Chapter 15

PATTERN AND PROCESS IN SAVANNA ECOSYSTEMS

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1. Introduction

The spatial pattern of vegetation is both a cause and effect of variation in resource availability in semiarid ecosystems. At landscape to regional scales, climatic and geologic constraints on soil moisture and nutrient availability are primary determinants of vegetation structural pattern in semiarid ecosystems. Similarly, at local to landscape scales, the patchy vegetation structural mosaic serves to redistribute the availability of soil moisture and nutrients in ways that have important consequences for structural dynamics and community composition.

The investigation of vegetation organization as a means to understand underlying patterns in the environment originates in the first ecological writings and continues throughout the history of the discipline. Theophrastus (3rd Century BC) observed the distribution of deciduousness and evergreenness with respect to climate (Hort, 1916; Morton, 1981) and experimentally transplanted plants to areas outside their natural range to determine if they would grow (or flower). The pioneering work of the early American ecologist, Henry Chandler Cowles (Cowles, 1899) documented the succession of vegetation as the cause of spatial variation in composition observed across dune formations of different ages. In this work, Cowles anticipated both the individualistic nature of the response of plant species to their environments (e.g. Gleason, 1927) and the "continuum concept" of species distribution along environmental gradients (McIntosh, 1967; Austin, 1985). Indeed, the historical foundation of plant ecology in biogeography (Humboldt, 1807) is itself an indication of the critical interactions between the large-scale spatial organization of the physical environment and the distribution of vegetation in the landscape. These same relationships were observed 3 millennia earlier by Theophrastus, who noted the positive relationship between altitude and latitude with respect to their climates and vegetation.

Today as in the past, relationships observed between environmental conditions and plant occurrences are fundamental to the study of plant ecology (Greig-Smith, 1979; Grime 1979; Tilman 1982; Weiher and Keddy, 1999). The concept that ecological processes are evident in vegetation patterns was formalized by Watt (1947), and this paradigm has often been used to investigate the relationships between the spatial structure of vegetation and the nature of competition, disturbance, and resource heterogeneity across a range of ecosystems. Even still, many outstanding issues in plant ecology are directly related to our incomplete understanding of the dynamics and persistence of spatial patterns (Levin, 1992). These include:

1) the relationship between competition/facilitation, spatial pattern, and the persistence of biodiversity;
2) the relative importance of biotic and abiotic factors in structuring vegetation communities;
3) the role of both current and former plant patterns in determining the spatial distribution of resource availability; and

4) the time and space scales over which various disturbances affect spatial pattern and the consequences of spatial disturbances on long-term stability of vegetation communities.

Semi-arid ecosystems (most notably savannas), exhibit a number of characteristics relevant to the investigation of these unresolved issues in spatial ecology. A most striking characteristic of savannas is their pronounced functional diversity in the form of tree/grass coexistence. The maintenance of this functional diversity is directly tied to question (1) above. Though extensive in distribution, savannas exhibit a high degree of small-scale spatial heterogeneity and maintain strong interactions between biotic and abiotic determinants of both soil moisture (see Chapter 7) and nitrogen availability. These factors make savannas ideally suited to address questions (2) and (3). In addition, disturbances such as fire and herbivory are ubiquitous in savanna vegetation and the importance of these disturbances is at the core of question (4).

The ecological relevance of savannas has encouraged many studies and theories regarding the nature of spatial patterns and the consequences of pattern on the dynamics of savanna vegetation. In this chapter, we will summarize the methods used to assess spatial pattern in savannas and the conceptual frameworks employed to integrate pattern and process in savanna ecosystems. Where possible, we will connect these methods and concepts with results from our own investigations on the nature and consequences of pattern in the Kalahari savannas of southern Africa. Although our examples are drawn mostly from savannas and our own results are specifically from southern African savannas only, many of the methods and concepts are equally applicable to other semi-arid vegetation communities.

2. Southern African Savannas

Savanna ecosystems vary systematically along gradients of available moisture and available soil nutrients (Scholes and Walker, 1993) and they are profoundly influenced by wildfire, by grazing animals, and by human modification to both fire and grazing regimes (Walker and Noy-Meir, 1982). Savannas are not a narrow "transition" vegetation between conditions that favor grasses and conditions that favor trees (Jeltsch, 1998). Rather, they occupy a substantial part of natural gradient of soil moisture and nutrients as well as a considerable portion of the arable land in Africa. In southern Africa, tropical savannas are extensive but varied, ranging from partially-closed woodlands to sparsely-covered scrublands (Scholes *et al*., 2002). Many tropical savannas are found in semi-arid climates where a constantly changing distribution of soil moisture is supplied by predominately convective storms that vary considerably in both frequency and depth (Sala and Laurenroth, 1982; McCown and Williams, 1990; Hutley *et al.,* 2001).

The Kalahari Transect (KT) provides a unique opportunity to investigate vegetation pattern in semi-arid savanna ecosystems across a number of spatial scales. The distribution of Kalahari sands occupies a third of southern Africa (Scholes and Parsons, 1997). The KT is one of a number of IGBP transects designated throughout the world (Koch *et al*., 1995), and spans a latitudinal rainfall gradient varying from 250 mm/year in the south to 1000 mm/year in the north. Although low frequency periodicities in annual rainfall have been observed for most of southern Africa (Tyson, 1986), rainfall events in the Kalahari are largely convective, and locations throughout the Kalahari Transect experience large variability in inter-annual rainfall amounts. The coefficient of variability in annual rainfall for the 20th century ranges from a minimum of 16% in the north to over 40% at the transect's southern extreme. The large gradient in both the mean and variation of annual rainfall results in dramatic changes in vegetation structure across the study sites (Scholes, *et al*., 2002; Caylor *et al.*, 2003; Privette *et al*., 2003), and vegetation type ranges from partially closed woodlands in the north to open shrub land in the south. Throughout the KT, the mixed life-form composition characteristic of savanna communities is maintained. The consistency in geomorphology over the entire region -

primarily deep Kalahari sands (Thomas and Shaw, 1991) - allows for an analysis of vegetation structure and ecosystem processes independent of soil type. These structural changes, coupled with the regional rainfall gradient lead to changes in the relative contribution of trees and grasses to vegetation productivity across the transect (Dowty *et al*., 2000; Caylor *et al*., 2004).

3.   A conceptual organization of spatial pattern and process in savannas

The persistence and extensive distribution of savannas has spawned a number of theoretical models of tree-grass coexistence. These differ in their underlying assumptions about the importance of soil moisture and nutrient limitation and the ways in which trees and grasses access and use soil moisture and nutrients. Initial dynamic models of tree-grass coexistence assumed that soil moisture is horizontally homogeneous (Eagleson and Segarra, 1985), and that competition for soil moisture is sufficient to explain observed patterns of vegetation in semi-arid systems (Yeaton and Cody, 1976; Phillips and MacMahon, 1981). Walter (1971) postulated a niche-differentiation model to explain a balance of trees and grasses at equilibrium. This model was based on tree and grass roots using different soil different layers for their water supplies - trees having deep roots and grasses having shallower roots. Due to a lack of direct evidence of a two-tiered layering of root structure in many savanna environments (Seghieri, 1995; Mordelet *et al*., 1997; Hipondoka *et al*., 2003), the importance of vertical niche-differentiation as a means of stabilizing savanna dynamics has been questioned. Accordingly, the Walter model has been modified in a number of ways to better approximate field observations (Eagleson and Segarra, 1985; Scholes and Archer, 1997).

As an alternative to vertical variation in soil moisture access, the role of horizontal heterogeneity in maintaining savanna vegetation structure has been increasingly explored. A striking characteristic of savanna vegetation (and semi-arid vegetation in general) is the pronounced patchiness exhibited across scales ranging from tens of meters to tens of kilometers. A particular challenge in understanding the importance of this patchy structure is that the characterization of horizontal spatial pattern depends strongly on the manner in which the pattern itself is conceptualized. The differences in these conceptualizations and how they affect the interpretation of spatial pattern is the focus of this chapter. To this end, we define three "types" of vegetation pattern: (1) Individual-based; (2) Patch-based; and (3) Intensity-based. Figure 1 provides a summary of these three types of pattern characterization for a single representation of hypothetical vegetation structure, and Table 1 provides a summary of the ways in which these conceptualizations are manifested in analyses of semi-arid ecosystems. Before discussing the methods used to describe and analyze these various types of spatial patterns, we will briefly distinguish how observations of patterns and process are coupled to develop conceptual models of pattern dynamics in semi-arid ecosystems.

4.   Links between pattern and process

Any observation of spatial pattern is associated with a distinct conceptual framework that determines how pattern is characterized, as well as how pattern is used to inform dynamics of vegetation structure (Table 1). The basis of all vegetation pattern is the distribution of individual plants. The individual-based distribution of plants may be described along a single dimension as a transect, or within a two-
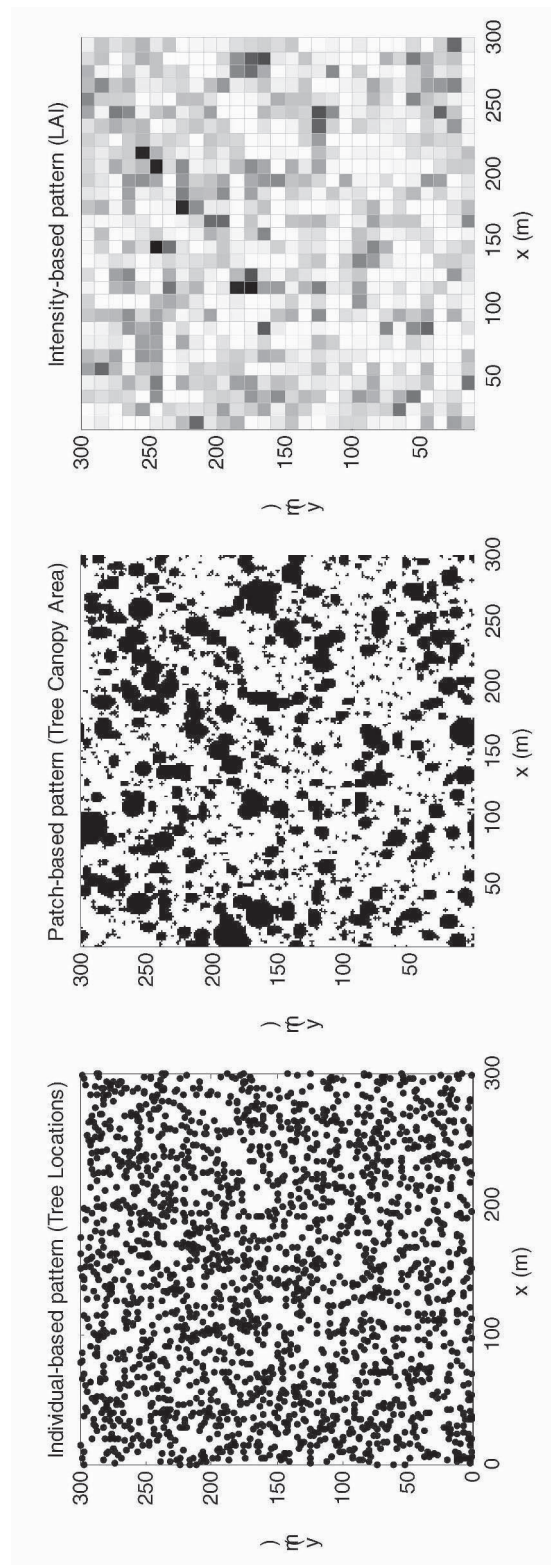
Figure 1. Three different views of vegetation pattern for a single hypothetical dataset of savanna vegetation structure. The individual-based pattern depicts the location of each tree in a 300 x 300 meter area. The patch-based pattern displays the projected canopy area of the canopy trees, and the intensity-based pattern depicts leaf area index aggregated to a 10-meter grid. The individual-based distribution provides the most information on competition and spacing, while the patch and intensity-based patterns provide greater information on the scale of landscape patchiness, and heterogeneity

Table 1 Summary of pattern observations and conceptualizations commonly employed in savanna vegetation. Citations to recent articles employing each method are provided, as well as references to example figures and analysis provided in this chapter.

Observations of savanna spatial pattern

Vegetation pattern as...	Pattern is described by...	Analysis techniques	Recent examples for semi-arid vegetation
... a discrete distribution of individuals (cf. Figure 1a)	Mapped plant positions within a study area	1 – Nearest neighbor 2 – K-function [Figures 2 & 3] 3 – Fourier analysis	1– Miriti et al., 2001 2 – Caylor et al., 2003; Schenk et al., 2003; Barot et al., 1999 3 – Couteron, 2001
... a continuous distribution of landscape components or patches (cf. Figure 1b)	Spatially contiguous field-based or remotely-sensed observations of landscape patches	1 – Change detection [Figure 4] 2 – Patch size distribution [Figure 5] 3 – Scaling analysis [Figure 6]	1 – Archer et al., 1998; Hudak & Wessman, 2001 2 – Li and Archer, 1997 3 – Ludwig et al., 2000
... a continuous distribution of intensity (cf. Figure 1c)	Spatially contiguous field-based or remotely-sensed observations of vegetation intensity (e.g. NDVI, LAI)	1 – Autocovariance & autocorrelation 2 – Fractal dimension [Figure 8] 3 – Scale analysis [Figure 9]	1 – Pearson, 2002 2 – Chen et al., 2002 3 – Caylor et al., in review; Qi and Wu, 1996

Conceptualizations of savanna spatial pattern

Vegetation pattern as...	Relevant spatial conceptualization is...	Modeling techniques	Recent examples for semi-arid vegetation
... a spatially interactive distribution of individuals	The spatial location of each individual	1 – Individual-based models 2 – Spatial moment-closure models	1 – Higgins et al., 2000; Simioni et al., 2000 2 – Bolker & Pacala, 1999
... a non-spatially interactive mosaic of patches	The relative abundance of each "patch" component	1 – Non-spatial patch models [Figure 7] 2 – Markov transition models	1 – Breshears & Barnes, 1999; Caylor et al., in press 2 – Bestelmeyer et al., 2003
... a spatially interactive mosaic of patches	The spatial location of each individual patch	1 – Cellular automata 2 – Interactive landscape models	1 – Van Wijk & Rodriguez-Iturbe, 2001 2 – Couteron & Lejeune, 2001; Boone et al., 2002; Ludwig et al., 1999

dimensional plot, three-dimensional canopy space, and even four-dimensional time series of change. Studies that attempt to characterize the density of individuals as well as the distances between individuals focus on this most basic of vegetation pattern description. Individual-based models of vegetation originated with forestry models in the mid-1960's. The initial models were well ahead of the digital computers of the time. They featured explicit 3-dimensional canopy interactions among trees, for example (see Shugart 1998 for review). In the early 1970's, simplifications in the competition algorithms under the rubric of "gap models" (Shugart and West 1980) allowed for an expansion of these applications into a large number of natural vegetation types (mostly forests). The consideration of forest "gaps" indicates the importance of mortality and regeneration in individual-based models, and therefore a key consideration in these models is the coupled spatial and demographic structure of the vegetation pattern. Unfortunately, the radical differences in scale of resource exploitation in the competition algorithm among plants of very different sizes (trees and grasses), as well as lack of a clear characteristic "gap size" has limited the development of individual-based models in savannas (Menaut et al., 1990). For savanna ecosystems the first such model was developed for West African palm savanna (Gignoux et al. 1995, Simioni et al. 2000). This model, called the LAMPTO model for its geographical location simulated the interactions among trees but treated the grasses as a homogeneous collection of leaf biomass. Peters (2002) has developed an individual-based grass-shrub model that is based on an earlier model of interaction of small alpine plants (Humphries et al. 2002, derived in turn from the ZELIG forest model of Urban et al. (1991)). Jeltsch et al. (1996) and Higgins et al. (2000) also presented cellular automata models of individual tree growth and demographics. These models contain greater detail regarding woody vegetation demography, but reduced emphasis on biophysical fluxes of carbon, nitrogen and water. All of these models emphasize the spatial distribution of individual trees, with reduced emphasis on the spatial organization of grasses. The challenge of "scaling-up" individual-based models to landscape-scale representations of vegetation structural pattern and structural change is an important and ongoing research task (Bolker and Pacala, 1999).

In many cases, the absence of clear scaling rules for individual-interactions makes it difficult to predict changes in vegetation structure and pattern at landscape scales. In addition, the presence of distinctly "patchy" structure in such varied ecosystems as semi-arid woodlands (Whittaker et al., 1979), annual grasslands (Wu and Levin, 1994) and rocky-intertidal marine communities (Levin and Paine, 1974) has fostered the development of a patch-based mosaic theory of vegetation dynamics (Levin et al., 1993). The division of a landscape into discrete land cover types is an obvious example of a patch-based pattern description, while the conceptualization of a savanna into "tree" and "grass" patches is another. In most patch-based descriptions of spatial pattern, information regarding the exact location (and size) of individual organisms is eliminated in favor of a more conceptually tractable description of the overall landscape organization. The applications of patch-based pattern to understand the dynamics of savanna vegetation include both spatially interactive and non-spatial mosaic models, as well as stochastic Markov-transition models. Patch-based models incorporate spatial processes either through spatially-explicit landscape-scale spatial heterogeneity (Coughenour, 1992) or grid-based cell automata (Gignoux et al., 1995; Jeltsch et al., 1998; Wijk and Rodriguez-Iturbe, 2002). These spatially-interactive mosaic models have proven to be particularly useful in diagnosing the dynamics of banded semi-arid vegetation mosaics, such as "tiger bush" (Lefever and Lejeune, 1997; Lejeune and Tlidi, 1999), where limited soil moisture and sloping terrain lead to the formation of alternating bands of bare soil and vegetation that organize in response to anisotropic gradients of soil moisture availability. Non-spatial patch models include classic "equilibrium-based" models that focus on competition for soil moisture (e.g. Walker et al., 1981), as well as more modern biogeochemical models that include nutrient cycling and disturbance (Daly et al., 2000). The use of pseudo-spatial patch models that allow various degree of interaction between landscape components (Breshears and Barnes, 1999; Caylor et al., in press) have proven particularly adept at examining the dynamic balance between structural pattern, vegetation dynamics and resource availability in savanna ecosystems. Markov-transition models describe the savanna landscape as a series of discrete states, with transition probabilities associated with the conversion of each state into any other (Shugart, 1998). These models have been applied in rangeland management (Bestelmeyer et al., 2003), but generally lack the mechanistic detail to accommodate changes in environmental factors without extensive parameterization.

A third way of expressing the structure of vegetation communities is the description of spatial pattern as the spatially-explicit intensity of a continuous variable such as biomass or leaf area. This intensity-based pattern description is often associated with remotely-sensed data, and is rapidly emerging as the most common representation of vegetation pattern over large areas. The incorporation of these intensity-based patterns into a conceptualization of savanna dynamics is most difficult, since the abstraction of savanna pattern as a continuous distribution of leaf area or biomass eliminates most of the demographic and structural information necessary to predict vegetation change. The availability of remotely-sensed data has allowed to large-scale estimates of

vegetation productivity (Prince and Goward, 1995), and recent Dynamic Global Vegetation Models (DGVM's) include modules that simulate the behavior of different life forms of plants and apply these in regional scale patches for global simulations of vegetation dynamics (Potter et al. 1993, Woodward et al. 1995, Delire et al. 2003). The same approach can be used to represent the productivity of different life forms of savanna plants using remote sensing products that estimate intensities off grass, trees, shrubs, and bare ground at smaller scales. Development of canopy productivity models in semi-arid ecosystems (Hanan *et al.*, 1997; Dowty *et al.*, 2000) has allowed for smaller-scale estimate of vegetation production derived from either field-based or remotely-sensed intensity-based observations of canopy structure (Caylor and Shugart, 2004; Caylor *et al.*, 2004). The relationships between environmental variability and vegetation function derived from these small-scale canopy production models can be incorporated into larger-scale simulations of regional production to yield estimates of changes in tree/grass production associated with climatic variability (Hély *et al.*, 2003a) or regional fuel load production and biomass burning (Hély *et al.*, 2003b). This multi-scale approach of nesting biophysical canopy production models into large scale landscape productivity models should be extended into the patch-based and individual-based approaches in order to simulate multi-year changes in structural pattern and composition (Shugart, 2000; Shugart *et al.*, in prep). The difficulty encountered integrating these various approaches (i.e. combining canopy production models with individual-based demographic models) highlights the conceptual challenges facing a synthesis of pattern and process in semi-arid ecosystems.

Of the three types of pattern descriptions (individual, patch, and intensity), the individual-based description requires the greatest amount of field-data collection, while the patch- and intensity-based descriptions are highly sensitive to the spatial resolution of observation. Each conceptualization leads to distinctly different approaches for predicting the nature of spatial pattern and structural dynamics in savanna ecosystems. While no single method is appropriate or practical in all instances, certain methods are better suited to address certain questions than others. In addition, as the spatial scale of observation increases, the abstraction of vegetation spatial pattern tends to become greater so that there exist correlations between each of these conceptualizations and the scale at which they are applied. It is our strong belief that any synthesis regarding the important role that spatial ecology plays in savanna ecosystems depends on a proper appreciation of the diversity of strengths, weaknesses, and assumptions that underlie the observation and application of each of these three conceptualizations of spatial pattern, as well as the development of methods that integrate patterns observed across the various spatial scales and conceptual frameworks.

5.   Spatial pattern as a distribution of individuals

A primary method of vegetation pattern analysis is the assessment of the distribution of individuals within a study area. The locations of plants are usually mapped so that the data are a series of zero-dimension point locations which exist in a plane (e.g. Figure 1a). Of particular interest in this type of analysis is the relative amount of aggregation or dispersion between individuals. In general, the significance of the observed pattern is derived from statistical inferences regarding the expected distribution of points, which is assumed to be generated according to a poisson process acting within the region considered (Diggle, 1983). The deviation between the observed distribution and the poisson process allows for the classification of spatial pattern as a continuum moving from highly aggregated communities to regularly spaced or hyper-dispersed communities, with random distribution patterns (i.e. showing no effect of either pattern) occupying the middle of the continuum (Ripley, 1976). The presence of a particular pattern is often associated with the operation of ecosystem-specific processes that serve to structure the community in a non-random manner (Dale, 1999).

The occurrence of hyper-dispersed (also termed "uniform" or "regularly spaced") community patterns has been explained as the result of density-dependent mortality associated with competition for a homogeneously distributed resource (Beals, 1968). In contrast, the observation of clumping in savanna ecosystems has been associated with high rates of disturbance or the presence of nurse sites for seedling establishment (Raffaele and Veblen, 1998). In particular, it has been hypothesized that clumping in savanna communities is a response to high fire disturbance (see Chapter 16 for a more complete analysis of fire regimes), as vegetation in the centers of clumps tends to persist after a fire (Gignoux *et al.,* 1995). It is important to realize that regardless of the particular pattern found, the observation of pattern itself cannot elucidate the process of cause without appropriate experimental manipulation of the community under investigation (Cale *et al.,* 1989). Regardless, the observation of a particular pattern serves to establish the presence of non-random structuring mechanisms within a community and to indicate the direction in which experimental investigations should proceed.

5.1. INDIVIDUAL-BASED OBSERVATIONS

5.1.1.   Nearest Neighbor methods

The low-density and seemingly uniform spacing of woody vegetation in many arid systems has fostered the hypothesis that individuals in savanna communities exhibit a high degree of competitive exclusion. Consequently, there have been a variety of studies investigating the spatial pattern of woody vegetation, many of these focusing on the interaction between species pairs using nearest neighbor techniques (Pielou, 1962). Work in the Mojave and Sonoran deserts (Yeaton and Cody, 1976; Yeaton *et al.,* 1977) shows size-dependent species dispersion patterns between *Yucca schidigera, Opuntia acanthocarpa* and *O. ramosissima.* Cody (1986) found that levels of positive and negative associations in nearest-neighbor distance were species dependent for a range of woody shrubs in a diverse Mojave Desert community. These patterns were attributed to differences in root system structure and germination requirements. In southern Africa, Smith and Goodman (1987) explored spacing relationships between *Acacia nilotica* and *Euclea divinorum* in the Mkuzi Game Reserve, South Africa. Their work showed a clear size-dependent nearest-neighbor exclusion pattern in mature *Acacia* individuals and understory *Euclea*, supporting the hypothesis of density-dependent spatial regulation of water-limited savanna systems.

5.1.2.   Second moment analysis

In addition to nearest-neighbor analysis the spatial pattern of a community can be examined across a range of spatial scales, and therefore provide a more comprehensive picture of vegetation pattern at a site (Clark and Evans, 1954; Ripley, 1977).   Phillips and MacMahon (1981) found numerous instances of aggregated dispersion patterns for saplings of 11 different species in 9 different sites across the same region, with little tendency for larger individuals to form aggregated dispersion patterns. The tendency for individuals to change from aggregated to random and occasionally uniform distributions with increasing size (and decreasing density) was taken as evidence of density-dependent mortality associated with the homogeneous distribution of soil moisture in a moisture-limited environment. Skarpe (1991) investigated the dispersion of *Acacia erioloba* and *Acacia mellifera* in both mono-specific and mixed plots near Naojane, Botswana, and found a tendency for saplings of both species to exhibit aggregated distributions. Mature individuals in her plots exhibited a random spatial distribution. More recently, Jeltsh *et al.* (1999) used aerial photography to examine vegetation patterns in the Kalahari Gemsbok Park in southern Botswana. They found patterns that were generally aggregated at four out of six study sites, and random at the other two. Both Skarpe and Jeltsch's sites were located in the southern portion of the Kalahari Desert.

The interpretation of spatial pattern in a particular vegetation community necessarily depends on an understanding of how the observed pattern differs from the null hypothesis of complete spatial randomness. When individuals are distributed according to a Poisson process, the expected number of individuals within some distance t of any particular individual is $K(t)=\rho\pi t^2$, where ρ is the density of individuals. This K-function can be further transformed into an L-function such that $L(t)=K(t)-\rho\pi t^2=0$. Since the L-function, $L(t)$, is only valid for individuals distributed under an ideal Poisson process, it is necessary to compare observed results at a field site with the results of multiple simulated calculations using the same density of individuals distributed randomly in an identically sized sample area. The use of sufficient simulations allows for minimum and maximum confidence intervals ($L_{min}(t)$ and $L_{max}(t)$, respectively) to be put on the expected values of $L(t)$ for any distance within the plot. Values of $L_{obs}(t)$ calculated for the actual distribution of individuals sampled in the field plot can then be compared to these thresholds to determine the significance of observed distribution patterns in the sampled data. Since the analysis is essentially a measure of the deviation between the number of observed events and the expected deviation under complete spatial randomness, values greater than $L_{max}(t)$ indicate significantly clumped or aggregated patterns within the plot, and values less than $L_{min}(t)$ indicate significantly uniform or hyper-dispersed patterns. Values of $L_{obs}(t)$ falling between $L_{max}(t)$ and $L_{min}(t)$ indicate random distributions. Using this technique, it is possible to determine the character of spatial pattern within each site. Furthermore, subsets of community data based on vegetation characteristics can be analyzed to examine the distribution patterns peculiar to that population. Care should be taken when forming these subsets, as pattern may be the result of interactions between events not contained within the subset itself. For example, $L(t)$ functions for small size-classes of individuals (e.g. saplings and seedlings) can be difficult to interpret independently of the distribution of large individuals, due to the high possibility of asymmetric effects between large and small individuals (Keddy, 1989).

Figure 2 provides an example of the L-function results for a single site along the Kalahari Transect, while Figure 3 provides a summary of individual-based spatial pattern across the entire transect. The lack of uniform

spacing in large individuals across the range of sites calls into question the idea of density-dependent processes as a means for determining vegetation structure in these systems. The high degree of aggregation in the spatial distribution of small individuals suggests that distribution of suitable regeneration sites and subsequent patterns of establishment may be critical phenomena in determining the spatial pattern of vegetation (Higgins *et al.,* *2000*).
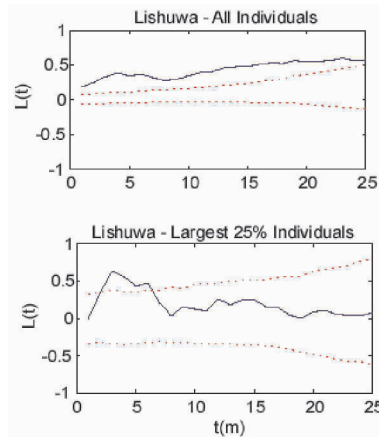

Figure 2. Individual-based pattern of distribution for all trees and the largest 25% trees at the northern-most Kalahari Transect site derived from second moment analysis as presented in Caylor et al. (2003). The L(t) function represents the departure of pattern from the hypothesis of complete spatial randomness, with L(t)>0 indicating aggregation, L(t)<0 indicating hyper-dispersion and L(t)=0 representing a purely random distribution. Dashed lines represent the 95% confidence intervals for a series of monte carlo simulations. At all distances, the distribution of the entire community is observed to be significantly aggregated, while the distribution of large individuals is observed to be predominately random, with some significant aggregation observed at spatial scales of 3-7 meters. These results suggest that the smaller individuals are causing the highly aggregated pattern observed for all individuals.

5.2. SPATIAL PATTERN AS A DISTRIBUTION OF PATCHES

In contrast to the view of savanna vegetation as the distribution of individual plants, it can be convenient to define savanna landscapes into a finite number of elements or patches. Typically, distinctions are made between tree cover, grass cover, and bare soil so that the landscape can simply be described as the fraction of each component present. More complex patches can be defined when data permit – often patches with small trees or mature tree patches with grass are considered independently. The complexity of patch definition is usually associated with the detail included in the field survey, with the most detailed approaches converging on individual-based techniques described above.

5.2.1.   Patch-based observations
In many semi-arid ecosystems the primary patch-based distinctions made are between woody canopy vegetation and non-woody canopy portions of the landscape. An underlying assumption of any patch-based pattern analysis is that the patch definitions (e.g. "tree patches" and "non-tree patches") are an ecologically meaningful description of savanna landscapes. The significance of this portioning is supported by the many studies that have investigated the effect of tree canopies on various components of soil water balance and nutrient availability. Observed effects of tree canopies include an increase in soil moisture storage and drainage under tree canopies (Joffre and Rambal, 1993); an increase in soil temperature, soil drying time and soil water deficit between tree canopies (Breshears *et al.,* 1997; Breshears *et al.*, 1998); and strong contrasts in light availability, temperature and soil moisture between the under-canopy and between-canopy environment (Belsky *et al.*, 1989; Belsky *et al.*, 1993). More recently, Jackson and Wallace (1999) described as much as a 40% reduction in bare soil evaporation under tree canopies in a Kenyan agro-forestry plantation and Smit and Rethman (2000) report increased infiltration and evapotranspiration of experimentally thinned plots of Mopane woodland (*Hardwikia mopane*). The difference between soil moisture under and between tree canopies has been used to explain observed patterns of herbaceous productivity of humid West African savannas (Menaut and Cesar, 1979; Mordelet and Menaut, 1995).
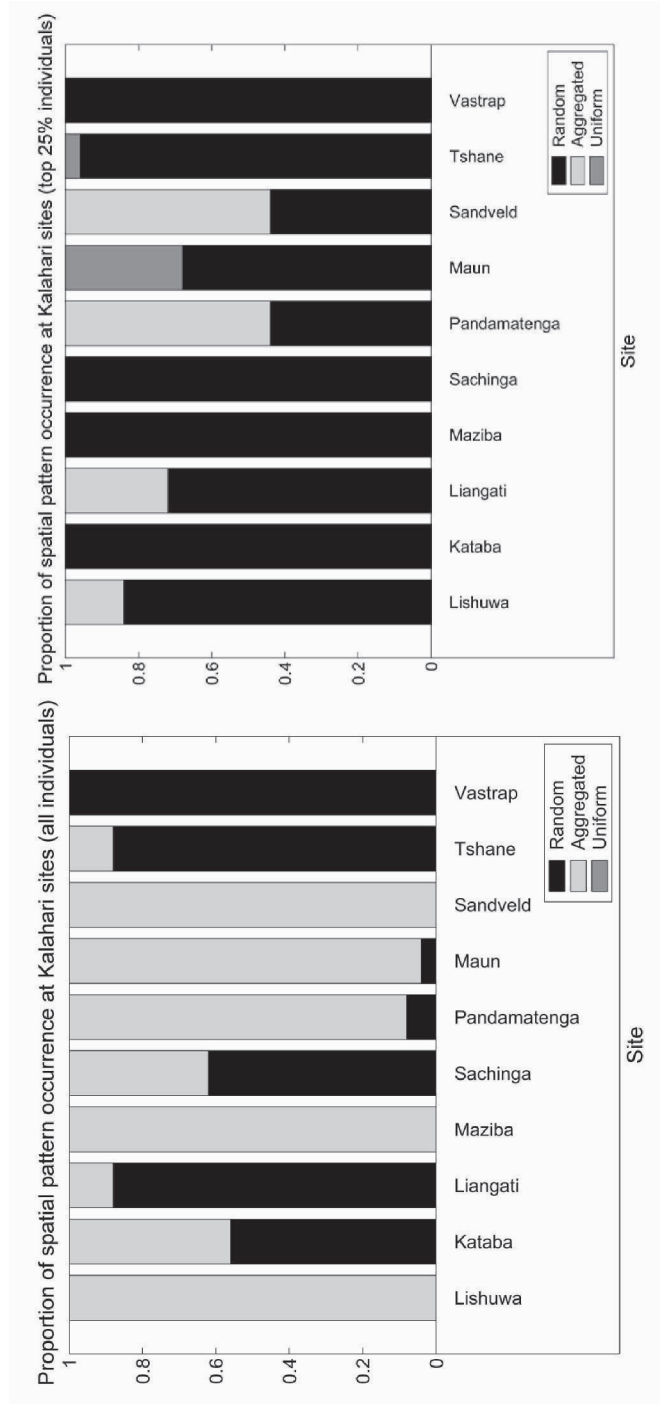
Figure 3. Individual-based pattern of distribution for all individuals and large trees at each of the 10 sites across the Kalahari Transect derived from second moment analysis as presented in Caylor et al. (2003). At most sites, the distribution of large individuals is observed to be more random than the distribution of all individuals, which is predominately aggregated. Some aggregation of large trees occurs at four out of ten sites, and uniform distributions are only observed in large individuals at two out of ten sites.

Tree canopy-related soil moisture changes have been shown to impact seedling germination of southern African woody vegetation (Keya, 1997; Wilson and Witkowsk, 1998) and woody species distribution patterns (Smith and Grant, 1986; Smith and Goodman, 1987). However, the effect of tree canopies is not always consistent; observed differences in canopy microclimate led to higher productivity of grass under trees in a low-rainfall savanna, but a lower relative productivity of under-canopy grasses in a high-rainfall savanna (Belsky *et al.*, 1993). Similar patterns were observed by Ludwig *et al*. (2001), who found that the effect of tree canopies on herbaceous productivity was determined by a balance of tradeoffs between facilitation and competition, with varying outcomes dependent on annual rainfall.

Patch-based approaches offer a distinct benefit over individual-based approaches by allowing for the incorporation of remotely-sensed data such as aerial photography. Such data are usually the greatest source of historical vegetation patterns in remote regions (Dunn *et al*., 1990). Kadmon and Harari-Kremer (1999) demonstrate the viability of image texture derived from aerial photography as a means for characterizing vegetation structure, particularly in heterogeneous environments. In open savannas, tree canopies can often be distinguished from the grass/bare soil background, so that a binary image of "tree patches" and "bare soil/grass patches" can be generated (e.g. Figure 1b). Such images allow for analysis of canopy cluster size, fraction of tree cover, and – when time series of data are present - rates of woody cover change. Archer *et al* (1998) use aerial photos to document 40+ years of woody vegetation change in southern Texan savannas. Their analysis of the aerial photography includes measurements of canopy patch density, size and spacing. In southern Africa, Hudak and Wessman (1998) use historical aerial photographs to estimate historical woody plant distribution in savanna regions of South Africa.
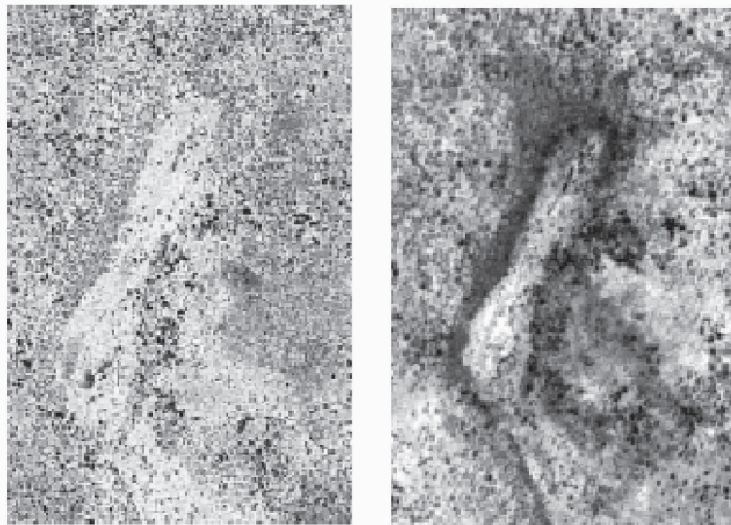

Figure 4. An example of observed change in vegetation in the Kalahari savannas as presented in Dowty et al. (2000). A comparison of declassified satellite (CORONA) data from 1967 (A) and an aerial photograph from 1995 (B) for a location in the Caprivi Strip region of Namibia show an expansion of vegetation along the edges of a shallow depression. Overall change in estimated woody cover is 27% over the 28-year period. In both images, the resolution is sufficient to discern individual tree canopies.

As a supplement to sparse aerial photography, satellite photographs from the recently declassified Corona project can also be used to infer historical patterns of vegetation structure

(Shugart *et al.*, 2001). Corona photographs meet three important criteria in regards to vegetation pattern observation and change detection: They have high resolution, are regional in extent, and are old enough to extract historical rates of change. In certain cases, individual trees and shrubs can be identified using Corona imagery taken in the 1960s, making it an excellent potential tool for exploring vegetation pattern and change in vegetation structure in semi-arid ecosystems. The suitability of Corona imagery for vegetation analysis in the KT region has been examined using two strips of Corona film taken in September of 1967 (Dowty *et al.*, 2000). The strips are sequential negatives taken by the forward facing camera on the KH-4B platform during Corona flight 120, which was launched on the 15th of September, 1967. This was the first flight to carry the KH-4B camera which had 2 meter ground resolution, and therefore the mission's acquisition represents the earliest available sub-5m resolution photos of the Earth's surface from space (McDonald, 1997). Figure 4 demonstrates the utility of the Corona data for analyzing vegetation change in semi-arid regions. Both the Corona image and an aerial photograph taken in 1995 are sufficiently detailed to discern individual trees. The observation of a 27% increase in woody cover between the 1967 Corona image and the 1995 aerial photograph is almost identical to the observed change in woody cover found in other regions of southern Africa over a similar time period (Hudak and Wessman, 2001).
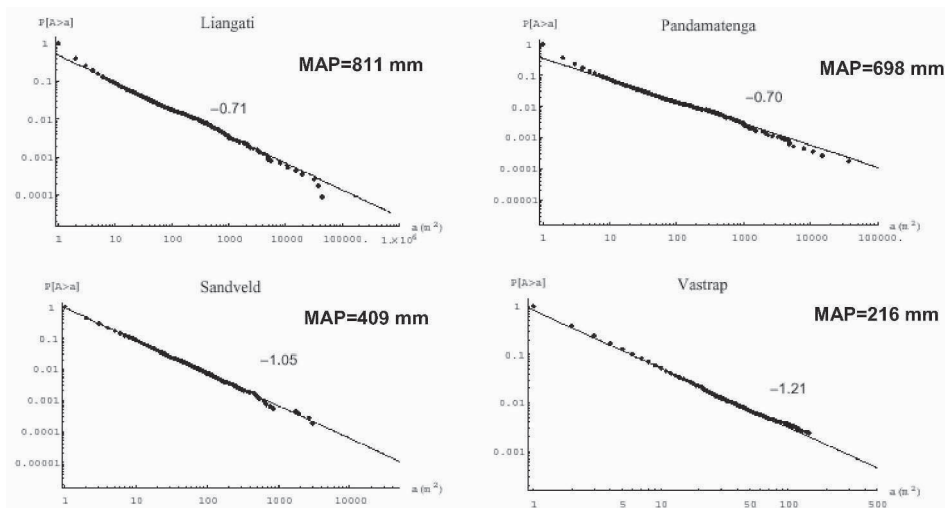

Figure 5. Probability distribution of the size of vegetation canopy cluster sizes. The size distribution at each site follows a power law probability distribution ($P[A \geq a] \propto a^\beta$). The slopes of the fitting lines are: (β=-0.71) Liangati; (β=-0.70) Pandamatenga; (β=-1.05) Sandveld; and (β=-1.21) Vastrap. As mean annual rainfall decreases, the slopes decrease indicating a decrease in the maximum cluster size observed at each site (note changes in the x-axis scale).

The application of fractal geometry to spatial analysis has extended descriptions of landscape patchiness described by classical Euclidean analysis of points, polygons and lines into the description of spatial configurations that are irregular, fragmented and disjointed. At the core of fractal geometry is the concept of scale-independence or self-similarity of patterns (Mandelbrot, 1983), such that observations of pattern at one scale inform the description of pattern at other scales through distinct scaling laws. Such patterns are often found in natural systems (Brown *et al.*, 2002), and can be easily demonstrated such diverse areas as the organization of stream networks (Rodriguez-Iturbe, 1997) mountain terrain (Dietler and Zhang, 1992), and plant morphology (Niklas, 1994). The application of fractal analysis to patterns of

vegetation structure has proceeded through a variety of methods (see Li, 2000 for a recent review). These include scaling properties of area-perimeter relationships in patch sizes (Krummel *et al.*, 1987), patch size distributions (Li and Archer, 1997), and the spatial autocorrelation of landscape pattern (Burrough, 1981).

Satellite-based assessments of the fractal patterns evident in savanna vegetation structural pattern can be achieved using recently available high-resolution commercial sensors. As example, we have used 1-m panchromatic data from the IKONOS satellite to determine the scaling properties of the size distribution of vegetation canopy clusters at four sites along the KT. The contrast between the bright, uniform sandy soils and dark vegetation canopies found across the Kalahari Transect makes the extraction of canopy features possible using simple binary threshold algorithms. In this case, we use the method described by Otsu (1979), which generates a black and white (binary) image from a grayscale image by minimizing the intraclass variance of the thresholded black and white pixels. The resulting binary matrix of vegetation canopies is then transformed into discrete clusters using 8-pixel adjacency to find contiguous vegetation canopies. The distribution of cluster sizes (Figure 5) is seen to follow a site-specific power law probability distribution, suggesting that the spatial structure of vegetation is scale invariant.

Any use of remote sensing data must contain a determination of what types of pattern (and change in pattern) can be detected based on observations at a given resolution. Woody vegetation dynamics are dependent on a number of factors (Skarpe, 1992), and the detection of change requires high-resolution spatial data over substantial time scales (Fransen *et al.*, 1998; Skarpe, 1991;Whiteman and Brown, 1998). These issues are particularly problematic in savanna ecosystems, where the small-scale interactions between individual organisms exert a strong control on the overall system dynamics and patterns of vegetation structure (Barot *et al.*, 1999). Therefore, in any discussion of remotely-sensed spatial patterns, it is critical to note that analysis techniques can only capture spatial pattern across a range of finite scales (namely the minimum scale of resolution). In order to demonstrate the critical role of spatial resolution in describing structural pattern, high-resolution data sets can be successively aggregated and parameters of vegetation structure can be repeatedly estimated. Using a simple unsupervised classification scheme with a 95% convergence threshold, we have derived estimates of woody vegetation cover in a 100 km area of savanna in the Caprivi Strip region of Namibia over a range of resolutions (5 to 1000 meters). As expected, our results demonstrate that estimates of percent tree cover exhibit a high degree of sensitivity to underlying data resolution, particularly at fine scales (Figure 6). In particular, where the sensor resolution is not sufficient to discern individual tree canopies, the effect appears to be an under-estimation of total woody vegetation cover.

5.3. SPATIAL PATTERN AS A DISTRIBUTION OF INTENSITY

The previous section discussed a number of patch-based descriptions that have been employed to conceptualize the pattern and important pattern-related processes that occur in savanna ecosystems. In many types of ecosystems these descriptions are often both a useful conceptual abstraction and an appropriate characterization of the overall landscape pattern. Indeed, the use of patch-based descriptions of savannas has led to substantial theoretical synthesis of savanna dynamics (Breshears and Barnes 1999). Unfortunately, the fine-scale structural heterogeneity present in savannas implies that many savanna landscapes exist not as distinct patches, but instead as surfaces of continuous variation. As such, the overall landscape pattern cannot be easily described using methods that presume the existence of clearly defined homogeneous units (i.e. "tree patches" and "grass patches"). In a recent study of northern Australian savannas, Pearson (2002) demonstrates that the treatment of savanna landscapes as homogenous units over-simplifies the complexity of their spatial structure, even in highly disturbed savannas. Furthermore, such over-simplification may lead to a reduced ability to monitor current and future changes in landscape health and quantify structural change.
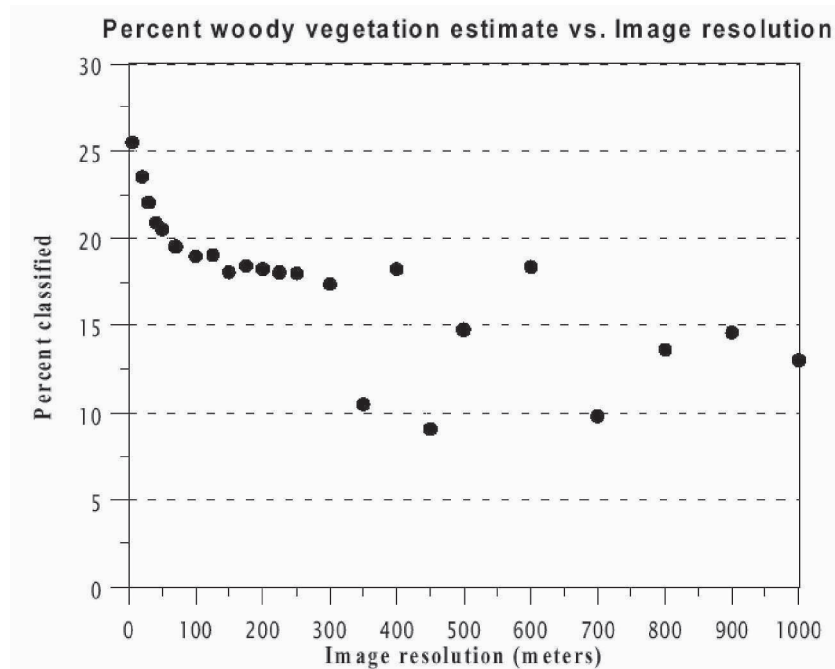
Figure 6. Effect of image resolution on percent woody cover estimation of declassified CORONA satellite data using a three-level unsupervised classification algorithm (adapted from Dowty et al., 2000). Increases in image resolution initially lead to lower estimates of total percent tree cover. At intermediate resolutions, the estimate of tree cover is highly variable with shifts in image resolution.

The introduction of multi-spectral remotely-sensed data has provided an additional incentive to define an "intensity-based" analysis of spatial pattern. Remote sensing data products such as the 18-year record of normalized difference vegetation index (NDVI) and emerging data sets such as the MODIS Leaf Area Index (LAI) product provide an aggregated sampling of the relative abundance of vegetation at a specific resolution. In contrast to the individual-based analysis of plant distributions or the patch-based segregation of the landscape into distinct spatial units, these data describe the continuous variation of a spatially extensive variable at discrete spatial scales (e.g. Figure 1c). When the resolution of the remotely-sensed data is sufficient to resolve individual plants, the distinction between "individual", "patch" and "intensity"-based pattern descriptions are blurred, although a passive sensor is never capable of re-creating the underlying individual-based data when the spatial extent of individuals overlaps. The use of spectral un-mixing approaches allows for patch-based inferences of pixel composition that can be derived from time series of intensity data (e.g. Scanlon *et al*., 2002). The use of radar-based observations for the delineation of individual tree canopies (Treuhaft *et al.*, 2002; Weishampel *et al.*, 1994), suggest that these intensity-based and individual-based approaches may exhibit greater overlap in the near future.

5.3.1. Intensity-based Observations

The use of intensity-based observations of vegetation structure requires spatial statistics to quantify patterns within the image data (*Stein et al.*, 1998). Spatial autocorrelation in image data can often be associated with physical properties of vegetation such as tree density and height (Bruniquel-Pinel *and* Gastellu-Etchegorry, 1998; Wulder and Boots, 1998). In addition to autocorrelation techniques, the semi-variogram can be used to estimate the scale and range of variation in an image (St-Onge and Cavayas*, 1995). To some extent, all measures of landscape variability are dependent upon the spatial resolution of measurement (Qi and Wu, 1996) and the methods of aggregation between resolutions (Bian and Butler, 1999).
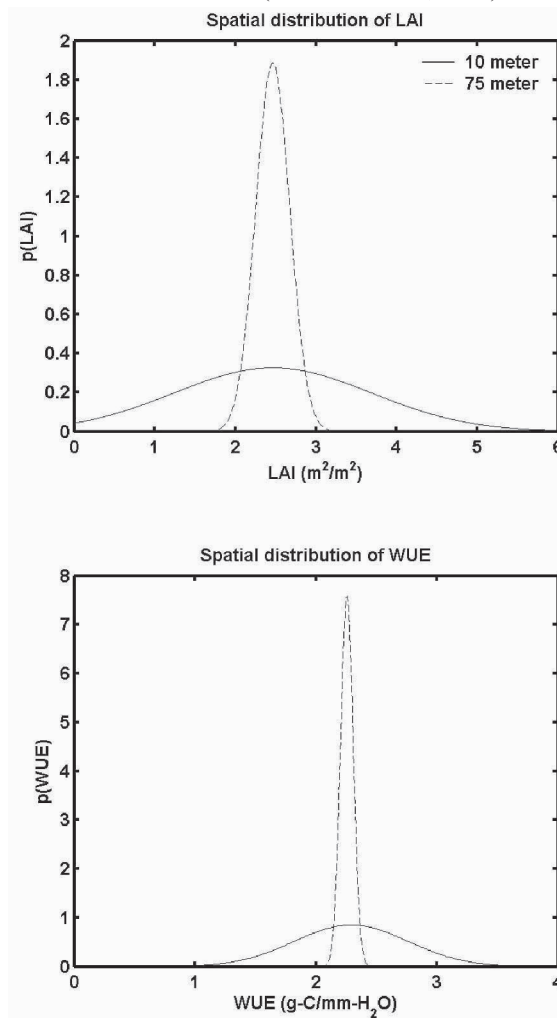

Figure 7. Effect of pattern resolution on simulation of processes in a non–spatially interactive savanna mosaic. The normalized distribution of tree leaf area (A) is provided at both 10 and 75-meter resolution (100m^2 and 5625m^2 pixels respectively) for a woodland site in western Zambia. The resulting distribution of simulated annual water use efficiency at each scale are also provided (B). Increases in the size of patch used for structural parameterization lead to rapid reductions in the range and variability of a key component of vegetation performance. The elimination of "extremes" in the distribution of water use efficiency and vegetation structure leads to an inability to discern demographic processes such as regeneration and mortality, which underlie the patchy mosaic structure.

Therefore, the accurate characterization of vegetation structural change depends not only on the presence of historical data, but also on an understanding of scale effects in heterogeneous tree/grass savanna mosaics (Figure 7). Characterization of vegetation structure using radar sensors has been performed in both forested areas (Sun and Ranson, 1998) and semi arid rangelands (Musick *et al*., 1998).

The fractal dimension, *D*, can be used to characterize the complexity of autocorrelation in image data across spatial scales. Because of the non-rectifiable nature of fractal patterns, the fractal dimension exceeds the topological dimension, *d*, but is less than *d+1*, so that in the case of 2-dimensional spatial pattern, *2<D<3*. Larger fractal dimensions are characteristic of patterns that exhibit short-range variation, and smaller fractal dimensions imply long-range variation. In practice, the fractal dimension can be derived from the slope of the semivariogram in a doubly logarithmic plot (Burrough, 1983; Lam and Cola, 1993; Chen *et al.*, 2002). Although patterns that exhibit self-similarity maintain the same fractal dimension across all scales, structured patterns such as those found in characteristic semi-arid vegetation mosaics yield scale-dependent measures of fractal dimension. Therefore, estimates of fractal dimension must be performed across a range of scales (Palmer, 1988). The scale-dependent fractal nature of spatial patterns in savanna ecosystems has been analyzed using the Corona data described above. Figure 8 displays the estimated fractal dimension of three different landscape types estimated at a range of scales. The three landscape types – pastoral, or undisturbed vegetation; township or settlement vegetation; and agricultural vegetation vary in their fractal dimension at high spatial resolutions, but converge as the resolution of the image is reduced. The undisturbed vegetation pattern exhibits the greatest fractal dimension, indicating that natural savanna vegetation is dominated by short-range variation characterized by the patchy distribution of individuals. The agricultural landscape is made up of a mosaic of small agricultural fields, which have a longer range of variation, and therefore the lowest fractal dimension.
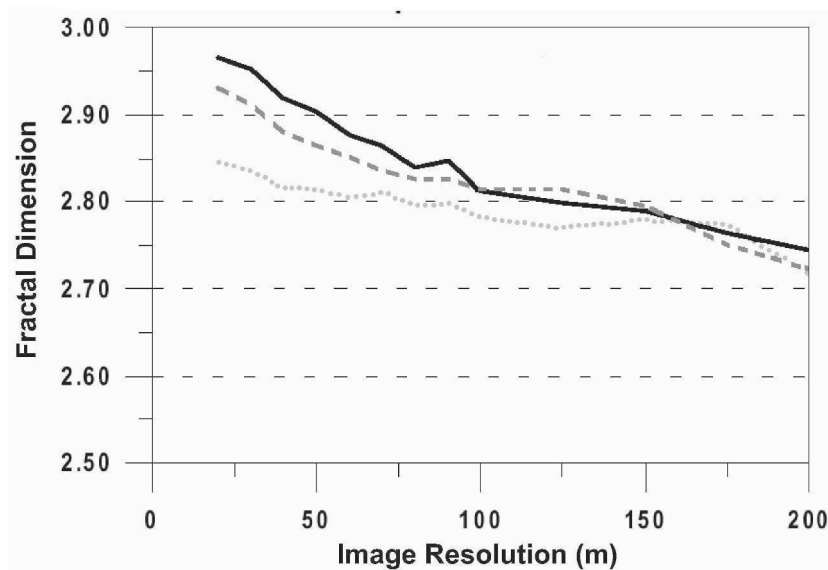

Figure 8. Landscape fractal dimension derived from semivariogram analysis as a function of image resolution and landcover type (adapted from Dowty et al., 2000). Pastoral (undisturbed) savanna vegetation [—] exhibits a greater fractal dimension at higher resolutions than either township [--] or agricultural [··] landscape mosaics. At coarser resolutions (>100m), the difference between the fractal dimension of landscape types is eliminated.

The availability of large-scale multi-resolution data sets of biophysical surface parameters has led to a number of insights into the scaling behavior of parameter fields across a wide range of spatial scales (Justice *et al*., 1989; Townshend and Justice, 1990; Smith *et al.,* 1992). Although studies of land-atmosphere interaction have demonstrated that the scaling of biological parameters will both be altered by and contribute to the formation of observed scaling patterns in physical parameters, few studies have investigated the scaling properties of vegetation structure directly (e.g., Sole and Manrubia, 1995; Chen *et al.*, 2002). High-resolution satellite imagery has been used to address the scaling properties of the variance in NDVI at scales ranging from 16-m^2 to 90,000 m^2 at four savanna and woodland locations across a large regional moisture gradient. Preliminary analyses of spatial patterns of NDVI show a change in scaling regime between the patch and the landscape scales. This is evidenced by log-log plots of the variance of NDVI as a function of the scale over which NDVI is averaged (Figure 9). A deviation in the expected linear decrease indicates a change in dominant pattern generating process. In the case of study sites on the Kalahari Transect there is a break in the linearity of the log variance curve that occurs at systematically larger scales as one transitions from the drier to the wetter end of the Transect. This change in breakpoint appears to be a consequence of plant canopy processes controlling pattern at small scales and other landscape processes then controlling pattern at larger scales. This implies that satellite data collection systems with differing resolutions might monitor the consequences of different processes and that for particular resolutions the same sensors might detect the consequences of different processes in different parts of the same region.
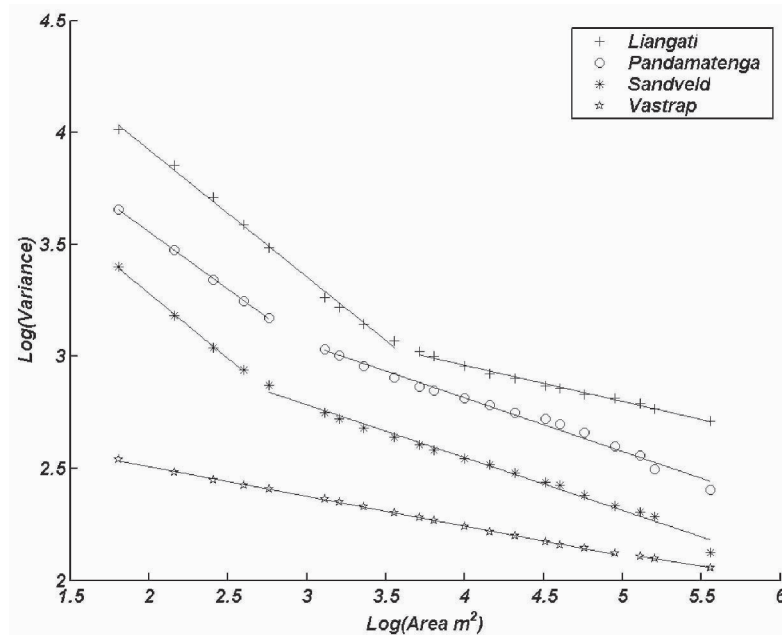

Figure 9 - Realization of the multi-scale nature of savanna ecosystems, depicting the variance of the NDVI field as a function of the area over which the field is averaged. The threshold scales between the distinct patch and landscape regimes are: (3600 m^2) Liangati; (576 m^2) Pandamatenga; and (400 m^2) Sandveld. No threshold scale is observed for the southernmost site, Vastrap. It is likely that the minimum scale of 16 m2 is insufficient to resolve the individual-patch scale pattern at the southernmost site, where vegetation is sparse and consists of small shrubs and isolated grass clumps.

6.   Conclusions

In this review we have compared various conceptualizations used to both observe and simulate spatial pattern in semi-arid ecosystems. A series of examples using field-based as well as both historical and recent satellite imagery has demonstrated the diversity of these approaches for measuring and interpreting spatial pattern in southern African savannas. These results contribute to the growing evidence of a multi-scale organization of vegetation in southern African savannas. Although the overall pattern of vegetation cover for the KT savanna is determined by mean annual rainfall and nutrient availability, small-scale patterns of vegetation structure are highly organized by internal processes, which operate at local scales. This conclusion has significant implications for 1) understanding how changes in global climate affect savanna ecosystems, 2) understanding how changes in savanna ecosystems affect the entire Earth system, and 3) monitoring vegetation at different resolutions in time and space, a central issue in the interpretation of remotely-sensed data collection.

Advancement in our understanding of the dynamics of semi-arid ecosystems depends on our capacity to understand how spatial patterns arise from (and modify) ecosystem processes. However, our ability to unravel the importance of multi-scale determinants of vegetation structure depends on the manner by which vegetation structural pattern is characterized in semi-arid ecosystems. In particular, the strong control that vegetation exerts on water availability and the subsequent impact of soil moisture on energy and nutrient cycles implies that key spatial processes occur at the scale of individual tree canopies. However, the observed scaling of patchy structure in savanna ecosystems as well as the presence of large-scale disturbances such as herbivory and fire suggest that these individual-based determinants of structure and function are hierarchically embedded within a suite of organizing processes operating across a wide range of temporal and spatial scales. In this chapter we have attempted to highlight the fact that any observation of spatial pattern necessarily includes assumptions regarding the importance of various pattern-forming mechanisms, and methods of pattern observation vary across time and space scales. Therefore, we suggest approaches that successfully integrate the information and assumptions contained in the diversity of pattern conceptualizations (i.e. individual stem maps at tens of meters to regional distribution of LAI over thousands of kilometers) will lead to new insight into the multi-scale patterns and processes that govern the dynamics of semi-arid vegetation.

7.   Acknowledgements

8.   References

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