

Relationship between small-scale structural variability and simulated vegetation productivity across a regional moisture gradient in southern Africa

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Abstract

The observed variability in vegetation structure within landscapes was used as the basis for model estimates of the range of annual productivity of landscape patches at four sites along a moisture gradient in southern Africa ranging from 879 to 365 mm mean annual rainfall. Principal components of patch-scale variability in leaf area, woody biomass and vertical leaf profiles were derived from intensive characterization of the small-scale spatial structure of woody vegetation at each site. For each site, the mean and extremes of the principal component distribution parameterized an ecophysiology model of vegetation productivity. Vegetation was most heterogeneous at intermediate locations along the rainfall gradient. Variability in vegetation structure led to a range of annual productivity within one site (600 mm) that accounted for 68% of the total range in mean productivity across all sites. Patch-scale estimates of tree productivity were found to be primarily correlated to annual rainfall ($r^2 = 0.66$, $P = 0.001$) and not woody leaf area ($r^2 = 0.01$, $P = 0.75$), while grass productivity was found to be related to values of woody leaf area ($r^2 = 0.77$, $P < 0.001$) and not annual rainfall ($r^2 = 0.11$, $P = 0.29$). This result indicates that life-form interactions have a significant role in controlling vegetation productivity across the rainfall gradient. The findings of this study emphasize the importance of considering heterogeneity rather than mean structure when modeling productivity, particularly when considering dynamic vegetation structure, where differences between landscape patches may not be well represented in the mean structure.

Keywords: heterogeneity, net primary productivity, principal components analysis, vegetation structure

Introduction

Large areas of the subtropics are made up of mixed life-form, heterogeneous vegetation in the form of shrublands, savannas and open woodlands (Bourliere & Hadley, 1970; Walker & Noy-Meir, 1982). The importance of spatial pattern in African savannas is demonstrated in the findings of numerous studies characterizing the spatial distribution of vegetation in these ecosystems (e.g. Smith & Goodman, 1986; Skarpe, 1990; Greig-Smith, 1991; Caylor *et al.*, 2003). The mechanisms leading to patch-scale structural variability in savannas are diverse, although the primary structur-

ing disturbances in southern African savannas are fire (Booyesen & Tainton, 1984) and herbivory (Ben-Shahar, 1996). The patchy nature of savanna structure leads to the possibility of complex spatial interactions between individuals. Smith & Goodman (1986) described competitive interactions that governed the spatial and temporal patterns of vegetation in an *Acacia nilotica*–*Euclea divinorum* savanna in South Africa. A series of studies conducted in Kenyan savannas (Belsky, 1992, 1994) found that moisture and light availability varied between subcanopy and inter-canopy locations, suggesting that the influence of biological structure on physical properties of the environment could be significant at the scale of large canopy individuals.

Many mechanistic production models have been developed, some of which include a detailed consideration of leaf physiology, canopy radiation and gas

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exchange (Friend, 1995; Woodward *et al.*, 1995; Foley *et al.*, 1996; Sellers *et al.*, 1996). Although savannas are important at both regional and global scales due to high productivity (Scholes & Hall, 1996) and frequent and extensive vegetation fires (Justice *et al.*, 1996), few productivity modeling efforts have directly addressed savanna ecosystems (cf. Simioni *et al.*, 2000; Ludwig *et al.*, 2001). The characterization of structural heterogeneity at the patch scale requires intensive field characterization of vegetation structure. For this reason, the functional implications of horizontal patchiness are often ignored in productivity modeling of savannas, despite the fact that recent work has demonstrated the role of spatial heterogeneity in controlling the vegetation dynamics and productivity of savannas along the North Australian Tropical Transect (Liedloff *et al.*, 2001; Ludwig *et al.*, 2001). Field-based measurements of vegetation productivity from Africa reflect a clear positive relationship with mean annual precipitation. For example, 9.5 ton ha⁻¹ yr⁻¹ is estimated at 623 mm mean annual precipitation (Nylsvley, South Africa, Scholes & Walker, 1993), 11.3 ton ha⁻¹ yr⁻¹ at 989 mm (Mana Pools, Zimbabwe, Dunham, 1989) and 21.5–35.8 ton ha⁻¹ yr⁻¹ at 1300 mm (Lamto, Côte d'Ivoire, Menaut & Cesar, 1979).

Studies of primary production derived from eddy covariance measurements of CO₂ flux are rare for tropical and subtropical mixed life-form vegetation types (Ruimy *et al.*, 1995). Eamus *et al.* (2001) have investigated the canopy conductance and water use of savannas in northern Australia, and Hanan *et al.* (1998) characterized the productivity of a Sahelian savanna. A new project associated with the Okavango Research Centre at Maun provides multi-year flux observations in Botswana (E. Veenendaal *et al.*, this issue), and the efforts of Scanlon *et al.* (this issue) present additional short-term eddy flux measurements in a range of ecosystems in southern Africa.

The Kalahari Group sediments (Thomas & Shaw, 1991), which occur across the central portion of southern Africa, form one of the largest sand basins in the world (Baillieux, 1975; McKee, 1979). The Kalahari transect is a research initiative designed to exploit both the systematic climatic gradient and the relatively

uniform soils in the Kalahari region for global change and resource management research (Chanda *et al.*, 1998; Scholes *et al.*, 2002). Vegetation type ranges from partially closed woodlands in the north to open shrubland in the south. Along the Kalahari transect, moisture availability is a fundamental determinant of vegetation cover and productivity at the landscape scale (Scholes & Parsons, 1997). The sites included in this study cover a latitudinal rainfall gradient varying from ~350 mm yr⁻¹ in the south to ~900 mm yr⁻¹ in the north.

To some extent, the net primary production (NPP) of woody vegetation is always dependent on vegetation structure, since the maximum rate of carbon uptake is constrained by total leaf area, and the rate of carbon loss is constrained by total woody biomass. Grass production is also limited by total leaf area, and can be further limited by woody vegetation structure through shading and soil moisture depletion. The objective of this study was to evaluate the direct effect of vegetation structural heterogeneity on productivity at four sites along the Kalahari transect in order to assess the role of vegetation structure as a control on vegetation productivity in this region. The use of a large climatic gradient allows for a comparison between the range in productivity associated with vegetation heterogeneity at a site, and the range in productivity associated with increasing resource limitation between sites.

Methods

Field data collection

Site locations and summaries are provided in Table 1 and Fig. 1. Detailed methodology and site descriptions are provided in Scholes *et al.* (2002). At each site, tree location (stem maps), species, diameter, height, and major and minor axes of crown dimensions were measured for each individual taller than 1.5 m. For multi-stemmed individuals, the diameter of each stem was recorded separately. Individual locations were determined to be the center of the main stem, or the estimated center when multiple-stemmed individuals were sampled. Canopy area was calculated to be an ellipse

Table 1 Site location, rainfall, plot size and vegetation type for the four sites used in the study

Site	Latitude	Longitude	Mean annual rainfall (mm)	Site dimensions (m)	Vegetation type (dominant genus)
Kataba	15.44°S	23.25°E	879	50 × 50	Miombo woodland (<i>Brachystegia</i>)
Pandamatenga	18.66°S	25.50°E	698	50 × 100	Woodland (<i>Schinziophyton</i>)
Maun	19.93°S	23.59°E	460	50 × 50	Woodland (<i>Colophospermum</i>)
Tshane	24.17°S	21.89°E	365	100 × 100	Wooded grassland (<i>Acacia</i>)

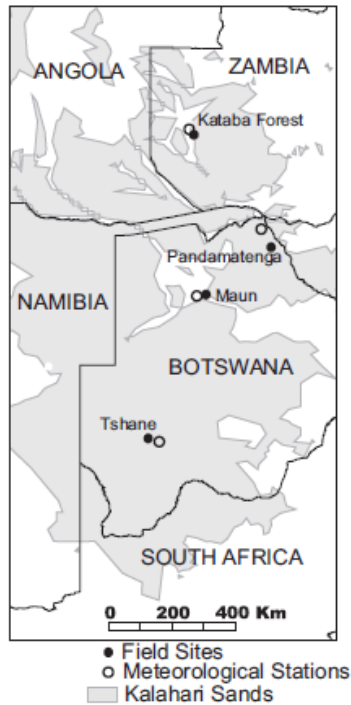


Fig. 1 Location of study sites and meteorological stations used in the study.

defined by the two major axes of measurement. Canopy height was estimated using a clinometer. Grass biomass was determined by harvesting 10–20 1 m² quadrats at each site. Samples were oven-dried and weighed to determine dry grass biomass per square meter.

Climate/meteorological data

The productivity model used in this study requires a suite of daily meteorological data, including average daily temperature, daily mean relative humidity and rainfall. These data are often unavailable for many locations in the Kalahari, and the use of distant station data is problematic due to the highly convective and patchy nature of rainfall in the Kalahari region. Therefore, simulations of annual productivity were conducted using daily climate data based on a combination of both stochastic and empirical modeling techniques.

The annual patterns of daily temperature and relative humidity were generated using a coarse-scale empirical model of mean temperature and humidity patterns derived specifically for the Kalahari region. For the purposes of this study's simulations, stochastic variation in temperature and relative humidity were ignored, and an empirically derived fifth-degree polynomial approximation of daily temperature and

humidity was to estimate average daily meteorological conditions. Data contained in the NCDC global summary of the day, Version 6 data set from 1994 to 2000 (NCDC, 2001), were used to determine the parameters of fifth-degree polynomials describing daily average temperature and daily average relative humidity at three of the four sites – Tshane, Maun and Pandamatenga. Because of the scarcity of NCDC data reported for western Zambia, a separate 2-year record of daily meteorological data at Mongu (Zambia) was used to generate the polynomial parameters for the Kataba site. These meteorological data for Mongu (Zambia) were previously reported in Dowty *et al.* (2000). In all cases, except Pandamatenga, the meteorological stations used are located within 40 km of the field sites. At the Pandamatenga site, the nearest meteorological station is located at Kasane, 100 km away. The locations of field sites and the meteorological stations are presented in Fig. 1.

In contrast to the empirical method used for temperature and relative humidity, rainfall was modeled stochastically using the probabilistic rainfall delivery method developed by Rodriguez-Iturbe *et al.* (1999), with parameters inferred from Porporato *et al.* (2003). Although daily rainfall was modeled as a purely stochastic process, the simulated yearly pattern used was constrained to be within 5% of the long-term mean annual rainfall at each site (Table 1). Although wind speed varies during the course of the growing season, long-term data were unavailable at the study locations, and the model demonstrates very little sensitivity to changes in mean daily wind speed. Therefore, daily wind speed was taken to be an average and constant value of 1 m s⁻¹. Climatic data used to simulate vegetation productivity at each site are provided in Fig. 2.

Vertical structure analysis

The volumetric distribution of woody vegetation leaf area was determined using a combination of field data and allometric relationships. The two-dimensional structure of canopies at each site was revealed using field observations of individual crown dimensions, while the vertical structure of canopies was generated using field observations of canopy height and average canopy depth. This detailed specification of canopy geometry produced a three-dimensional representation of canopy structure for each site at a resolution of 1 m. A toroidal edge-correction technique was employed to remove bias associated with plot boundaries. Leaf biomass and whole-tree biomass were estimated for each individual using generalized allometric relationships developed in Goodman (1990). Field measurements of

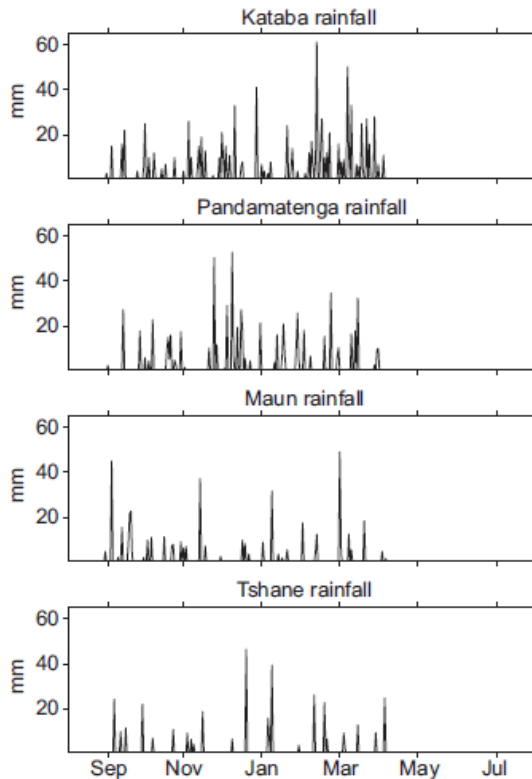


Fig. 2 Simulated daily climate for the four sites used in the study. Rainfall is simulated stochastically, and daily meteorological data are empirically derived from available station data.

specific leaf area ($\text{m}^2 \text{kg}^{-1}$) were used to calculate the leaf area from each tree's allometrically determined leaf biomass. Each individual's leaf area was then distributed evenly throughout the individual's canopy volume to arrive at a leaf area per unit volume or leaf area density ($\text{m}^2 \text{m}^{-3}$). Where canopy volumes intersected, leaf area density at intersecting locations was taken to be the sum of the contributing canopies' leaf area densities. The mean vertical leaf area profiles were developed for each site by taking the plot-wide leaf area density at each vertical level.

The structure of vegetation across the Kalahari transect is highly variable. This patch-scale variation leads to distributions of structural parameters such as leaf area, height and vertical distribution of the canopy that are impossible to describe in simple statistical terms such as mean and variance. In order to characterize both the horizontal and vertical components of variability in canopy structure, each research plot was divided into $10 \times 10 \text{ m}^2$ subplots. The vertical profile of leaf area was then determined for each subplot by taking the subplot-wide leaf area density at

each vertical level. This produced a total of 200 subplot leaf area profiles (Kataba $n = 25$; Pandamatenga $n = 50$; Maun $n = 25$; Tshane $n = 100$) across the four sites. Each subplot consisted of a vertical profile of leaf area resolved at 1 m increments, from 1 to 14 m in height (the maximum observed height). These 200 subplot profiles, each containing leaf area at 14 heights, were submitted to a principal components analysis (PCA) in order to determine the nature of variability in vertical woody vegetation structure both within and between sites.

In this study, our emphasis is on understanding how the range of structural variability at each site leads to differences in estimates of simulated vegetation productivity. Therefore, three samples of vegetation structure were selected from the distribution of subplots at each site based on their distribution within the PCA factor-space: the 'minimum extreme', 'maximum extreme' and 'mean'. The extremes of vegetation structure at a site were established using a linear regression model fit to the distribution of subplot scores for Factors 1 and 2. The two 'extreme' subplots were then sampled by finding the subplots located closest to maximum and minimum observed values of the linear regression model. A third sample representing the mean PCA score for the site was taken by sampling the subplot most closely located to the mean of all the subplot scores for Factors 1 and 2.

Model description

The productivity model developed by Dowty (1999) simulates CO_2 uptake by photosynthesis, respiration and evapotranspiration on a daily basis, and is similar in many respects to the canopy model developed by Woodward *et al.* (1995). The leaf physiology component of the model includes routines for C_3 tree (Farquhar *et al.*, 1980) and C_4 grass (Collatz *et al.*, 1992) photosynthesis, stomatal conductance (Ball *et al.*, 1987), and CO_2 and water diffusion through the stomata. The leaf model is embedded in a multi-layer canopy model that considers radiation attenuation through the canopy and allocates nitrogen to the leaf layers according to irradiance as described in Woodward *et al.* (1995). The calculation of mean daily radiation is based on hourly solar-earth geometry and the assumption of clear sky conditions, and photosynthetically active radiation is taken to be 50% of the total incoming radiation (Jones, 1992). Grasses and trees have distinct distributions of root mass through a three-layer soil profile (0–10, 10–30, 30–300 cm) (Scholes & Walker, 1993). In each case, root mass is a fixed ratio of whole-plant mass with a fixed breakdown to each soil layer. The tree root distributions through these layers are 5%, 15% and 80%, respectively. The grass root distributions are 60%, 40% and 0%. The

timing and, to a lesser extent, the rate of leaf flush and leaf fall are dependent primarily on the intensity and persistence of available soil moisture conditions. The effect of soil moisture on leaf physiology is included through an additional empirically derived constraint on stomatal conductance as presented in Woodward *et al.* (1995). An earlier application of the model has shown it

to represent adequately the dynamics and magnitude of Kalahari vegetation productivity in response to inter-annual variation in rainfall (Dowty *et al.*, 2000). Although this study focused on annual NPP, the simulated daily productivity for the PCA mean subplot at Kataba is depicted in Fig. 3 as an example of the daily productivity model output.

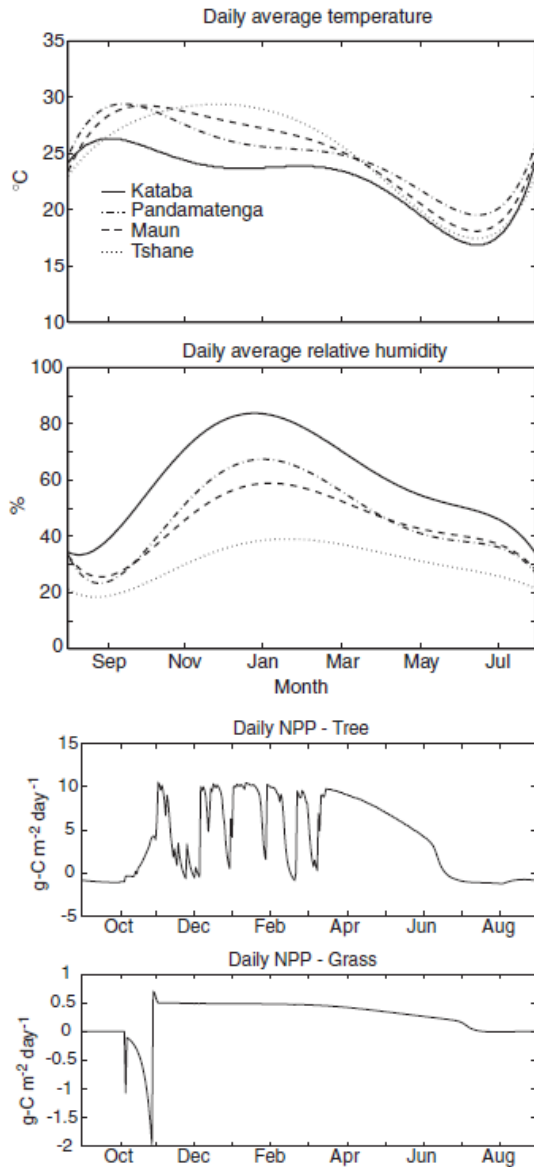


Fig. 3 Simulated daily tree and grass net primary production (NPP) for Kataba using mean principal components analysis (PCA) subplot structure (leaf area index (LAI) = $2.14\text{m}^2\text{m}^{-2}$; woody biomass = 5.24kgm^{-2}).

Model simulations

In order to simulate annual productivity of the tree/grass mosaic at each of the four study sites, the ecophysiology model was parameterized using results of the vegetation structure analysis described above, including maximum tree leaf area (at full flush), tree biomass and maximum grass biomass (at full flush). Relevant vegetation parameters and their values are provided in Table 2. Year-long simulations were started during the dry season (September 1) and a total of 12 simulations were conducted (four sites \times three runs per site). In many southern African savannas, leaf flush precedes the onset of rain (Fuller & Prince, 1996). Therefore, initial woody and herbaceous were set to be 10% of maximum values at the start of the simulation. The modeled daily NPP was integrated throughout the year and resolved into tree and grass components to arrive at an annual NPP for each component. Tree and grass productivity were correlated to both woody leaf area and annual rainfall in order to assess the role of these factors in controlling vegetation productivity across the study sites.

Results

Patterns of average vertical canopy structure exhibited marked changes between sites along the rainfall gradient. Average site-level leaf area distribution moved from the top of the canopy in the two northern wetter sites towards the bottom of the canopy in the two southern more arid sites (Fig. 4). In order to distinguish the ranges of structural variability that underlay this general pattern, the variance in structure both within and between sites was analyzed in more detail using PCA. The PCA resulted in three factors with eigenvalues greater than one, and these three factors, respectively, explained 44.3%, 24.0% and 13.8% of the variance in subplot vertical structure (Fig. 5). Since the PCA was performed using leaf area density at each height as the independent variables, PCA results describe the generalized patterns of vertical leaf area observed across all four sites, and also include information about the canopy height and total leaf area. Factor 1 is positively loaded at all heights, whereas Factors 2 and 3 exhibit shifts in loading with

Table 2 Productivity model parameters for the 12 simulations used in the study

Site	PCA extreme 1 simulation		PCA extreme 2 simulation		PCA mean simulation			
	LAI ($\text{m}^2 \text{m}^{-2}$)	Woody biomass (kg m^{-2})	LAI ($\text{m}^2 \text{m}^{-2}$)	Woody biomass (kg m^{-2})	LAI ($\text{m}^2 \text{m}^{-2}$)	Woody biomass (kg m^{-2})	Canopy height (m)	Maximum grass biomass (kg m^{-2})
Kataba	0.93	1.62	3.84	9.04	2.14	5.24	11.0	0.042
Pandamatenga	0.02	0.10	5.53	18.97	1.48	5.39	10.4	0.156
Maun	3.19	4.13	0.35	0.42	2.11	2.66	9.4	0.055
Tshane	1.63	2.30	2.40	8.56	0.62	1.45	7.0	0.097

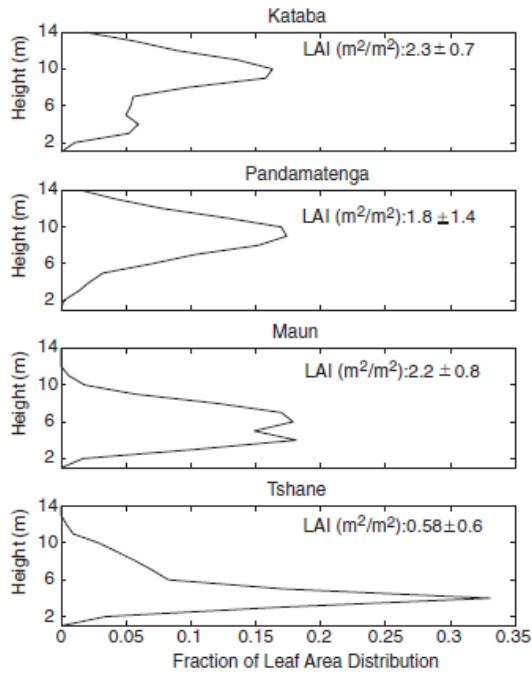


Fig. 4 Average, standard deviation and vertical distribution of leaf area index at Kataba (879mm yr^{-1}), Pandamatenga (698mm yr^{-1}), Maun (460mm yr^{-1}) and Tshane (365mm yr^{-1}).

height (Fig. 5). Subplot scores for both Factors 1 and 2 reveal within- and between-site variability in vegetation structure (Fig. 6). Within sites, Maun and Tshane are seen to be most highly loaded on Factor 2, while Pandamatenga and Kataba are loaded on Factor 1. The distribution of points around the origin in the factor space plot is decidedly non-uniform, largely due to the relatively small variance in Tshane subplots with respect to Factor 1 (Fig. 6).

Results from the model simulations show decreasing mean annual productivity across the moisture gradient, with grasses contributing more to the total productivity at the southern end of the transect (Fig. 7a). The

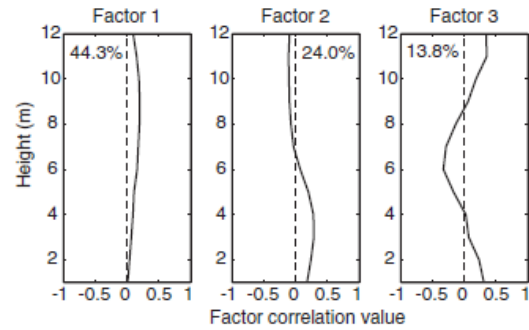


Fig. 5 Factor loadings and percent of total variance explained for the first three factors derived from the principal component analysis of patch-scale vegetation structure across the four study sites. Factor 1 is weighted strongly for almost all heights, and Factors 2 and 3 exhibit a tradeoff between different heights in the canopy. In total, these three factors account for 82.1% of the total variance in vegetation structure across the four sites.

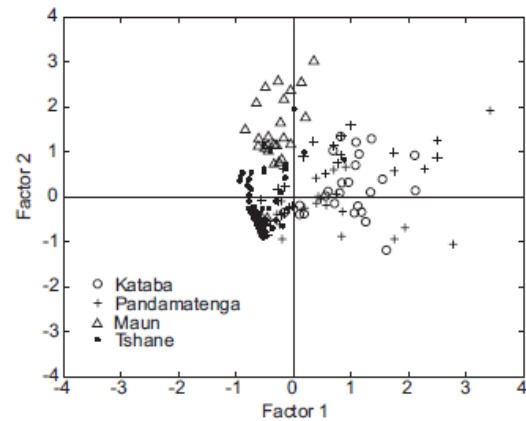


Fig. 6 Distribution of subplot factor scores for Factors 1 and 2 derived from the principal component analysis of patch-scale vegetation structure across the four study sites. Maun and Tshane vary mostly along the Factor 2 axis, while Kataba and Pandamatenga vary mostly along the Factor 1 axis.

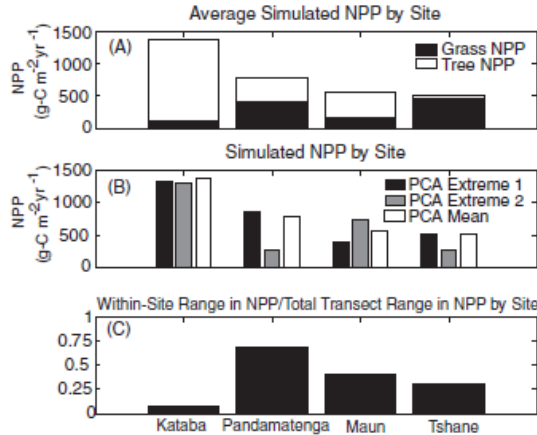


Fig. 7 Simulated net primary production (NPP) by model run (a), average simulated NPP (b), and ratio of within-site to total transect range in simulated NPP results (c) at Kataba (879 mm yr⁻¹), Pandamatenga (698 mm yr⁻¹), Maun (460 mm yr⁻¹) and Tshane (375 mm yr⁻¹).

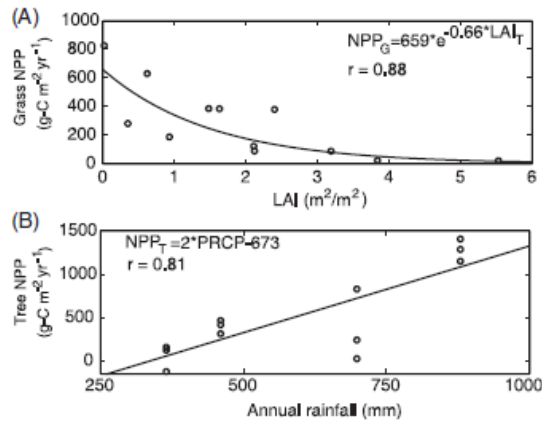


Fig. 8 Correlations between grass productivity and tree leaf area (a), as well as tree productivity and annual rainfall (b) for the 12 model simulations. No relationship existed between grass productivity and rainfall or tree productivity and tree leaf area.

heterogeneity in structure leads to wide ranges of simulated total NPP within each site (Fig. 7b). The ratio of within-site to across-site range in NPP peaks at Pandamatenga (Fig. 7c), where the within-site range in NPP was 68% of the range across all sites. A significant negative exponential relationship was found between patch-scale simulations of grass annual productivity and woody leaf area within the patch ($r^2 = 0.77$, $P < 0.01$; Fig. 8a). In addition, a positive linear relationship was found between tree annual productivity and annual rainfall ($r^2 = 0.66$, $P = 0.01$; Fig. 8b). No significant relationships were found between simulated

annual grass productivity and annual rainfall ($r^2 = 0.11$, $P = 0.29$) or simulated annual tree productivity and woody leaf area ($r^2 = 0.01$, $P = 0.75$).

Discussion

The analysis of structural heterogeneity across large climate gradients requires the development of detailed vegetation characterization as well as methodologies for comparing the variability of vegetation at disparate sites. The vertical profiles of leaf area and the decline in leaf area across the Kalahari transect are similar to patterns reported for other semi-arid climatic gradients in West Africa (Menaut, 1982), and a research transect with a 1000 mm rainfall gradient in northern Australia (Williams *et al.*, 1996; Cook *et al.*, 2002). Despite these general patterns in vegetation structure, simple means and variances of vegetation structural parameters are poor representations of structural heterogeneity in semi-arid ecosystems, where patch-scale structural parameters are not normally distributed across the landscape (Pearson, 2002). The PCA analysis presented allows the range of vegetation structure to be sampled in a way that preserves variability at each site, but does not depend on any assumptions regarding the underlying distribution of structural parameters. The clustering of subplots from Tshane and Maun along Factor 2 indicates the wider variability in vertical profile found in these sites, although total leaf area is more constant than at the Kataba and Pandamatenga sites, which demonstrates a larger response to Factor 1. The high degree of overlap between sites within the factor space (Fig. 6) indicates that the degree of structural variability within sites is comparable to the structural variability observed between sites. The results of the patch-scale simulations imply that climate forcing is the primary control on productivity of established woody vegetation, while the controls on grass and herbaceous productivity at these sites seem more dependent on biological forcing (Fig. 8). The results in Fig. 8 agree with the observed effects of tree canopies on grass productivity in western African savannas (Mordelet *et al.*, 1995). Furthermore, the high dependence of grass productivity on woody vegetation structure (Fig. 8) suggests that the small-scale pattern of woody vegetation structure may be an important control on regeneration of trees in the Kalahari, as seedlings directly compete with grass for available resources (Higgins *et al.*, 2000).

In conclusion, this study has demonstrated that the degree of heterogeneity in vegetation structure can lead to a wide range in simulated estimates of vegetation productivity across a large climatic gradient in the Kalahari. As expected, the patch-scale productivity of

woody vegetation is positively correlated with increasing mean rainfall across the sites included in this study. This general pattern is underlain by a large variability in vegetation structure at the patch level, which leads to a range of productivity at a single site in the middle of the transect that is 68% of the observed range across all sites. Woody vegetation structure at the patch level has a cascading effect on grass/herbaceous productivity. These results point to the importance of patch-scale variability in estimates of vegetation productivity, and the role of vegetation structure as a control on productivity in savanna ecosystems.

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