# Predicting the Wavelength of Vegetation Patterns using Mathematical Models

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This talk can be downloaded from my web site

www.ma.hw.ac.uk/ $\sim$ jas



#### Outline

- Ecological Background
- Detailed Calculation of Possible Wavelengths
- Effects of Changing Rainfall Levels
- Wavelength Selection: Two Examples
- Further Reading



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- Ecological Background
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Further Reading

- 3 Effects of Changing Rainfall Levels
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#### Ecological Background

Detailed Calculation of Possible Wavelengths Effects of Changing Rainfall Levels Wavelength Selection: Two Examples Further Reading

#### **Vegetation Patterns**

# Vegetation Patterns

#### High rainfall: uniform vegetation



#### Very low rainfall: no vegetation





Further Reading

Wavelength Selection: Two Examples

Vegetation Patterns

Pattern Wavelength: A Quantitative Statisti Mathematical Model of Klausmeier Typical Solution of the Model

# Vegetation Patterns

High rainfall: uniform vegetation



Low rainfall: patterned vegetation



W National Park, Niger Average patch width 50 m

Very low rainfall: no vegetation



#### **Vegetation Patterns**



Bushy vegetation in Niger



Mitchell grass in Australia
(Western New South Wales)

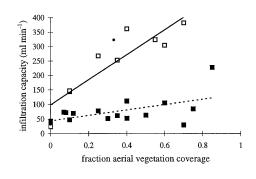
- Banded vegetation patterns are found on gentle slopes in semi-arid areas of Africa, Australia and Mexico
- Plants vary from grasses to shrubs and trees



#### Vegetation Patterns

Pattern Wavelength: A Quantitative Statistic Mathematical Model of Klausmeier Typical Solution of the Model Homogeneous Steady States

#### 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



#### Pattern Wavelength: A Quantitative Statistic

 The wavelength of vegetation bands is probably the most accessible quantitative statistic for vegetation patterns.



 Our topic: how to predict pattern wavelength using mathematical models



#### Mathematical Model of Klausmeier

$$\label{eq:Rate of change = Rainfall - Evaporation} \begin{array}{ll} - \mbox{ Uptake by } + \mbox{ Flow} \\ \mbox{ of water } & \mbox{ plants } & \mbox{ downhill } \end{array}$$

$$\label{eq:Rate of change = Growth, proportional - Mortality} & + \mbox{ Random } \\ & \mbox{plant biomass} & \mbox{to water uptake} & \mbox{dispersal} \\ \end{aligned}$$

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

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

#### Mathematical Model of Klausmeier

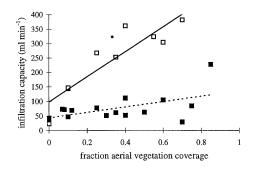
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The nonlinearity in  $wu^2$  arises because the presence of plants increases water infiltration into the soil.



#### Mathematical Model of Klausmeier



$$wu^2 = w \cdot u \cdot \left( \begin{array}{c} \text{infiltration} \\ \text{rate} \end{array} \right)$$

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#### Mathematical Model of Klausmeier

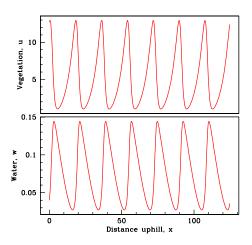
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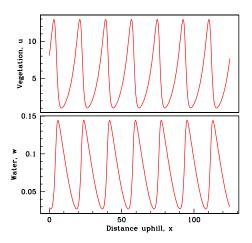
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Parameters: A: rainfall B: plant loss  $\nu$ : slope

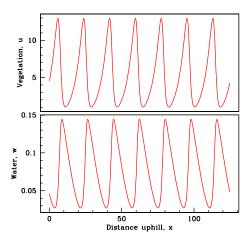


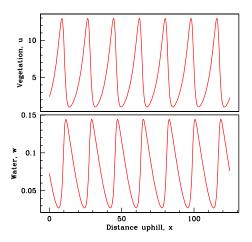




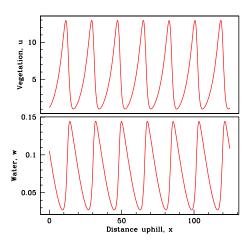


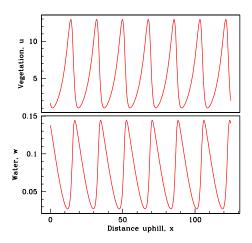




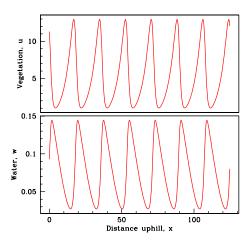




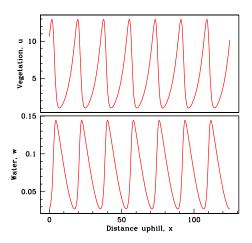


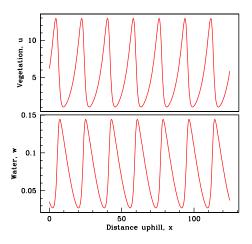


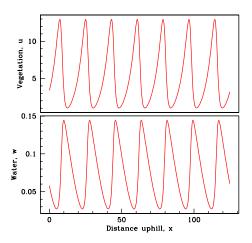


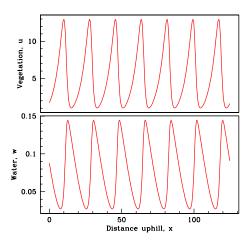




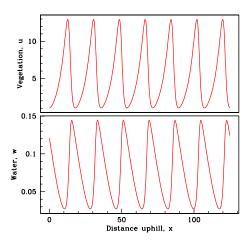




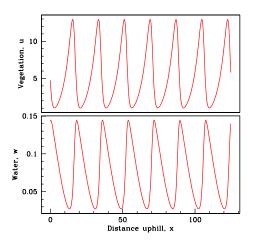






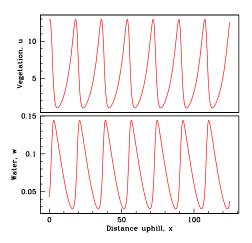




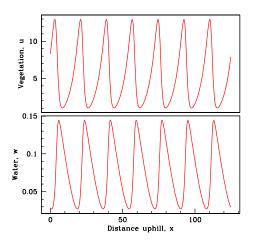


Further Reading

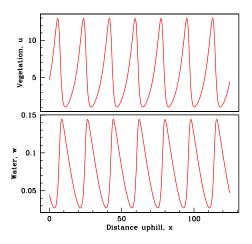
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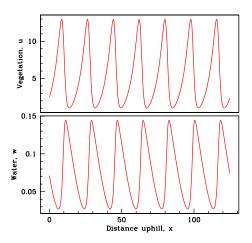


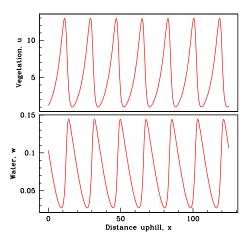


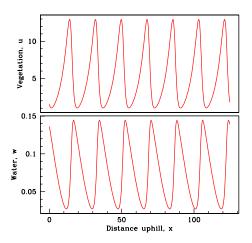




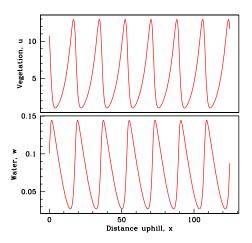


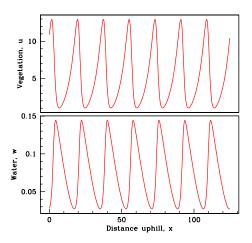


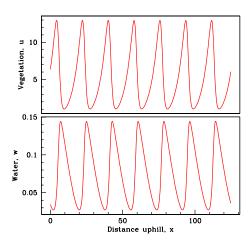




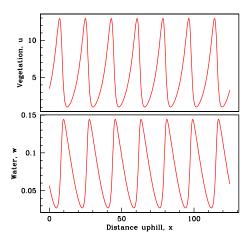


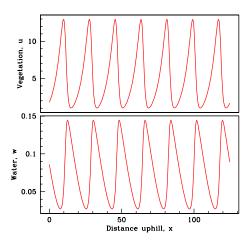


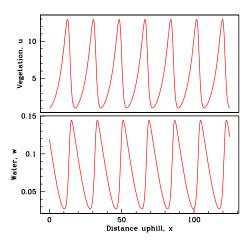


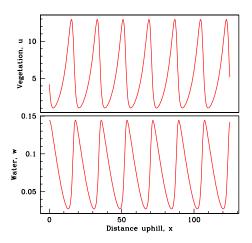




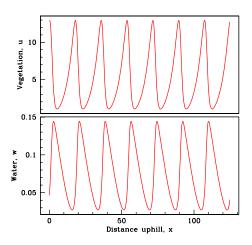




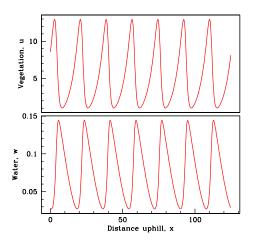




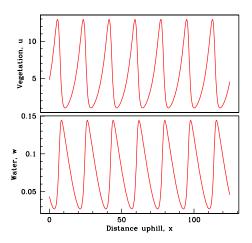




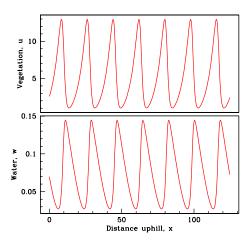


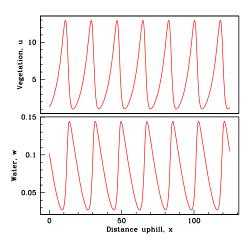




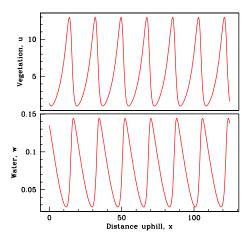


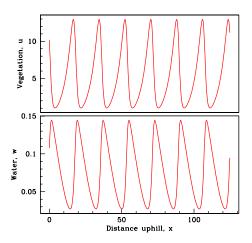








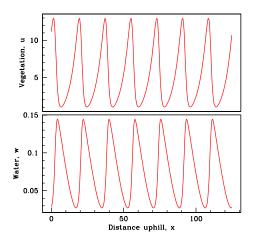


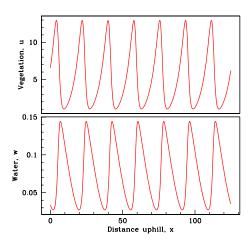




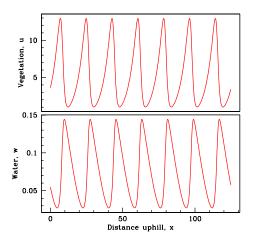
Further Reading

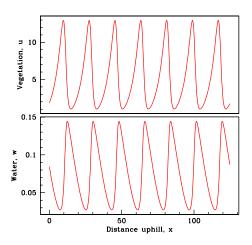
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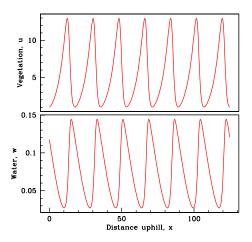




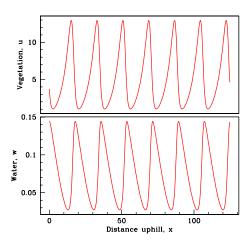




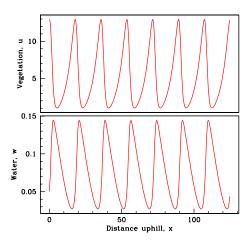








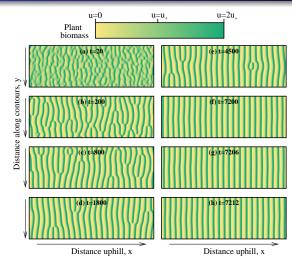




Detailed Calculation of Possible Wavelengths Effects of Changing Rainfall Levels Wavelength Selection: Two Examples Further Reading

Typical Solution of the Model

### Typical Solution of the Model in Two Dimensions





# Homogeneous Steady States

- The starting point for mathematical study of vegetation patterns is to determine homogeneous steady states
- Recall the model equations:

$$\frac{\partial w}{\partial t} = A - w - wu^{2} + \nu \frac{\partial w}{\partial x}$$
  
$$\frac{\partial u}{\partial t} = wu^{2} - Bu + \frac{\partial^{2} u}{\partial x^{2}}$$

For homogeneous steady states 
$$A = w + wu^2$$
,  $Bu = wu^2$   
 $\Rightarrow u = 0$ ,  $w = A$  or  $uw = B$ ,  $A - w - B^2/w = 0$ 

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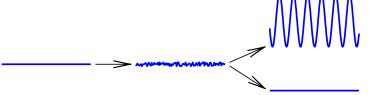
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- For all parameter values, there is a stable "desert" steady state u = 0, w = A
- When  $A \ge 2B$ , there are also two non-trivial steady states satisfying  $w^2 Aw + B^2 = 0$ , u = B/w



### Stability of Homogeneous Steady States I

 Patterns can arise when a homogeneous steady state is unstable



- To determine stability:
  - (i) Linearise the model about the steady state

$$\begin{array}{rcl} \partial \hat{\boldsymbol{w}}/\partial t & = & -(1+u_s^2)\hat{\boldsymbol{w}} - 2B\hat{\boldsymbol{u}} + \nu\partial\hat{\boldsymbol{w}}/\partial x \\ \partial \hat{\boldsymbol{u}}/\partial t & = & u_s^2\hat{\boldsymbol{w}} + B\hat{\boldsymbol{u}} + \partial^2\hat{\boldsymbol{u}}/\partial x^2 \\ & & (\hat{\boldsymbol{w}} = \boldsymbol{w} - \boldsymbol{w}_s, \quad \hat{\boldsymbol{u}} = \boldsymbol{u} - \boldsymbol{u}_s) \end{array}$$

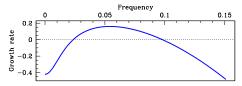


# Stability of Homogeneous Steady States II

- To determine stability:
  - (i) Linearise the model about the steady state
  - (ii) Consider sinusoidal solutions:

$$(\hat{u}, \hat{w}) = \underbrace{(u_s, w_s)}_{\substack{\text{steady}\\ \text{state}}} + \underbrace{(\tilde{u}, \tilde{w})}_{\substack{\text{small}\\ \text{constants}}} \cdot \underbrace{e^{\lambda t}}_{\substack{\text{cos}\\ \text{cos}}} \cdot \underbrace{\sin(2\pi f x)}_{\substack{\text{cos}\\ \text{frequency } f}}$$

Substituting into the model gives  $\lambda(f)$  ("dispersion relation")

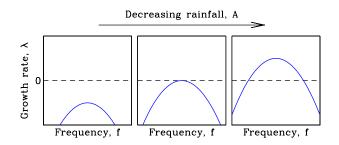


(iii) The steady state is unstable if Re  $\lambda(f) > 0$  for some f



### Stability of Homogeneous Steady States III

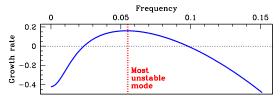
The steady state loses stability as rainfall A is decreased





### Stability of Homogeneous Steady States IV

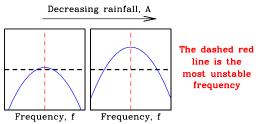
In many cases the pattern wavelength corresponds to the most unstable frequency (wavelength=1/frequency).





# Stability of Homogeneous Steady States IV

In many cases the pattern wavelength corresponds to the most unstable frequency (wavelength=1/frequency).



When *A* is just small enough for patterns, the most unstable frequency gives a reliable guide to wavelength. For smaller *A*, wavelength selection is more complicated.



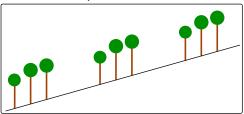
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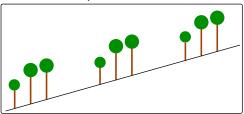




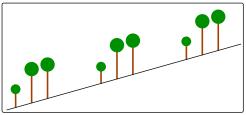
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WATER FLOW
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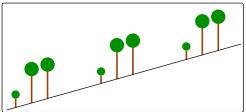


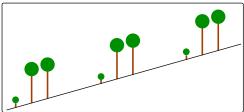




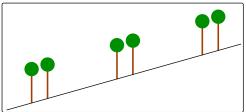


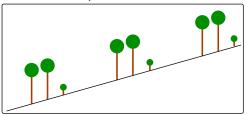


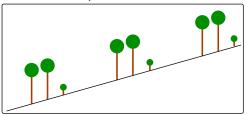


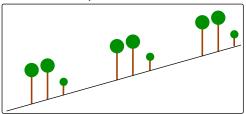


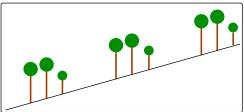


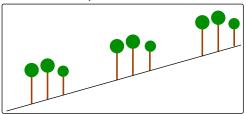


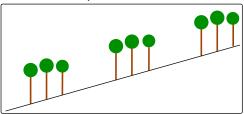




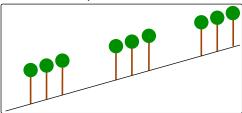














## Travelling Wave Equations

The patterns move at constant shape and speed  $\Rightarrow u(x,t) = U(z), w(x,t) = W(z), z = x - ct$   $d^2 U/dz^2 + c dU/dz + WU^2 - BU = 0$   $(\nu + c)dW/dz + A - W - WU^2 = 0$ 

Patterns are periodic (limit cycle) solutions of these equations Calculation of all possible patterns is done in three steps.

#### Step 1: Calculate the Locus of Hopf Bifurcations

Patterns are periodic (limit cycle) solutions of the equations

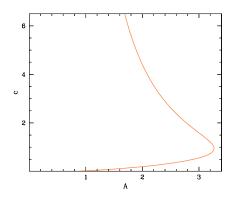
$$d^2U/dz^2 + c dU/dz + WU^2 - BU = 0$$
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Patterns lie on a solution branch that starts at a Hopf bifurcation point (in most cases)

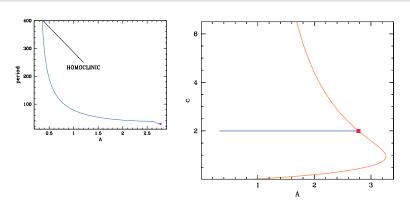
Step 1: Calculate the locus of Hopf bifurcations in the *A–c* plane



## Step 1: Calculate the Locus of Hopf Bifurcations



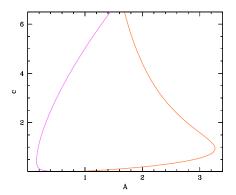
#### Step 2: Calculate Some Branches of Pattern Solutions



Step 2: Calculate some branches of pattern solutions. These end at a homoclinic solution

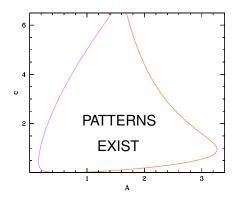


#### Step 3: Calculate the Locus of Homoclinic Solutions



Step 3: Calculate the homoclinic locus, approximated by the locus of patterns of a fixed, very long period

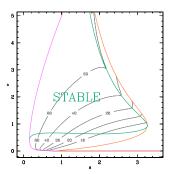
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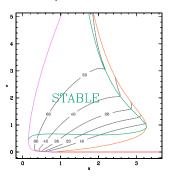
## Pattern Stability

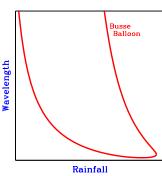
Not all of the possible patterns are stable as solutions of the model equations.



## Pattern Stability

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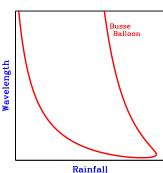
The parameter region with stable patterns is known as the "Busse balloon".

## Pattern Stability

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

#### Key Result

For many rainfall levels, there are stable patterns with a range of wavelengths.



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 
$$u(z,t) = U(z) + e^{\lambda t} \overline{u}(z)$$
 with  $|\overline{u}| \ll |U|$   
 $w(z,t) = W(z) + e^{\lambda t} \overline{w}(z)$  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: 
$$\overline{u}(0) = \overline{u}(L)e^{i\gamma}$$
  $(0 \le \gamma < 2\pi)$ 

$$\overline{w}(0) = \overline{w}(L)e^{i\gamma} \quad (0 \le \gamma < 2\pi)$$

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

$$W(2,t) = W(2) + C W(2) \quad \text{with } |W| \leq |W|$$

$$\Rightarrow$$
 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: 
$$\overline{u}(0) = \overline{u}(L)e^{i\gamma}$$
  $(0 \le \gamma < 2\pi)$ 

$$\overline{w}(0) = \overline{w}(L)e^{i\gamma} \quad (0 < \gamma < 2\pi)$$

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

$$\Rightarrow$$
 Eigenfunction eqn:  $\lambda \overline{u} = \overline{u}_{zz} + c\overline{u}_z + f_u(U, W)\overline{u} + f_w(U, W)\overline{w}$   
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Boundary conditions: 
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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 
$$u(z,t) = U(z) + e^{\lambda t} \overline{u}(z)$$
 with  $|\overline{u}| \ll |U|$   
 $w(z,t) = W(z) + e^{\lambda t} \overline{w}(z)$  with  $|\overline{w}| \ll |V|$ 

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

$$\Rightarrow$$
 Eigenfunction eqn:  $\lambda \overline{u} = \overline{u}_{zz} + c\overline{u}_z + f_u(U, W)\overline{u} + f_w(U, W)\overline{w}$   
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Boundary conditions: 
$$\overline{u}(0) = \overline{u}(L)e^{i\gamma}$$
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PDE model: 
$$u_t = u_{zz} + cu_z + f(u, w)$$
  
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Periodic wave satisfies: 
$$0 = U_{zz} + cU_z + f(U, W)$$

$$0 = \nu W_z + cW_z + g(U, W)$$

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

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

$$\lambda w = \nu w_z + c w_z + g_u(O, vv)u + g_w(O, vv)v$$

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

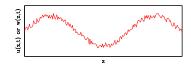
$$\lambda \overline{w} = \nu \overline{w}_z + c\overline{w}_z + g_u(U, W)\overline{u} + g_w(U, W)\overline{w}$$

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

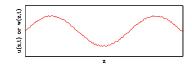
Eigenfunction eqn: 
$$\lambda \overline{u} = \overline{u}_{zz} + c\overline{u}_z + f_u(U, W)\overline{u} + f_w(U, W)\overline{w}$$

$$\lambda \overline{w} = \nu \overline{w}_z + c\overline{w}_z + g_u(U, W)\overline{u} + g_w(U, W)\overline{w}$$

Here 
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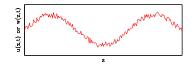




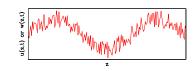
Eigenfunction eqn: 
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$$\lambda \overline{w} = \nu \overline{w}_z + c\overline{w}_z + g_u(U, W)\overline{u} + g_w(U, W)\overline{w}$$

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







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

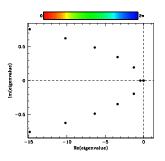
 solve numerically for the periodic wave by continuation from a Hopf bifn point in the travelling wave eqns

$$0 = U_{zz} + cU_z + f(U, W)$$

$$0 = \nu W_z + cW_z + g(U, W) \quad (z = x - ct)$$

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

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

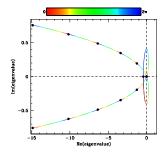


$$\lambda \overline{u} = \overline{u}_{zz} + c\overline{u}_z + f_u(U, W)\overline{u} + f_w(U, W)\overline{w}, \quad \overline{u}(0) = \overline{u}(L)e^{i\gamma}$$

$$\lambda \overline{w} = \nu \overline{w}_z + c\overline{w}_z + g_u(U, W)\overline{u} + g_w(U, W)\overline{w}, \quad \overline{w}(0) = \overline{w}(L)e^{i\gamma}$$

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- solve numerically for the periodic wave by continuation from a Hopf bifn point in the travelling wave eqns
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- $\odot$  continue the eigenfunction equations numerically in  $\gamma$ , starting from each of the periodic eigenvalues

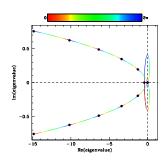


$$\lambda \overline{u} = \overline{u}_{zz} + c\overline{u}_z + f_u(U, W)\overline{u} + f_w(U, W)\overline{w}, \quad \overline{u}(0) = \overline{u}(L)e^{i\gamma}$$

$$\lambda \overline{w} = \nu \overline{w}_z + c\overline{w}_z + g_u(U, W)\overline{u} + g_w(U, W)\overline{w}, \quad \overline{w}(0) = \overline{w}(L)e^{i\gamma}$$

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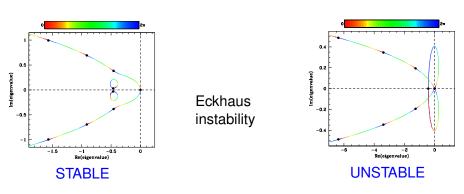
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This gives the eigenvalue spectrum, and hence (in)stability



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



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.

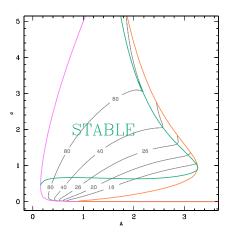
In fact, stable/unstable boundaries can be computed accurately by numerical continuation of the point at which

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

(Eckhaus instability point)



## Stability in a Parameter Plane

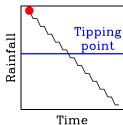


#### Outline

- Ecological Background
- Detailed Calculation of Possible Wavelengths
- 3 Effects of Changing Rainfall Levels
- Wavelength Selection: Two Examples
- Further Reading

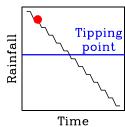


## The Onset of Patterning



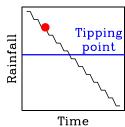


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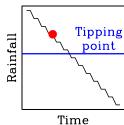


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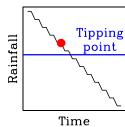


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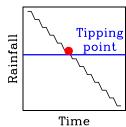


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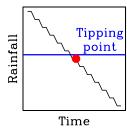


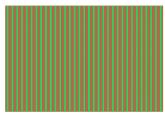
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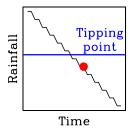


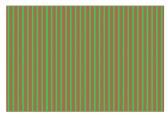


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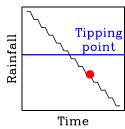


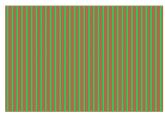




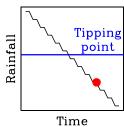


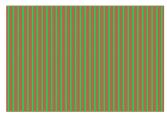
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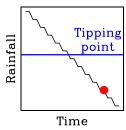


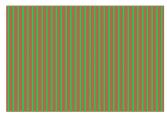
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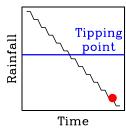


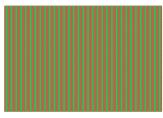
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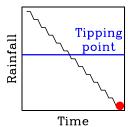
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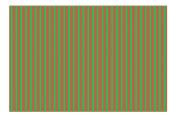




### The Onset of Patterning

At high rainfall levels, vegetation is uniform. The transition to patterns is a "tipping point"





The tipping point occurs when the homogeneous steady state becomes unstable.

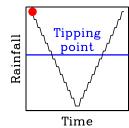


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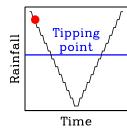
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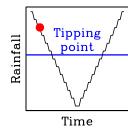
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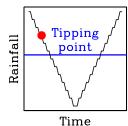
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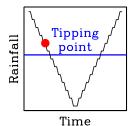


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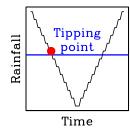


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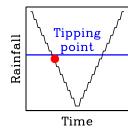
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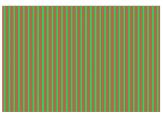




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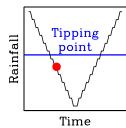
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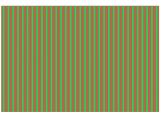




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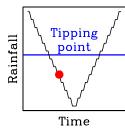
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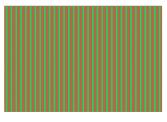




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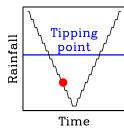
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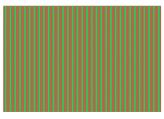




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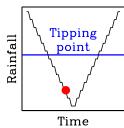
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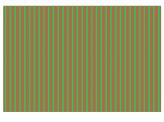




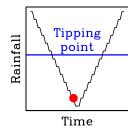
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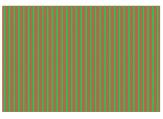
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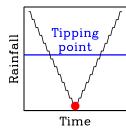
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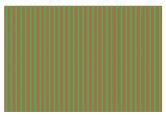




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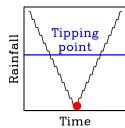
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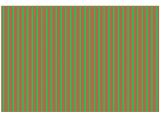




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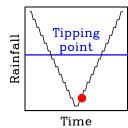


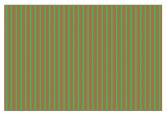


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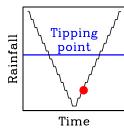
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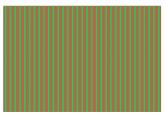
www.macs.hw.ac.uk/~jas





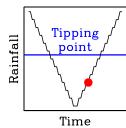
At high rainfall levels, vegetation is uniform. The transition to patterns is a "tipping point"

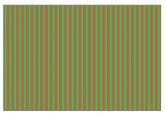




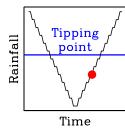
## The Onset of Patterning

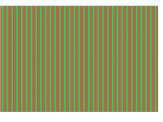
At high rainfall levels, vegetation is uniform. The transition to patterns is a "tipping point"



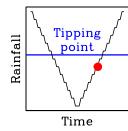


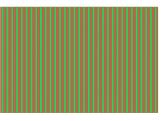
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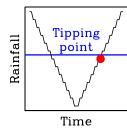
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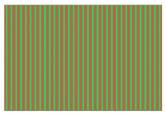




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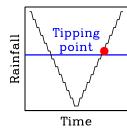
At high rainfall levels, vegetation is uniform. The transition to patterns is a "tipping point"

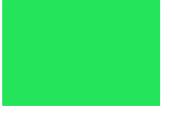




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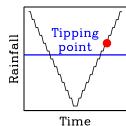
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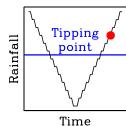
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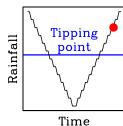
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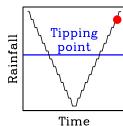
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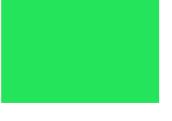
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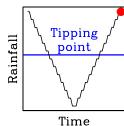
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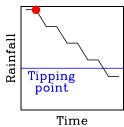
#### Desertification

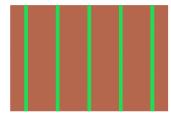
At very low rainfall, vegetation cannot survive even in patterns, and there is another tipping point, giving full-blown desert.



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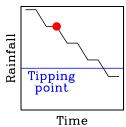


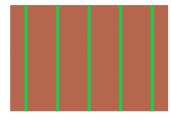


The Onset of Patterning Desertification History-Dependent Patterns Mathematical Explanation of Hysteresis Ecological Conclusions

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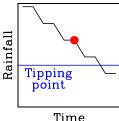




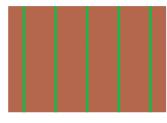
Desertification

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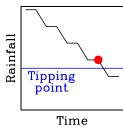
Time



The Onset of Patterning Desertification History-Dependent Patterns Mathematical Explanation of Hysteresis Ecological Conclusions

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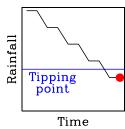




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The Onset of Patterning Desertification History-Dependent Patterns Mathematical Explanation of Hysteresis Ecological Conclusions

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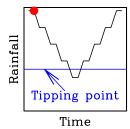
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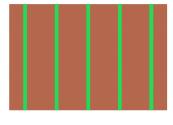


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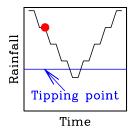


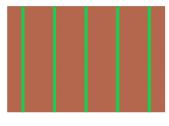


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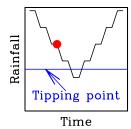


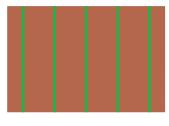


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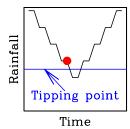


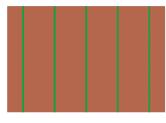


The Onset of Patterning Desertification History-Dependent Patterns Mathematical Explanation of Hysteresi Ecological Conclusions

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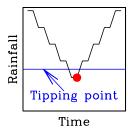




The Onset of Patterning Desertification History-Dependent Patterns Mathematical Explanation of Hysteresis Ecological Conclusions

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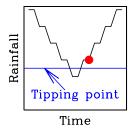




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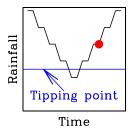




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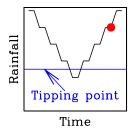




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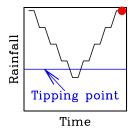




The Onset of Patterning Desertification History-Dependent Patterns Mathematical Explanation of Hysteresis Ecological Conclusions

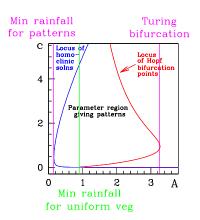
### Desertification

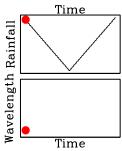
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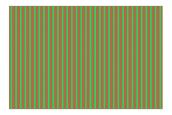


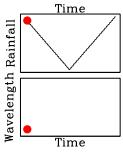


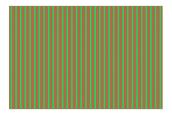
## Stability in a Parameter Plane

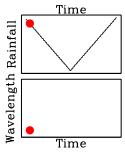


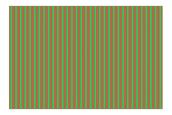


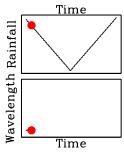


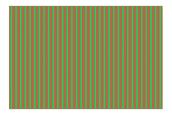


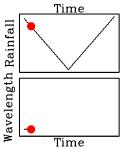


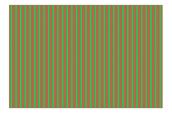


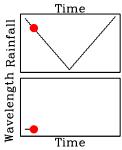


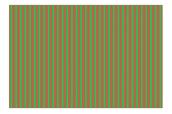


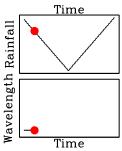


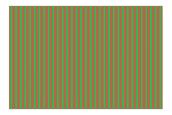


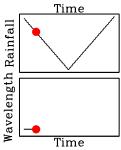


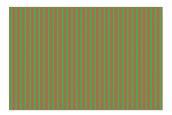


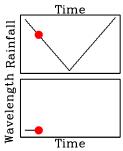


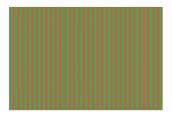


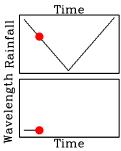


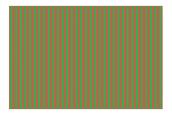


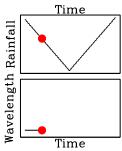


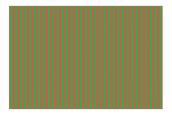


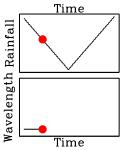


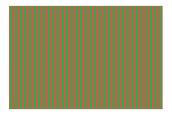


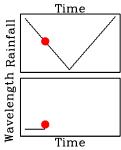


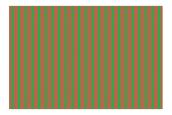


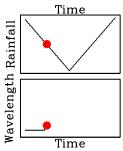


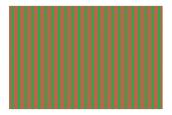


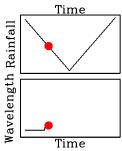


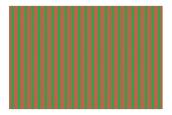


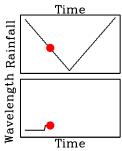


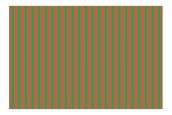


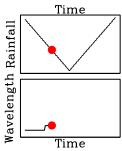


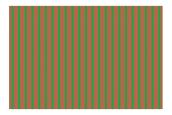


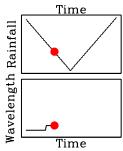


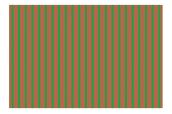


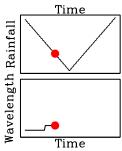


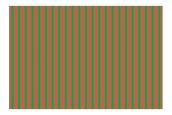


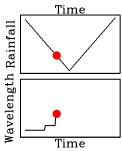


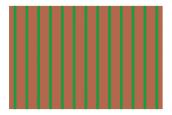


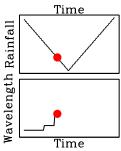


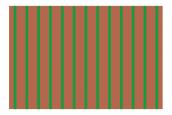


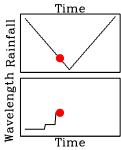


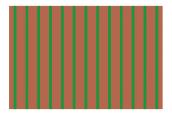


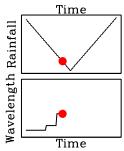




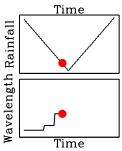


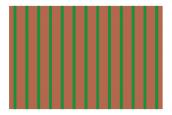


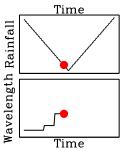




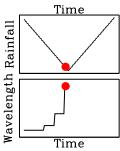


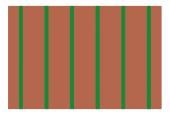


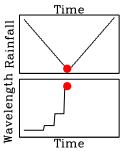




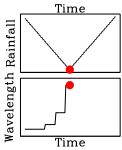




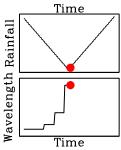


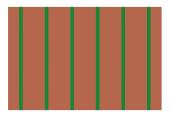


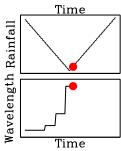


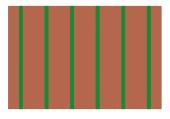


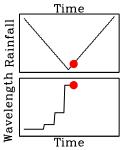


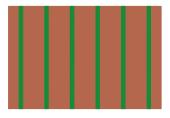


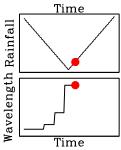


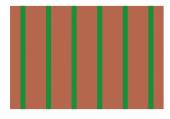


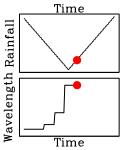


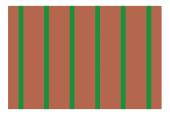


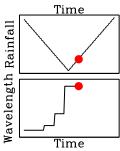




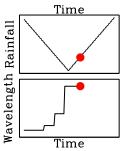


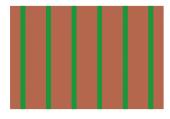


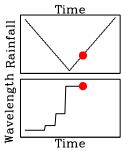




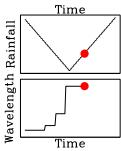


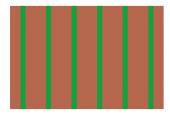


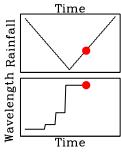




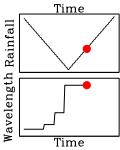




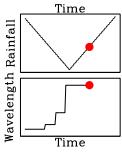




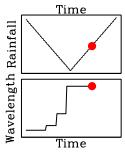




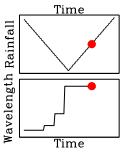




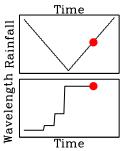




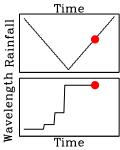


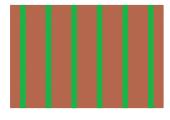


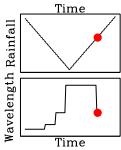




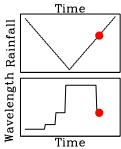




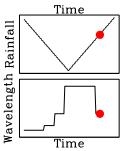


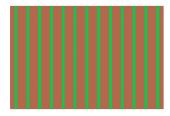


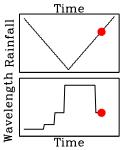




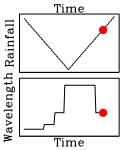




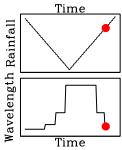


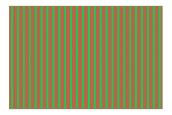


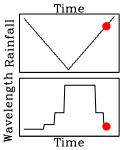


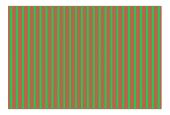


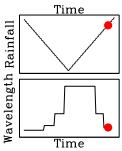


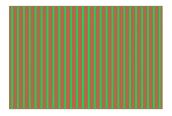


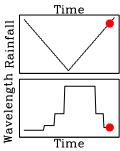


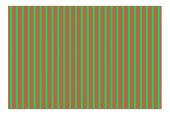


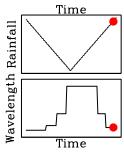


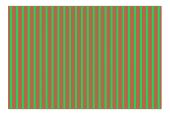


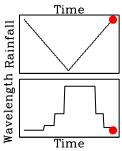


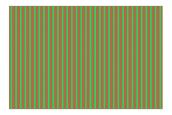


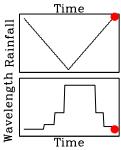


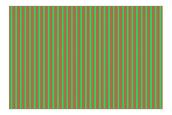


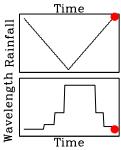


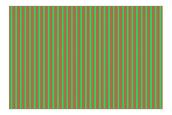






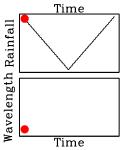


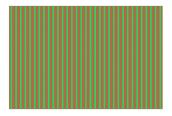


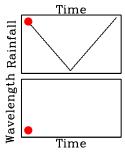


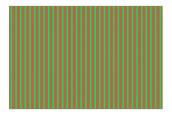
The Onset of Patterning
Desertification
History-Dependent Patterns
Mathematical Explanation of Hysteresi
Ecological Conclusions

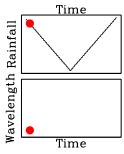
# History-Dependent Patterns (Animation)

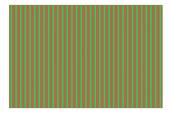


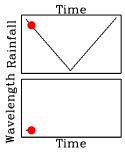


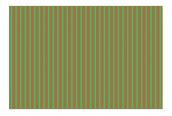


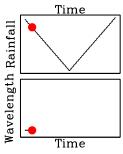


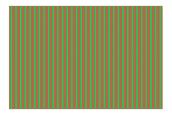


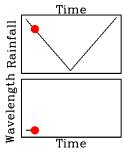


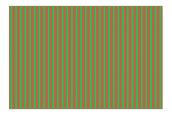


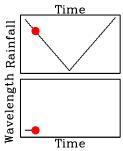


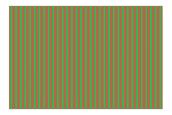


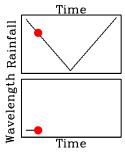


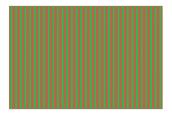


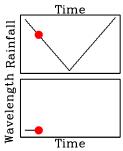


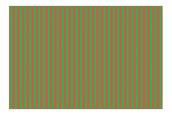


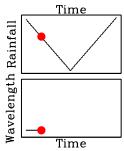


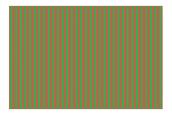


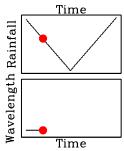


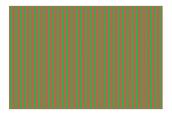


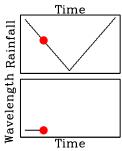


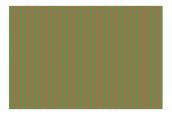


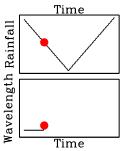


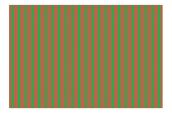


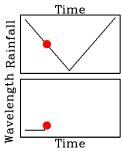


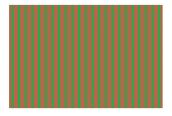


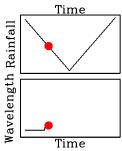


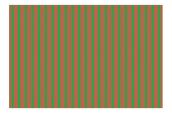


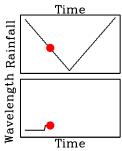


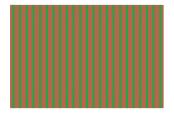


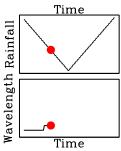


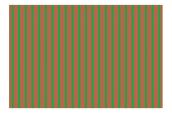


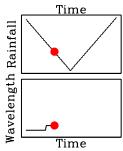


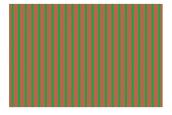


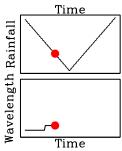


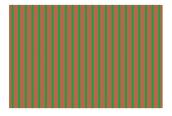


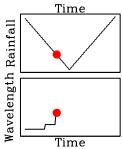




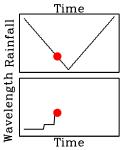




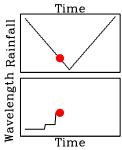


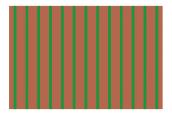


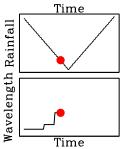




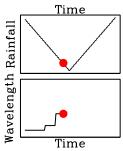




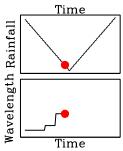




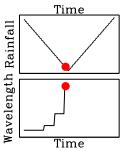


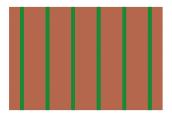


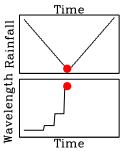


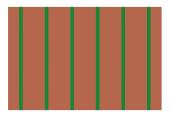


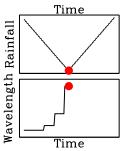


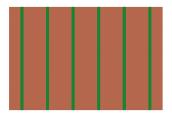


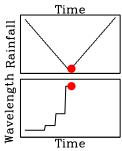




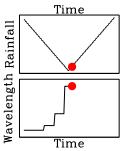


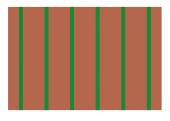


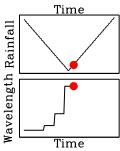


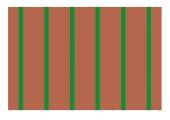


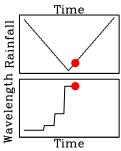


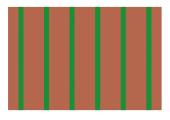


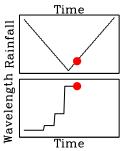


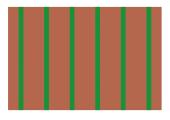


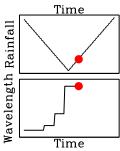


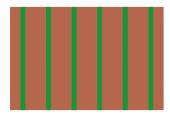


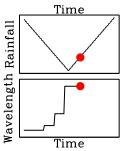


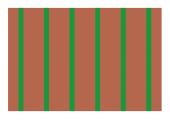


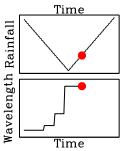


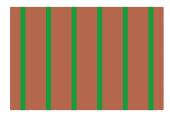


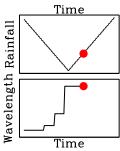


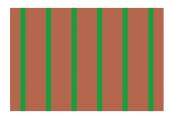


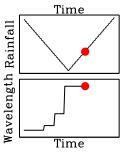




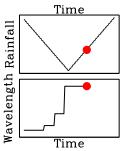




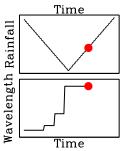




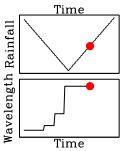




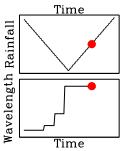




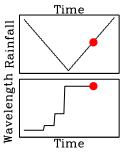




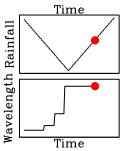




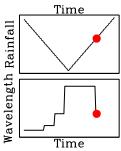


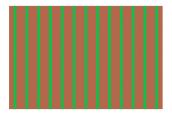


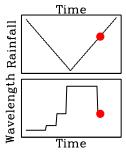




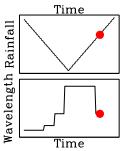




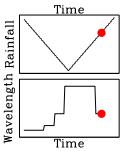


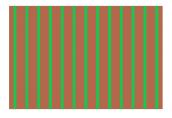


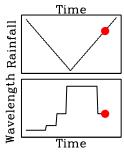




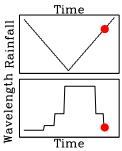


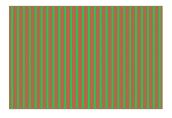


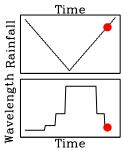


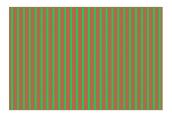


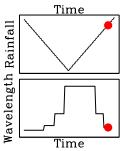


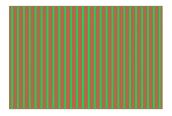


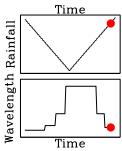


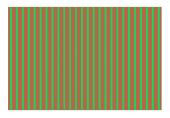


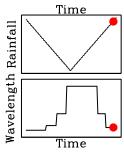


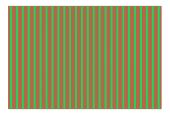


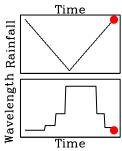


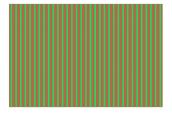


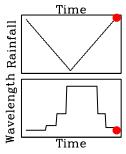


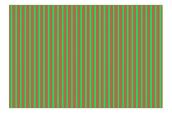


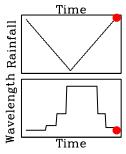


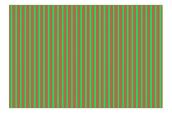








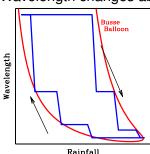




The Onset of Patterning
Desertification
History-Dependent Patterns
Mathematical Explanation of Hysteresis
Ecological Conclusions

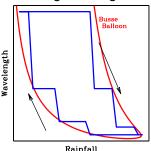
## Mathematical Explanation of Hysteresis

Wavelength changes abruptly at the edge of the Busse Balloon.



## Mathematical Explanation of Hysteresis

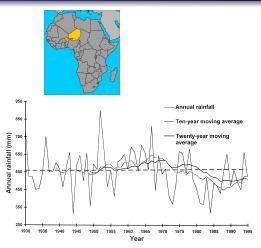
Wavelength changes abruptly at the edge of the Busse Balloon.

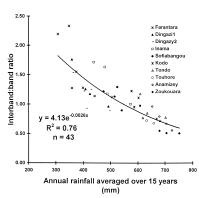


The Busse Balloon can be calculated using the software package WAVETRAIN (www.ma.hw.ac.uk/wavetrain)



## Data on the Effects of Changing Rainfall





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



The Onset of Patterning
Desertification
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Ecological Conclusions

## **Ecological Conclusions**

The mathematical model has predicted answers to the following 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?
- What determines the wavelength of vegetation bands?



## **Ecological Conclusions**

The mathematical model has predicted answers to the following 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?
- What determines the wavelength of vegetation bands?
   Wavelength depends on both parameters and patterning history.



#### Outline

- Ecological Background
- Detailed Calculation of Possible Wavelengths
- 3 Effects of Changing Rainfall Levels
- Wavelength Selection: Two Examples
- Further Reading



Ecological Background Detailed Calculation of Possible Wavelengths Effects of Changing Rainfall Levels Wavelength Selection: Two Examples Further Reading

# The Origin of Vegetation Patterns How to Predict Pattern Wavelength Wavelength for Degradation of Uniform Vegetation When Does Vegetation Colonise Bare Ground? Comparison of Wavelengths

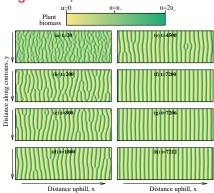
#### The Origin of Vegetation Patterns

Vegetation patterns develop via either degradation of uniform vegetation, or colonisation of bare ground.



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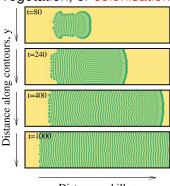


#### The Origin of Vegetation Patterns

How to Predict Pattern Wavelength Wavelength for Degradation of Uniform Vegetation When Does Vegetation Colonise Bare Ground? Comparison of Wavelengths

## The Origin of Vegetation Patterns

Vegetation patterns develop via either degradation of uniform vegetation, or colonisation of bare ground.



Distance uphill, x



Ecological Background Detailed Calculation of Possible Wavelengths Effects of Changing Rainfall Levels Wavelength Selection: Two Examples Further Reading The Origin of Vegetation Patterns How to Predict Pattern Wavelength Wavelength for Degradation of Uniform Vegetation When Does Vegetation Colonise Bare Ground? Comparison of Wavelengths

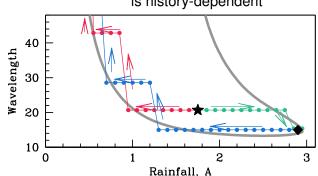
#### How to Predict Pattern Wavelength

Pattern wavelength is history-dependent



## How to Predict Pattern Wavelength

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#### How to Predict Pattern Wavelength

Pattern wavelength is history-dependent

 $\parallel$ 

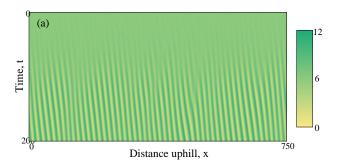
We must focus on the onset of patterning

/

Degradation of uniform vegetation Colonisation of bare ground



#### Wavelength for Degradation of Uniform Vegetation



For degradation of uniform vegetation, pattern wavelength can be calculated via the stability of the homogeneous steady state: wavelength=1/(most unstable frequency).



#### When Does Vegetation Colonise Bare Ground?

#### $\mathsf{Downhill} \longleftrightarrow \mathsf{Uphill}$

Very low rainfall: an isolated vegetation patch dies out

Time

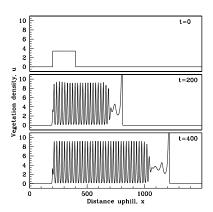
Slightly larger rainfall: both edges move uphill

Larger rainfall: the patch expands both uphill and downhill



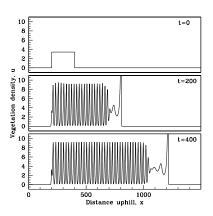
#### When Does Vegetation Colonise Bare Ground?

The key critical case is when the downhill edge is stationary



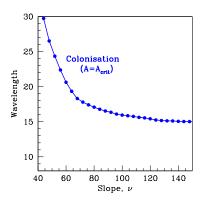
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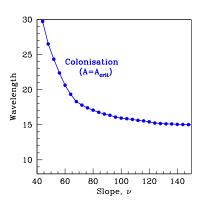


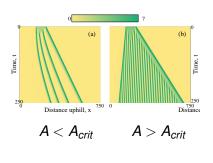
Wavelength can be calculated via numerical simulations in which rainfall A is chosen so that the downhill edge is stationary  $(A = A_{crit}, say)$ .

#### Comparison of Wavelengths

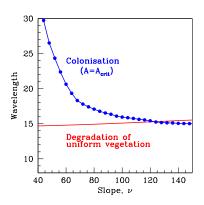


#### Comparison of Wavelengths





#### Comparison of Wavelengths



Degradation of uniform vegetation and colonisation of bare ground give patterns with different wavelengths.

#### Outline

- Ecological Background
- Detailed Calculation of Possible Wavelengths
- 3 Effects of Changing Rainfall Levels
- Wavelength Selection: Two Examples
- 5 Further Reading



## **Further Reading**

- Dagbovie AS, Sherratt JA (2014) Pattern selection and hysteresis in the Rietkerk model for banded vegetation in semi-arid environments. J R Soc Interface 11:20140465
- Klausmeier CA (1999) Regular and irregular patterns in semiarid vegetation. Science 284:1826-1828.
- Sherratt JA (2005) An analysis of vegetation stripe formation in semi-arid landscapes. J. Math. Biol. 51:183-197.
- Sherratt JA (2013) History-dependent patterns of whole ecosystems. Ecological Complexity 14:8-20.
- Siero E, Doelman A, Eppinga MB, Rademacher J, Rietkerk M, Siteur K (2015) Stripe pattern selection by advective reaction-diffusion systems: resilience of banded vegetation on slopes. Chaos 25:036411
- Siteur K, Siero E, Eppinga MB, Rademacher J, Doelman A, Rietkerk M (2014) Beyond Turing: the response of patterned ecosystems to environmental change. Ecological Complexity 20:81-96



#### List of Frames



#### **Ecological Background**

- Vegetation Patterns
- Pattern Wavelength: A Quantitative Statistic
- Mathematical Model of Klausmeier
- Typical Solution of the Model
- Homogeneous Steady States



#### Detailed Calculation of Possible Wavelengths

- Banded Patterns on Slopes Move Uphill
- Travelling Wave Equations
- Pattern Stability



#### Effects of Changing Rainfall Levels

- The Onset of Patterning
- Desertification
- History-Dependent Patterns
- Mathematical Explanation of Hysteresis
- Ecological Conclusions



#### Wavelength Selection: Two Examples

- The Origin of Vegetation Patterns
- How to Predict Pattern Wavelength
- Wavelength for Degradation of Uniform Vegetation
- When Does Vegetation Colonise Bare Ground?
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Further Reading

