Vegetation Patterns in Semi-Deserts

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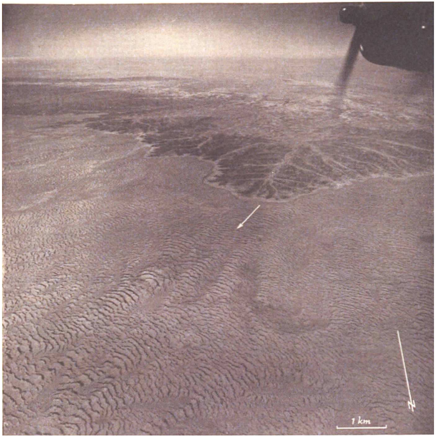
Heriot-Watt University

University of Sussex, 14 March 2013

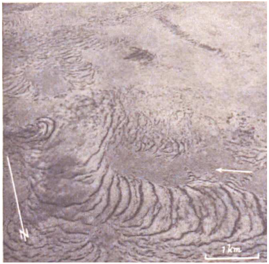
This talk can be downloaded from my web site

www.ma.hw.ac.uk/∼jas

Vegetation Patterns



1950



(William MacFadyden,
Geogr. J. 115: 199-211, 1950)

Vegetation Patterns

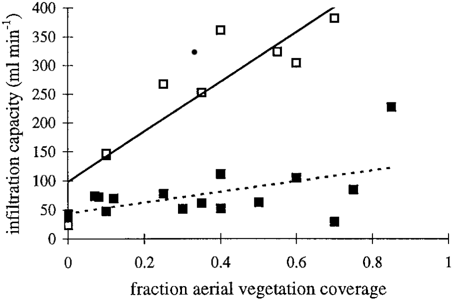
Bushy vegetation in Niger

Mitchell grass in Australia

(Western New South Wales)

- Banded vegetation patterns are found on gentle slopes in semi-arid areas of Africa, Australia and Mexico
- Plants vary from grasses to shrubs and trees
- Typical wavelength 1km for shrubs and trees

Why Do Plants Form Patterns?



Data from Burkina Faso

Rietkerk et al
Plant Ecology 148: 207-224, 2000

More plants ⇒ more roots and organic matter in soil
⇒ more infiltration of rainwater

Banded Patterns on Slopes

- On slopes, water flow downhill causes stripes which move uphill

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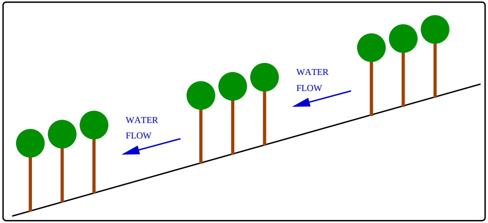

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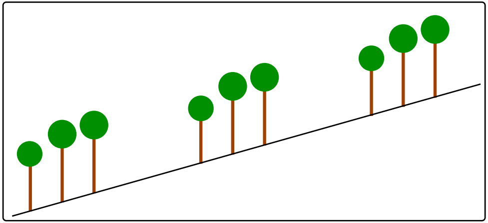

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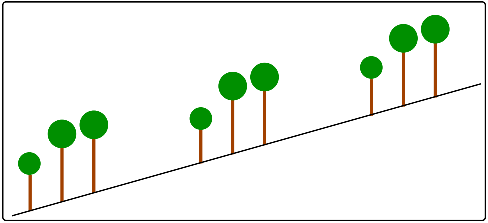

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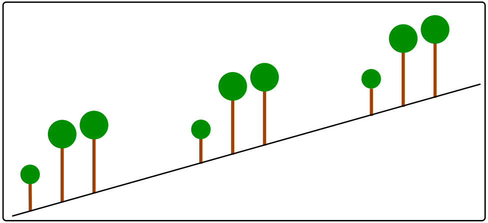

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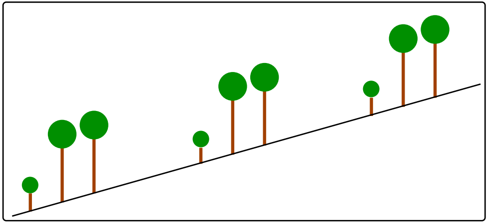

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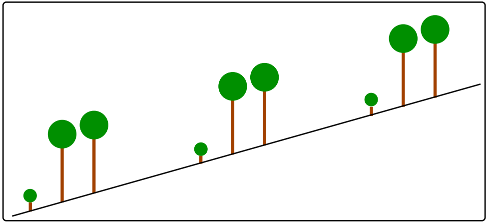

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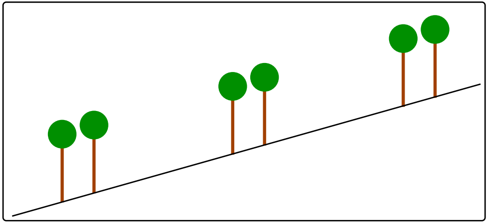

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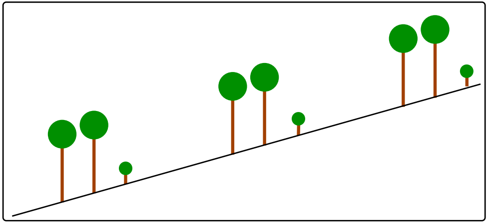

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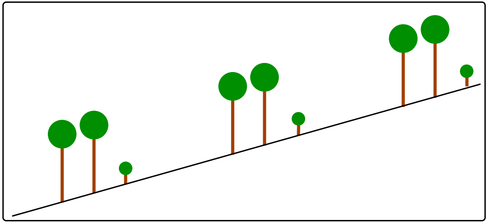

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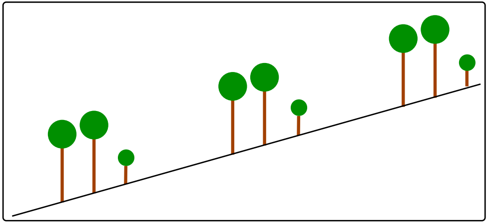

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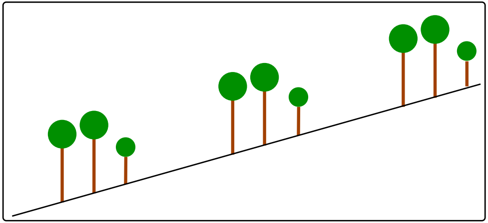

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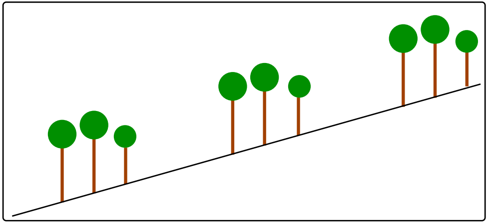

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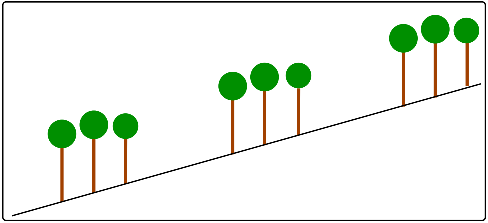

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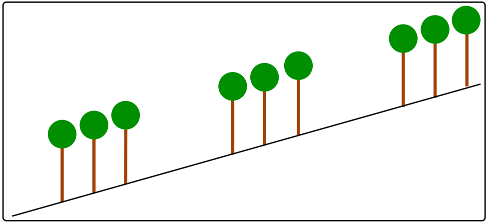

Key Ecological Questions

- At what rainfall level is there a switch from uniform vegetation to patterns?
- At what rainfall level is there a transition to desert?
- How does the spacing of the vegetation bands depend on rainfall, herbivory and slope?

Outline

Mathematical Model of Klausmeier

Rate of change of water = Rainfall – Evaporation – Uptake by plants + Flow downhill

Rate of change plant biomass = Growth, proportional to water uptake – Mortality + Random dispersal

$$\partial w/\partial t = A - w - wu^2 + \nu \partial w/\partial x$$

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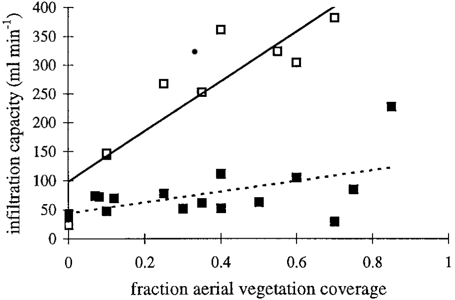

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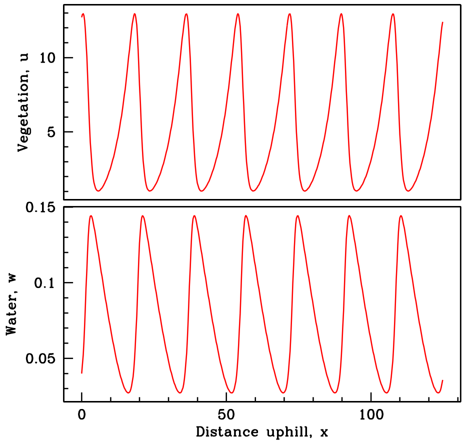
Parameters: A: rainfall B: plant loss ν: slope

Typical Solution of the Model



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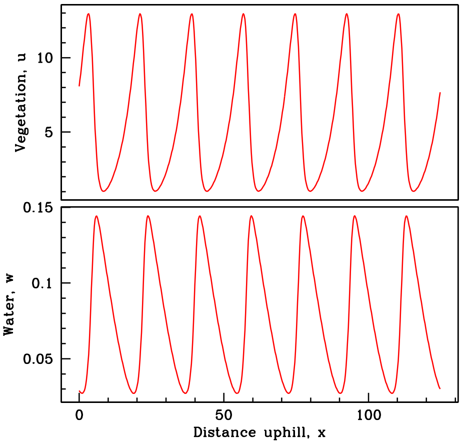

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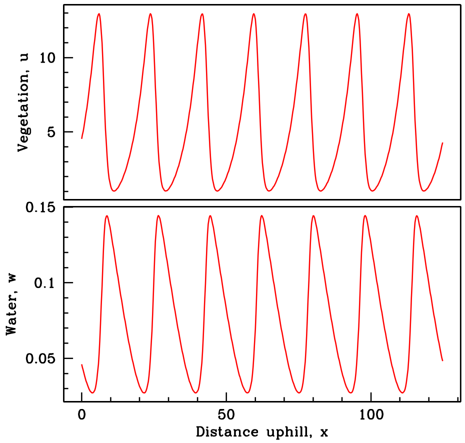

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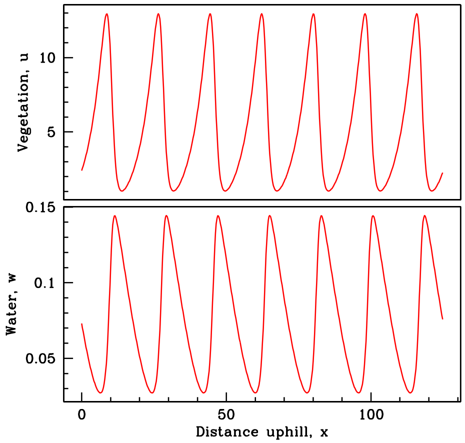

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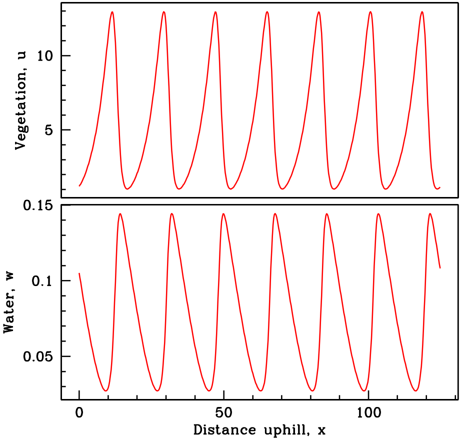

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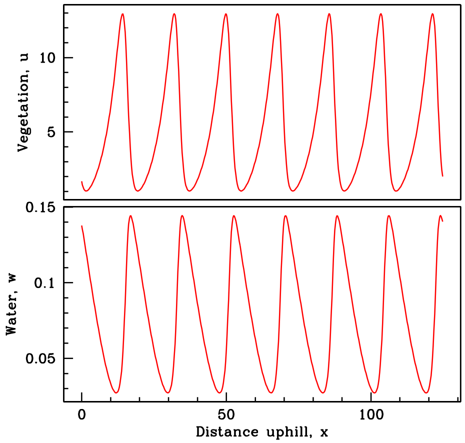

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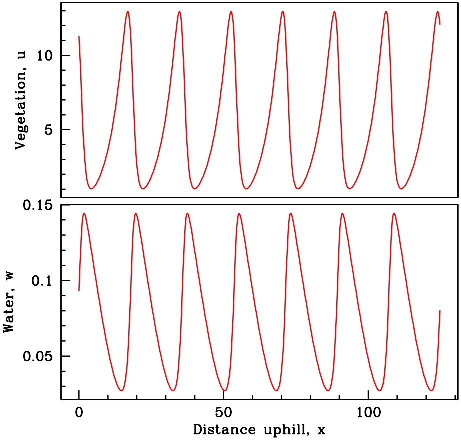

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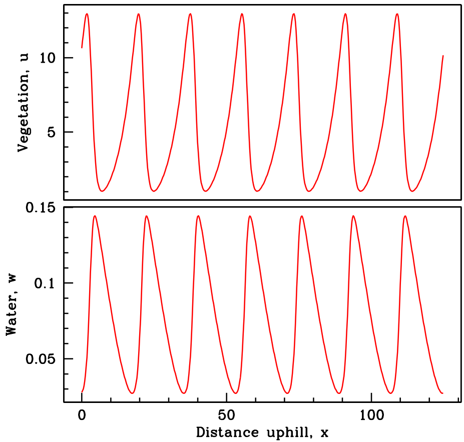

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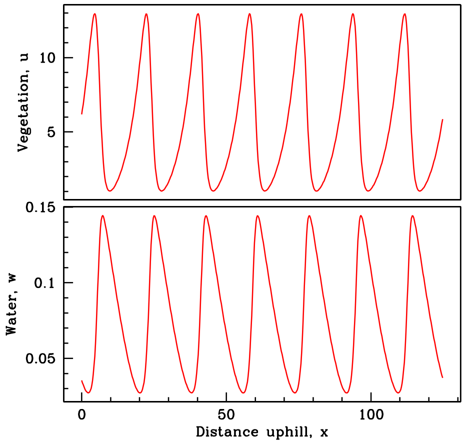

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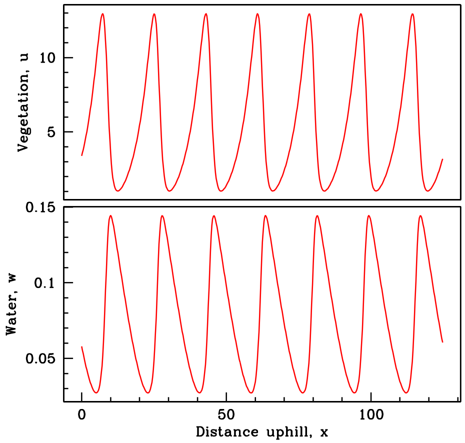

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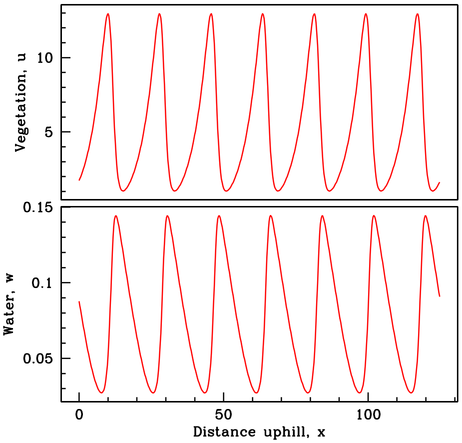

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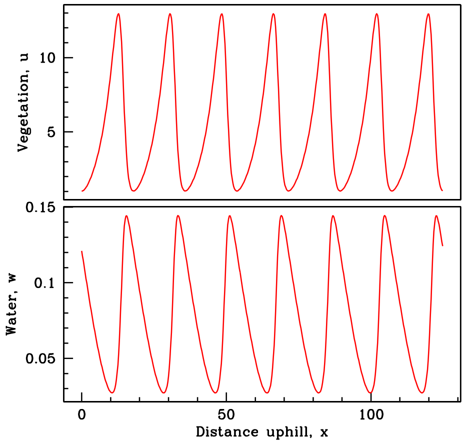

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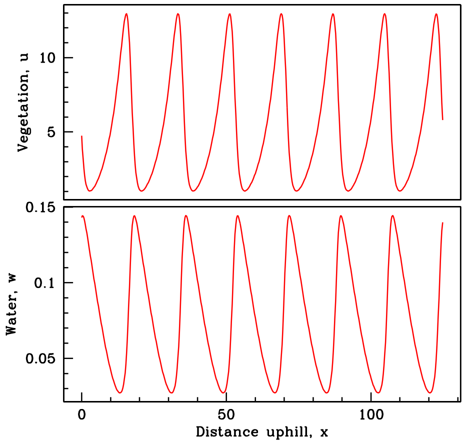

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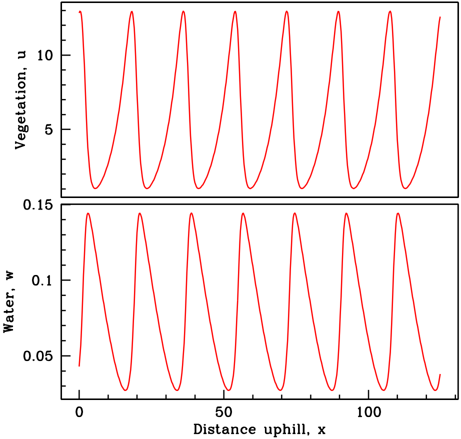

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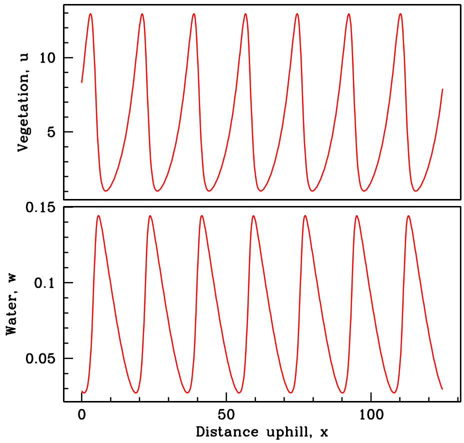

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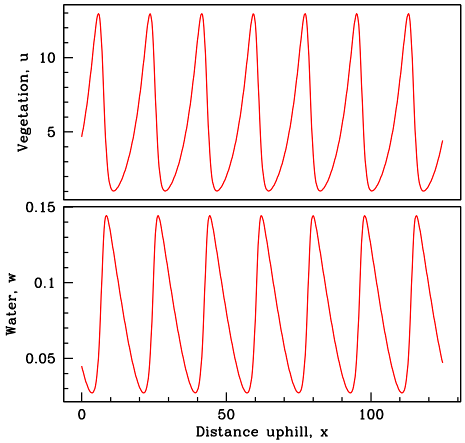

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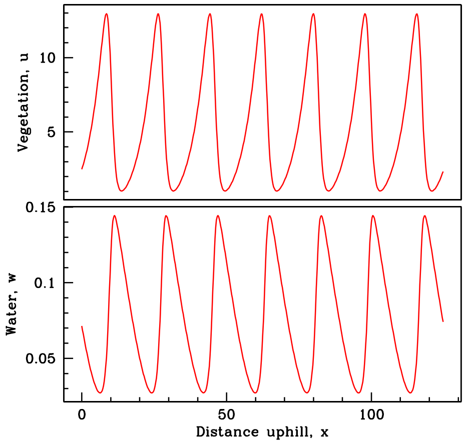

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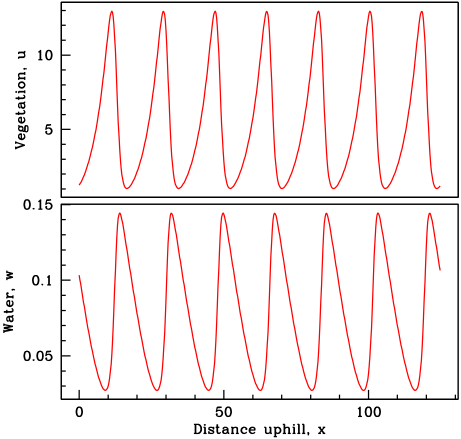

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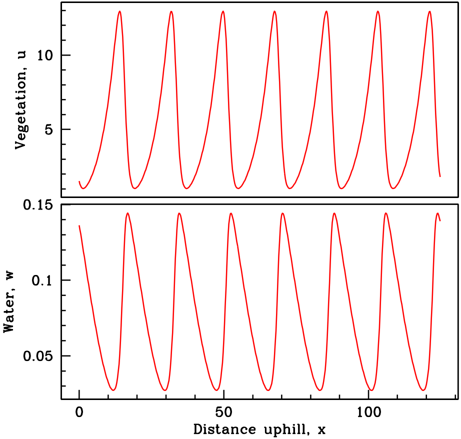

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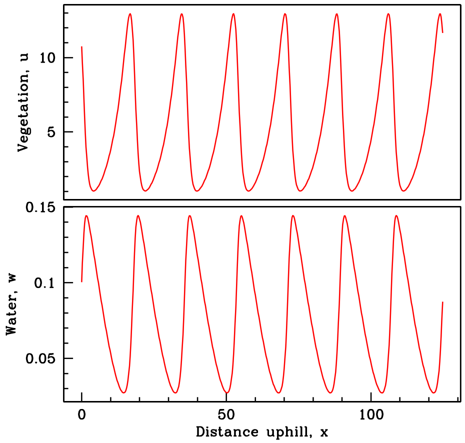

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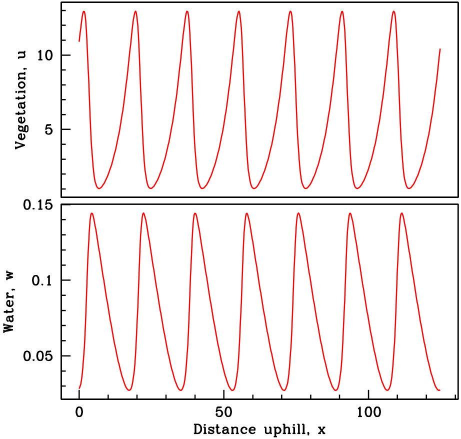

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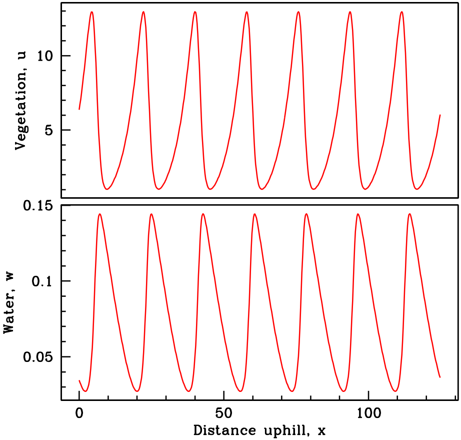

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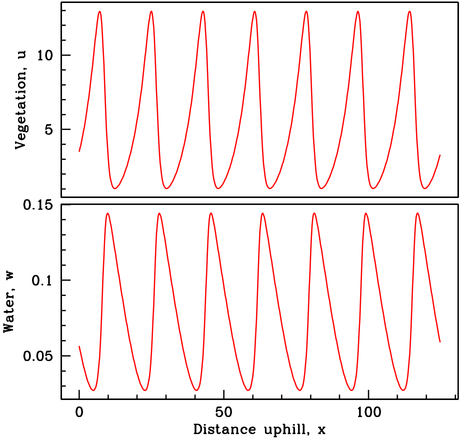

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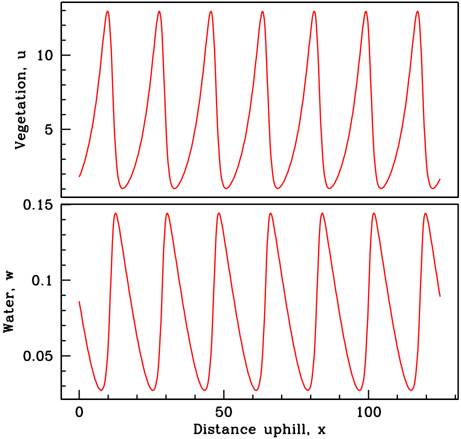

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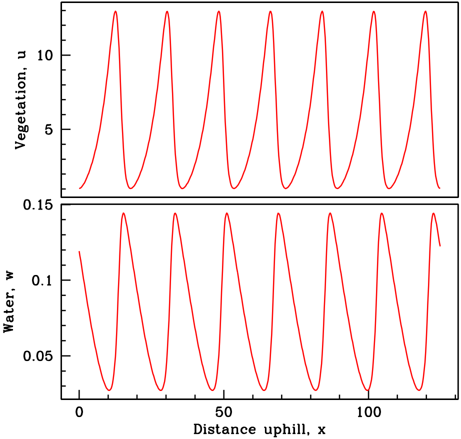

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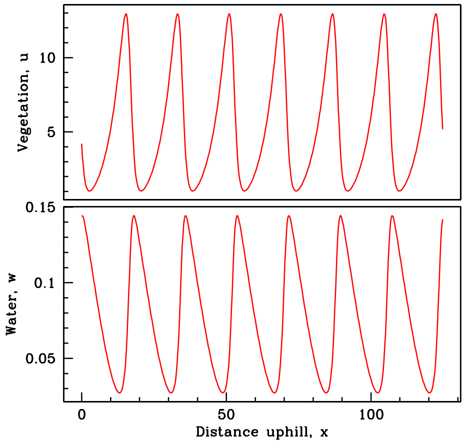

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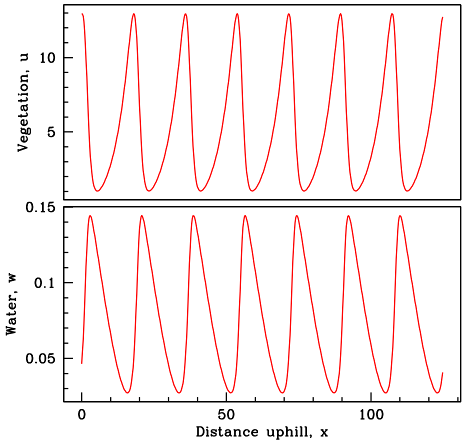

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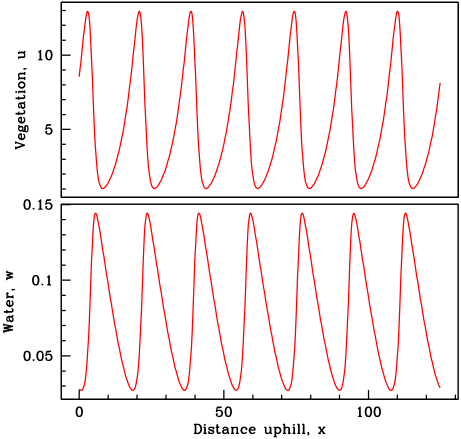

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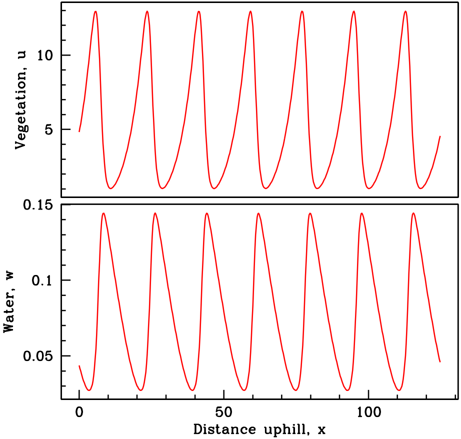

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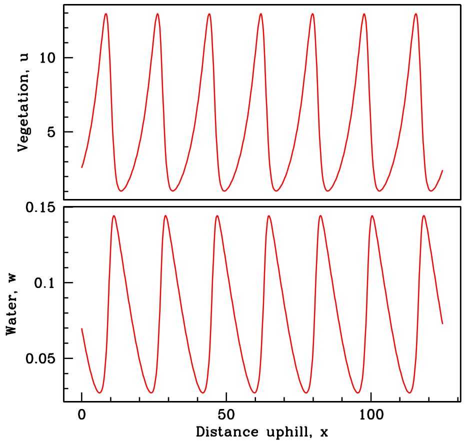

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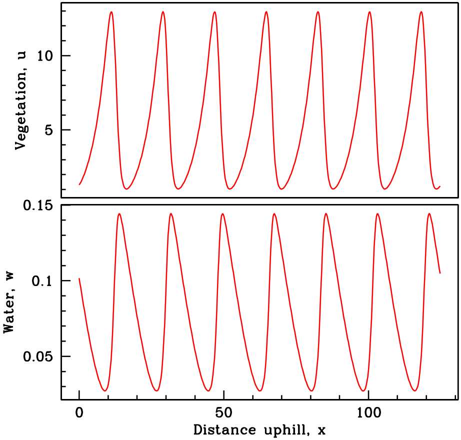

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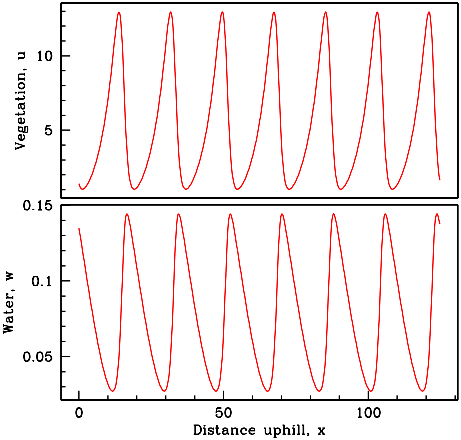

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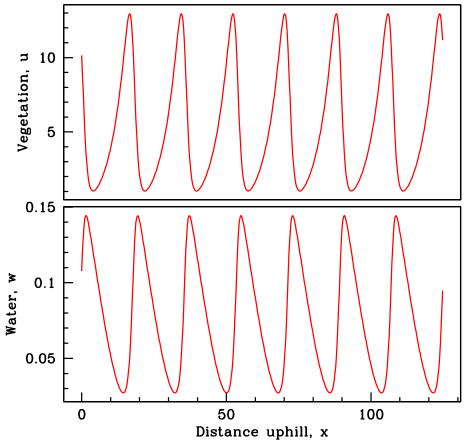

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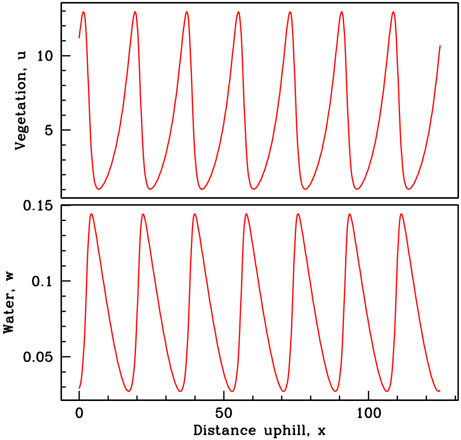

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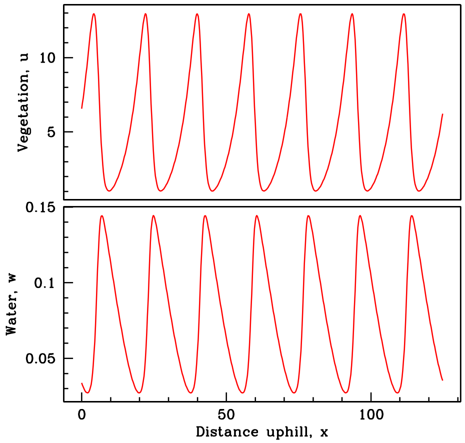

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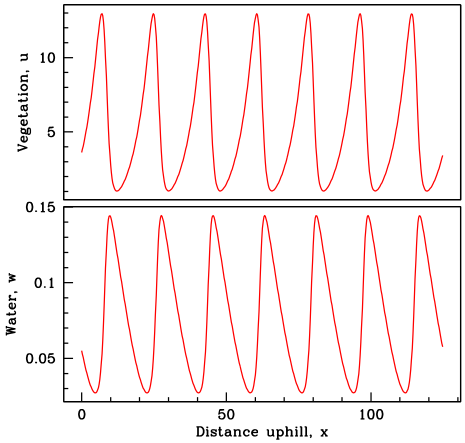

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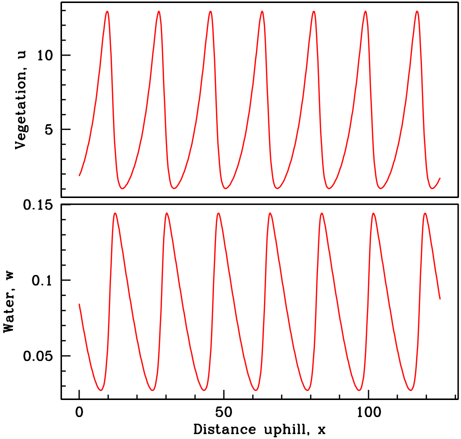

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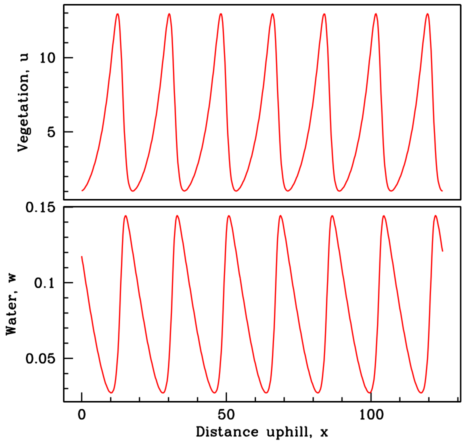

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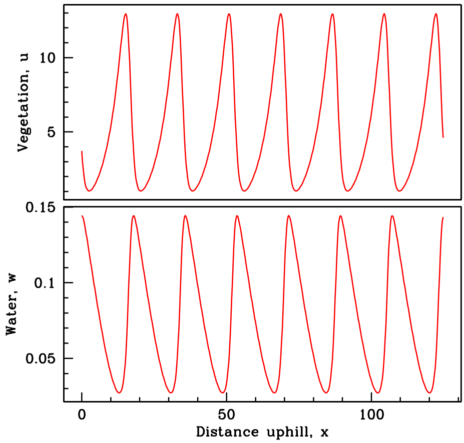

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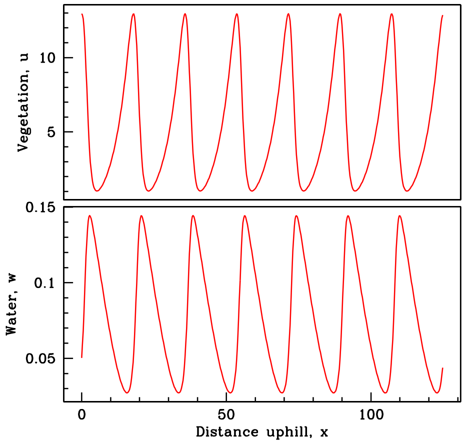

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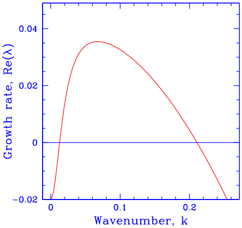
- When $A \geq 2B$, there are also two non-trivial steady states, one of which is unstable to homogeneous perturbations
- The other steady state (u_s, w_s) is stable to homogeneous perturbations but can be unstable to inhomogeneous perturbations $\Rightarrow$ pattern formation

Approximate Conditions for Patterning

Look for solutions $(u, w) = (u_s, w_s) + (u_0, w_0)\exp\{ikx + \lambda t\}$



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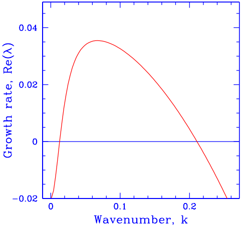

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To leading order for large ν, the condition for pattern formation is

$$A < B^{5/4}\nu^{1/2}\left(\sqrt{2}-1\right)^{1/2}$$

Back to Key Ecological Questions

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Outline

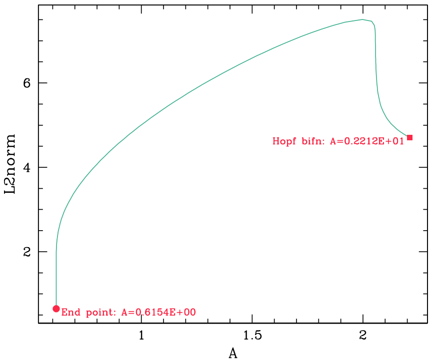
Travelling Wave Equations

The patterns move at constant shape and speed
$\Rightarrow u(x,t) = U(z)$, $w(x,t) = W(z)$, $z = x - ct$

$$\begin{aligned} d^2U/dz^2 + c\,dU/dz + WU^2 - BU &= 0 \\ (\nu + c)dW/dz + A - W - WU^2 &= 0 \end{aligned}$$

The patterns are periodic (limit cycle) solutions of these equations

Bifurcation Diagram for Travelling Wave Equations



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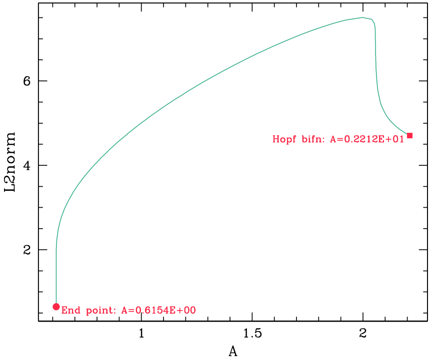
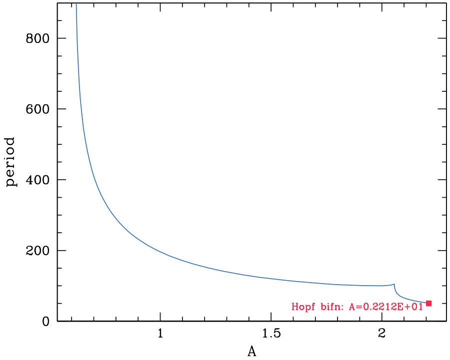
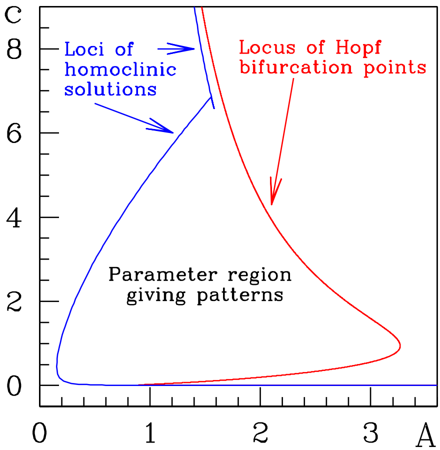
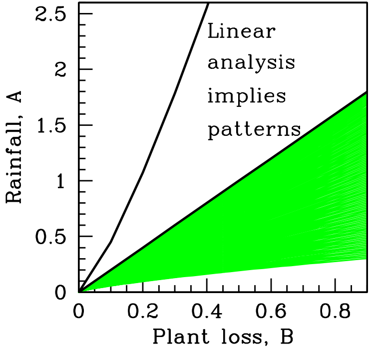




When do Patterns Form?



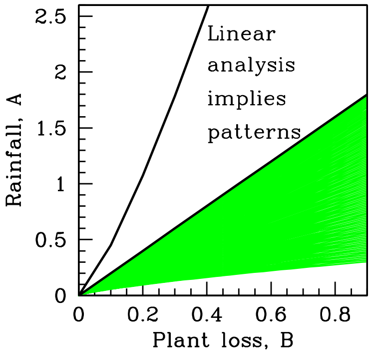
Pattern Formation for Low Rainfall

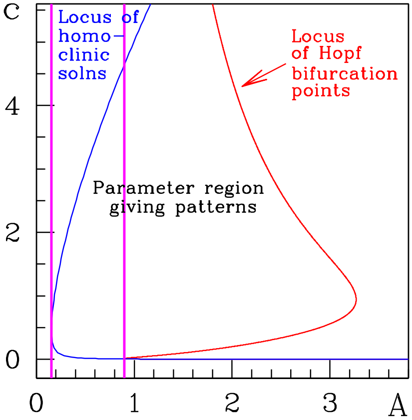


Recall: the homogeneous steady state only exists for $A \geq 2B$

Patterns are also seen for parameters in the green region.

Pattern Formation for Low Rainfall





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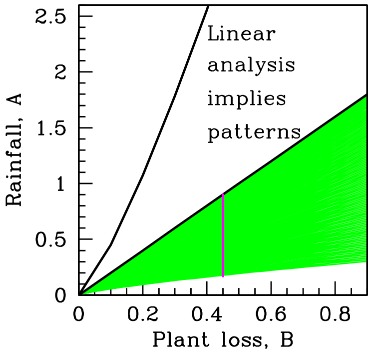
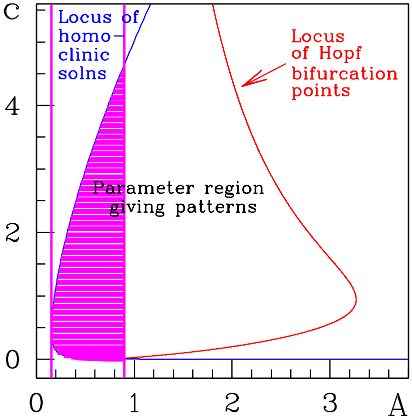
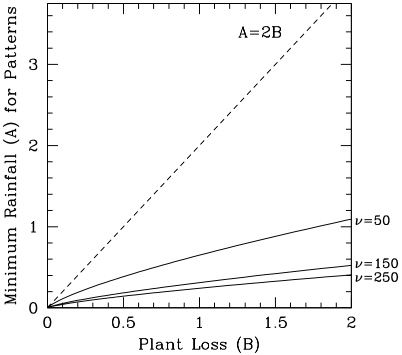




Minimum Rainfall for Patterns



Back to Key Ecological Questions

- At what rainfall level is there a switch from uniform vegetation to patterns?
- At what rainfall level is there a transition to desert?
- How does the spacing of the vegetation bands depend on rainfall, herbivory and slope?

Outline

The Eigenvalue Problem

PDE model:
$$u_t = u_{zz} + cu_z + f(u,w)$$
$$w_t = \nu w_z + cv_z + g(u,w)$$

Periodic wave satisfies:
$$0 = U_{zz} + cU_z + f(U,W)$$
$$0 = \nu W_z + cW_z + g(U,W)$$

Consider
$$u(z,t) = U(z) + e^{\lambda t}\overline{u}(z) \quad \text{with } |\overline{u}| \ll |U|$$
$$w(z,t) = W(z) + e^{\lambda t}\overline{w}(z) \quad \text{with } |\overline{w}| \ll |W|$$

$\Rightarrow$ Eigenfunction eqn:
$$\lambda\overline{u} = \overline{u}_{zz} + c\overline{u}_z + f_u(U,W)\overline{u} + f_w(U,W)\overline{w}$$
$$\lambda\overline{w} = \nu\overline{w}_z + c\overline{w}_z + g_u(U,W)\overline{u} + g_w(U,W)\overline{w}$$

Boundary conditions:
$$\overline{u}(0) = \overline{u}(L)e^{i\gamma} \quad (0 \le \gamma < 2\pi)$$
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Here $0 < z < L$, with $(\overline{u},\overline{w})(0) = (\overline{u},\overline{w})(L)e^{i\gamma}$ $(0 \leq \gamma < 2\pi)$

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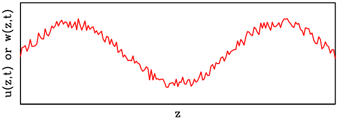
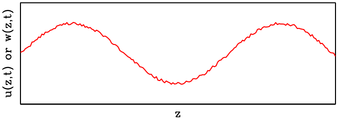


$\text{Re}(\lambda) < 0$

$\longrightarrow$



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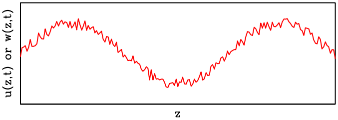

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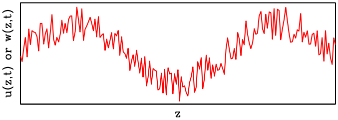

Numerical Calculation of Eigenvalue Spectrum

(based on Jens Rademacher, Bjorn Sandstede, Arnd Scheel Physica D 229 166-183, 2007)

1. solve numerically for the periodic wave by continuation from a Hopf bifn point in the travelling wave eqns

$$
\begin{aligned}
0 &= U_{zz} + cU_z + f(U, W) \\
0 &= \nu W_z + cW_z + g(U, W) \quad (z = x - ct)
\end{aligned}
$$

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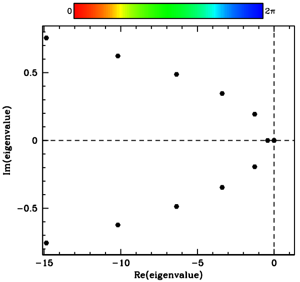
1. solve numerically for the periodic wave by continuation from a Hopf bifn point in the travelling wave eqns
2. for $\gamma = 0$, discretise the eigenfunction equations in space, giving a (large) matrix eigenvalue problem



$$\lambda \overline{u} = \overline{u}_{zz} + c\overline{u}_z + f_u(U,W)\overline{u} + f_w(U,W)\overline{w}, \quad \overline{u}(0) = \overline{u}(L)e^{i\gamma}$$
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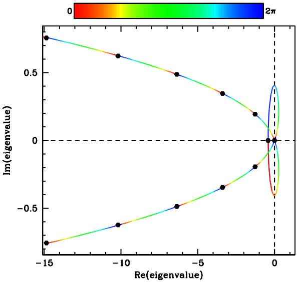

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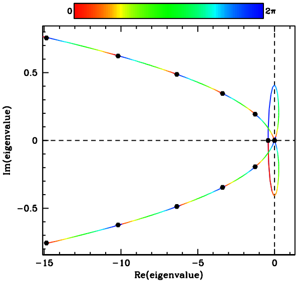

This gives the eigenvalue spectrum, and hence (in)stability

Numerical Calculation of Eigenvalue Spectrum

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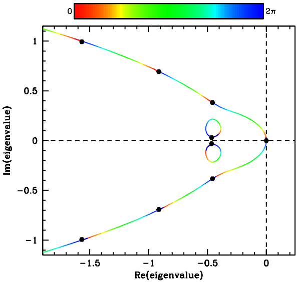
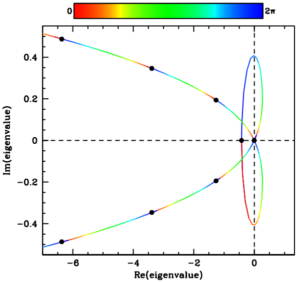


STABLE

Eckhaus instability



UNSTABLE

This gives the eigenvalue spectrum, and hence (in)stability

Stability in a Parameter Plane

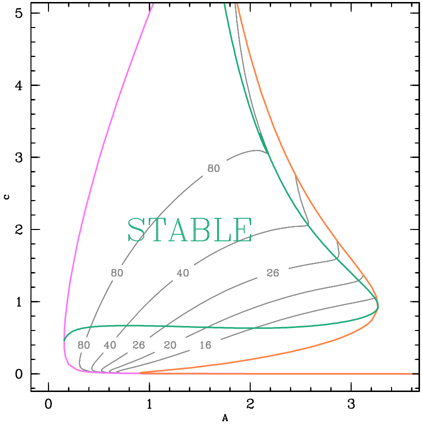
By following this procedure at each point on a grid in parameter space, regions of stability/instability can be determined.

In fact, stable/unstable boundaries can be computed accurately by numerical continuation of the point at which

$$\mathrm{Re}\lambda = \mathrm{Im}\lambda = \gamma = \partial^2 \mathrm{Re}\lambda / \partial \gamma^2 = 0$$

(Eckhaus instability point)

Stability in a Parameter Plane



Pattern Stability: The Key Result

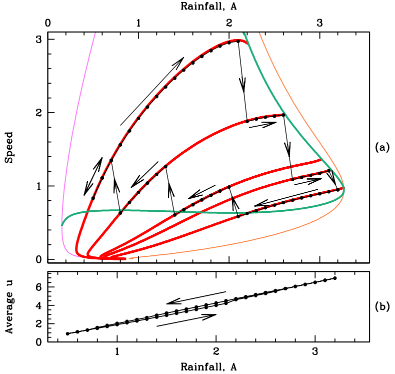
Key Result

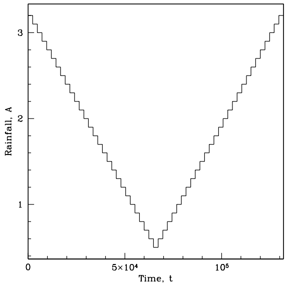
Many of the possible patterns are unstable and thus will never be seen.

However, for a wide range of rainfall levels, there are multiple stable patterns.

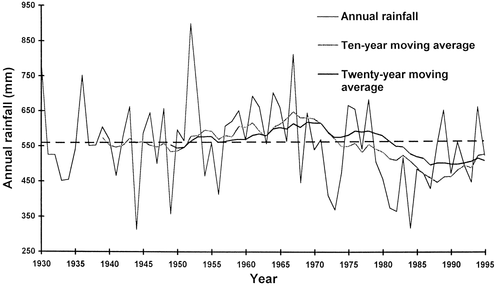
Variations in Rainfall: Hysteresis

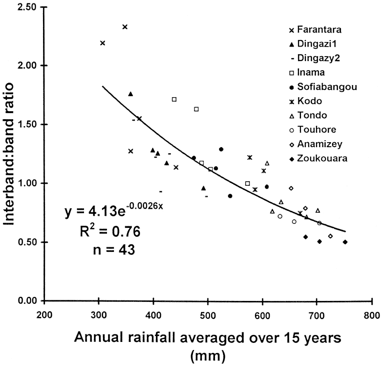
The existence of multiple stable patterns suggests the possibility of hysteresis.





Data on the Effects of Changing Rainfall





Data from 1950-1995 (C. Valentin & J.M. d'Herbès, Catena 37:231, 1999)

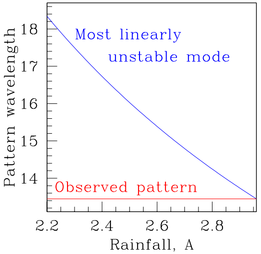
Back to Key Ecological Questions

- At what rainfall level is there a switch from uniform vegetation to patterns?
- At what rainfall level is there a transition to desert?
- How does the spacing of the vegetation bands depend on rainfall, herbivory and slope?

Predictions of Pattern Wavelength

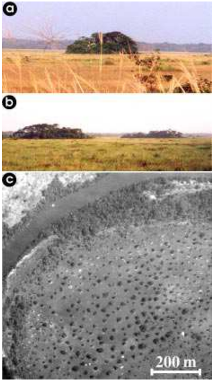
- In general, pattern wavelength depends on initial conditions
- When vegetation stripes arise from homogeneous vegetation via a decrease in rainfall, pattern wavelength will remain at its bifurcating value.

$$\text{Wavelength} = \sqrt{\frac{8\pi^2}{B\nu}}$$



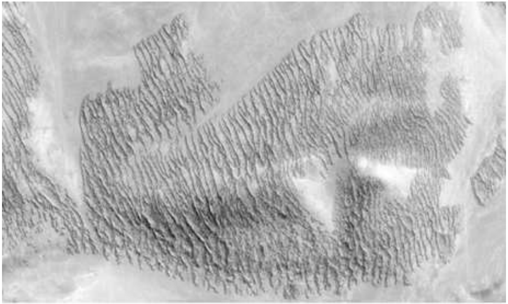
Outline

Tree Patches in Savannah Grasslands



(Olivier Lejeune et al, Phys. Rev. E 66: 010901, 2002)

Pattern of Fog-Dependent Vegetation in Chile



Aerial photo over Atacama Desert, Northern Chile

(Borthagaray et al, J. Theor. Biol. 265: 18-26, 2010)

Tillandsia landbeckii

Ribbon Forest in Colorado, USA

Photo taken by David Buckner

Mudflat Pattern in The Netherlands

(Weerman et al, Am. Nat. 176: E15-E32, 2010)

Mussel Bed Pattern in the Wadden Sea

In the Wadden Sea, mussel beds self-organise into striped patterns

Aerial photo of a mussel bed

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J.A. Sherratt: History-dependent patterns of whole ecosystems. *Ecological Complexity* in press.

J.A. Sherratt: Pattern solutions of the Klausmeier model for banded vegetation in semi-arid environments V: the transition from patterns to desert. Submitted.

List of Frames