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Structural, physiognomic and aboveground biomass variation in savanna-forest transition zones on three continents. How different are co-occurring savanna and forest formations?

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Abstract

Through interpretations of remote sensing data and/or theoretical propositions, the idea that forest and savanna represent "alternative stable states" is gaining increasing acceptance. Filling an observational gap, we present detailed stratified floristic and structural analyses for forest and savanna stands mostly located within zones of transition (where both vegetation types occur in close proximity) in Africa, South America and Australia. Woody plant leaf area index variation was related in a similar way to tree canopy cover for both savanna and forest with substantial overlap between the two vegetation types. As total woody plant canopy cover increased, so did the contribution of middle and lower strata of woody vegetation to this total. Herbaceous layer cover also declined as woody cover increased. This pattern of understorey grasses and herbs being progressively replaced by shrubs as canopy closure occurs was found for both savanna and forests and on all continents. Thus, once subordinate woody canopy layers are taken into account, a less marked transition in woody plant cover across the savanna-forest species discontinuum is observed compared to that implied when trees of a basal diameter > 0.1 m are considered in isolation. This is especially the case for shrub-dominated savannas and in taller savannas approaching canopy closure. An increased contribution of forest species to the total subordinate cover is also observed as savanna stand canopy closure occurs. Despite similarities in canopy cover characteristics, woody vegetation in Africa and Australia attained greater heights and stored a greater concentration of above ground biomass than in South America. Up to three times as much aboveground biomass is stored in forests compared to savannas under equivalent climatic conditions. Savanna/forest transition zones were also found to typically occur at higher precipitation regimes for South America than for Africa. Nevertheless, coexistence was found to be confined to a well-defined edaphic/climate envelope consistent across all three continents with both soil and climate playing a role as the key determinants of the relative location of forest and savanna. Taken together these observations do not lend support the notion of alternate stable states mediated

through fire-feedbacks as the prime force shaping the distribution of the two dominant vegetation types of the tropical lands.

1 Introduction

In general terms, "savannas" may be defined as woody vegetation formations types having a fractional axylale (herbaceous) ground cover of at least 0.1; but also with a woody species composition quite distinct from "forests"; the latter also typically (though not always) with axylales absent (Torello-Raventos et al., 2013). Together forest and savanna dominate the tropical vegetated regions covering 0.15 to 0.2 of the earth's surface (Walter and Mueller-Dombois, 1971).

At a broad scale it has long been recognized that the distributions of these two biomes are principally governed by precipitation and its seasonality (Schimper, 1903). Nevertheless, it is sometimes possible to find these different vegetation formation types in climatic zones where they are not usually occurring. For example, stands dominated by species usually associated with forest vegetation formation types ("forest outliers") may be found in Australia at mean annual precipitations (P_A) of $< 1.0\,\mathrm{m\,a^{-1}}$ in both Australia (Fensham, 1995) and South America (Killeen et al., 2006). Conversely, savannas are often seen on sandy soils under precipitation regimes usually associated with forest ($P_A > 2.0\,\mathrm{m\,a^{-1}}$) with such "savanna inliers" having been reported for South America, Australia and Africa (Hopkins, 1992; Lloyd et al., 2008; Torello-Raventos et al., 2013).

There are also discrete regions where the two biomes intercept – often referred to as "ecotones" or "Zones of (Ecological) Tension" (ZOT) – where both forest and savanna exist as discrete "patches" under similar climatic conditions. Although the influence of soil structure in shaping vegetation distributions within such ZOT has long been recognised (Cochrane, 1989; Ratter, 1992; Thompson et al., 1992; Hoffmann et al., 2009; Lehmann et al., 2011; Saiz et al., 2012), the observation that the artificial exclusion of fire from savanna areas within ZOT is followed by invasion of forest species has led to the idea that forest and savanna stands may represent alternate stable states modulated by fire-mediated feedbacks (Warman and Moles, 2009; Hoffmann et al., 2012a; Murphy and Bowman, 2012). Here the regular recurrence of fire in savanna systems is considered to prevent these vegetation formations from becoming dominated by fire sensitive forest species, with grasses and savanna trees characterised by adaptations to a pyrogenically susceptible environment dominating (Gignoux et al., 2009; Hoffmann et al., 2012a; Murphy and Bowman, 2012). The observation that the exclusion of fire over prolonged periods often leads to transition of mesic savanna to forest is also seen as strong evidence for such feedbacks; see for example Hopkins and Jenkin (1962), Louppe et al. (1995), Swaine et al. (1992) and Geiger et al. (2011).

The notion of fire-mediated bistability has gained increasing acceptance through analysis of a global tree canopy cover data set (MOD44B; Hansen et al. (2002). A number of studies have interpreted the observation of a lack of canopy cover around 0.6 range (fractional cover) in this data set to provide planetary scale evidence of alternative states with forest and savanna considered to exist above or below this threshold (Hirota et al., 2011; Staver et al., 2011a, b; Murphy and Bowman, 2012). Fire mediated feedbacks also form the basis of several models of tropical vegetation structure both across the ZOT and within savanna systems (Van Langevelde et al., 2003; Staver et al., 2011a; Higgins and Scheiter, 2012) with conceptual origins lying in theoretical frameworks of non-linear ecosystem population dynamics (May, 2001).

Hanan et al. (2013) have, however, recently pointed out that gaps in the distribution of the global vegetation cover data set may be the result of statistical procedures of calibration rather than low frequency occurrences of crown cover classes in the real world. Alternative explanations for the existence of observed tropical cover distribution patterns such a plant water demand (Bertram and Dewar, 2013) and herbivory (Pachzelt et al., 2013) have also been used in modelling studies to explain woody cover patterns not solely dependent on fire mediated feedbacks.

Moreover, direct ground based observational evidence for forest-savanna discontinuities and the existence of alternative stable states does not seem to have been actively sought. Nor has the structural and/or floristic (dis)similarity in structure of forests and savannas in the transition been studied across continents in any sort of systematic manner. We do know, however, that fire adapted woody species in vegetation types usually defined as “savannas”, can attain forest-like woody canopy covers under certain circumstances (Torello Raventos et al., 2013).

In this paper we attempt to fill this obvious data gap by providing detailed ground-based observational information on vegetation structure changes across the forest-savanna boundary. An emphasis is placed on the evaluation of all layers of the canopy, particularly the lower shrub and grass/herb (“axylale”) layers: these being particularly important in the categorisation of the different tropical vegetation formations (Torello-Raventos et al., 2013), even though often excluded in definition and analysis of tropical forest structure. Our detailed field-based data thus include woody vegetation layers below 5 m and trees with diameter < 0.1 m. Indeed, these layers sometimes represent a substantial component of both forest and savanna total woody cover and with some savannas even dominated by these shorter woody vegetation types (Eiten, 1972; Haase and Beck, 1989; Gentry, 1995; Killeen et al., 1998; Oberle et al., 2009; Torello-Raventos et al., 2013).

Our analysis utilises a global data set of newly established sample plots – mostly located in ZOT – but also including specifically selected savanna inliers and forest outliers as well as low precipitation savanna formations, with a delineation of these into forest, woodland or savanna through a consistent set of rules designed to define tropical vegetation formation types globally (Torello Raventos et al., 2013). To our knowledge our present analysis of structure of the plots used by Torrello Raventos et al. (2013) represents the first attempt to describe changes across ZOT on a field data basis and at a global scale. As well as describing structural differences, we also provide some first estimates of biomass differences for forest and savanna stands growing in close proximity with data coming from Australia, South America and Africa and with the anticipation that such data will be of considerable importance for global land-use change carbon emission estimates (Malhi, 2010; Gloor et al., 2012; Houghton, 2012). Specific questions addressed include:

1. Is there a really a marked discontinuity in dominant strata canopy cover distributions for tropical woody vegetation formation types as suggested by remote sensing products? And if so, is this associated with an abrupt transition from (i) vegetation formation types characterised by an obvious axylale layer and dominated by fire-adapted woody species (savannas) to (ii) contrasting closed formations characterised by a very different woody species composition and with both axylales and fire virtually absent (forests)?
2. Does any such apparent marked continuity in woody plant cover continue to exist once variations all strata are taken into account? Specifically, around the point of upper-strata canopy closure, is there a replacement of axylales by shrubs and small trees not included in most ground-based inventories and – most likely – also not detected by remote sensing products?
3. Do forest vs. savanna trees differ in their allometry? And if so, along with differences in woody plant density – especially in the subordinate layers, how is this translated into differences in stand level biomass?
4. Given the obvious influence of soils as key modulators of tropical vegetation structure, to what extent might edaphic factors provide an explanation for both savanna and forest sometimes being found under apparently identical conditions? And if the soil effect is considerable, is an invocation of "alternative stable states" then necessary for an understanding of the otherwise enigmatic distribution patterns of forest and savanna vegetation formation types across the tropical lands.

2 Materials and methods

With an objective of quantifying what factors define changes in vegetation structure and physiognomy across savanna-forest boundaries in so called *Zones of Tension* (ZOT), measurements of forest and savanna vegetation structure were made in ZOTs located in Australia, Africa and South America. Sites had been selected with a view to maximising differences in climate and soils to allow an analysis of global applicability. The criteria of plot selection and establishment are detailed in Torello-Raventos et al. (2013). Drier savanna and forest plots were also examined in Australia, Bolivia and West Africa and with higher precipitation forest and savanna sites also studied in Brazil and Australia. A map showing all plot locations is given in Fig. 2 of Torello-Raventos et al. (2013) with a list of all plots studied, their location, vegetation formation type, basic climatology and soil type also provided here (see Table S1 in Appendix A of Supplement). Nomenclature of the various vegetation types follows Torello-Raventos et al. (2013) and in what follows all that is not referred to as some form of "Forest" is, by definition, considered part of the "Savanna Domain". This includes all "grassland", "savanna" and "woodland" types.

In terms of natural and human-mediated disturbances, some sites were fire-protected and with domestic animal grazing specifically excluded, but some others, especially in West Africa, farm animals were observed grazing in or nearby the sample plots. For all plots, there were no barriers placed to the grazing of vegetation by the natural fauna. Table A1 of Torello-Raventos et al. (2013) gives details of plot histories (in terms of those previously or newly established), plot protection status and perceived anthropogenic influences (grazing and fire protection or promotion).

2.1 Study sites

Measurements were made from July 2006 to March 2009 in five field campaigns, each over a period of ca. two months with as many plots as possible sampled within the allocated time and summarized as follows: West Africa (Ghana, Burkina Faso and Mali: 14 plots; August to October 2006), Bolivia (11 plots; February to May 2007) Cameroon (8 plots; November to December 2007), Brazil (17 plots; April to June 2008) and Australia (11 plots; February to April 2009). All sampling campaigns had been timed to coincide with the end of the wet season and associated expected maximum plant physiological activity and standing herbaceous biomass.

2.2 Tree and shrub canopy area index

Defining a canopy area index (C) as the sum of individual tree canopy projected area (including the skylight transmitted component) divided by the ground area as detailed in Torello-Raventos et al. (2013), C was estimated separately for three woody strata within each plot *viz.* for the upper (U), mid-stratum (M), and subordinate (S) layers as defined on the basis of with a stem diameter at breast height (1.3 m) D, and individual tree height (H). Data used here is as presented in Torello-Raventos et al. (2013), with precise definitions of C_U, C_M and C_S given in their Table 1. In short, the upper stratum was considered to consist of all woody elements $D > 0.1$ m; the middle stratum all woody elements with $H > 1.5$ m and 25 mm $< D < 0.1$ m and the lower stratum all other woody plant present (*viz.* less than 1.5 m high and/or $D < 25$ mm).

For some analyses presented here the woody canopy cover component was also divided into trees and shrubs, these being segregated as in Torello-Raventos et al. (2013). In brief, shrubs are defined as woody species with either a single stem (bole) of length at least 1.5 m, but with height less than 3 m, or a woody species with a stem length prior to branching of less than 1.5 m (also being less than 5 m height). The associated canopy area indices are designated as C_t and C_Sh and are formally defined in Table 1 of Torello-Raventos et al. (2013).

Also considered separately here is a division of the woody vegetation according to height, with the total woody plant canopy cover (all trees and shrubs taller than 1.5 m; C_W) and seedling canopy cover (all trees and shrubs less than 1.5 m tall; C_Se), again as defined in Table 1 of Torello-Raventos et al. (2013).

2.3 Fractional canopy covers

Assuming a random distribution of trees and/or shrubs, the crown cover; *viz.* the fraction of ground covered by crowns (including within-crown light gaps) referred to here as the *fractional crown cover* (ς) can be estimated for any combination of layers (Z) as

$$\varsigma_Z = 1 - \exp\left(-\sum\nolimits_{i=1}^{n} C_i\right), \tag{1a}$$

where n is the number of layers. For example, for $Z = W = U + M$ then $n = 2$ and

$$\varsigma_\mathrm{W} = 1 - \exp\left(-C_\mathrm{U} - C_\mathrm{M}\right). \tag{1b}$$

Likewise for a single layer or vegetation form (e.g. shrubs) then

$$\varsigma_\mathrm{Sh} = 1 - \exp\left(-C_\mathrm{Sh}\right). \tag{1c}$$

Savanna vegetation may, however, be clumped and so we tested for complete spatial randomness (CSR) using a G function (Bivand et al., 2008) via the `R spatstat` package (Baddeley and Turner, 2005). The G function measures the distribution of distances from an arbitrary event to its nearest event and comparisons of the theoretical expectation for CSR against that actually observed. There were only minor indications of clumping for those plots tested plots suggesting little if any underestimation of fractional covers using Eq. (1) (see Fig. S1 in Appendix B of Supplement).

Estimates of various ς so estimated are used extensively throughout this paper (and with subscripts always as above) and here we note that estimates of fractional crown cover are not numerically or conceptually the same as those often presented for (fractional) *woody canopy cover* which – in remote sensing studies – is defined as "the portion of the skylight orthogonal to the surface which is intercepted by trees" (e.g. Hansen et al., 2002). Defining then α as the proportion of light intercepted on average by the tree crowns, and noting that canopy cover as so defined above is essentially equivalent to the fractional foliage cover or projective foliar cover of the stratum in question, ζ (Lloyd et al., 2008) it then follows that $\zeta = \alpha\varsigma$ where α is the average proportion of skylight passing through each tree.

Estimates of the fractional canopy cover of grasses and herbs in the ground layer (referred to here as "axylales") are as in Torello-Raventos et al. (2013). In brief, the axylale fractional cover (ζ_a) was visually recorded along a series of transects with a typical sampling intensity of 110 × 1.0 m^2 quadrants per 1 ha plot.

2.4 Canopy height

Upper stratum tree heights (H) were estimated as described in Feldpausch et al. (2011) and Torello-Raventos et al. (2013). In short, site specific allometric equations were developed to calculate 0.95 quantile and average woody plant heights for the upper stratum ($D \geq 0.10$ m), these being denoted as H^* and $\langle H \rangle_\mathrm{U}$ respectively.

2.5 Stand-level leaf area index

Leaf area index of trees and shrubs taller than 1.5 m (L) was assessed using hemispherical photography. True-colour images were taken under diffuse light conditions (mostly sunrise and sunset) with a Nikon Coolpix 8800VR camera and Nikon Fisheye Lens FC-E9 set at aperture 8.0 with a 2 step underexposure (Zhang et al., 2005). At most sites 10 to 25 images were taken at the centre of 25 m × 25 m grid cells but for a few sites with a very sparse woody cover, hemispheric images were taken from randomly selected trees. This is because of a potentially problematic determination of L from grid hemispherical images in open vegetation ($L \lesssim 1.5$) as detailed by Ryu et al. (2010).

Images were analysed with the Gap light Analyser software Version 2 (Frazer et al., 1999) and in applying the technique two or more observers independently determined image specific threshold and contrast settings to reduce observer error. For each image, L was calculated from an integration over the zenith angles 0–75° after trunk and/or branch elements had been removed through manual editing. If images contained individual trees with non-overlapping crowns, fraction canopy cover in the image was also measured for each image by blackening total canopy area and determining canopy openness. Canopy-level L was then determined by dividing image L by image canopy fraction and L for plots where only images of individual trees were taken was then determined by multiplying the average individual tree estimates of L by the C_W. Comparison of results of this calculation with L determined from grid cell images (if sites had images with non-overlapping crowns) gave comparable results particularly if $L < 1.0$.

Estimates for end of season L for the axylale layer were determined from clipping standing biomass (by drying to constant weight) in five to ten randomly selected 1 m^2 plots. Leaf area of these samples was determined by scanning the fresh surface of a subsample of the clipping before determination of specific leaf area.

2.6 Shrub and seedling dominance indices

To quantify the relative dominance of shrubs in the ground layer relative to herbs and grasses (axylales), we defined a "shrub dominance index" (χ_1) as

$$\chi_1 = \frac{\varsigma_{\mathrm{Sh}} - \zeta_{\mathrm{a}}}{\varsigma_{\mathrm{Sh}} + \zeta_{\mathrm{a}}}, \tag{2a}$$

where (as defined above) ς_{Sh} is the shrub crown projected cover and ζ_{a} is the axylale fractional cover. A second metric which quantifies competition between herbaceous and woody elements of the subordinate layer, a "seedling dominance index", χ_2, was also defined, *viz*.

$$\chi_2 = \frac{\varsigma_{\mathrm{Se}} - \zeta_{\mathrm{a}}}{\varsigma_{\mathrm{Se}} + \zeta_{\mathrm{a}}}, \tag{2b}$$

where ς_{Se} is the crown projected cover of all tree and shrub seedlings (as defined above). The two indices (which can both potentially vary from −1 to +1) differ in that χ_1 quantified the relative dominance of shrubs over axylales in the understorey (but ignoring any tree seedlings or tree saplings) whereas χ_2 provides a measure of the relative abundance of both tree and shrub seedlings relative to herbaceous cover extent.

2.7 Tree, shrub and liana biomass

2.7.1 Forests

For all forest plots *sensu* Torello-Raventos et al. (2013) we applied a global equation for predicting above ground biomass (B) from diameter at breast height (D) and tree height (H) and density (ρ) using the "dry forest" equation of Chave et al. (2005) for all trees of $D \geq 25$ mm (see Eq. S1 in Table S2 of Supplement Appendix C). Wood density values were obtained from Zanne et al. (2009) for Africa and South America and Ilic et al. (2000) for Australia. Unknown species densities are calculated using the mean values at closest taxon. For forest shrubs we developed our own generic equations for predicting B from basal area (A_B) or crown diameter (D_C) these being based on destructive measurements of 63 randomly selected individuals of the species *Acacia tenuifolia*, *Croton argyroglossus*, *Tetrapterys racemulosa* and two unidentified *Acacia* species harvested at the Tucavaca stunted forest and shrub-rich woodland site in Bolivia (TUC-01 and TUC-02). The resulting parameterisation (see Eqs. S2 and S3 in Table S2 of Supplement Appendix C) gave rise to similar predictions to another derived independently for Indian understorey forest shrubs (Singh and Singh, 1991) suggesting a general applicability. For lianas we applied an equation from Schnitzer et al. (2006) and for palms the equation of de Castilho et al. (2006) both these parameterisations predicting B from D (see Eqs. S4 and S5 in Table S2 of Supplement Appendix C)

2.7.2 Savannas

For taller savanna trees in the African humid savannas of Burkina Faso, Cameroon and Ghana ($H > 10$ m) we applied a generic allometric relationship for predicting B from D and H, originally developed for miombo woodland trees (Malimbwi et al., 1994). This parameterisation (see Eq. S6 in Table S2 of Supplement Appendix C), tested for African savanna trees using unpublished data from Ivory Coast (Menaut, 1971), was confirmed as a good predictor for large trees ($H > 10$ m) but with a tendency to underestimate B for medium to smaller sized trees. For the more humid West African and Cameroon savanna plots we therefore developed new equations for all trees of $D > 25$ mm and $H < 10$ m using the Menaut (1971) data set (see Eqs. S7 and S8 in Table S2 of Supplement Appendix C). For trees in the Sahelian savanna plots (HOM-01 and HOM-02) we used a parameterisation from Henry et al. (2011) using D as the predictor variable (see Eq. S13 in Table S2 of Supplement Appendix C) with the biomass parameterisations for trees in the Guinean savannas BDA-01 and BDA-02 (Alexandre and Kaïré, 2001) also as given in Henry et al. (2011) with B derived from basal area (A_B) measurements (see Eq. S14 in Table S2 of Supplement Appendix C). For shrubs at these drier sites we used an equation from Skarpe (1990) with B estimated from crown area (A_C) measurements (see Eq. S10 in Table S2 of Supplement Appendix C). For the subligneous fire resprouter shrub *Cochlospermum planchonii* (dominant in the Burkina Faso plots DAN-01 and DAN-02) a separate equation was developed (see Eq. S9 in Table S2 of Supplement Appendix C) with B calibrated against A_C. For shrubs and trees in South American cerrados we used an equation taken from Ribeiro et al. (2011) with B derived from D, H and ρ (see Eq. S11 in Table S2 of Supplement Appendix C). Biomass of Australian trees and shrubs with $D > 25$ mm were estimated following Williams et al. (2005) with B derived from D and H (see Eq. S12 in Table S2 of Supplement Appendix C).

2.8 Climate

As in Torello-Raventos et al. (2013) we also estimated an index of plant water supply in relation to evaporative demand, W, this being calculated as (Berry and Roderick, 2002):

$$W = P_\mathrm{A} - Q_\mathrm{s}/(\rho\lambda) \tag{3}$$

where P_A is mean annual precipitation rate, Q_s is mean annual global solar radiation, ρ is the density of liquid water and λ is the latent heat of evaporation for H_2O. Temperature and precipitation climatologies for all sites were obtained from the interpolated dataset from WorldClim dataset (see http://www.worldclim.org/) with mean annual solar radiation data obtained from NASA's Langley Atmospheric Sciences Data Center Distributed Active Center (DAAC) assimilated from daily records (1983 to 2005).

2.9 Soil cation status

Soil sampling and exchangeable cation determination methods are as described in detail in Quesada et al. (2010) and Quesada et al. (2011) and are thus only briefly summarised here. In short, exchangeable aluminium, calcium, magnesium, potassium and sodium *viz.* $[\mathrm{Al}]_\mathrm{E}$, $[\mathrm{Ca}]_\mathrm{E}$, $[\mathrm{Mg}]_\mathrm{E}$, $[\mathrm{K}]_\mathrm{E}$ and $[\mathrm{Na}]_\mathrm{E}$, were determined by the silver-thiourea method (Pleysier and Juo, 1980) with a simple measure of soil fertility defined here, this being the "total major nutrient cations", N^+:

$$N^+ = [\mathrm{Ca}]_\mathrm{E} + [\mathrm{Mg}]_\mathrm{E} + [\mathrm{K}]_\mathrm{E}, \tag{4}$$

with all cation concentrations expressed as $\mathrm{meq}^+\ \mathrm{kg}^{-1}$ and integrated across the top 0.3 m of soil depth.

2.10 Statistical analysis

All analyses used the `R` statistical platform (R-Development-Core-Team, 2012). Mixed effects models (Figs. 1 and 2) were developed using the `mgcv` and/or `nlme` packages (Wood, 2006; Pinheiro et al., 2012) allowing for heterogeneity in variances considered in model fits using `varClasses` functions. Breakpoint regression analyses (Fig. 3) were with the `segmented` package (Muggeo, 2008); robust (rank-based) linear regression analyses (Figs. 4–7) used the high breakpoint (HBR) option of `wwest` (Terpstra and McKean, 2005) and standard major axis regression (Fig. 9) was undertaken using `smatr` (Warton et al., 2012).

3 Results

3.1 Leaf vs. canopy area index

The relationship between woody vegetation leaf area index estimates from hemispherical photographs (L) and woody plant canopy area index (C_W) values obtained from ground-based inventories is shown in Fig. 1. Here, as in most subsequent diagrams, sites have first been grouped into vegetation domain *viz*. savanna and forest; these being differentiated on the basis of both floristics and structure (Marimon et al., 2006; Torello-Raventos et al., 2013). Both vegetation formation types are also further categorised into three structural groups and with continents identified by colour. In brief, for the forests, the prefix "stunted" applies to those forests with a mean canopy height (upper stratum) of less than 12 m and "tall forests" have an upper stratum 0.95 quantile height of more than 36 m. For the savanna domain, "shrub savannas" have a mean canopy height of less than 6 m (also with a canopy area index between 0.3 and 0.7) with "tall savannas" having a mean upper stratum canopy height greater than 12 m.

Figure 1 suggests a uniform but non-linear relationship across vegetation types and continents, tending towards an asymptote at $C_W \simeq 2$ (at which $L \simeq 2.7$). Below this point the ratio L/C_W is reasonably constant indicating a reasonably constant leaf area density (leaf area per unit projected canopy area; ℓ_D) of around 1.25, declining to less than 1.0 at high L. Thus under conditions permitting only limited foliage development variations in L are a direct consequence of variations in C_W (with a more or less constant ℓ_D). But at higher C_W there is a compensatory reduction in ℓ_D. Most importantly, Fig. 1 shows that, although the relationship between L and C_W is non-linear, C_W provides a reasonable proxy for stand-level L that is broadly consistent across both vegetation type and continent.

3.2 Variations in canopy structure

Changes in fractional crown cover (ς) as C_W increases are shown for the upper (U), middle (M) and subordinate (S) woody strata in Fig. 2a–c. This shows ς_U saturating beyond $C_W \simeq 2$, and with both ς_M and ς_S accounting for most of the increase in C_W beyond that (left side panels). Overall, there is little to suggest systematic differences between continents and, although overlap is limited, little to suggest any systematic difference between forest and savanna. Figure 2a also shows an apparent gap in the data around $0.55 \le \varsigma_U \le 0.65$ for the upper stratum but with both forest and savanna stands occurring above and below this break at around $C_W \simeq 1.5$. By contrast, no similar discontinuity is observed for either ς_M or ς_S.

The same data is also shown in Fig. 2d and Fig. 2e but in this case divided into trees (t) and shrubs (Sh). As C_W increases ς_t shows a saturating function similar to ς_U though with much less variability (though with two Australian forests occurring at unusually low rainfalls as clear outliers). The shrub fractional cover is clearly more variable (Fig. 2e). At least in part this can be attributed to the presence of shrub dominated savannas at some of the lowest C_W (these occurring on all three continents and for clarity enclosed by the dotted-line polygon in Fig. 2e). And so the line shown has been parameterised excluding these shrub-dominated sites so as to give an indication of how ς_U varies with C_W just for those savanna and forest formations with a distinct upper-stratum dominated by trees. This suggests a rapid increase in ς_{Sh} at $C_W \simeq 1$, peaking around $C_W = 1.5$ and maintained around ς_{Sh} at higher C_W, at least for the forests within the ZOT as examined here. This increase in ς_{Sh} at $C_W \simeq 1$ is observed first in tree-dominated savannas and stunted forests and it is only at $C_W \geq 2$ where the data is dominated by forest sites that ς_{Sh} tends to level out at a values of about 0.2.

Figure 2f shows axylale fractional cover (ζ_a) to decline with increasing C_W, first reaching a minimum at $C_W \simeq 2$ for both forest and savanna formation types. There is a reasonably strong relationship between ζ_a and axylale leaf area index (see Fig. S6 in Appendix D of Supplement) and so taken in conjunction with Fig. 2e, it can be concluded that as canopy closure occurs beyond $C_W \simeq 1$ that the herbaceous layer (generally dominated by C_4 grasses in these ecosystems) declines, being replaced by an increasingly dominant shrub layer. Importantly, this change in dominance is not associated with a transition from savanna to forest, but is rather first observed in the woodier savanna formation types.

The consequences of any attempt to define tropical vegetation formations solely on the basis of changes in upper stratum cover can be seen in Fig. 3 where the estimated stand level crown cover is plotted against that of the upper stratum only. Here the shaded area between the fitted segmented regression line (Muggeo, 2008) and the

1 : 1 relationship shows the average woody cover overlooked by an "upper stratum only" approach. Differences are greatest for $\varsigma_\mathrm{U} \lesssim 0.2$ and $0.5 \lesssim \varsigma_\mathrm{U} \lesssim 0.7$: these being associated in the first instance with the presence of shrub-dominated savannas and in the second instance with the higher relative dominance of shrub cover for vegetation characterised by $1 \geq C_\mathrm{W} \geq 2$.

3.3 Shrub and seedling dominance

The relative dominance of shrubs within the understorey in relation to axylale cover as affected by the upper-canopy cover is illustrated through a plotting of the shrub-dominance index (χ_1: Eq. 2a) as a function of ς_U in Fig. 4a. This shows χ_1 to increase with increasing ς_U both as savanna tree density increases and across the savanna/forest transition. There are, however, distinct outliers as detected by the robust regression fitting technique, these being (long-grassed) savanna woodlands in Africa and tall savanna woodlands in Australia. When the seedling dominance index (χ_2) is applied (i.e. including tree seedlings, but excluding any shrubs taller than 1.5 m) then most of the Australian tall savanna woodlands then fall into line (Fig. 4b) but with the long-grassed African savanna woodlands still identified as clear outliers. Thus, although there are exceptions, there is a clear tendency for grasses and herbs to be replaced by seedlings and shrubs in the lower strata as canopy closure occurs higher up. This is seen first in woodier savannas (beyond $\varsigma_\mathrm{U} \simeq 0.3$) extending then to the higher leaf area forest vegetation formation types.

3.4 Species composition of understorey

The presence of forest and savanna species in the middle and subordinate layers of savanna vegetation formation types plots is examined as a function of total fractional cover (this consisting mainly though not exclusively of savanna tree species) in Fig. 5a. This shows that associated with the upper canopy closure within savanna vegetation formation types beyond $\varsigma_\mathrm{U} \simeq 0.4$ is a marked increase in the abundance of forest species. On the other hand, there is no relationship between ς_U and the cover of subordinate savanna tree and shrub species for these same stands (Fig. 5b).

3.5 Crown-cover/height allometry

Upper stratum quantile height (H^*) is examined as a function of the associated upper canopy crown cover (ς_U) in Fig. 6. This illustrates, for the South American savannas in particular, that there is relatively little variation in H^* across a wide range of intermediate ς_U. At any given ς_U it can be seen that H^* is lower for South American savanna and/or forest than for Africa or Australia. There is also rapid increase in H^* associated with the transition from savanna to forest in South America that is more gradual on the other continents, especially once the stunted forests associated with unusually low precipitation (see Table S1 in Appendix 1 of Supplement) are taken into account.

3.6 Biomass/height allometry

The relationship between crown cover and biomass of the upper stratum (B_U: $D \geq 0.1$ m) – this being the only layer usually studied for estimates of forest biomass (e.g., Feldpausch et al., 2012) – is shown in Fig. 7a. Here we find a strong inverse reciprocal relationship and, although there is a rapid increase in B_U for $\varsigma_U > 0.8$ (including a few savanna plots) there is also considerable variation in B_U beyond this point with differences of over 300 t ha^{-1} possible at any given $\varsigma_U > 0.8$. A generally more consistent relationship is observed when biomass and crown canopy cover are examined at the whole stand level (Fig. 7b) and with some overlap between savanna and forest observed in both cases. The higher biomass of the tall savanna types is also clearly demonstrated by this diagram which also shows that, even at a ς_U of only 0.5, some Australian tall savanna formations can have a biomass approaching that of much higher crown cover South American and African forest formations.

3.7 Forest-savanna biomass differences

Figure 8 plots the biomass of all forest and savanna plots (excluding seedlings) as a function of the mean annual water availability, W, as calculated in Eq. (3). For each continent, forest and savanna are shown separately and with plots located within ZOT shown by the shaded area (ZOT here being defined as regions occurring at the intersection of major savanna/forest areas and with neither vegetation domain type clearly dominating at the scale of 10 km or less). Biomass estimates ($\hat{B}$) for each plot are also shown separately for the upper and middle strata and for lianas and with additional forest $\hat{B}$ (upper stratum only) coming from Feldpausch et al. (2012) indicated by an asterisk. Apart from showing that the ZOT investigated occur at different W for different continents, the presence of stunted forests in areas significantly drier than the studied ZOT is illustrated, as is the occasional presence of savanna at low W. The most substantial increase in biomass associated with a transition from savanna to forest is for the South American ZOT (this being markedly less than for the sites sampled in Australia and Africa). There is also an important contribution of the middle stratum (trees and shrubs with $D < 25$ mm) to the total biomass of plots within the ZOT in some cases; and for the South American savannas in particular.

3.8 Inter-continental differences in the location of the forest-savanna boundary

The location of all sampled plots in terms of both W and soil cation nutrient status (N^+; Eq. 4) is shown in Fig. 9 where with the $N^+ \cap W$ environmental space encompassed by ZOT (as identified in Fig. 8) shown through the shaded ellipse and with the fitted SMA regression line through these data points also shown. This shows that, not only is the presence of the ZOT within South America at a more negative W associated with soils of a lower exchangeable base cation status, but also that variations in the locations of individual plots within ZOT on each continent are also explicable in terms of the same N^+; W relationship. Generally speaking, forests are found above the fitted line and savanna formation types below. Savannas were, however, found at higher W for both

South America and Australia, these being associated with low N^+. On the other hand, the stunted forests of both South America and Australia exist at relatively high N^+ (and reasonably negative W). Also of note is a lack of observations where W is strongly negative and N^+ also low.

The general notion that the location of forest-savanna transition zones may differ between continents is examined further in Fig. 10, where the frequency of occurrence of savanna vegetation formation types in terms of P_A is shown for all of Africa and South America binned into 0.2 m P_A classes (original data from the vegetation map based study of Lloyd et al. (2008) undertaken at $1^\circ \times 1^\circ$ resolution). Here, observations to the right of the frequency diagrams are mostly forest-type vegetation types and those on the left arid vegetation type formations. This confirms a clear difference between the two continents in terms of savanna distribution in relation to rainfall. Specifically, the maximum frequency of savanna occurrence occurring at a P_A at least 0.2 m greater for South America than is the case for Africa. It was not, unfortunately, possible to include Australia in such an analysis due to the very limited area of tropical forest present.

4 Discussion

The idea that forest and savanna present fire mediated alternate stable states has recently been being supported by analyses of bi- or tri- model distributions of tree canopy cover in a remotely sensed global tree cover dataset (Hirota et al., 2011; Staver et al., 2011b; Murphy and Bowman, 2012) with this notion having been underwritten by models also simulating such dichotomies (Van Langevelde et al., 2003; Staver et al., 2011a; Higgins and Scheiter, 2012). This has led to the general view that such alternative stable states can exist under the same environmental conditions now becoming widespread – see for example Warman and Moles (2009) and Hoffmann et al. (2012a). However Hanan et al. (2013) have pointed that gaps in the distribution patterns in the global tree cover data set may be caused by statistical procedure rather than representing true abundance differences. Unequivocal evidence supporting the notion of alternative stable states should therefore be sought elsewhere.

Here we have reported an as complete as possible set of observations of structural changes across savanna and forest formations across ZOT on three continents. Our expectation was that, should alternative stable states driven by fire mediated feedbacks exist, then associated with that should be abrupt disjunctions in vegetation structure observable across forest/savanna boundaries. Also, as argued previously by Warman and Moles (2009) and Murphy and Bowman (2012) it would also not be expected that the our studied zones of transition would be found to be located in some sort of consistently common climate/soil environmental space.

4.1 Disjunction vs. continua in the forest-savanna transition

In terms of disjunction of vegetation structure, Figs. 1 and 2 show much more a continuum, particularly if all layers of vegetation are taken into account. Specifically it would seem that, around the point that canopy closure occurs, that the shrub layer of both forest and savanna becomes increasingly important (Fig. 2e); effectively replacing the grass layer in both woodland and open forest systems (Figs. 2f and 4). Confounding comparison with remote sensing products is, however, also the observation that many (shrub dominated) savannas can have a considerable canopy cover but with almost all of this contributed by trees < 5 m tall. Such low stature vegetation was apparently not included in the calibration of the global vegetation cover data set Hansen et al. (2003) and is presumably less accurately quantified as a result. This calls for caution when using such *in silico* datasets as a proxy for real world ecosystem level woody cover measurements and the relative distribution of forest and savanna formations in zones of transition.

We do, of course, acknowledge that the transitional vegetation formations described in our study do not present a spatially explicit frequency distribution of all savanna and forest formations present across the planet. They are, however, representative of the commonly found formations in our study areas as they were specifically selected for this purpose (Torello-Raventos et al., 2013). We do therefore not expect the analysis of the differences in structural layers as savanna transforms to forest to be fundamentally different in other sites. Most formations studied by us – with the exception of the MDJ-05 transitional forest plot in Central Africa - specifically selected as being in active transition (Mitchard et al., 2009) and NXV-02 in Brazil (Franczak et al., 2011) – can therefore be assumed on the basis of history and stand age to reflect the recent climate, soil and land management activities. Although soil organic matter $^{13}C/^{12}C$ ratios (G. Saiz and TROBIT Consortium, unpublished data) do suggest that some forest plots in Cameroon may have had savanna vegetation in a fairly recent (centennial timescale) past – see Table S1 in Appendix A in Supplement as well as Torello-Raventos et al. (2013).

4.2 The importance of the shrub layer

The observed increase in understorey wood plant density around the stage of full upper canopy closure is at the expense of the axylale cover and may be a consequence of the relative inefficiency of the C_4 photosynthetic pathway typical of tropical grasses in shaded environments – as is also suggested by the axylale species persisting in dense savanna and forest formations at relatively low abundances actually being of the C_3 photosynthetic mode (Torello-Raventos et al., 2013). In this context we also note that Laubenfels (1975) working in North America and limiting his observations to “vegetation cover showing a minimum of disturbance, particularly by chopping, by heavy grazing and by fire” noted a natural discontinuity between “woodland” and “forest” in terms of their upper canopy cover (the forest being “continuous” and the woodland “rarely more than 40 %”). This transition was accompanied by substantial differences in understorey structure (changing from a dominance of grasses to that of shade adapted understorey shrubs) analogous to those described here for the savanna/forest transformation. Effectively then, be it in the temperate zone or in the tropics, a new understorey environment is created around the stage that climatic and edaphic conditions combine to allow full upper-canopy closure to first occur. In both cases the resulting shaded understorey environment is very different to the high insolation and high evaporative demand ground layer of the more open vegetation formation types. In the tropics this then favours relatively high canopy cover shade adapted C_3 shrubs and – to a lesser extent – C_3 grasses. Put another way, as a result of a "new niche creation" at or around $C_U = 1$ it turns out that once conditions are suitably favourable for upper canopy closure to be achieved, then a rapid increase in total stand-level woody plant cover ensues with a "filling up" of this newly created shaded understorey environment by suitably adapted woody species. Thus, when considering all woody canopy layers together there is probably very little difference in the climatic/edaphic conditions necessary to support a stand of $C_W = 2$ as opposed to $C_W = 1$. And with fire-mediated feedbacks not necessary to account for this phenomenon. Figures 1 and 2 also suggest that beyond $C_W \gtrsim 2$ the upper-canopy strata become increasingly more dominant and with shade adapted shrubs expected eventually outcompeted by taller shade adapted tree species and a preponderance of regenerating seedlings representing species of all strata. Though interestingly the extent to which specialist shrubs can persist beneath the denser canopies of the moister tropical forests seems to vary from continent to continent (LaFrankie et al., 2006).

4.3 Species traits and stand structure

We also found evidence of the presence of forest species in the subordinate layers of some plots within ZOT but with savanna species dominating the upper stratum (Fig. 5a). This increase of the proportion of forest species with an increase in canopy closure for savanna formations in ZOT, could be taken to suggest that fire suppression through a dense savanna tree upper-canopy reducing herbaceous fuel loads (Fig. 2f) serves to promote the likelihood of survival of forest species. For this suggestion some empirical evidence exists (Hennenberg et al., 2006; Geiger et al., 2011). Alternatively, the increased abundance of understorey forest species relative to their savanna counterparts in such environments may simply be due to their typically greater shade tolerance (Hoffmann et al., 2012a, b) through the "niche creation" mechanism discussed above.

Although not always explicitly stated, theoretical models of fire mediated feedbacks assume implicitly that stand structure and tree functional traits are correlated. For example, fire is argued to persist in savanna formation types through the persistence of flammable grasses which in turn require a relatively open canopy to be of sufficient biomass for fires to be able to spread (Hennenberg et al., 2006; Hoffmann et al., 2012a). Necessarily associated with this are woody species with typical fire-adapted traits such as a relatively thick bark and a high re-sprouting ability as well as a high light requirement for growth (Ratnam et al., 2011; Hoffmann et al., 2012b). Our field data on vegetation formations in the ZOT show, however, that the supposed trait/canopy structure association is not obligatory. With some woodland formations dominated by species more usually associated with pyranogenic environments attaining forest like structures. Though sometimes also with an appreciable abundance of forest species in subordinate layers. (Fig. 5). Our findings thus underline the importance of understanding canopy cover closure differences in response to varying climatic drivers or CO_2 increases (Higgins and Scheiter, 2012) as well as in association with the often cited explanation of fire reduction being the cause of the rapid expansion of forest species in the ZOT savanna woodlands of Central Africa, Australia (Mitchard et al., 2009; Bowman et al., 2010) or Brazil (Marimon et al., 2006).

4.4 Above-ground biomass differences

Forest vegetation formations generally showed a much higher aboveground biomass than savanna formations (Fig. 8), albeit with a smaller belowground trend in the opposite direction likely (Lloyd et al., 2009). The transition of forest to savanna therefore has large implications for carbon stocks in above ground vegetation. As reported before in this study woody biomass increases rapidly with canopy closure beyond a fractional crown cover of 0.6 (Fig. 7). Within any particular region, B for ZOT savanna vegetation formation types (*sensu lato*) are generally much less than for forests (Fig. 8) but globally speaking the variation in B for both forest and savanna formation types within ZOT is large: with tall woodlands in Australia having a biomass similar to forests within

South American ZOT. For both forest and savanna, the lower woody strata may contribute significantly to the total biomass (up to 20 %) this being particularly important for the South American plots. This may be of consequence not only for the accurate estimation of carbon losses associated with the extensive removal of such vegetation in the ZOT's for economic development but also in assessing changes in biomass associated with climate change induced shifts in vegetation distribution (Malhi et al., 2009). A better understanding of the savanna type replacing the forest vegetation is needed for such accurate predictions.

Continental differences were also observable with biomass and canopy height generally lower in South American plots compared to Africa and Australia. The tendency for South American trees to be shorter for a given D (Fig. 6) has also been observed in tropical forest allometric studies (Feldpausch et al., 2011). One possibility to account for this may be the extremely low cation status of many Amazonian forest and savanna soils (Cochrane, 1989; Quesada et al., 2010; Quesada et al., 2011). The notion that nutrients limit the development of forest has been previously put forward through a simple analysis of total ecosystem nutrient stocks but with the overall evidence for this notion currently considered equivocal at best (Bond, 2010).

4.5 Soils and the distribution of forest vs. savanna

Biome distribution and ZOT locations differ between continents when considered in relation to climatic variables, in particular precipitation (Lloyd et al., 2008; Lehmann et al., 2011). Combining soil information on total base nutrient cations (N^+) and W in Fig. 9 shows, however, that the ZOT globally occurs across a consistent climate/soil space continuum with savannas generally in drier and forest in wetter environments than the ZOT. Although savannas may vary greatly in biomass in the ZOT, the mere fact that this climate/soil space exists argues against the overriding importance of fire mediated feedbacks as the main driver of forest savanna transitions.

Of course, according to some rationales the evidence of Fig. 10 that savanna-forest ecotones exist at different P_A for different continents could also be presented as some sort of evidence for a fire-mediated feedbacks (Murphy and Bowman, 2012). Nevertheless, fires actually much more common in the savanna regions of Africa than South America (Giglio et al., 2013) – the opposite of what would expect should a greater intensity and/or frequency of fires be associated with ZOT occurring at higher P_A than would otherwise be the case. More likely is as indicated by Fig. 9: that these intercontinental differences may be more related to differences in soil fertility as has also been suggested by Lehmann et al. (2011). An ordination study of Lloyd et al. (2009) similarly showed soil cation status to be a key determinant of vegetation formation type distributions across tropical South America. Such conclusions are, of course, not necessarily at odds with the notion that the frequency and magnitude of fire occurrences – both natural and anthropogenic – can substantially affect savanna vegetation structure. Nor is it at odds with the regular and persistent anthropogenic use of fire to maintain landscapes that would otherwise support forest vegetation formation types in a more open savanna-type state.

Supplementary material related to this article is available online at http://www.biogeosciences-discuss.net/11/4591/2014/bgd-11-4591-2014-supplement.pdf.

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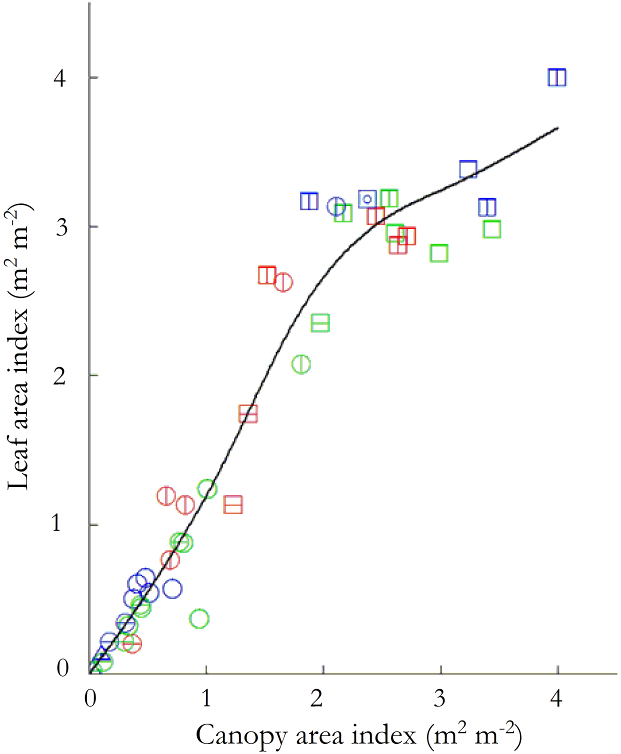

Fig. 1. Relationship between woody plant canopy area index (C_W) and leaf area index (L) Symbols; (△) grassland and grassland savanna; (⊖) shrub rich savanna formation types; (○) savanna and woodland formation types; (⦶) tall woodlands; (⊟) stunted forests; (□) forest; (◫) tall forest. Vegetation nomenclature follows Torello-Raventos et al. (2013). Blue symbols, Africa; Green symbols, South America; Red symbols, Australia. The fitted line represents a quadratically penalised generalised general linear model fit with the variance modelled as an exponential function of C_W.

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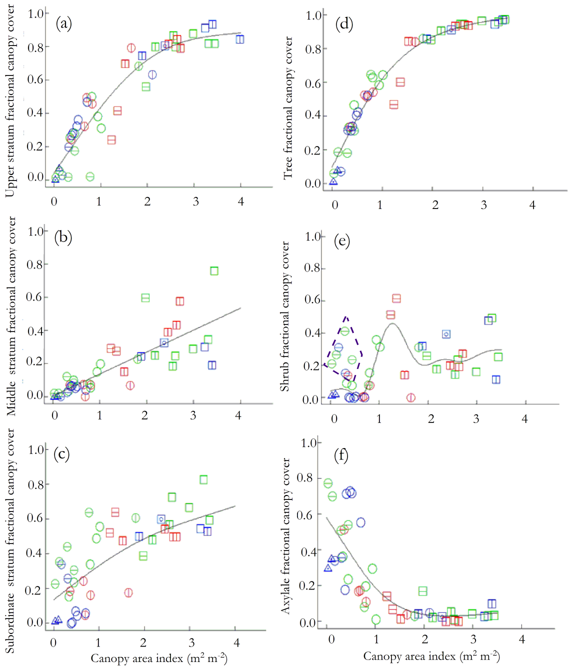


Fig. 2. Relationship between various measures of canopy structure and woody plant canopy area index. The three left hand side panels separate the woody vegetation forms according to stratum *viz*. upper, middle and subordinate; the three right hand panels separate according to physiognomic form viz. trees, shrubs and axylales (= herbs and grasses). **(a)** Upper stratum = all trees with $D > 0.1$ m; **(b)** middle stratum = all trees and shrubs ($25\,\text{mm} < D < 0.1$ m and $H > 1.5$ m); **(c)** subordinate stratum = all tree and shrub species ($H > 1.5$ m); **(d)** all tree species (including seedlings); **(e)** all shrub species (including seedlings) and **(f)** non-woody plants (axylales). Symbols as in Fig. 1. The fitted lines represent a quadratically penalised generalised general linear model fit which for **(d)** and **(e)** excludes the shrubby savannas (enclosed in the dotted-lined polygon in **(e)**: see also text).

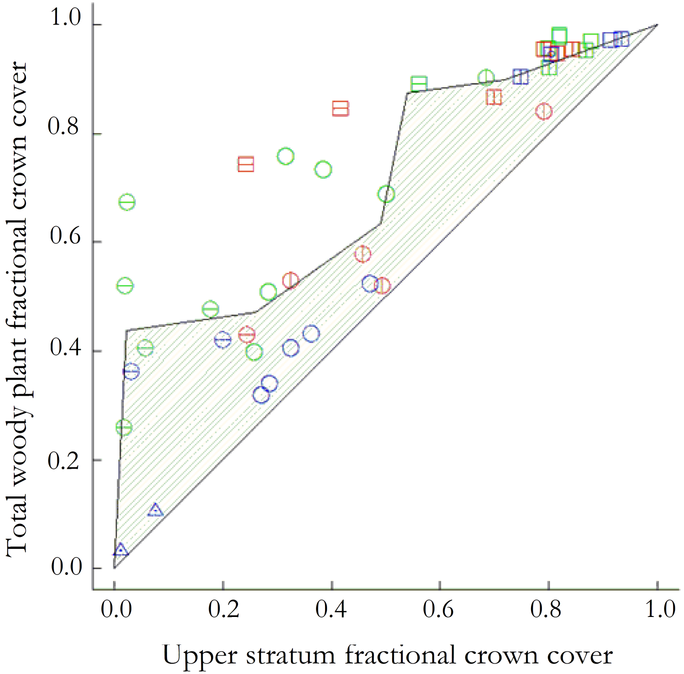


Fig. 3. Fractional cover of all woody layers combined (including seedlings) vs. the fractional cover of the upper stratum only (ζ_U; all trees with $D > 0.1$ m). The upper (disjointed) line represents the result from a segmented regression fit to the data ($r^2 = 0.84$) with the bottom line representing the 1 : 1 relationship. The hatched area therefore shows the average difference between the two estimates for which the area is greatest at $\zeta_U \lesssim 0.25$ and $0.55 \lesssim \zeta_U \lesssim 0.80$. Symbols as in Fig. 1

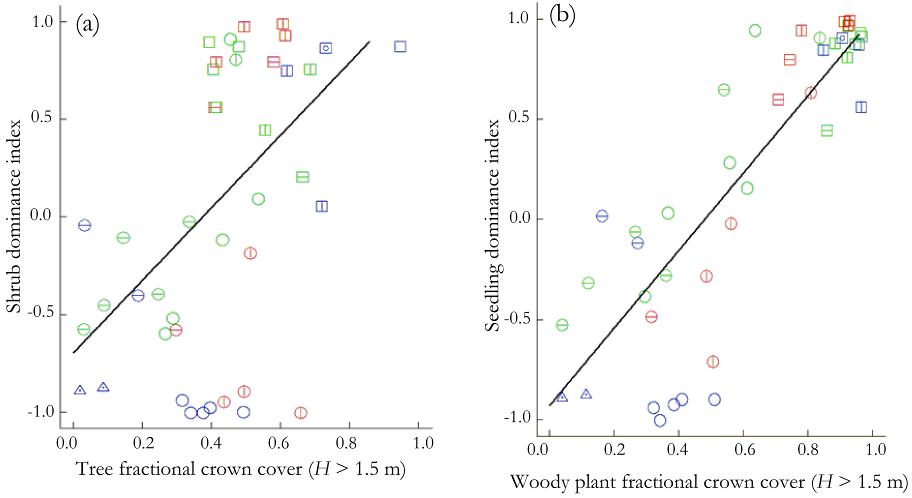
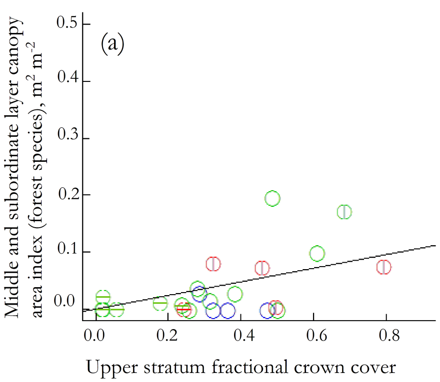


Fig. 4. Relationships between upper stratum woody plant canopy dominance and measures of shrub/seedling competition in the lower layers. **(a)** Relationship between a shrub dominance index (χ_1: Eq. 3a) and the total fractional cover of all tree species with a height (H) > 1.5 m; **(b)** a measure of (tree + shrub) seedling dominance (χ_2: Eq. 3b) and the total woody crown cover (H > 1.5 m). Symbols as in Fig. 1. The fitted line comes from the application of a linear robust (high breakpoint) regression fit to the data



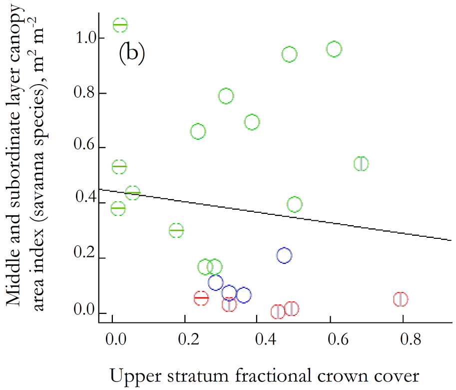


Fig. 5. Dependence upon upper stratum woody plant crown cover in plots for characterised as savanna vegetation formation types and geographically located in the ZOT of **(a)** [middle + subordinate] forest-species canopy area index and **(b)** savanna species [middle + subordinate] layer canopy area index. Symbols as in Fig. 1. Note the different scales for the y-axes.

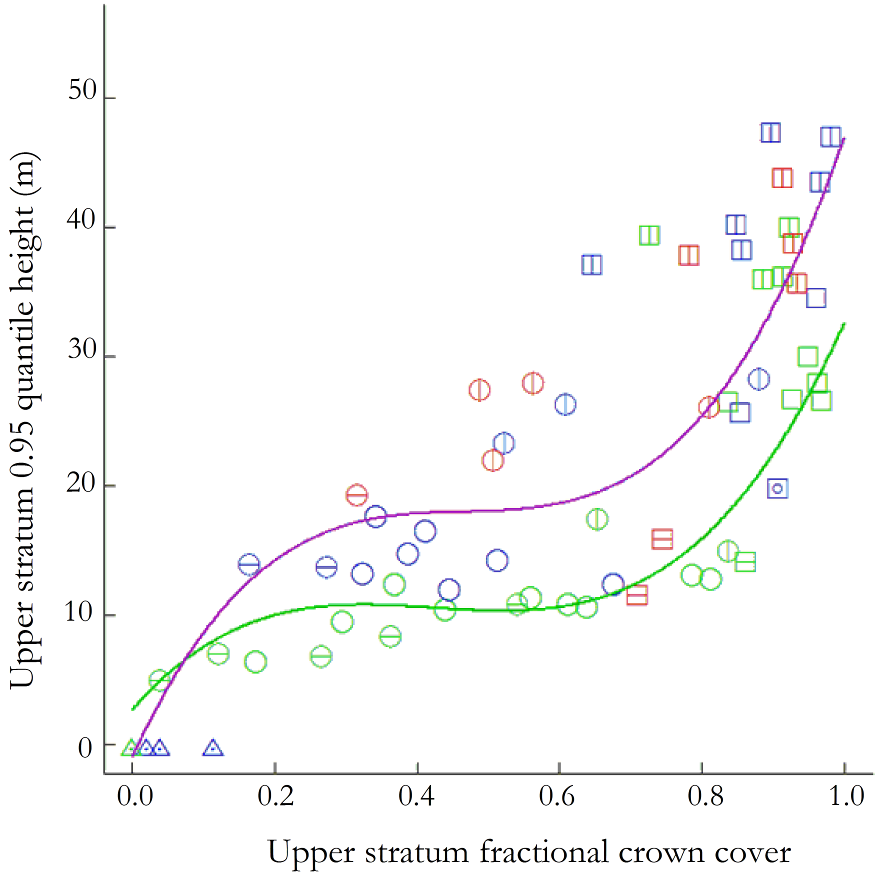


Fig. 6. Relationship between the upper stratum 0.95 quantile height and total woody plant crown cover ($H > 1.5$ m. Symbols as in Fig. 1. The lines show results of rank based linear model regression fits for which South America (green line) is significantly different to Africa and Australia (which in turn do not differ from each other: purple line).

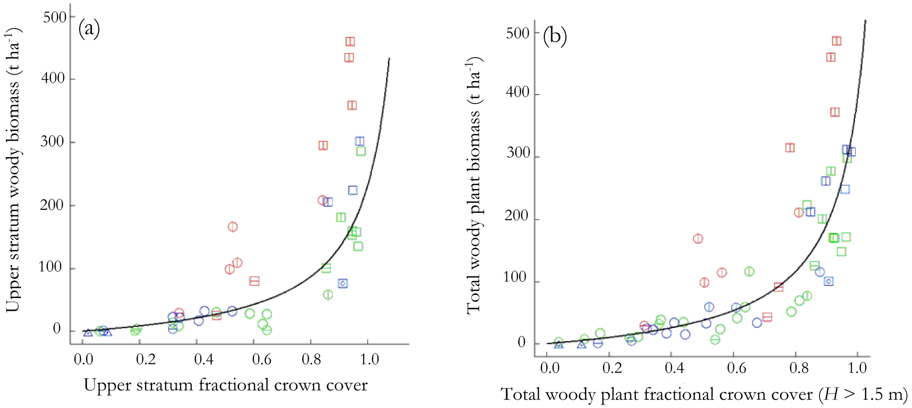


Fig. 7. Relationship between **(a)** biomass and fractional crown cover for the upper canopy stratum only, and **(b)** biomass and fractional cover for all trees and shrubs taller than 1.5 m. Fitted curves represent a simple reciprocal relationship (*viz.* $1/y = a + b/x$) and have been fitted using a rank based linear model regression. Symbols as in Fig. 1.

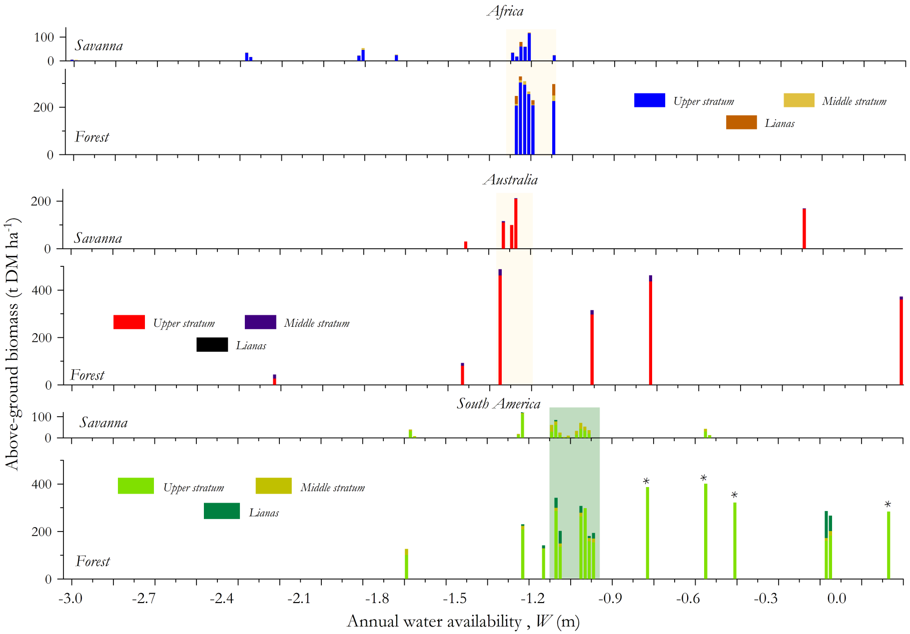


Fig. 8. Variations in estimates of biomass of forest and savanna across the three continents studies divided into the upper canopy stratum (diameter at breast height, $D > 0.1$ m), middle canopy stratum ($0.1\,\text{m} < D < 25$ mm) and lianas plotted as a function of mean annual water availability, W (Eq. 3). For each continent, the approximate location of the main studied forest/savanna transition zone(s) are indicated by grey shading. For South America, extra sites at low W (upper stratum only) have also been included and these are indicated by an asterisk.

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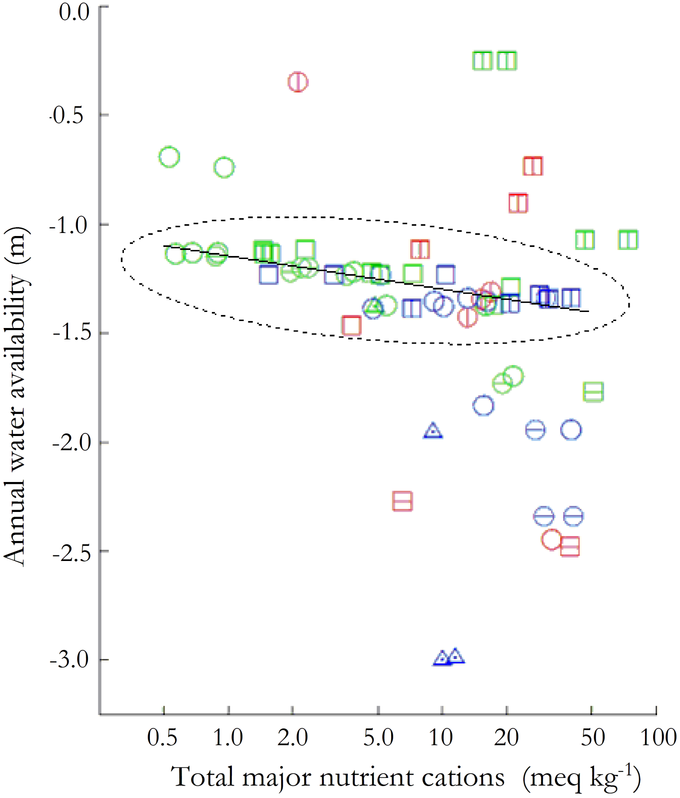

Fig. 9. Location of sample plots in relation to their mean annual cumulative soil water deficit (defined as in Eq. 3) and exchangeable nutrient cation content for the top 0.3 m of soil (Eq. 4). Symbols as in Fig. 1. The ovoid encompasses all sites located within zones of transition as shown in the grey shading of Fig. 8 through which is also shown the best fit standard major axis regression line. Blue symbols, Africa; Green symbols, South America; Red symbols, Australia.

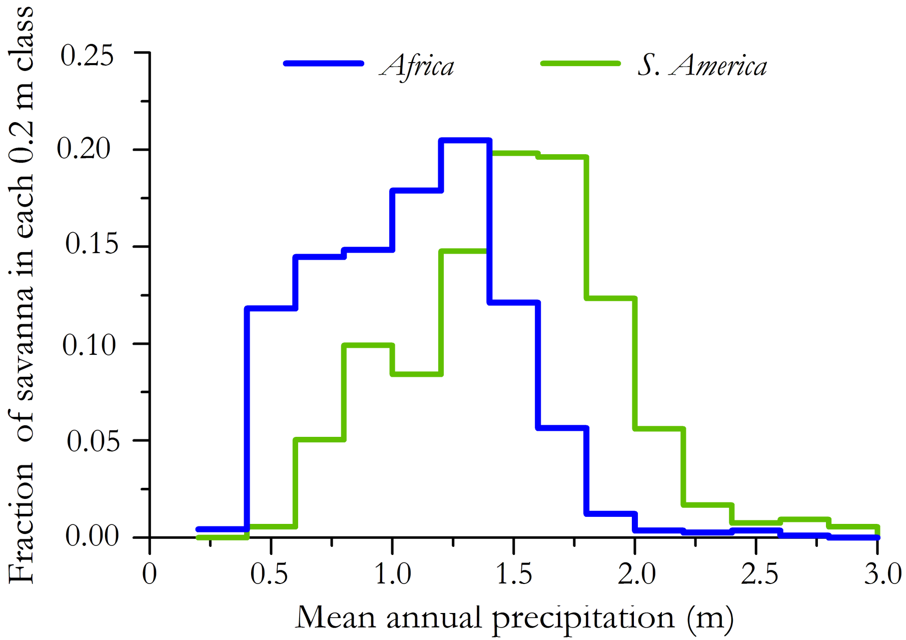

Fig. 10. Distribution of savanna vegetation formation types (including grasslands) in Africa and South America in relation to mean annual precipitation. Original data from Lloyd et al. (2008).