

SPATIAL DECOUPLING OF FACILITATION AND COMPETITION AT THE ORIGIN OF GAPPED VEGETATION PATTERNS

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Abstract. Spatially periodic vegetation patterns, forming gaps, bands, labyrinths, or spots, are characteristic of arid and semiarid landscapes. Self-organization models can explain this variety of structures within a unified conceptual framework. All these models are based on the interplay of positive and negative effects of plants on soil water, but they can be divided according to whether they assume the interactions to be mediated by water redistribution through runoff/diffusion or by plants' organs. We carried out a multi-proxy approach of the processes operating in a gapped pattern in southwest Niger dominated by a shrub species. Soil moisture within the root layer was monitored in time and space over one month of the rainy season. Soil water recharge displayed no spatial variation with respect to vegetation cover, but the stock half-life under cover was twice that of bare areas. A kernel of facilitation by the aboveground parts of shrubs was parameterized, and soil water half-life was significantly correlated to the cumulated facilitative effects of shrubs. The kernel range was found to be smaller than the canopy radius (81%). This effect of plants on soil water dynamics, probably through a reduction of evaporation by shading, is shown to be a better explanatory variable than potentially relevant soil and topography parameters. The root systems of five individuals of *Combretum micranthum* G. Don were excavated. Root density data were used as a proxy to parameterize a kernel function of interplant competition. The range of this kernel was larger than the canopy radius (125%). The facilitation-to-competition range ratio, reflecting the above-to-belowground ratio of plant lateral extent, was smaller than 1 (0.64), a result supporting models assuming that patterning may emerge from an adaptation of plant morphology to aridity and shallow soils by means of an extended lateral root system. Moreover, observed soil water gradients had directions opposite to those assumed by alternative mathematical models based on underground water diffusion. This study contributes to the growing awareness that combined facilitative and competitive plant interactions can induce landscape-scale patterns and shape the two-way feedback loops between environment and vegetation.

Key words: allometry; aridity; Niger; root–shoot ratio; self-organization; symmetry-breaking instability; vegetation patterns.

INTRODUCTION

Heterogeneity of the vegetation cover in semiarid and arid environments is commonly seen as the consequence of resource concentration mechanisms, in which vegetated patches intercept water runoff or sediments carried away from open areas by wind or water erosion (Schlesinger et al. 1990, Wilcox et al. 2003, Ludwig et al. 2005, Breshears 2006). Such patterned vegetations can attain very high levels of organization (Tongway et

al. 2001), in which landscapes display contrasted phases of bare and densely vegetated areas with well-defined scale and symmetry across entire geographic regions.

Progress toward a general theory for these spatially periodic patterns is provided by self-organization models (Lefever and Lejeune 1997, HilleRisLambers et al. 2001, von Hardenberg et al. 2001). Their fundamental prediction is that the interplay of short-range facilitation and long-range competition is a necessary condition for pattern formation. These positive and negative interactions between plants are supposed to be mediated by limiting resources, and more specifically, water. However, mechanisms actually at work in these systems remain to be investigated. Most models

Manuscript received 5 March 2007; revised 3 August 2007; accepted 10 October 2007. Corresponding Editor: J. A. Jones.

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(Klausmeier 1999, Rietkerk et al. 2002, Meron et al. 2004) hypothesize a movement of water either via surface runoff or diffusion in the soil. Field evidence for runoff transfers are limited to the case of tiger bush, i.e., banded patterns generally aligned along topographic contours over slightly sloping terrains (see Tongway et al. 2001 for a review). Bands, however, are not the only type of periodic patterns encountered in semiarid areas: gaps, labyrinths, and spots are other typical symmetries observed under varying climate or geomorphologic conditions (e.g., White 1970, Leprun 1999). To explain these isotropic patterns, inter-patch runoff transfer mechanisms would require particular topographic setups, such as the regular humps hypothesized by Klausmeier (1999). Evidence supporting this hypothesis is lacking, and we could even show, for the study site considered here, that there was no clear relationship between the vegetation pattern and micro-elevation (Barbier et al. 2006). Besides topography, differential infiltration (due to a better soil structure under vegetated patches) and underground moisture gradients have been proposed as potential drivers of subsoil water redistribution on flat terrain (HilleRisLambers et al. 2001, von Hardenberg et al. 2001). An alternative mechanistic explanation to runoff/diffusion transfers is provided by the Lejeune and Lefever model (Lefever and Lejeune 1997, Lefever et al. 2000, Lejeune et al. 2004). In this model (see the *Methods* section), the fundamental unit is not the vegetation patch, but the individual plant, which interacts with other plants through both its above- and belowground organs. Large scale patterns emerge when competition by the root systems has a longer spatial range than facilitation by the aboveground parts.

To investigate the relevance of the self-organization hypothesis in determining periodic patterning in vegetation and decide between possible mechanisms, we undertook a multi-proxy approach within a gapped periodic pattern in southwest Niger (see pictures of the site in Barbier et al. [2006]). We focused both on plant allometric proportions and on the spatial and temporal dynamics of soil water resources within the root zone in order to address the following questions: (1) Are soil water dynamics in the root zone compatible with the hypothesis of either belowground or aboveground water transfers from bare to vegetated patches? (2) Is root distribution/architecture compatible with a long range competition? (3) Can we evidence a mechanism of short range facilitation through the monitoring of soil water dynamics? (4) Can we determine the spatial distribution of these facilitative and competitive effects to parameterize Lejeune and Lefever's model?

METHODS

Modeling background

In most published self-organization models, plants influence the water budget locally, and this effect is further propagated through water movement due to hydraulic gradients between densely and sparsely

vegetated areas. Surface water is either assumed to run off from bare patches to thickets as a result of increased infiltration under vegetation, even in the absence of a ground slope (HilleRisLambers et al. 2001, Gilad et al. 2004) or to diffuse below ground from bare to vegetated patches as a result of increased uptake by vegetation (von Hardenberg et al. 2001). All the models of this class are based on equations of the reaction–diffusion type exhibiting a modulation instability which spontaneously onsets a self-organizing process of pattern formation.

There is nevertheless a second class of models (Lefever and Lejeune 1997, Lefever et al. 2000, D'Odorico et al. 2006), which implicitly assumes that the dynamics of the water resource in the shallow root zone is directly determined by the cumulative, opposite effects of individual plants. Facilitative effects on neighbors are exerted by the aerial part of the plants, which are known to improve the water budget in the soil (e.g., Callaway 1995), whereas competitive effects result from lateral resource uptake by the root systems. Patterns appear when competition is exerted at a longer range than facilitation. The fundamental mechanism is therefore that, as a response to increased aridity, plants tend to grow large, superficial root systems with respect to canopy size to extract enough water from the topsoil (a general trend confirmed by Schenk and Jackson [2002]). The resulting facilitation-to-competition range ratio thus decreases as a function of water scarcity, and beyond a given aridity threshold, this ratio becomes small enough to allow self-organized patterning to occur.

In this class of models, equations are integro-differential and integrals account for the cumulative effect of the biomass of neighboring vegetation on a given plant (resources are not modeled explicitly) located at a focal space point \mathbf{r} . Let $b(\mathbf{r} + \mathbf{r}')$ be the biomass at a location $\mathbf{r} + \mathbf{r}'$ relative to the focal point. One can define the mean field potential, M_i , which is the integration over space of individual plant influences exerted at \mathbf{r} as

$$M_i = \int \Phi_i(|\mathbf{r}'|)b(\mathbf{r} + \mathbf{r}')d\mathbf{r}' \quad (1)$$

with $i = f$ for the potential expressing facilitative influences or $i = c$ (competition potential). Space and biomass units are normalized by the crown radius (L_a) and the biomass of an average, fully grown individual (b_a), respectively. The integrals are based on kernel functions, Φ_i , which aim at expressing how the influence of biomass on its neighbors decreases with distance. Different kernels have to be used to model either the facilitative influence, Φ_f , induced by the aerial structures of the plants or the competitive action, Φ_c , exerted by the root systems. The kernels are positive, definite, monotonic, decreasing functions, g , of the distance $|\mathbf{r}'|$, namely,

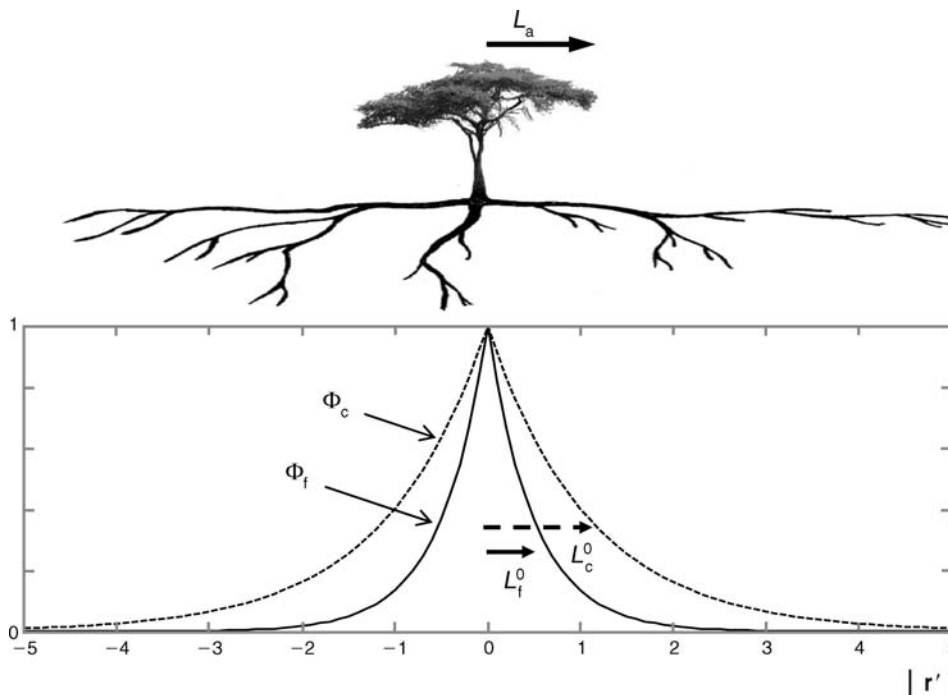


FIG. 1. Schematic one-dimensional representation of the aboveground, $\Phi_i(|r'|)$, and belowground, $\Phi_c(|r'|)$, kernel functions with their respective range parameters L_i^0 and L_c^0 . An exponential function is assumed for both kernels. L_a represents the unit distance (scaling parameter) corresponding to the canopy radius of a fully grown-up individual.

$$\Phi_i = g \left[\frac{|r'|}{L_i^0 b(\mathbf{r} + \mathbf{r}')^p} \right] \quad (2)$$

with $i = c, f$.

The spatial modeling of facilitation or competition effects (Fig. 1) is therefore determined by the choice of function g (e.g., Gaussian, exponential ...) and by a range parameter specific to each type of interaction, i.e., L_i^0 for facilitation and L_c^0 for competition. Following Gilad et al. (2004), the range of the interactions is modulated by the biomass. This modulation is assumed to follow an allometric rule to be fitted to local conditions via the exponent p . It is important to note that the range parameter does not correspond to the total extent of the kernel, but rather to its “standard deviation.” As mentioned before, a necessary condition for large scale patterns (wavelength $\gg L_i^0$) to emerge is to have $L_i^0/L_c^0 < 1$.

We hereafter assume isotropic kernels, which means neglecting, for instance, anisotropic root plasticity in competition as well as the effect of dusk and dawn sun inclinations in shading effects, as in other studies (Wu et al. 1985, Walker et al. 1989).

Testing modeling assumptions

The mechanistic hypotheses defining the classes of models reviewed here can be tested in the field, as each of them assume very specific features in either soil water spatiotemporal dynamics or in plant architectures. If differential infiltration is the key process, stock recharge

at rooting depth should be much smaller under bare soil. Underground diffusive transfers, on the other hand, necessitate a significant recharge in bare areas, and at least temporarily (after a rain shower) a lower stock under vegetation due to greater transpiration. Finally, for the model based on morphological plasticity to be substantiated, both plant architecture and soil water dynamics should match the hypothesis of a short-range facilitation mediated by canopies and a long range competition mediated by roots.

Study site

The study site has already been described in previous accounts (Barbier et al. 2006). It was located within a Biosphere Reserve (Parc W), in southwest Niger (12°22'43" N, 2°24'12" E). Its vegetation presented a characteristic spatially periodic gapped pattern (see Plate 1a) and was dominated by *Combretum micranthum* G. Don. This species accounted for 44% of the total count of the 3000 inventoried individuals and 65% of the biovolume of the aerial parts, as assessed by the product of crown area and total height (ellipsoidal approximation). This 2–3 m tall deciduous shrub species is usually abundant in west African periodic patterns (Seghieri and Galle 1999, Couteron et al. 2000, Couteron 2001) and features a multi-stemmed morphology with a general hemispherical aspect. The very heterogeneous (patchy) grass and herb layer was composed of shallow-rooted annuals. The only patches presenting a significant

TABLE 1. General soil properties for the study site.

Property	N	Mean	CV
Clay (%)	48	24.03	0.30
Fine silt (%)	48	8.30	0.17
Coarse silt (%)	48	10.16	0.22
Fine sand (%)	48	27.73	0.15
Coarse sand (%)	48	29.78	0.26
Gravel (>2 mm; %)	31	24.57	0.63
pH water	48	4.90	0.04
pH KCl	48	3.87	0.04
Organic matter (calimetry; %)	48	1.53	0.40
Organic C (%)	48	0.89	0.40
Total N (‰)	48	0.69	0.36
C/N	48	12.57	0.08
Available P (Olsen; mg/kg)	48	6.10	0.26
Iron-pan depth (cm)	31	37	0.28
Bulk density (g/cm ³)	31	1.33	0.10

Notes: Volumetric samples were taken using a 250-cm³ cylinder. All proportions, except gravel content and bulk density, concern the 2-mm sieved soil samples. Soil analyses were performed by the CIRAD, Montpellier, France (US Analyses des eaux, sols et végétaux, ISO 9001). N, number of samples; CV, coefficient of variation.

biomass at the end of the rainy season were dominated by *Pennisetum pedicellatum* Trin., a 1 m tall Poaceae, and located where shrub cover exceeded 60%. The substratum was typical of the iron-capped plateaus on which periodic vegetation is observed in southwestern Niger (White 1970, Tongway et al. 2001; see Plate 1b). Those plateaus are overtopped by shallow sandy-clayey soils (Table 1). Soil pits revealed that the moderately hardened iron pan clearly prevented the *Combretum*'s root system to penetrate below a mean depth of 37 cm. Both average clay fraction and gravel content presented a two-fold increase at a 25 cm depth (data not shown) as compared to the top 5 cm values presented in Table 1, showing a probable illuviation process. Other soil parameters indicated a poor, compact, and acid soil, but some of these parameters, such as organic matter content, showed a substantial spatial variation linked to the presence of vegetation. Such feedbacks of vegetation on soil properties have been described in most semiarid and arid areas (Callaway 1995, Tongway et al. 2001).

The rainy season in southwest Niger is between June and September, with a mean annual rainfall of 705 mm (La Tapoa, Niger; 1981–2002), subject to an important interannual variation (coefficient of variation up to 30%). Annual mean potential evapotranspiration is very high (2700 mm, La Tapoa, Niger; 1981–2002).

Root systems characterization

The root systems of five individuals of *Combretum micranthum* G. Don, of various sizes and locations within the periodic pattern, were excavated (see Plate 1c). Soil porous materials were cautiously removed using pulsed air at supersonic speed (Soil Pick; MBW, Slinger, Wisconsin, USA), a very efficient methodology to observe roots of >1 mm in diameter (Nadezhkina and Cermak 2003).

The shallowness of the root zone justified a two-dimensional description of the root systems in the plane of the soil surface, i.e., without accounting for depth. For each individual, root diameters were thus measured within 30° angular sectors and at increasing lateral distances from each stem clump. Estimation of the root density, d , was obtained by dividing the sum of root diameters for a given sector and distance by the circle arc length at that distance. The description by angular sectors allowed accounting for the observed plasticity of the root system when its extension was limited or deviated in sectors containing stem clumps of other individuals. Root density data were used as a proxy to estimate the competition kernel, $\Phi_c(|\mathbf{r}'|)$ (Fig. 1). However, as fine roots are the only ones effectively involved in water and nutrient uptake (Smit 2000), we only considered roots having diameters ≤ 5 mm. Results were not sensitive to small variations in this threshold value.

We estimated the parameters L_c^0 and p along with the form of the function, g , of Eq. 1 using least squares fittings of root density data variation in function of the distance to the clump. Measures from all angular sectors around all studied shrubs were considered as individual observations. After a first outlook at the data, it appeared that the choice for the kernel function, g , could be restrained to the family of decreasing exponentials of “order q ,” that is,

$$d(|\mathbf{r}'|) \propto \exp\left\{-\left[\frac{|\mathbf{r}'|}{L_c^0 b(\mathbf{r} + \mathbf{r}')^p}\right]^q\right\}. \quad (3)$$

The parameter q allows the choosing of the shape of the kernel function according to the fit with field data (e.g., $q = 2$ gives a Gaussian function, while $q = 1$ gives a simple exponential). Parameter estimation was performed using the ln-transform of equation 3, so as to obtain $\gamma = (1/L_c^0)^q$ directly as the slope of the linear fit

$$\ln d = -\gamma \left[\frac{|\mathbf{r}'|}{b(\mathbf{r} + \mathbf{r}')^p}\right]^q + \text{constant}. \quad (4)$$

The normalized biomass, $b(\mathbf{r} + \mathbf{r}')$, was estimated as the ratio of the biovolume (i.e., the ellipsoidal approximation of the crown using its two diameters times the total height) to that of the largest excavated individual. Values obtained for b for the five excavated individuals varied in the range 0.1–1.

Soil water monitoring

We measured soil moisture variation in the root zone, in both space and time, just after the onset of the rainy season (21 June to 24 July 2004). At this time of the year, all shrubs had leaf foliage, while the annual grass layer was only starting to develop. It was therefore the most favorable moment to observe feedback of shrubs on soil water. During the studied period, the on-site rain gauge indicated six rain episodes each yielding >10 mm of rain, among which five were ~ 40 mm. Ninety-eight gypsum conductivity sensors (Eijkelkamp soil moisture

blocks; Giesbeek, The Netherlands) were buried at a 20-cm depth at 5-m intervals on two 30×30 m grids, one centered on a thicket area, the other one surrounding a bare area. All sensors were calibrated at complete water saturation. Gypsum block readings are linearly dependant on soil water potential between wilting point and field capacity (Stenitzer 1993, Hillel 1998, Johnston 2000). Ten sensors were damaged by termites, and their readings were excluded from subsequent analyses, leaving 43 and 45 sensors for each of the two sites, respectively.

Field survey of vegetation and micro-elevation

To investigate the effect of plant aerial parts and topography on soil moisture dynamics, a survey was conducted within two 50-m side quadrats, centered around the lattices of buried conductivity sensors. All shrubs above 1.5 m were mapped in x, y coordinates and measured (height and two perpendicular diameters of the crown), and soil surface elevation was surveyed every five meters. Mapping was performed using a tacheometer consisting of an optical theodolite (Metland MTXO; Ecuelles, France) to which a laser telemeter was adapted (Leica Disto; Heerbrugg, Switzerland).

Influence of facilitation on soil water dynamics

Knowing the position of both shrubs and sensors, it was possible to model the cumulative effect (mean field potential; Eq. 1), M_f , of individual shrubs' facilitative kernels, Φ_{fj} , above each sensor. To ease the comparison between above- and belowground ranges of shrub influence, Φ_f was given the same form as the one obtained for the competitive kernel, Φ_c (Eq. 2, same p and q values, see *Results*). In fact, preliminary attempts at fitting with distinct kernel functions for Φ_f and Φ_c did not give better results. To account for saturation effects in shading, the mean field potential was computed as a product of facilitation kernels: $M_f = 1 - \prod_j [1 - \Phi_{fj}(|r'|)]$, with $0 \leq \Phi_{fj} \leq 1$, rather than by a direct sum. The optimal value of L_f^0 was estimated through least-square linear fits between M_f and soil water half-life during the seven dry days following a 37.5 mm rainfall event that occurred on 30 June. In theory, it should be possible to explore the effect on soil water dynamics of the modeled competitive potential (root systems) and estimate the parameters of Φ_c using a similar approach. But the attempts we made only gave poor fits, possibly due to the small number of sensors, to the important effect of root plasticity and also to the very strong impact of the facilitative processes on soil water dynamics.

Influence of soil properties and topography on soil water dynamics

Volumetric (250 cm^3) soil samples were taken at the soil surface above each humidity sensor for the site surrounding a bare area ($N=43$ sensors). Granulometric fractions (densimetry) and organic matter content (calimetry) were measured by the CIRAD, Montpellier,

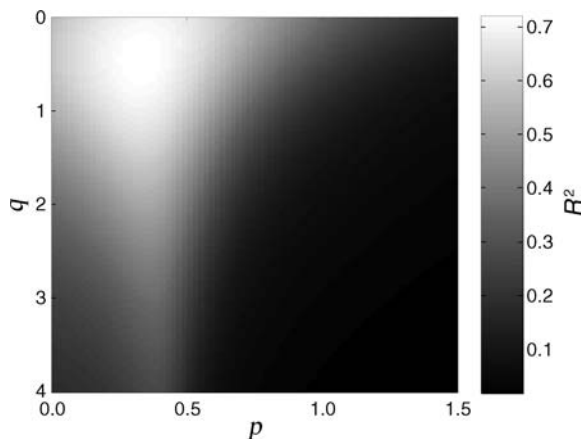


FIG. 2. Assessment of shape and range of the competitive kernel function (Φ_c). The gray-scale (R^2 value) measures the influence of parameters p (allometric exponent) and q (choice of the function shape) on the linear fit between root density (left-hand term of Eq. 4) and relative distance to clump center (right-hand term of Eq. 4).

France (service unit [US] Analyses des eaux, sols, et végétaux, ISO 9001).

The influence of topography was assessed both directly via relative elevation and using a topography-derived hydrological index, the topographic moisture index (TMI). This index is a good approximation of the propensity of a location to receive and capture run on, considering solely local and global topography (Beven and Kirkby 1979). The TMI was computed on the basis of a 1-m resolution digital elevation model interpolated over the 50-m side-surveyed area. It is given, in each cell, by $TMI = \ln(\alpha/\tan[\beta])$, where β is the local slope and α is the upslope contributing area computed following the multiple direction flow algorithm of Quinn et al. (1995).

On the basis of these data, we investigated effects of plants vs. abiotic factors on soil water content. The independent explanatory power of the facilitation mean field potential, M_f , on soil water dynamics was compared to the independent effects of soil parameters and topography, through the method of hierarchical partitioning (HP; Chevan and Sutherland 1991, Mac Nally 2000). For each predictor variable, the method computes multiple regression models in combination with an increasing number of the other variables (hierarchies). The increases in the values of the coefficient of determination (R^2) brought by that variable are then averaged, allowing assessment of its “independent” (vs. “joint”) explanatory power (sensu Chevan and Sutherland 1991). This approach is especially useful in the presence of substantial colinearity between explanatory variables.

RESULTS

Least squares estimation of the parameters of the competitive kernel (Φ_c ; see Eqs. 2 and 4) gave optimal values for $q = 1/2$ and $p = 1/3$ (Fig. 2). The best fits

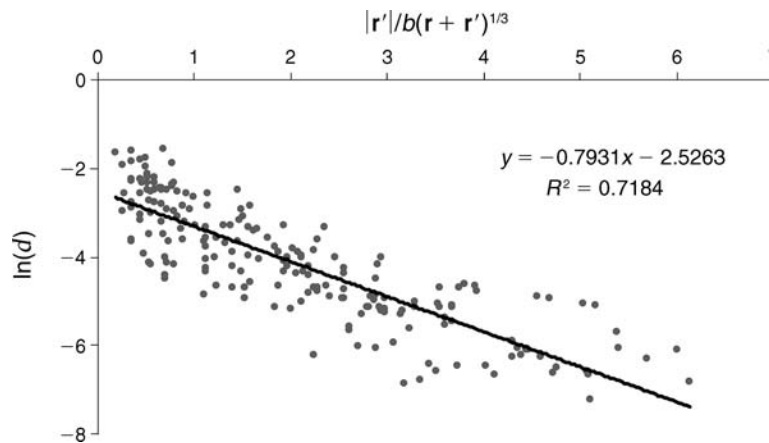


FIG. 3. Estimation of the competitive range (L_c^0). Linear fit between root density, d (left-hand term of Eq. 4), and “relative distance” (right-hand term of Eq. 4, in abscissa), with parameter values of $q = 1$ and $p = 1/3$. The slope of the linear regression directly gives $-1/L_c^0$.

between the \ln -transformed root density and the weighted distance, $|r'|/[b(r+r')^p]$, presented R^2 values >0.72 . There was only a slight decrease of R^2 (i.e., R^2 still >0.7) by setting $q = 1$, i.e., using a simple exponential form of the kernel. This value will therefore be used in what follows, as it is mathematically more convenient for future modeling efforts. Varying p values, on the contrary, had important consequences as points belonging to individuals of different sizes tended to align along different slopes. Even slight departures from this optimum produced significant differences between individual slopes, as assessed via a test of the homogeneity of the slopes in a general linear model (GLM). The slope (i.e., $-1/L_c^0$) obtained with $p = 1/3$ and $q = 1$ indicated the value of the competitive kernel range, i.e., $L_c^0 = 1.27$ (Fig. 3).

Soil water recharge ~ 12 hours after a 37.5-mm rainfall event was spatially homogeneous, with limited influence of the vegetation cover (Fig. 4), at least at a 20 cm depth, i.e., at medium depth of the shrubs root systems. In fact, after each of the six main rain events that occurred during the study period, the mean water stock increase was never lower in bare areas compared to vegetated areas, as shown by an ANOVA test ($P < 0.001$). The main difference rather occurred during the dry days following each of the rain events. Indeed, the soil water stock decreased in bare areas at a much faster rate than under cover (see after 1.5 and 3 days in Fig. 4). Subsequently, variations of these decay rates could also be observed between different places within the thickets.

To ease comparison between the decay curves, we derived the half-life time of the water stock, i.e., the time needed to reach half of the initial, after-rain stock value. Linear regressions between the facilitation mean field potential, M_f , computed for each sensor location and soil water half-life gave an optimal R^2 value of 0.47 (peak in Fig. 5a) for a facilitation range of $L_f^0 = 0.81$. However, the relationship was obviously nonlinear (Fig.

5b), and fitting a sigmoid function allowed us to better account for the threshold effect observed at M_f values of ~ 0.6 ($R^2 = \sim 0.5$), for which the mean half-life time jumped from about 3 days to 6 days. In any case, half-life of soil water stock within the root zone under cover was clearly twice that of bare areas. Since the maximum moisture values observed for all sensors were identical, this difference was only due to discrepancies in decay rates and not to changes in the field capacity, as was observed by Joffre and Rambal (1988, 1993) in a different context.

Some insight into causal relationships behind the observed soil water dynamics could be obtained by looking at the variance hierarchical partitioning of either the soil moisture increase (recharge) or the half-life time (discharge) after the 37.5-mm rainfall. To limit the number of soil sample analyses, only one of the study plots, the one surrounding a bare area ($N = 43$ sensors), was considered here. Predictors (explanatory variables) likely to influence soil water budget, such as soil textural and structural parameters and relative elevation. The approach by hierarchical partitioning allows assessing which part of the variance explained by a predictor in a first order model (i.e., a simple regression) is shared (J) or not (I) with other variables in higher order models (i.e., multiple regressions). In the case of the stock recharge (Fig. 6a), all predictors presented a small total ($I + J$) explanatory power. The highest total and independent effects were detained by relative elevation, and were lower than 0.15, meaning that only 15% of the variability in recharge was correlated to elevation. In the case of discharge (Fig. 6b), on the other hand, M_f explained the most important share of half-life time variability ($I + J = 0.55$ and $I = 0.27$), well above the variability explained by any soil or topography variables. Important joint effects (J) were observed, as can be expected in light of the well-known feedbacks exerted

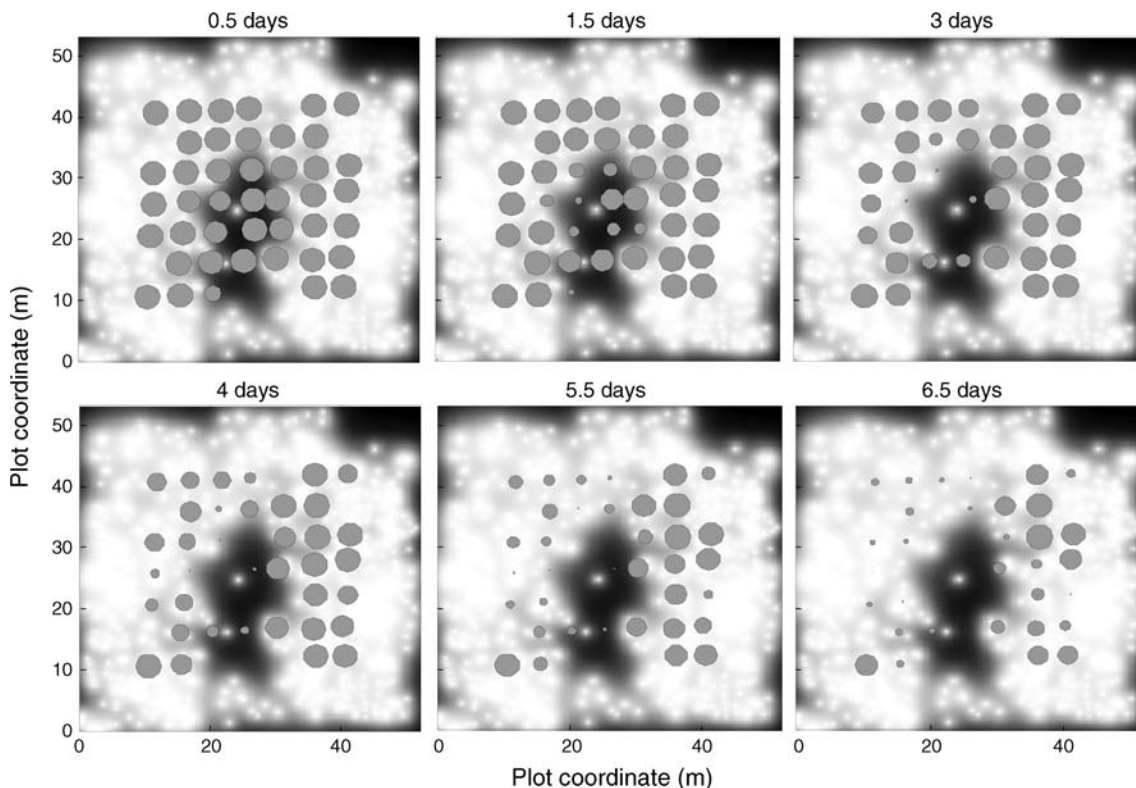


FIG. 4. Spatiotemporal dynamics of the soil water moisture at a 20-cm depth in the plot surrounding a bare area (gap) after a 37.5-mm rain event. Gray circle diameters are proportional to soil wetness between wilting point and field capacity. All sensors represented by a circle at day 0.5 (upper left panel) were monitored during subsequent days. The background gray level map indicates values taken by the facilitative mean field (black, $M_f = 0$; white, $M_f = 1$).

by plants on soil properties in semiarid areas. The second most important explanatory variable, organic matter ($I + J = 0.39$, $I = 0.15$), is indeed correlated to variations in the cover, as indicated by its large joint effect ($J > I$). It is also worth noting that information derived from soil micro-topography, and especially the topographic moisture index (TMI), did not allow explaining any substantial amount of the variability of soil water dynamics, not even for recharge.

DISCUSSION

The results presented here show that distinct mechanisms of facilitation and competition coexist in the periodic system under study and can be evidenced and quantified as consequences of the dual role of below- and aboveground parts of the plants. The observed facilitation-to-competition range ratio, which reflects the morphological ratio of the plants, is smaller than 1 ($L_f^0/L_c^0 = 0.64$). Such a fundamental result agrees with the theory explaining landscape-scale periodic vegetation patterning as the outcome of plants' morphological adaptation to aridity via laterally extended root systems (Lefever and Lejeune 1997, Lejeune and Tlidi 1999, Lejeune et al. 1999, 2004, Lefever et al. 2000). Our field results show that this theory is able to provide a complete explanation for periodic pattern formation.

This also means that more attention should be paid to root systems characteristics in periodic vegetation systems.

Unfortunately, previous field descriptions (e.g., Tongway et al. 2001) rarely mention rooting architecture, making it still difficult to generalize the results obtained in this study to all semiarid and arid periodic vegetation patterns. However, shrubs having superficial roots extending far away from the limits of the canopy have been reported in periodic vegetations dominated by other shrub species in Somalia (Gillett 1941, Glover 1951). More generally, large and superficial root systems are a common strategy in semiarid and arid areas (Walter 1963, Schenk and Jackson 2002, Esler et al. 2003). References to shallow soils, though not systematic, are not rare in field descriptions of periodic systems (Boaler and Hodge 1964, Wickens and Collier 1971, Mabbutt and Fanning 1987, Tongway and Ludwig 1990). In west Africa, and more particularly in Niger, periodic vegetation patterns have always been reported on iron-capped plateaus with shallow soils (White 1970, Leprun 1999, Tongway et al. 2001), which determine superficial rooting.

On the other hand, assumptions on resource redistribution by aboveground runoff and belowground diffusion (HilleRisLambers et al. 2001, von Hardenberg et al.

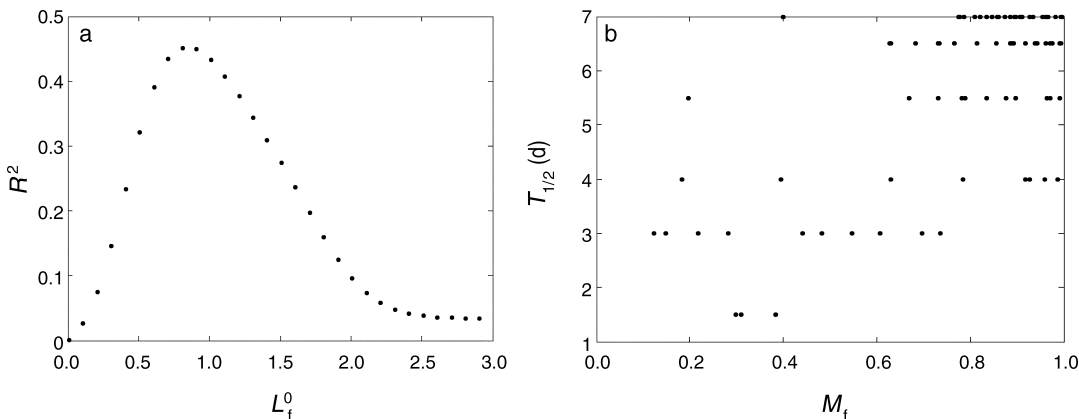


FIG. 5. Estimation of the facilitative range (L_f^0). (a) Coefficient of determination for linear regressions between soil water half-life (response) and M_f as a function of the unknown parameter, L_f^0 . (b) Observed relationship between soil water half-life ($T_{1/2}$) and facilitation mean field computed with the optimal value found, i.e., $L_f^0 = 0.81$. $N = 88$ sensors.

2001) were not verified at our study site (which is representative—in terms of constitutive species, substratum conditions, pattern characteristics, and climate—of the periodic gapped vegetation of southwest Niger). Stock recharge in the shallow root zone, monitored during a whole month of rainy season, has been observed to be homogeneous, irrespective of the vegetation cover, topography, and soil heterogeneities. In fact, the shallow rooting zone can even be completely saturated after modal rainfall events, even in bare areas (Fig. 4). Infiltrometry measurements were made (results not presented), and as can be expected, a higher infiltration was generally observed under cover due to a better soil structure. However, both texture and structure are taken into account in our analysis (for instance, see Fig. 6), and the results clearly show that these variables—and therefore infiltration rate—do not make any significant difference in the budget of the shallow root zone. In presence of a substantial and consistent ground slope, with associated contour-oriented vegetation bands (tiger bush), other studies showed that water recharge was higher under the thickets than in bare areas due to runoff collection (Bromley et al. 1997, Galle et al. 1999, 2001), although these studies rarely mention rooting depth. It is however clear that the redistribution of water runoff from bare to vegetated areas cannot have the same importance for the more isotropic vegetation gaps, labyrinths, or spots, as these vegetation types occur extensively in areas without major slope variation (e.g., White 1970) or other favorable topographic setup (Barbier et al. 2006). The notion of a subsurface diffusive flow toward vegetated areas (von Hardenberg et al. 2001) can also be discarded for our field site, as the differential evaporation determines a spatial gradient of soil humectation in which thickets are at the wetter end. Hence these theories seem to lack completeness in light of the gapped periodic patterns which are extensively found in tropical west Africa.

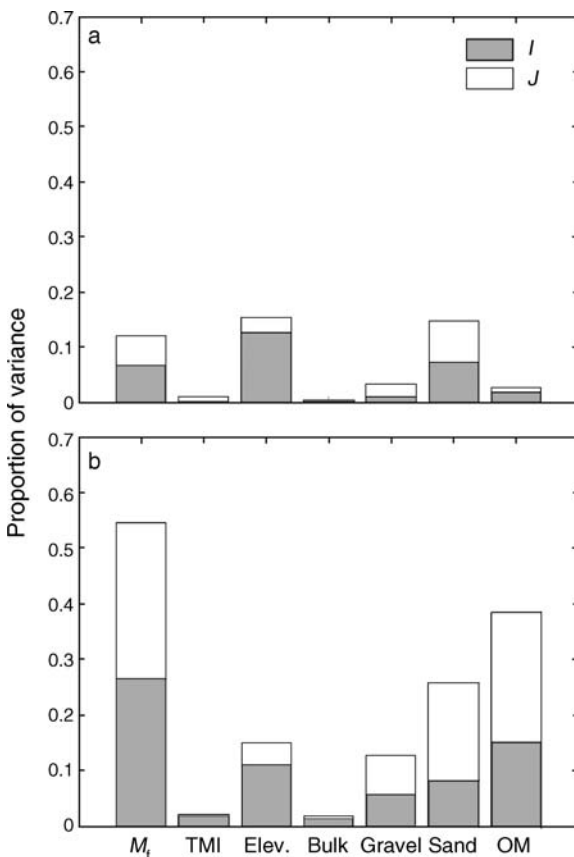


FIG. 6. Hierarchical partitioning of the coefficients of determination (R^2) found in multiple linear regression models explaining (a) soil recharge and (b) soil water half-life after a 37.5-mm rainfall event on the site surrounding a bare area. $N = 43$ sensors. Predictors are: M_f , facilitation mean field potential (computed for $L_f^0 = 0.81$, ensuring the best R^2); TMI, topographic moisture index; Elev., relative elevation; Bulk, bulk density; OM, organic matter content. For further specifications and units, see Table 1. Gray bars show independent effect (I); white bars show joint effect (J); $I + J = R^2$ of the first order model (simple linear regression).

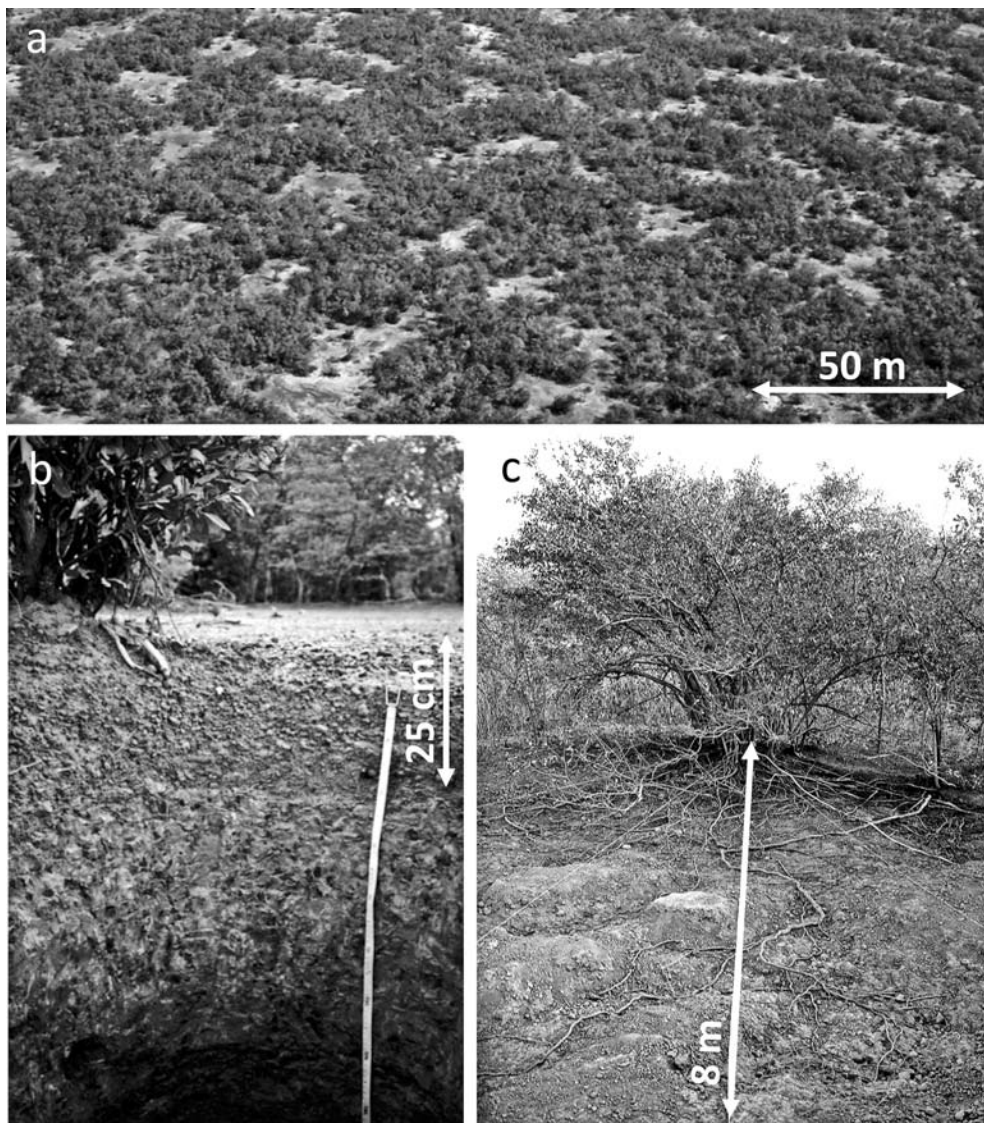


PLATE 1. (a) Oblique aerial view of the study site. (b) Soil profile showing the shallow root zone and the iron pan below 25 cm. (c) Excavated root system of a *Combretum micranthum* G. Don. Photo credits: N. Barbier.

The facilitation mechanism appears to be the consequence of a reduction of soil evaporation mediated by the aerial parts of shrubs. The facilitative potential (M_f) we used to model such influences indeed displayed a substantially higher independent explanatory effect on observed decay rates of the water stock than other relevant soil variables (e.g., texture or organic matter content). This is consistent with what Tuzet et al. (1997) call the “shade” and “wake” effects induced by shrub’s crowns. Shrubs are indeed known to constitute important radiative and convective shields, that significantly decrease soil evaporation rate in their shade zone (Slatyer 1961, Wallace and Holwill 1997, Breshears et al. 1998, Pugnaire et al. 2004, Wayne and Van Auken 2004). As soil evaporation is often a large component of the total evapotranspiration in arid environments

(Dugas et al. 1996, Tuzet et al. 1997, Kurc and Small 2004), shading effects can have a measurable positive influence on the undergrowth, and in particular on the grass layer and the shrub’s own recruitment (Tiedemann and Klemmedson 1977, Hastwell and Facelli 2003). Such positive feedback is known to be very strong in resource-limited environments, where competition for resources can effectively be balanced, and sometimes obliterated by the local improvement of resources availability induced by plants (Holmgren et al. 1997, Pugnaire and Luque 2001, Callaway et al. 2002, Maestre et al. 2003). The results presented in this paper confirm the pervasiveness of plant–plant facilitative interactions in resource-starved ecosystems. This is all the more true that, when estimating the facilitation potential, we did not measure the complete positive impact of shrub

shading on soil water conservation but rather the balance between shading and water uptake by plants. Transpiration by vegetation is indeed likely to be stronger in the thickets, due to a higher shrub root density. But, on the other hand, water uptake by the sciaphilous annual grass *Pennisetum pedicellatum* was not taken into account by our measures made during the first part of the rainy season, when grass biomass was low. At the end of the rains, transpiration by grasses may diminish the facilitative effect at least in the first 10 centimeters of the profile.

Although the importance of facilitation in plant communities is increasingly recognized in the literature (Callaway 1995, Bruno et al. 2003), the awareness that plant interactions, of different natures or even of opposite effects, could actually have distinct spatial distributions and ranges is only slowly developing. Yet the concepts of single-ring influence circles (Zinke 1962, Boettcher and Kalisz 1990), phytogenic (Uranov 1965, Yastrebov 1996), or ecological fields (Wu et al. 1985, Walker et al. 1989) are important conceptual steps in that direction. Self-organization of semiarid vegetation demonstrates that space does matter to understand the dynamic outcome of the interplay between opposite plant influences.

ACKNOWLEDGMENTS

We are most grateful to European project ECOPAS, park Regional W for technical, scientific and financial support during field missions, as well as to the Department of Biology, UAMN, Niger, for fruitful collaboration. We also thank Paolo D'Odorico and one anonymous referee for very constructive comments.

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