

Research Article

## Scale-dependent influence of topography-based hydrologic features on patterns of woody plant encroachment in savanna landscapes

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Received 21 October 2004; accepted in revised form 20 January 2005

**Key words:** *Prosopis glandulosa*, Ecohydrology, Tree–grass interactions, Parkland, Vegetation change, Wetness index, Scale multiplicity, Woody plant encroachment, Southwestern USA

### Abstract

Rainfall in drylands is erratic. Topographic features of landscapes can dampen or amplify temporal variability by spatially influencing patterns of water loss and accumulation. The extent to which portions of a landscape may differentially capture or retain scarce water and nutrient resources is an important determinant of vegetation patterns, particularly with respect to the distribution of woody plants. We therefore hypothesized that historic changes in woody cover on landscapes experiencing similar climate and disturbance regimes would vary with catena-to-catena (hillslope-to-hillslope) variation in topography-based hydrologic features. We tested this hypothesis by comparing topographic wetness index (TWI) values on replicate landscapes where woody plant abundance has increased over the past 100 yr. These landscapes are characterized by savanna parklands on coarse-textured upland portions of catenas that grade (1–3% slopes) into closed-canopy woodlands on fine-textured (lowland) portions of catenas. TWI values for woody and herbaceous communities were comparable within uplands, suggesting factors unrelated to surface/subsurface hydrology determine patterns of woody cover in these catena locations. TWI values for upland savanna parklands were significantly lower than those of closed-canopy woodlands occupying catena footslopes. Furthermore, uplands adjoining historically static woodland boundaries had lower TWI values than those where woodland boundaries had moved upslope  $2.1 \text{ m yr}^{-1}$  from 1976 to 1995. Results suggest runoff–runon relationships influence patterns of woody plant cover and change at the catena scale and may override constraints imposed by soil texture. As a result, changes in woody cover potentially accompanying changes in disturbance regimes, climate or atmospheric chemistry are likely to be constrained by topoedaphic settings. Models of vegetation dynamics may therefore need to explicitly account for rainfall–topography–soil texture relationships and associated scale-dependent mechanisms to accurately predict rates and patterns of change in woody and herbaceous plant abundance.

### Introduction

Savanna ecosystems are characterized by mixtures of two contrasting plant life forms: woody plants

and grasses. The size, cover and density of woody plants in savannas varies markedly, is dynamic and is influenced by interactions between climate (primarily amount and seasonality of rainfall) and

disturbances (grazing, browsing and fire) as constrained by soils (primarily texture and depth) (Johnson and Tothill 1985; Walker 1987; Scholes and Archer 1997; Walker and Langridge 1997; Rodriguez-Iturbe et al. 1999; Jeltsch et al. 2000). Changes in climate, atmospheric CO<sub>2</sub> levels, nutrient status or disturbance regimes can alter woody–herbaceous ratios. In recent decades, woody plant abundance has increased dramatically in many temperate, subtropical and tropical savanna systems (see 150+ references in Archer et al. 2001). The relative importance of climatic, atmospheric and disturbance factors in causing this shift towards greater domination by trees and shrubs has been the topic of active debate (Archer et al. 1995; House et al. 2003; Köchy and Wilson 2001; Van Auken 2000).

Although woody plant encroachment has been widely observed, quantification of the rates and patterns of woody plant proliferation in drylands is limited. Available information suggests changes in woody plant abundance can be non-linear (Archer 1996) and locally mediated by edaphic features such as soil texture (e.g., McAuliffe 1994). Woody plant clumping or clustering is common in many arid and semiarid landscapes (Fuentes et al. 1984; Haase et al. 1996) and is particularly prevalent in savannas (Franco-Pizana et al. 1995; McPherson et al. 1988; Vitousek and Walker 1989; Whittaker et al. 1979). However, the potential role of soils in regulating these patterns of tree–shrub distribution is not well known. In other drylands, woody plants may occur in distinct bands that may migrate slowly across the landscape in response to the topographic redistribution of water (e.g., Tongway et al. 2001). In the Rio Grande Plains of southern Texas, patterns of woody plant cover are strongly influenced by topography and soils (Figure 1). Sandy loam uplands have a savanna parkland physiognomy, consisting of discrete clusters and groves of woody vegetation embedded in a grassy matrix; adjoining clay loam lowlands are characterized by closed-canopy woodlands. These patterns are the opposite of those reported in other savannas, where woodlands occur on coarse-textured soils and savannas on fine-textured soils (e.g., Johnson and Tothill 1985; Knoop and Walker 1985). What might explain these discrepancies in plant–soil relationships?

Previous work on the landscapes in Figure 1 has shown that woody plant cover has increased since

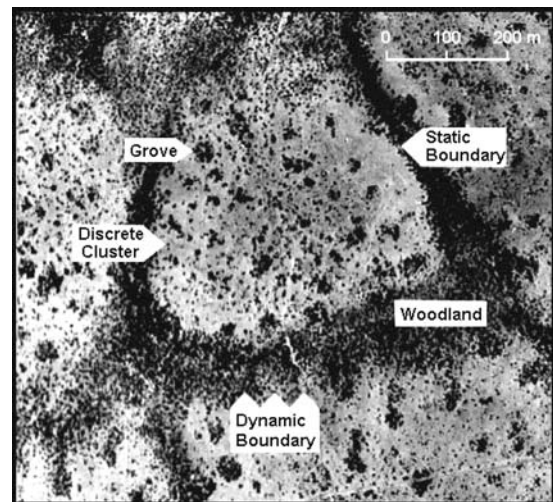


Figure 1. Savanna parklands on convex sandy loam uplands of southern Texas are characterized by small, discrete clusters (argillic horizon present) and large groves (argillic horizon poorly expressed) of woody plants (black) embedded in a matrix of herbaceous vegetation (gray). These grade (<3% slopes) into clay loam intermittent drainages characterized by closed-canopy woodlands. Woodland boundaries on some catenas have been static from 1976 to 1995, whereas the boundary on other catenas has migrated upslope an average of 39.7 m over this same period.

the 1940s (Archer 1995a). These increases in woody cover were the result of the initiation of new shrub clusters and the expansion of established clusters in sandy loam uplands occurring in conjunction with the upslope migration of woody plants from clay loam lowlands. However, the magnitude of woody cover change ranged from 150% on some catenas (hill-slope gradients) to 338% on others; and for some catenas, the boundary of lowland woodland communities has remained static since the 1940s, whereas for others, this boundary has moved significantly upslope.

Explanations for the observed differences in woody cover change between landscapes remain elusive. These landscapes and the catenas comprising them were in close (<2 km) geographic proximity, ruling out climate, atmospheric CO<sub>2</sub> enrichment and N-deposition differences as viable explanations. Furthermore, these landscapes had comparable land management histories since the late 1800s (cattle grazing, no known fire). Detailed examinations of soil physical and chemical properties along upland-to-lowland transects spanning static and dynamic woodland boundaries have also failed to reveal differences (Stroh 1995; Stokes

1999). What then, might account for local contrasts in the rate, pattern and extent of woody cover change? Given the strong linkage between runoff and vegetation in drylands (Noy-Meir 1973; Ludwig et al. 1997; Bergkamp 1998; Tongway et al. 2001; Wilcox et al. 2003), we hypothesized that the distribution of contrasting woody plant communities on landscapes and the nature of their boundaries are an ecohydrological function of topography (specifically, slope steepness and length) and associated runoff–runon relationships. If this is the case, then differences in rates and patterns of woody cover change between landscapes experiencing similar climate and disturbance could be the result of landscape-to-landscape variation in topography-based hydrologic features that regulate woody and herbaceous patch abundance and distribution.

To test this hypothesis, we quantified topography-based hydrologic features of the upland and lowland portions of landscapes using a topographic wetness index (TWI). The TWI represents the potential, relative moisture content of a given location in a catchment based on slope inclination and upslope catchment area (Beven and Kirkby 1979; O'Loughlin 1981). For any given point or pixel, TWI values increase with increasing upslope catchment area and decrease when the capacity for drainage by gravitational forces (as implied by slope inclination) increases (Del Barrio et al. 1997). This index has been applied with good results in landscape classification and modeling studies (Del Barrio et al. 1997; Irvin et al. 1997), in site selection for riparian wetland restoration (Kentula 1997; O'Neill et al. 1997), and in estimating herbaceous biomass under different grazing regimes (Todd et al. 1998).

Most indices used in landscape studies lack a built-in linkage to ecological processes (Li and Wu 2004), although they can be used to represent landscape patterns that correlate to landscape functions such as hydrological processes (Wu et al. 2000; Ludwig et al. 2002). A notable exception is the 'leakiness' index developed by Ludwig et al. (2002) that assesses the capacity for landscapes to retain resources such as water and soil based on functional mechanisms. The TWI, like the leakiness index, is based on physical mechanisms that regulate hydrological processes. As such, it is a tool in the emerging field of ecohydrology (Rodriguez-Iturbe 2000; Nuttle 2002) for exploring how hydrological processes may influence vegetation patterns on

landscapes. In contrast to the leakiness index built explicitly on spatial structures of vegetation and a simpler topographic representation, the TWI is based solely on topography and does not take into account the potentially important influence of vegetation patches on landscape water movement (e.g., Ludwig et al. 1997; Bergkamp 1998; Wilcox et al. 2003). It can only account for hydrological processes determined by topography; but as such, can serve as a null model for exploring the role of vegetation and soil patterning in regulating hydrological processes on landscapes. In contrast to the leakiness index and other landscape-level indices, the TWI provides distributed measures for individual locations within a landscape. Thus, multiple-scale analyses focusing on different elements and levels of landscape organization are possible.

Our objectives in this study were to (1) compute TWI values for landscape components in savanna parkland/woodland landscapes; (2) use TWI values to assess the potential influence of topography-based hydrologic features in shaping vegetation pattern at various spatial scales, and (3) determine if observed differences in rates and patterns of woody plant encroachment on landscapes experiencing similar climate and land management are associated with differences in topography-based hydrologic features represented by TWI values.

## Methods

### *Study site*

The potential role of topography-based hydrologic features in regulating the woody plant cluster distributions and woodland boundaries was examined on savanna landscapes at the Texas A&M Agriculture and Extension Service La Copita Research Area (LCRA) 65 km west of Corpus Christi, Texas, USA (27°40' N; 98°12' W; elevation 75–90 m a.s.l.). Contemporary vegetation of the region has been described by McMahan et al. (1984). The 1103 ha LCRA is situated in the eastern Rio Grande Plains of the Tamaulipan Biotic Province (Dice 1943). Climate of the area is subtropical with warm winters, hot summers (mean annual temp = 22.4 °C) and a highly variable mean annual rainfall of 680 mm (CV > 35%; Le Houerou and Norwine 1988).

Vegetation of the study site, which has been grazed by cattle since the 1800s, consists of savanna parklands in sandy loam uplands. These gently grade (1–3% slopes) into closed-canopy woodlands on clay loam intermittent drainages (Figure 1). Small discrete clusters with numerous woody species and patches of herbaceous vegetation occur on portions of the upland where an argillic (Bt or ‘clay pan’) horizon is well-defined starting at ca. 40 cm depth; where this horizon is poorly expressed, large groves have developed (Archer 1995a). Wooded landscape elements are typically dominated by *Prosopis glandulosa* var. *glandulosa* (honey mesquite) in both uplands and lowlands. Associated understory woody plants in upland and lowland habitats consist of a diverse, ubiquitous mixture of evergreen, winter-deciduous, and summer-deciduous species. Additional details on climate, soils, vegetation history and succession can be found in Archer (1995a), Boutton et al. (1998) and Scifres and Koerth (1987).

#### Approach

Landscapes of the LCRA, defined here as convex sandy loam uplands and their neighboring clay loam intermittent drainages (Figure 1), were delineated and their vegetation classified in ERDAS Imagine (ERDAS 1998) using 1-m resolution Digital Orthophoto Quadrangles (DOQ) data derived from 1995 NAPP aerial photographs (black and white, nominal scale 1:40,000). Lowland woodland and upland savanna parkland areas were manually delineated and digitized. Upland savanna parkland portions of landscapes from the entire (1103 ha) site, exclusive of areas known to have been disturbed by chemical or mechanical manipulation of the woody vegetation (based on LCRA ranch management records), were subjected to an unsupervised classification using Iterative Self-Organizing Data Analysis (ISODATA; ERDAS 1998). This classification initially grouped pixels into 40 classes based on reflectance value similarities. These 40 classes were subsequently collapsed into one of two categories: woody or herbaceous. Pixels classified as ‘woody’ in the uplands were further classified as either ‘clusters’ or ‘groves’ based on the size of the woody patches. Based on past fieldwork at the site, woody

patches  $>100 \text{ m}^2$  were classified as groves; and those  $<100 \text{ m}^2$  as clusters. In order to match the resolution of the TWI data, the classification was re-sampled to  $4 \times 4 \text{ m}$  resolution.

Classification accuracy was assessed based on visual classification of the aerial photo at 200 randomly selected reference points (94 woody and 106 herbaceous) in the uplands. The overall accuracy of the classification was 94.5%. Producer’s and user’s accuracies (measures of omission and commission error, respectively) were  $>91\%$ . Field-based accuracy assessments for classifications of historical photography are not possible. However, assessments based on visual interpretation work well in our case, which involved simple and sharply contrasting landscape elements on high quality, high resolution aerial photos. Confidence in our visual interpretation-based accuracy assessments was bolstered by the fact we have conducted intensive field research on this site since 1984 and are thus intimately familiar with the vegetation.

TWI values were determined for individual pixels on all the landscapes of the LCRA. The TWI used was defined as,  $\text{TWI} = \ln A_s / \tan \beta$ , where  $A_s$  was the specific catchment area (the cumulative upslope area draining through a location per contour unit length), and  $\beta$  the local slope inclination (Beven and Kirkby 1979; O’Loughlin 1981). Specific catchment area was represented using ‘flow accumulation’ (number of upslope pixels draining into a pixel) and local inclination was represented by the slope gradient for a pixel, derived from a digital elevation model (DEM) in ArcView Spatial Analyst (ESRI 1998). DEM grids (4-m resolution) were developed using the ArcInfo TOPOGRID command (ESRI 1994) based on contour lines manually digitized from USGS 1:24,000 quadrangle maps. Slope inclination and upslope catchment area interact to affect the TWI value. For example, a TWI value of 8.3, the average TWI for the LCRA landscapes (range 3.7–20.6), could be that of a pixel with  $0.5^\circ$ ,  $5^\circ$ , or  $45^\circ$  slope and 35, 350, or 4000 units of upslope catchment area, respectively. As the TWI is a relative measure of the potential wetness of a location, it is best used for comparative studies.

The potential regulation of woodland boundaries by topography-based hydrologic features was evaluated on three LCRA landscapes with no known history of brush management. A pair of a static and a dynamic lowland woodland boundary

segments (ranging from 150 to 350 m in length) were identified in each landscape based on a comparison of 1976 and 1995 aerial photographs. Positive transparencies of the 1976 NRCS aerial photography (nominal scale 1:58,000) were scanned and registered to the 1995 imagery. Lowland woodland boundaries on the 1976 imagery were then manually delineated and digitized on each of the three selected landscapes. For each dynamic boundary segment, the area of upslope expansion from 1976 to 1995 was delineated and TWI values determined for each pixel within that area. For each static boundary segment, TWI values were calculated for upslope pixels within 40 m of the boundary (the approximate average distance of upslope expansion observed along the dynamic boundary segments). ArcView Spatial Analyst was used to generate frequency distributions of TWI values for (a) upland savanna parkland vs. lowland woodland pixels of all LCRA landscapes; (b) herbaceous vs. grove vs. cluster pixels within the savanna parkland uplands of all LCRA landscapes; and (c) pixels within the 1976–1995 expansion zone of dynamic woodland boundaries vs. upslope pixels within 40 m of the static woodland boundaries on the three selected LCRA landscapes. Statistical comparisons between mean TWI values of pixel groups were conducted using two-sample unequal variance *t*-tests (S-PLUS, MathSoft 1998) on 250 randomly selected pixels for each group. Statistical comparisons between pairs of frequency distributions of TWI values were also conducted using two-sample Kolmogorov–Smirnov goodness of fit tests that ascertain whether two sets of observations could reasonably have come from the same distribution.

Differences in TWI frequency distribution of pixels representing various landscape elements would support the hypothesis that topography-based hydrologic features are differentially influencing the spatial distribution and abundance of woody and herbaceous community types at the landscape scale. However, if TWI distributions are comparable, this would suggest factors other than surface/subsurface hydrology may be responsible for differences in land cover from one area to another when climate and disturbance are held equal. We therefore examined the TWI over a range of spatial scales ranging from the local patch level (e.g., herbaceous vs. cluster vs. grove) to the landscape level (upland savanna parkland vs.

lowland woodland boundaries). From these hierarchical comparisons, we could ascertain if the importance of topography-based hydrologic features as a determinant of vegetation structure might change with spatial scale.

## Results and discussion

### *Patch-scale upland vegetation pattern*

The shrub clusters and groves comprising today's savanna parklands at the La Copita site are known to have developed relatively recently (Boutton et al. 1998), but the pattern and extent of their development has varied from landscape to landscape within an area experiencing similar climate and land use (livestock grazing and no fire) (Archer 1995a). What is the cause for these local differences in grass–woody plant abundances? Within the sandy loam upland portions of catenas classified as savanna parkland, mean ( $\pm$ SD) TWI values for herbaceous ( $8.19 \pm 1.37$ ), grove ( $8.18 \pm 1.41$ ), and cluster ( $8.24 \pm 1.34$ ) elements were not statistically different ( $p > 0.1$ ) and their frequency distributions were similar ( $p > 0.1$ ) (Figure 2a). Thus, the hypothesis that topography-based hydrologic features are differentially affecting herbaceous, cluster and grove communities in upland portions of catenas was not supported.

The inference that coarse surface hydrology is not of primary importance in structuring the vegetation in uplands is consistent with other studies on this site which suggest that (a) establishment of the dominant woody plant, *Prosopis glandulosa*, appears to be primarily a function of patterns of dispersal of its seed by ungulates and protection from fire (Archer 1995b; Brown and Archer 1987, 1999); (b) establishment of understory woody plants is the result of facilitation by *P. glandulosa* (Archer 1995a); and (c) subsurface (>40 cm) variation in the clay content of the B horizon of upland soils exerts significant control over woody plant growth rates (Miller et al. 2001), species composition (Archer, unpubl. data), and the extent of grove expansion (Stokes 1999). The fact that TWI distributions were not different between clusters (argillic horizon well-developed at 40–100 cm depth) and groves (argillic horizon poorly developed) suggests that surface topography indices are not a viable surrogate for, nor an indicator of

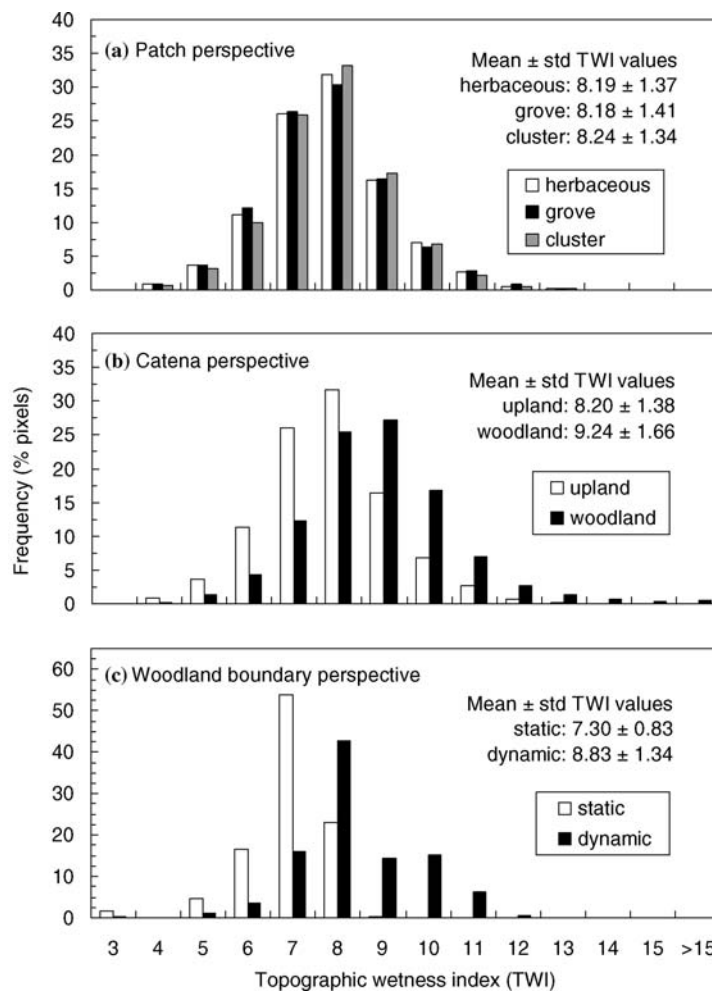


Figure 2. Frequency distribution and mean ( $\pm$ SD) of topographic wetness index (TWI) values from three perspectives: (a) patch perspective: herbaceous, grove, and cluster pixels in uplands, (b) catena perspective: pixels in upland savanna parkland vs. pixels in lowland woodland, and (c) woodland boundary perspective: pixels within known expansion zones of dynamic woodland boundaries vs. pixels from comparable upslope zones within 40 m of static woodland boundaries. Two-sample unequal variance *t*-tests using randomly selected pixels ( $n=250$  per group) indicated no significant differences in TWI values ( $p>0.1$ ) between herbaceous, grove, and cluster pixels, a significant difference in TWI values ( $p<0.001$ ) between savanna uplands and lowland woodlands, and a significant difference in TWI values ( $p<0.001$ ) between pixels associated with static vs. dynamic woodland boundaries. Statistical comparisons between pairs of frequency distributions of TWI values using two-sample Kolmogorov–Smirnov goodness of fit tests gave the same results as the *t*-tests.

potential subsurface flows (O’Loughlin 1990) that might regulate the distribution, dynamics and abundance of these contrasting upland woody community types. The TWI approach as used here, does not allow us to evaluate the potential importance of finer-scale runoff–runon patterns, i.e., runoff from herbaceous or bare patches with low infiltration rates and capture by woody patches with higher infiltration rates known to be significant in some systems (Anderson and Hodgkinson

1997; Schachak et al. 1998; Galle et al. 1999; Seghier and Galle 1999).

#### *Catena-scale vegetation pattern*

In dryland landscapes, the linkage between runoff and vegetation is a particularly close one (Ludwig et al. 1997; Wilcox et al. 2003). In our Rio Grande Plains landscapes, the frequency distribution of

TWI values for the lowland woodland and upland savanna parkland elements differed significantly ( $p < 0.001$ ), with areas classified as woodland having greater mean ( $\pm$ SD) TWI values ( $9.24 \pm 1.66$ ) than those classified as upland savanna parkland ( $8.20 \pm 1.38$ ) (Figure 2b). This suggests patterns of runoff and runon are a significant determinant of woody plant cover, stature and pattern of distribution at the landscape or catena scale. Surface runoff has been recorded from upland woody and herbaceous patches at this site (Weltz and Blackburn 1995), but studies quantifying runon to low-lying sites have not yet been conducted. However, the logical expectation that clay loam runon areas are wetter than sandy loam runoff areas is supported by spot-checks of soil moisture that indicated a rank order (wettest to driest) of woodland (=catena footslope) > woodland margin > savanna parkland (catena apex) (Stokes 1999).

Runoff–runon relationships likely interact over time with soil texture and annual rainfall amount and intensity to uniquely affect woody plant cover and density from site to site and region to region. For example, models of woody plant abundance in savannas based on regional and sub-continental assessments (e.g., Johnson and Tothill 1985; Williams et al. 1996) typically predict declines in woody plant cover and density with decreasing rainfall and increasing topsoil clay content. Local assessments also confirm that sites with fine-textured soils may support open savanna grasslands (grasses with their shallow, fibrous root systems are favored by clayey soils that retain water in upper layers), whereas nearby sites on coarse-textured soils support woodlands (trees and shrubs with deeper, more extensive root systems are favored by sandy soils that allow percolation of rainfall to deeper depths) (e.g., Knoop and Walker 1985). However, on La Copita landscapes, local patterns of woody plant cover run counter to these generalizations in that closed-canopy woodlands occur on fine – rather than on coarse-textured surface soils and the more open savanna parklands occur where surface soils are coarse-textured rather than fine-textured.

The explanation for this seeming contradiction appears to reflect the fact that when other factors are held equal then (a) runoff reduces the effectiveness of annual rainfall and limits woody plant size and cover such that parklands rather than

woodlands develop on uplands; and (b) runoff from upland portions of the landscape sufficiently augments annual rainfall on lowland intermittent drainages to offset the advantage that might otherwise allow grasses to dominate the clay loam soils on these landscape positions. At the La Copita site, supplementation of annual rainfall by runon from uplands is apparently sufficient to support woody plants of a size and density that enabled formation of woodlands on fine-textured lowland landscape locations.

The topographic setting that has favored the development of woodlands at the La Copita site (mean annual rainfall 680 mm) may not favor woody plants over grasses (other factors held equal) where annual rainfall is lower (resulting in fewer and smaller runoff events) or higher (excessive runon resulting in increased frequency and duration of ponding and flooding). Disturbances such as grazing, browsing and fire and the effects of atmospheric CO<sub>2</sub> enrichment and N-deposition, all known to affect woody–herbaceous ratios, are superimposed on this topography–soil texture–rainfall template to further influence the pattern and rate of change in woody plant size, density and cover. Novel combinations of these factors may thus account for local and regional differences in rates and patterns of woody cover and community development.

#### *Woodland boundary dynamics*

The importance of local landscape runoff–runon phenomena in regulating woody plant community dynamics was further illustrated by the fact that the frequency distribution of TWI values varied such that portions of the landscape where woodlands had migrated upslope between 1976 and 1995 had significantly ( $p < 0.001$ ) greater mean ( $\pm$ SD) TWI values ( $8.83 \pm 1.34$ ) than the comparable upslope areas adjoining woodland boundaries that had remained static ( $7.30 \pm 0.83$ ) (Figure 2c). The properties of these static vs. dynamic woodland boundaries and their behavior since the 1940s has been documented in more detail elsewhere (Stroh 1995; Stokes 1999), and soil samples collected along transects spanning their boundaries have failed to reveal differences in physical properties that might explain their different behaviors. Our results indicate that the

dynamics of woodland boundaries at the lowland-upland interface may be determined by catena-specific differences in catchment area and slope inclination. This inference is further supported by observations that (a) woodland boundaries tend to move upslope during relatively wet decades (periods of higher moisture that would augment runoff from uplands), and retreat during relatively dry decades (periods of less potential runoff from uplands) (Archer et al. 1988); and (b) while mean upslope movement of dynamic woodland boundaries was  $39.7 \pm 16.3$  m over the 19-yr-period of observation in this study ( $2.1 \text{ m y}^{-1}$ ), migration distances ranged from 11 to 72 m ( $0.6\text{--}3.8 \text{ my}^{-1}$ ) at specific locations along dynamic boundary segments. These combined observations support the hypothesis that woody plant dynamics on catena gradients are affected by differences in the amount of runoff and by variation in the capture of that runoff at footslope locations.

#### *Implications for tree–grass interactions*

Explanations accounting for grass–woody plant interactions are often based on how the contrasting root systems of these two life forms access moisture from coarse vs. fine-textured soils (e.g., Scholes and Archer 1997; Breshears and Barnes 1999; Rodriguez-Iturbe 2000). However, our data suggest topographic redistribution of water can override soil texture effects that might otherwise dictate the relative abundance of woody vs. herbaceous plants. Redistribution and concentration of water is an important determinant of the structure and productivity of vegetation in drylands (Noy-Meir 1973; Bergkamp 1998), particularly with respect to the banded or ‘tiger-stripe’ patterns of woody plant distribution (e.g., Montana 1992; Ludwig et al. 1997, 1999; Wu et al. 2000; Tongway et al. 2001). In our system, differences in catena-scale runoff–runon phenomena, as assessed with TWI based on catchment area and local slope inclination, appear to offer a reasonable explanation for observed differences in the spatial distribution of savanna parkland vs. woodland vegetation types along topoedaphic gradients. Furthermore, catena-scale variation in TWI values helps explain why savanna–woodland boundaries may be relatively static on some landscapes and

more dynamic on others. Observed differences in TWI values suggest that experimental manipulations and quantification of surface runoff/runon and subsurface flows and soil moisture levels along contrasting catena gradients would be instructive next steps in gaining a mechanistic understanding of the ecohydrology of tree–grass dynamics.

Spatial patterns of woody and herbaceous vegetation in these savanna parkland landscapes were characterized by scale multiplicity (Wu 2004) in that they were hierarchically structured, with distinct ecological mechanisms operating at different domains of scale (Wiens 1989). Our data support results from other studies that suggest patch-scale upland vegetation patterns are controlled primarily by differences in subsoil texture (Archer 1995a); and indicate that catena-scale vegetation patterns are controlled primarily by topography-mediated surface hydrological processes. It is expected that changes in woody–herbaceous ratios caused by changes in disturbance regimes (e.g., grazing, browsing, fire) or atmospheric chemistry ( $\text{CO}_2$  enrichment; N-deposition) will be constrained by scale-dependent topography–soil texture relationships and will play out differently in areas of higher or lower annual rainfall. Models of vegetation dynamics may therefore need to explicitly account for rainfall–topography–soil texture relationships and associated scale-dependent mechanisms to accurately predict the future rate and pattern of changes in woody and herbaceous plant abundance.

#### **Acknowledgements**

This work was supported by a NASA grant NAG5-11238 and NSF Grants DEB-9815607, 0303886 and 9981723. Our sincere thanks to Xiaolian Ren for her assistance in developing the GIS database for the La Copita, processing aerial photo images and conducting preliminary data analyses. The efforts of Dave McKown, manager of the La Copita Ranch, in facilitating this research are also appreciated. We thank John Ludwig, David Breshears, Brad Wilcox, Rusty Feagin, and three anonymous reviewers whose constructive comments helped improve the manuscript.



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