



On soil moisture–vegetation feedbacks and their possible effects on the dynamics of dryland ecosystems

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[1] Soil moisture is the environmental variable synthesizing the effect of climate, soil, and vegetation on the dynamics of water-limited ecosystems. Unlike abiotic factors (e.g., soil texture and rainfall regime), the control exerted by vegetation composition and structure on soil moisture variability remains poorly understood. A number of field studies in dryland landscapes have found higher soil water contents in vegetated soil patches than in adjacent bare soil, providing a convincing explanation for the observed preferential establishment of grasses and seedlings beneath tree canopies. Thus, because water is the limiting factor for vegetation in arid and semiarid ecosystems, a positive feedback could exist between soil moisture and woody vegetation dynamics. It is still unclear how the strength of such a feedback would change under different long-term rainfall regimes. To this end, we report some field observations from savanna ecosystems located along the south-north rainfall gradient in the Kalahari, where the presence of relatively uniform sandy soils limits the effects of covarying factors. The data available from our field study suggest that the contrast between the soil moisture in the canopy and intercanopy space increases (with wetter soils under the canopy) with increasing levels of aridity. We hypothesize that this contrast may lead to a positive feedback and explore the implications of such a feedback in a minimalistic model. We found that when the feedback is relatively strong, the system may exhibit two stable states corresponding to conditions with and without tree canopy cover. In this case, even small changes in environmental variables may lead to rapid and largely irreversible shifts to a state with no tree canopy cover. Our data suggest that the tendency of the system to exhibit two (alternative) stable states becomes stronger in the more arid regions. Thus, at the desert margins, vegetation is more likely to be prone to discontinuous and abrupt state changes.

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1. Introduction

[2] The interaction between vegetation and soil moisture dynamics contributes to structure and function in arid and semiarid ecosystems [e.g., *Noy-Meir*, 1973; *Walker et al.*, 1981; *Scholes and Archer*, 1997; *Rietkerk and van de Koppel*, 1997]. The establishment and growth of dryland vegetation depends on the availability of soil water resources [e.g., *D’Odorico and Porporato*, 2006], which, in turn, result from plant interactions with the soil water balance [e.g., *Greene*, 1992; *Greene et al.*, 1994; *Breman and Kessler*, 1995; *Bhark and Small*, 2003]. Patchy distributions of vegetation are a recurrent feature of dryland landscapes [e.g., *Greig-Smith*, 1979; *Schlesinger et al.*, 1990; *Belsky*,

1994], where a mosaic of vegetated and bare soil areas is usually associated with heterogeneous patterns of root zone soil moisture. Subcanopy soils are frequently found to be moister than intercanopy patches [*Walker et al.*, 1981; *Greene*, 1992; *Greene et al.*, 1994, 2001; *Breman and Kessler*, 1995; *Scholes and Archer*, 1997, *Bhark and Small*, 2003; *Zeng and Zeng*, 1996; *Zeng et al.*, 2004], suggesting the possible existence of a positive feedback between vegetation and soil water content.

[3] Vegetation–soil moisture feedback has important implications for dryland ecosystems in that it may lead to pattern formation [*Lefever and Lejeune*, 1997; *von Hardenberg et al.*, 2001; *Hillerislambers et al.*, 2001]. Recent theories [e.g., *Lejeune et al.*, 2002] recognize that the moister subcanopy environment facilitates seedling establishment beneath the canopy of existing plants [e.g., *Scholes and Archer*, 1997; *Caylor et al.*, 2003], while the exploitation of soil water resources by competing lateral root systems makes intercanopy patches unsuitable for vegetation establishment and growth [*Casper et al.*, 2003]. These facilitation-competition processes can explain the composition and structure of vegetation in water-limited ecosystems [e.g.,

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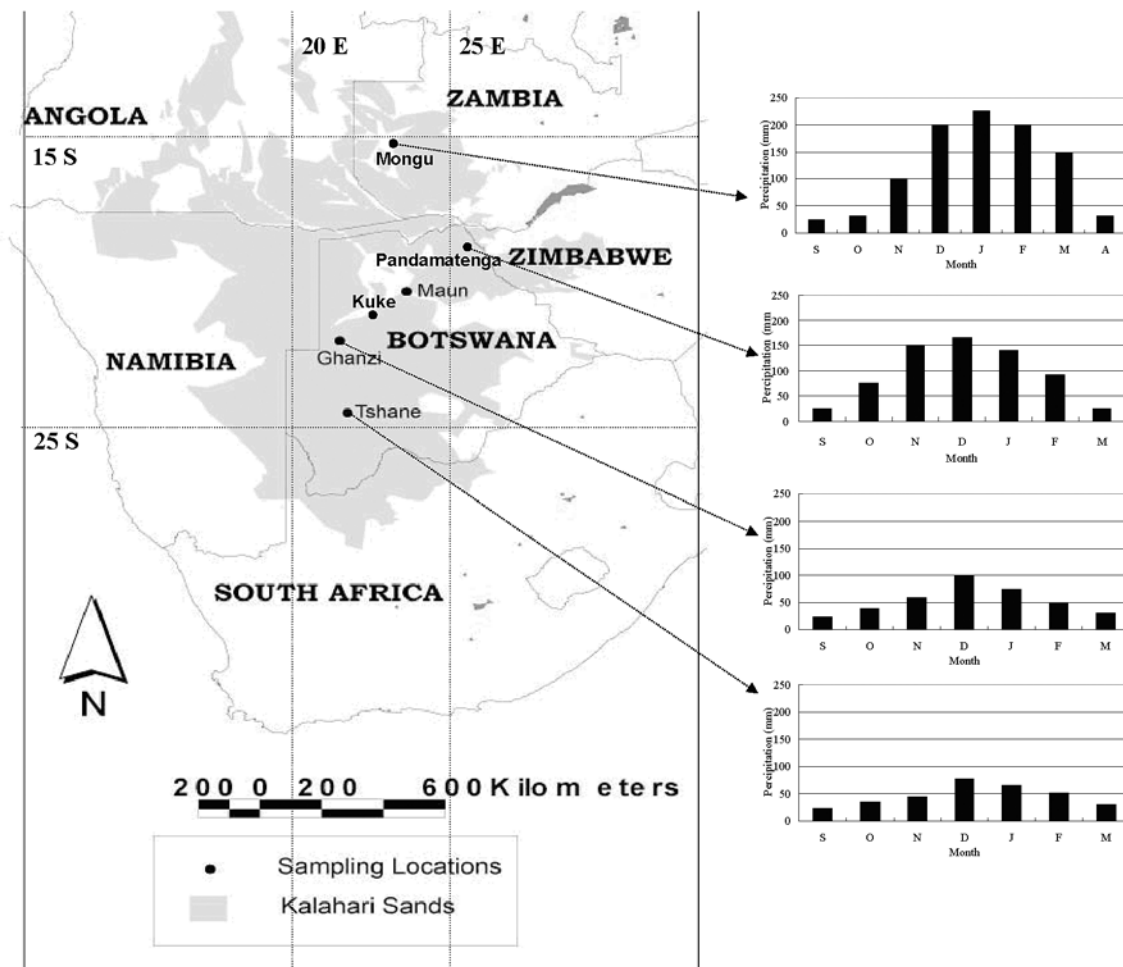


Figure 1. Spatial extent of the Kalahari sands and sites selected for this study. Insets show mean annual distribution of precipitation [Scholes *et al.*, 2002].

Coueron and Lejeune, 2001; Lejeune *et al.*, 2002; Caylor *et al.*, 2006].

[4] Spatial patterns characterized by intercanopy soils that are too dry for woody vegetation growth and survival, contrasting with moister subcanopy soils that are capable of sustaining seedling establishment and growth, are indicative of vegetation–soil moisture feedbacks and suggest the presence of two stable states [e.g., Walker *et al.*, 1981; Wilson and Agnew, 1992; Rietkerk and van de Koppel, 1997; Scheffer *et al.*, 2001; Zeng *et al.*, 2004]. For example, once the existing vegetation is removed, the system remains locked in a (stable) dry, bare soil state from which the

system recovers only in the unlikely event that other factors (e.g., climate drivers or disturbances) destabilize the desert (i.e., bare soil) state. Because of the nonlinearities introduced in these dynamics by vegetation–soil moisture feedbacks, changes in climate forcing and disturbance regime may lead to rapid shifts from (sparsely) vegetated to bare soil conditions. The abrupt character of these shifts has been often related to the rapid pace of desertification occurring in a number of regions around the world [Zeng and Zeng, 1996; Rietkerk and van de Koppel, 1997; Nicholson, 2000]. Thus stronger positive feedbacks favor the emergence of bistable dynamics (i.e., with vegetated and bare soil con-

Table 1a. Site Characteristics^a

Site	Location Latitude, Longitude	Rainfall, mm/a	Dominant Tree Species	Percent Tree Cover	Dominant Grass Species
Tshane	24.17°S, 21.89°E	365	Open Acacia savanna	14%	<i>Schmidtia pappophoroides</i> , <i>Eragrostis lehmanniana</i>
Ghanzi	21.78°S, 21.57°E	400	Acacia-Terminalia savanna	20%	<i>Eragrostis lehmanniana</i> , <i>Stipagrostis suniolumis</i>
Kuke	20.90°S, 22.75°E	~400	Acacia-Terminalia savanna	20%	<i>Schmidtia pappophoroides</i> , <i>Eragrostis lehmanniana</i>
Maun	19.92°S, 23.59°E	460	Mopane woodland	36%	<i>Schmidtia pappophoroides</i>
Pandamatenga	18.66°S, 25.50°E	698	Baikia woodland	40%	<i>Schmidtia pappophoroides</i> , <i>Panicum Maximum</i> , <i>Digitaria spp.</i>
Mongu	15.44°S, 23.25°E	879	Miombo woodland	65%	<i>Digitaria spp.</i> , <i>Eragrostis spp.</i>

^aRainfall values are based on historical data reported by Scholes *et al.* [2002] and Williams and Albertson [2004]. Data on tree species are from Scholes *et al.* [2002].

Table 1b. Period of Record for Soil Moisture Measurements

Site	2004–2005 Wet Season		2005–2006 Wet Season	
	Start	End	Start	End
Tshane	1 Oct 2004	1 May 2005	1 Oct 2005	12 Jan 2006
Ghanzi	1 Nov 2004	15 May 2005	15 Nov 2005	19 Jan 2006
Pandamatenga	1 Oct 2004	1 Apr 2005	1 Nov 2005	30 Jan 2006

ditions being both stable states of the system), thereby enhancing the catastrophic character of possible ecosystem shifts in response to natural or anthropogenic disturbances.

[5] It is still unclear how, by affecting the strength of this feedback, changes in the rainfall regime may modify the ecosystem sensitivity to disturbances (i.e., the ecosystem resilience). For example, a trend of decreasing precipitation is expected to enhance the likelihood of shifts to desert conditions, however, it is not clear whether it could also either strengthen or weaken the feedback between woody vegetation and soil moisture, thereby increasing or decreasing the system susceptibility to abrupt shifts to conditions with no tree cover in response to disturbances and climate trends. To address this point, we present the results from some soil moisture observations along a rainfall gradient (~ 180 – 900 mm/a, where a is year) in the Kalahari region of southern Africa. The presence of uniform sandy soil along this gradient provides a unique opportunity to assess how mean annual precipitation affects the strength of the contrast between soil moisture values observed in canopy and intercanopy soils. We also develop a minimalist model to speculate on the possible implications of these feedbacks on the stability and resilience of savanna ecosystems in the Kalahari.

2. Methods

[6] The south-north rainfall gradient existing in the Kalahari occurs on homogeneous sandy soils [Wang *et al.*, 2007], which occupy a third of southern Africa [Scholes

and Parsons, 1997]. The research sites used for this study (Figure 1) are located along the Botswana–West Zambia portion of the Kalahari Transect, one of a number of International Geosphere-Biosphere Programme transects designated throughout the world [Koch *et al.*, 1995]. Rainfall in this region is highly seasonal and for the most part confined to the October–March wet season. Table 1a provides relevant information regarding site characteristics including mean annual rainfall and vegetation cover. Tree phenology varies by species, but many species have leaves on the canopy at the start of the season that are then replaced by a new flush just before or after the first rains. Others are drought deciduous but leaf out before the first rains. Generally, we can expect some leaf area in the canopy at the time of first rains, although peaks occur between January and February. Phenology of these tree species is poorly characterized, and hard to assess from remote sensing data, since grass/tree differences are not well resolved. In this system areas with no tree cover are not necessarily bare but typically exhibit a grass cover (Table 1a, see also Figure 2). Nevertheless we will refer to them as “intercanopy patches” or “intercanopy states”, meaning that are areas with no tree canopies, but with sparse grass cover (Figure 2).

[7] In water-limited ecosystems, soils remain dry for most of the time, while relatively high soil water contents exist only for short periods subsequent to rainfall events [Noy-Meir, 1973]. To detect differences in soil moisture dynamics between sites with different vegetation cover, field measurements need to capture these soil moisture pulses; thus continuous soil moisture measurements are needed [Bhark and Small, 2003]. Soil moisture monitoring (Table 1b) began at the onset of the 2004–2005 wet season when soil moisture probes were installed at three sites (Tshane, Ghanzi, and Pandamatenga) out of the six sites considered in this study. Two soil profiles were instrumented for soil moisture measurements at each site: one of them beneath a tree canopy, and the other in an adjacent

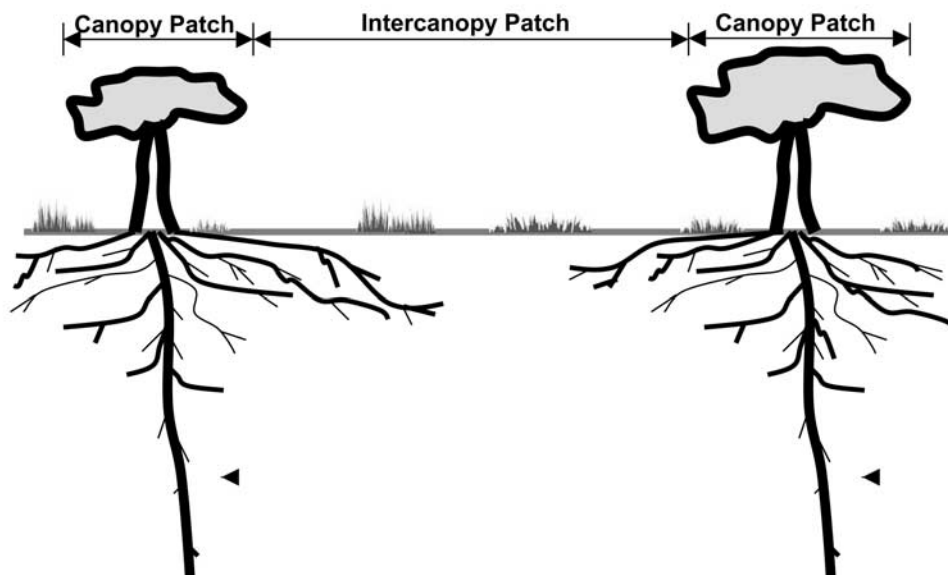


Figure 2. Typical patchy distribution of vegetation with areas covered by tree canopies, or “canopy patches” and “intercanopy patches” with sparse grasses and bare soil.

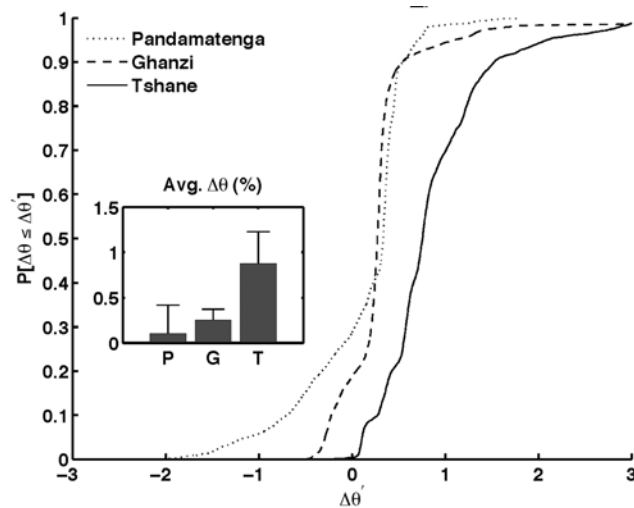


Figure 3. Differences, $\Delta\theta$, in root zone average soil moisture under canopies and between canopies at three Kalahari Transect sites. The cumulative distribution function is given for $\Delta\theta$ at Pandamatenga (dotted lines, $n = 4178$; MAP = 698 mm), Ghanzi (dashed lines, $n = 5664$; MAP = 400 mm) and Tshane (solid lines, $n = 5591$; MAP = 365 mm). Inset provides the mean difference at each site over all observations. Overall, root zone average soil moisture was higher under canopies 71% of the time at Pandamatenga (P), 80% of the time at Ghanzi (G), and 100% of the time at Tshane (T). The average difference was greatest at the southernmost site (Tshane) and lowest at the northernmost site (Pandamatenga). Bars report standard deviation of volumetric soil moisture, measured in 2-h intervals for the periods in Table 1b.

intercanopy patch. The tree chosen to establish the “canopy” microsite was selected among those of the dominant species at each site (Table 1a), while the “intercanopy” microsite was established in an open area (i.e., not covered by tree canopies, see Figure 2) within a distance of 8–10 m from the tree stem. Four DECAGON ECH₂O probes (Probe-20 cm) were used for each soil profile to monitor soil moisture at the depths of 0.10 m, 0.30 m, 0.50 m, and 1.00 m. Despite its sensitivity to temperature the ECH₂O probe provides accurate and precise measurements [Czarnomski *et al.*, 2005]. Soil moisture measurements were logged into a HOBO Weather Logger at 2-h intervals. Because of the lack of replication and to the spatial variability of soil moisture, soil temperature, and vegetation distribution, the canopy and intercanopy profiles investigated at each site are not necessarily representative of all canopy and intercanopy soils at that site.

[8] In addition to the direct soil moisture measurements, the depth of carbonate-rich soil horizon was used as an indicator of the long-term soil moisture regime [Schlesinger, 1985; Birkeland, 1999]. In March 2005, two soil pits were dug to at least 1 m depth at each of six sites along the Kalahari Transect (Tables 1a and 1b), one underneath a large tree canopy and the other in an adjacent intercanopy space. In each pit, subsurface soil horizons were identified by differences in color, texture, hardness, or structure.

Horizons were classified in the field using standard classification criteria [Soil Survey Staff, 2003].

3. Results

[9] Figure 3 shows differences between depth-average soil moisture values measured beneath tree canopies and in open areas at the three sites instrumented with soil moisture probes. It is observed that at the most humid site (Pandamatenga, mean annual precipitation (MAP) = 698 mm) only small differences in soil moisture exist between the intercanopy the subcanopy soils. A stronger difference exists at the dryer site (Tshane, MAP = 365 mm), where moister soils are found beneath the tree canopy. The intermediate site (Ghanzi, MAP = 400 mm) exhibits a slightly larger difference in soil moisture between canopy and intercanopy patches than the (wetter) Pandamatenga site. Figure 4 shows an example of soil moisture time series. A major difference between the two time series is the minimum soil moisture values, which are higher for the subcanopy site, consistently with a greater clay fraction (at 10-cm depth) found beneath tree vegetation or with greater soil evaporation and water uptake by shallowly rooted herbaceous plants growing between the canopies of woody plants.

[10] A closer inspection of the soil moisture data reveals important differences in the soil moisture–vegetation relations with depth. Figure 5 shows the probability that surface soil moisture at the canopy microsite is greater than in the intercanopy for different sites and soil moisture classes. It is found that at 10 cm depth (Figure 5a) a negative relation exists between soil moisture and canopy cover for low soil moisture values, while the relation becomes positive for high soil moisture values. When the whole root zone (i.e., top 1 m, consistently with field observations of root profiles [Wang *et al.*, 2007]) is considered, the trend is reversed: the relation is positive at the dryer sites, while at the wetter site it is positive only when the entire root zone is dry and negative when it is wet (Figure 5b). Thus, when the surface soils are wet, they are wetter under canopies; when surface soils are dry, they are drier under canopies. Opportunities for seedling establishment presumably occur in the periods

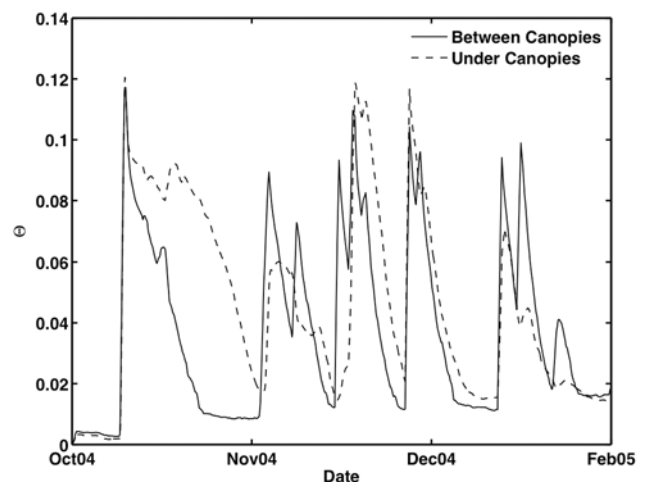


Figure 4. Example of time series of surface (10-cm-depth) soil moisture (data from the Tshane site).

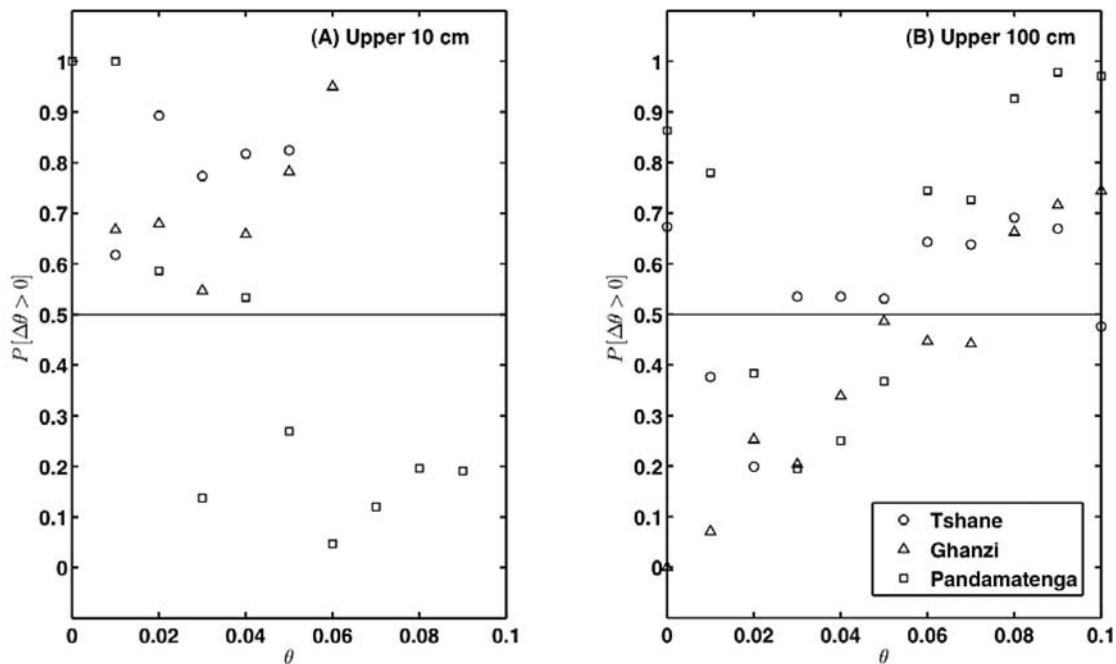


Figure 5. Probability that soil moisture under the canopy is greater than in the intercanopy (a) at 10-cm depth and (b) for depth-average soil moisture in the top 1 m. Values on the x axis represent mean values of θ between canopy and intercanopy microsites.

of relatively wet soil following rainfall occurrences. At all sites these opportunistic periods are better under the canopy than in the intercanopy (Figure 5b), suggesting the possible existence of a positive feedback between soil moisture and vegetation in terms of opportunities for seedling establishment rather than in terms of drought avoidance. Once seedling roots reach deeper layers, the drier sites may exhibit a positive feedback between woody vegetation and soil moisture, in that root zone soil moisture remains higher under the canopy for most of the time (Figure 5b), while at the wetter site root zone soils are more often wetter in the intercanopy than under the canopy.

[11] The results in Figure 3 show how soil moisture differences between subcanopy and intercanopy soils change at three points along the Kalahari Transect. The soil moisture measurements available for this study are relatively short and include two rainy seasons. The first season had a rather anomalous pattern of seasonal precipitation: in summer 2004–2005 soils were on average moister in the part of the transect with lower mean annual precipitation. To determine if the observed pattern of differences in soil moisture in Figure 3 are due to an anomalous hydrologic behavior of the system during that particular rainfall season, we used the depth of carbonate-rich horizons as an indicator of the long-term soil moisture dynamics. To this end, subsurface horizons in the soil pits followed a predictable pattern with one or more Bw (cambic) horizons overlying one or more Bk (calcic) horizons. Cambic horizons form in soils that have only undergone a slight degree of weathering and translocation of materials, mainly iron oxides. They indicate young soils or soils forming in low-weathering environments. Calcic horizons form when calcium carbonate accumulates in the subsoil as a result of excess evaporation and little or no movement of water downward through the bottom of the

soil. The depth of calcic horizons is related to the depth of leaching and is influenced by the long-term balance between infiltration/leaching and evaporation.

[12] A horizons were only present in the northernmost sites under canopies (Mongu and Pandamatenga) where significant staining of sands were seen at the surface due to the relatively high presence of organic matter. Bk horizons were generally much harder than Bw horizons and exhibited coarse angular blocky structure, whereas Bw horizons were either granular or fine angular blocky. In the southern, drier sites (Tshane and Kuke), Bk horizons were generally darker in color than overlying Bw horizons, probably due to the translocation of clays into the lower horizons. No argillans (i.e., clay films) were observed in the Bk horizons, however, and these soils do not have sufficient clay content to qualify as Bt (argillic) horizons. In the northern, wetter sites (Mongu and Pandamatenga), soils became progressively lighter with depth due to staining of overlying layers by organic matter.

[13] For soils in intercanopy spaces, the depth to the Bk horizon varied along the transect (Table 2), with the deepest intercanopy Bk horizons at Mongu and the shallowest at Tshane. This pattern reflects the differing amount of moisture, or average depth of wetting, at these sites along the transect. For soils underneath tree canopies, the depth to the Bk horizon was always greater than that of adjacent intercanopy spaces, and this difference became smaller with increasing mean annual precipitation. This result is consistent with greater infiltration of water underneath canopies than in intercanopy spaces. The average depth to the Bk horizon was 62 cm and was generally deeper at wetter sites than at drier sites. The Bk horizon depth under trees was shallowest at the Maun site, probably due to differences in soil texture at this site relative to other sites. The soil at Maun

Table 2. Depth of the Carbonate-Rich Horizon^a

	Under Tree	Intercanopy
Tshane	60	19
Ghanzi	n/a	n/a
Kuke	60	23
Maun	45	39
Pandamatenga	70	60
Mongu	75	70

^aDepth is given in cm; n/a indicates not available.

is composed of floodplain sediments, whereas Kalahari Sands underlie the other sites along the transect [Ringrose *et al.*, 1998].

4. Model-Based Analysis of Woody Vegetation Dynamics

[14] To speculate on the possible impact of soil moisture–tree vegetation feedbacks on dryland ecosystems along the Kalahari we develop a simple model of vegetation dynamics. To this end, we use a minimalist representation of the temporal dynamics of woody vegetation without accounting for the spatial interactions of trees with other landscape units. The goal of this model is to show some possible dynamical effects of the interactions between vegetation and soil moisture dynamics, rather than providing an accurate representation of all the complex processes affecting these dynamics. Thus we will not account for the effect of herbivory and fires on the stability and resilience of dryland vegetation, as the emergence of multiple stable states from the interaction of herbivory and fires with vegetation dynamics has been already investigated by other authors [Noy-Meir, 1975; Walker *et al.*, 1981; Dublin *et al.*, 1990; Anderies *et al.*, 2002; D'Odorico *et al.*, 2006a]. We account mainly for the feedback between woody vegetation and soil moisture regime, i.e., for the effect of tree canopies on the water content of the soil beneath their vertical projection. Because these feedbacks act at scales as small as an individual tree canopy, the model will provide a framework to investigate the feedback effect on the temporal dynamics of woody vegetation at the patch scale. We express the temporal variability of woody/vegetation biomass, V , as a logistic function [e.g., Murray, 1989]

$$\frac{dV}{dt} = \alpha V(V_{cc} - V) \quad (1)$$

with α being the reproduction rate and V_{cc} being the patch scale carrying capacity for woody vegetation. We follow Ridolfi *et al.* [2006] and model V_{cc} as a function of the controlling environmental factors, i.e., of the average volumetric soil water content, $\bar{\theta}$, in the growing season. Thus $V_{cc} = 0$ for $\bar{\theta} < \bar{\theta}_w$, with $\bar{\theta}_w$ being a critical value of soil moisture for woody vegetation survival. For larger values of $\bar{\theta}$, V_{cc} is an increasing function of $\bar{\theta}$ and asymptotically tends to a maximum value. We normalize V with respect to its maximum value (i.e., $0 \leq V \leq 1$) and express V_{cc} as (Figure 6a)

$$V_{cc} = \begin{cases} 0 & (\text{if } \bar{\theta} \leq \bar{\theta}_w) \\ \frac{\bar{\theta} - \bar{\theta}_w}{\zeta + (\bar{\theta} - \bar{\theta}_w)} & (\text{if } \bar{\theta} > \bar{\theta}_w) \end{cases} \quad (2)$$

with ζ being a dimensionless parameter that determines the rate of convergence of V_{cc} to 1 (Figure 6a).

[15] The dependence of $\bar{\theta}$ on V due to vegetation–soil moisture feedbacks can be expressed as $\bar{\theta} = f(V) = \bar{\theta}_0 + \beta V$, with $\bar{\theta}_0$ being the average seasonal value of soil moisture when the soil is with no canopy cover (i.e., $V = 0$). The parameter β expresses the strength of the feedback: when the feedback is positive, β is larger than zero and the soil water content increases with increasing values of V . Bistable dynamics are expected to emerge only if $\bar{\theta}_0 < \bar{\theta}_w < \bar{\theta}_0 + \beta$. In fact in this case the state $V = 0$ is a stable state of the system because it is associated with a moisture content, $\bar{\theta} = \bar{\theta}_0 < \bar{\theta}_w$, that does not allow for any sustainable growth of woody vegetation (i.e., $V_{cc} = 0$). On the other hand, as V increases, conditions may be reached in which $\bar{\theta} = \bar{\theta}_0 + \beta V > \bar{\theta}_w$. In this case the carrying capacity is positive and the establishment/growth of some woody vegetation can be sustainable.

[16] These features of woody vegetation dynamics can be better understood by looking at the shape of the potential function, U , associated with the process (1): the right-hand side of equation (1) can be expressed as a function, $h(V)$, of V using equation (2) and $f(V)$. The potential is defined as $U(V) = \int_V h(V)dV$. Minima of $U(V)$ are associated with stable states of the system [e.g., Murray, 1989]. To visualize the transient dynamics of the system toward its stable state(s), the shape of the potential function is often thought of as a hilly landscape, and the state of the system as a ball rolling down toward the valley bottom (stable state). When the system is bistable, the potential exhibits two minima and the initial conditions determine the stable state toward which the system evolves. Figure 6b shows a few examples of potential functions. When $\bar{\theta}_0 + \beta V < \bar{\theta}_w$ (dashed line), soil moisture is insufficient for woody vegetation establishment even when V is initially larger than 0. Thus the system has only one stable state at $V = 0$. When $\bar{\theta}_0 > \bar{\theta}_w$ (dotted line) the state with no canopy cover is unstable because, the carrying capacity is positive even when $V = 0$. This fact suggests that after a disturbance removes the existing woody vegetation the system is able to recover and reverts back to the stable state with canopy cover. When $\bar{\theta}_0 < \bar{\theta}_w < \bar{\theta}_0 + \beta$ (solid line), the system is bistable; that is, the system can be stable both with and without canopy cover. In these conditions a disturbance may switch the system to a stable unvegetated state in which the dynamics would remain locked without being able to recover.

[17] To speculate on how stable and unstable states of woody vegetation change along the Kalahari rainfall gradient, we take the average moisture content of the soil with no canopy cover, $\bar{\theta}_0$, as a proxy for mean annual precipitation and plot the states of the system as a function of $\bar{\theta}_0$ (Figure 6c). As expected, high values of $\bar{\theta}_0$ are associated with stable vegetated conditions (i.e., with canopy cover). Low values of $\bar{\theta}_0$ correspond to the case of a system that is stable in the absence of canopy cover. For intermediate values of $\bar{\theta}_0$ bistable conditions emerge as a result of the vegetation–soil moisture feedback. The likelihood that the system switches from a stable state to another is known as resilience [Holling, 1973] and can be measured by the distance between this state and the intermediate unstable conditions. Figure 6c shows how as $\bar{\theta}_0$ decreases, the resilience of dryland woody vegetation decreases, suggesting that smaller and smaller disturbances are needed to

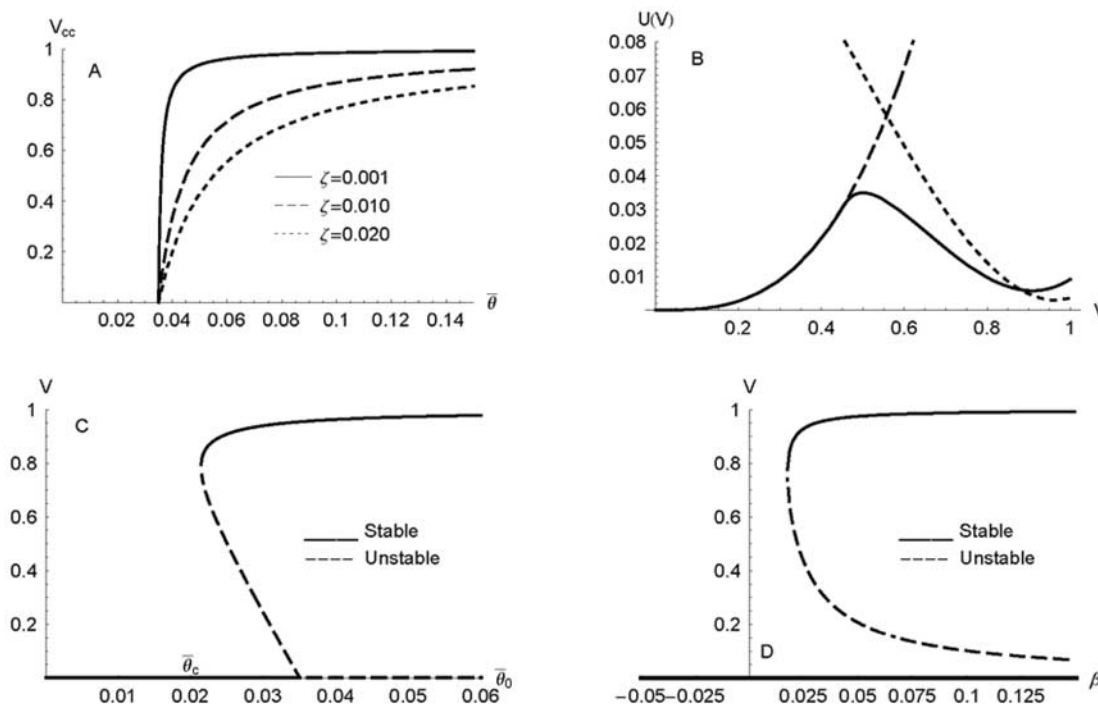


Figure 6. (a) Dependence between ecosystem carrying capacity and average seasonal soil moisture (equation (2)) calculated for $\bar{\theta}_w = 0.035$ and different values of the parameter K . (b) Potential function, $U(V)$, associated with vegetation dynamics (equations (1) and (2)) calculated with $\beta_1 = 0.022$, $\bar{\theta}_w = 0.035$ and $\bar{\theta}_0 = 0.025$ (solid line), $\bar{\theta}_0 = 0.01$ (dashed line), and $\bar{\theta}_0 = 0.04$ (dotted line). (c) Stable and unstable states of the system as a function of $\bar{\theta}_0$ (with $\beta_1 = 0.022$ and $\bar{\theta}_w = 0.035$). (d) Stable and unstable states as a function of the strength of the feedback, β (with $\bar{\theta}_0 = 0.025$ and $\bar{\theta}_w = 0.035$).

cause the transition to conditions with no canopy cover. Below a critical value of $\bar{\theta}_0$ ($\bar{\theta}_0 = \bar{\theta}_c \approx 0.02$) the vegetated stable state (i.e., with canopy cover) disappears and the system catastrophically shifts to conditions with no canopy cover [e.g., Walker *et al.*, 1981; Rietkerk and van de Koppel, 1997]. Because the soil moisture–vegetation feedback can operate at scales as small as a tree canopy, states with and without canopy cover can coexist in the same landscape, partly explaining the patchy configuration of woody vegetation, i.e., the mosaic of canopy and intercanopy patches typical of arid and semiarid systems. However, the model proposed in this study does not account for spatial dynamics and is therefore unable to explain vegetation pattern formation. Moreover, because the model lacks spatial dynamics, the carrying capacity parameter used in equation (1) should be interpreted at the local (i.e., patch) scale rather than at the landscape scale. Further, because of the relatively small scales at which the feedback between woody vegetation and soil moisture may be active, the shift to intercanopy conditions does not imply necessarily that the whole landscape shifts to desert conditions, unless the shift is induced by a large-scale disturbance.

[18] To assess the effect of the feedback strength on the dynamics of dryland ecosystems, we investigated the stable states of the system as a function of the parameter β (Figure 6d). As expected, the resilience of woody vegetation decreases as the feedback becomes weaker. In fact, a decrease in β is associated with smaller domains (in the

parameter space) of the bistable dynamics; thus a smaller perturbation is needed to shift the system from the canopy state to (stable) intercanopy conditions. Moreover, Figure 6d shows that bistable dynamics arise only when the feedback is positive. In fact, negative values of β correspond to conditions in which soil moisture is higher in the intercanopy soil than in canopy patches because plants are not able to favor their own establishment through mechanisms of self-facilitation. In this case, if on intercanopy plots soil moisture is smaller than $\bar{\theta}_w$ (i.e., $\bar{\theta}_0 < \bar{\theta}_w$), no vegetation is sustainable with the available water resources. Conversely, if $\bar{\theta}_0 > \bar{\theta}_w$, the system tends to its (state-dependent) carrying capacity. In either case the dynamics exhibit only one stable state.

5. Discussion and Conclusions

[19] The results presented in sections 3 and 4 indicate that interesting relations exist between vegetation and soil moisture along the Kalahari Transect. An analysis of the soil moisture time series (Figure 4) indicates that immediately after a rainstorm soils are wetter in the intercanopy patches presumably due to the absence of canopy interception. However, intercanopy soils tend to dry out at a faster rate than canopy patches, presumably due to the higher solar irradiance and resulting soil evaporation. For this drier site, the subcanopy soils stay relatively moist due to reduced soil evaporation, an effect that overcomes the presence of

canopy interception. Our relatively short soil moisture records suggest that the relations between soil moisture and vegetation are overall positive (i.e., wetter soils under the intercanopy) at the dry end of the transect and weak to perhaps neutral at the wet end. Soil profile analyses, indicate deeper wetting beneath tree canopies at all sites. However, these differences become less pronounced as mean annual precipitation increases. Both soil moisture measurements and soil profiles indicate that a positive relation exists at the dry end of the transect, and that its strength decreases while going from arid to semiarid or subhumid areas (i.e., β is reduced). These relations may be suggestive of feedbacks between soil moisture and vegetation dynamics. Our minimalist ecohydrological model of woody vegetation dynamics showed that positive feedbacks between soil moisture and vegetation may lead to the existence of two stable states (i.e., “canopy” and “intercanopy” conditions) in the dynamics of dryland woody vegetation, while bistability does not emerge when the feedback is either negative (i.e., $\beta < 0$) or weakly positive (i.e., small positive values of β).

[20] The possible existence of stronger positive feedbacks at the dry end of the Kalahari is also supported by the vegetation patterns observed along the transect; *Caylor et al.* [2003] found a significantly larger number of seedlings and juvenile trees growing beneath the canopies of older (i.e., 25% largest) trees at Tshane, while no significant difference existed between canopy and intercanopy patches at the (wetter) Pandamatenga site. At sites drier than Tshane (Vast-rap, MAP \approx 200 mm/a) most of the seedlings and younger trees were found to grow outside the vertical projection of the canopy of larger individuals. Similar patterns can be found along other aridity gradients [e.g., *Holzappel et al.*, 2006]. Thus, at sites with relatively high values of MAP (MAP \approx 600 mm/a) subcanopy soils are not preferential sites for seedling establishment. Under very dry climate conditions (MAP $<$ 200 mm/a) only a very sparse woody vegetation exists, with new seedlings establishing away from the older trees to avoid competition, though other processes may also explain the different seedling survival rates between the two microsites (e.g., different exposure to disturbance by herbivores). In intermediate conditions (e.g., Tshane) soils under the canopy are preferential sites for seedling establishment [*Caylor et al.*, 2003], suggesting that a positive feedback may exist between woody vegetation and the limiting resource, i.e., soil moisture. In these locations it can be argued that the dynamics of woody vegetation are more likely to be bistable and prone to disturbance-induced abrupt shifts to intercanopy conditions, as discussed by *Rietkerk and van de Koppel* [1997]. On the other hand, the relatively strong interannual rainfall fluctuations typical of the drier climates [*D'Odorico et al.*, 2006b] along with spatial interactions associated with resource redistribution and plant encroachment [*van de Koppel and Rietkerk*, 2004; *Scanlon et al.*, 2007] may enhance the ecosystem resilience and reduce the likelihood of abrupt shifts to the intercanopy state. In fact, it has been shown [*D'Odorico et al.*, 2005] that interannual fluctuation can stabilize the system in an intermediate state (i.e., between the two stable states of the deterministic dynamics).

[21] Because of the presence of lateral roots trees extract water both from the canopy and the intercanopy soils

[*Casper et al.*, 2003, *Wang et al.*, 2007]. However, the canopy can have a local effect on the soil moisture regime underneath the canopy. When canopy soils are wetter than in the intercanopy patches, positive feedback between soil moisture and (woody) vegetation may exist. Despite the important implications of positive feedbacks between soil moisture and woody vegetation, there is yet no general consensus on the ecohydrological processes explaining the existence of higher soil moisture values in the soils beneath tree canopies. Three major mechanisms can play an important role in the interactions between plants and soil moisture:

[22] 1. Vegetation may enhance soil infiltration capacity [e.g., *Lyford and Qashu*, 1969; *Walker et al.*, 1981; *Rietkerk and van de Koppel*, 1997] through the reduction in rain splash compaction, root action, and other biotic factors [*Greene*, 1992; *Greene et al.*, 1994; *Breman and Kessler*, 1995; *Devitt and Smith*, 2002; *Bhark and Small*, 2003]. This mechanism is often invoked to explain the formation of banded vegetation [e.g., *Klausmeier*, 1999; *Tongway et al.*, 2001] in low-permeability soils with textures ranging between clayey sands and sandy clays [*Greene et al.*, 2001].

[23] 2. Evaporative losses may be lower in subcanopy soils due to tree or grass shading [*Scholes and Archer*, 1997; *Zeng et al.*, 1996; 2004; *D'Odorico et al.*, 2005].

[24] 3. Stem flow contributes to higher soil moisture at the base of trees and shrubs by funneling rain water down to the ground surface [*Pressland*, 1976; *Martinez-Meze and Whitford*, 1996; *Whitford et al.*, 1997].

[25] While stem flow alone is not likely to be able to explain the higher soil water contents beneath tree/shrub canopies, the other two processes may offset the evaporative losses associated with canopy interception [e.g., *Tromble*, 1988] in the canopy patches thereby causing higher soil water contents in the subcanopy soils.

[26] The effect of trees on soil infiltration capacity is a likely explanation for possible vegetation–soil moisture feedbacks in the clayey soils such as those found in areas exhibiting banded vegetation. In the case of the Kalahari the effect of woody vegetation on evaporative losses is a more plausible mechanism responsible for the higher soil water contents existing beneath tree canopies in the sandy soils of the Kalahari. In fact, in this region infiltration is seldom limited by soil permeability, as suggested by the lack of tracks of significant infiltration-excess runoff and the low degree of landscape dissection by drainage networks.

[27] It is possible for woody vegetation to map onto preexisting topoedaphic features and thus it might be argued that trees in the southern Kalahari are simply taking advantage of preexisting edaphic heterogeneity. Heterogeneity in edaphic characteristics that appear to influence woody vegetation arise from spatially discontinuous argillic horizon development on surfaces with different age or parent material, presumably due to the reduced permeability of these clay-rich subsurface horizons [*McAuliffe*, 1994; *Archer*, 1995; *Hamerlynck et al.*, 2000; *Stroh et al.*, 2001]. At our sites, we argue that the underlying edaphic heterogeneity does not cause the distribution of woody vegetation, but rather that the trees themselves influence soil formation [e.g., *Sandvig and Phillips*, 2006]. First, we saw no evidence for the formation of an argillic horizon at any of our sites, and the highly mature, sandy characteristics of Kala-

hari soils would make the creation of argillic horizons unlikely. In studies elsewhere, the argillic horizon seems to be necessary for controlling below groundwater relations. The calcic horizons that were observed at our sites were not continuous or indurated enough to plausibly influence the permeability of the soils to the degree that an argillic horizon would. Second, in these flat aeolian deposits, there is no plausible geomorphic mechanism for the creation of fine-scale (e.g., on the scale of individual trees) soil heterogeneities like those seen on bajadas in the Mojave and Sonoran deserts [McAuliffe, 1994; Hamerlynck et al., 2000] or in floodplains of the Rio Grande valley [Archer, 1995; Stroh et al., 2001]. Finally, mapped tree distributions are consistent with competition-facilitation interactions among trees, rather than abiotic structuring of the landscape by edaphic heterogeneity [Caylor et al., 2004].

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