

BELOW GROUND BIOMASS PATTERNS IN ARID LANDS

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Summary. Vegetation patterns have been observed in many arid zones around the world. This particular spontaneous arrangement of the vegetation optimizes the use of the scarce water resources and could be imitated to restore vulnerable ecosystems; at the same time, the patterns of vegetation act as an early warning signal of the fact that fragile ecosystems may suddenly undergo irreversible shifts, thus, they deserve a special attention. The formation of vegetation patterns is the object of many theoretical and experimental studies, nevertheless, in previous works, the interest that is deserved to below ground biomass allocation is minor as compared to the effort that is spent to describe the organization of vegetation above ground.

In general, the distribution, growth, and mortality of vegetation is more sensitive to the hydrological cycle than to any other factor. Modelling root water uptake and the interrelated spatial and temporal variations in soil water content is a particularly challenging area.

A simple model for the study of vegetation patterns in arid lands has been used here to investigate the interrelations between plant ecology and hydrology, and the interplay between above and below ground biomass patterns.

The model is a set of partial differential equations for soil moisture, plant biomass (above and below biomass of one or more species) and surface water balance, and describes the dynamics of vegetation organization in space and time. Competition and vegetation survival strategies are accounted for within the biomass balance according with a classical mathematical biology approach. The preferential allocation of biomass below ground may be a survival strategy that plants adopt when they compete with other species that are superior competitor above ground or under particular stress e.g.: fire or grazing. By numerical simulations several crucial eco-hydrological mechanisms may be investigated: the impact of root distribution on patterns of above ground biomass with different survival strategy, competition among species that under less productive conditions tend to allocate resources to roots, the impact of alteration in root biomass distribution due to fire or grazing in water limited ecosystem.

Recent literature results are revised and presented here together with a new model outcome that advances our comprehension of relevant eco-hydrological feedbacks with special focus on the role of above and below ground biomass partitioning.

1 INTRODUCTION

Below ground growth of biomass is especially relevant in arid areas. The coexistence of desert vegetation species and their above ground arrangement depends to a large extent from differences in root system morphology [Cody, 1986]. Vegetation bands alternating with bands of bare soil (that are a particular type of mosaic vegetation) can consist either of grass, trees shrubs or trees and shrubs [Valentin et al., 1999]. Below ground, different vegetation species are expected to lead to very diverse root systems, even though, in general, root system in arid environment must evolve for optimal uptake of water. Not enough effort has been spent so far in understanding below ground biomass form and functioning, as well as the interconnection between the soil moisture patterns and the below ground biomass organization.

The origin of regular vegetation patterns in arid and semiarid lands has been ascribed to a mechanism of preferential infiltration in the vegetated area [Valentin et al., 1999]. Soil moisture accumulates locally in the root zone and influences the root growth and the above-ground biomass organization. The soil moisture spatial distribution depends on soil properties [Rietkerk et al., 2002, Fernando and Cortina, 2002 Ursino, 2005], plant physiology [Ursino, 2007], and on rainfall seasonal and daily variability [Ursino and Contarini, 2006, Nordbotten et al. 2007, De Michele et al., 2008].

Subterranean growth form is an important aspect of the study of vegetation in arid areas, but the plant root system, opposite to the above-ground component, is not easily accessible and far less studied. Root systems must evolve for optimal uptake for water leading eventually to competition among different types of vegetation via rapid root growth and relocation. Some roots are contractile and can move the plant both laterally and vertically. Vegetation type diversity in arid zone may be ascribed to differences in the way of exploiting subterranean resources and differences in root system morphology [Cody, 1986].

In this paper, the formation of regular vegetation patterns in arid lands, has been investigated via numerical analysis, for different root distributions. Despite the complexity of the soil-vegetation-atmosphere system invites a stochastic analysis, a deterministic modeling approach has been undertaken here in order to better clarify the relevant interconnections between root parameter setup, vegetation patterns and vegetation survival strategy. Conclusions on the efficiency of different below ground biomass patterns, depending on the vegetation growth rate function, are inferred from the results of the numerical simulations.

2 MODEL

According to Ursino [2009] a simple, bucket model for soil moisture (w) plant biomass (n) and surface water (o) balance, defined on a one dimensional domain indexed by x as a function of time t is solved here for a soil transect transverse to the bands of vegetation. A

soil depth H , corresponding to the mean root depth is considered, and soil related variables are averaged over H . The schematic representation of the root distribution is defined by H and by the mean lateral root length l_r [Gilad et al., 2004]. Below ground biomass allocation is proportional to the above ground biomass density and is represented by the gaussian kernel

$$K(x) = \frac{1}{l_r \sqrt{2\pi}} \exp\left[-\frac{1}{2}\left(\frac{x}{l_r}\right)^2\right] \quad (1)$$

Where $\int_{-\infty}^{\infty} K(x) dx = 1$.

The model dimensionless set of equations is the following (the reader is referred to Ursino [2009] for the dimensional form of the model and related parameters.):

$$\begin{aligned} \frac{\partial w}{\partial t} &= \ell_0 \frac{n + k_2 k_3}{n + k_2} - ew - \beta \int_{-\infty}^{\infty} f(w(x), n(x+s)) \cdot K(s) ds + d \frac{\partial^2 w}{\partial x^2} \\ \frac{\partial n}{\partial t} &= \beta \int_{-\infty}^{\infty} f(w(x+s), n(x)) \cdot K(s) ds - mn + d_n \frac{\partial^2 n}{\partial x^2} \\ \frac{\partial o}{\partial t} &= a - \ell_0 \frac{n + k_2 k_3}{n + k_2} + d_o \frac{\partial^2 o}{\partial x^2} \end{aligned} \quad (2)$$

Model (2) is based on the simplistic hypothesis of uniform net rainfall a on a flat soil. A more realistic hypothesis on the distribution of the net rainfall would not change the main conclusions reported in this paper [Ursino and Contarini, 2006].

The net dimensionless rainfall a infiltrates preferentially where plants grow, inducing a feedback mechanism that is accounted for by the term $\ell_0 \frac{n + k_2 k_3}{n + k_2}$, where $k_2 = 10$ and

$k_3 = 0.1$, $\ell_0 k_3$ is the minimum infiltration rate of surface water in the absence of plants and $\ell_0 = 1$ is the maximum infiltration rate [HilleRisLambers et al., 2001]. The water loss due to evaporation and leakage is ew with $e = 1 + w^{-1} \exp[\kappa \cdot (w - 1)]$ and $\kappa = 9$. The term mn represents the plant biomass loss due to mortality; $d = 1$, $d_n = 0.5$ and $d_o = 2.5$ are the soil moisture, biomass and surface water diffusion coefficients. Both the soil moisture and the surface water balance must be evaluated in order to account for the crucial runoff-runon mechanism from the bare zones to the vegetated area that sustains the mosaic vegetation patterns.

$\int_{-\infty}^{\infty} f(w(x), n(x+s)) \cdot K(s) ds$ is the plant water uptake within the first line of (2),

whereas $\int_{-\infty}^{\infty} f(w(x+s), n(x)) \cdot K(s) ds$, in the biomass balance equation, describes the growth rate of vegetation. The function $f(w, n)$ defines how much biomass is produced as a function of soil moisture availability and below ground biomass allocation. Thus, it identifies how efficiently the scarce water resources may be exploited, and consequently the characteristic survival strategy of the corresponding species.

Two different biomass growth rates $f(w, n)$ have been postulated and confronted. The first one is:

$$f(w, n) = n \left[g \left(\frac{w}{k_I} + w \right) - m \right] \quad (3)$$

where $m = 2.74$, $k_I = 0.075$ and $g = 5$.

Equation (3) has been proposed by Hillerislambers et al. [2001] and is referred here as the growth rate of type 1 vegetation. The second is:

$$f(w, n) = -m \cdot n \cdot \left[1 - \left(\frac{rw}{m} \right) n \right] \quad (4)$$

where $m = 0.45$ and $r = 0.36$.

Equation (4) was proposed by Klausmeier [1999] and is referred here as the growth rate of type 2 vegetation.

Klausmeier [1999] attributes banding to soil moisture redistribution, whereas Hillerislambers et al. [2001] demonstrated that vegetation banding is a consequence of the feedback between preferential infiltration and biomass growth. It is, indeed, the plant survival strategy that determines whether soil moisture redistribution or preferential infiltration counts more: the apparently contradictory results obtained by Klausmeier [1999] and Hillerislambers et al. [2001] may be explained by realizing that, since they postulated two different biomass growth rate functions, they modeled similar vegetation patterns for different reasons [Ursino 2007]. Ursino [2009], by comparing patterns of species with different average root length, demonstrated that the root length does not have a significant impact on the soil moisture patterns relative to the vegetation patterns indeed, whatever the root length, soil moisture accumulates below the vegetation bands of type 1 vegetation and in between the bands of the type 2 vegetation, consequently the plant survival strategy determines which hydrological process counts more (whether preferential infiltration or redistribution) and root parameter setup apparently does not change this tenet. Furthermore, Ursino [2009] demonstrated that the vegetation patterns exhibit characteristic lengths that depend on both: vegetation self organization and root distribution, depending on $f(w, n)$.

Extreme events such as fire and grazing have been observed to have an impact on the

survival strategy of many plants that react to the associated stress by allocating biomass preferentially below ground. This fact is modeled here by varying the parameter β that simplistically resembles the ration between roots and shoots within model (2).

3 RESULTS

In the following, different root over shoot ratios β as well as different mean root lengths ℓ_r and depths H have been postulated. Model (2) has been numerically integrated over time. An Euler explicit method has been adopted. At long simulation time the system reaches a steady state, and at that time the biomass spatial distribution has been investigated in order to verify if regular vegetation patterns established.

Figure 1 shows the threshold values of the couple of parameters a and ℓ_r that are the parameter values where, according to the model prediction, the formation of vegetation patterns changes from uniform field to banded field.

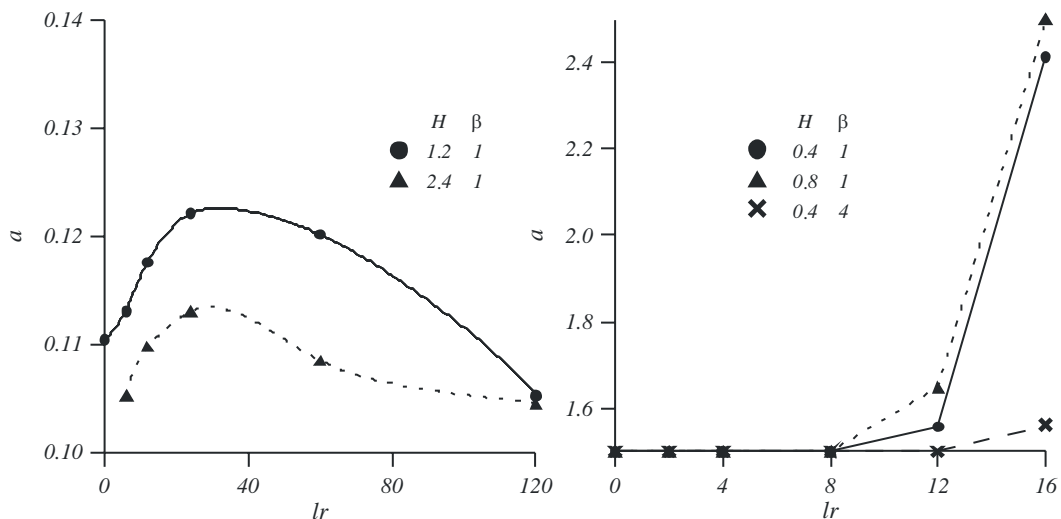


Figure 1: Threshold $(a - \ell_r)$ values that separate fields where the model predicts the formation of regular vegetation patterns and neighboring fields where the model predicts uniform vegetation cover. Left panel: type 1 vegetation. Right panel: type 2 vegetation.

The formation of type 1 vegetation patterns is very sensitive to changes of all the parameters: ℓ_r, H and β . For a smaller than the threshold value the model predicted banding, according to the common instability criteria. There is a particular ℓ_r that maximize the threshold value of a , suggesting that root distribution may contribute to optimize the use of the scarce water resources by the vegetation bands. Deeper roots lead to the replacement of vegetation patterns with uniform vegetation cover (triangles), and with increasing biomass

allocation below ground the bands disappeared: the case $H = 0.4, \beta = 4$, has been considered, but it is not shown in Figure 1, since it led to uniform vegetation patterns always (for all a).

For type 2 vegetation, as ℓ_r increases, persistent vegetation patterns established independently from the amount of net rainfall a . The variations of H did not have a significant impact on the results. Increasing β the field of uniform vegetation cover extended to higher ℓ_r (crosses). According to Ursino [2009], in this case, the patterns exhibit a characteristic length that resemble the one of the subterranean biomass distribution and patterning may be attributed to root distribution.

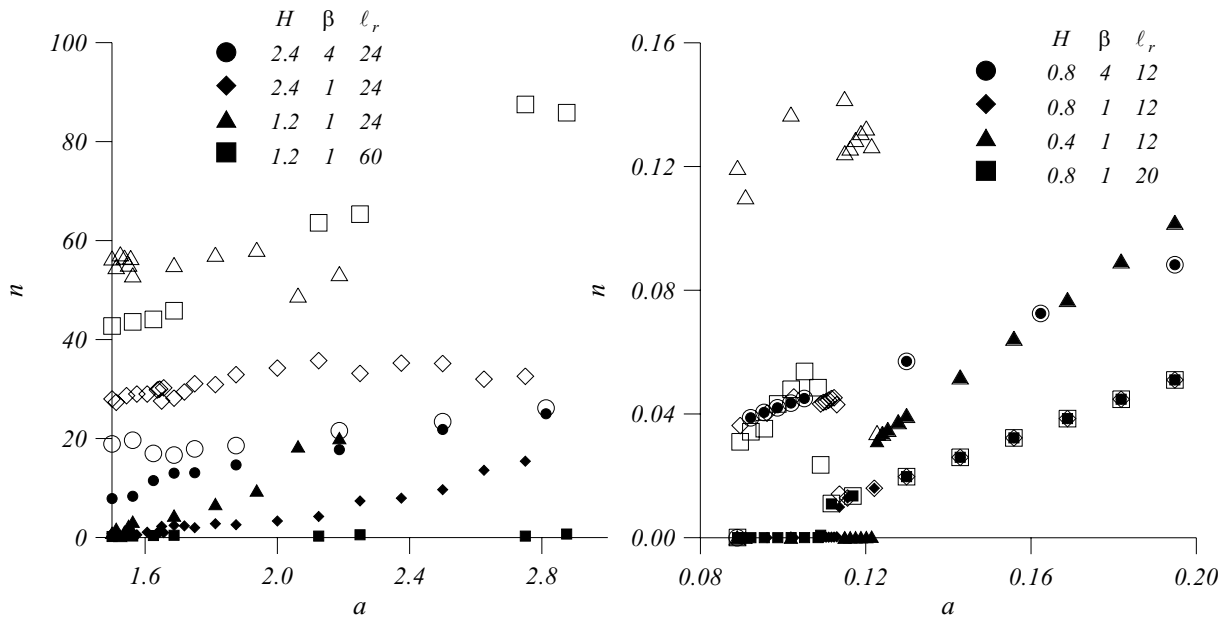


Figure 2: Maximum (solid symbols) and minimum (opened symbols) values of biomass density (n) at steady state versus a . Left panel: type 1 vegetation. Right panel: type 2 vegetation.

In Figure 2 maximum and minimum biomass density along the transect transverse to the bands have been plotted versus a , for different root distribution (different sets of the parameters H, β, ℓ_r). The two extreme n values of course coincide in case of uniform vegetation cover (left panel).

Allocating biomass preferentially below ground (increasing β) favors the development of biomass patterns of type 1 vegetation, whereas leads type 2 vegetation to a scenario of almost uniform vegetation cover, with maximum and minimum biomass density very close to each other (circles). Opposite, increasing the root length (ℓ_r) always favors the formation of type 2 vegetation bands, and the one of type 1 vegetation at small a only (squares). Shallow roots

(low H) optimize the use of the scarce resource in any case, increasing the biomass production (triangles).

4 DISCUSSION

The presence of regular vegetation patterns may be attributed either to the instability of the homogeneous steady state solution of the set of equations (3) or to the below ground root distribution (particularly in case of type 1 vegetation cover), according to Ursino [2009].

In any case, addressing the existence of an optimal distribution of roots, is of great relevance for the restoration and management of arid land, and the results presented in this paper envision the possibility of predicting if an optimal root distribution exists for a given vegetation type, demonstrating that it depends on the survival strategy of the plants.

Further investigation could attempt to model such optimal development of the roots in a more dynamic way, mimicking the contemporary redistribution of soil moisture and biomass, in order to demonstrate if such optimal below ground organization may be reached by the vegetation during its life cycle.

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