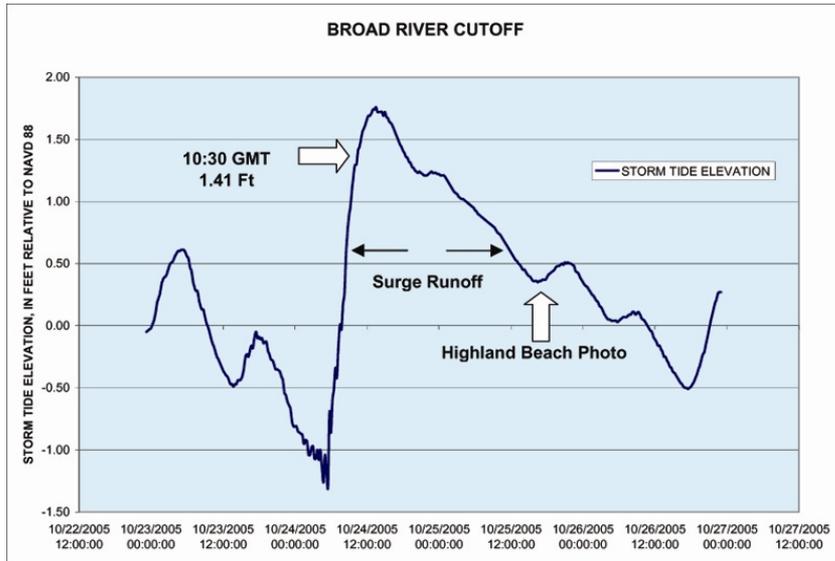
Fields of Neighborhood (Berger, 2000)

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

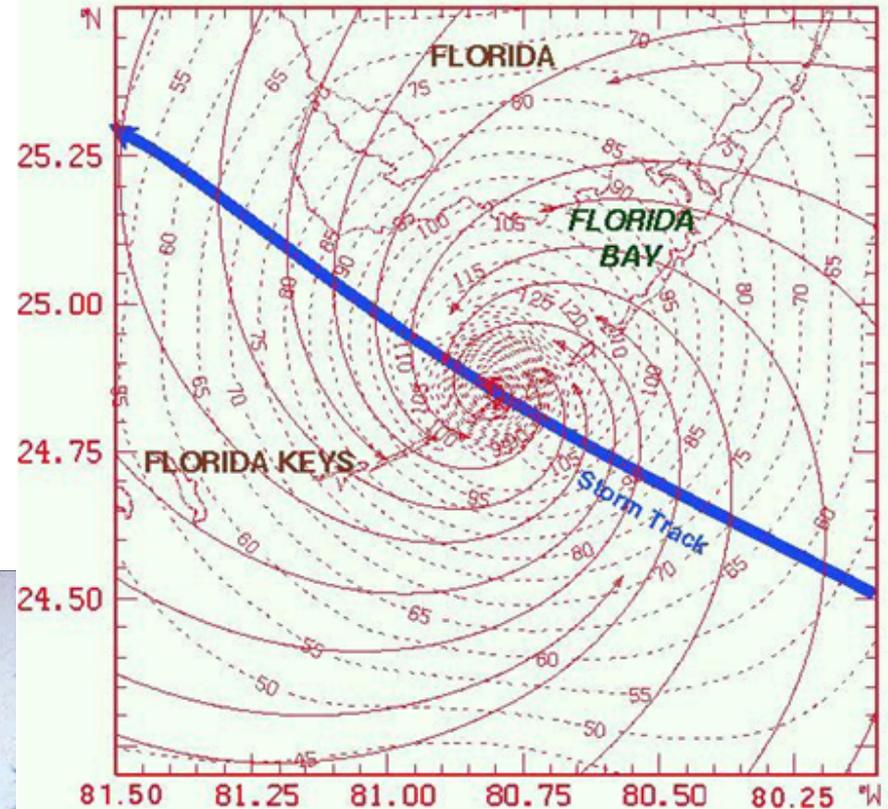


Sometimes the monitoring stations don't survive the storm surge

The direct effects have been estimated by reconstructing the wind field of the hurricane...



Labor Day Hurricane - 0300 UTC 3 Sept. 1935
10-min mean winds (kt) @ 10 m for marine exposure



1935 Labor Day Hurricane Wind Field

Wind speed = 60 meters/second

Basin: Florida Bayv2 <key>

Storm: C:/slosh.pkg/sloshdsp/rexfiles/download/1935ke

SLOSH Wind field

1 min avg KTS(MPH)



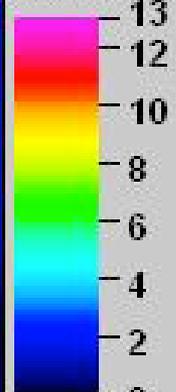
Envelope of High Water



Cape Sable

Straits of Florida

Stm Tide ft
Abv Grid Cell



Tide level:
0.2 ft

... and created a storm surge

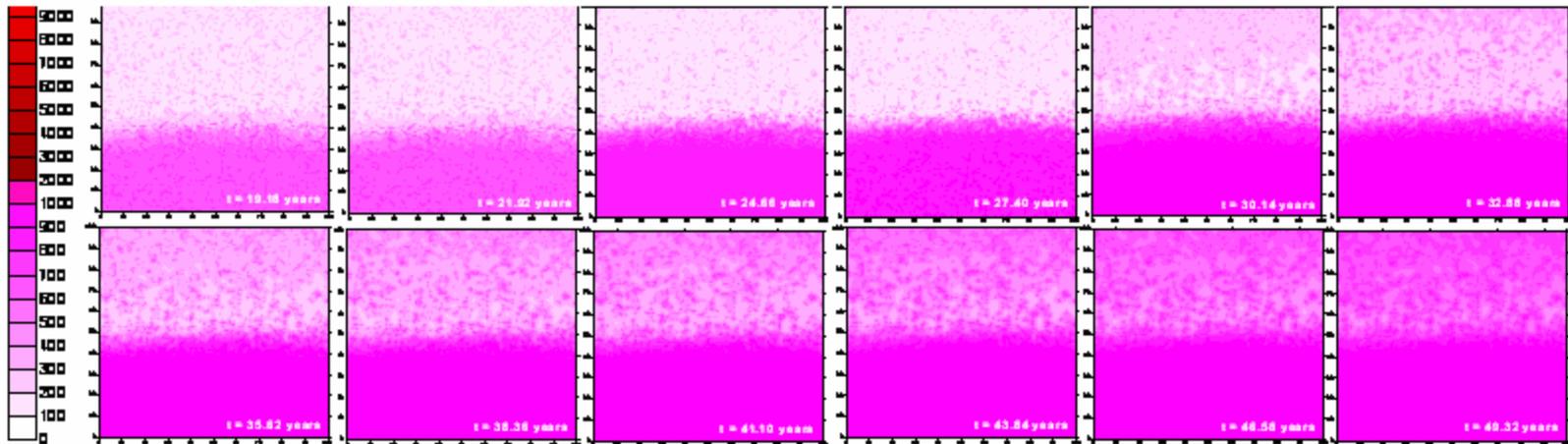
Slide from Dennis Krohn

....and we have simulations that tend to show this can happen

This all tends to require detailed simulations... but

19.18 years

27.4 years ; storm surge



Darker magenta is higher mangrove density

50 ye

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.

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

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

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

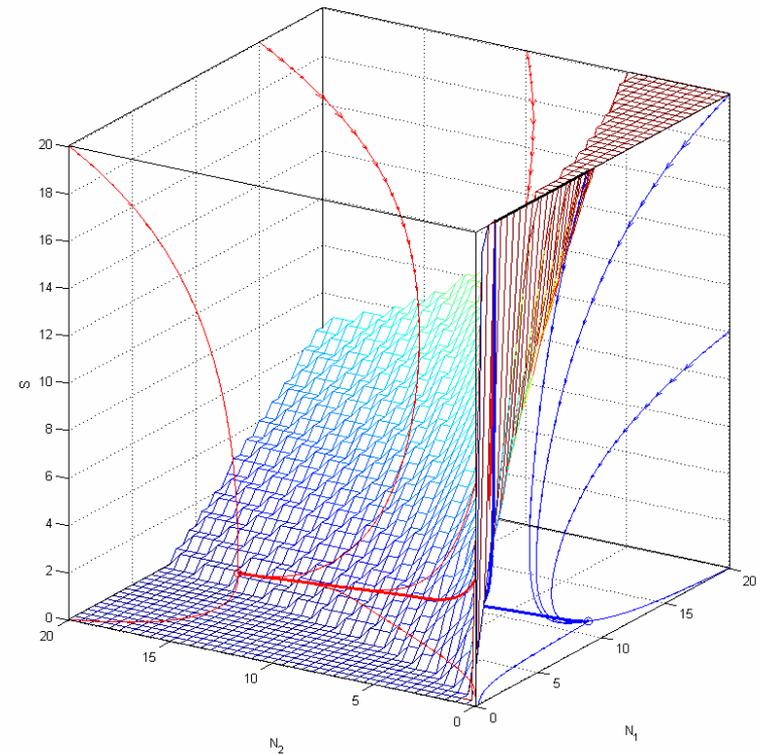
where D is the diffusion coefficient, z is distance from the seaward edge of the landscape. The groundwater salinity, g, was arbitrarily chosen to represent the spatial heterogeneity of the system. It is assumed that g is 30 ppt at the seaward edge and 0 at the landward edge.

Mangrove – Hammock Ecotone

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

Objectives

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

Burkhead &
Trexler



Bluegill
Lepomis macrochirus



Coastal Shiner
Notropis petersoni



Least killifish
Heterandria formosa



Pygmy Sunfish
Elassoma evergladii



Sailfin molly
Poecilia latipinna



Striped Mullet
Mugil cephalus



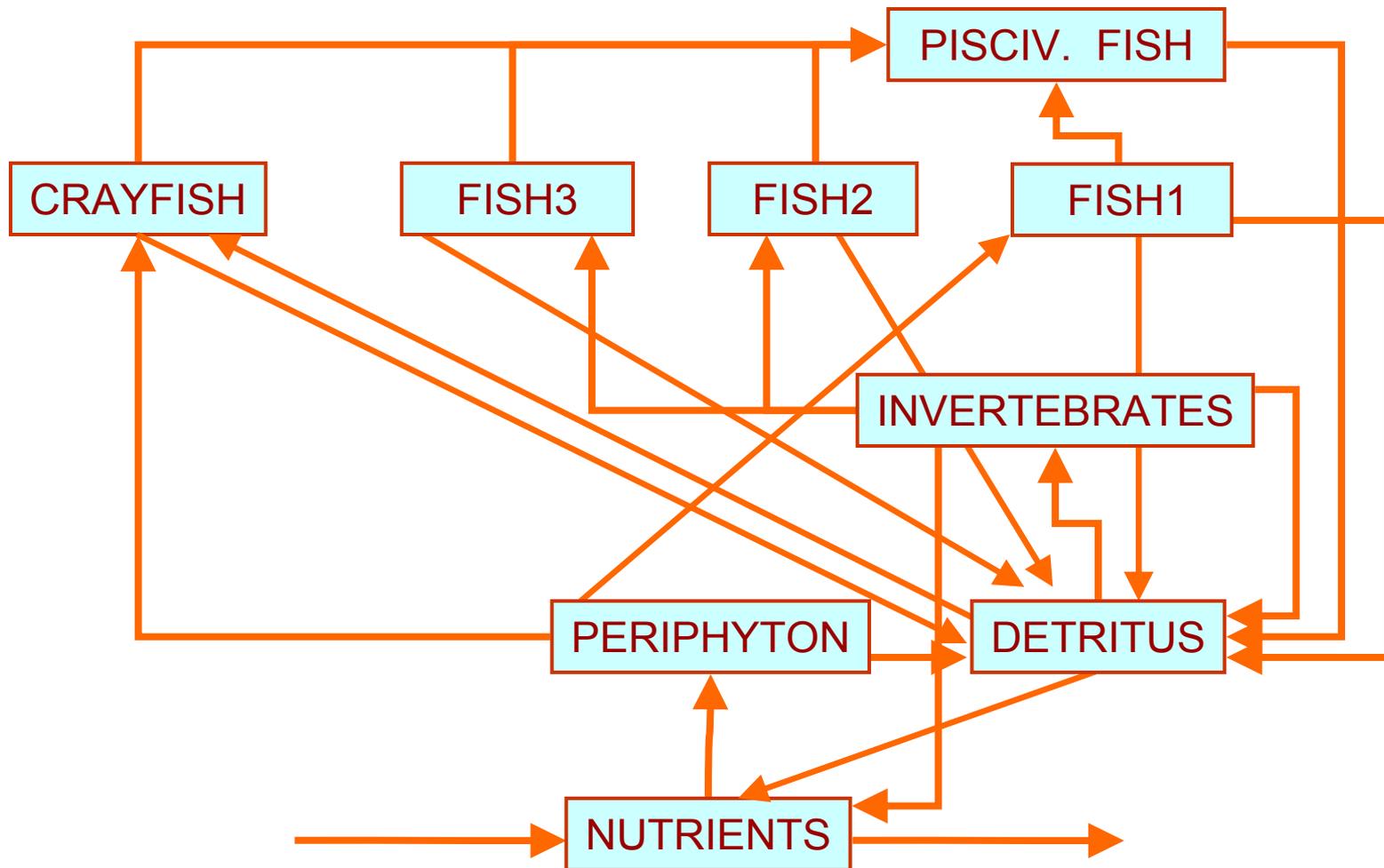
Swamo Darter
Etheostoma fusiforme



Model Structure

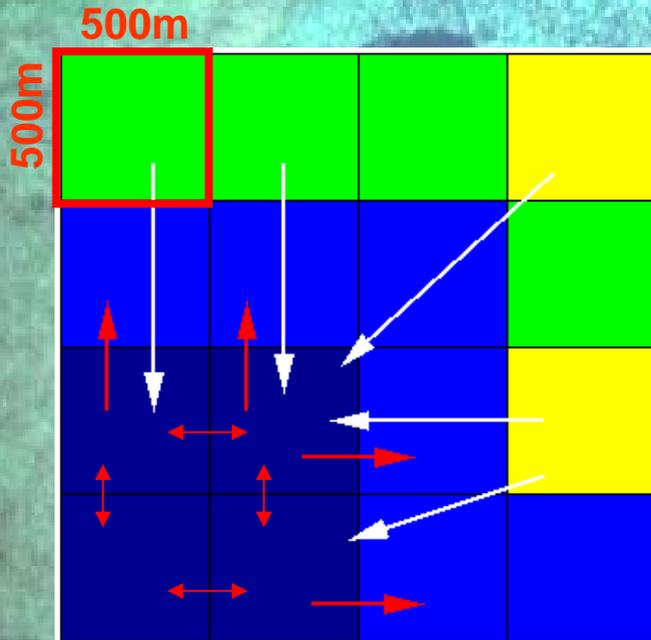
- Classical food web model
- Part 1: ODE describe structure and the fluxes between spatial cells
 - Functional responses, recycling
- Part 2: rules for movement of migratory species between cells
- Spatially explicit, grid-based ($n \times 10k$)

GEFISH Complex Food Web



GEFISH: Movement Rules for Fish

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

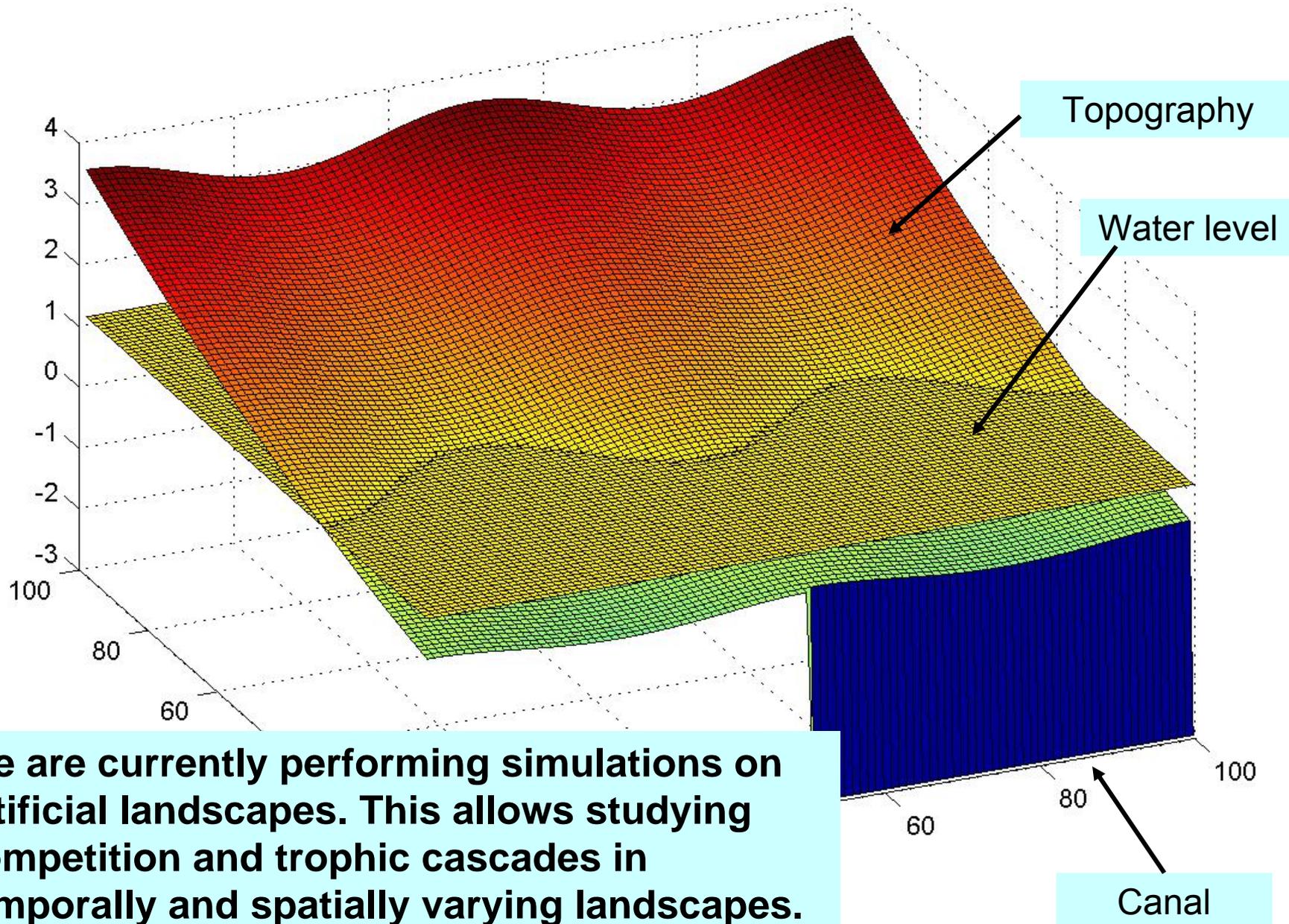


Red: net diffusional movement from high fish density to low density areas

Water Level: Day = 220

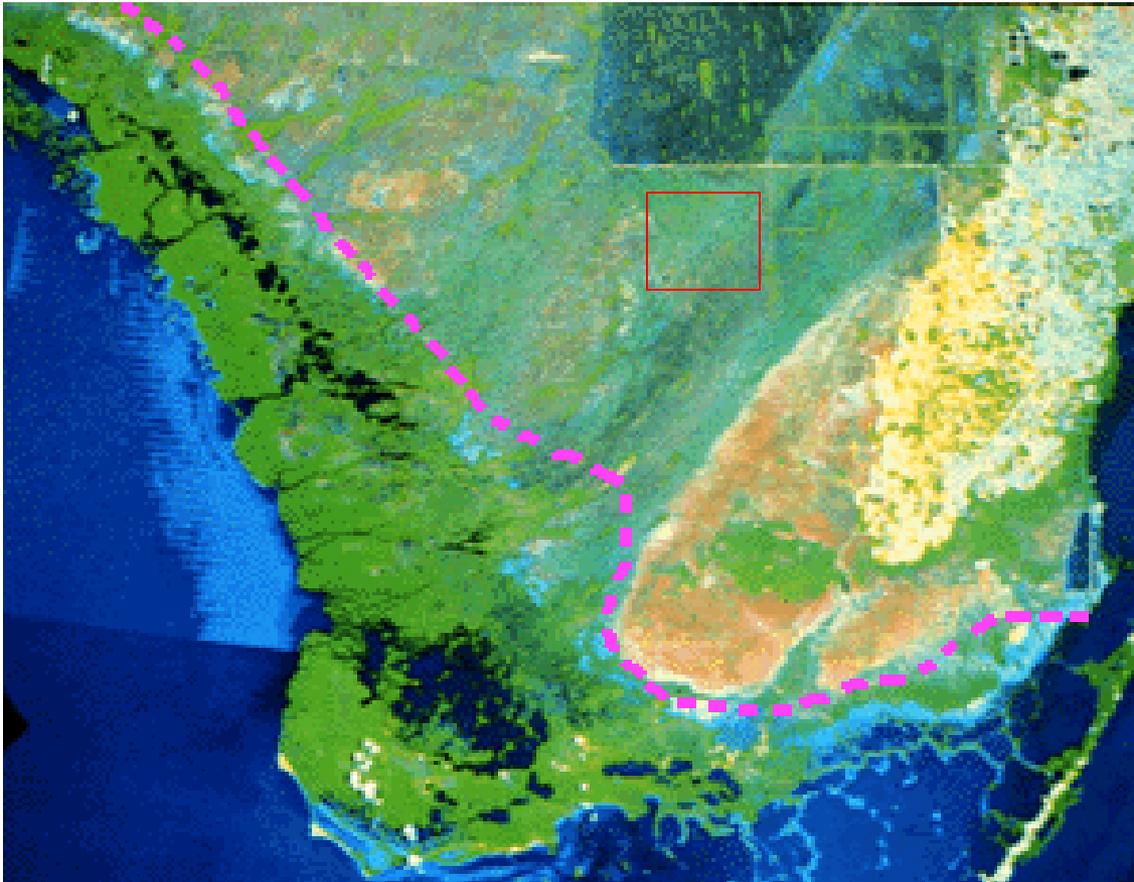
Amplitude = 0.85

MWL = 1.45



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

Analytic Version

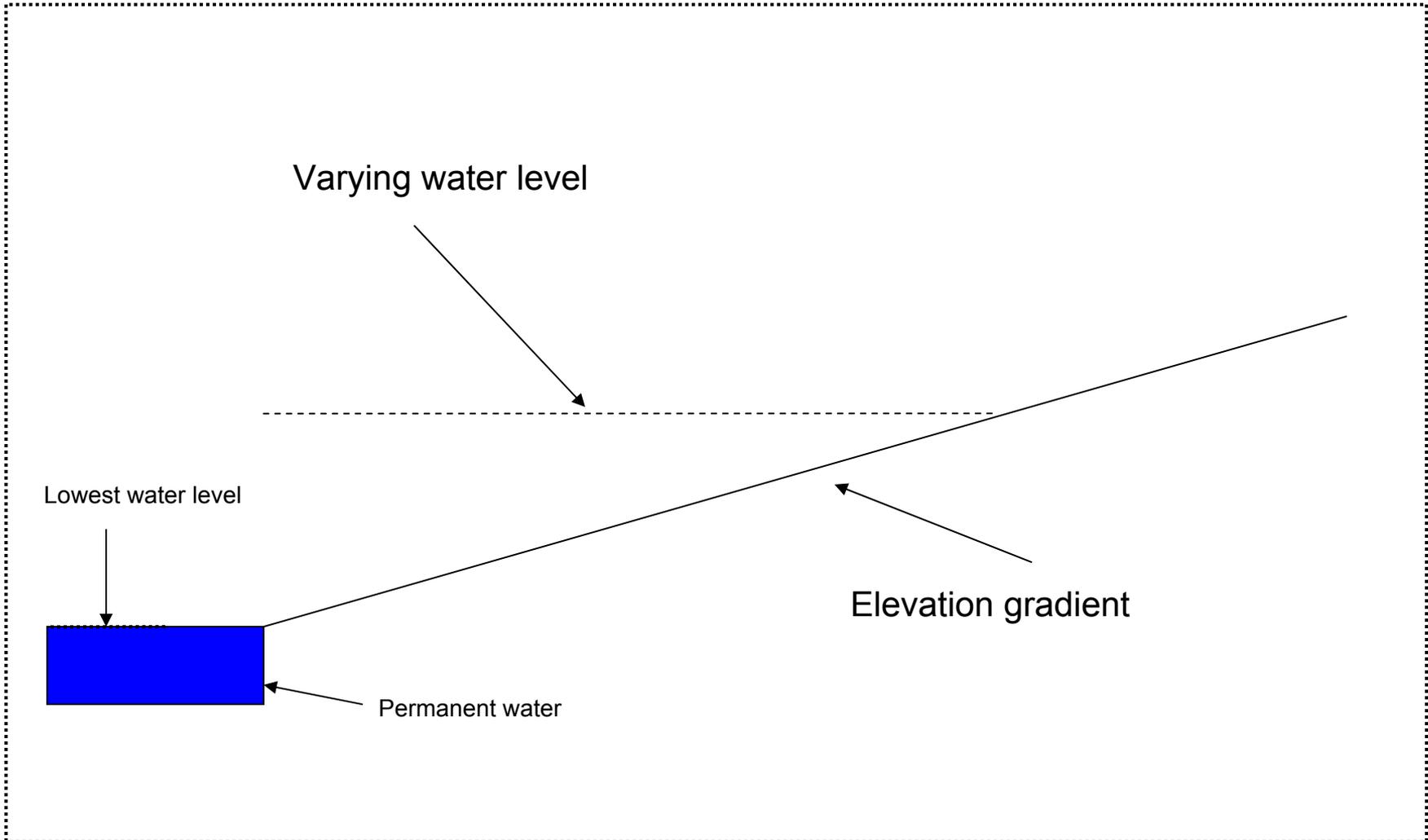
If we assume that the fish can follow a resource gradient, where the resource emerges immediately as an area becomes wetted. We have the equations:

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

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

We call this the ‘dynamic IFD hypothesis’.

We can model the landscape in a very simple way



Analytic Version

We also used an alternative pure diffusion model, in which we used estimates of the diffusion rate, D ,

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

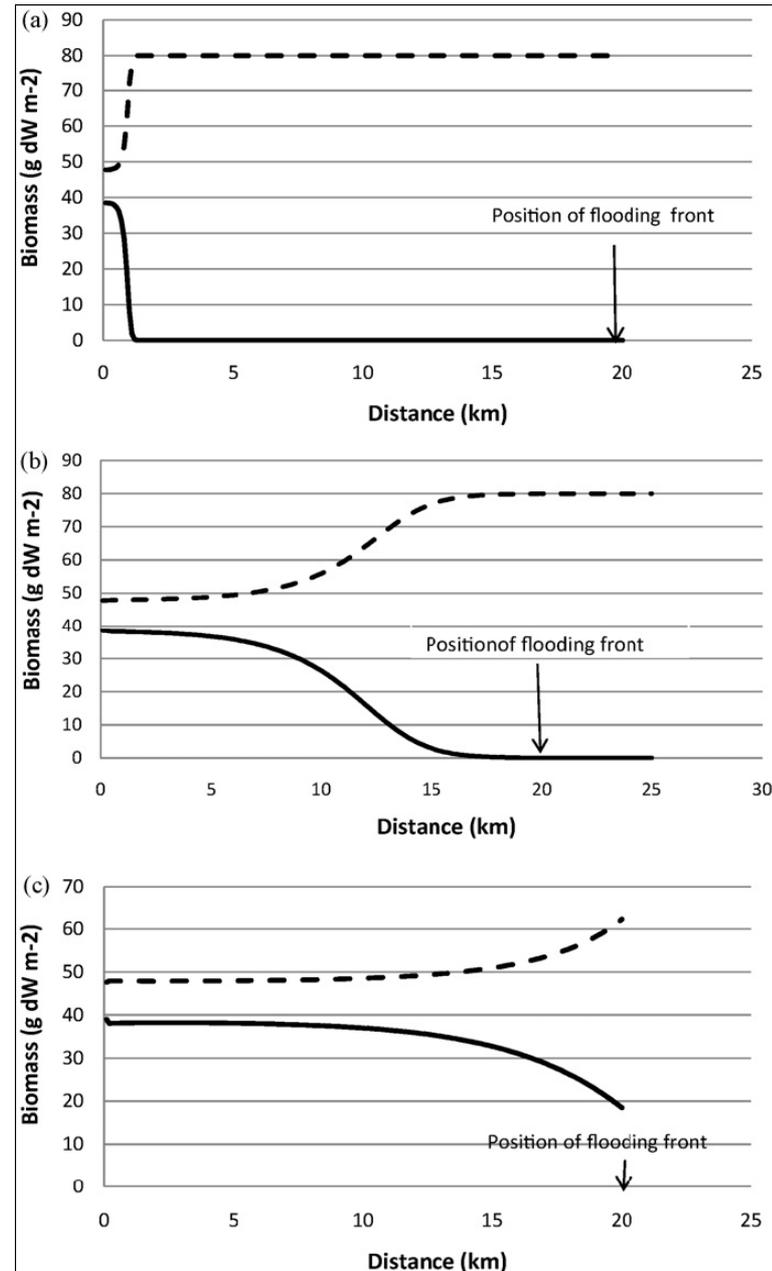
$$\frac{\partial F(s,t)}{\partial t} = \frac{\gamma fR(s,t)F(s,t)}{1 + hfR(s,t) + wfF(s,t)} - mF(s,t) + D \frac{\partial^2 F(s,t)}{\partial s^2} ,$$

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

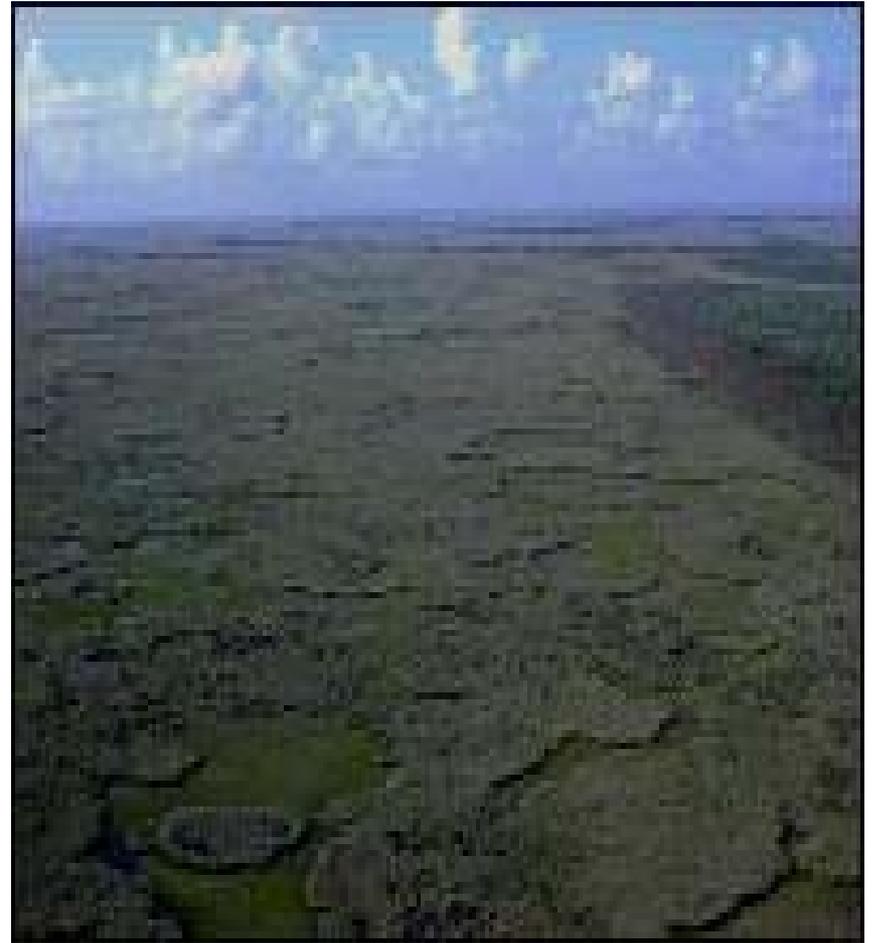
- The Everglades is characterized by large areas of 'ridge and slough' landscape.
- [see Larsen et al., *Ecological Monographs* 77:591-614, 2007; Ross et al., *Hydrobiologia* 569:37-59, 2006)]



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



A DELICATE BALANCE: ECOHYDROLOGICAL FEEDBACKS GOVERNING LANDSCAPE MORPHOLOGY IN A LOTIC PEATLAND

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Abstract. The Everglades ridge and slough landscape is characterized by elevated sawgrass ridges regularly interspersed among lower and more open sloughs that are aligned parallel to the historic flow direction. Landscape degradation, characterized by topographic flattening, has coincided with a century of drainage, levee construction, nutrient enrichment, and flow reductions. Here we develop a conceptual model of Everglades landscape dynamics based on a literature synthesis and supported by the numerical model PeatAccrete. We propose that two feedback mechanisms govern landscape characteristics. The first, simulated with PeatAccrete, involves differential peat accretion governed by water level and phosphorus concentration, leading to the attainment of an equilibrium ridge elevation relative to slough. Differential peat accretion, however, cannot produce a characteristic ridge width or landscape wavelength. Instead, we propose that feedback between channel morphology and sediment mass transfer controls lateral and longitudinal topographic features, consistent with processes in anabranching rivers. This sediment transport feedback was critical in pattern initiation and evolution, and sediment redistribution from slough to ridge provides a plausible mechanism for preventing gradual ridge expansion. However, PeatAccrete model results show that, in the absence of sediment transport, ridges expand only on the order of meters per century. This result suggests that a combination of factors has driven the widespread disappearance of sloughs over the past century, including altered vertical peat accretion rates that lead to slough infilling. Sensitivity tests indicated that changes in duration and depth of surface water inundation, phosphorus supply, and redox potential have altered differential peat accretion rates in a way that favors topographic flattening. These factors are relatively well defined compared with the role of sediment transport, which requires further quantification. Because both positive and negative feedback processes interact in the Everglades, the trajectory of landscape evolution in time will depend upon current conditions, with areas of remnant ridge and slough topography being more likely than areas of degraded topography to respond to changes in water management in ways that enhance landscape heterogeneity over human timescales. Dual feedbacks between peat accretion and sediment transport are likely important controls on landscape evolution in low-gradient peatlands worldwide with pulsed, unidirectional flow.

Key words: anabranching; Everglades; Florida; geomorphology; landscape ecology; peatland; ridge-slough; wetland; wetland hydrology.

INTRODUCTION

Landscape heterogeneity and patterning increase environmental complexity and biodiversity (Kolasa and Rollo 1991). In lotic ecosystems and floodplains, physical and biological heterogeneity affect and/or are influenced by flow patterns and processes, species distribution and persistence, flux of materials and energy among ecosystem compartments, and predator-prey interactions (Palmer and Poff 1997). Fluvial dynamics often play a major role in regulating ecosystem heterogeneity, and changes in flow management can disrupt the interactions that create heterogeneity, resulting in decreased biodiversity (Ward et al. 1999).

Many low-gradient, lotic wetlands exhibit spatial heterogeneity and even patterning in vegetation distri-

bution, which may develop parallel (longitudinal) or perpendicular to the flow. Examples of wetlands with longitudinal patterning include the ridge and slough landscape (RSL) of the Florida Everglades (Science Coordination Team 2003, Ogden 2005), water tracks in boreal fens (Glaser et al. 1981), the Okavango Delta (Ellery et al. 2003, Gumbrecht et al. 2004), morichal wetlands in Colombia and Venezuela (San Jose et al. 2001), buritizal wetlands in the Brazilian Pantanal (Silva et al. 1999), and some floodplain riparian wetlands (Hupp 2000, Steiger and Gurnell 2003). In these wetlands, islands or ridges with trees or herbaceous vegetation are interspersed among open-water conduits and aligned parallel to the flow direction. Here, mechanisms for creating and maintaining environmental heterogeneity are complex, involving feedback between physical and biological processes including peat and organic matter production and redistribution of material

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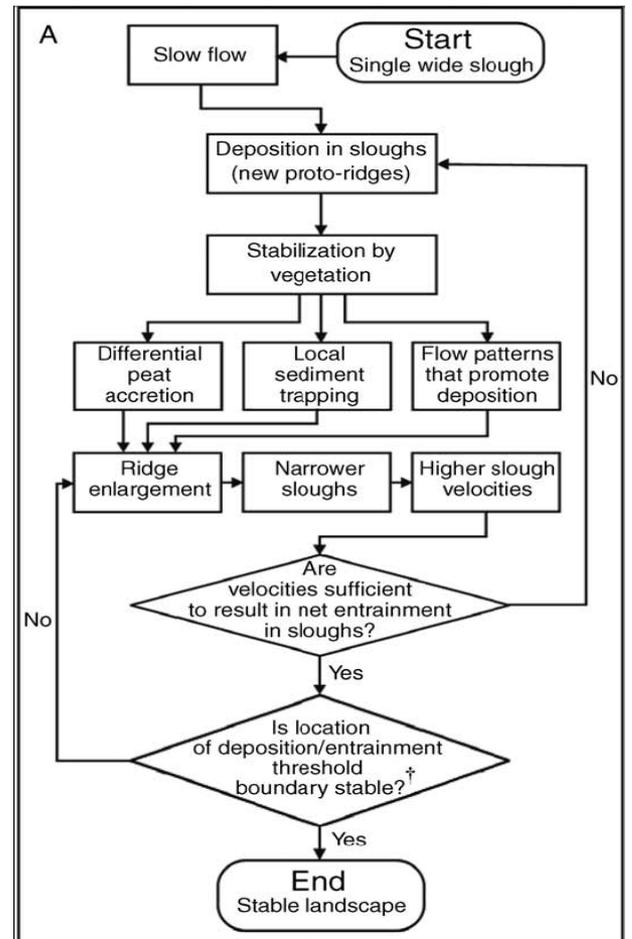
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- To address this problem, the processes that create and maintain patterns must be understood.
- Geologist/ecologists addressed this using hypothesized mechanisms in a detailed process model; e.g., Laurel Larsen et al. (2007), Larsen and Harvey (2011).

- **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.**

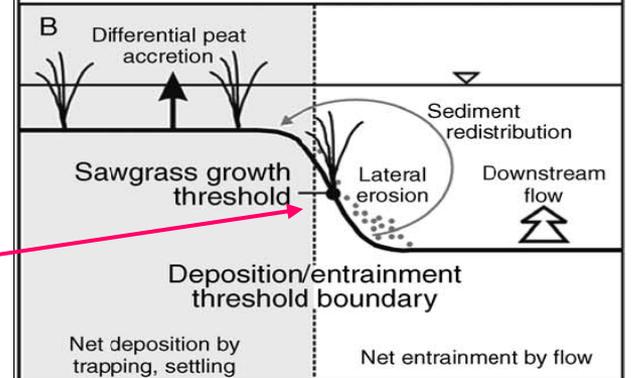
- **Under the differential peat accretion hypothesis, these sawgrass patches may have also accreted peat more rapidly than sloughs, causing further topographic differentiation to an equilibrium elevation difference between ridge and slough.**
- **Once the incipient proto-ridges were initiated, current 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.**





$$\frac{\partial(\text{peat elevation})}{\partial t} = \frac{\partial^2(\text{peat elevation})}{\partial x^2} + \text{Net Peat Accretion}(x)$$

The gravity erosion is a diffusional process



Spatial population dynamics

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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Netherlands Institute of Ecology, Centre for Limnology

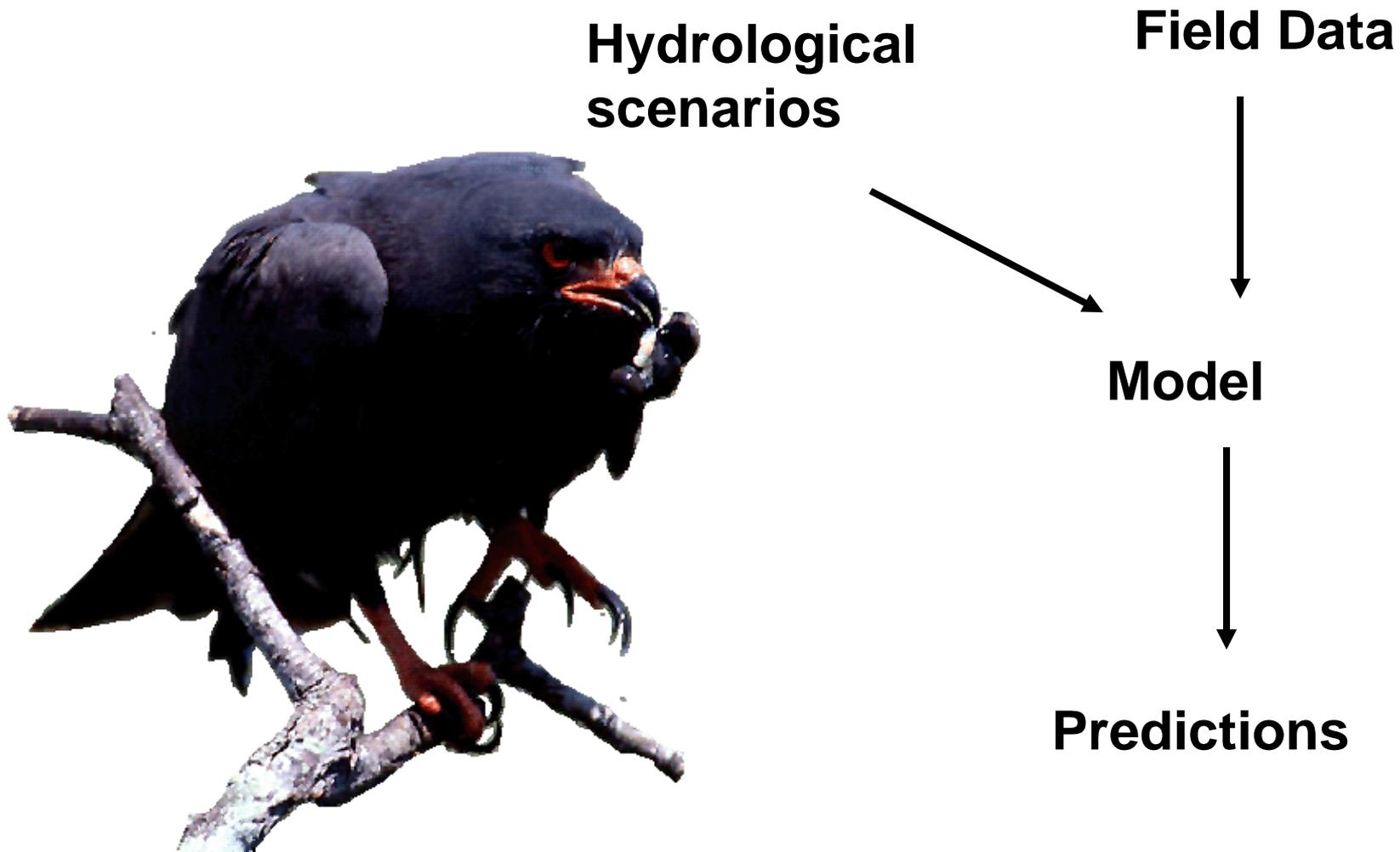
Program website: atlss.org

Mooij, W. M., R. E. Bennetts, W. M. Kitchens, and D. L. DeAngelis. 2002. Exploring the effect of drought extent and interval on the Florida snail kite: Interplay between spatial and temporal scales. *Ecological Modelling* 149 (1-2):25-39.

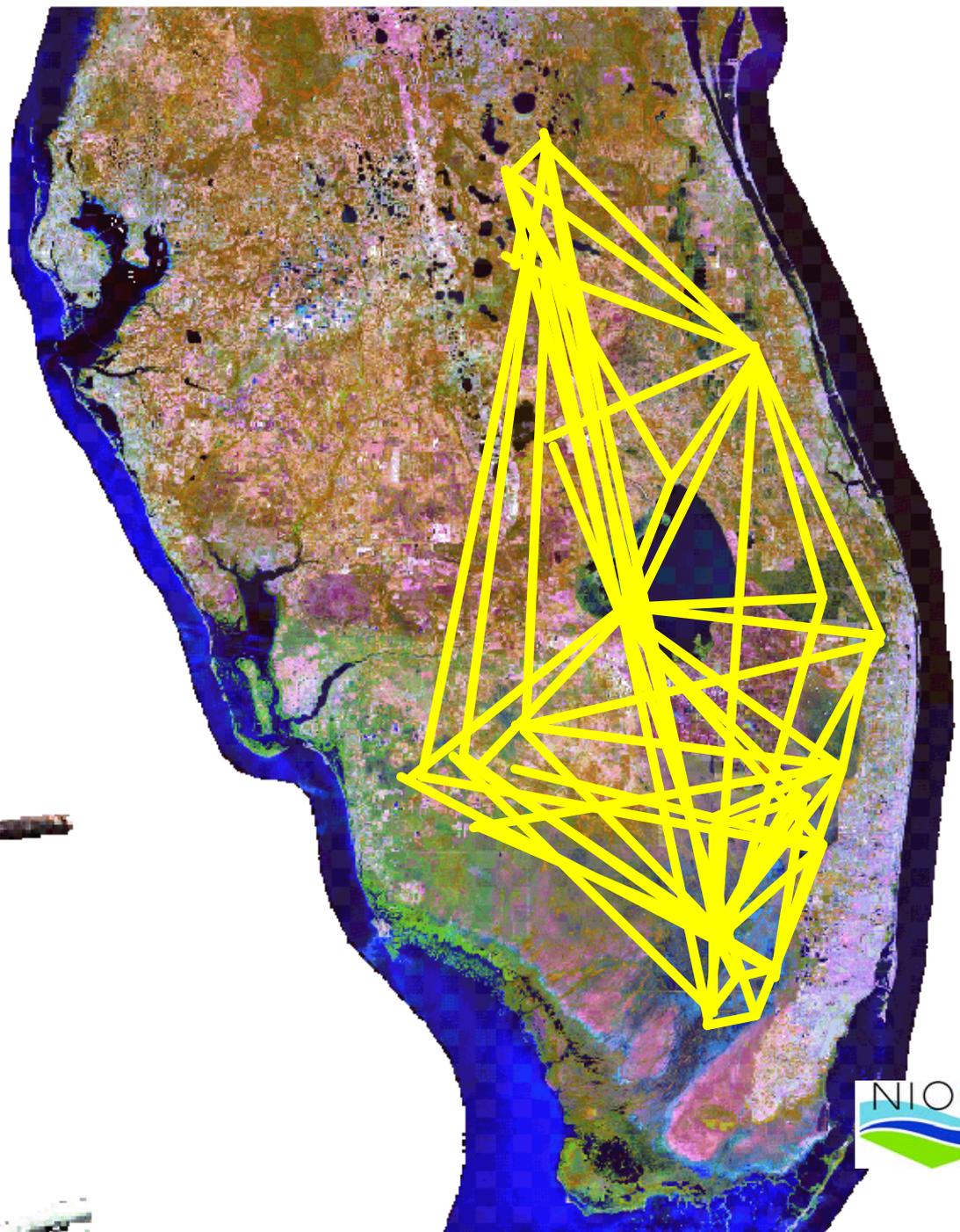
Why model the snail kite?

- 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.

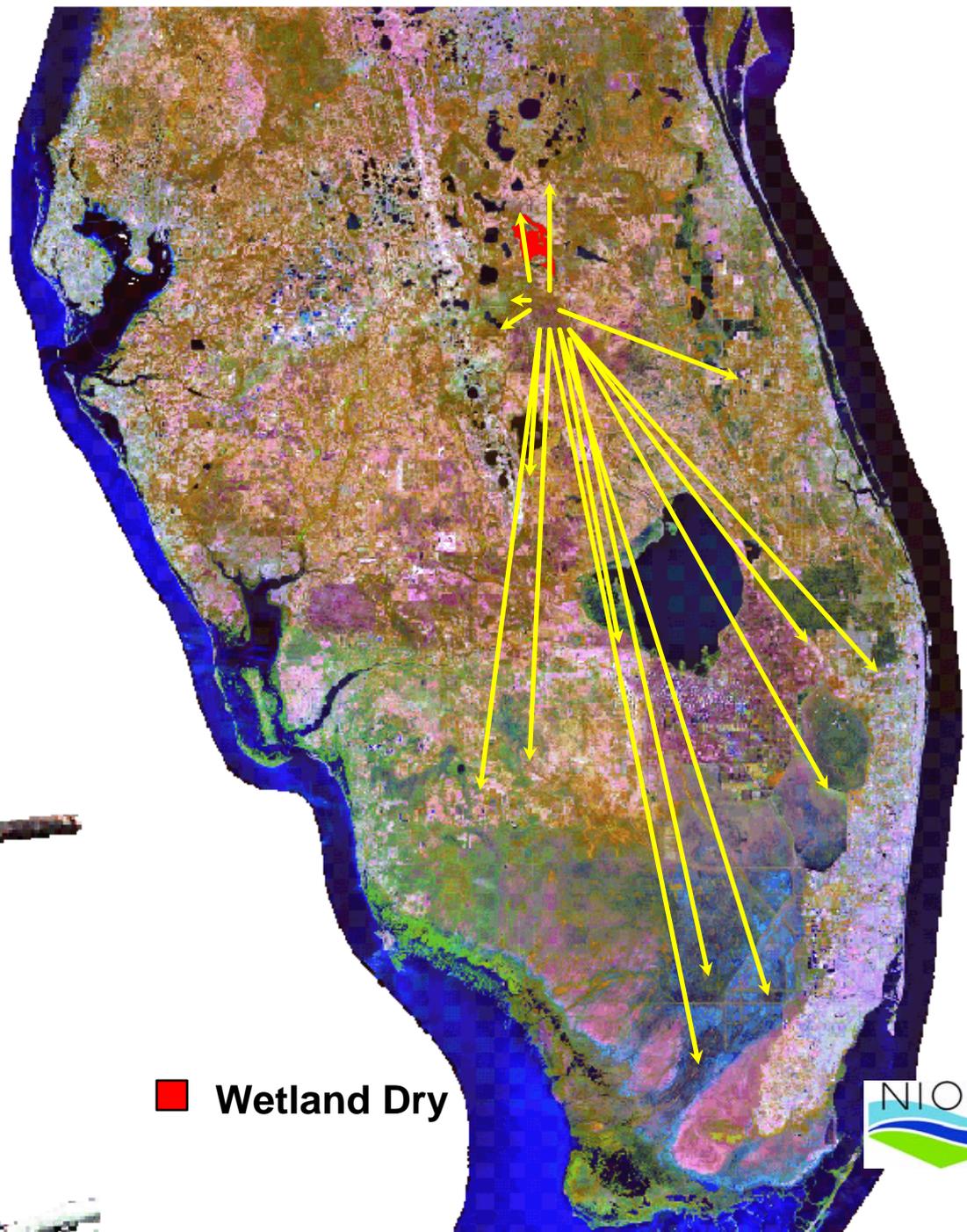
The model incorporates field data on the snail kite to allow examination of its population dynamics under different hydrologic scenarios



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.

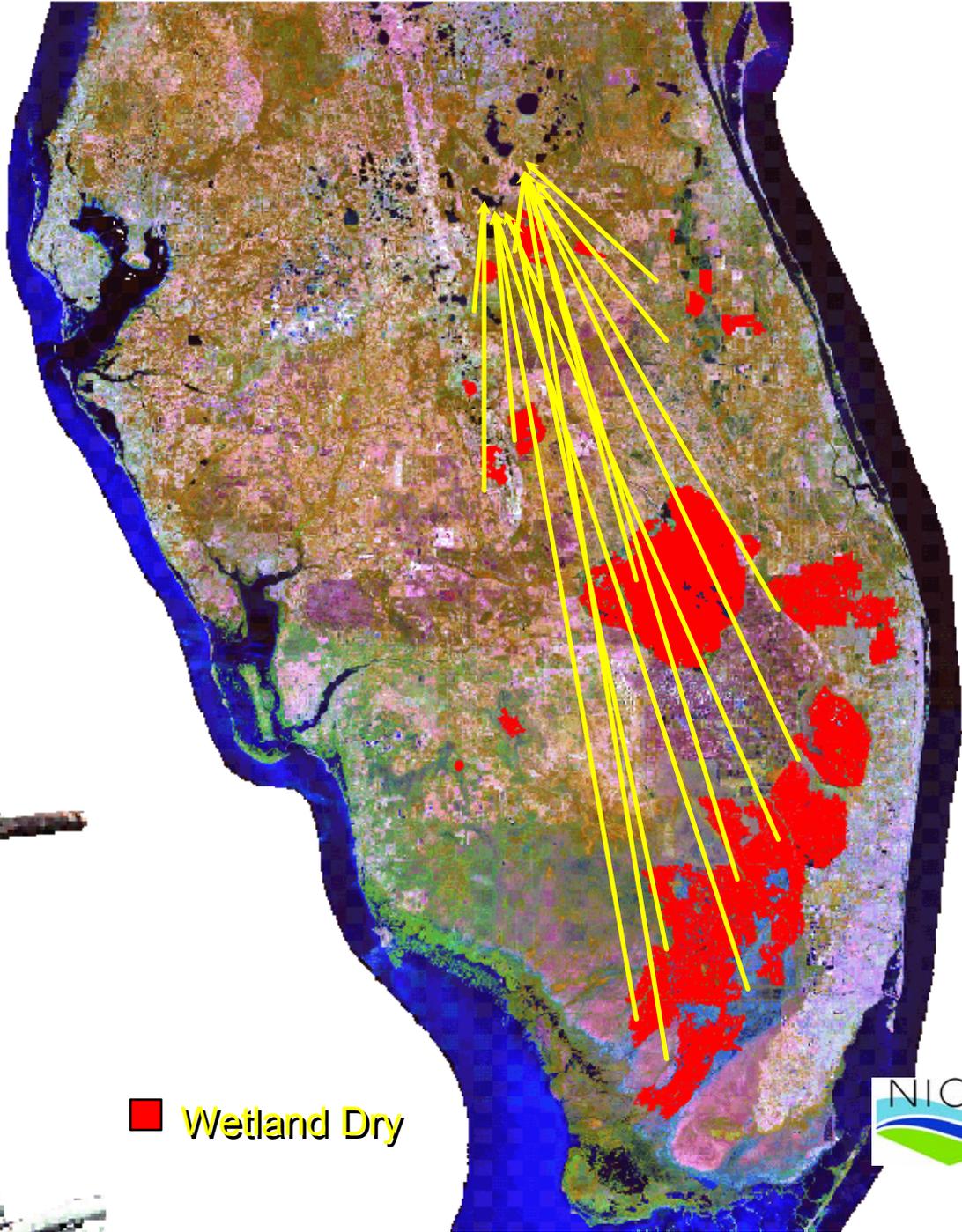


■ Wetland Dry



Widespread Drying Event

Spatially correlated droughts pose a threat



■ Wetland Dry



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 (λ , 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., λ 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.

Tree islands, energy flow and nutrients

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

Shu Ju, Department of Biology, University of Miami

Rongsong Liu, Department of Mathematics, University of Wyoming, Laramie, Wyoming

John P. Bryant, Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska

Stephen A. Gourley, University of Surrey, Guildford, Surrey, United Kingdom

Ju, S. and D. L. DeAngelis. 2009. The R^* rule and energy flux in a plant-nutrient ecosystem. *J. Theor. Biol.* 256:326-332

Ju, S. and D. L. DeAngelis. 2010. Nutrient fluxes at the landscape level and the R^* rule. *Ecological Modelling* 221:141-146

CONTRIBUTION TO THE ENERGETICS OF EVOLUTION*

BY ALFRED J. LOTKA

SCHOOL OF HYGIENE AND PUBLIC HEALTH, JOHNS HOPKINS UNIVERSITY

Communicated, May 6, 1922

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...

It has been pointed out by Boltzmann¹ that the fundamental object of contention in the life-struggle, in the evolution of the organic world, is available energy.² In accord with this observation is the principle³ that, in the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient⁴ in directing available energy into channels favorable to the preservation of the species.

The first effect of natural selection thus operating upon competing species will be to give relative preponderance (in number or mass) to those most efficient in guiding available energy in the manner indicated. Primarily the *path* of the energy flux through the system will be affected.

But the species possessing superior energy-capturing and directing devices may accomplish something more than merely to divert to its own advantage energy for which others are competing with it. If sources are presented, capable of supplying available energy in excess of that actually being tapped by the entire system of living organisms, then an opportunity is furnished for suitably constituted organisms to enlarge the total energy flux⁵ through the system. Whenever such organisms arise, natural selection will operate to preserve and increase them. The result, in this case, is not a mere diversion of the energy flux through the system of organic nature along a new path, but an increase of the total flux through that system.

Again, so long as sources exist, capable of supplying matter, of a character suitable for the composition of living organisms, in excess of that actually embodied in the system of organic nature, so long is opportunity furnished for suitably constituted organisms to enlarge the total mass of the system of organic nature. Whenever such organisms arise, natural selection will operate to preserve and increase them, provided always that there is presented a residue of untapped available energy. The result will be to increase the total mass of the system, and, with this total mass, also the total energy flux through the system, since, other things equal, this energy flux is proportional to the mass of the system.

Where a limit, either constant or slowly changing,⁶ is imposed upon the total mass available for the operation of life processes, the available energy per unit of time (available power) placed at the disposal of the organisms, for application to their life tasks and contests, may be capable of increase by increasing the rate of turnover of the organic matter through the life cycle. So, for example, under present conditions,⁷ the United States produce annually a crop of primary and secondary food amounting to

*Lotka, A. J. 1922. Contribution to the energetics of evolution. Proceedings of the National Academy of Sciences 8:147-151.

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?

RESOURCE COMPETITION BETWEEN PLANKTONIC ALGAE: AN EXPERIMENTAL AND THEORETICAL APPROACH¹

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Abstract. The results of 76 long-term competition experiments between two species of freshwater algae (*Asterionella formosa* and *Cyclotella meneghiniana*) grown along a resource gradient agree with the predictions of two different models of resource competition. Both models are based on the functional resource-utilization response of each species to limiting resources. The Monod model and the Variable Internal Stores model of competition made similar predictions. *Asterionella* was observed to be competitively dominant when both species were phosphate limited; *Cyclotella* was dominant when both species were silicate limited; and both species stably coexisted when each species was growth-rate limited by a different resource. Almost 75% of the variance in the relative abundances of these two species along a natural silicate-phosphate gradient in Lake Michigan is explained by the Monod model.

Key words: Competition models; diatoms; functional response; Michaelis-Menten; Monod; phosphate; resource competition; resource gradient; resource utilization; silicate.

INTRODUCTION

Many recent theoretical studies of interspecific competition have dealt with the dependence of competition on the resource utilization abilities of each species. The models used in these studies may be classified as being of two types. One uses the classical Lotka-Volterra competition equations, estimating the coefficient of competition, α , from some measure of the resource utilization overlap between species (MacArthur 1969, 1970; Orians and Horn 1969; May 1975). The other approach employs models which explicitly include the availability (concentration) of the resource and the functional dependence of growth of each species on the availability of the resource (Stewart and Levin 1973; Greeney et al. 1973; MacArthur 1972; O'Brien 1974; Petersen 1975; Taylor and Williams 1975; Titman 1976). The work reported here is an experimental test of the latter type of mechanistic model. The results of 76 long-term competition experiments between two species of freshwater algae grown under controlled-culture laboratory conditions along a two-resource gradient are compared with the predictions of resource-utilization models of interspecific competition. This is a test of the utility of species-specific resource acquisition and utilization information in predicting the steady-state outcome of competition between two species potentially limited by two resources.

Asterionella formosa Hass. and *Cyclotella meneghiniana* Kutz., freshwater diatoms which are seasonally abundant in midlatitude, mesotrophic lakes (Kopczynska 1973; Stoermer and Kopczynska 1967), were the two species studied. The two potentially limiting resources for this study were phosphate

and silicate, the nutrients which most often limit algal growth in such lakes (Lund et al. 1963; Powers et al. 1972; Schelske and Stoermer 1971; Kilham 1971).

The nutrient kinetics of the clones of *Asterionella* and *Cyclotella* used in these competition experiments are reported elsewhere (Tilman and Kilham 1976). With this information on the ability of each species to acquire and utilize resources, two different models of resource competition are used to predict the steady-state outcome of interspecific competition for potentially limiting silicate and phosphate. The first model (Model I) is based on the Monod equations (Monod 1950; Herbert et al. 1956; Taylor and Williams 1975). The second model (Model II) is based on a variable internal stores model of growth (Droop 1974). Both competition models are founded on models of the functional acquisition and growth response of a single species to a single resource.

The experiments were designed to test how well such single species physiological information can predict the outcome of competition. To avoid variability in the outcome of competition that could be attributed to genetic changes in the populations (cf., Park et al. 1964), the same clone of each species was used throughout all the experiments. Both clones were bacteria-free isolates. Sterile technique was used throughout the experiments to eliminate the possible complication of bacterial competition for limiting resources. Competition experiments were allowed to proceed for between 30 to 40 days, to assure that the results observed were the steady-state outcome of interspecific competition. Two single-species culture controls were performed for all conditions at which competition experiments were performed, thus verifying that each species could exist by itself under all conditions tested. It was hoped that these precautions would minimize the variance in the outcome of the competition experiments, allowing a better test of the relationship between the resource utilization abilities of a species and its competitive abilities.

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Getting back to tree islands.

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

They seem to exist through self-organizing processes

Tree–Grass Coexistence in the Everglades Freshwater System

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ABSTRACT

Mosaic freshwater landscapes exhibit tree-dominated patches—or *tree islands*—interspersed in a background of marshes and wet prairies. In the Florida Everglades, these patterned landscapes provide habitat for a variety of plant and animal species and are hotspots of biodiversity. Even though the emergence of patchy freshwater systems has been associated with climate histories, fluctuating hydrologic conditions, and internal feedbacks, a process-based quantitative understanding of the underlying dynamics is still missing. Here, we develop a mechanistic framework that relates the dynamics of vegetation, nutrients and soil accretion/loss through ecogeomorphic feedbacks and interactions with hydrologic drivers. We

show that the stable coexistence of tree islands and marshes results as an effect of their both being (meta-) stable states of the system. However, tree islands are found to have only a limited resilience, in that changes in hydrologic conditions or vegetation cover may cause an abrupt shift to a stable marsh state. The inherent non-linear and discontinuous dynamics determining the stability and resilience of tree islands should be accounted for in efforts aiming at the management, conservation and restoration of these features.

Key words: Tree islands; Peatland; Tree-grass coexistence; Alternative stable states; Resilience; Savanna; State shift.

INTRODUCTION

The Everglades freshwater wetlands exhibit a heterogeneous landscape with marshes and wet prairies punctuated by patches of woody vegetation, including trees (for example, Sklar and van der

Valk 2002). These tree patches are typically more elevated than the surrounding marshes, and are therefore known as “tree islands,” in that they often remain above the water level while the rest of the landscape is flooded. Tree islands are typically richer in nutrients, provide habitat to diverse communities of plants and animals (Sklar and van der Valk 2002), sustain high levels of productivity (Naiman and Decamps 1997; Mitsch and Gosselink 2000), and contribute to carbon storage (for example, Richardson 2000). Tree islands are a characteristic feature of the Florida Everglades (Figure 1A), though similar landforms can be found in other tropical/subtropical freshwater landscapes (for example, Okefenokee Swamp, GA;

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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.

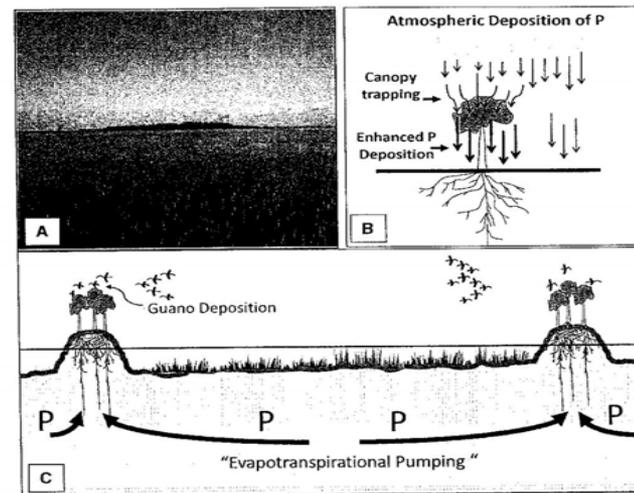


Figure 1. A A profile view of a tree island surrounded by grasses and herbaceous marsh species in Everglades National Park. Schematic representation of the P enrichment due to the deposition feedback (B), and guano deposition or evapotranspirational pumping (C).

the Pantanal wetland in Brazil, Prance and Schaller 1982; the Okavango delta, Botswana, for example, McCarthy and Ellery 1994; the wetlands of northern Belize, Macek and others 2009); and boreal bogs (Glaser 1987, 1992; Richardson 2000).

Tree islands occurring in the ridge and slough habitat of the Everglades formed during periods of extended drought between 3500 and 500 years before present (Willard and others 2006). With the initiation of large-scale drainage projects and other hydrologic manipulations in this region, approximately one half of the tree island area in the Everglades has been lost (Davis and others 1994). Conservation of the remaining islands and the restoration of their historic aerial extent is a primary objective of Everglades restoration efforts. Ecogeomorphic models of the causal mechanisms leading to their formation and persistence are needed to guide this effort.

Despite the diversity and spatial organization of vegetation within the tree and grass plant communities, the landscape of the Everglades freshwater wetlands exhibits the features of a two-phase system with a distinct contrast between tree islands and marshes. Tree islands are more elevated, dominated by woody vegetation, and rich in phosphorus, whereas marshes are vegetated by herbaceous

vegetation (that is, graminoids, grasses, and forbs, hereafter generically referred to as "grasses") and phosphorus-poor (Wetzel and others 2005, 2009). A parallel has recently been drawn between the tree-grass mosaic of tree island-marsh systems and patchy vegetation typical of dryland ecosystems, particularly of savannas (van der Valk and Warner 2009). This comparison is useful to appreciate the complexity of vegetation dynamics in heterogeneous wetland landscapes as well as to capitalize on a relatively rich literature on savanna and dryland vegetation (for example, Sarmiento 1984; Schlesinger and others 1990; Scholes and Walker 1993; Scholes and Archer 1997; Ridolfi and others 2008; D'Odorico and others 2006) to formulate research questions and hypotheses that could advance our understanding of these complex systems. Fundamental among those questions is how trees and grasses coexist in patchy freshwater landscapes and how this coexistence is affected by changes in environmental conditions. Known as "the savanna question" (Sarmiento 1984), the coexistence of trees and grasses or other herbaceous species in wetlands remains poorly investigated. In this study, we show how the stable coexistence of marshes and tree islands in the Everglades may emerge as the result of positive feedback mechanisms that

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.

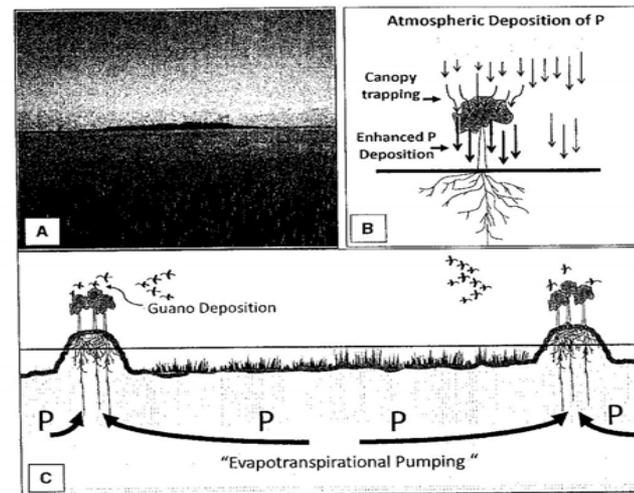


Figure 1. A A profile view of a tree island surrounded by grasses and herbaceous marsh species in Everglades, National Park. Schematic representation of the P enrichment due to the deposition feedback (B), and guano deposition or evapotranspirational pumping (C).

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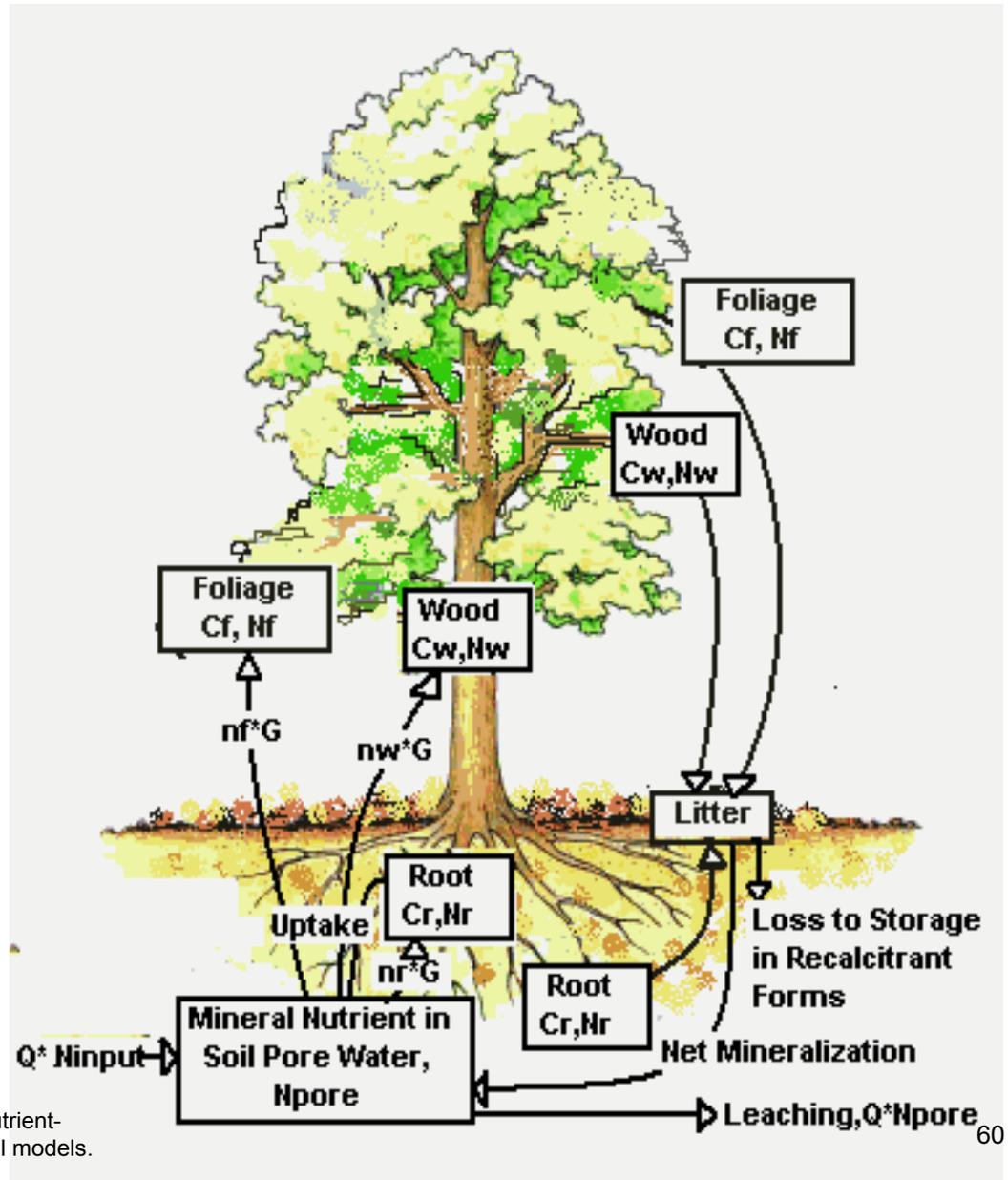
Modeling Plants, Nutrients, and Energy

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.

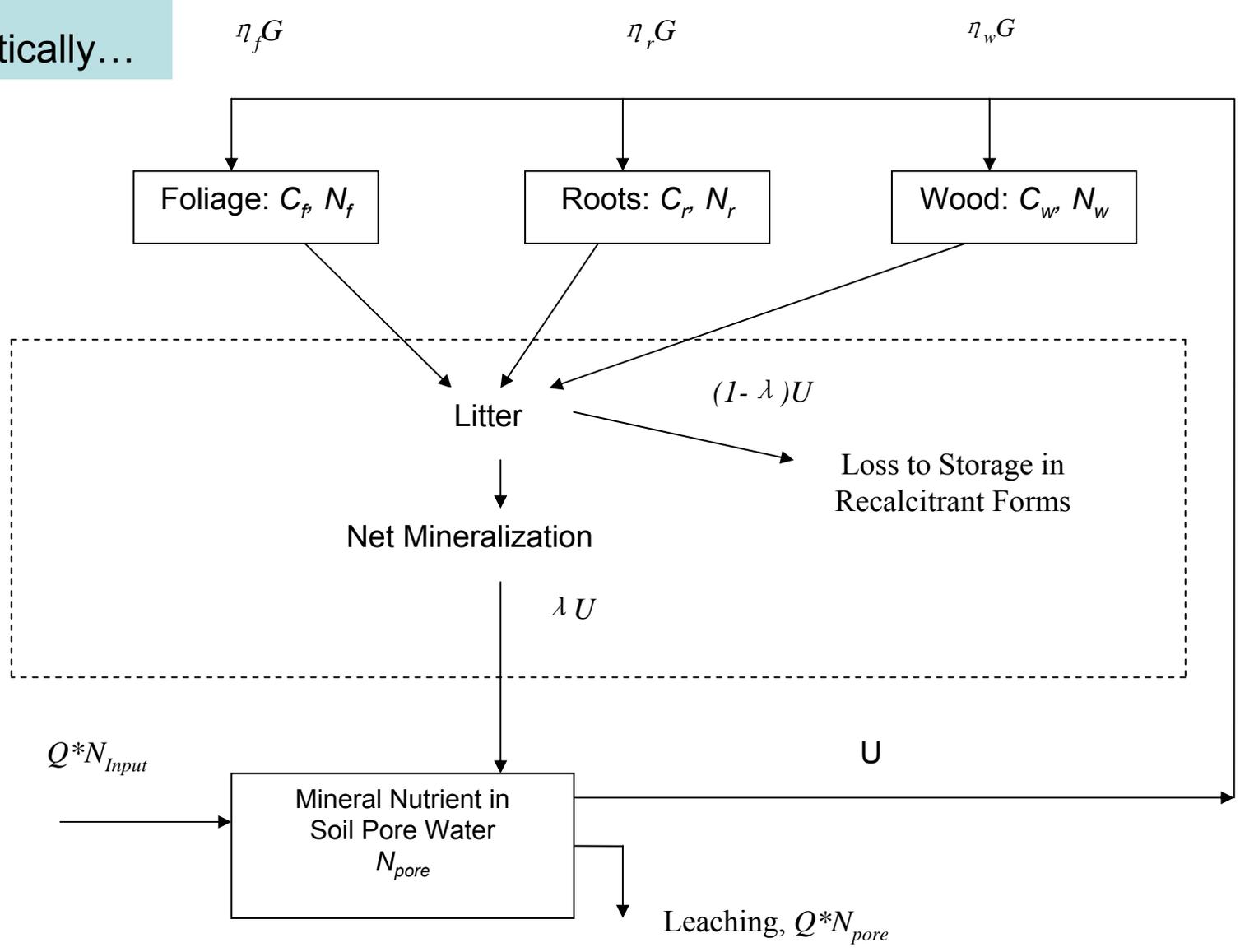
Under given circumstances (e.g., external nutrient input, whether or not the tree is competing with other trees with other strategies), what is the best way to allocate the energy; that is, for greatest primary production.

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.



*Comins, HN, and McMurtrie, RE (1993) Long-term response of nutrient-limited forests to CO₂ enrichment; equilibrium behavior of plant-soil models. *Ecol Appl* 3: 666-681.

More schematically...



$$\eta_f + \eta_r + \eta_w = 1$$

Basic Model Equations

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

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

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

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

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

$$\frac{dN_f}{dt} = \left(\overset{\text{Uptake}}{\downarrow} U - \eta_w v_w G \right) \frac{\eta_f}{\eta_f + \rho \eta_r} - \gamma_f N_f$$

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

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

The $-\eta_w v_w G$ represents fixed N:C allocation to wood

Equations for Nutrient Uptake and Pore Water Nutrient Dynamics

$$U = \left(\frac{g_N N_{pore}}{k_N + N_{pore}} \right) \left(1 - e^{-k_r b_r C_r} \right) \quad \text{Uptake rate}$$

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

↗ ↘
↑
↖ ↗

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 η_f, η_r, η_w that maximizes G^* .

(Actually, we fix allocation to wood, η_w)

Does this also minimize N_{pore}^* ?

Methods

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.

$$F(S, G^*, N_{pore}^*) = G^* - G_0 \left[\left(\frac{g_N N_{pore}^*}{k_N + N_{pore}^*} \right) \left(1 - e^{-k_r b_r \eta_r G^* / \gamma_r} \right) - \eta_w v_w G^* \right] \left[\frac{1 - e^{-k_f b_f \eta_f G^* / \gamma_f}}{G^* v_0 (\eta_f + \rho \eta_r)} \right]$$
$$= 0 \quad (1)$$

In the expression $F(S, G^*, N_{pore}^*)$, N_{pore}^* can be expressed simply in terms of G^* in the second order equation.

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

and where

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

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...

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

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

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

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

That implies that when $\eta_r G^*$ reaches a maximum, N_{pore}^* will reach a minimum.

Analytic Results

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

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 $\text{Min}(R^*)$ or $\text{Max}(G^*)$.

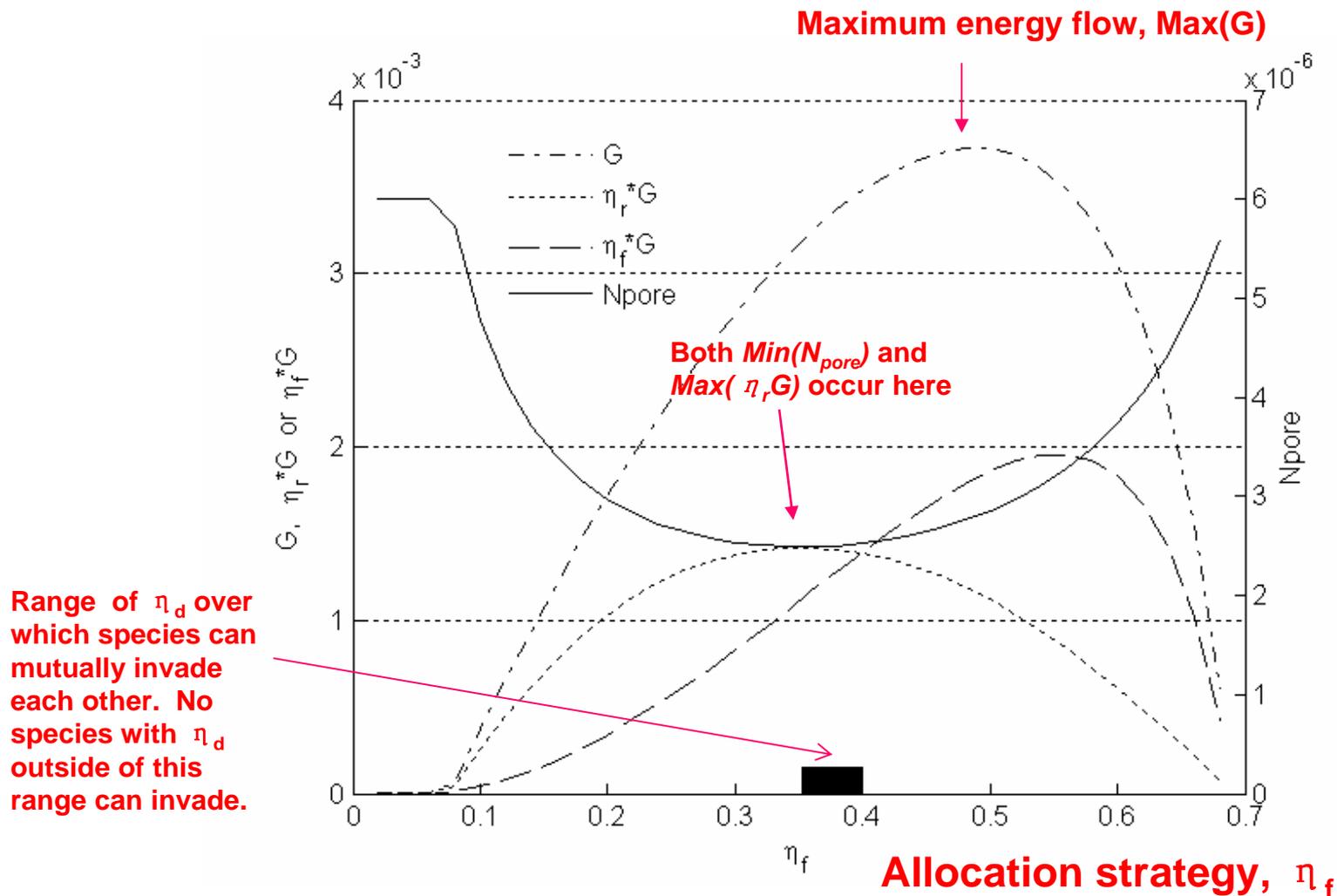


Figure 3a. Net carbon production, G^* , energy flux to roots, $\eta_r G^*$, energy flux to foliage, $\eta_f G^*$, and soil pore water nitrogen, N_{pore} , as functions of allocation fraction of carbon to foliage, η_f , for fixed η_w . Nutrient input, $N_{input} = 2.0 \times 10^{-8}$; best competitor has strategies in range $\eta_f = 0.35-0.4$. $\lambda = 0.99$, $Q = 5.0$, $\eta_w = 0.2$.

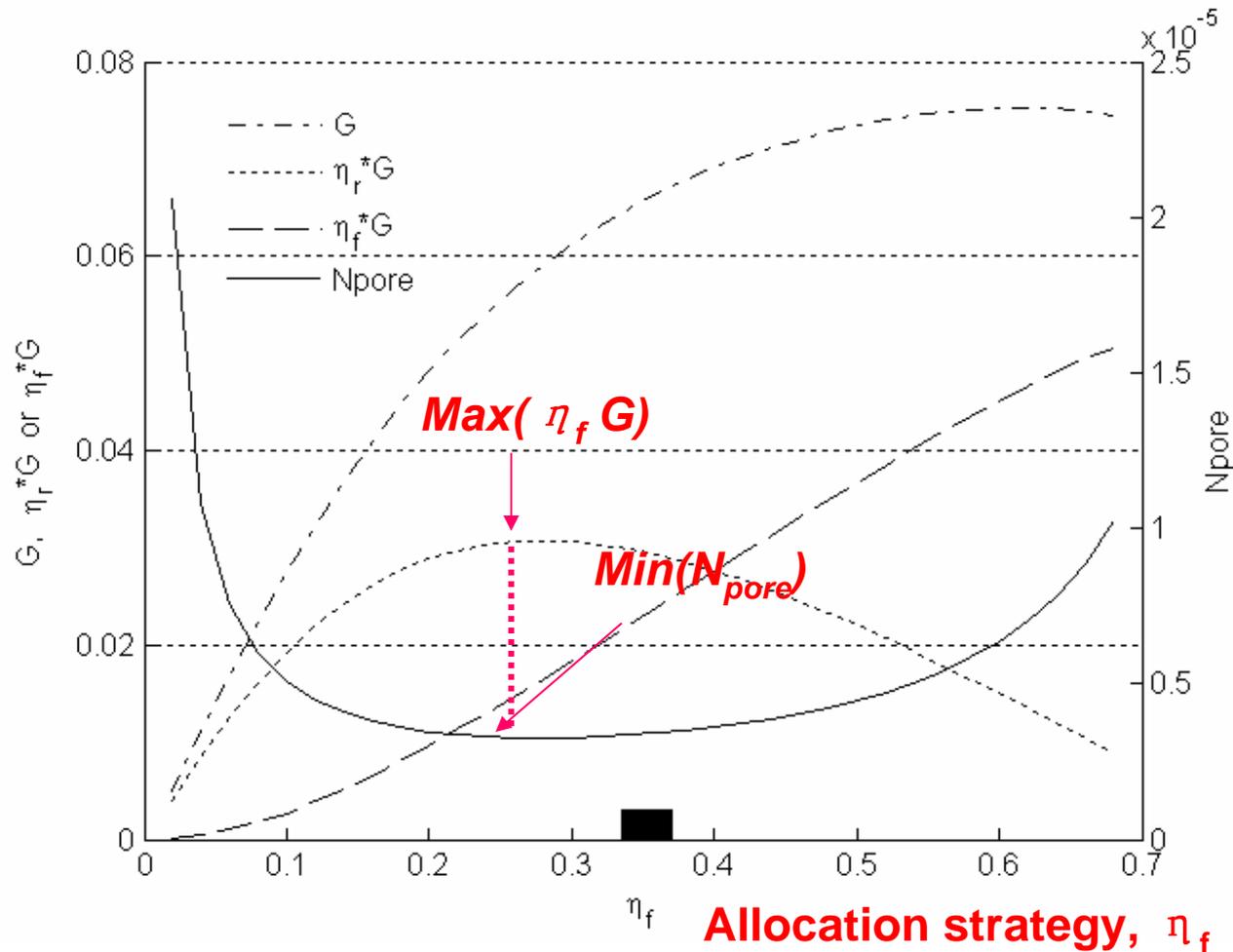


Figure 3b. Net carbon production, G^* , energy flux to roots, $\eta_r G^*$, energy flux to foliage, $\eta_f^* G^*$, and soil pore water nitrogen, N_{pore} , as functions of allocation fraction of carbon to foliage, η_f , for fixed $\eta_w \cdot N_{input} = 10.0 \times 10^{-8}$; best competitor has strategies in range $\eta_f = 0.33-0.37$. $\lambda = 0.99$, $Q = 5.0$, $\eta_w = 0.2$.

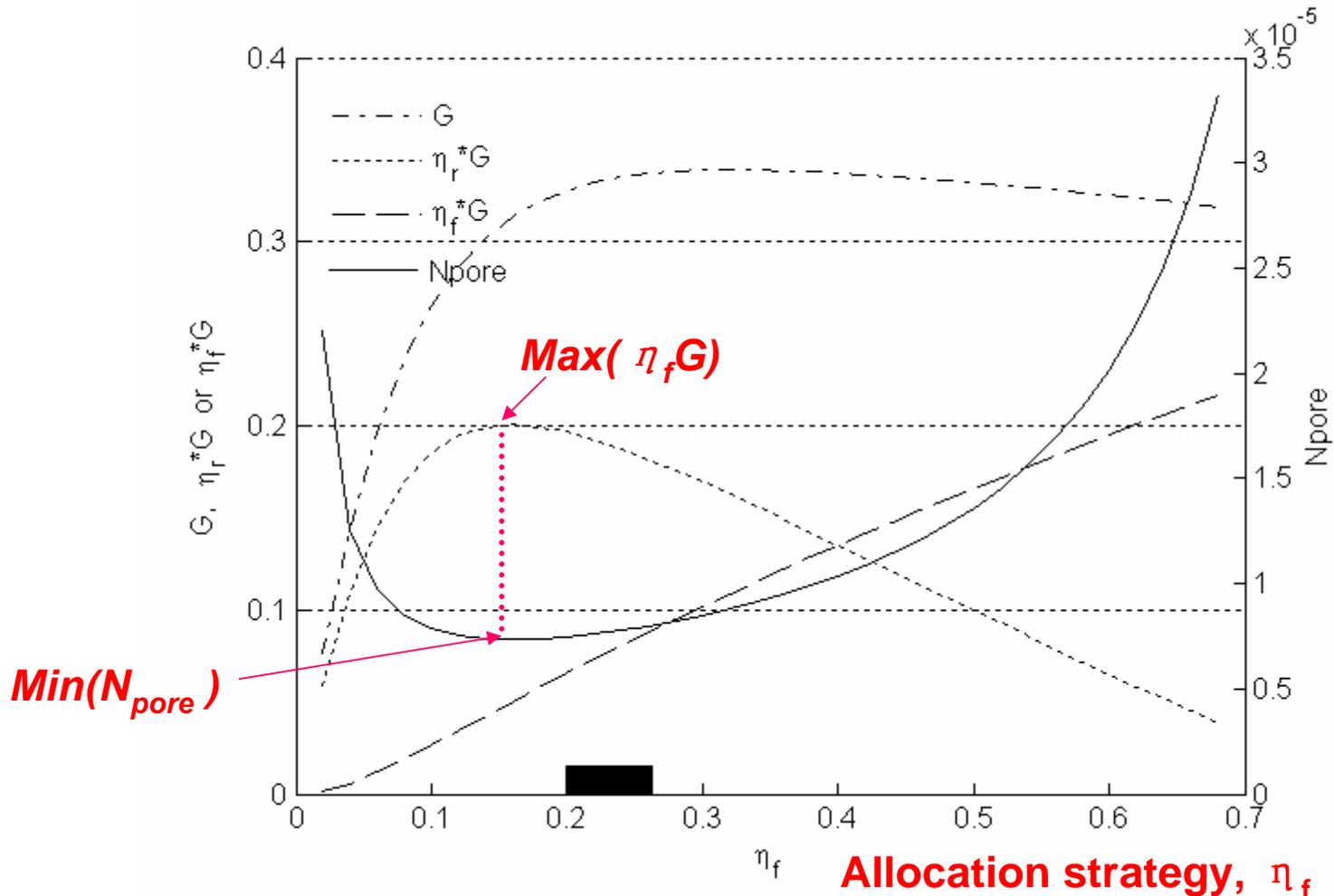


Figure 3c. Net carbon production, G^* , energy flux to roots, $\eta_r G^*$, energy flux to foliage, $\eta_f^* G^*$, and soil pore water nitrogen, N_{pore} , as functions of allocation fraction of carbon to foliage, η_f , for fixed $\eta_w \cdot N_{input} = 12.5 \times 10^{-8}$; best competitor has strategies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

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.

Extension to Landscape

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?



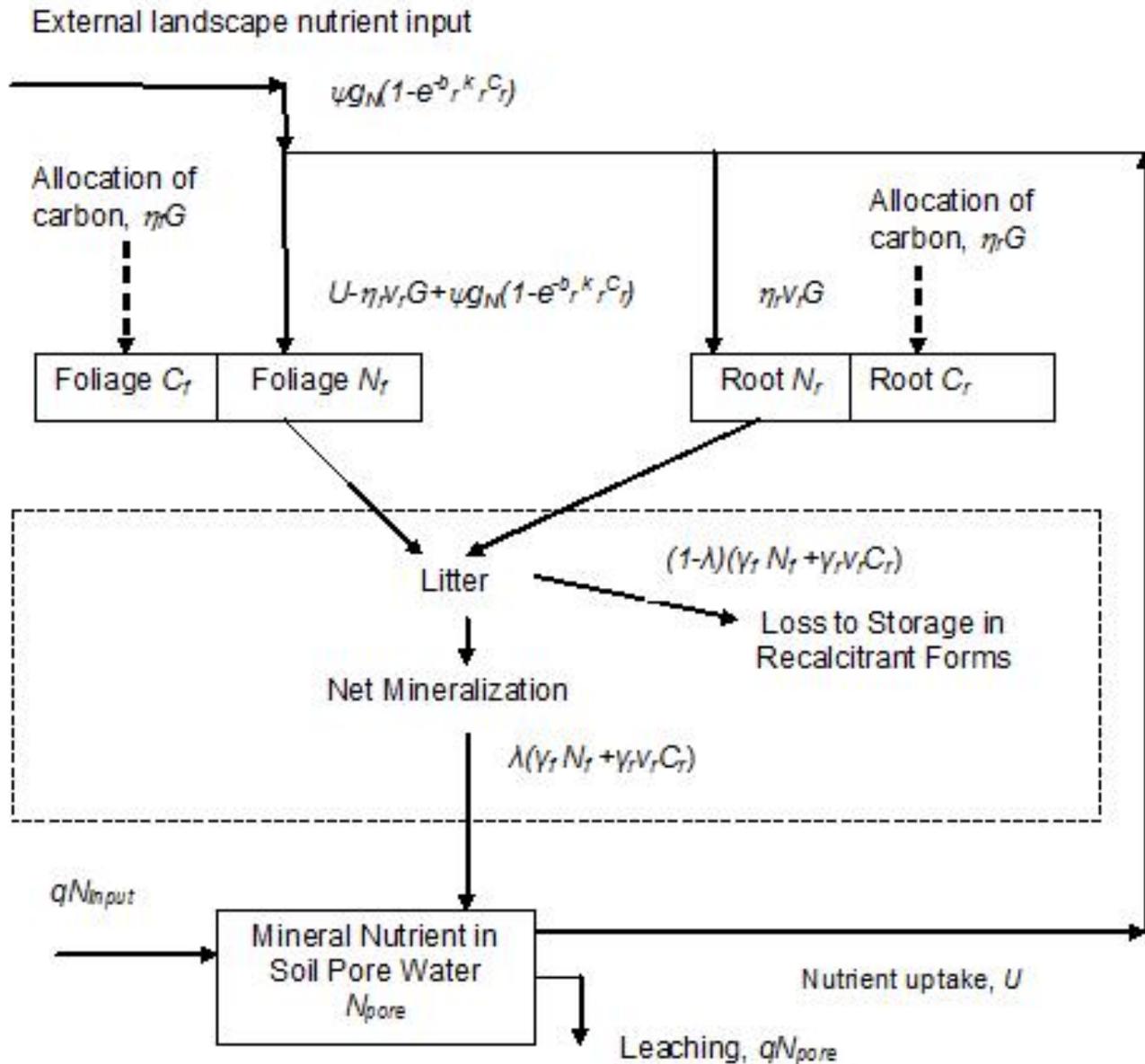


Fig. 1. Schematic of model used in this paper. It is a modified version of the G'DAY model (Comins and McMurtrie, 1993), with the details of litter decomposition and soil processes omitted, but an available soil pore water nutrient pool added. The foliage and root compartments have separate variables for carbon and nutrient. Nutrient fluxes are represented by solid lines and carbon fluxes by dashed lines.

Main Results

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^* .

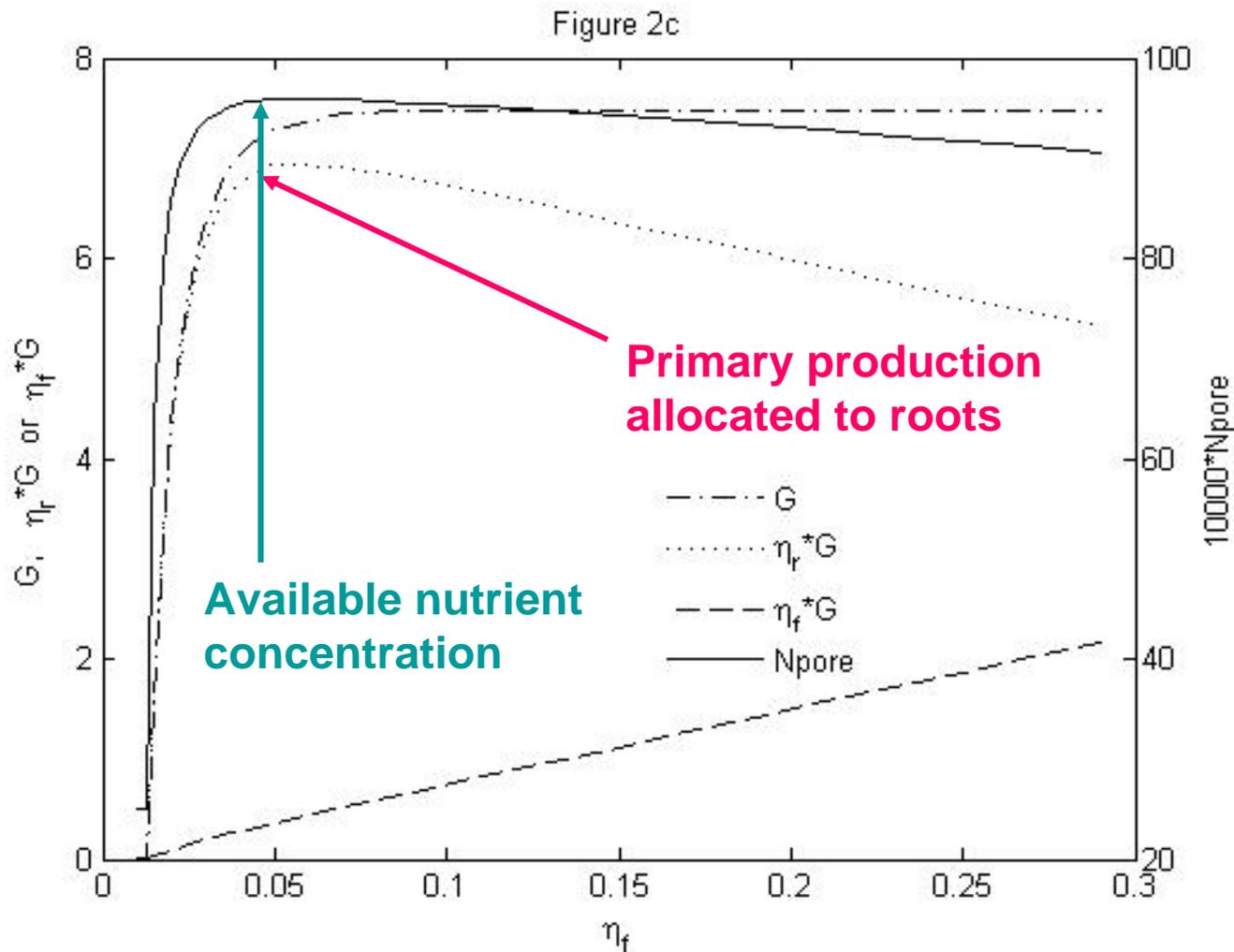


Fig. 2c. Tree growth rate (carbon fixed per unit time), G^* , carbon flux to roots, $\eta_r G^*$ carbon flux to foliage, $\eta_f G^*$ and soil pore water nutrient, N_{pore}^* ($\times 10^4$), as functions of allocation fraction of carbon to foliage, f , for four different values of the biomass-dependent external nutrient input, Ψ . (c) $\Psi = 0.000035$. Other parameters are $\alpha = 0.9993$, $q = 0.005 \text{ kg m}^{-2} \text{ yr}^{-1}$, $v_r = 0.008$, $\gamma_f = 0.10 \text{ yr}^{-1}$, $\gamma_r = 0.30 \text{ yr}^{-1}$, $G_0 = 7.56 \text{ kg Cm}^{-2} \text{ yr}^{-1}$, $\gamma_0 = 0.06$, $g_N = 3.00$, $k_N = 0.01$, $br = 1.0 \text{ m}^2 \text{ kg}^{-1}$, $bf = 2.5 \text{ m}^2 \text{ kg}^{-1}$, $kf = 0.50$, $kr = 0.01$, and $N_{\text{input}} = 0.0025 \text{ kg kg}^{-1}$.

Figure 2d

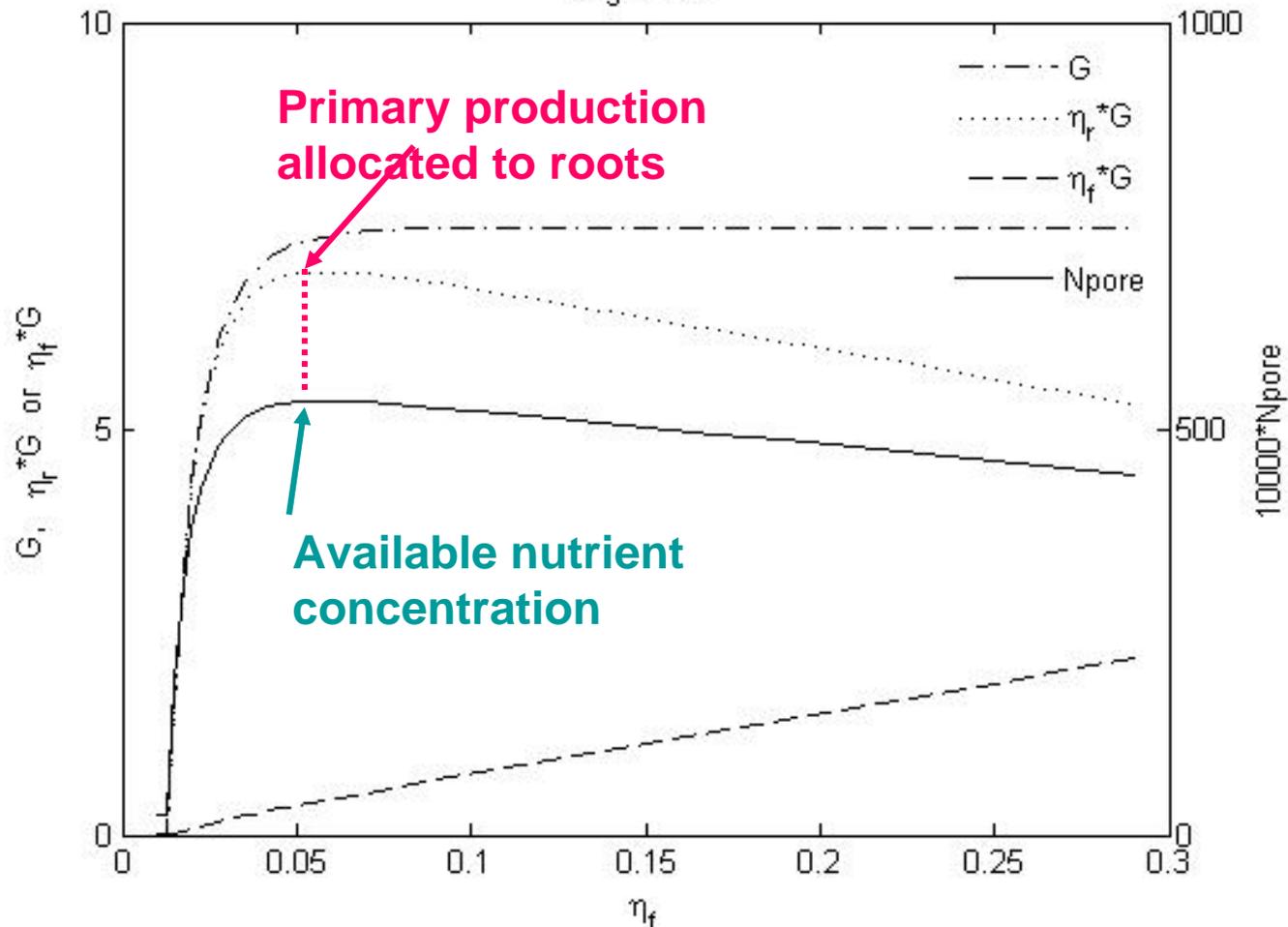


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Conclusions

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