Secondary seed dispersal in the Klausmeier model of vegetation for sloped semi-arid environments

Giancarlo Consolo a* and Giovanna Valenti b

a Department of Mathematical, Computer, Physical and Earth Sciences
University of Messina (Italy)
V.le F. D’Alcontres 31, I-98166 Messina, Italy.
b Department of Engineering, University of Messina (Italy)
C.da di Dio s/n, I-98166 Messina, Italy.
*corresponding author: gconsolo@unime.it

Abstract

The effects of secondary seed dispersal on the dynamics of banded vegetation are investigated in the framework of a generalized version of one of the easiest tools for the description of pattern formation along the hillsides of semi-arid environments: the Klausmeier model. The generalization here considered consists in augmenting the evolution equation for the vegetation biomass with an advection term mimicking the anisotropic dispersal of seeds by overland flow. Linear stability analysis is used to deduce the threshold condition for the occurrence of wave instability as well as to obtain approximated explicit expressions for some key quantities: pattern speed, locus of stationary patterns and excited wavenumber. The generalized model is also integrated numerically considering two different sets of initial conditions that yield pattern dynamics originating from degradation of uniform vegetation or colonization of bare ground. These numerical simulations are performed to corroborate the analytical predictions, to characterize more deeply the propagating character of the edges of vegetation patches and to emphasize how distinct initial conditions may lead to significantly different ecological scenarios.

Keywords: wave instability, non-stationary vegetation patterns, primary and secondary seed dispersal, linear stability analysis, Maxwell points.
1 Introduction

In many semi-arid environments, vegetation along hillsides is spatially self-organized in regular patches with suitable and unsuitable sites for establishment. A lot of theoretical efforts have been spent to develop analytical and numerical tools capable to predict the transitions that such ecosystems may experience. In particular, a relevant body of research focuses on the modeling of those complex phenomena that contribute to the formation, modulation, resilience and propagation of vegetation patterns [1]-[22].

In this context, the Klausmeier model is certainly one of the easiest tools able to predict pattern formation in sloped semi-arid environments [2]. In its original formulation, it is a two-compartments model for surface water and vegetation biomass that admits an advection-driven instability through which vegetated patches may form and undergo an upslope migration.

This latter feature has been the subject of a long debate since very few field observations on this phenomenon were reported in the literature, especially due to the difficulty in performing the corresponding long-time experiments.

The origin of the above discrepancy is believed to be attributed to the phenomenon of seed dispersal [17]-[23]. It is indeed known from the literature that the overall process of seed dispersal, which includes the stages of mobilization, transport and germination, is quite critical in reproductive biology and ultimately affects the spatial organization of dryland ecosystems [22]. In particular, in sloped semi-arid environments, seeds generally undergo a primary, isotropic, dispersal from the plant to the ground, followed by a secondary, anisotropic, dispersal due to their transport in overland flow. Several theoretical works have also concluded that, as long as the anisotropic effects arising from secondary seed dispersal are accounted for, the movement of banded vegetation may be retarded or even suppressed [17],[19],[20]. These results have been obtained in the frameworks of Saint-Venant equations, HilleRisLambers et al. model, Rietkerk et al model (to cite a few), where seed dispersal is treated as a short or a long range phenomenon [5],[17],[18],[19],[20].

However, to the best of our knowledge, very few investigations have been addressed in the context of the Klausmeier model which, in its original formulation, accounted for the primary dispersal but not for the secondary one [2]. In Ref.[24], for instance, the authors took into account the “modified” version of this model by assuming that both the state variables (surface water and vegetation biomass) undergo diffusion and advection, and studied the resilience of banded vegetation on flat and sloped terrains.

With this in mind, in the present manuscript we consider a generalization of the original Klausmeier model which simply consists in augmenting the evolution equation for the vegetation biomass with an advection term representing the downslope motion of seeds carried by surface water. Therefore, differently from the “modified” version, the present model ignores water diffusion since the advection contribution is generally dominant on slopes.
Then, in order to inspect the possibility of originating migrating patterns, we shall deduce the threshold condition for wave instability [6],[16],[24],[25]. Moreover, with the goal of properly characterizing such patterns, we shall provide explicit expressions for the most relevant ecological quantities here involved: pattern speed, locus of stationary patterns and excited wavenumber.

Analytical predictions will be corroborated by numerical simulations that also aim at elucidating the role played by initial conditions. In particular, by considering two distinct setups, we shall trigger pattern dynamics from degradation of uniform vegetation or colonization of bare ground. Through these examples, we shall point out how the choice of initial conditions crucially affects the propagating character of the edges of the vegetated patches and how it leads to significantly different ecological scenarios [13].

The manuscript is organized as follows. In Section 2, we introduce the generalized Klausmeier model and discuss the ecological meaning of all the quantities here involved. In Section 3, we investigate the local stability character of each steady state admitted by the model against spatially homogeneous and non-homogeneous perturbations. This study will serve as a starting point to establish which steady state may undergo the instability required to trigger non-stationary patterns. At the end of this section, we also deduce an approximate, but explicit, expression for the most relevant ecological quantities characterizing the excited patterns. In Section 4, we introduce the numerical framework and discuss the ecological implications arising from our results. Some final remarks are addressed in Section 5.

2 The model

We consider the following one-dimensional advection–reaction–diffusion model:

\[
\begin{align*}
\frac{\partial U}{\partial T} - k_3 \frac{\partial^2 U}{\partial X^2} - k_8 \frac{\partial U}{\partial X} &= k_1 W U^2 - k_2 U \\
\frac{\partial W}{\partial T} - k_7 \frac{\partial W}{\partial X} &= k_4 - k_5 W - k_6 W U^2
\end{align*}
\]

(1)

where \(U(X, T)\) and \(W(X, T)\) represent the plant biomass and surface water density at time \(T\) and position \(X\), respectively. The space variable runs along the uphill direction and all the ecological coefficients \(k_i\) (\(i = 1, \ldots, 8\)) are positive quantities. In detail, the diffusive term \(k_3 \frac{\partial^2 U}{\partial X^2}\) mimics the primary, isotropic, seed dispersal from the plant to the ground, while the advection term \(k_8 \frac{\partial U}{\partial X}\) accounts for the secondary, anisotropic and short-range, seed dispersal due to the transport of seed biomass by overland flow.

It is easy to see that, in the particular case \(k_8 = 0\), system (1) specializes to the original Klausmeier model [2] where the only advection term there included, \(k_7 \frac{\partial W}{\partial X}\), describes the downhill water flow due to the hillslope.

The reaction terms are unchanged with respect to the original Klausmeier model [2] and make use of the following assumptions: the per capita rate of water uptake is proportional to plant biomass; the plant growth rate is proportional to water uptake; the plant loss has a linear
form (and may include both natural and herbivory effects); rainfall is included via its mean annual value.

In order to reduce the number of parameters involved in the model, we rescale the governing equations (1) by introducing the following dimensionless variables and parameters

\[
\begin{align*}
    u &= U \sqrt{\frac{k_6}{k_5}} \\
    w &= W \frac{k_1}{\sqrt{k_6 k_5}} \\
    t &= k_5 T \\
    x &= X \sqrt{\frac{k_5}{k_3}} \\
    B &= k_2 \frac{k_5}{k_1} \\
    A &= k_1 k_4 \frac{k_5^{3/2}}{k_6^{1/2}} \\
    \nu &= \frac{k_7}{\sqrt{k_3 k_5}} \\
    \psi &= \frac{k_8}{\sqrt{k_3 k_5}}
\end{align*}
\]

so that we get the dimensionless system:

\[
\begin{align*}
    u_t - u_{xx} - \psi u_x &= w u^2 - B u = f(u, w) \\
    w_t - \nu w_x &= A - w - w u^2 = g(u, w)
\end{align*}
\]

where the parameters \(A\) and \(B\) are now related to rainfall and plant loss, respectively, while \(\psi\) and \(\nu\) correspond to the advection velocities of seeds and water, respectively.

The governing system (4) is supplemented with initial data and periodic boundary conditions.

Moreover, since advection in surface runoff is considered to be primarily responsible for seed transport downslope, hereafter we assume \(\psi < \nu\) [20],[24] and we also consider \(B \leq 2\) in agreement with realistic parameter values for plant growth in semi-arid environments [2],[9].

## 3 Estimation of key features of pattern dynamics

In this section we address linear stability analysis to estimate some key features of pattern dynamics. Firstly, we establish the bifurcation threshold for pattern formation and, then, we determine the conditions under which such patterns may migrate or be stationary.

### 3.1 Uniform steady states and linear stability analysis

The model (4) admits spatially-homogeneous steady states \(E^* = (u^*, w^*)\) whose number depends upon the value of the rainfall \(A\), namely:

- for \(A < 2B\) \(\Rightarrow\) desert state only: \(E^*_D = (0, A)\)
- for \(A \geq 2B\) \(\Rightarrow\) three steady states: \(E^*_D, E^*_L = \left( u_L, \frac{B}{u_L} \right), E^*_R = \left( u_R, \frac{B}{u_R} \right)\)

where

\[
\begin{align*}
    u_L &= \frac{A - \sqrt{A^2 - 4B^2}}{2B} < 1 < u_R = \frac{A + \sqrt{A^2 - 4B^2}}{2B}.
\end{align*}
\]
In order to inspect the local stability character of each steady state (5) under small non-homogeneous perturbations, we linearize the governing system (4) around $E^*$ by looking for solutions of the form

$$E = E^* + \tilde{E} \exp(\omega t + ikx)$$

being $\omega$ the growth factor, $k$ the wavenumber and $i$ the imaginary unit. Therefore, inserting (7) into (4), the following complex characteristic equation for $\omega$ is obtained:

$$\omega^2 + (c_1 - ikc_2)\omega + d_1 - ikd_2 = 0$$

with

$$c_1 = k^2 - (f_u^* + g_w^*)$$
$$c_2 = \nu + \psi$$
$$d_1 = f_u^* g_w^* - f_w^* g_u^* - k^2 (g_w^* + \nu\psi)$$
$$d_2 = \nu (k^2 - f_u^*) - \psi g_w^*$$

where the asterisk denotes that the functions are evaluated at $E^*$ and the subscripts stand for partial derivative with respect to the indicated variables.

As known, a steady state is linearly stable if the real part of all roots of the characteristic equation are negative $\forall k$. This leads to the following propositions.

**Proposition 1.** The desert steady state $E_D^*$ is always stable, and in particular it behaves as a node or a focus with respect to homogeneous or non-homogeneous perturbations, respectively.

**Proof.** Taking into account that:

$$f_u(E_D^*) = -B < 0, \quad f_w(E_D^*) = 0, \quad g_u(E_D^*) = 0, \quad g_w(E_D^*) = -1 < 0$$

the explicit solutions of Eq.(8) evaluated at $E_D^*$ are:

$$\omega_1 = -(B + k^2) + ik\psi, \quad \omega_2 = -1 + ik\nu$$

which are both real and negative for $k = 0$ (stable node) while have negative real part for $k \neq 0$ (stable focus), so that $E_D^*$ is always a stable steady state. $\square$

**Proposition 2.** The steady state $E_L^*$ is always unstable (a saddle point) with respect to both homogeneous and non-homogeneous perturbations whereas $E_R^*$ is stable with respect to homogeneous perturbations but it can lose stability with respect to non-homogeneous ones.

**Proof.** Taking into account that:

$$f_u(E_{L,R}^*) = B > 0, \quad f_w(E_{L,R}^*) = u_{L,R}^2 > 0,$$
$$g_u(E_{L,R}^*) = -2B < 0, \quad g_w(E_{L,R}^*) = -(1 + u_{L,R}^2) < 0.$$
the roots of Eq. (8) evaluated at $E_{L,R}^*$ are:

$$\omega_{1,2} = \frac{1}{2} \left\{ -c_1 - ikc_2 \pm \sqrt{c_1^2 - k^2c_2^2 - 4d_1 + ik\left(4d_2 - 2c_1c_2\right)} \right\}$$

which, in the case of uniform perturbations ($k = 0$), reduce to:

$$\omega_{1,2} = \frac{1}{2} \left\{ \left( B - u_{L,R}^2 - 1 \right) \pm \sqrt{(B - u_{L,R}^2 - 1)^2 - 4B(u_{L,R}^2 - 1)} \right\}.$$  

Considering that $u_L < 1 < u_R$, we may conclude that $E_L^*$ is always unstable with respect to both homogeneous and non-homogeneous perturbations whereas $E_R^*$ is stable with respect to homogeneous perturbations but it can lose stability with respect to non-homogeneous ones. □

### 3.2 Wave instability

Since we are interested in the occurrence of advection-driven instability giving rise to oscillating vegetation patterns [6],[16], hereafter we will restrict our attention to the dynamics observed around the steady state $E_R^*$, which represents the only good candidate for this purpose. In particular, since the excited spatially-periodic patterns are expected to be non-stationary, we search for the conditions under which the so-called wave instability takes place. As known, in parabolic reaction-diffusion systems with no advection terms, wave instability requires at least three interacting species [26]. On the other hand, in the presence of advection, two species suffices to generate such an instability [2],[6],[16],[25]. Therefore, the non-stationary patterns observed in the present work are not due to the coupling of a Hopf oscillation with a stationary Turing solution [27]-[33].

Mathematically speaking, we thus look for solutions of the characteristic equation (8) having null real part, $\text{Re}\{\omega\} = 0$ and $\text{Im}\{\omega\} \neq 0$, for some $k \neq 0$. From such a requirement, we obtain the following sixth-order equation for $k$:

$$\alpha_3 k^6 + \alpha_2 k^4 + \alpha_1 k^2 + \alpha_0 = 0$$

being:

$$\begin{align*}
\alpha_3 &= 1 + u_R^2 \\
\alpha_2 &= 2 - 3B + \left(\nu - \psi\right)^2 + \left[4 - B + \left(\nu - \psi\right)^2\right]u_R^2 + 2u_R^4 \\
\alpha_1 &= 1 + 3B^2 - B\left[4 + \left(\nu - \psi\right)^2\right] + \left[3 - B\left(4 + B + \left(\nu - \psi\right)^2\right) + 3u_R^2 + u_R^4\right]u_R^2 \\
\alpha_0 &= B\left(u_R^2 - 1\right)\left(1 + u_R^2 - B\right)^2
\end{align*}$$

Consequently, the bifurcation locus of the wave instability is implicitly defined by:

$$27\alpha_6^2\alpha_3^2 - \alpha_1^2\alpha_2^2 + 4\alpha_1^3\alpha_3 + 4\alpha_2^3\alpha_0 - 18\alpha_0\alpha_1\alpha_2\alpha_3 = 0$$
Owing to the algebraic complexity of such a locus, significant information are extracted through numerical investigations.

In Figure 1 we represent the bifurcation locus (17) in the \((B, A)\) parameter space for a fixed value of the slope gradient \(\nu = 182.5\) and varying the seed advection speed \(\psi\) in the range \([0, \nu]\). The bifurcation diagram so obtained consists of three regions: the region below the line \(A = 2B\), that is characterized by the absence of vegetation, being the desert state \(E_D^*\) the only steady state here admitted; the intermediate area delimited by \(A = 2B\) and the bifurcation locus, that corresponds to the pattern-forming region; the area above the wave bifurcation locus, where also the homogeneous vegetated state \(E_R^*\) exists and is stable. In this latter region, intuitively one expects that when rainfall is sufficiently high, a localized introduction of plant biomass will invade and colonize the bare ground, i.e. large rainfall values are enough to sustain plant growth.

It is interesting to notice that the instability region shrinks with the increase of seed advection speed and vanishes for \(\psi = \nu\), i.e. when all seeds falling into the ground are entirely dispersed via surface runoff. In other words, this result suggests that the presence of secondary seed dispersal reduces the instability region in which vegetation patterns can be observed.

![Bifurcation Diagram](image)

Figure 1: (Main panel) Bifurcation diagram in the \((B, A)\) parameter space, obtained by fixing the water advection speed \(\nu = 182.5\) and varying the seed advection speed \(\psi\). (Inset) Zoom of the bifurcation diagram around the value \(B = 0.45\). The marked points are: \(P_1 = (0.45, 2.5)\), \(P_2 = (0.45, 3.0)\) and \(P_3 = (0.45, 3.2)\).
To gain additional information on how the system behaves when the model parameters are varied, and in particular to check the validity of the analytical expression of the bifurcation locus (17), we now fix the slope gradient at $\nu = 182.5$ and vary the seed advection speed. We then investigate the character of the roots of the characteristic polynomial (8) in correspondence of the points $P_1 = (0.45, 2.5)$, $P_2 = (0.45, 3.0)$ and $P_3 = (0.45, 3.2)$, marked in the $(B, A)$ parameter space reported in the inset of Figure 1. The real and imaginary parts of the roots obtained for $\psi = 0, 10, 50$ are depicted in Figs. 2, 3 and 4, respectively. In these figures, the root $\omega_1$ is denoted through solid lines, whereas $\omega_2$ through dashed lines. Notice that $\text{Re}\{\omega_2\}$ is always negative and its value is significantly outside the used scale, so that it is not represented to improve the intelligibility of the figures. The stability character is thus determined by the behavior of the root $\omega_1$.

In detail, a direct inspection of Figure 2 reveals that, for $\psi = 0$, there exists a range of unstable wavenumbers independently of the value we choose for the parameter $A$. From the mathematical viewpoint, these results confirm that the points $P_1, P_2$ and $P_3$ fall into the pattern-forming region. Moreover, the imaginary part associated to such unstable wavenumbers is always negative. This ecological scenario, characterized by the absence of secondary seed dispersal, corresponds to the excitation of a non-stationary vegetation pattern which migrates uphill. In fact, as also reported by Klausmeier [2], if the eigenvalue which determines the instability is complex with a negative (positive) imaginary part, the resulting patterns oscillate in time and the stripes move uphill (downhill).

Figure 3, obtained for $\psi = 10$, shows that for $A = 2.5$ (point $P_1$) and $A = 3.0$ (point $P_2$) there exists a region of unstable wavenumbers but the corresponding imaginary parts are now positive. On the contrary, for $A = 3.2$ (point $P_3$) there are no unstable modes, being the real part always negative. In the former two cases, the system is thus within the instability region and the behavior of the roots corresponds to the excitation of a non-stationary pattern which migrates downhill. In the last case, the characteristic polynomial evaluated at $E^*_R$ has all roots with negative real parts, so that the homogeneous vegetated state $E^*_R$ is stable so confirming that the point $P_3$ is outside the pattern-forming region.

From the analysis of the results reported in Figure 4, obtained for $\psi = 50$, we notice that the setup with $A = 2.5$ (point $P_1$) represents the only situation in which patterns may form and migrate downhill. In all other cases ($A = 3.0$ and $A = 3.2$), the characteristic polynomial has all roots with negative real parts and indeed the points $P_2$ and $P_3$ fall outside the pattern-forming region.

All these results confirm that the increase of secondary seed dispersal $\psi$ reduces the region of the parameter space in which patterns can emerge and it may even reverse the direction of pattern migration.
Figure 2: The case $\psi = 0$. Real (left panels) and Imaginary (right panels) parts of the roots $\omega_{1,2}$ of the characteristic polynomial (8) as a function of the wavenumber, obtained for $\nu = 182.5$. Solid red lines stand for $\omega_1$, black dashed lines stand for $\omega_2$. Figs.(a-b), (c-d) and (e-f) correspond to the points $P_1 = (0.45, 2.5)$, $P_2 = (0.45, 3.0)$ and $P_3 = (0.45, 3.2)$, respectively, as reported in the $(B, A)$ parameter space depicted in the inset of Fig.1.
Figure 3: The case $\psi = 10$. Real (left panels) and Imaginary (right panels) parts of the roots $\omega_{1,2}$ of the characteristic polynomial (8) as a function of the wavenumber, obtained for $\nu = 182.5$. Solid red lines stand for $\omega_1$, black dashed lines stand for $\omega_2$. Figs.(a-b), (c-d) and (e-f) correspond to the points $P_1 = (0.45, 2.5)$, $P_2 = (0.45, 3.0)$ and $P_3 = (0.45, 3.2)$, respectively, as reported in the $(B, A)$ parameter space depicted in the inset of Fig.1.
Figure 4: The case $\psi = 50$. Real (left panels) and Imaginary (right panels) parts of the roots $\omega_{1,2}$ of the characteristic polynomial (8) as a function of the wavenumber, obtained for $\nu = 182.5$. Solid red lines stand for $\omega_1$, black dashed lines stand for $\omega_2$. Figs.(a-b), (c-d) and (e-f) correspond to the points $P_1 = (0.45, 2.5)$, $P_2 = (0.45, 3.0)$ and $P_3 = (0.45, 3.2)$, respectively, as reported in the $(B, A)$ parameter space depicted in the inset of Fig.1.
3.3 Approximate locus of stationary patterns

One of the most significant information extracted from the previous figures is that the sign of the imaginary part of the eigenvalue which exhibits the fastest growth rate determines the direction of band migration. Of course, since we are in the context of linear stability analysis, the previous statement is strictly valid close to the onset of instability [6],[16]. In the following, we then aim at determining the locus of null-migration velocity, bearing in mind that quantitative information can be extracted in the proximity of the bifurcation locus (17) only.

To this goal, let us recast the two roots of (8) as:

\[ \omega_{1,2} = \frac{1}{2} \left\{ -(c_1 - i k c_2) \pm \sqrt{c_1^2 - k^2 c_2^2 - 4d_1 + i k (4d_2 - 2c_1 c_2)} \right\} \]  

whose straightforward manipulation yields:

\[
\begin{align*}
\text{Re} \{ \omega_{1,2} \} &= \frac{1}{2} \left\{ -c_1 \pm \left[ \frac{1}{2} \left( c_1^2 - k^2 c_2^2 - 4d_1 + \sqrt{(c_1^2 - k^2 c_2^2 - 4d_1)^2 + k^2 (4d_2 - 2c_1 c_2)^2} \right) \right]^{1/2} \right\} \\
\text{Im} \{ \omega_{1,2} \} &= \frac{1}{2} \left\{ k c_2 \pm \left[ \frac{1}{2} \left( 4d_1 + k^2 c_2^2 - c_1^2 + \sqrt{(c_1^2 - k^2 c_2^2 - 4d_1)^2 + k^2 (4d_2 - 2c_1 c_2)^2} \right) \right]^{1/2} \right\} 
\end{align*}
\]  

For simplicity, we denote such roots as

\[ \omega_1 = \gamma + i \delta, \quad \omega_2 = -\alpha + i \beta \]  

If we limit the discussion in a small range of wavenumbers centered around the mode with the fastest growth rate, called \( k_{\text{max}} \), we can safely assume \( \gamma, \alpha, \beta \in \mathbb{R}^+ \), as it can be verified from Figures 2–4. On the other hand, as mentioned before, the sign of real and imaginary parts of \( \omega_2 \) do not vary with \( k \), so that the dynamical behavior of the system is entirely ruled by \( \omega_1 \). Consequently, at \( k_{\text{max}} \), the value of the velocity of band migration, i.e. \( \text{Im}\{\omega_1\} = \delta \), will determine the migrating/stationary character of patterns. In particular, consistently with literature [2], we have:

\[ \delta(k_{\text{max}}) < 0 \Rightarrow \text{uphill migrating patterns} \]
\[ \delta(k_{\text{max}}) = 0 \Rightarrow \text{stationary patterns} \]
\[ \delta(k_{\text{max}}) > 0 \Rightarrow \text{downhill migrating patterns} \]  

Therefore, from (8),(9),(20) and imposing the condition for the maximum of the growth rate \( \left( \frac{d\gamma}{dk} = 0 \right) \), after some algebraic manipulations, we end up with a system of five equations
in five unknowns \((\gamma, \delta, \alpha, \beta, k)\):

\[
\begin{align*}
    k^2 &= \alpha - \gamma - 1 - u_R^2 + B \\
    (\nu + \psi) k &= \beta + \delta \\
    (1 + u_R^2 - \nu \psi) k^2 &= B (1 - u_R^2) - \alpha \gamma - \beta \delta \\
    k [\nu (k^2 - B) + \psi (1 + u_R^2)] &= \alpha \delta - \gamma \beta \\
    (\nu + \psi) \{ (\alpha + \gamma) [2k (1 + u_R^2 - \nu \psi + \gamma) + \beta (\nu + \psi)] + \\
    + (\beta - \delta) [\nu (k^2 - B) + \psi (1 + u_R^2) - \alpha (\nu + \psi)] \} &= 2k (\beta - \delta) (\psi \delta - \beta \nu)
\end{align*}
\]

Due to the complexity of this system, we consider two reasonable simplifying assumptions: \(\psi \ll \nu \) and \(\beta \gg \delta\). The first one originates from ecological arguments, as it implies that only a relatively small portion of seeds that fall into the ground is transported downhill by water flow.

The second one is mathematically justifiable by the fact that the typical value of this dimensionless parameter, \(\nu = 182.5\), is generally much larger than that of any other coefficient present in the model [2],[6],[9],[10]. Therefore, if the imaginary parts \(\beta\) and \(\delta\) (given in (19)2) are evaluated at leading order in \(\nu\), they result of the order of \(k \nu\) and 0, respectively, i.e. they differ by at least one order of magnitude. This conclusion is also consistent with the results depicted in Figures 2–4.

The above assumptions allow to get an approximate, but explicit, expression for the dimensionless pattern speed \(\delta\):

\[
\delta \approx \beta \psi \frac{\left(1 + u_R^2\right)^2 + \beta^2 - 2Bu_R^2 \nu}{(1 + u_R^2)^2 + \beta^2}
\]

from which we extract the locus of stationary patterns:

\[
\psi \left(1 + u_R^2\right)^2 + \beta^2 = 2Bu_R^2 \nu
\]

where:

\[
\beta = \left[ \frac{\nu^3 (1 + u_R^2) \left\{ \nu^2 \left[ 2B \nu u_R^2 - \psi (1 + u_R^2) \right] - 2\nu (B + 1 + u_R^2 - \psi \nu) (u_R^2 + u_R^2 (2 - 3B) + B + 1) \right\}^{1/4}}{2 \nu^4 - 2\nu^2 (B + 1 + u_R^2) + (1 + u_R^2)^2} \right]^{1/4}
\]

Firstly, we notice that such a locus (24) exists if and only if \(\psi \neq 0\) so that, in the absence of secondary seed dispersal, downhill migration is prevented and we retrieve the classical results obtained in the original Klausmeier model that, as known, admits uphill migration only [2]. Moreover, the locus here obtained has the advantage of being an explicit function of the model parameters \((A, B, \nu\) and \(\psi)\) and independent of the excited wavenumber \(k\).

The locus of stationary bands (24) is depicted in Figure 5 for \(\nu = 182.5\) and for different values of seed advection speed \((\psi = 1.0, 1.5, 2.5)\). In the figure, the two differently hatched areas
indicate patterns migrating uphill or downhill, whereas the boundary between them represents the no-migration locus. As it is easy to see, the pattern-forming region becomes progressively dominated by the downhill motion as the parameter $\psi$ is increased. In particular, for a seed advection $\psi = 2.5$, that corresponds to a very small percentage of water advection ($\psi \approx 0.01 \nu$), the instability region is almost entirely characterized by a downhill motion. In other words, a small seed-to-water advection ratio suffices to make the patterns stationary or even to reverse the direction of band propagation.

Moreover, from (22), it is possible to deduce the expression of the wavenumber associated to the fastest growing mode:

$$k_{\text{max}} \simeq \frac{\beta}{\nu} \left[ \frac{\nu^2 \left( 2Bu_R^2 - \psi (1 + u_R^2) \right) - 2\nu (B + 1 + u_R^2 - \psi \nu) (u_R^4 + u_R^2 (2 - 3B) + B + 1)}{2\nu \left( \nu^4 - 2\nu^2 (B + 1 + u_R^2) + (1 + u_R^2)^2 \right)} \right]^{1/4}$$

(26)

We notice that, by evaluating (26) at leading order in $\nu$, we get $k_{\text{max}} \sim O(1/\nu^{1/2})$, in agreement with previous literature results [6].

Figure 5: Bifurcation diagram augmented by the locus of stationary bands, for three different values of seed advection speed: (a) $\psi = 1.0$, (b) $\psi = 1.5$ and (c) $\psi = 2.5$. 
4 Numerical simulations

In this section we report the results of simulations arising from numerical integration of the
system (4). This study has a twofold goal. Firstly, it aims at validating the analytical results
illustrated in the previous section, with a particular emphasis on establishing the limit of validity
of the approximated locus of stationary patterns. Secondly, it focuses on elucidating the role
played by initial conditions.

To achieve these purposes, we integrate numerically the governing system (4) through COM-
SOL Multiphysics®[34] over the domain $x \in [0, L]$ together with periodic boundary conditions
that allow to mimic an infinite domain through the analysis of the behavior of a small section
of a hillslope. Moreover, the use of periodic boundary conditions constitutes a quite natural
choice in this context since the scale of the observed patterns is small compared to the size of
the computational domain [1],[2],[12],[35]-[39].

Preliminarily, we aim at validating numerically the results obtained analytically in the
previous Section. As illustrative example, we inspect the spatio-temporal dynamics obtained by
varying the seed advection speed $\psi$, for fixed values of water advection speed $\nu = 182.5$, rainfall
$A = 3.0$ and plant loss $B = 0.45$ (representative of point $P_2$). In particular, we observe the
behavior obtained for $\psi = 0, 10, 50$ in order to enable a direct comparison with results depicted
in Figs.2,3,4 (c-d). In performing such an investigation, we set the domain size to $L = 200$
and consider, as initial condition, a small random perturbation of the homogeneous vegetated
state $E^*_R$. Patterns generated from such initial conditions are referred to as ”degradation of
homogeneous vegetation” (DHV).

Results shown in Figure 6 reveal an excellent agreement with the analytical predictions.
Indeed, for $\psi = 0$, the system exhibits a transition from the spatially-uniform state toward a
patterned state and, in particular, the emerging vegetation bands are spatially-periodic and
migrate uphill (see Fig.6a). The observed dynamics is consistent with the results depicted in
Fig.2(c-d), being associated to the presence of an unstable mode with negative imaginary part.
For $\psi = 10$, the system exhibits a transition from the spatially-uniform state toward a patterned
state with spatially-periodic bands that migrate downhill (see Fig.6b). This is in agreement
with results depicted in Fig.3(c-d), because of the presence of an unstable mode with positive
imaginary part. Finally, for $\psi = 50$, after a given transient, the system relaxes towards the
spatially-uniform steady state (see Fig.6c) in accordance with the absence of unstable modes
as in Fig.4(c-d).

Let us now address a different investigation in which we analyze the pattern generation
from different initial conditions. In particular, we aim at comparing patterns originated from
the above-mentioned ”degradation of homogeneous vegetation” (DHV) with those arising from
the so-called ”colonization of bare ground” (CBG). In this latter case, surface water is assumed
to be initially distributed homogeneously over the entire domain whereas vegetation biomass is
at its steady-state value within a limited region of arbitrary width and is absent outside it. As
widely discussed by J.Sherratt in Ref.[13], the choice of initial conditions is crucial as it may
give rise to significantly different ecological scenarios. In fact, pattern dynamics originated from
these initial conditions may provide information on the direct or inverse relationship between pattern wavelength and ground surface slope that, in turn, may be used to infer the historical origin of semiarid vegetation bands. Here we show that the initial conditions also affect the behavior of both edges of a vegetated patch as the secondary seed speed is varied.

To perform such an analysis, we now keep the advection speeds constant at the values $\nu = 182.5$ and $\psi = 1$ whereas the domain size is set to $L = 600$. Moreover, we numerically implement the initial conditions corresponding to CBG as follows:

\[
\begin{align*}
  u(x, 0) &= \begin{cases} 
    u_R & \text{for } x \in [50, 250], \\
    0 & \text{for } x \not\in [50, 250],
  \end{cases} \\
  w(x, 0) &= A & \text{for } x \in [0, 600]
\end{align*}
\]  

(27)

It is worth noting that pattern formation originated from DHV is expected to be in accordance with analytical predictions, at least close to the bifurcation threshold where patterns are characterized by small amplitude. This agreement arises from the fact that, in both analytical and numerical approaches, a small perturbation of the steady-state is applied. On the contrary, in the CBG case, numerical results are not easily predictable since the associated nonlinear ”invasion” problem is quite difficult to be treated analytically as it involves a transition between two locally stable states [13],[40].

Let us then analyze the spatio-temporal pattern dynamics resulting from numerical simulations using the two proposed initial conditions.

In Figures 7 and 8 we show the results obtained in the cases DHV and CBG, respectively. In these figures, the rainfall parameter is fixed at $A = 1$ whereas the plant loss is set at $B = 0.4$ (figures (a)) or $B = 0.2$ (figures (c)) in order to explore the behavior within the regions of uphill or downhill motion, respectively. For what concerns figures (b), we have chosen $B = 0.32$ for DHV and $B = 0.26$ for CBG since the loci of stationary patterns obtained numerically in the two cases are different.
Results depicted in Figure 7 reveal clearly that, in the DHV case, all vegetation bands exhibit the same direction of propagation or are all stationary, independently of the parameter values. Moreover, from (26), the expected value of the pattern wavelength \( \lambda = 2\pi/k_{\text{max}} = 50.15 \) is in excellent agreement with the numerical one \( \lambda = 51 \), so further validating the analytical predictions.

A different scenario is revealed in the CBG setup. In this case, comparing the different patterns obtained as the plant loss is varied, the only common feature is the uphill motion of the top edge of the initial vegetation patch, see Figure 8. This result is, of course, consistent with the presence of a larger soil moisture in the proximity of the top part of the pattern which creates the tendency of uphill migration, independently of the plant loss value [6],[16].

The behavior of the bottom edge of the patch constitutes another significant information extracted from Figure 8.

In detail, for \( B = 0.4 \), the bottom edge of the patch moves uphill too (see Figure 8(a)). This means that, for a fixed value of rainfall and provided that the strength of the secondary seed dispersal is not so relevant, the considered value of plant mortality is large enough to prevent the seeds from germinating along the bottom side of the pattern. Despite this apparent analogy with the DHV case, the CBG setup yields an excited wavelength that is roughly three times larger.

In contrast, for \( B = 0.2 \), the bottom edge of the patch moves downhill (see Figure 8(c)). This implies that the smaller value of mortality now favors the growth of vegetation even along the downhill direction. Numerical simulations indeed reveal that even a small percentage of seeds transported downslope by surface runoff suffices to create such a tendency of patterns to migrate downhill.

Figure 7: Spatio-temporal patterns obtained numerically from DHV. The rainfall parameter is set to \( A = 1 \) in all figures, whereas the plant loss is equal to: (a) \( B = 0.4 \), (b) \( B = 0.32 \) and (c) \( B = 0.2 \). The figures show the behavior obtained once the transient regime is expired.
The last interesting case involves dynamics obtained for an intermediate value of plant loss $B = 0.26$, that makes the only bottom edge of the pattern stationary (see Figure 8(b)). Hence, when reducing the plant loss value, the lower edge of the vegetation patch experiences a reversal of the direction of motion, from uphill to downhill, while the top edge continues moving uphill. In other words, patterns generated from CBG can never be entirely stationary and the only feature controllable by model parameters is the direction of propagation of the lower edge of the patch.

In the literature, the condition under which an extremum of a traveling wave may change direction of propagation and becomes stationary is referred to as "Maxwell point" [13]. The occurrence of such a Maxwell point may have some ecological grounds since it combines two competing effects. On the one hand, as known, bare soils and vegetated patches are characterized by different infiltration rates and this creates higher levels of moisture at the uphill edge of the band which, as said, favors the tendency of patterns to migrate uphill. On the other hand, the presence of secondary seed dispersal favors accumulation of seeds, and the consequent preferential growth of vegetation, at the downslope edge of vegetated patches. Therefore, the downslope seed transport acts as a stabilizing mechanism that justifies the low rates (or even the absence) of upslope migration of vegetation bands reported experimentally [17],[20],[22]. The occurrence of a downslope movement of vegetation bands has not been observed so far so that, from the theoretical viewpoint, it should be treated with caution. Indeed, some previous works suggest to interpret the regions of the parameter space in which such a phenomenon takes place as a regime in which pattern migration is precluded [20].

For the sake of completeness, it should be remarked that the above-mentioned competing dynamics become mutually exclusive when patterns are generated from DHV. In fact, in this case the control parameters may only determine the common direction of band propagation and select which of those effects really takes place.

Let us finally analyze the bifurcation diagrams obtained in the investigated cases. They are depicted in Figures 9(a) and (b) for DHV and CBG, respectively. In both figures the pattern-forming region is delimited by the black line and the red curve, representative of the condition $A = 2B$ and the wave bifurcation locus (17), respectively. The approximated locus
of stationary patterns deduced analytically in (24) is here denoted by a dashed green curve. In Figure 9(a), the dotted blue curve denotes the locus of stationary patterns obtained numerically in the DHV case. As one can see, a quantitative agreement is found close to the bifurcation threshold. The agreement becomes just qualitative away from the onset, consistently with the fact that linear stability analysis cannot predict the dynamical behavior far from the instability threshold, where patterns have non-negligible amplitude. In Figure 9(b), the dotted blue curve represents the locus of Maxwell points in the CBG case. This locus is numerically deduced by monitoring the position of the downhill edge of the vegetated patch (located initially at $x = 50$) at the final stage of simulation ($t = 100$). In such a procedure, we set a numerical tolerance to 1%. Moreover, we span the pattern-forming region in the $(B, A)$ parameter space through a rectangular computational grid as fine as $0.01 \times 0.02$. As expected, there is no quantitative agreement with analytical results, even close to the bifurcation threshold, and a poor qualitative agreement holds everywhere. However, the trend exhibited by this curve for small values of the rainfall parameter (about $A < 3$) is quite similar to the one obtained in the DHV case, so that a certain degree of similarity between the two cases may be still retrieved.

![Figure 9: Bifurcation diagram augmented by the loci of stationary patterns deduced analytically (dashed green curves) and numerically (dotted blue curves), obtained for (a) DHV and (b) CBG. The pattern-forming region is delimited by the line $A = 2B$ (solid black line) and the wave bifurcation locus (solid red curve).](image)

5 Final remarks

In this paper we have considered a generalization of the original Klausmeier model to account for the effects of secondary seed dispersal on the dynamics of vegetation patterns in sloped semi-arid environments.
Using standard tools of linear stability analysis, we have established the character of the spatially-homogeneous steady-states and derived the conditions for the occurrence of wave instability that is generally associated to the formation of non-stationary patterns. Moreover, we have deduced analytically the approximated expressions for the pattern speed, the locus of stationary patterns and the excited wavenumber. These expressions, which are strictly valid close to the bifurcation threshold, bring the advantage of depending explicitly on the model parameters only.

The most relevant results arising from our analytical calculations are: (i) the pattern-forming region shrinks as the seed advection speed increases and it disappears as the advection speeds of seed and water become equal to each other; (ii) stationary patterns may only exist in the presence of secondary seed dispersal so that, in its absence, patterns may only migrate uphill; (iii) a small percentage of seed transport by overland flow suffices to create the tendency of patterns to migrate downhill.

The analytical results so obtained have been validated through numerical simulations carried out by considering two sets of initial conditions that give rise to vegetation patterns from ‘degradation of homogeneous vegetation’ (DHV) or ‘colonization of bare ground’ (CBG). In the former case, the analytically-deduced locus of stationary patterns agrees qualitatively with the one obtained numerically and they are even in quantitative agreement close to bifurcation threshold, as expected. On the other hand, due to the intrinsic nonlinear nature of the problem associated to the CBG setup, only a poor qualitative agreement with analytical results holds everywhere.

The use of different initial conditions has allowed to extract additional information, useful from the ecological viewpoint. In particular, our simulations clearly indicate that the proper choice of initial conditions becomes crucial for the characterization of patterned vegetation dynamics. Among the most relevant numerical results, we have found that, when patterns are generated from DHV, vegetation bands move together in the same direction (uphill or downhill) or are all stationary. In contrast, when patterns originate from CBG, the top edge of the vegetation patch moves always uphill whereas the lower edge may reverse its direction of propagation according to the values of control parameters.

Our numerical experiments thus point out that overland flow and seed dispersal influence vegetation establishment and patch dynamics. In particular, these results confirm that the downslope seed transport in overland flow has a stabilizing effect and may be used to properly characterize the observed low migration rates or even the absence of a net motion of vegetation bands [13],[14],[17],[20]. The proposed combined analytical-numerical study may be useful in acquiring a better understanding on the dynamics of non-stationary vegetation patterns typically observed along the hillsides of semi-arid environments.
Acknowledgments

The authors gratefully acknowledge Jonathan Sherratt for helpful comments. This work has been supported by INdAM-GNFM and, partially, by Italian MIUR through project PRIN2017 ”Multiscale phenomena in Continuum Mechanics: singular limits, off-equilibrium and transitions” (project number: 2017YBKNCE).

References

[23] F. van Langevelde et al., Ecological Modelling 337, 253 (2016)
[34] www.comsol.com, ver.5.3