History-Dependent Patterns of Whole Ecosystems

Jonathan A. Sherratt

Department of Mathematics
and Maxwell Institute for Mathematical Sciences
Heriot-Watt University

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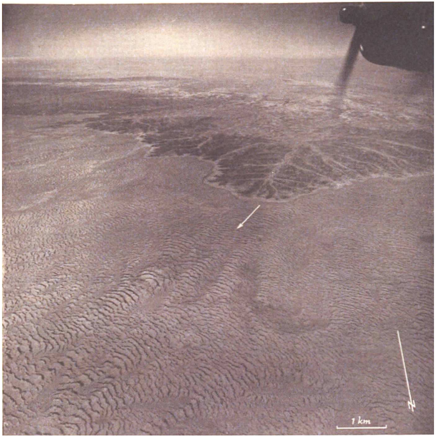
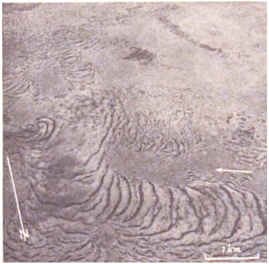
This talk can be downloaded from my web site

www.ma.hw.ac.uk/∼jas

Vegetation Patterns



1950



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

Vegetation Patterns

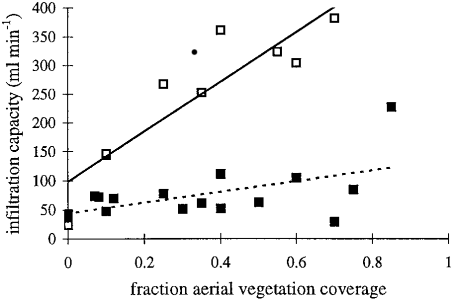
Bushy vegetation in Niger

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 $\Rightarrow$ more roots and organic matter in soil
$\Rightarrow$ more infiltration of rainwater

Banded Patterns on Slopes

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

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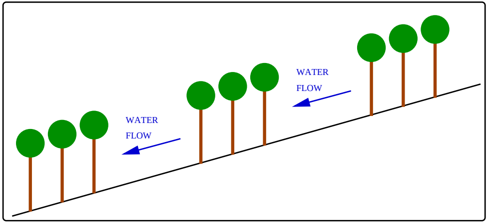

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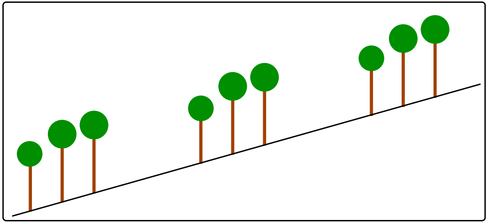

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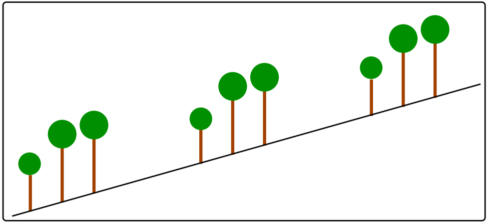

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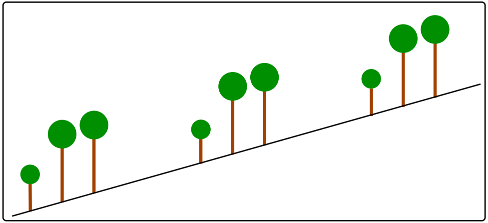

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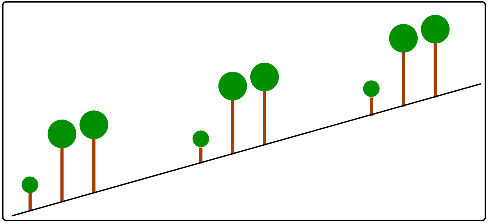

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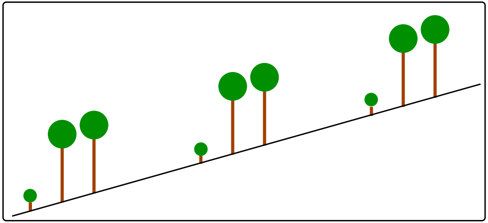

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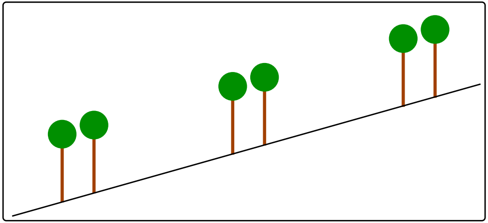

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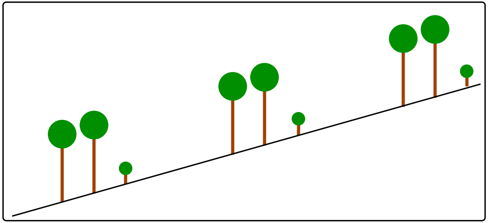

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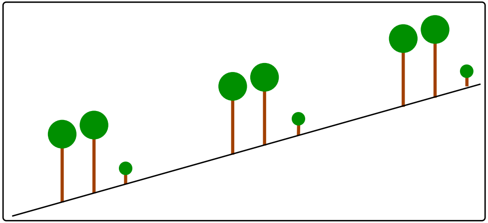

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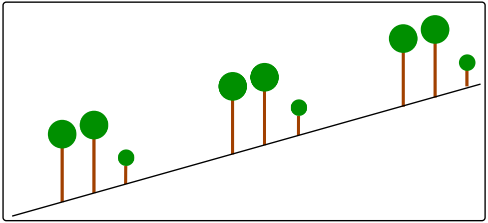

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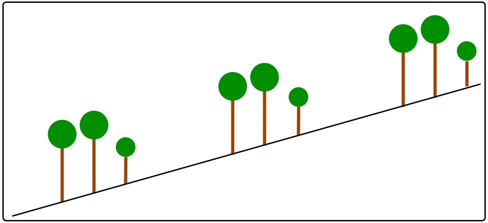

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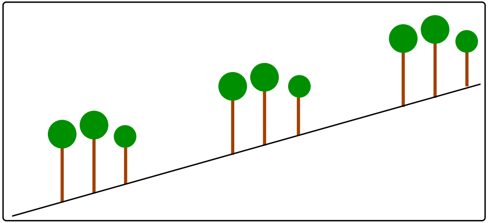

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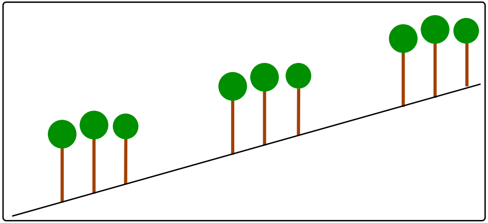

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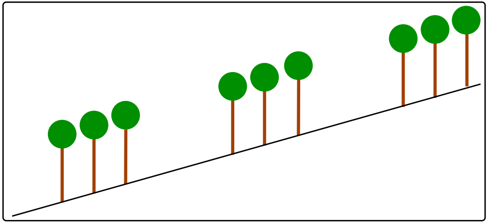

Key Ecological Questions

- 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

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

$$\partial u/\partial t = wu^2 - Bu + \partial^2 u/\partial x^2$$

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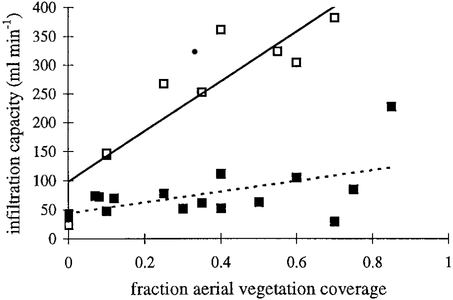

$$wu^2 = w \cdot u \cdot \begin{pmatrix} \text{infiltration} \\ \text{rate} \end{pmatrix}$$

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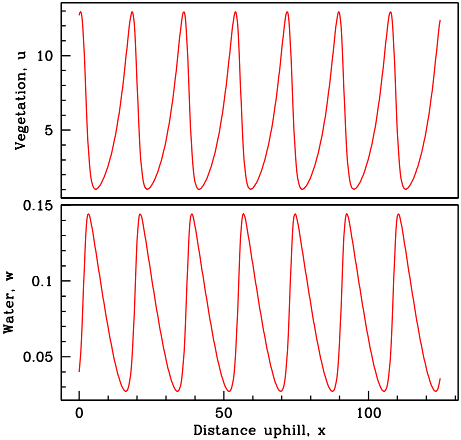
Parameters: A: rainfall B: plant loss ν: slope

Typical Solution of the Model



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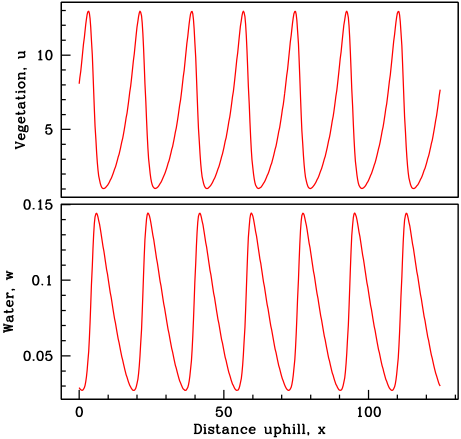

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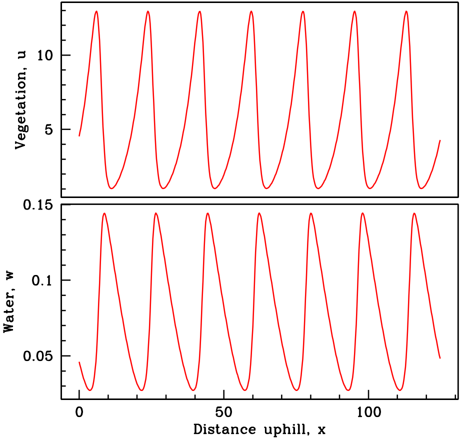

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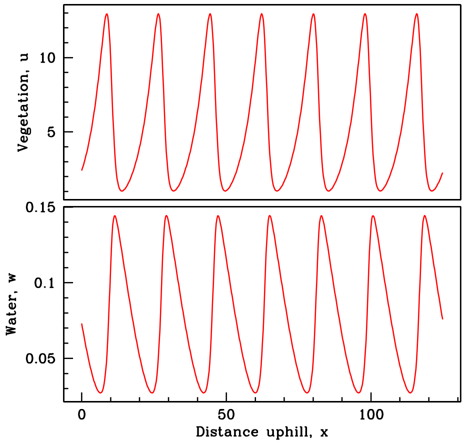

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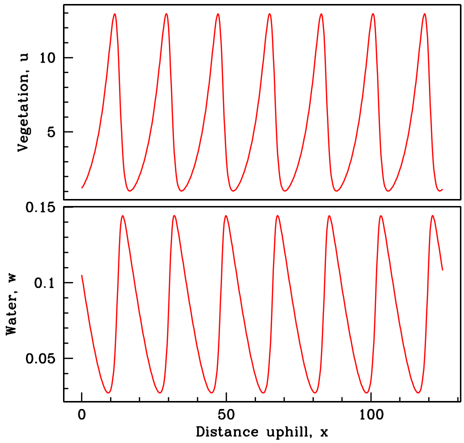

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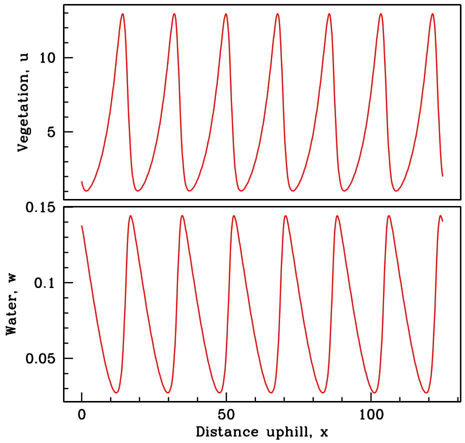

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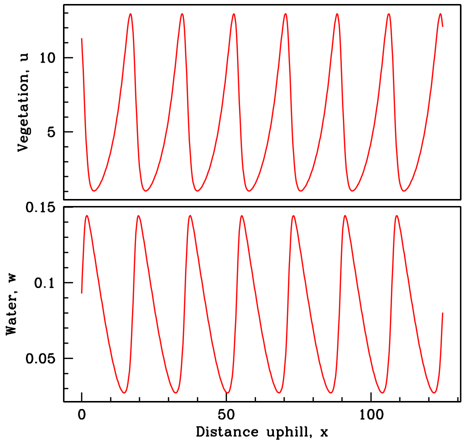

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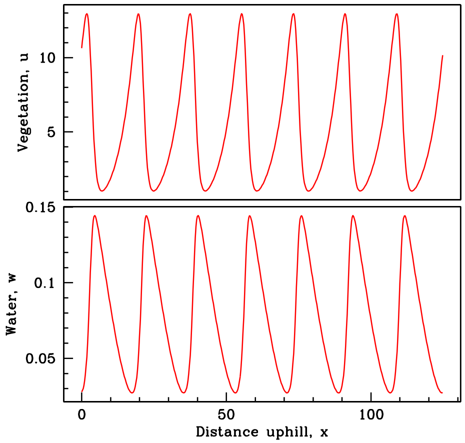

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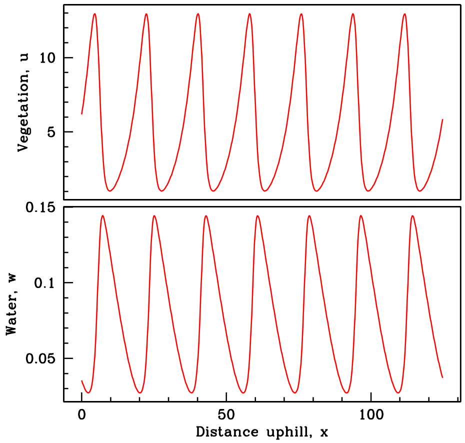

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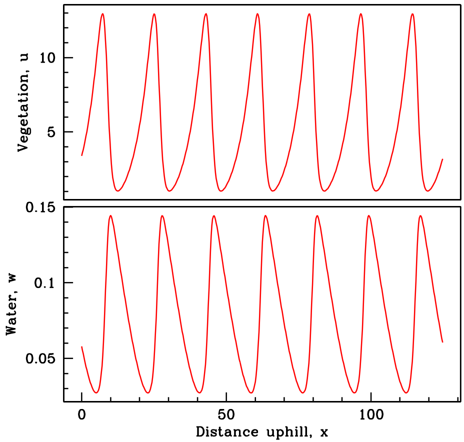

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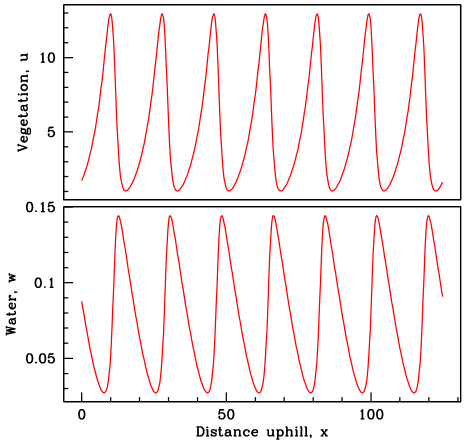

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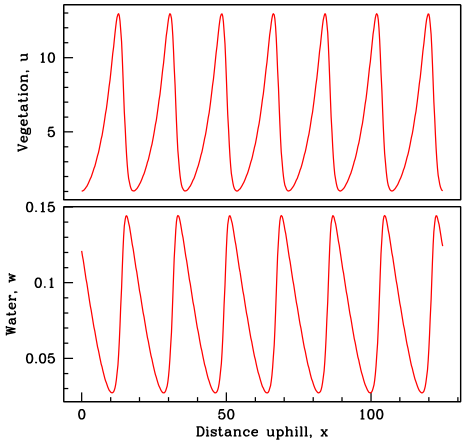

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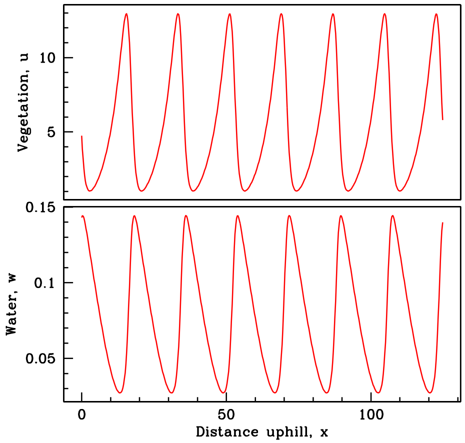

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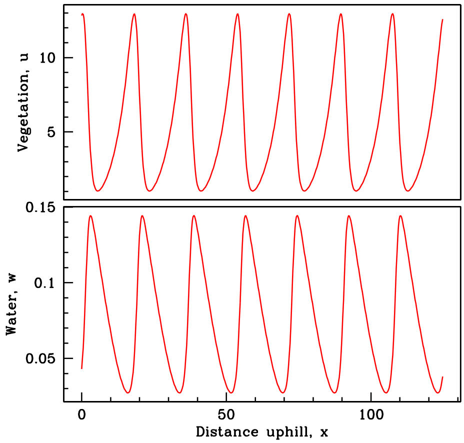

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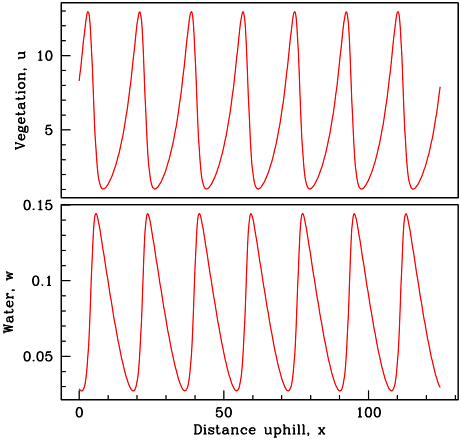

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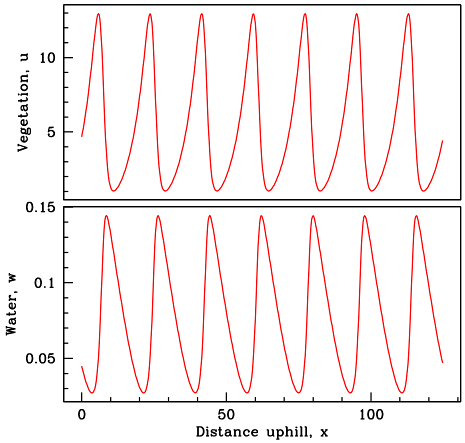

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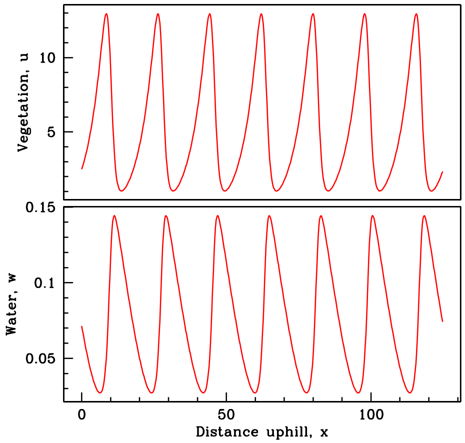

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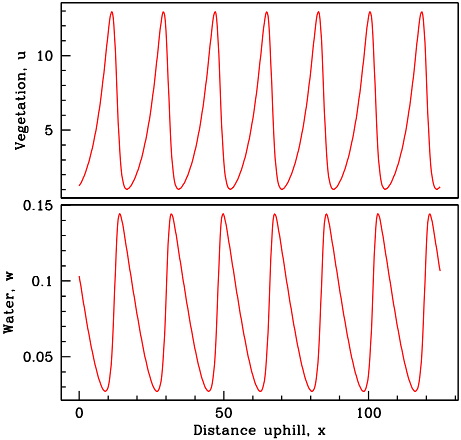

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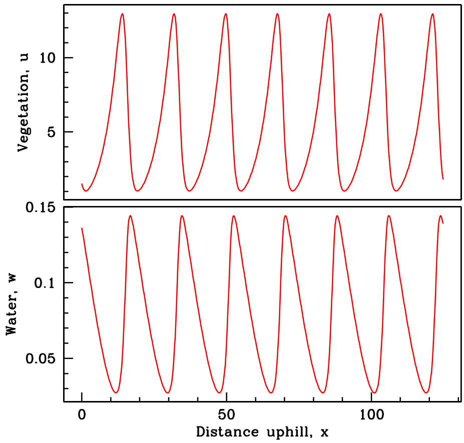

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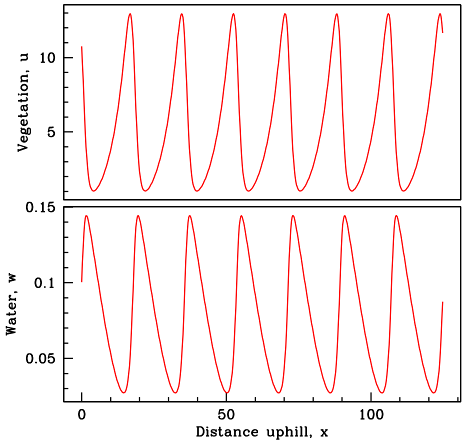

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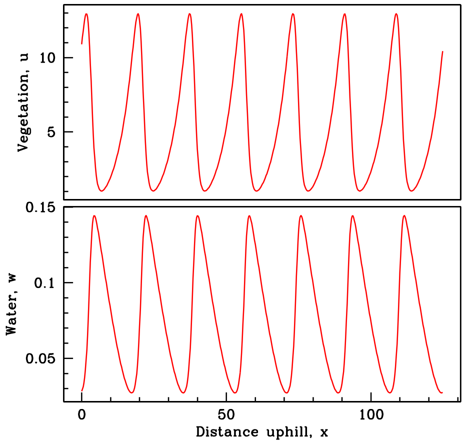

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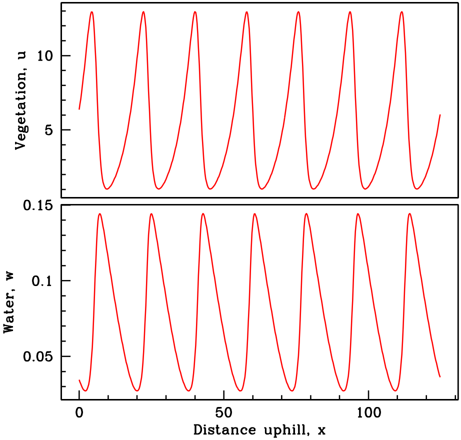

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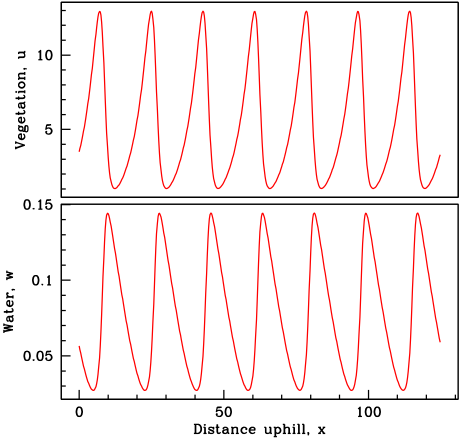

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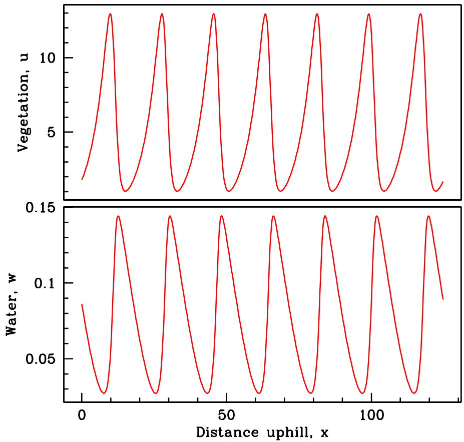

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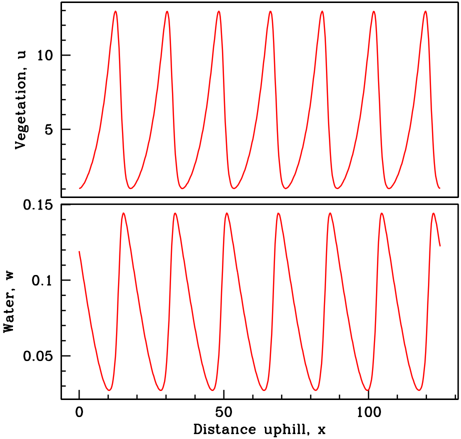

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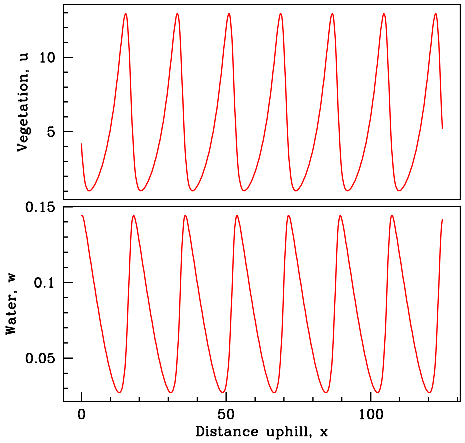

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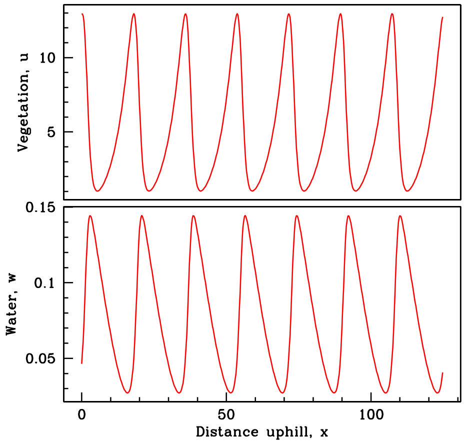

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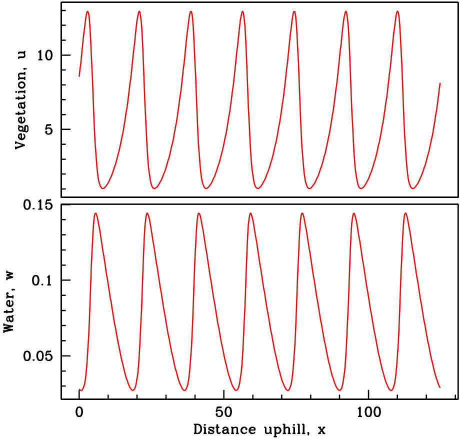

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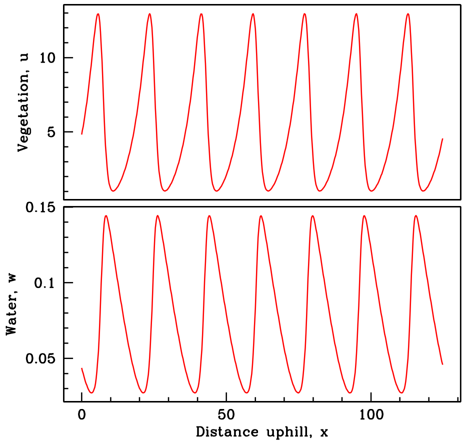

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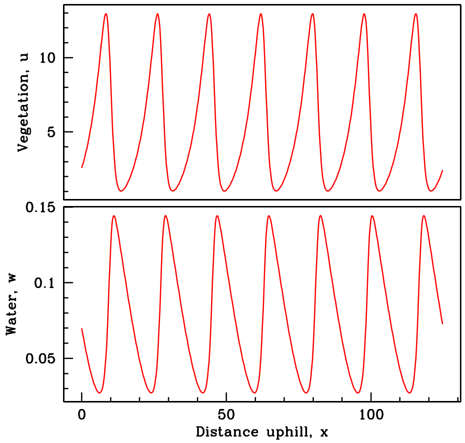

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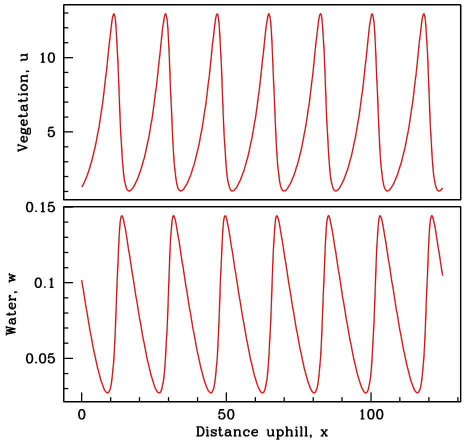

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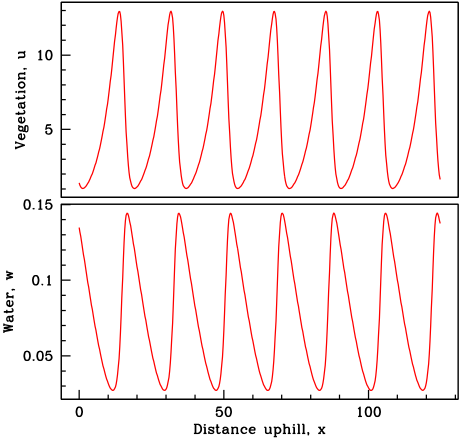

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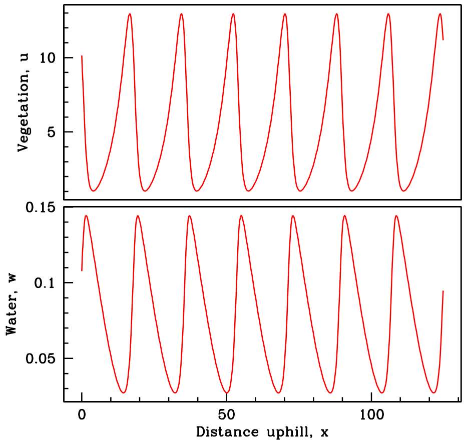

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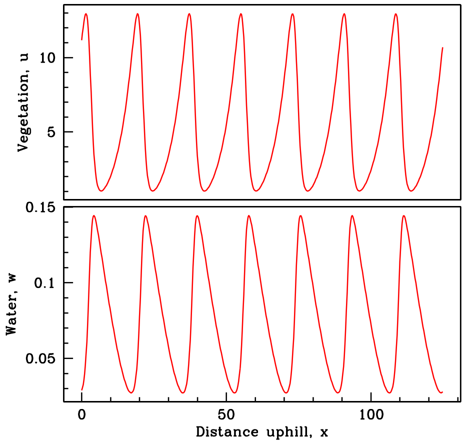

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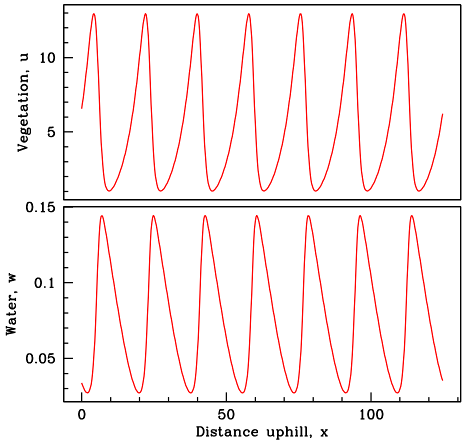

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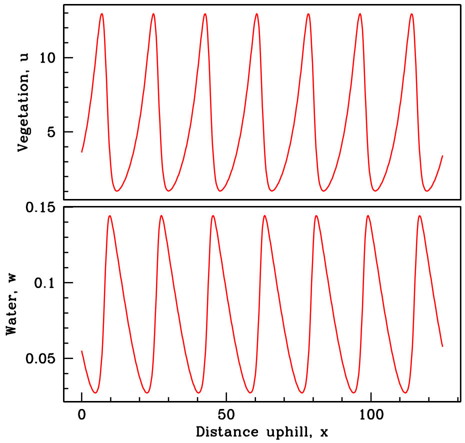

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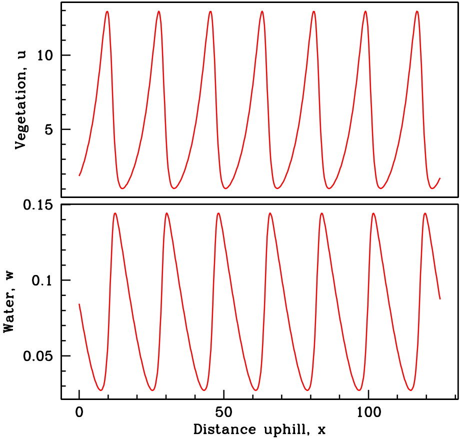

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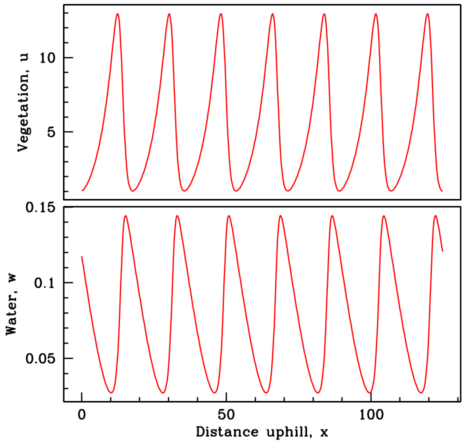

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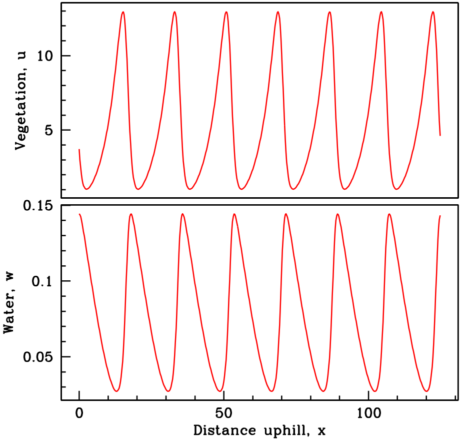

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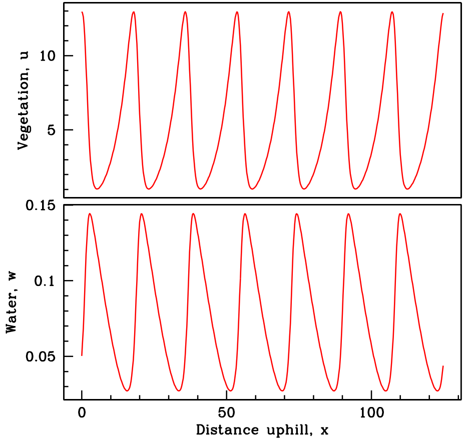

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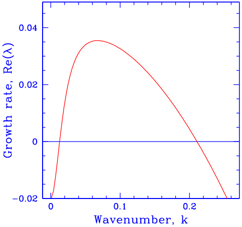
- When $A \geq 2B$, there are also two non-trivial steady states, one of which is unstable to homogeneous perturbations
- The other steady state (u_s, w_s) is stable to homogeneous perturbations but can be unstable to inhomogeneous perturbations $\Rightarrow$ pattern formation

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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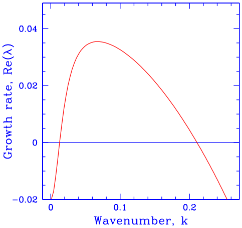

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To leading order for large ν, the condition for pattern formation is

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

Back to Key Ecological Questions

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- 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

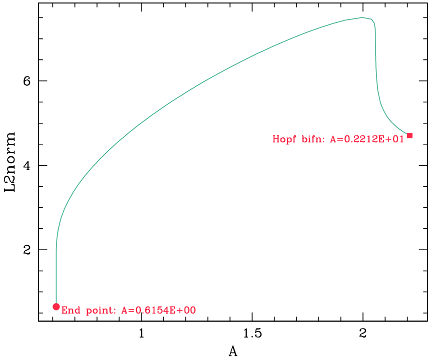
Travelling Wave Equations

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

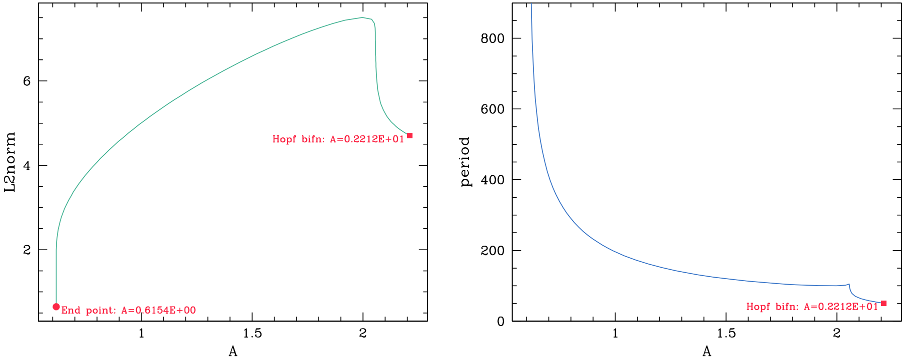
$$\begin{aligned} d^2U/dz^2 + c\,dU/dz + WU^2 - BU &= 0 \\ (\nu + c)dW/dz + A - W - WU^2 &= 0 \end{aligned}$$

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

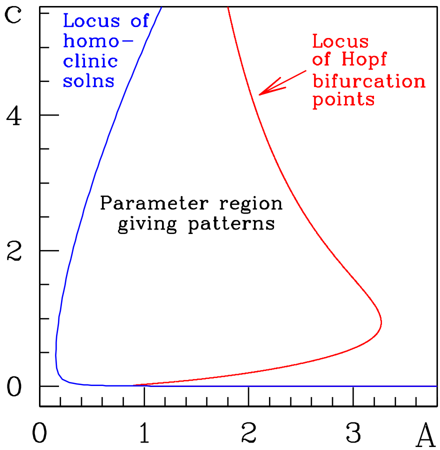
Bifurcation Diagram for Travelling Wave Equations



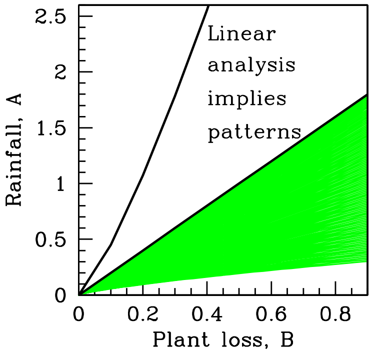
Bifurcation Diagram for Travelling Wave Equations



When do Patterns Form?



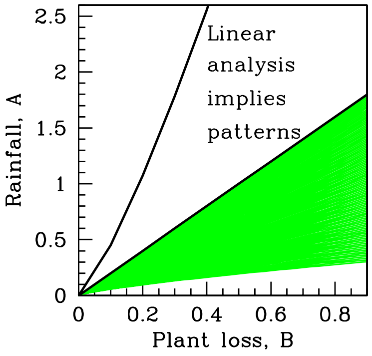
Pattern Formation for Low Rainfall

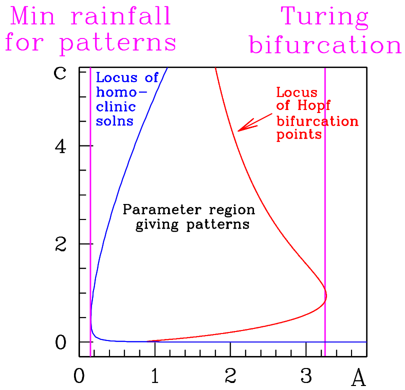


Recall: the homogeneous steady state only exists for $A \geq 2B$

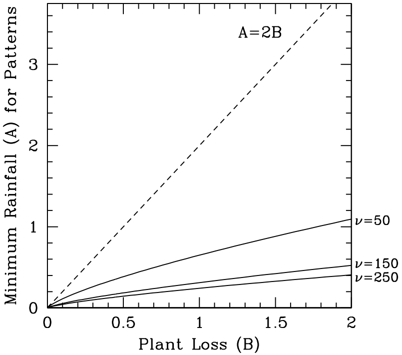
Patterns are also seen for parameters in the green region.

Pattern Formation for Low Rainfall





Minimum Rainfall for Patterns



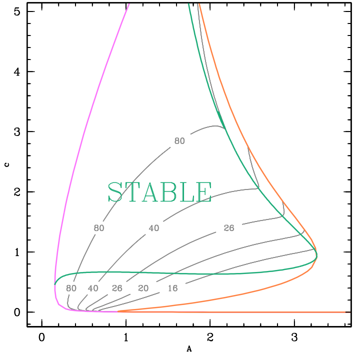
Back to Key Ecological Questions

- 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

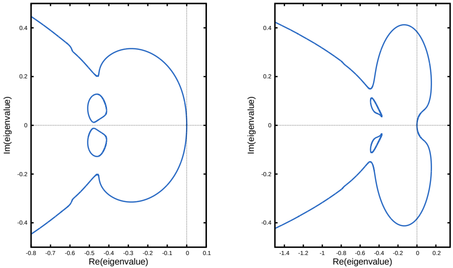
Pattern Stability

Not all of the possible patterns are stable as solutions of the model equations.



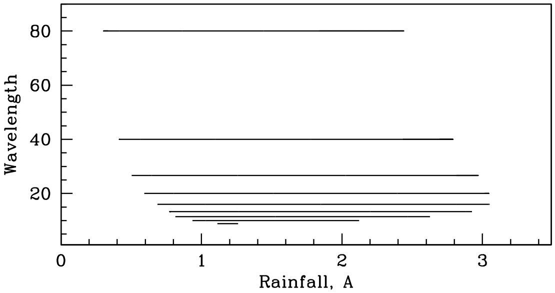
Pattern Stability: Numerical Approach

The boundary between stable and unstable patterns can be calculated by numerical continuation of the essential spectrum.



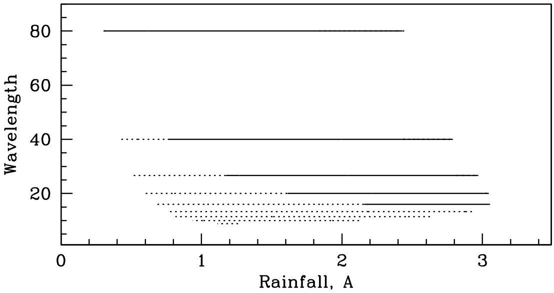
Calculations of this type can be performed using the software package WAVETRAIN (www.ma.hw.ac.uk/wavetrain).

Pattern Stability: Wavelength vs Rainfall



The wavelengths shown are those compatible with periodic boundary conditions on a domain of length 80.

Pattern Stability: Wavelength vs Rainfall



The wavelengths shown are those compatible with periodic boundary conditions on a domain of length 80.

Pattern Stability: The Key Result

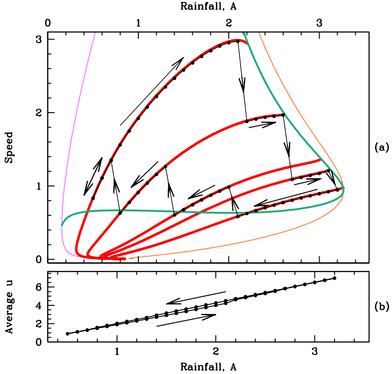
Key Result

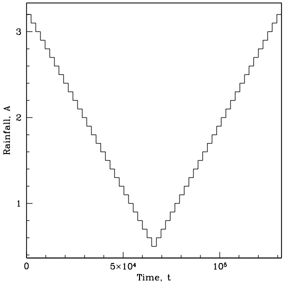
Many of the possible patterns are unstable and thus will never be seen.

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

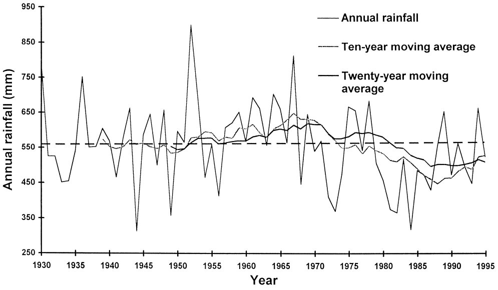
Variations in Rainfall: Hysteresis

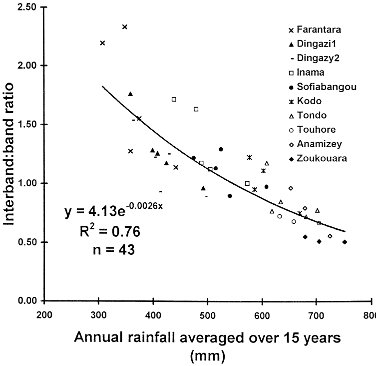
The existence of multiple stable patterns suggests the possibility of hysteresis.





Data on the Effects of Changing Rainfall





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

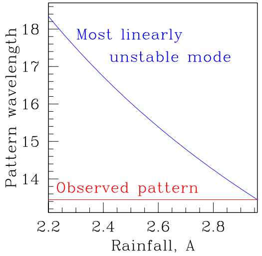
Back to Key Ecological Questions

- 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

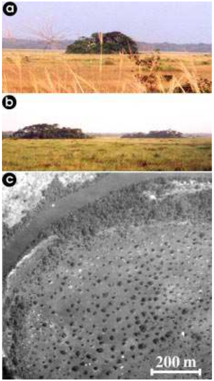
- In general, pattern wavelength depends on initial conditions
- When vegetation stripes arise from homogeneous vegetation via a decrease in rainfall, pattern wavelength will remain at its bifurcating value.

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



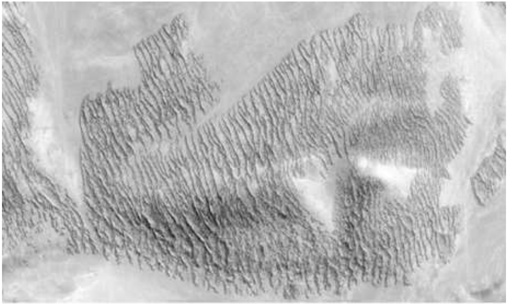
Outline

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)

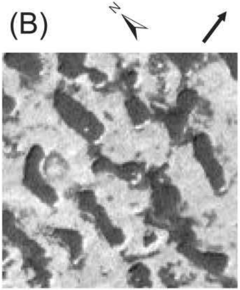
Mussel Bed Pattern in the Wadden Sea

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

Aerial photo of a mussel bed

Mussel Bed Pattern in the Wadden Sea

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



25 m by 25 m

Aerial photo of a mussel bed

Mussel Bed Pattern in the Wadden Sea

Model of van de Koppel *et al*

(Am Nat 165: E66, 2005)

$$a(x,t) = \text{density of algae}$$
$$m(x,t) = \text{density of mussels}$$

$$\frac{\partial a}{\partial t} = \overbrace{\beta\,\partial a/\partial x}^{\text{advection by tide}} + \overbrace{\alpha(1-a)}^{\text{transfer to/from upper water layers}} - \overbrace{am}^{\text{eaten by mussels}}$$
$$\frac{\partial m}{\partial t} = \underbrace{\partial^2 m/\partial x^2}_{\text{random movement}} + \underbrace{\delta am}_{\text{birth}} - \underbrace{\gamma\, m/(1+m)}_{\text{dislodgement by waves}}$$

Aerial photo of a mussel bed

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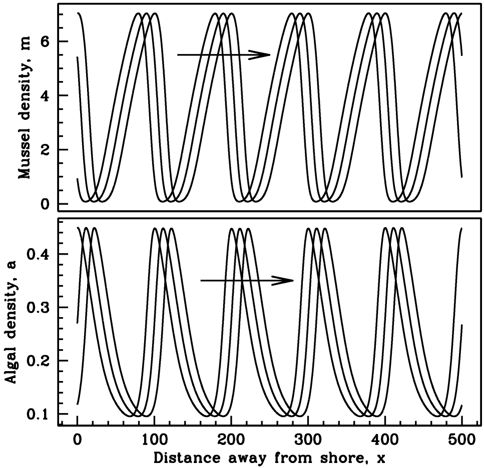
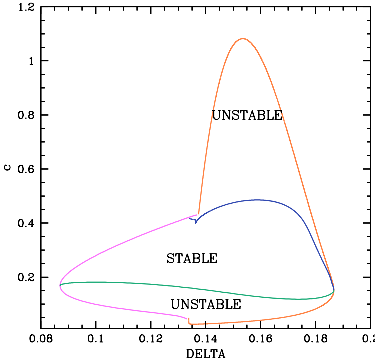
Aerial photo of a mussel bed

Typical Pattern Solution

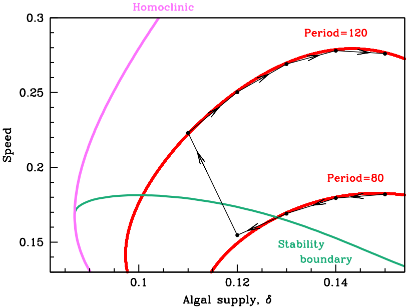


Pattern Existence and Stability



The parameter δ reflects the supply rate of algae

Hysteresis in Mussel Bed Patterns



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List of Frames