

# Turing Patterns in Deserts

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**Abstract.** Self-organised patterns of vegetation are a characteristic feature of many semi-arid regions. In particular, banded vegetation is typical on hillsides. Mathematical modelling is widely used to study these banded patterns, because there are no laboratory replicates. I will describe the development of spatial patterns in an established model for banded vegetation via a Turing bifurcation. I will discuss numerical simulations of the phenomenon, and I will summarise nonlinear analysis on the existence and form of spatial patterns as a function of the model parameter that corresponds to mean annual rainfall.

## 1 Introduction

Self-organised patterns of vegetation are a characteristic feature of semi-deserts. The most striking and best studied example is striped patterns on gentle slopes (see [1, 2] for review). These occur in many parts of the world, and are particularly well documented in Australia [3, 4], Mexico/South-Western USA [5, 6] and sub-Saharan Africa [7–9]. Bands of grass, shrubs or trees run along contours, separated by bare ground; wavelengths of about 1km are typical for trees and shrubs, with shorter wavelengths observed for grasses.

There are no laboratory replicates of banded vegetation, so that empirical study is limited to observation of existing patterns. Because the timescale of pattern evolution is very slow (decades), such observational data is ineffective as a basis for assessing the implications of changes in environmental parameters such as rainfall. Therefore theoretical models are an important and widely used tool for studying these patterns [10]. This paper is concerned with pattern formation in one model for banded vegetation, due originally to Klausmeier [11]. It comprises coupled partial differential equations for plant and water densities, and is the basic model for patterning due to water redistribution. Many extensions of the Klausmeier model have been proposed over the last decade. Most of these involve separate variables for soil and surface water [12–16]. Some authors have also incorporated features such as rainfall variability [17–19] and a herbivore population [20]; see [21, 22] for other recent extensions. Note also that the Klausmeier model and its extensions are not the only theoretical explanation for vegetation stripes. Lejeune and coworkers [23–26] have studied in detail a model based on the combination of short-range activation and long-range inhibition between neighbouring plants. Here the activation is due to shading of one plant

by another, while competition for water results in inhibition; the difference in length scales of these processes is due to the root system within the soil being much more extensive than the parts of the plants above ground. In this model, slope acts as a selector rather than an initiator of spatial patterning.

This paper is concerned with the original Klausmeier model [11]. I will present a detailed discussion of pattern solutions of this model, which arise via a Turing bifurcation in the model partial differential equations. I will show that studying these pattern solutions can provide valuable new ecological insights into the formation and maintenance of vegetation patterns in semi-deserts.

## 2 Model Equations

The dimensionless form of the Klausmeier model is:

$$\begin{aligned} \frac{\partial u}{\partial t} &= \overbrace{wu^2}^{\text{plant growth}} - \overbrace{Bu}^{\text{plant loss}} + \overbrace{\partial^2 u / \partial x^2}^{\text{plant dispersal}} & (1a) \\ \frac{\partial w}{\partial t} &= \underbrace{A}_{\text{rain-fall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{wu^2}_{\text{uptake by plants}} + \underbrace{\nu \partial w / \partial x}_{\text{flow downhill}}. & (1b) \end{aligned}$$

Here  $u(x, t)$  is plant density,  $w(x, t)$  is water density,  $t$  is time and  $x$  is space in a one-dimensional domain of constant slope, with the positive direction being uphill. The (dimensionless) parameters  $A$ ,  $B$  and  $\nu$  reflect rainfall, plant loss and slope gradient respectively. For full details of the dimensional model and nondimensionalisation, see Klausmeier (1999), Sherratt (2005) or Sherratt & Lord (2007).

For all parameter values, (1) has a stable trivial steady state  $u = 0$ ,  $w = A$ , corresponding to bare ground, without vegetation. When  $A \geq 2B$ , there are also two other homogeneous steady states which arise from a saddle node bifurcation:

$$\begin{aligned} u = u_1 &\equiv \frac{2B}{A - \sqrt{A^2 - 4B^2}}, & w = w_1 &\equiv \frac{A - \sqrt{A^2 - 4B^2}}{2} & (2) \\ \text{and } u = u_2 &\equiv \frac{2B}{A + \sqrt{A^2 - 4B^2}}, & w = w_2 &\equiv \frac{A + \sqrt{A^2 - 4B^2}}{2}. & (3) \end{aligned}$$

The first of these (2) is always unstable to homogeneous perturbations; the second is the key equilibrium from which patterns develop. This steady state is linearly stable to homogeneous perturbations whenever  $B < 2$ . For larger values of  $B$  and small  $A$ , (3) can become unstable, giving complicated local dynamics including a limit cycle, but realistic parameter values for semi-arid environments imply that  $B < 2$ .

For large values of the rainfall parameter  $A$ , (3) is also stable to inhomogeneous perturbations, so that the model predicts the spatially uniform vegetation that characterises temperate parts of the world. However as  $A$  is decreased a Turing bifurcation occurs: (3) becomes unstable to some spatially inhomogeneous

perturbations, and spatial patterns develop. The patterns consist of periodically repeating peaks and troughs of vegetation (Figure 1), and as the rainfall parameter  $A$  is decreased further, these solutions gradually increase in amplitude, resembling more closely the empirically observed patterns. In the prototypical Turing system of two coupled reaction-diffusion equations, the patterns arising from a Turing bifurcation are stationary. However the advection term in (1a) causes the patterns to move, in the positive  $x$  direction (uphill). There has been a long-running debate in the ecological literature about this uphill migration, with some field studies reporting stationary patterns (e.g., [3]). However, the majority of data sets spanning a time period sufficient to address this issue do indicate uphill migration, with speeds in the range  $0.2\text{--}1\text{ m year}^{-1}$  (see Table 5 of [1]). A recent and very detailed study using photographic data from satellites [27, Chapter 10] confirms migration, with speeds in this range, for three out of six geographical locations. The ecological cause of uphill migration is that moisture levels are higher on the uphill edge of the bands than on their downhill edge, leading to reduced plant death and greater seedling density [28, 29].

### 3 Travelling Wave Solutions

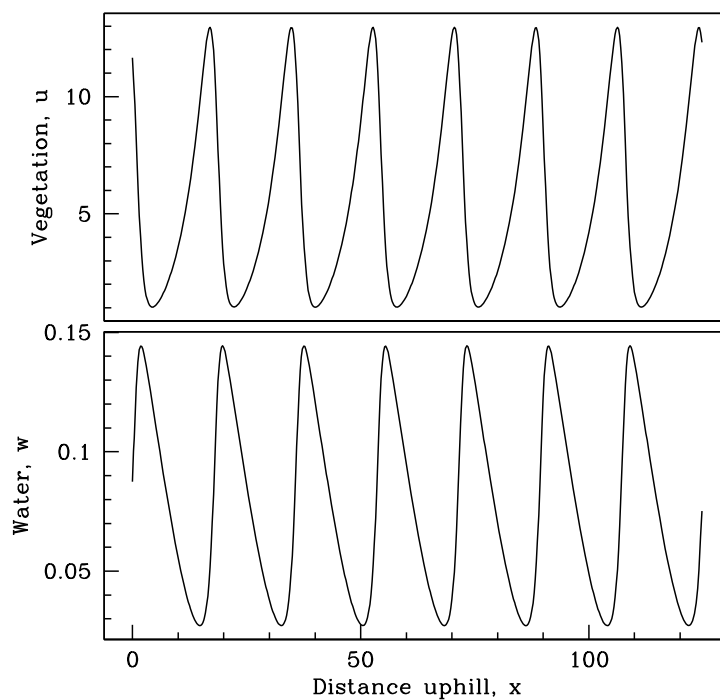
Mathematically, patterns moving with constant shape and speed can be studied via the ansatz  $u(x, t) = U(z)$  and  $w(x, t) = W(z)$ , where  $z = x - ct$  with  $c$  being the migration speed. Substituting these solution forms into (1) gives the travelling wave equations

$$d^2U/dz^2 + c dU/dz + WU^2 - BU = 0 \quad (4a)$$

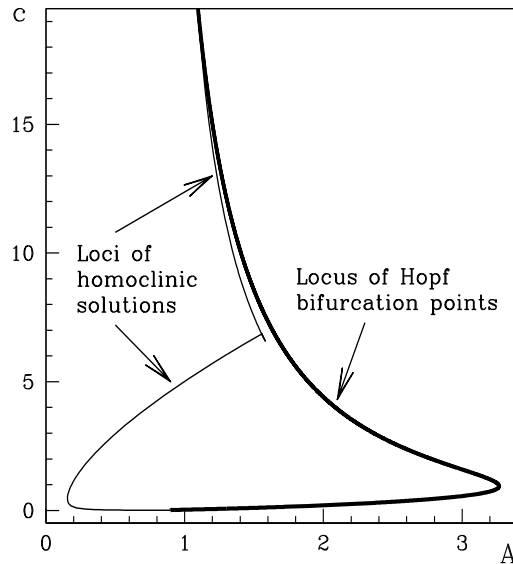
$$(\nu + c)dW/dz + A - W - WU^2 = 0. \quad (4b)$$

Patterned solutions correspond to periodic solutions of (4). In [30], Gabriel Lord and I used numerical bifurcation analysis to study these periodic solutions. We showed that for a given value of the migration speed  $c$ , patterns occur for a range of rainfall parameter values  $A$ . For most values of  $c$ , this range is bounded by a Hopf bifurcation point for (3,4) and a homoclinic solution of (4). However for some values of  $c$  there is a fold in the branch of periodic travelling wave solutions, and this then constitutes an end of the rainfall range for patterns [31, 32]. A typical result is illustrated in Figure 2, which shows the loci of the Hopf bifurcation point and the homoclinic solution in the  $A$ - $c$  parameter plane, for fixed values of  $B$  and  $\nu$ .

Analytical study of (1) is made more complicated by the advective term in the  $u$ -equation. For example, linear stability analysis of (3) to investigate the Turing bifurcation is significantly more complicated in (1) than for a system of two reaction-diffusion equations [34], and indeed one cannot obtain an exact closed-form expression for the value of  $A$  at which the bifurcation occurs. However, the slope parameter  $\nu$  is much larger than  $A$  and  $B$ : Klausmeier [11] estimated  $\nu = 182.5$ ,  $A = 0.1\text{--}3.0$  and  $B = 0.05\text{--}2.0$ . This large value is not due to the slope itself being steep: banded vegetation is restricted to slopes of a few percent, and



**Fig. 1.** An illustration of a typical vegetation pattern, as predicted by the Klausmeier model (1). There is a periodic pattern of peaks in vegetation density  $u$ , separated by regions in which vegetation is almost absent. The surface water density  $w$  also has a periodic form; it is largest on the uphill side of a vegetation stripe, and gradually decreases with distance uphill to the next stripe. The pattern moves slowly uphill; in this case the (dimensionless) migration speed is approximately 0.9. The parameter values are  $A = 2.5$ ,  $B = 0.45$ ,  $\nu = 182.5$ , which are in the range of Klausmeier's (1999) parameter estimates for grass. The equations were solved numerically using a finite difference scheme (see [30] for details) on the domain  $0 < x < 125$  with periodic boundary conditions.



**Fig. 2.** A typical example of the part of the  $A$ - $c$  parameter plane in which there are patterned solutions of (1), which corresponds to limit cycles in (4). I plot the loci of Hopf bifurcation points (—) and homoclinic solutions (—) in (4), which bound the pattern region. The other parameters are  $B = 0.45$  and  $\nu = 182.5$ . The plot is truncated at  $c \approx 20$ : patterns actually exist for values of  $c$  up to about 50. The numerical solutions were performed using AUTO [33]. The loci of homoclinic orbits are approximations; they are in fact the loci of solutions of a fixed but very long wavelength (3000). Further details of the numerical continuation approach are given in [30].

on steeper slopes, different processes occur because rainwater generates gullies. Rather,  $\nu$  is large because the plant diffusion coefficient is small compared to the advection rate of water, and it is the relative values of these quantities that determines the nondimensional parameter  $\nu$  [11, 34]. By exploiting this large value of  $\nu$  it is possible to obtain leading order approximations for various key points in the  $A$ - $c$  parameter plane. In particular:

- The Turing bifurcation occurs at  $A = (\sqrt{2}-1)^{1/2}\nu^{1/2}B^{5/4}$ ,  $c = A^2/(2B^2\nu) + B^3\nu/(2A^2)$  [32].
- The maximum migration speed for patterns is  $c = \nu B/(2 - B)$  [31].
- The base of the “tusk-shaped” region (see Figure 2) occurs at  $c = 0.881B^{3/4}\nu^{1/2}$  [35, 36].
- Pattern solutions exist for arbitrarily small values of the migration speed  $c$  [32].

## 4 Conclusion

Ecological pattern formation at the level of whole ecosystems is a new, exciting, and rapidly growing research area, whose study is influenced strongly by Turing's ideas [37]. Vegetation patterns in semi-arid regions represent one example of such patterns, but there are many others, including regular isolated spots of trees and shrubs in savanna grasslands [38, 39], patterns of open-water pools in peatlands [40, 41], labyrinthine patterns in mussel beds [42, 43], striped patterns of tree lines ("ribbon forests") in the Rocky Mountains [44, 45]. Mathematical modelling is an important tool for the study of landscape patterns, and the Klausmeier model (1) is one of the most generic models: as well as semi-arid vegetation, it has been used to model fog-dependent plant ecosystems [46] and (with a slight modification) mussel beds in river estuaries [47]. I have outlined the mathematical analysis of pattern formation in the Klausmeier model, showing how such analysis can make clear and quantitative predictions concerning critical levels of the rainfall level and wave speed.

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