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## Mechanisms of vegetation-ring formation in water-limited systems

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## ABSTRACT

A common patch form in dryland landscapes is the vegetation ring. Vegetation patch formation has recently been attributed to self-organization processes that act to increase the availability of water to vegetation patches under conditions of water scarcity. The view of ring formation as a water-limited process, however, has remained largely unexplored. Using laboratory experiments and model studies we identify two distinct mechanisms of ring formation. The first mechanism pertains to conditions of high infiltration contrast between vegetated and bare soil, under which overland water flow is intercepted at the patch periphery. The decreasing amount of water that the patch core receives as the patch expands, leads to central dieback and ring formation. The second mechanism pertains to plants with large lateral root zones, and involves central dieback and ring formation due to increasing water uptake by the newly recruited individuals at the patch periphery. In general the two mechanisms act in concert, but the relative importance of each mechanism depends on environmental conditions. We found that strong seasonal rainfall variability favors ring formation by the overland-flow mechanism, while a uniform rainfall regime favors ring formation by the water-uptake mechanism. Our results explain the formation of rings by fast-growing species with confined root zones in a dry-Mediterranean climate, such as *Poa bulbosa*. They also explain the formation of rings by slowly growing species with highly extended root zones, such as *Larrea tridentata* (Creosotebush).

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## 1. Introduction

Water-limited landscapes are inherently patchy. Contributing to this patchiness are self-organization processes in which positive biomass-water feedbacks operating at sub-patch scales induce vegetation patterns at landscape scales. Much effort has been devoted recently to modeling water-limited landscapes and accounting for the emergence of self-organized patchiness (Borgogno et al., 2009; Deblauwe et al., 2008; Gilad et al., 2004, 2007a; Rietkerk et al., 2004). Very few model studies, however, have been devoted to patterns that emerge at the single-patch scale, such as spots, rings and crescent-like patches, and to the biomass-water relationships associated with them (Meron et al. 2007; Sheffer et al. 2007; Tlidi et al., 2008). Model and empirical studies, both at the patch and landscape scales, are significant for understanding the relationships among spatial heterogeneity, community structure and ecosystem function (Lovett et al., 2005). In addition, empirical studies of patch formation are more

feasible at the patch scale and can thus help in examining self-organizing phenomena at larger spatial scales.

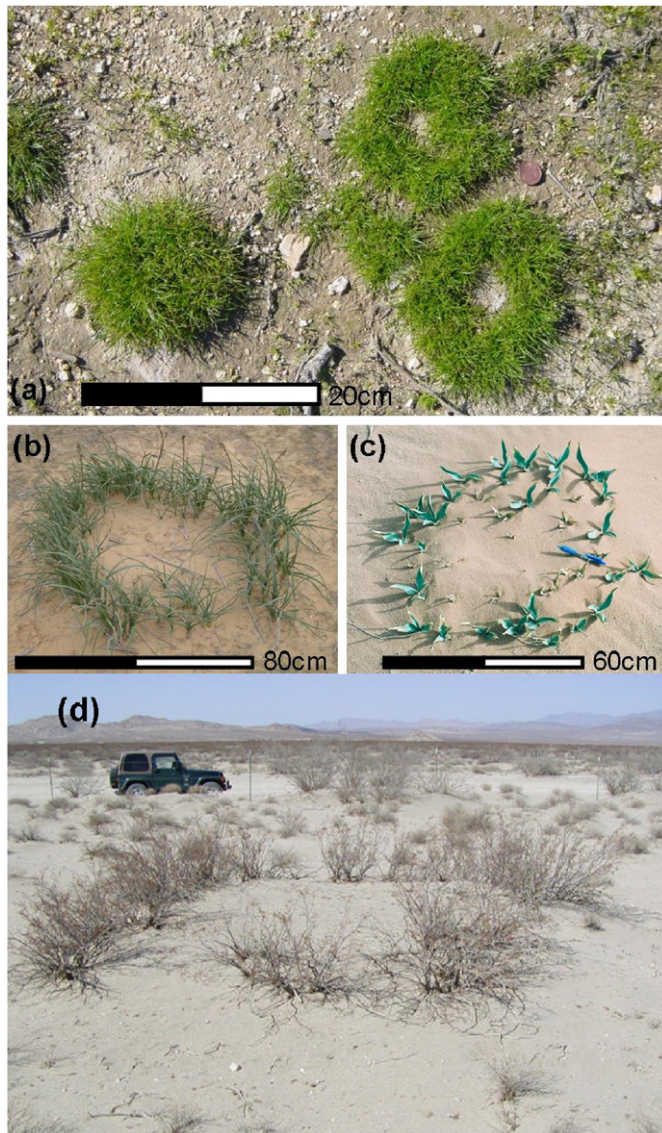
Isolated patch forms in water-limited systems often assume ring shapes. Such shapes are observed in a wide variety of plant species, as Fig. 1 indicates. Most examples are found in clonal plants with confined root zones in the lateral dimensions, such as *Poa bulbosa* (Fig. 1a), *Urginea maritime* (Fig. 1b), and *Asphodelus ramosus* (Fig. 1c). However, examples of ring forming species with extended root zones exist as well. Most notable is *Larrea tridentata* (Creosotebush; Fig. 1d), a xerophytic evergreen shrub dominant in the arid regions of the southwestern United States. Depending on environmental conditions, these species may also exhibit spot-like and crescent-like patches. Ring diameter is species dependent and varies over two orders of magnitude, from about 0.1 m in the case of *P. bulbosa* to about 10 m for *L. tridentata*.

Several mechanisms of ring formation have been suggested. Some authors have argued that low density of individuals in the ring center (low ramet density) is a result of endogenous factors, such as architectural patch development or aging, rather than a result of exogenous factors, such as external stress, resource limitation or disturbance (Adachi et al., 1996; Briske, 1991; Briske and Derner, 1998; Danin, 1996; Danin and Orshan, 1995; Harper 1985). Other studies have suggested the release of allelopathic substances as a mechanism that controls patch (genet)

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**Fig. 1.** Ring patterns in nature. (a) Mixtures of rings and spots of *Poa bulbosa* L. observed in the Northern Negev, Israel ( $150 \text{ mm yr}^{-1}$ ); (b) An *Asphodelus ramosus* L. ring observed in the Negev desert, Israel ( $170 \text{ mm/yr}$ ); (c) A ring of *Urginea maritime* (L.) Baker observed in Wadi Rum, Jordan ( $50 \text{ mm yr}^{-1}$ ); (d) Ring of *Larrea tridentata* (DC.) Coville in Lucerne Valley, California, USA ( $98 \text{ mm yr}^{-1}$ ). Photography by J. von Hardenberg (a), H. Yizhaq (b, c) and F. Rodrigue (d).

shape and ring-formation in clonal species (Gatsuk et al., 1980). There is little information on the effect of vegetation rings on ecological processes, but some studies indicate that ring formation impacts ecosystem function through habitat engineering (Fogel et al., 2004; Ravi et al., 2010).

The recent view of vegetation patchiness in drylands as a self-organization phenomenon associated with long-range competition over the limited water resource (Gilad et al., 2007a; Meron, 2011; Rietkerk and Van de Koppel, 2008; Valentin et al., 1999), motivated a similar view of ring formation (Meron et al., 2007; Sheffer et al., 2007). According to this approach ring formation is tightly related to the different positions of individuals within a patch, which affect their accessibility to water, and not a result of endogenous or physiological properties such as growth architecture and age, or exogenous non-uniform water supply. Patches consisting of individuals of similar age that are subjected to uniform but limited water supply, can still show ring formation due to the harsh competition over the water resource

that develops at the patch core as the patch grows in size. Additional factors, such as interspecific competition (Bonanomi et al., 2005), the release of allelopathic substances (Gatsuk et al. 1980; Wikberg and Mucina, 2002) and aeolian processes (Ravi et al., 2008), may induce or contribute to ring formation in some cases, but do not appear necessary for ring formation under conditions of water stress.

This view has been tested in controlled and manipulated greenhouse experiments on *P. bulbosa*. In these experiments we showed that ring-shaped patches are formed as a result of differential biomass growth across the patches in spite of uniform water supply. In the experiments we found that water scarcity created a difference in above-ground biomass production between the genet core and the periphery, which favored ring formation. In contrast, improved water availability led to biomass growth at the genet core, counteracting ring formation. Root biomass patterns were consistent with these findings supporting our suggested explanation that differences in above-ground biomass growth are related to competition for water among neighboring individuals within the clone (Sheffer et al., 2007). However, water manipulation experiments cannot directly reject central dieback as a result of other endogenous differences among individuals.

The long term effects of increased competition for water at the patch core have been studied using a spatially explicit mathematical model for vegetation growth in water-limited systems (Meron et al., 2007; Sheffer et al., 2007). In these studies a time-periodic rainfall regime has been used, which accounts for the seasonal variability in Mediterranean climate. The main finding was that rings are formed by species with highly confined root zones in the lateral directions, such as *P. bulbosa*, *Carex humilis*, *U. maritime* and other clonal plants. These results, however, do not explain the formation of rings by species such as *L. tridentata*, whose root zone extends far beyond the plant canopy (Brisson and Reynolds, 1994; Reynolds 1986).

This paper extends the previous studies in two directions; a new experiment is conducted to rule out physiological differences as a significant factor affecting ring formation under conditions of water scarcity, and a new mechanism of ring formation is identified using the model equations. Unlike the mechanism reported in previous studies (Meron et al., 2007; Sheffer et al., 2007) the new mechanism applies to species with highly extended root zones, and may explain the formation of rings by *L. tridentata*.

## 2. Methods

### 2.1. Controlled greenhouse experiments with *P. bulbosa*

We carried out a greenhouse experiment to test whether ring formation is caused by internal factors or external conditions, using *P. bulbosa* L. as an experimental plant model. *Poa bulbosa* is a small geophytic grass (see Fig. 1a) common to Israel and the Mediterranean region, central and north Europe and the central parts of Asia (Feinbrun-Dotan, 1986). This grass forms small green biomass tufts or ring-shaped patches that vary in size between 10 and 100  $\text{cm}^2$  and form dense genets of ca. five individuals per  $\text{cm}^2$  (Ofir and Kerem, 1982). *Poa bulbosa* is found mostly in rangelands on shallow soils where it plays an important role in stabilizing the soil and preventing erosion. Visible rings of *P. bulbosa* are commonly found in the drier parts of the plant's distribution in Israel (Mechanic-Perberski, 1962), whereas in humid habitats several genets may aggregate to form continuous patches of a few square meters (Seligman et al., 1959; Tsukanova, 1995).

*Poa bulbosa* propagates clonally by developing below-ground bulbs or above-ground bulbets. The bulbs and bulbets remain dormant during the summer until the emergence of new shoots

and roots at the beginning of the following rainy season. The propagation of daughter bulbs increases patch density and causes its radial expansion. We relate to *P. bulbosa* ramets as individuals since, as in many bulb-forming clonal plants, newly formed ramets become disconnected and independent of their mother ramets soon after their formation (Pitelka and Ashmun, 1985). Control over the number of daughter bulbs is unknown, but a positive correlation was found between ramet size and rate of ramet propagation in similar plants (Hutchings and Barkham, 1976; Wijesinghe and Whigham, 1997; Wikberg and Svensson, 2005).

Two hypotheses of ring formation in *P. bulbosa* have been examined: (i) ring formation is determined by internal differences among individuals, where the intrinsic rate of biomass production of individuals in the core is lower than for those in the periphery; (ii) the higher rate of biomass production in the periphery compared to the core is due to higher competition for water in the core. To test these hypotheses we experimentally grew *P. bulbosa* clones, collected from a field site at the beginning of the growth season, in pots. We compared core and periphery biomass growth of intact genet with the growth of the same parts grown in separate pots by dissecting the genets before transplanting them into the pots (Fig. 2). *Poa bulbosa* pots received uniform equal irrigation throughout the growth season. At the end of the growth season, after leaves senesced we collected and compare core and periphery above-ground biomass production. Using biomass measures and area size analyses we calculated the density of biomass in the core and periphery of the experimental clones. More details on the experimental procedures are presented in Appendix A. The effects of position within the patch (periphery vs. core) and growth treatment (intact vs. separated parts) on biomass density were tested using standard *t*-test, or ANOVA using statistical software (JMP version 4, SAS Institute, 2000).

## 2.2. Model studies

We use here the model introduced by Gilad et al. (2004, 2007a), which has already been studied in a variety of contexts including vegetation patterns and pattern transitions along environmental-stress gradients (rainfall, grazing; Gilad et al., 2004, 2007a), productivity-resilience tradeoffs in banded vegetation on hill slopes (Yizhaq et al., 2005), plants as ecosystem engineers (Gilad et al., 2004, 2007a, 2007b; Meron et al., 2007), transition from competition to facilitation in woody-herbaceous systems along rainfall gradients (Gilad et al., 2007b), effects of rainfall intermittency on vegetation patterns (Kletter et al., 2009), and the emergence of scale-free patterns (von Hardenberg et al., 2010).

The model consists of a system of nonlinear partial integro-differential equations for three dynamical variables: (i) a biomass variable  $b(\vec{r}, t)$ , representing the plant's biomass above-ground level per unit area of ground surface, (ii) a soil-water content variable,  $w(\vec{r}, t)$ , representing the amount of soil water available to the plants per unit area of ground surface, and (iii) a surface water variable,  $h(\vec{r}, t)$ , representing the height of a thin water layer above ground level. A detailed presentation of the model appears in Appendix B.

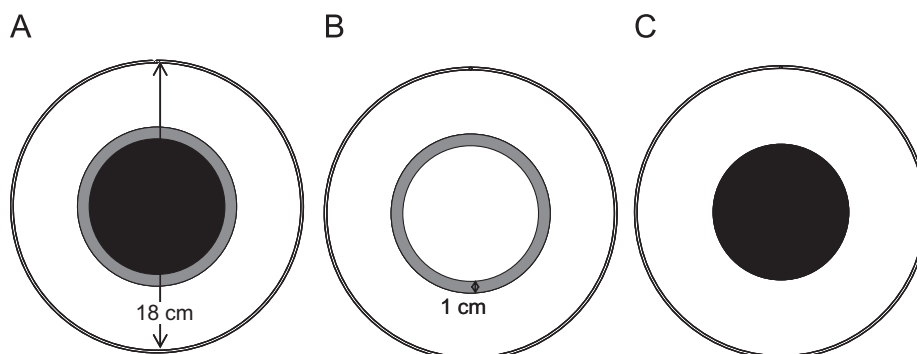
Two water-transport processes affect the local availability of soil-water in the model, assuming flat topography: (i) surface-water flow from bare areas towards vegetation patches because of higher infiltration rates in vegetated areas (Eldridge et al., 2000), (ii) water uptake by plants' roots that may extend far beyond the plants' canopies. The first process is controlled by a dimensionless parameter  $f$  that varies between zero and unity (Gilad et al., 2007a) and in terms of which we can define an *infiltration contrast* ( $c$ ) between vegetated and bare areas as  $c = f^{-1} - 1 \geq 0$ . Values  $c \ll 1$  ( $f \approx 1$ ) imply low infiltration contrasts, as in sandy soils, whereas values  $c \gg 1$  ( $f \ll 1$ ) imply high infiltration contrasts, occurring mostly when biological or physical soil crusts impede the infiltration rate in bare soil. The second transport process is controlled by a root-augmentation parameter  $\eta$ , that quantifies the extent to which the lateral extension of the root system  $L$  increases as the above-ground biomass increases:  $\eta \propto dL/db$ . Larger  $\eta$  values imply larger root-to-shoot ratios and vice versa. The value  $\eta = 0$  describes root zones of fixed sizes independent of the above-ground biomass.

Another important parameter in this study is the rainfall rate,  $p$ . This should generally be a time dependent parameter that accounts for seasonal rainfall variations as well as inter-annual variations. In the present study we neglect inter-annual rainfall variations and choose  $p$  to be time-periodic with an annual period consisting of an  $n$ -month rainy period followed by an  $m$ -month dry period, where  $m + n = 12$ . We will concentrate here on the case of  $n = 4$ , representing a Mediterranean climate with strong seasonal variability, and  $n = 12$ , representing climates with weak or no seasonal variability.

The process of ring formation involves two main phases, a latent-ring phase, during which the ring is not apparent but the biomass in the periphery is higher than in the core; and a visible-ring phase, where there is no biomass in the core. To quantify ring formation we introduce a ring index (Sheffer et al., 2007),  $\Delta$ , defined as

$$\Delta = (b_{\max} - b_{\text{core}}) / b_{\text{core}},$$

where  $b_{\max}$  is the maximal biomass in the patch and  $b_{\text{core}}$  is the biomass in the patch core. According to this definition, spots are characterized by a zero ring index,  $\Delta = 0$ , while visible rings are



**Fig. 2.** Experimental set up of genets grown in pots in three experimental treatments. The outer circle represents the pot boundaries (a view from above, 18 cm in diameter), the dark solid circle represents a *Poa bulbosa* genet growing in the pot. The genet consists of a 1 cm wide periphery area, denoted by the gray circle at the outer rim of the genet, and a core area denoted by the solid black circle. Experimental treatments consisted of (A) intact genets—periphery and core areas growing together, (B) separately growing periphery area, and (C) separately growing core area. Core size varies according to intact genet size, ranging from 10 to 15 cm in diameter.



characterized by a ring index equal to unity,  $\Delta = 1$ . Intermediate index values,  $0 < \Delta < 1$ , describe latent rings. Thus, the process of ring formation from an initial spot is quantified by the temporal increase of the ring index from zero to unity.

To simulate the situation in the field, we integrated the equations on grids representing systems that are large in comparison to the size of individual spots or rings. An integration time corresponding to 50 years was chosen to ensure the patterns appear stable for an ecological long-term. Since most ecosystems are subjected to disturbances, studying long transients is often as important as understanding the asymptotic dynamics.

### 3. Results

#### 3.1. Experimental results

The results of the greenhouse experiment indicate that when the core and the periphery parts were grown separated, above-ground biomass density of the ramets was similar for both (one-way ANOVA  $p = 0.84$ , Fig. 3). When the genets were intact core biomass was significantly lower than periphery ( $t$ -test  $p = 0.036$ ,  $n = 10$ ) and demonstrated latent ring pattern. This is a further indication that the differences between core and periphery biomass densities are due to their position in the genet and not caused by internal factors. In Sheffer et al. (2007) we also found that high water input improved water availability and allowed core individuals to grow more biomass. Our results show that core and periphery individuals have a similar growth potential thus rejecting the hypothesis that ring formation is determined by internal differences among individuals. Ring formation in the control genets (where peripheries and cores grew together) support the hypothesis that the decreased rate of biomass production in the core compared to the periphery is due to within clone competition and not to differences in production potential. Results from our previous experiments showed that with high water input the difference between periphery and core biomass

production decreased and that root biomass was high below genet core (Sheffer et al., 2007). We learned from these results that the main cause for periphery to core differences was higher competition for water in the core.

#### 3.2. Model results

##### 3.2.1. Ring formation at constant precipitation

Studying the model equations with constant precipitation rate we found that any of the two water transport processes, surface water flow and water uptake by plant roots, independently of the other, can induce ring formation from initial small spot-like patches. Figs. 4a and b show changes in the ring index  $\Delta$  and ring radius respectively as a function of time for high infiltration contrast between bare soil and vegetation patches ( $f = 0.1$  or  $c = 9$ ) and no root-augmentation ( $\eta = 0$ ). This situation corresponds to no lateral growth of the root zones as the plants grow, and leads to highly confined root systems, like in a deep and confined tap root. Under these conditions water transport from the bare area to the biomass patch is mainly due to overland flow of surface water that infiltrate mostly at the patch periphery. As the patch area grows (Fig. 4b) less and less surface water reaches the patch center, a process that results in intense competition for water at the patch core and consequently in central dieback and ring formation (Fig. 4a). We refer to this mechanism of ring formation as the “overland-flow mechanism”.

Fig. 4c and d show an analogous behavior for the case of no infiltration contrast ( $f = 1$  or  $c = 0$ ) and moderate root augmentation ( $\eta = 1.0$ ). Under these conditions water transport from the bare area to the above-ground biomass patch predominantly occurs by water uptake and conduction through root systems that extend far beyond the patch. As the patch grows more and more individuals take up water from the patch center, a competitive process that results in central dieback and ring formation. We refer to this mechanism of ring formation as the “water-uptake mechanism”. We note that when  $\eta$  is sufficiently big (for given rainfall rate  $p$ ) water uptake at the forefront of the patch can deplete the soil-water content down to a level where no further growth is possible, before central dieback takes place. This results in a spot-like patch which, unlike rings, asymptotes in time to a stationary fixed size form. The long-term dynamics of rings generally involve the convergence to spot or stripe patterns (Gilad et al., 2004, 2007a).

Although both mechanisms induce ring formation, the dynamics of the process are quite different. In the overland-flow mechanism the patch expands at a constant rate or speed (Fig. 4b). The expansion rate is independent of the patch size and shape because it is determined by local processes occurring at the patch periphery only (apart of the initial phase in which the patch is still small enough for the overland flow to reach any point in the patch). By contrast, in the water-uptake mechanism the expansion rate does depend on patch size and shape, as the variable-slope graph of the patch radius shown in Fig. 4d indicates. The patch first goes through rapid expansion because of the effective water uptake by the extended root zones. As it grows the water content in the patch forefront decreases owing to the increase in number of individuals, and the patch expansion slows down. Meanwhile the competition for water in the patch center increases as well and eventually leads to central dieback of core individuals and ring formation. Central-dieback, in turn, reduces the competition for water at the forefront of the patch, thereby increasing the expansion speed. The information contained in the ring-radius temporal-development graphs (Fig. 4b and d) can be regarded as a “finger print” of the mechanism of ring formation; constant slope indicates the dominance of the overland-flow mechanism, and variable slope indicates the dominance of the water-uptake mechanism.

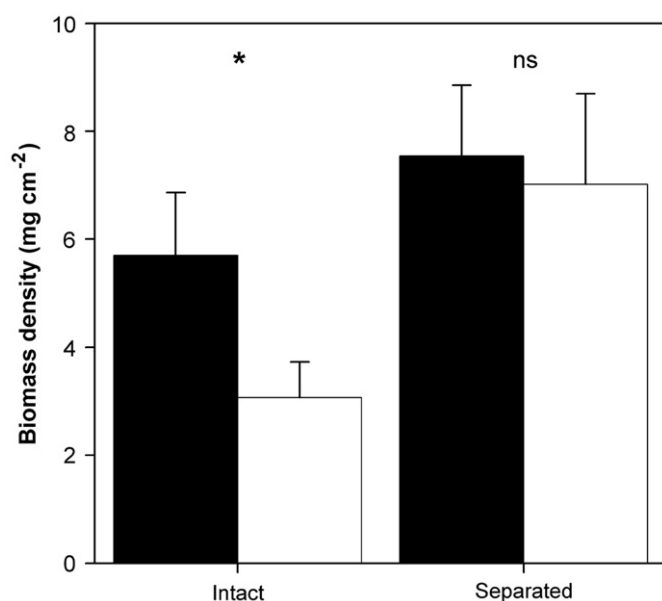
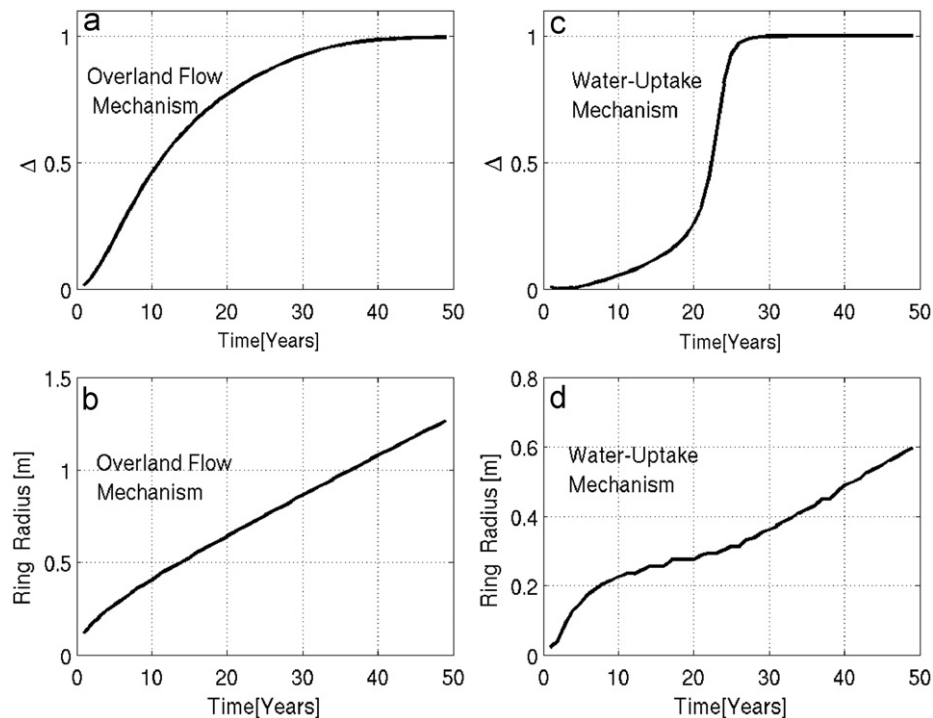


Fig. 3. Above-ground biomass production in intact and dissected *P. bulbosa* genets. The effect of core (white bars) and periphery (black bars) parts growing together (intact treatment) vs. splitting core and periphery parts to grow in different pots (separated treatment) on above-ground biomass density of *P. bulbosa* genets at the end of the experiment ( $n = 11$  and  $n = 10$ , respectively).



**Fig. 4.** Ring indices (a, c) and radii (b, d) development, showing the difference between the two mechanisms of ring formation. The graphs were obtained by solving numerically the model equations under conditions of uniform rainfall (no seasonal variability). In the overland-flow mechanism ( $\eta=0, f=0.1$ ) the ring radius grows at constant rate (b), while in the water-uptake mechanism ( $\eta=1, f=1$ ) ring growth rate varies in time (d).

### 3.2.2. Effects of rainfall regime

In general, the two mechanisms of ring formation act in concert. We now show that the relative importance of each mechanism depends on the rainfall regime. Fig. 5a shows the ring index  $\Delta$ , as a function of  $\eta$  for a climate with strong seasonal variability ( $n=4$  rainy months a year) and for a climate with no seasonal variability ( $n=12$ ), keeping the total annual rainfall and  $f$  equal in both cases. Changing  $\eta$  while keeping  $f$  fixed amounts to changing the importance of the water-uptake mechanism relative to the overland-flow mechanism. In the case of strong seasonal variability rings develop as  $\eta$  is decreased, implying that ring-formation under this rainfall regime is primarily generated by the overland-flow mechanism. By contrast, in the case of no seasonal variability rings develop as  $\eta$  is increased, implying the dominance of the water-uptake mechanism. Indeed, as Fig. 5b shows, the graph of the ring radius development in the case of strong seasonal variability has a constant slope, similar to that shown in Fig. 4b, while in the case of no seasonal variability the graph has variable slope, similar to that shown in Fig. 4d.

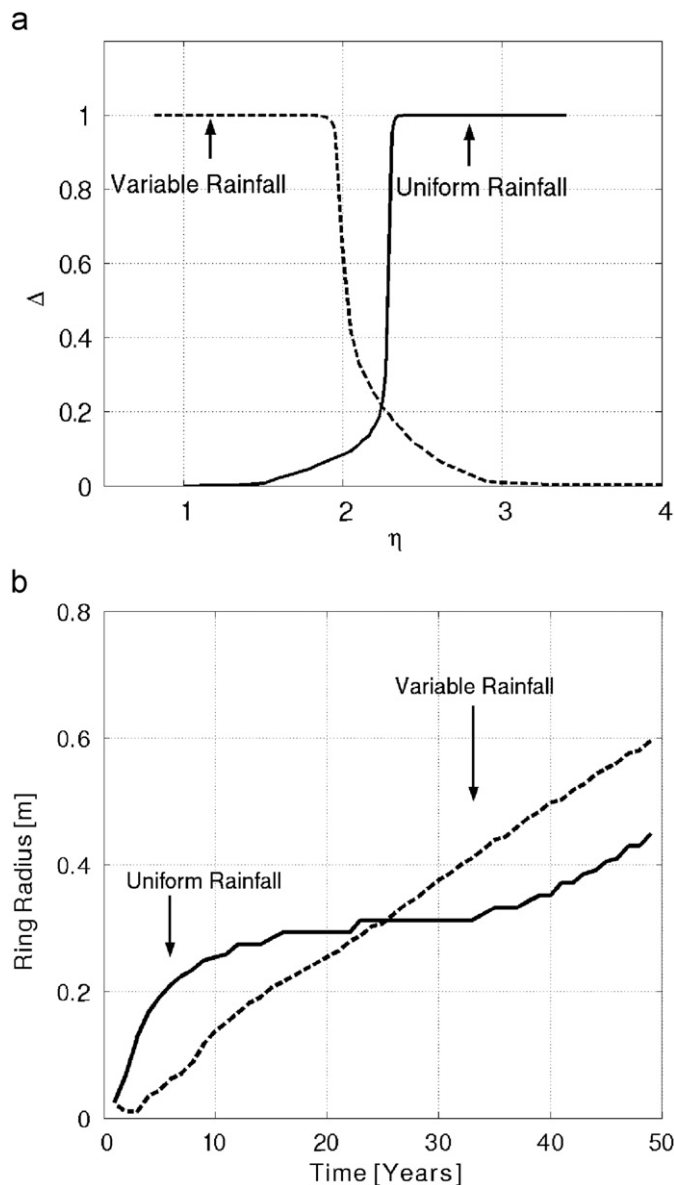
How can we understand the shift in ring-formation mechanism upon changing the precipitation regime? In the case of strong seasonal rainfall variability, a species with highly confined root zone, that grows fast enough to follow seasonal rainfall variations, can exploit the high rainfall rate during the wet season to expand and thus grow a ring-shaped patch by the overland-flow mechanism. When the same annual rainfall amount is evenly spread over the year the spots of the same species may not develop to rings because of the lower rainfall rate and their confined roots which limit the area around the patch that is available for water uptake. However, species with extended root zones may still form rings by the water-uptake mechanism, compensating for the lower precipitation rate with their ability to collect more water from larger areas available for uptake.

Another view of the shift in ring-formation mechanism upon changing the precipitation regime is given in Fig. 6, which shows

the soil-water content ahead of the patch as a function of time for the two precipitation regimes. In the case of strong seasonal variability the patch periphery experiences high levels of water content during the short rainy period. If in addition the species has confined roots (small  $\eta$ ), individuals at the patch center hardly affect the water availability at the patch front, apart of a short initial transient during which the patch size still does not exceed the root-zone size. As a result, the soil-water profile ahead of the patch is constant in time and the patch expands at a constant rate. In the case of no seasonal variability and species with extended root systems (large  $\eta$ ), the soil-water content ahead of the patch is relatively low throughout the year, and shared by all individuals in the patch. As the patch grows, the soil-water content surrounding the patch first decreases as more and more individuals take up water due to their extended roots, but once central dieback takes place the soil-water content starts increasing.

## 4. Discussion

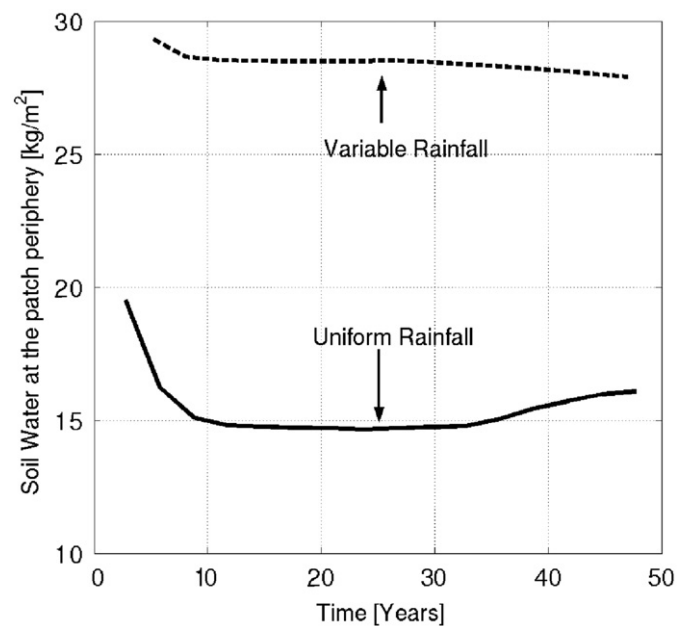
Pattern formation involve self-organization processes whereby small-scale interactions of individuals with their proximate environments (biotic and abiotic) give rise to large-scale biomass patch dynamics (Camazine et al., 2001; Rietkerk et al., 2004). We studied these processes empirically, using *P. bulbosa* as an experimental model, and theoretically, using a mathematical model. In earlier reports of our experimental studies (Sheffer et al., 2007) we demonstrated that *P. bulbosa* genets growing in dry conditions with strong seasonality displayed patterns of latent rings. Water deficiency promoted ring formation while water profusion enhanced biomass throughout the genet, decreasing ring formation. These results suggest that ring formation is driven by water and root mediated mechanisms, and that the growth of each individual is controlled by the interaction



**Fig. 5.** Effect of rainfall regime on ring-formation mechanism. Under variable rainfall regime ( $n=4$  rainy months a year) rings develop ( $\Delta$  approaches unity) as the root zone decreases in size ( $\eta$  decreases) by the overland-flow mechanism (constant expansion rate), as the dashed lines in (a) and (b) show. When the rainfall is uniform throughout the year ( $n=12$ ) rings form as the root-zone size increases by the water-uptake mechanism (variable expansion rate), as the solid lines in (a) and (b) show. Parameters:  $p=0.88$  (corresponding to 220 mm/y),  $f=0.1$ . To allow ring formation in both rainfall regimes we chose in (b)  $\eta=1.2$  for variable rainfall and  $\eta=2.5$  for uniform rainfall. Other parameter values are given in Appendix B.

between water availability and the effects of other individuals in its surrounding. Here we report on an experiment that further supports the claim that ring formation is driven by self-organization within a patch. In this experiment core and periphery parts of a patch were grown separately. The results show that without core to periphery interaction, biomass production of core individuals was similar to individuals from genet periphery. This implies that there are no intrinsic differences, e.g. physiological or age, among the individuals except for their position within the genet.

The experimental results highlight the dominant role of local water availability in patch dynamics, and justify the application of the Gilad et al. (2004, 2007a) model to study ring formation. In



**Fig. 6.** Annually averaged values of soil-water content at the patch periphery during ring development, for a variable rainfall regime (dashed line), and for a uniform rainfall regime (solid line). In the case of variable rainfall, after an initial transient the soil water content approaches a constant value (the slight decline at later times is due to boundary effects). In the case of uniform rainfall the soil-water content ahead of the patch first decreases significantly as more and more individuals take up water due to their extended roots, but once central dieback takes place the surrounding-soil-water content starts increasing. Parameters:  $p=0.88$  (corresponding to 220 mm/yr),  $f=0.1$  and  $\eta=1.2$  (2.5) for variable (uniform) rainfall. Values of other parameters are given in Appendix B.

Sheffer et al. (2007), we simulated the response of a latent ring to low and high precipitation rates, and reproduced the short time trends we observed in experiments. We further used the model to study the long-term dynamics of water-limited patches, focusing on a rainfall regime representing strong seasonal variability. The main finding was that ring formation under conditions of strong seasonal variability is obtained in species whose root zones are sufficiently confined (in the lateral directions), such as *P. bulbosa*. In the current model study we identified another possible mechanism of ring formation that may explain the formation of rings by species with highly extended root zones, such as *L. tridentata*.

By isolating the effects of the two water transport processes, surface water flow and water uptake by plant roots, we identified two distinct mechanisms of ring formation. The first mechanism (*overland flow*) applies to species with highly confined root zones in the lateral directions, and is characterized by patches that grow at constant rates (constant expansion speeds). The mechanism involves overland flow that is intercepted at the patch periphery, due to higher infiltration rates in vegetated areas compared to bare (crusted) soil, and declines as the flow approaches the patch center. This induces central dieback and ring formation once the growing patch becomes large enough. The second mechanism (*water uptake*) applies to species with extended lateral root zones and is characterized by a variable patch-growth process, consisting of an initial phase of decelerated patch growth, followed by a phase of accelerated growth, and a final phase of constant growth. The initial slowing down of patch growth is due to the depletion of soil-water at the forefront of the patch as a result of an increasing number of individuals, whose roots are long enough to reach that area. While this process is taking place, the competition for water at the patch center increases, leading eventually to central dieback. The decline in core biomass, in turn, reduces the uptake ahead of the patch and increases the expansion rate.

An important factor affecting patch growth is the rainfall regime. Increase in the mean annual rainfall rate leads to ring formation, independently of the governing mechanism, but for a given mean annual rainfall rate, the intra-annual rainfall distribution can favor one mechanism over the other. Strong seasonal rainfall variability favors ring formation by the overland-flow mechanism, which applies to species with confined root zones. This mechanism may explain why most *P. bulbosa* genets we measured in our experiments formed a latent ring pattern. Examples of other species that fall in this category are *Bouteloua gracilis* (Ravi et al., 2008), *Urginea maritima* (L.; Fig. 1b) and *Asphodelus ramosus* L. (Fig. 1c). By contrast, a uniform rainfall regime favors ring formation by the water-uptake mechanism, which applies to species with extended root zones in the lateral directions.

The model studies reported here were carried out for species whose growth rates are fast enough to follow seasonal rainfall variations. The results obtained with uniform rainfall, however, may also apply to slowly growing perennial species that do not follow fast seasonal variability and respond only to the mean annual rainfall. For such species our results suggest that ring formation is likely to occur by the water-uptake mechanism. A possible example of this case is *Larrea tridentata* (Creosotebush), which depicts many homologous properties to our theoretical findings (Briones et al., 1996; Fonteyn and Mahall, 1981; Phillips and MacMahan, 1981).

Besides the rainfall regime there are other factors affecting patch growth that should be considered when analyzing field observations. Here we examined ring formation of individual patches and did not analyze patch dynamics of many interacting patches. At the landscape level sparsely scattered patches may expand and form rings, while a pattern of closely packed patches, under the same environmental conditions, is likely to consist of stable spots rather than rings (Gilad et al., 2004, 2007a). In a similar way, neighborhood effects of other plant species interspersed between spots may impede patch growth and ring-formation. One of these causes may explain the observations of spot patterns of *L. tridentata* in drylands other than the Mojave Desert (Barbour, 1973; Ebert and McMaster, 1981).

The rings obtained in the model simulations are transient patch forms. They keep expanding and converge asymptotically to spot patterns or stripe patterns or combinations thereof, depending on the precipitation rate. The expansion rate, however, is much slower than the local biomass growth rate. This is unlike spots in the bistability range of bare soil and spot patterns, which can form stable localized structures, presumably due to homoclinic snaking (Knobloch, 2008). We believe that vegetation rings observed in nature are transient patch forms as well, although this may not be easily noticeable. As far as we know this question has never been studied empirically. Since ecological systems are generally subjected to disturbances, asymptotic behaviors, obtained after tens or even hundreds of years, may not be of much interest in practice.

More studies are needed to prove the validity of the two mechanisms we suggest for ring formation in water-limited systems. Observations of positive correlations between constant patch-expansion rate and confined root zones, and between variable patch-expansion rate and extended root zones, will support the suggested mechanisms.

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## Appendix A

*Poa bulbosa* clones were collected from Adulam nature reserve, Israel (31° 39' N 34° 56' E, 400 mm yr<sup>-1</sup> average rainfall, Sheffer and Shkedy, 2008), at the beginning of the rainy season, after ca. 120 mm of precipitation. We collected only genets that appeared to be completely covered with emerging new leaves. We transplanted individual genets, 10–15 cm in diameter, into 4 L pots (18 cm diameter, 20 cm height) filled with vermiculite and irrigated to saturation. The experiments were carried out in a greenhouse. In the transplant procedure we dissected each of ten *P. bulbosa* genets and divided them into periphery (1–2 cm from the perimeter) and core (rest of the genet). We planted the separated parts of the genets as well as ten intact genets. Irrigation treatment consisted of 630 ml of water per pot per week, equivalent to 500 mm of annual rainfall. We harvested above-ground biomass twice during the experiment, at the onset and at the end of the experiment, after all the leaves had dried. At each harvest we clipped and collected separately the periphery and core biomass in order to compare biomass growth within the genet and measure the dynamics of ring formation. In intact genets the biomass separation was achieved by collecting the biomass of the outer 1 cm periphery of the genet and that of the rest (core) separately. We then weighed the collected biomass after it was oven dried at 60 °C for three days. The core and periphery areas were calculated by manually delineating these parts from scaled digital images, photographed after biomass removal, using ERDASS IMAGINE (ERDAS, 1999) and in intact genets by using an inner 1 cm buffer zone application in ArcMap software (ESRI, 2004).

## Appendix B

Expressed in non-dimensional form and for flat topography, the model equations read:

$$\frac{\partial b}{\partial t} = G_b b(1-b) - b + \delta_b \nabla^2 b, \quad (\text{B.1})$$

$$\frac{\partial w}{\partial t} = lh - v(1-\rho b)w - G_w w + \delta_w \nabla^2 w, \quad (\text{B.2})$$

$$\frac{\partial h}{\partial t} = p - lh + \delta_h \nabla^2 (h^2). \quad (\text{B.3})$$

Tables 1 and 2 contain definitions of the non-dimensional variables and parameters appearing in these equations, and a description of their dimensional counterparts. For a detailed explanation of the model equations we refer the reader to Gilad et al. (2007a) and Meron (2011). Here, we only describe those aspects of the model equations that are most relevant to the present study.

Surface-water flow from bare areas towards vegetation patches is described by Eq. (B.3) with a biomass dependent infiltration rate of the form

$$I = \alpha \frac{b(\vec{r}, t) + qf}{b(\vec{r}, t) + q}, \quad 0 \leq f \leq 1, \quad (\text{B.4})$$

and constant or time-dependent precipitation rate  $p$ . High infiltration contrast between vegetated areas and crusted soil, and thus strong overland flow towards vegetation patches, is captured



**Table 1**

Definitions of the non-dimensional variables and parameters appearing in Eqs. (B.1)–(B.3) in terms of their dimensional counterparts. A description of the dimensional parameters and their units appear in Table 2.

Quantity	Scaling	Quantity	Scaling
$b$	$B/K$	$P$	$\Delta P/MN$
$w$	$\Delta W/N$	$\delta_b$	$D_B/MS_0^2$
$h$	$\Delta H/N$	$\delta_w$	$D_W/MS_0^2$
$q$	$Q/K$	$\delta_h$	$D_HN/MA S_0^2$
$\nu$	$N/M$	$\zeta$	$\Delta Z/N$
$\alpha$	$A/M$	$\rho$	$R$
$\eta$	$EK$	$t$	$MT$
$\gamma$	$\Gamma K/M$	$x$	$X/S_0$

**Table 2**

Description of the model parameters and their units.

Parameter	Unit	Description
$K$	kg/m <sup>2</sup>	Maximum standing biomass
$Q$	kg/m <sup>2</sup>	Biomass reference value beyond which infiltration rate under a patch approaches its maximum
$M$	yr <sup>−1</sup>	Rate of biomass loss due to mortality and disturbances
$A$	yr <sup>−1</sup>	Infiltration rate in fully vegetated soil
$N$	yr <sup>−1</sup>	Soil water evaporation rate
$E$	(kg/m <sup>2</sup> ) <sup>−1</sup>	Root augmentation per unit biomass
$\Lambda$	(kg/m <sup>2</sup> ) <sup>−1</sup> yr <sup>−1</sup>	Biomass growth rate per unit soil water
$\Gamma$	(kg/m <sup>2</sup> ) <sup>−1</sup> yr <sup>−1</sup>	Soil water consumption rate per unit biomass
$D_B$	m <sup>2</sup> /yr	Biomass lateral expansion (vegetative or by seeds) coefficient
$D_W$	m <sup>2</sup> /yr	Transport coefficient for soil water
$D_H$	m <sup>2</sup> /yr (kg/m <sup>2</sup> ) <sup>−1</sup>	Bottom friction coefficient between surface water and ground surface
$S_0$	m	Minimal root length
$Z(X)$	mm	Topography function
$P$	kg/m <sup>2</sup> yr <sup>−1</sup>	Precipitation rate
$R$	–	Evaporation reduction due to shading
$f$	–	Infiltration contrast between bare soil and vegetation

by values  $f \ll 1$ . The parameter  $\delta_h$  is a transport coefficient, inversely proportional to the friction between the overland water flow and the ground surface.

Water uptake by plants' roots is captured by the uptake rate

$$G_w(\vec{r}, t) = \gamma \int_{\Omega} g(\vec{r}', \vec{r}, t) b(\vec{r}', t) d\vec{r}', \quad (\text{B.5})$$

where the kernel  $g$  represents the spatial extent of the root zone and is modeled by the Gaussian function

$$g(\vec{r}', \vec{r}, t) = \frac{1}{2\pi} \exp \left\{ -\frac{|\vec{r} - \vec{r}'|^2}{2[1 + \eta b(\vec{r}', t)]^2} \right\}. \quad (\text{B.6})$$

According to Eqs. (B.2) and (B.5) water uptake at a point  $\vec{r}$  depends on all plants at points  $\vec{r}'$  in the neighborhood  $\Omega$  of  $\vec{r}$  whose roots extend to the point  $\vec{r}$ . The spatial extent of the root zone  $L$  (the Gaussian width), depends on the above-ground biomass  $b$  through the relation

$$L = 1 + \eta b, \quad (\text{B.7})$$

where the proportionality parameter  $\eta$  is a measure of the root-to-shoot ratio,  $\eta = dL/db$ . The effect of  $\eta$  on the size of the root zone, however, is enhanced by a positive feedback between below-ground biomass (root) and above-ground biomass (shoot), which is captured by the following expression for the biomass

growth rate:

$$G_b(\vec{r}, t) = v \int_{\Omega} g(\vec{r}, \vec{r}', t) w(\vec{r}', t) d\vec{r}'. \quad (\text{B.8})$$

As a plant grows its root zone extends in size and probes new soil regions where water can be taken up from. According to Eq. (B.8), this increases the plant's growth rate, which in turn, increases even further the root-zone size  $L$  (through  $b$ ).

In all simulations throughout this study we used the following (non-dimensional) parameter values:  $\alpha=4$ ,  $\gamma=5$ ,  $\nu=4$ ,  $\rho=1$ ,  $q=0.05$ ,  $\delta_b=0.02$ ,  $\delta_w=2$ ,  $\delta_h=200$ . Values used for other parameters are displayed in the figure captions.

## References

- Adachi, N., Terashima, I., Takahashi, M., 1996. Mechanisms of central die-back of *Reynoutria japonica* in the volcanic desert on Mt. Fuji. A stochastic model analysis of rhizome growth. *Ann. Bot.* 78, 169–179.
- Barbour, M.G., 1973. Desert dogma reexamined: root/shoot productivity and plant spacing. *Am. Midl. Nat.* 89, 41–57.
- Bonanomi, G., Rietkerk, M., Dekker, Mazzoleni, S., 2005. Negative plant-soil and positive species interaction in a herbaceous plant community. *Plant Ecol.* 181, 269–278.
- Borgogno, F., D'Odorico, P., Laio, F., Ridolfi, L., 2009. Mathematical models of vegetation pattern formation in ecohydrology. *Rev. Geophys.* 47 (RG1005), 1–36.
- Briones, O., Montana, C., Ezcurra, E., 1996. Competition between three chihuahuan desert species: evidence from plant size-distance relations and root distribution. *J. Veg. Sci.* 7, 453–460.
- Briske, D.D., 1991. Developmental morphology and physiology of grasses. In: Heitschmidt, R.K., Stuth, J.W. (Eds.), *Grazing Management: An Ecological Perspective*. Timber Press, Portland, Oregon, pp. 85–108.
- Briske, D.D., Derer, J.D., 1998. Clonal biology of caespitose grasses. In: Cheplick, G.P. (Ed.), *Population Biology of Grasses*. Cambridge University Press, Cambridge, pp. 106–135.
- Brisson, J., Reynolds, J.F., 1994. The effect of neighbors on root distribution in a creosotebush (*Larrea tridentata*) population. *Ecology* 75, 1693–1702.
- Camazine, S., Deneubourg, J.L., Franks, N.R., Sneyd, J., Theraulaz, G., Bonabeau, d E., 2001. *Self-Organization in Biological Systems*. Princeton University Press, NJ.
- Danin, A., 1996. *Plants of Desert Dunes*. Springer, Berlin and Heidelberg, p. 177.
- Danin, A., Orshan, G., 1995. Circular arrangement of *Stipagrostis ciliata* clumps in the Negev, Israel and near Goakeb, Namibia. *J. Arid Environ.* 30, 301–313.
- Deblauwe, V., Barbier, N., Couteron, P., Lejeune, O., Bogaert, J., 2008. The global biogeography of semi-arid periodic vegetation patterns. *Global Ecol. Biogeogr.* 17, 715–723.
- Ebert, G.S., McMaster, S., 1981. Regular pattern of desert shrubs: a sampling artefact? *J. Ecol.* 69, 559–564.
- Eldridge, D.J., Zaady, E., Shachak, M., 2000. Infiltration through three contrasting biological soil crusts in patterned landscapes in the Negev, Israel. *Catena* 40, 323–336.
- ERDAS Inc. (Earth Resources Data Analysis), 1999. *IMAGINE version 6.4*. Atlanta, Georgia.
- ESRI, 2004. *ArcView GIS*. Environmental Systems Research Institute, Redlands, CA.
- Feinbrun-Dotan, N., 1986. *Flora Palestina*, vol.4. Jerusalem: Israel Academy of Sciences and Humanities.
- Fogel, B.N., Crain, C.M., Bertness, M.D., 2004. Community level engineering effects of *Triglochin maritima* (seaside arrowgrass) in a salt marsh in northern New England, USA. *J. Ecol.* 92, 589–597.
- Fonteyn, P.J., Mahall, B.E., 1981. An experimental analysis of structure in a desert plant community. *J. Ecol.* 69, 883–896.
- Gatsuk, L.E., Smirnova, O.V., Vorontzova, L.I., Zaugolnova, L.B., Zhukova, L.A., 1980. Age states of plants of various growth forms: a Review. *J. Ecol.* 68, 675–696.
- Gilad, E., von Hardenberg, J., Provenzale, A., Shachak, M., Meron, E., 2004. Ecosystem engineers: from pattern formation to habitat creation. *Phys. Rev. Lett.* 93, 098105.
- Gilad, E., von Hardenberg, J., Provenzale, A., Shachak, M., Meron, E., 2007a. A mathematical model of plants as ecosystem engineers. *J. Theor. Biol.* 244 (4), 680–691. doi:10.1016/j.jtbi.2006.08.006.
- Gilad, E., Shachak, M., Meron, E., 2007b. Dynamics and spatial organization of plant communities in water limited systems. *Theor. Popul. Biol.* 72, 214–230.
- Harper, J.L., 1985. Modules, Branches, and the capture of resources. In: Jackson, J.B.C., Buss, L.W., Cook, R.E. (Eds.), *Population Biology and Evolution of Clonal Organisms*. Yale University Press, New Haven, pp. 1–33.
- Hutchings, M.J., Barkham, J.P., 1976. An investigation of shoot interactions in *Mercurialis Perennis* L., a rhizomatous perennial herb. *J. Ecol.* 64, 723–743.
- Kletter, A., von Hardenberg, J., Meron, E., Provenzale, A., 2009. Patterned vegetation and rainfall intermittency. *J. Theor. Biol.* 256, 574–583.
- Knobloch, E., 2008. Spatially localized structures in dissipative systems: open problems. *Nonlinearity* 21, T45.
- Lovett, G.M., Jones, C.G., Turner, M.G., Weathers, K.C. (Eds.), 2005. *Ecosystem Function in Heterogeneous Landscapes*. Springer.

- Mechanic-Perberski, N., 1962. Investigations in populations of *Poa bulbosa* L. M.Sc. Thesis, Hebrew University of Jerusalem (in Hebrew).
- Meron, E., Yizhaq, H., Gilad, E., 2007. Localized structures in dryland vegetation: forms and functions. *Chaos* 17, 037109.1–037109.9.
- Meron, E., 2011. Modeling dryland landscapes. *Math. Model. Nat. Phenom.* 6, 163–187.
- Ofir, M., Kerem, D., 1982. The effects of temperature and photoperiod on the onset of summer dormancy in *Poa bulbosa* L. *Ann. Bot.* 50, 259–264.
- Phillips, D.L., MacMahon, J.A., 1981. Competition and spacing patterns in desert shrubs. *J. Ecol.* 69, 97–115.
- Pitelka, L.F., Ashmun, J.W., 1985. Physiology and integration of ramets in clonal plants. In: Jackson, J.B.C., Buss, L.W., Cook, R.E. (Eds.), *Population Biology and Evolution of Clonal Organisms*. Yale University Press, New Haven, CT, pp. 399–435.
- Ravi, S., D'Odorico, P., Wang, L., Collins, S., 2008. Form and function of grass ring patterns in arid grasslands: the role of abiotic controls. *Oecologia* 158, 545–555.
- Ravi, S., Breshears, D.D., Huxman, T.E., D'Odorico, P., 2010. Land degradation in drylands: interactions among hydrologic-aeolian erosion and vegetation dynamics. *Geomorphology* 116, 236–245.
- Reynolds, J.F., 1986. Adaptive strategies of desert shrubs with special reference to the creosotebush (*Larrea tridentata* [DC] Cov). In: Whitford, W.G. (Ed.), *Pattern and process in desert ecosystems*. University of New Mexico Press, Albuquerque, New Mexico, USA, pp. 19–49.
- Rietkerk, M., Dekker, S.C., De Ruiter, P.C., Van de Koppel, J., 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305, 1926–1929.
- Rietkerk, M., Van de Koppel, J., 2008. Regular pattern formation in real ecosystems. *Trends Ecol. Evol.* 23, 169–175.
- SAS Institute, 2000. JMP Version 4. SAS Institute, Cary, North Carolina, USA.
- Seligman, N., Rosenzaft, Z., Tadmor, N., Katzenelson, J., Naveh, Z., 1959. Natural Pasture in Israel. Sifriat poalim, Merhavia, Israel, pp. 378 (In Hebrew, English summary).
- Sheffer, E., Shkedy, Y. (Eds.), 2008. *Adulam Long-term Ecological Research—Summary of Three Years of Research*. Science division. Israel Nature and Parks Authority, Jerusalem.
- Sheffer, E., Yizhaq, H., Gilad, E., Shachak, M., Meron, E., 2007. Why do plants in resource deprived environments form rings? *Ecol. Compl.* 4 (1), 192–200. doi:10.1016/j.ecocom.2007.06.008.
- Tlidi, M., Lefever, R., Vladimirov, A., 2008. On vegetation clustering: localized bare soil spots and fairy circles. *Lect. Notes Phys.* 751, 381–402.
- Tsukanova, S.K., 1995. *Poa bulbosa* L. in the Central Kara Kum. *Probl. Desert Dev.* 1, 30–35.
- Valentin, C., D'Herbes, J.M., Poesen, J., 1999. Soil and water components of banded vegetation patterns. *Catena* 37, 1–24.
- Von Hardenberg, J., Kletter, Y.A., Yizhaq, H., Nathan, J., Meron, E., 2010. Periodic versus scale free patterns, in dryland vegetation. *Proc. R. Soc. B* 277, 1771–1776.
- Wijesinghe, D.K., Whigham, D.F., 1997. Costs of producing clonal offspring and the effect of plant size on population dynamics of the woodland herb *Uvularia perfoliata* (Liliaceae). *J. Ecol.* 85, 907–919.
- Wikberg, S., Mucina, L., 2002. Spatial variation in vegetation and abiotic factors related to the occurrence of a ring-forming sedge. *J. Veg. Sci.* 13, 677–684.
- Wikberg, S., Svensson, B.M., 2005. Ramet dynamics in a centrifugally expanding clonal sedge: a matrix analysis. *Plant Ecol.* 183, 55–63.
- Yizhaq, H., Gilad, E., Meron, E., 2005. Banded vegetation: biological productivity and resilience. *Physica A* 356 (1), 139–144. doi:10.1016/j.physa.2005.05.026.