

Vegetation structure characteristics and relationships of Kalahari woodlands and savannas

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Abstract

The Kalahari Transect is one of several International Geosphere–Biosphere Programme (IGBP) transects designed to address global change questions at the regional scale, in particular by exploiting natural parameter gradients (Koch *et al.*, 1995). In March 2000, we collected near-synoptic vegetation structural data at five sites spanning the Kalahari's large precipitation gradient (about 300–1000 mm yr⁻¹) from southern Botswana (~24°S) to Zambia (~15°S). All sites were within the expansive Kalahari sandsheet. Common parameters, including plant area index (PAI), leaf area index (LAI) and canopy cover (CC), were measured or derived using several indirect instruments and at multiple spatial scales. Results show that CC and PAI increase with increasing mean annual precipitation. Canopy clumping, defined by the deviation of the gap size distribution from that of randomly distributed foliage, was fairly constant along the gradient. We provide empirical relationships relating these parameters to each other and to precipitation. These results, combined with those in companion Kalahari Transect studies, provide a unique and coherent test bed for ecological modeling. The data may be used to parameterize process models, as well as test internally predicted parameters and their variability in response to well-characterized climatological differences.

Keywords: clumping, Kalahari, leaf area index, SAFARI 2000, savanna, scaling, semi-arid, vegetation structure

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Introduction

Vegetation structure, the three-dimensional spatial and angular distribution of plant biomass, has become increasingly recognized as an important factor in the transfer of mass and energy between soil, vegetation and the atmosphere, in vegetation succession and in biomass burning. Its parameterization in ecological and climatological modeling has become widespread (e.g., Potter *et al.*, 1993, 1998; Sellers *et al.*, 1996).

Nevertheless, knowledge of vegetation canopy structure remains incomplete in many remote areas, such as sub-Saharan Africa. First, comparatively small changes in precipitation patterns and soil type can substantially change canopy characteristics. Second, remote sensing

methods used to estimate canopy structural parameters have limited spatial resolution and are hampered by mixed vegetation classes. Third, sub-Saharan Africa undergoes extensive biomass burning on a frequent basis, leading to a high degree of patchiness in structural characteristics, even under a similar climate and soil. At the landscape scale, herbivory by domestic and wild animals and shifting agriculture also contribute to such patchiness.

In this article, we report canopy structural relationships determined for five sites visited during the Kalahari Transect Campaign (March 2000) of the Southern African Regional Science Experiment 2000 (hereafter referred to as SAFARI). SAFARI is an organizational umbrella for various environmental studies, which together should improve understanding of the sources, transformations, dynamics, sinks and impacts of trace gases and atmospheric aerosols in

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southern Africa (Swap *et al.*, 2002). Vegetated areas can be intimately involved in the atmospheric processes, since vegetation can be a source of matter (fires and natural vegetation emissions), can impact and be affected by regional climate and may rely on wet and dry atmospheric deposition for its nutrients. Further, a major component of SAFARI is remote sensing research and validation of NASA's Earth Observing System (EOS). Indeed, SAFARI represents one of the most comprehensive tests of EOS to date (Myneni *et al.*, 2002; Privette *et al.*, 2002).

Roughly 40 scientists worked together during the Kalahari Transect Campaign to characterize vegetation structure at five sites extending from Mongu, Zambia to Tshane, Botswana. The investigators used various instruments and sampling techniques, and worked within three nested sampling grids. This scheme facilitated extrapolation of detailed structural measurements and correlation of different measurements. Nearly simultaneous measurements from several satellites were acquired to allow extrapolation to a larger area.

The present study was conducted to determine which vegetation structural parameters, if any, are correlated with mean annual precipitation (MAP) along the Kalahari Transect. We focused on three aspects of structure: (1) the values of key parameters (canopy cover (CC), plant area index (PAI) and clumping index), (2) the correlative relationships among the parameters and (3) the trends in values and relationships as a function of MAP. We also develop equations relating the various parameters, and describe their implications.

The data and results provided here, together with others emanating from the SAFARI Kalahari Transect Campaign, form an extensive and coherent test bed for ecological modeling of global change scenarios. The near-simultaneity of the measurements provides a synoptic snapshot of biological responses to well-characterized climatological variables (primarily MAP and solar insolation) in the absence of strongly differing nutrient availability and land use.

Methods

Kalahari Transect campaign

The Kalahari Transect campaign (Dowty *et al.*, 2000; Otter *et al.*, 2002) was designed to quantify landscape parameters near peak foliar biomass (approximately March 2000) across a large precipitation gradient. The campaign was designed to provide wet season vegetation data that could be analyzed synergistically with data acquired during the SAFARI aircraft campaign held in the subsequent dry season (August–September 2000; Swap *et al.*, 2002b).

The campaign commenced in late February at Mongu, Zambia, proceeded to four sites in Botswana and concluded in mid-March at Tshane, Botswana (960 km or 8.7° latitude south of Mongu). The difference in MAP between the northernmost site (Mongu) and the southernmost site (Tshane) was about 650 mm yr⁻¹ (Shugart *et al.*, 2003). Campaign participants typically spent 3 days at each site. Canopy structural data were collected on nested transects immediately upwind (i.e., in the fetch) of a portable tower-based eddy covariance system.

Spring 2000 coincided with an anomalously high precipitation period that caused extensive flooding in the southeast part of the subcontinent. Precipitation anomalies at the study sites were considerably less, ranging from slightly below average seasonal precipitation in Mongu to slightly above average precipitation over the southern sites.

Field sites

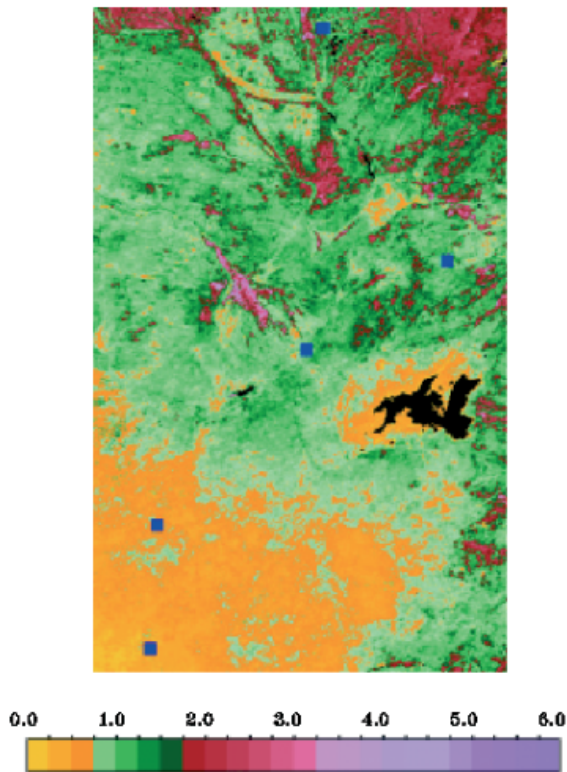
The Kalahari Transect is marked by fairly constant arenosol soils, typically tens of meters deep (the Kalahari sands). The Transect's vegetation includes near-continuous Kalahari woodlands (Miombo woodland on sand) to the north and increasingly sparser woodlands and savannas southward (Fig. 1). All field sites were on the southern African plateau with elevations of about 1000 m. All sites in Botswana exhibited signs of light grazing. Summary information is provided in Table 1, following Otter *et al.* (2002). Further details are available in Dowty *et al.* (2000), Frost (2000; Mongu only) and Scholes *et al.* (2002).

Sampling grids

Campaign participants used a nested sampling scheme designed to allow spatial extrapolation of the more labor-intensive measurements, and to characterize structure over an area roughly commensurate with moderate resolution (~1 km) remote sensing products. Three grid patterns were established with stake flags, including:

1. a 50 m × 50 m completely sampled plot (sometimes expanded to 50 m × 100 m) flagged at 10 m intervals (hereafter referred to as the 'Small Grid'),
2. a 300 m (east–west) × 250 m (north–south) grid flagged at 50 m intervals ('Medium Grid'), and
3. a 750 m (east–west) × 500 m (north–south) grid flagged at 25 and 250 m intervals, respectively ('Large Grid').

At least one gridline of each grid coincided with a gridline of the others. Although configurations varied



GREEN LEAF AREA INDEX: MODIS A2, Day136 2000

Fig. 1 Relative proximity of test site locations (blue squares from top to bottom: Mongu, Pandamatenga, Maun, Okwa, Tshane) superimposed on the leaf area index (LAI) product from NASA's MODIS instrument on EOS Terra (Acquisition date: 18 May 2000). The significant LAI gradient approximately follows the mean annual precipitation gradient along the Kalahari Transect. The Makgadigadi Pans (large black shape, right side of scene), the Okavango Delta (light purple, middle of scene) and the Cuando and Zambezi River basins (pink, NW-SE trending linear features at top of scene) provide spatial reference.

slightly by site, a typical layout is shown in Fig. 2. In general, investigators used more manual techniques (e.g., determining stem maps with tape measures) over the smaller grids and more automated, indirect measurements (e.g., hemispherical photography) over the larger grids. Below, we briefly describe key instruments and techniques relevant to this article.

Instrumentation

Plant canopy analyzer (PCA)

The PCA (LAI-2000, LICOR Inc., Lincoln, NE, USA) provides estimates of PAI and gap fraction (GF) based on the ratio of canopy-transmitted to top-of-canopy radiation (<490 nm) (Welles & Norman, 1991). Specifically, PCA samples the overhead hemisphere in five

concentric conical rings (0–13°, 16–28°, 32–43°, 47–58°, 61–74° view zenith angle). PCA theory assumes a random horizontal spatial distribution of canopy elements. Because this assumption was violated disproportionately at different sites, two strategies were used. We sampled precisely at the stake flags at sites where vegetation was less clumped (Pandamatenga and Maun). A 90° lens mask was used to minimize operator shadowing. At sites where vegetation was highly clumped (Okwa and Tshane), we noted the primary vegetation 'endmember' (grass, shrub or tree) at each flag, then moved the detector as necessary such that the five concentric cones viewed only that endmember. A 270° mask was used to isolate the single endmember. We positioned the PCA at ground level for measurements at Maun, Okwa and Tshane. At Pandamatenga, we sampled with the PCA at two levels (surface and ~1.5 m height) to allow separation of over- and understory. In all cases, measurements were taken when direct irradiance was negligible (dawn, dusk or overcast skies). A co-calibrated instrument was positioned with an unobscured view of the sky for irradiance measurements. PCA data were collected on both the Medium and Large Grids (Tian *et al.*, 2002), but have not been analyzed for Mongu.

Tracing architecture and radiation of canopies (TRAC)

The relatively new TRAC instrument (3rd Wave Engineering, Ottawa, Canada) contains pyranometers sensitive to photosynthetically active radiation (400–700 nm) (Chen & Cihlar, 1995; Chen, 1996; Leblanc *et al.*, 2001). The instrument was hand-carried, with the detector ~70 cm above ground, along the 750 m transects during periods of direct sunlight (i.e., non-cloudy conditions). TRAC measures sunfleck size and frequency by recording the photosynthetic photon flux density (PPFD) at 32 Hz, which translates to a sampling interval of about 1.6 cm on the 750 m transects (Privette *et al.*, 2002).

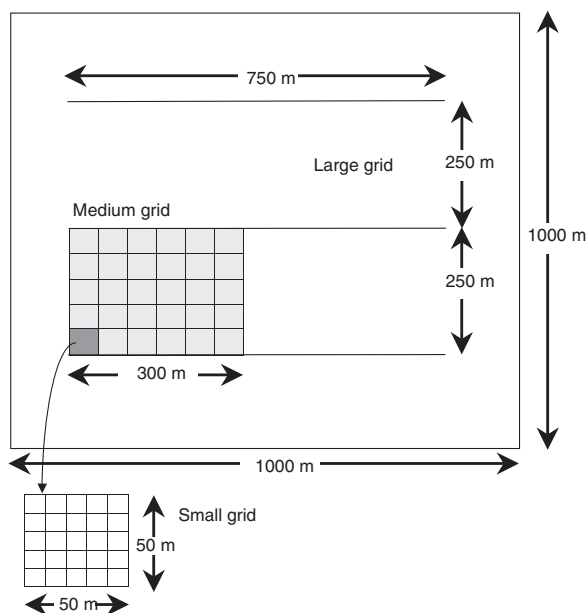
Proprietary TRAC software (TRACW in v.2.3.3) was used to determine the GF and clumping index (Ω) of the overstory from an uplooking pyranometer (Leblanc *et al.*, 2001). Clumping is estimated by determining the deviation of the measured gap size distribution from that of randomly distributed foliage. The clumping index was used to determine the true PAI from the effective PAI (PAI_{eff}), which assumes non-clumped foliage, as (Chen, 1996)

$$PAI = PAI_{eff} / \Omega \quad (1)$$

When plant material is randomly distributed, $\Omega = 1$. When the material is regularly spaced, $\Omega > 1$, and when material is clumped (in spatially discrete collections, such as produced by tree crowns), $\Omega < 1$. An increase in

Table 1 Field site characteristics of the Kalahari Transect campaign

Site	Location	Elevation (m a.s.l.)	Mean annual rainfall (mm yr ⁻¹)	Predominate vegetation	Comment
Mongu, Zambia	15.44°S 23.25°E	1084	879	Kalahari woodland dominated by <i>Brachystegia spiciformis</i> with sparse woody understory; overstory height ~ 12 m	Bordered Kataba local forest which undergoes subsistence harvesting; EOS validation core site; 30 m tower
Pandamatenga, Botswana	18.66°S 25.5°E	1065	698	Open woodland dominated by <i>Schinzophyton rautanenii</i> , <i>Baikiaea plurijuga</i> and <i>Burkea Africana</i> ; patches of high grass	Near Agricultural Research Station; measurements in woodland that undergoes light grazing
Maun, Botswana	19.92°S 23.59°E	929	460	<i>Colophospermum mopane</i> woodland with patches of <i>Terminalia sericea</i> thicket	Harry Oppenheimer Okavango Research Centre; Measurements were 3 km east of a permanent flux tower
Okwa River Crossing, Botswana	22.41°S 21.71°E	1089	407	Open Kalahari shrubland dominated by <i>Acacia mellifera</i> , <i>Terminalia sericea</i> and <i>Grewia flava</i>	Measurements within a soil and vegetation transitional area on the edge of a fossil (dry) river bed
Tshane, Botswana	24.16°S 21.89°E	1115	232	Open savanna dominated by <i>Acacia leuderitzii</i> and <i>Acacia mellifera</i>	Land-use gradient: grazing intensity increases between the site and Tshane village

**Fig. 2** Schematic representation of the three sampling grids (adapted from Tian *et al.*, 2002).

clumping coincides with an increase in solar radiation reaching the surface.

TRAC was used exclusively on the Large Grid. Data were not collected on the northernmost transect at Maun, since most plant material (shrub) was located at

or below detector level. For the same reason, accurate results for Okwa were not expected.

Hemispherical photography

A digital camera (Coolpix 950, Nikon Corporation, Tokyo, Japan) with a fish-eye lens was used to photograph the overstory at each flag on the Large Grid. The camera was mounted on a tripod with an average height of 1.42 m. Hemispherical photography is best suited to tall canopies such as forests, due in part to the bias introduced when the lens is too close to the vegetation components. This was observed at some sites, particularly at Okwa where the canopy was short. As a result, no results are presented for Okwa. Estimates of GF, as a function of view zenith angle, are readily obtained from hemispherical images.

Images were classified into vegetation and sky components using an automated unsupervised classification procedure. The classified images were then segmented into zenith and azimuth bins (10° and 5°, respectively) from which estimates of the GF were obtained.

PAIs were determined from data for each segment between 20° and 70° zenith angle. Van Gardingen *et al.* (1999) suggested that PAI obtained using this angular configuration are more reliable since, at large zenith angles, the GF is often zero due to the increased path length reducing the gap probability, with the reverse true at low zenith angles. Estimates of PAI were derived

using the non-linear elimination approach, which is solved using a generalized extinction coefficient. For further details, refer to Norman & Campbell (1989). Clumping was not considered in the PAI calculations.

Ceptometer

Ceptometers (AccuPAR, Decagon, Inc., Seattle, WA, USA) were used to sample both the Medium and Large Grids. Only that of the Medium Grid is reported here. The instrument contains 80 PAR sensors fixed at 1 cm intervals along a wand and connected to a control box. The distribution of sensors allows estimation of local GF. Data were collected at ground level at each flag two times with widely differing solar zenith angles. Processing followed the semi-empirical algorithm detailed in Campbell (1986). The canopy shape factor was calculated first, based on the different GF measured at the two times, and then PAI_{eff} was calculated.

Manual techniques

On the Small Grid, stem maps were created via variable-width belt-transect sampling of tree location, species, diameter, height and major and minor axes of crown dimensions (Caylor *et al.*, 2003a). Only stems taller than 1.5 m were measured. For multi-stemmed individuals, the diameter of each stem was recorded separately. Canopy area was calculated to be an ellipse defined by the two axes of the crown ellipses. Canopy height was estimated using a clinometer. On the Medium Grid, tree basal area and height (clinometer) were measured in circular quadrats of 4–8 m radius, and overstory cover was estimated by the line intercept technique (Scholes *et al.*, 2002). Line intercept methods were separately applied to the understory (<1 m) where present. At the Mongu site, a spherical densitometer and basal area prism were also used (Frost, 2000). The leaf area index (LAI) was estimated by applying allometric equations to each measured stem circumference (Scholes *et al.*, 2003).

Determination of overstory and understory PAI

We focused our analysis on PAI and CC, as these parameters are common parameters in many process models and are estimated through remote sensing methods (DeFries *et al.*, 2000; Myneni *et al.*, 2002). Our methods primarily determined overstory PAI, where we define overstory as vegetation above ~ 0.7 m height. For each method, we determined the mean PAI over the grid on which it was measured.

An estimate of the understory LAI (primarily grasses, forbs and short shrub) is possible by correcting the PCA's (understory + overstory) PAI for clumping, and

then subtracting the TRAC (overstory) PAI. The method assumes that:

- the clumping index of the total canopy equals that of the overstory;
- all understory plant material is herbaceous;
- PCA and TRAC provide comparable PAI results for given conditions.

We tested the latter assumption using TRAC's clumping value, Eqn (1) and the PCA's overstory PAI_{eff} data collected at Pandamatenga.

Determination of CC

CC is the fraction of ground area directly covered by the overstory, where for the purposes of this study, overstory is defined as shrub and tree material above the recording height of the sensors (~ 0.7 m). For the PCA and hemispherical photography, we first determined the overstory GF_0 from the subset of observations with view zenith angles closest to zero, then took the complement ($1 - GF_0$) to estimate CC. The line transect data estimate CC directly. TRAC, however, detects plant material only along the sensor-sun vector, which is typically not normal to the ground. So, to estimate CC from TRAC, we normalized the derived GF to the case where the sun is directly overhead. We did this by applying Beer's Law and assuming $\Omega(0^\circ) = \Omega(\theta_s)$, where Ω is the clumping index and θ_s is the solar zenith angle at the time of measurement, i.e.,

$$\begin{aligned} CC_{\text{TRAC}} &= 1.0 - GF_0 \\ &= 1.0 - \exp[-G(\theta_s)\Omega(\theta_s)PAI / \cos(\theta_s = 0)] \\ &= 1.0 - \exp[-0.5\Omega(\theta_s)PAI], \end{aligned} \quad (2)$$

where we assume G , a species-dependent leaf angle distribution function, is 0.5 (i.e., random).

Variability of structure with annual precipitation

To assess trends with aridity, we correlated the mean TRAC (PAI) and PCA (PAI_{eff}) values with MAP. Okwa data were not used, since this site had sparser woody vegetation (bushes) relative to the surrounding landscape. The variability of CC with MAP was also determined.

Determining a predictive parameter for vegetation structure

To determine the best predictor of all other structural parameters, we computed the correlation matrix of the set $\{PAI, PAI_{\text{eff}}, \Omega, CC, GF(\theta_s)\}$ for each site (90 samples

Table 2 PAI as a function of site and method

Site	Ω	Large Grid			Medium Grid		
		PCA	Photography	TRAC	PCA	Ceptometer	Allometry
Mongu	0.76	N/A	1.04	2.09	N/A	1.86	1.70
Pandamatenga	0.69	1.21, 0.65	1.30	1.43	1.01/0.91	1.56	1.68
Maun	0.76	1.52	1.74	1.19	1.21	1.28	0.74
Okwa River	0.57	1.34	N/A	0.55	1.75	1.34	0.19
Tshane	0.72	0.75	0.25	0.64	0.78	0.83	0.51

PCA and Ceptometer data represent total plant area; all other data represent overstory plant area ($> \sim 1$ m) only. Ω denotes canopy clumping index. Values from the PCA, Photography and Ceptometer represent effective plant area indices (all material was assumed to be randomly distributed in space). Allometry values represent LAI. N/A indicates value not available. The first PCA value for Pandamatenga represents the total PAI, and the second value represents the overstory PAI only. PAI, plant area index; PCA, plant canopy analyzer; TRAC, tracing architecture and radiation of canopies; LAI, leaf area index.

per site, each representing a 25 m segment in the Large Grid). For this analysis, only TRAC data were used since they were collected at all sites, on the Large Grid, and since TRAC measures canopy clumping. Logical circularity is minimal since the core parameters (PAI, CC and Ω) are determined from different aspects of the native PPFD measurements.

Relationships between structural parameters

The ability to model semi-arid communities, and to estimate indirectly various structural parameters from remote sensing data, depends in part on mathematical relationships between parameters. Therefore, we fit the PAI vs. CC relationships using linear regressions. The resulting fit parameters (slopes and intercepts) were correlated with precipitation such that, with a map of MAP, a regional vegetation structural model can be inferred.

Results

Plant area index (PAI)

The mean PAI for each site and instrument is shown in Table 2. The TRAC results indicated increasing PAI with increasing precipitation. Both the digital photography and PCA results, however, suggested greater PAI at Maun than at Pandamatenga (which has a greater annual precipitation). The reason for this is not clear. Trends among the different sensors' estimations at the sites are not evident, suggesting that the biases of each sensor vary with the local conditions. Note that the ceptometer and PCA results represent total PAI (understory plus overstory), while the photography and TRAC PAI values represent overstory ($> \sim 1$ m) PAI only. The allometric method estimates LAI, for overstory only.

The results of understory LAI calculations at Pandamatenga (0.32), Maun (0.81) and Tshane (0.40) seem plausible in the absence of independent measurements. The value for Okwa (1.8), while more than double any of the others, may also be acceptable given the extensive grass and dense shrub understory at this site (for photographs of each site, see Privette *et al.*, 2002). This understory was generally below the TRAC sensor height, and therefore could not obscure the sensor from direct sunlight and be recorded as plant material. Indeed, there were few trees at this site. As noted in the methods, our estimation of understory LAI assumes that the PAI values from TRAC and PCA are equal. We were able to test this assumption at Pandamatenga (only), where we collected PCA data at both waist and ground level. The resulting PCA estimate of overstory PAI, corrected for clumping, was 0.94. This differs from the TRAC value (1.43) by 0.49 (34% relative), which is less than the sum of one standard deviation errors in Table 2.

On the Kalahari, clumping indices (Ω) were always less than unity and remarkably similar (Table 2). This suggests that the expected error in PAI_{eff} (vs. PAI) remains about the same for the different locations.

Canopy cover (CC)

First, we tested the validity of our TRAC GF approximation (Eqn (2)) by comparing measurements of GF provided by PCA, digital photography and TRAC. Representative plots for a northern (Pandamatenga) and a southern (Tshane) site are shown in Fig. 3, and suggest that Eqn (2) provides reasonable estimates of CC. The plots depict the normal decrease in GF with increasing θ . Analysis of all data suggests that the photography estimates of GF tend to exceed those of TRAC and PCA at all θ . This may be due to the relative heights of the sensors, since the PCA was held at

ground level and the camera was held at about 1.5 m. However, the error bars are large and overlapping among sensors.

The mean CC values for all sites and sensors are provided in Table 3. Again, PCA and ceptometer data represent CC for total vegetation (understory and overstory), whereas the photography, line intercept and TRAC provide overstory CC only, and line intercept counts small (<0.5 m) within-canopy gaps as part of the CC. Despite these methodological differences, there is reasonable agreement between the methods. For example, the difference among estimates on the Large Grid was less than 0.21 at each site, except Mongu. The lower estimates obtained by photography at Mongu and Tshane are exceptions, which might be explained by the height of the camera (1.5 m) relative to that of the other instruments (TRAC at 0.7 m, ceptometer and PCA at ground level). The TRAC CC result was low at Maun, possibly due to its use on just two of the transects there. PCA had an anomalously high

value on the Medium Grid at Okwa, where the vegetation differed among the different grids. Depending on the sensor, CC decreased by about 30% (absolute) over the Kalahari Transect, a trend consistent with PAI.

Variability of structure with annual precipitation

The variability of the mean TRAC (PAI) and PCA (PAI_{eff}) values with MAP is shown in Fig. 4. Okwa data were not used since the site presented anomalous vegetation conditions relative to surrounding landscape. Assuming a linear relationship, PAI and MAP were well correlated for TRAC ($r^2 = 0.95$), but only moderately correlated ($r^2 = 0.34$) for PCA. The variability of CC with MAP is shown in Fig. 5. Using an exponential curve, we found an excellent correlation ($r^2 = 0.97$) in the TRAC case, but again only a moderate correlation (0.56) in the PCA case.

Determining a predictive parameter for vegetation structure

Analysis of the covariance among the TRAC-derived structural parameters revealed that CC had the highest mean correlation ($r^2 = 0.65$) with the other parameters, while the clumping index had the lowest ($r^2 = 0.06$). This suggests that if a single structural variable were being measured to characterize semi-arid vegetation structure (or estimate the other parameters), CC would be a good candidate.

Relationships between parameters

Linear relationships between PAI and CC, and between PAI and clumping index, are detailed in Table 4. The consistency of the clumping index among the sites and

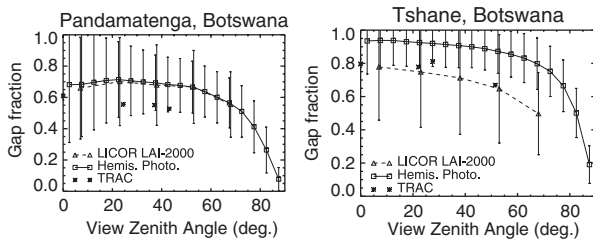


Fig. 3 Mean gap fraction with view angle (°) for a northern (Pandamatenga, left) and a southern (Tshane, right) site on the Kalahari. The plant canopy analyzer data were collected at about 1.5 m above ground level at Pandamatenga, but at ground level for Tshane. The error bars represent one standard deviation. The site-wide tracing architecture and radiation of canopies (TRAC) value for $\theta_v = 0$ was estimated with Eqn (2) and the three 750 m transect values (where $\theta_v \neq 0$ as shown); here, the error bars represent the range.

Table 3 CC (fractional) as a function of site and method

Site	Large Grid			Medium Grid		Small Grid
	PCA	Hemispherical photography	TRAC	PCA	Line intercept*	Stem map/dripline
Mongu	N/A	0.24	0.54	N/A	0.49	0.65
Pandamatenga	0.39/0.34	0.32	0.39	0.54/0.46	0.51	0.32
Maun	0.45	0.20	0.24	0.41	0.40	0.36
Okwa River	0.29	0.20	0.20	0.51	0.23	N/A
Tshane	0.22	0.07	0.20	0.16	0.20	0.14

*Line intercept method does not reflect within-crown gaps. The first value for PCA at Pandamatenga represents the total cover, and the second value represents the overstory only. The remaining PCA values represent the total cover. N/A indicates value not available. CC, canopy cover; PCA, plant canopy analyzer; TRAC, tracing architecture and radiation of canopies.

the variability of the other parameters led to very low correlations with clumping index. In general, none of the correlations varied with MAP. Representative plots of PAI vs. CC for the driest (Tshane) to wettest (Mongu) sites are shown in Fig. 6. The linearity of the relationship is obvious.

To allow rough estimation of the PAI vs. CC relationship over the entire region, we analyzed the regression coefficients (Table 4) with MAP. The relationships of PAI with CC had increasing slopes and decreasing constants with increasing precipitation as shown in Fig. 7. We fit the slope data with a logarithmic

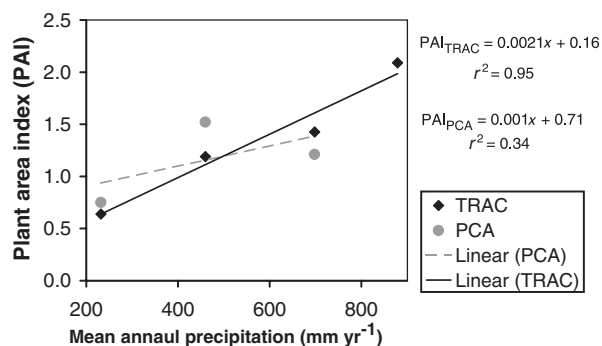


Fig. 4 Variability of plant area index (PAI) with mean annual precipitation for five sites along the Kalahari Transect.

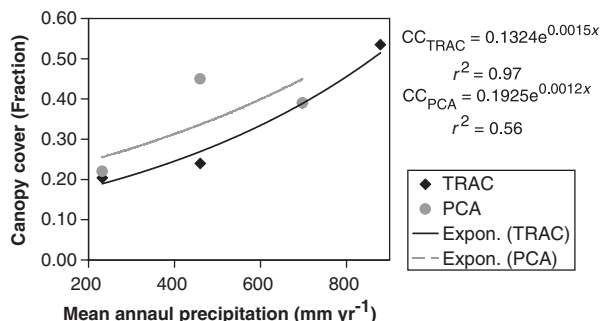


Fig. 5 Variability of canopy cover with mean annual precipitation for five sites along the Kalahari Transect.

curve, and the constant data with a linear curve. Correlations were very high ($r^2 = 0.99$ and 0.92 , respectively). For sites along the Kalahari gradient, these relationships provide a rough guide to estimating PAI from CC given MAP.

Discussion

The strong correlation of canopy structure with precipitation (Figs 4, 5 and 7) along the Kalahari has been reported previously (e.g., Ringrose & Chanda, 2000); however, the SAFARI Kalahari Campaign archive provides one of the richer and most synoptic (near-simultaneous) views of this variability.

Although the equations describing the parameter relationships as a function of precipitation (Figs 4, 5 and 7) are rough, their implications seem reasonable. In the case of PAI vs. CC over the Kalahari, the trends suggest that the PAI per unit CC (i.e., vertical plant material) increases with increasing precipitation. This result is consistent with observation (taller trees with more leaf area) and independent data (Scholes *et al.*, 2003). The linear PAI vs. CC site-wise relationship suggests that if the MAP increased (as it does further north of Mongu), trees would generate more foliage and continue to fill the between-crown gaps (increasing CC). Because canopy coverage is bounded [0,1] and PAI is in theory unbounded (in practice, $0 < \text{PAI} < \sim 12$), the linear trend would at some point transition to a near-asymptotic trend, where the PAI increases with little or no further increase in canopy coverage. This transition was not reached in these data.

The absence of a PAI vs. clumping relationship (Table 4) implies that the landscape PAI is not a function of the gap size distribution, and hence the spatial distribution of individuals, in these water-limited environments. Various theories of plant competition (e.g., Smith & Goodman, 1986) imply that clumped individuals may compete for scarce resources and hence be retarded in growth. Since the scarcity of resources decreases from south to north along the Kalahari, we hypothesized that

Table 4 Empirical relationships between measured structural parameters*

Y	X	Mongu			Pandamatenga			Maun			Okwa			Tshane		
		Const.	Slope	r^2	Const.	Slope	r^2	Const.	Slope	r^2	Const.	Slope	r^2	Const.	Slope	r^2
PAI	CC	-0.78	5.47	0.88	-0.40	5.00	0.81	-0.33	4.35	0.86	-0.12	3.18	0.88	-0.04	3.38	0.71
Ω	CC	0.68	0.17	0.07	0.59	0.28	0.08	0.82	-0.08	0.01	0.88	0.09	0.00	0.74	0.12	0.00
PAI	Ω	2.45	-0.25	0.00	1.94	-0.51	0.01	2.72	-1.86	0.15	1.13	-0.61	0.06	1.38	-0.91	0.20

*Data are from TRAC. Const., constant (y-intercept); PAI, plant area index; CC, canopy cover; TRAC, tracing architecture and radiation of canopies.

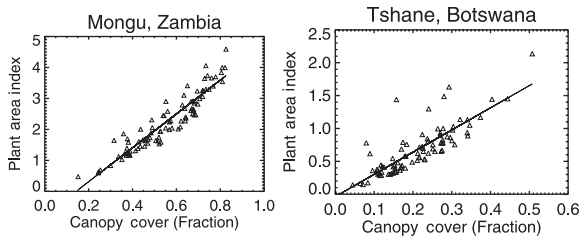


Fig. 6 Variability of plant area index with canopy cover for the wettest (Mongu, left) and driest (Tshane, right) sites visited during the Kalahari Transect. Data points represent TRAC-derived values obtained for each 25 m interval along the three 750 m transects.

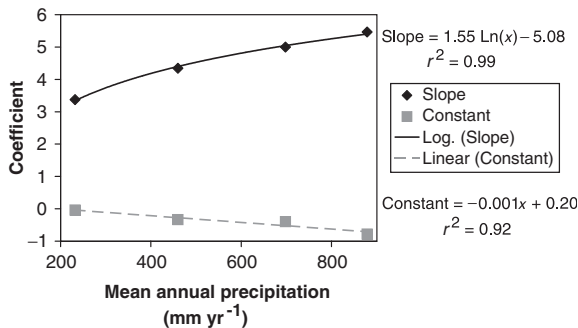


Fig. 7 Variability of linear equation coefficients relating plant area index to canopy cover (from Table 4), with precipitation. Note that a given slope value effectively represents sensitivity within a site, whereas the trend of the slope line represents the sensitivity of the relationship to precipitation.

the clumping index might indicate a trend in competition. It did not, although its fairly non-intuitive definition may not be suited towards competition characterization (type or intensity).

Further, the lack of correlation of the clumping index with other parameters (e.g., CC, LAI, PAI) is disappointing since this parameter currently cannot be determined from remote sensing, and few field instruments are able to retrieve it. Unfortunately, the TRAC software used to generate the clumping index is proprietary, i.e., the source code is not available to users. Therefore, the ability to derive actual PAI and LAI values from the more commonly measured effective values appears limited. Modern remote sensing methods (Myneni *et al.*, 2002), however, appear to be able to estimate directly actual LAI without recourse to a clumping parameter (although wavelength-independent structural parameters are used). Still, neither parameter is easily explained in terms of usefulness to ecologists.

It is encouraging that CC proved to have the greatest correlation with other structural variables (Table 4)

since it is easily measured in the field and may also be derived from remote sensing techniques. For example, Caylor *et al.* (2003b) used high spatial resolution IKONOS and CORONA imagery to determine CC in the Kalahari. The strong linear correlation of PAI vs. CC suggests that the more difficult-to-measure PAI (and LAI) can be determined through empirical equations. Further, the well-behaved trend in this relationship with MAP (Fig. 7), together with the consistency of the clumping index over all sites, suggests that vegetation structure over the entire region can likely be well characterized with remote sensing methods.

An obvious question for this study is whether any of the three sampling grids provides a valid statistical sample of local vegetation characteristics. Because a common technique was used on two grids, PCA data may be used to assess how well the Medium Grid represents the landscape population, represented here by the Large Grid statistics. The relative differences were 16.5%, 20.4%, 30.6% and 44.0% from Pandamatanga to Tshane, respectively, suggesting that the Medium Grid's capacity to represent the larger landscape increases with annual precipitation. This underscores the utility of nesting the plots such that extrapolation is possible.

We note that throughout this article, we reported PAI values rather than LAI values. The latter parameter is more commonly used in models and derived from remote sensing. To estimate LAI from light obscuration instruments used here, the probability of obscuration by a stem vs. by a leaf must be estimated. Green LAI can then be determined from the relation

$$\text{LAI} = \text{PAI} - \text{SAI}, \quad (3)$$

where SAI is the stem area index ($\text{m}^2 \text{m}^{-2}$), a measure of the non-photosynthesizing material (e.g., stems, dead leaves) in the canopy. Ideally, the ratio of SAI to LAI or PAI is determined via destructive measurements. These were not determined on the Kalahari Campaign, but may be estimated from ancillary data. For example, a comparison of the allometric LAI values and the PAI values measured in this campaign suggest that the SAI to be about 0.3 in the Kalahari; PAI measurements by ceptometer during the leafless period in similar vegetation at Skukuza, South Africa (600 mm MAP) suggests a similar value (R.J. Scholes, unpublished data).

Asner (1998) suggests a range $0.3 < \text{SAI} < 0.4$ for semi-arid savannas based on a large sample of North and South American systems. Using these estimates, the resulting green LAI values are qualitatively similar to those from remote sensing (i.e., EOS MODIS; see Fig. 1). Privette *et al.* (2002) conducted a quantitative comparison and showed that the TRAC and MODIS LAI are

consistent over all sites (including year-round at Mongu), and that the impact of SAI on PAI is substantially lower in the wet season relative to the dry season. That study and others (Tian *et al.*, 2002; Scholes *et al.*, 2003) help provide confidence in the global LAI product produced each 8 days from MODIS. However, many more studies linking satellite-derived products to field data are required, especially over other ecosystems and in different seasons, before the family of MODIS land products can be considered globally validated with well-characterized uncertainties.

Besides their use in ecological modeling, these results may be helpful in establishing optimal sampling schemes for semi-arid vegetation structure. Specifically, results from the labor-intensive and time-consuming measurements conducted on the Small Grid are likely correlated with the TRAC results collected over the Large Grid. By establishing appropriate relationships between these, results of the laborious tasks might be estimable from the TRAC results. This could reduce time, effort and expense in the field. Unfortunately, the mean site value comparisons provided here are not conclusive in that respect. A point-by-point comparison of the different instruments' results has not been conducted. Although these instruments were used on common transects, the varying fields-of-view and sampling styles make such a comparison challenging.

Conclusions

Using data from an ~20 day field campaign along ~950 km of the International Geosphere-Biosphere Programme (IGBP) Kalahari Transect, we found that the overstory PAI increases from about 0.64 at Tshane, Botswana (~350 mm MAP) to 2.1 at Mongu, Zambia (~960 mm MAP). Of this, stem material contributes about 0.3; thus the green LAI ranges from about 0.35 to 1.8. The overstory fractional CC ranges from 0.20 to 0.55 over the same gradient. Results from commonly used field instruments produced different estimates of both parameters; however, the spatial trends were similar among the instruments and matched those seen in the LAI product from NASA's Earth Observing System. CC was highly correlated with PAI over the entire Transect, and could act as a proxy variable in this environment.

The clumping factor was fairly consistent over the sites (mean value of ~0.73 if Okwa is ignored), which suggests that the actual LAI and PAI values exceed the effective values determined with common field instruments (e.g., LI-COR LAI 2000) by about 25%. We suggest that this magnification factor be applied to future data derived from LAI instruments, which do not explicitly account for clumping.

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The data described in this study are available via the Oak Ridge Data Active Archive Center's (DAAC) Mercury system (<http://mercury.ornl.gov/safari2k/>), and will form part of the SAFARI CDROM Series Vol. 3 (Nickeson *et al.*, 2003, available from the Oak Ridge National Laboratory's Distributed Active Archive Center (DAAC)). Associated satellite data are also available on the third CDROM volume as well as through the EOS Data Gateway (EDG), an online resource of the Land Processes DAAC at the US Geological Survey, Sioux Falls, South Dakota. The complete SAFARI 2000 data archive will be available at the SAFARI Regional Data Center operated by the University of the Witwatersrand.

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