

Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate[†]

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Summary To estimate the relative contributions of woody and herbaceous vegetation to savanna productivity, we measured the ¹³C/¹²C isotopic ratios of leaves from trees, shrubs, grasses and the surface soil carbon pool for 22 savannas in Australia, Brazil and Ghana covering the full savanna spectrum ranging from almost pure grassland to closed woodlands on all three continents. All trees and shrubs sampled were of the C₃ pathway and all grasses of the C₄ pathway with the exception of *Echinolaena inflexa* (Poir.) Chase, a common C₃ grass of the Brazilian cerrado. By comparing the carbon isotopic compositions of the plant and carbon pools, a simple model relating soil δ¹³C to the relative abundances of trees + shrubs (woody plants) and grasses was developed. The model suggests that the relative proportions of a savanna ecosystem's total foliar projected cover attributable to grasses versus woody plants is a simple and reliable index of the relative contributions of grasses and woody plants to savanna net productivity. Model calibrations against woody tree canopy cover made it possible to estimate the proportion of savanna productivity in the major regions of the world attributable to trees + shrubs and grasses from ground-based observational maps of savanna woodiness. Overall, it was estimated that 59% of the net primary productivity (*N_p*) of tropical savannas is attributable to C₄ grasses, but that this proportion varies significantly within and between regions. The C₄ grasses make their greatest relative contribution to savanna *N_p* in the Neotropics, whereas in African regions, a greater proportion of savanna *N_p* is attributable to woody plants. The relative contribution of C₄ grasses in Australian savannas is intermediate between those in the Neotropics and Af-

rica. These differences can be broadly ascribed to large scale differences in soil fertility and rainfall.

Keywords: carbon isotopes, cerrado, grasses, photosynthetic pathway, soil carbon pool.

Introduction

All areas containing a discontinuous tree stratum overlying a grassy ground layer and subject to a distinctly seasonal wet-dry tropical climate can be classified as part of the savanna biome (Walker and Menaut 1988). The relative dominance of trees versus grasses in savanna systems varies widely according to soil type (Williams et al. 1996) and fire history (Moreira 2000), as well as grazing intensity and the overall extent of past disturbances (Moleele and Perkins 1998, Burrows et al. 2002, van Langevelde et al. 2003). At continental scales, the relative abundances of trees versus grasses are influenced by rainfall amount (Sankaran et al. 2005) with seasonality also likely to be important.

Although savanna trees are invariably of the C₃ photosynthetic pathway, savanna grasses are mainly of the C₄ photosynthetic pathway (Downton and Tregunna 1968, House and Hall 2001), though C₃ herbs and a few C₃ grasses may also occur in savanna ground layers in subtropical and tropical regions (Klink and Joly 1989, Miranda et al. 1997, Medina et al. 1999). The difference in photosynthetic pathway between the woody plant and herbaceous layers gives rise to variation between the layers in the extent of discrimination at the ecosys-

[†] We dedicate this paper to Alexandre Santos, a close friend and colleague, who was killed in the Amazon plane crash of September 29, 2006.

^{††} Antonio Carlos Miranda died September 24, 2002.

tem level against the heavier, naturally occurring ^{13}C molecule versus ^{12}C during photosynthesis (Farquhar et al. 1989, Miranda et al. 1997). The resulting overall difference in vegetation carbon isotopic composition allows use of $^{13}\text{C}/^{12}\text{C}$ ratios as a natural indicator of vegetation change at a range of scales (e.g., Victoria et al. 1995, Bird et al. 2000), although the presence of C_4 grasses in savanna (as well as in other ecosystems) complicates the use of $^{13}\text{C}/^{12}\text{C}$ ratios in global carbon cycle studies (Lloyd and Farquhar 1994, Fung et al. 1997, Still et al. 2003). This is because the relatively low natural photosynthetic discrimination (Δ) of C_4 grasses is similar to that accompanying air-to-sea CO_2 exchange (Lloyd and Farquhar 1994). By contrast, Δ for C_3 plants is considerably greater, which allows spatial and temporal variations in atmospheric $^{13}\text{CO}_2/^{12}\text{CO}_2$ ratios to be used to partition ocean-atmosphere exchanges from land-atmosphere exchanges in global carbon cycle studies (Keeling et al. 1989).

An evaluation of the proportion of global terrestrial productivity accounted for by C_4 plants has been a focus of some research over the last decade, with recent estimates being 0.21 (Lloyd and Farquhar 1994), 0.23 (Still et al. 2003) and 0.27 (Fung et al. 1997). However, these studies have taken a simplistic approach, estimating the relative contribution of C_4 tropical grasses to the overall productivity of savannas either as a fraction of total productivity (0.50 for Lloyd and Farquhar 1994 and 0.75 for Fung et al. 1997) or on the basis of remotely sensed pixel classifications (woody versus non-woody vegetation; Still et al. 2003).

The natural variation in isotopic composition between trees and grasses in savanna systems provides a ready means to evaluate the relative contributions of trees and grasses to overall savanna ecosystem productivity, and this is the focus of the current study. Tree, shrub, herb, grass and soil $^{13}\text{C}/^{12}\text{C}$ ratios were considered for 22 savanna sites in Australia, Brazil and Ghana.

The relative contribution of C_4 grasses to the overall ecosystem productivity p_4 can be determined as:

$$p_4 = \frac{\delta_{\text{obs}} - \delta_3}{\delta_4 - \delta_3}; \quad p_3 = 1 - p_4 \quad (1)$$

where δ_{obs} is the estimated mean isotopic composition of the surface soil carbon pool (assumed here to be a natural integrator of ecosystem accumulated carbon), δ_3 is the ecosystem mean value for C_3 (tree) organic matter in the soil, δ_4 is the ecosystem mean value for C_4 (grass) organic matter and p_3 represents the relative contribution of C_3 trees to total ecosystem productivity.

In our study, plant and soil carbon isotope measurements were made in conjunction with measurements of vegetation structure for savannas in Australia, Brazil and Ghana. Variation in p_3 and p_4 was related to differences in the relative abundance of trees versus grasses for the 22 sites studied, and the derived model parameters were used to estimate the relative contributions of trees + shrubs and grasses to ecosystem net primary productivity for the major savanna areas of the world.

Materials and methods

Site descriptions

Measurements in Australia were made at sites along the Northern Australian Tropical Transect covering a strong rainfall gradient (Figure 1). We sampled on a range of soil types at Annaburroo ($12^\circ 48' \text{ S}$, $131^\circ 48' \text{ E}$), Douglas Daly ($13^\circ 54' \text{ S}$, $131^\circ 18' \text{ E}$), Willeroo ($15^\circ 06' \text{ S}$, $131^\circ 42' \text{ E}$), Kidman Springs ($16^\circ 06' \text{ S}$, $131^\circ 54' \text{ E}$) and Kalkaringi ($17^\circ 18' \text{ S}$, $131^\circ 48' \text{ E}$). According to the global database of New et al. (2002), mean rainfall for these sites is estimated as 1370, 1200, 960, 780 and 640 mm, respectively.

Measurements in Brazil were made at eight locations, six in the District Federal (close to Brasília: $15^\circ 48' \text{ S}$, $49^\circ 48' \text{ W}$) and two near the main highway west of the town of Barreiras in the state of Bahia ($12^\circ 06' \text{ S}$, $45^\circ 06' \text{ W}$). Around Brasília, all sites are characterized by a high rainfall for the savanna region (about $1560 \text{ mm year}^{-1}$) with the Barreiras sites being drier with a mean average rainfall of about $1110 \text{ mm year}^{-1}$. As in Australia, all sites are characterized by a seasonal rainfall pattern, with little or no rain for at least three months of the year.

Measurements in Ghana were made in Mole National Park ($9^\circ 36' \text{ N}$, $1^\circ 48' \text{ W}$), located in an area just north of the savanna-rain forest transition zone. Mean annual rainfall at Mole is around $1070 \text{ mm year}^{-1}$ and shows a more asymmetric seasonal pattern than at the other sites. Annual rainfall estimates quoted above and seasonal precipitation patterns in Figure 1 all come from the $0.5^\circ \times 0.5^\circ$ global terrestrial database of New et al. (2002).

Relative abundances of trees, shrubs and grasses

At each site, the crown cover (C) of trees and shrubs, which is the fraction of the sample site within the vertical projection of the periphery of tree and shrub crowns (dimensionless), was determined by the crown separation ratio technique (Penridge and Walker 1988, Walker et al. 1988). Crown widths and crown gaps for each stratum were measured separately, irrespective of species. Between eight and 20 measurements were made for each stratum.

Crown cover for each tree and shrub stratum was converted to the stratum fractional foliage cover, ζ (in situ foliar light interception per ground area), according to $\zeta = \alpha C$, where α is the canopy projected cover (the mean proportion of light intercepted by the canopy crowns), obtained by matching the observed openness of individual tree or shrub crowns with the photographs given in Walker and Hopkins (1990).

Foliage cover of the ground layer was determined by measuring the extent of foliar interception along a transect. A 50-m tape was laid out at the sample site, and looking vertically down onto the tape and foliage or branches or both of small shrubs in the ground layer, the amount of foliage intercepted along the tape was estimated and expressed as a percentage of the transect length (Walker and Hopkins 1990).

Two to four transects of at least 50 m were made within study areas of a broadly uniform vegetation structure and were taken to be representative of the vegetation and soil properties for an area of at least 1 ha.

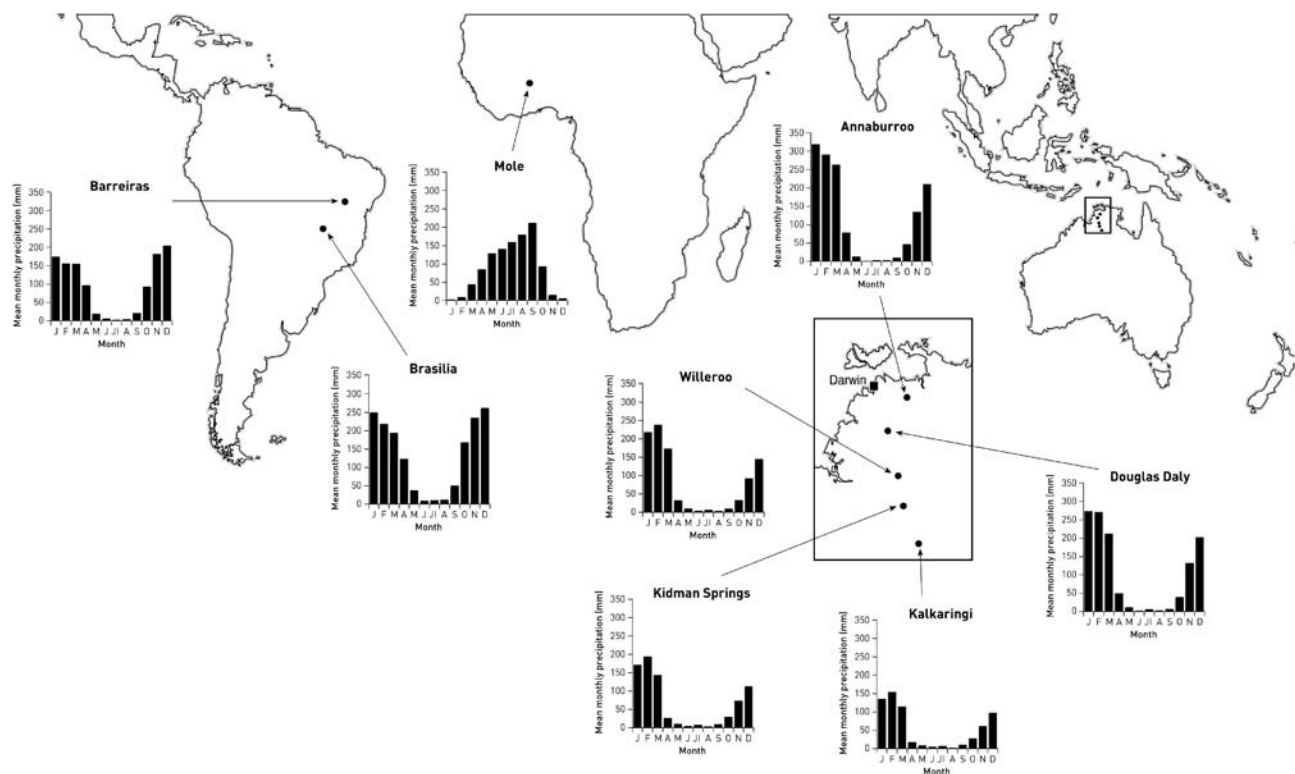


Figure 1. Locations of the sampling sites and their mean seasonal rainfall pattern (1961–1990) as given by New et al. (2002).

Isotopic composition of plant dry matter

For tree and shrub foliage, leaves were sampled from toward the top of the canopy and on the northern side in Australia and Brazil and on the southern exposed side in Ghana. About 10 leaves were taken from each tree, with up to 30 trees sampled at each site. Foliage was not sampled from trees clearly shaded by another tree for a significant proportion of the day. For each grass species, about 100 g fresh mass (FM) of leaf and blade was collected from around the study site. For selected trees and shrubs in the Australian study, the isotopic composition of trunk wood was also determined; a sample about 5 g FM being chiselled out of the trunk at breast height. All samples were dried in a forced convection oven at 75 °C for at least 24 h, before transportation to Canberra for $\delta^{13}\text{C}$ analysis.

Isotopic composition of soil carbon

The strategy for soil carbon sampling depended on the extent of tree and shrub cover at the site. Where the crown cover class was greater than about 0.25 (crowns touching or slightly separated), sampling was conducted along a 30- to 50-m transect (the same as that used to estimate foliage cover in the tree + shrub and grass layers) with samples being taken every 1.5 to 2.5 m. Where trees and shrubs were more isolated (crown cover class less than 0.25), 1–4 transects were carried out between individual trees, with samples being taken at intervals of about 0.5 m along the transect under, and in close proximity to, the isolated trees. Further away from the trees, the distance between samples was increased, typically being 2 m in the mid-

dle of the transect. These sampling procedures usually resulted in 15 to 25 soil samples per plot. Sampling was performed at 0.00 to 0.05 m depth after removing the surface litter. Each sample consisted of 50–200 g of soil. Samples were air dried in the field before transportation to Canberra for analysis. At the laboratory, samples were dried at 70 °C and subsequently analyzed for $\delta^{13}\text{C}$ composition, and soil carbon concentration was determined on the < 500 μm fraction as described by Bird et al. (1994). Results are expressed as parts per thousand (‰) deviation from the V-PDB- CO_2 scale with an analytical uncertainty of 0.1‰.

Mean plant and soil isotopic compositions and relative contributions of C_3 and C_4

For each of the major vegetation components (C_3 trees, C_3 shrubs, C_4 grasses), the mean foliar $\delta^{13}\text{C}$ was calculated as the arithmetic mean of all species sampled, with the C_3 grass *Echinochloa inflex* (Poir.) Chase, where present in Brazil, excluded from the calculations for Figure 3a, but with its presence accounted for by Equation 4 (see Results). For soils, estimates of the $\delta^{13}\text{C}$ of the surface soil pool are means of all samples along the transects, but weighted by the soil C content.

Tree and grass productivity for savannas at a global scale

To estimate the savanna grass and tree cover for Africa, we used ground-survey-based vegetation maps of South Africa (Acocks 1988, Low and Rebio 1998), Botswana, Malawi, Mozambique, Zimbabwe and Zambia (Wild and Fernandes 1967), Angola (Gossweiler 1939, Airy Shaw 1947), Tanzania,

Kenya and Uganda (Trapnell and Langdale-Brown 1972), Chad (Pias 1970), Sudan (Harrison and Jackson 1958), Ghana (Taylor 1952) Central African Republic (Guignon 1968), Nigeria (Keay 1953), Ethiopia and Somalia (Pichi-Sermolli 1957), Gabon and the Republic of the Congo (Congo (Brazzaville); Trochain and Koechlin 1958), Democratic Republic of the Congo (Congo (Kinshasa); Duvigneaud 1952, 1953, Mullenders 1955), Ivory Coast (Mangenot 1971) and Namibia (Burke et al. 2002), with remaining areas within Africa identified and classified according to White (1983). For Australia, we used Carnahan (1990) as the primary source, and for South America, detailed vegetation maps of Brazil (IBAMA 1993), Venezuela (Huber 1995) and Guyana (Huber et al. 1995). For Surinam, the one mappable savanna area (Sipiliwini) was identified on the basis of satellite maps as used by ter Steege and Zondervan (2000), also extending into Brazil where it is correctly mapped (IBAMA 1993). Depending on the resolution of the original map, vegetation categories were manually digitized at either $0.5^\circ \times 0.5^\circ$ or $1.0^\circ \times 1.0^\circ$ omitting smaller savanna areas such as in French Guiana. Large-scale seasonal wetlands such as the Pantanal (Brazil) were included in the analysis, as well as other significant seasonally flooded areas, although floodplains along the Amazon River were too small to include in this large scale analysis. These include the Llanos del Orinoco in Venezuela/Colombia and the Llano de Moxos in Bolivia (Hamilton et al. 2004) as well as a large area of seasonally flooded grasslands associated with the upper Nile floodplain (Harrison and Jackson 1958).

Net primary productivity of all identified savanna areas was estimated according to House and Hall (2001):

$$N_p = 11.0\Omega - 539 \quad (2a)$$

where N_p is estimated total net primary productivity of the ecosystem (trees plus grasses) in $\text{g DM m}^{-2} \text{ year}^{-1}$ and Ω is an index of soil water availability (of dimension days) calculated as a sum over 12 months according to Scholes and Hall (1996):

$$\Omega = \sum_{i=1}^{12} d_i w_i; w_i = \min\left\{\frac{R_i}{E_i}, 1.0\right\} \quad (2b)$$

where d_i is the number of days in month i , R_i is the mean monthly rainfall and E_i is the mean monthly potential evaporation. Constraining R/E to be equal to or less than 1.0 is equivalent to saying that evaporation cannot exceed rainfall and that stored soil water is not carried over between months. This is a conservative assumption, taken in the absence of detailed soil information (Scholes and Hall 1996).

All calculations were performed at $0.5^\circ \times 0.5^\circ$ resolution using the global climatological database of New et al. (2002) and restricted to areas for which the mean monthly temperature of the warmest month is greater than 20.5°C . This is slightly less than the 22.0°C crossover point for the relative dominance of C_4 versus C_3 grasses suggested by Collatz et al. (1998) for current atmospheric CO_2 concentrations, but this slightly lower threshold served to correctly account for the dominance of C_4

grasses, even on the high plateaus of South Africa below about 2900 m (O'Connor and Bredenkamp 1997). This defines tropical/subtropical (cf. temperate) savanna and grassland considered in this study.

Results

Vegetation characteristics

The sites sampled and the projected grass and tree ζ at each site are listed in Table 1. The table shows large variability in tree density among the 22 sites. Maximum tree canopy C values were 0.75 for Australia (open forest), 0.81 for Brazil (cerradão) and 0.52 for Ghana (Guinea savanna) with sites having $C = 0.01$ also being sampled on all three continents at grassland sites. Tree α was less variable across sites ranging from 0.34 (Brazil) to 0.60 (Australia). Ground shrub and herb ζ was generally less than 0.01, the exception being the woodier sites in Brazil and Ghana (cerrado denso, cerradão and Guinea savanna), where values greater than 0.1 were mostly attributable to a shrub layer less than 2 m high. By contrast, no discernible shrub layer was apparent in open forest types with high tree densities in Australia. Also included in the "ground shrub and herb" category were small palms, most notably dominant at the savanna parque site near Barreiras where *Syagrus campestris* (Mart.) H. Wendl and *Syagrus comosa* (Mart.) Mart. were quite abundant; accounting for about 0.8 of the non-grass ground cover layer.

Grass ζ varied less widely, with the lowest values being recorded in Brazil, either in Barreiras (0.20 and 0.29) or under the denser woody vegetation types (cerrado denso and cerradão). Highest grass ζ tended to be found in vegetation types where the woody component was scarce (low open woodlands in Australia, campo limpo and campo sujo in Brazil, grasslands in Ghana).

The relationship between the tree + shrub (woody) and grass and herb (ground) foliar projected cover (ζ_w and ζ_g , respectively) for all sites is shown in Figure 2. Although considerable variation existed, there was a generally negative relationship (as indicated by the line encompassing about 30% of the values). Thus, ζ_g was greater than about 0.8, whereas ζ_w was invariably low. For the Barreiras sites (circled in Figure 2), ζ_w was low (< 0.2) despite ζ_g also being low (< 0.3) with lots of open ground. For some moister Australian sites on sandy and loamy soils (also circled in Figure 2), values of ζ_w and ζ_g were relatively high.

Carbon isotope measurements

Figures 3a and 3b summarize the foliar $\delta^{13}\text{C}$ measurements for non-grass and grass vegetation types, respectively. The $\delta^{13}\text{C}$ distributions were similar for non-grass vegetation types across the three continents with an approximately Gaussian distribution and a median value of -28.4‰ . This indicates that all non-grass vegetation types sampled (including shrubs and herbs) were of the C_3 photosynthetic pathway. By contrast, grass foliar $\delta^{13}\text{C}$ signatures could be divided into two populations; the chief one having a median $\delta^{13}\text{C}$ of -13.2‰ , showing

Table 1. Soil texture and vegetation cover characteristics of the study sites. Terminology follows local sources, namely, Carnahan (1990) for Australia, Eiten (1983) for Brazil and Lawson (1966) for Ghana. Crown cover (C) = fraction of the sample site within the vertical projection of the periphery of tree and shrub crowns; canopy projected cover (α) = the mean proportion of light intercepted by individual canopy crowns; fractional foliar (projected) cover (ζ) is the estimated in situ proportion of light interception by the selected stratum. Crown cover for each tree and shrub stratum was converted to the fractional foliage cover according to $\zeta = \alpha C$.

Site	Soil texture	Vegetation cover type	C	α	Tree + shrub ζ	Ground shrub + herb ζ	Total non-grass ζ	Grass ζ
<i>Australia</i>								
Annabaroo	Loam	Open forest	0.75	0.45	0.34	0.01	0.35	0.75
Annabaroo	Sand	Open forest	0.68	0.55	0.37	0.02	0.39	0.50
Douglas Daly	Loam	Low woodland	0.52	0.55	0.29	0.05	0.34	0.67
Douglas Daly	Sand	Low open forest	0.50	0.60	0.30	0.07	0.37	0.52
Kalkaringi	Clay	Low open woodland	0.02	0.60	0.01	0.00	0.01	0.95
Kalkaringi	Loam	Low open woodland	0.03	0.45	0.01	0.01	0.02	0.53
Kidman Springs	Loam	Low open woodland	0.04	0.50	0.02	0.01	0.03	0.63
Kidman Springs	Sand	Low woodland	0.37	0.55	0.20	0.00	0.20	0.58
Willeroo	Clay	Low open woodland	0.09	0.40	0.04	0.00	0.04	0.63
Willeroo	Sand	Low woodland	0.51	0.45	0.23	0.04	0.27	0.43
<i>Brazil</i>								
Barreiras	Sand	Cerrado sensu strictu (aberta)	0.24	0.45	0.11	0.09	0.20	0.20
Barreiras	Loam	Savanna (parque)	0.02	0.40	0.01	0.10	0.11	0.29
Brasília	Rocky, sand	Campo limpo	0.00	0.00	0.00	0.00	0.00	0.85
Brasília	Loam	Campo sujo	0.04	0.34	0.02	0.04	0.05	0.85
Brasília	Loam	Cerradão	0.59	0.45	0.26	0.20	0.45	0.20
Brasília	Sand	Campo cerrado	0.17	0.45	0.08	0.00	0.08	0.80
Brasília	Loam	Cerrado sensu strictu	0.56	0.40	0.25	0.09	0.35	0.34
Brasília	Loam	Cerrado denso	0.81	0.39	0.31	0.12	0.43	0.21
<i>Ghana</i>								
Mole	Loam	Grassland	0.01	0.45	0.00	0.00	0.00	0.70
Mole	Sand	Guinea savanna	0.52	0.47	0.24	0.11	0.36	0.38
Mole	Sand	Open Guinea savanna	0.24	0.54	0.13	0.09	0.22	0.59
Mole	Loam	Tall moist grassland	0.00	0.00	0.00	0.02	0.02	0.85

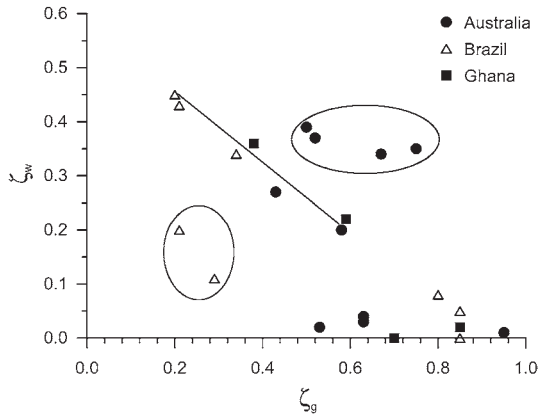


Figure 2. Relationship between tree + shrub (woody; ζ_w) and grass + herb (ground; ζ_g) foliar projected cover for a range of savanna sites in Australia, Brazil and Ghana. Circled values represent outliers for both Australia and Brazil. The straight line shows a more general relationship for other savannas with $\zeta_w > 0.2$.

the expected dominance of C_4 grasses in these subtropical environments (Collatz et al. 1998). In addition, Brazilian plots showed the signature of C_3 grasses, in this case entirely due to *Echinolaena inflexa*, which was found in all Brasília plots sampled (but not near Barreiras). The widespread existence of this C_3 grass in the Brazilian cerrado has long been established (Renvoize 1984, Klink and Joly 1989, Miranda et al. 1997).

As an index of the relative dominance of trees + shrubs versus grasses + herbs, we used a parameter ϕ :

$$\phi = \frac{\zeta_w}{\zeta_w + \zeta_g} \tag{3}$$

Figure 4 shows variations in C_3 and C_4 plant foliar $\delta^{13}C$ as a function of ϕ . For the C_3 plants, there was a tendency for $\delta^{13}C$ to become more negative as ϕ increased (significant at $P = 0.05$, weighted Type II regression, assumed error for $\phi = 0.1$ for all values), whereas no distinct trend was evident for the C_4 grasses. There was no significant correlation between mean annual precipitation and foliar $\delta^{13}C$ for either C_3 or C_4 plants ($P = 0.5$).

Figure 5 shows variations in estimated mean isotopic composition of the soil carbon pool, δ_{obs} , as a function of ϕ , with a fitted Type II regression line also shown. Also presented are the regression lines for foliar $\delta^{13}C$ as a function of ϕ for both C_3 and C_4 plants from Figure 4. This shows a nearly linear decline in δ_{obs} with a fitted slope of $-15.3\text{‰} \phi^{-1}$, very close to the mean difference between C_3 and C_4 plant foliar $\delta^{13}C$ (Figure 3). Nevertheless, the estimated intercept of $\delta^{13}C = -14.6\text{‰}$ ($\phi = 0.0$) was significantly different from the value of -12.5‰ determined from the type II regression for C_4 plant foliage at $\phi = 0.0$ (Figure 4).

Data in Figure 5 are for leaves only. For a range of trees sampled in Australia, the trunk and branch $\delta^{13}C$ is plotted as a function of foliar $\delta^{13}C$ in Figure 6. This shows a variable yet significant offset with trunks and branches being on average enriched 1.4‰ compared with foliage, consistent with results from previous studies (Leavitt and Long 1982). We also investigated differences among leaf, stem blade and root $\delta^{13}C$ for many of the Australian C_4 grass samples, but found no consistent or significant differences (data not shown).

Data analysis

To accommodate the offsets implicit in Figures 5 and 6 we attempted to fit a range of models by the maximum likelihood technique (Gilmour et al. 1995), the best of which was:

$$\delta_{obs} = \delta_4 + \psi + \phi(\delta_3 - \delta_4) + \beta\zeta_w + \gamma E + a_p \tag{4}$$

where ψ and β are fixed effects defining the offsets implicit in Figures 5 and 6, respectively, E is a variable indicating the presence or absence of *E. inflexa* and a_p is a random plot effect representing the residual error. Fitted values (\pm SE) were $\psi = -1.95 \pm 0.43\text{‰}$, $\beta = 5.24 \pm 3.80\text{‰}$ and $\gamma = -1.45 \pm 1.25\text{‰}$. The modeled versus fitted relationship is presented in Figure 7 which shows that the simple model gave a reasonably good fit to the data.

From Equation 1 we can write:

$$p_3 = \frac{\delta_{obs} - \delta_4}{\delta_3 - \delta_4} \tag{5a}$$

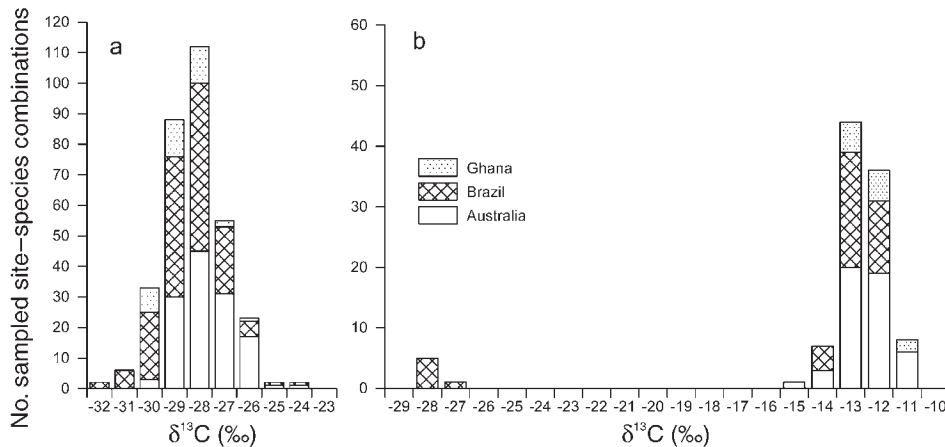


Figure 3. Distribution of foliar ^{13}C isotopic composition (expressed as $\delta^{13}C$) for all site–species combinations sampled. (a) Leaves from trees, shrubs and herbs; (b) leaves from grasses.

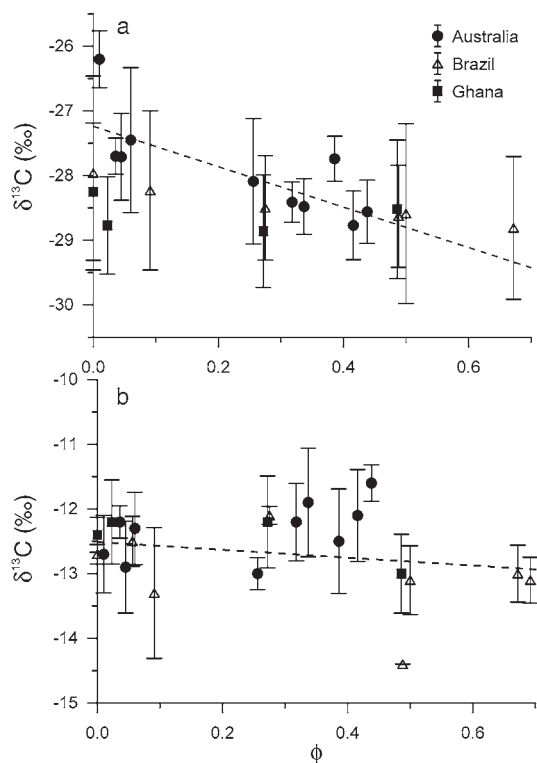


Figure 4. Relationship between mean ¹³C isotopic composition (expressed as δ¹³C) of sampled leaves and the proportion of the total ecosystem foliage projected cover accounted for by trees and shrubs (φ) for (a) C₃ and (b) C₄ plants. Values are means ± SD.

Likewise a rearrangement of Equation 4 less the random error term a_p gives:

$$\phi = \frac{\delta_{\text{obs}} - \delta_4 - \beta \zeta_w - \gamma E - \psi}{\delta_3 - \delta_4} \quad (5b)$$

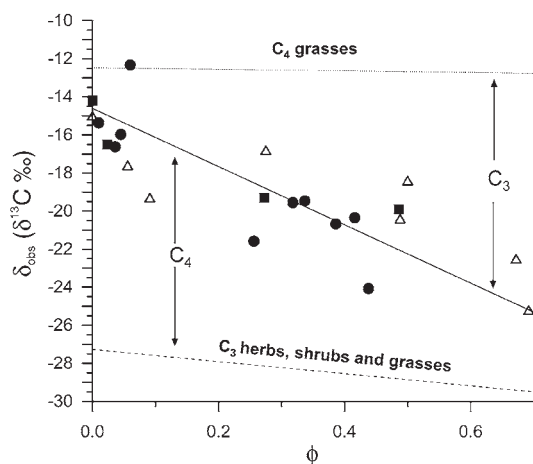


Figure 5. Relationship between mean (carbon weighted) soil surface ¹³C isotopic composition (δ_{obs}; expressed as δ¹³C) and the proportion of the total ecosystem foliage projected cover accounted for by trees and shrubs (φ). A Type II linear regression line of best fit is shown, as are the relationships for C₃ and C₄ foliage as shown in Figure 4.

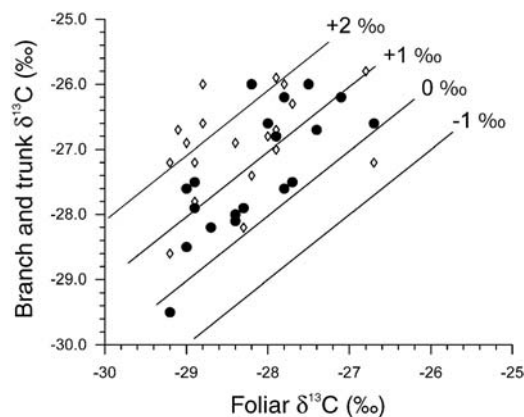


Figure 6. Relationship between branch (●) and trunk (◇) isotopic composition (expressed as δ¹³C) and foliar δ¹³C from the same tree. All samples are from Australia. Lines are drawn for 1:1 slopes with intercepts between -1 and +2‰.

The similarity in form between these two equations has three implications. (1) When trees, shrubs and *E. inflexa* are absent then $p_3 = 0$, $\phi = 0$, $\zeta_w = 0$ and $\gamma = 0$ and $\delta_{\text{obs}} = \delta_4 + \psi$. Thus, for pure C₄ grasslands, mean soil δ¹³C is, on average, about 2‰ less than the isotopic composition of the vegetation, similar to the offset observed by Bird and Pousai (1997). (2) The estimate for β is significant, suggesting that there is an opposing enrichment of δ_{obs} dependent on the absolute magnitude of the woody canopy cover. This is in addition to the influence of ζ_w on φ (Equation 3). (3) Where present, the C₃ grass *E. inflexa* reduces soil δ¹³C by about 1.5‰ compared with where it is absent. Taking these effects into account, a comparison of Equations 5a and 5b shows that the (observed) φ is numerically equivalent to the (theoretical) p_3 . This is because both terms have the same slope, namely $(\delta_{\text{obs}} - \delta_4)/(\delta_3 - \delta_4)$. Thus, referring to Equation 3, after taking account of points 1–3 above, the relative proportions in a savanna ecosystem of total foliar

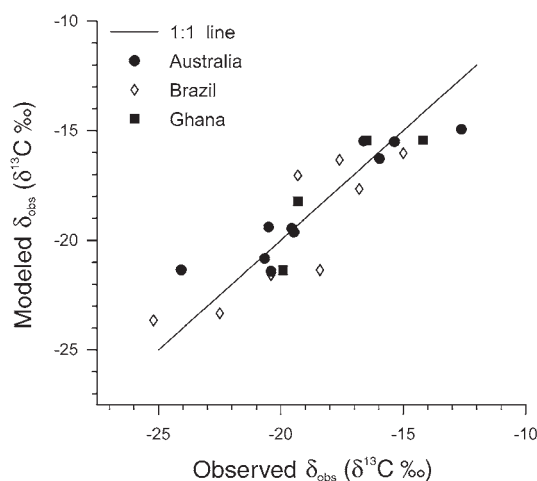


Figure 7. Relationship between modeled and observed mean (carbon weighted) soil surface ¹³C isotopic composition (δ_{obs}; expressed as δ¹³C) obtained using the restricted maximum likelihood model.

projected cover attributable to grasses and woody plants is numerically equivalent to their relative contributions to N_p deduced from stable isotope measurements.

It thus seems that ϕ may be a good quantitative indicator of the relative contributions of trees versus grasses to overall savanna productivity. Nevertheless, many larger-scale analyses have not examined the relative ζ of grasses and trees, as most savanna vegetation classifications measure the abundance of trees in terms of ζ_w or C (Pratt et al. 1966, Lind and Morrison 1974, Matthews 1983, White 1983, Carnahan 1990). We have thus plotted our estimated fraction of ecosystem N_p attributable to grasses ($= 1 - \phi$) as a function of ζ_w in Figure 8. The best fit to the data is given by a third-order polynomial which shows the biphasic nature of the response. After an initial decline with ζ_w , there is a plateau range where the relative contribution of grasses is relatively invariant at about 0.65 of total ecosystem N_p . Even at $\zeta_w = 0.4$, the relative contribution of grasses is still about 0.5 of total ecosystem N_p . However, the fitted relationship suggests a strong decline in the relative contribution of grasses for ζ_w greater than 0.4 with ecosystems with $\zeta_w > 0.5$ essentially grass free.

Global definitions

Only one published estimate of the fractional projected cover of trees and grasses was found—that being from Carnahan's (1990) study, which considered all vegetation in terms of four cover classes of which, for savanna-type vegetation, three are relevant: $0.3 < \zeta_w < 0.7$ (open forest or open scrub), $0.1 < \zeta_w < 0.3$ (woodland or shrubland) and $\zeta_w < 0.1$ (open woodland or open shrubland). Nevertheless, most ground-based vegetation maps use tree/shrub canopy cover in some way in their savanna classifications, usually in the form of C . For example, in his large scale map of all of Africa, White (1983) divides savanna into grassland ($C < 0.1$), wooded grassland ($0.1 < C < 0.4$) and woodland ($C > 0.4$); *Flora Zambesiaca* has four primary divisions, woodland, savanna woodland, tree savanna and grassland (Wild and Fernandes 1967); and the Brazilian system divides savanna (cerrado) vegetation into arborea densa (dense woodland), arborea aberta (open woodland), parque (parkland) and gramíneo-lenhosa (grassland with scattered shrubs). In many cases the exact C values associated with such definitions are unspecified in the map documentation. However, by referencing primary sources and literature syntheses, many of which include photographs (e.g., Keay 1953, Trapnell 1953, Trapnell and Clothier 1957, Eiten 1983, Acocks 1988) or profile diagrams (e.g., Keay 1953) for vegetation types associated with each particular classification, it was possible to classify each vegetation type broadly into five categories; $C = 0$ (denoted here as pure grassland); $0 < C < 0.05 =$ isolated trees; $0.05 < C < 0.2 =$ open savanna; $0.2 < C < 0.5 =$ open savanna woodland; and $0.5 < C < 0.8 =$ savanna woodland. The terminology for the different savanna types is based on that used by Keay (1949). In brief, in savanna woodland, the trees form a more or less complete canopy, in open savanna woodland, the trees are fairly closely and evenly spaced but do not form a closed canopy, whereas in open savanna, the trees are more widely separated.

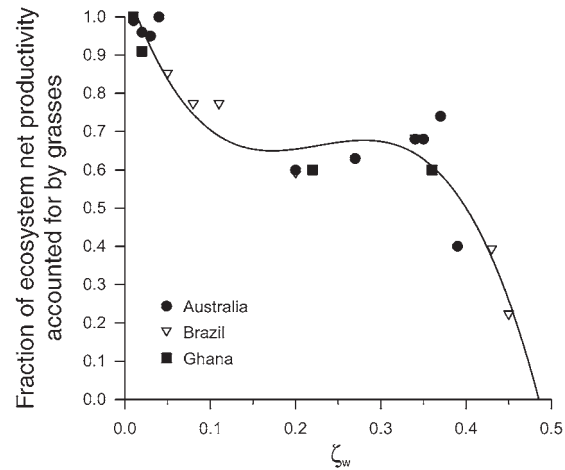


Figure 8. Relationship between the estimated fraction of the total ecosystem productivity accounted for by grasses and tree + shrub foliar projected cover (ζ_w).

Global estimates

Results by region are shown in Table 2 with the two grass dominated areas (grassland and isolated trees) pooled together, as is usually the case (e.g., Lind and Morrison 1974, White 1983, Carnahan 1990). Table 2 shows that Southern Africa (SnA), East Africa (EstA) and the Southern hemisphere Neotropical regions (ShN) have comparable areas of all vegetation types considered. The higher tree density woodland division is almost absent in Australia (Oz), and the intermediate open woodland savanna type is virtually absent in West Africa (WstA) and Central Africa (CeA). The northern hemisphere Neotropical region (NhN) is almost totally dominated by grasses and lacks significant areas of both open woodland and woodland categories with only small amounts of open savanna being identified. For WstA, EstA, SnA and Oz, there is a tendency for savanna N_p (ground area basis) to be higher for the woodier types. By contrast, for ShN (mostly the cerrado region of Brazil), N_p values are modeled to be uniformly high as is the case for open savanna in NhN. Modeled grassland productivities are considerably greater in CeA, ShN and NhN than in WstA or Oz, with EstA and SnA being intermediate between these two extremes.

Based on a mean tree/shrub foliar projected cover of 0.5 (cf. Table 1), the estimates for C above yield estimates of median ζ_w of 0.00, 0.01, 0.07, 0.17 and 0.33 for pure grassland, isolated trees, open savanna, open woodland savanna and woodland savanna, respectively, which from Figure 8 suggests $p_4 \approx 1.0, 0.95, 0.85, 0.60$ and 0.25 . Estimates based on these values of the proportions of N_p contributed by C_4 grasses in each region (p_4) are shown in the two rightmost columns of Table 2. Considering only the three savanna types, p_4 varies from 0.34 in CnA to 0.84 in NhN with an overall N_p -weighted mean of 0.59. Overall regional p_4 (including grassland) varies from 0.58 to 0.94 with an overall N_p mean (all continents examined) of 0.69.

Figure 9 shows the simulated distribution of the four as-

Table 2. Estimated areas ($\times 10^{12} \text{ m}^2$) and net primary productivity (N_p ; both on a ground area basis ($\text{mol m}^{-2} \text{ year}^{-1}$) and on a regional basis (Tmol year^{-1})) for grassland and savanna in Southern Africa, East Africa, West Africa, Central Africa and Australia, Southern hemisphere Neotropical savanna areas, Northern hemisphere Neotropical areas and their totals. Also shown in the two far-right-hand columns are the proportions of photosynthesis attributable to C_4 grasses, p_4 , both within the three savanna types only and for the region as a whole (grasslands and all three savanna types).

Parameter	Grassland	Savanna types			Region	Savanna p_4	Region p_4
		Open	Open woodland	Woodland			
<i>Southern Africa</i>							
Area	1.10	1.53	1.19	1.07	4.89		
N_p ($\text{mol m}^{-2} \text{ year}^{-1}$)	48.9	26.5	42.5	60.0	42.8	0.52	0.63
N_p (Tmol year^{-1})	53.7	40.5	50.7	64.5	209.5		
<i>East Africa</i>							
Area	0.46	1.26	0.60	0.35	2.67		
N_p ($\text{mol m}^{-2} \text{ year}^{-1}$)	43.7	36.9	65.1	73.4	49.2	0.62	0.68
N_p (Tmol year^{-1})	20.2	46.4	38.8	26.0	131.3		
<i>West Africa</i>							
Area	0.45	2.27	0.28	0.29	3.30		
N_p ($\text{mol m}^{-2} \text{ year}^{-1}$)	12.2	42.4	77.6	79.7	44.5	0.71	0.72
N_p (Tmol year^{-1})	5.6	96.3	21.9	22.7	146.5		
<i>Central Africa</i>							
Area	0.44	0.11	0.02	0.78	1.36		
N_p ($\text{mol m}^{-2} \text{ year}^{-1}$)	103.0	80.1	56.0	73.8	83.5	0.34	0.58
N_p (Tmol year^{-1})	45.2	9.1	1.4	57.6	113.2		
<i>Australia</i>							
Area	0.97	1.06	0.60	0.03	2.66		
N_p ($\text{mol m}^{-2} \text{ year}^{-1}$)	27.9	16.8	32.5	52.9	24.8	0.70	0.84
N_p (Tmol year^{-1})	27.0	17.8	19.5	1.8	66.2		
<i>Southern hemisphere Neotropical</i>							
Area	0.33	0.37	0.64	0.16	1.50		
N_p ($\text{mol m}^{-2} \text{ year}^{-1}$)	89.5	78.2	80.9	80.1	82.0	0.63	0.71
N_p (Tmol year^{-1})	29.2	28.8	51.6	13.1	122.8		
<i>Northern hemisphere Neotropical</i>							
Area	0.45	0.05	< 0.01	–	0.51		
N_p ($\text{mol m}^{-2} \text{ year}^{-1}$)	105.5	109.3	104.7	–	105.8	0.84	0.94
N_p (Tmol year^{-1})	47.8	5.4	0.3	–	53.5		
<i>Total</i>							
N_p (Pmol year^{-1})	0.229	0.244	0.184	0.185	0.843	0.59	0.69

signed vegetation types, illustrating the larger overall area of tropical savanna in Africa than in Australia or South America. Notable features include the areas of woody savanna surrounding the Congo rain forest to the north and south, but with the penetration of grasslands into the Congo Basin proper on its south west and eastern peripheries. Also of note is the relatively low density of woody vegetation in much of the band of savanna that extends from Liberia in West Africa almost to the Red Sea. Within South America, there are no systematic spatial patterns in woodiness as in Africa, with the occasional presence of savanna areas within the Amazon Basin. It can also be inferred from Table 2 that the most notable feature of Australian savannas in a global context is the low density of trees and shrubs compared with much of Africa and, to a lesser extent, South America.

Figure 10 shows the distribution of each vegetation class as

a function of rainfall for Africa (SnA, EstA, WesA and CeA combined), Australia (Oz) and the Neotropics (NhN and ShN combined). For Africa, there is a tendency for the woodier vegetation types to become more abundant as mean annual rainfall increases, but that grasslands are the predominant (non-rain forest) vegetation above mean annual precipitations of about $1700 \text{ mm year}^{-1}$ (Figure 10a). This is largely due to the presence of extended grasslands in high rainfall regions of CeA surrounding the Congo rain forest (Figure 9). For Australia, a pattern of increased woodiness of savanna vegetation with increases in rainfall is observed, although there is a virtual total absence of areas of woodland large enough to be mapped at $1.0^\circ \times 1.0^\circ$ (about $100 \times 100 \text{ km}$) resolution and, unlike Africa, grasslands are absent from high rainfall regions except for seasonally flooded areas (Figure 10b). For the savannas and grasslands of the Neotropics there is, by contrast,

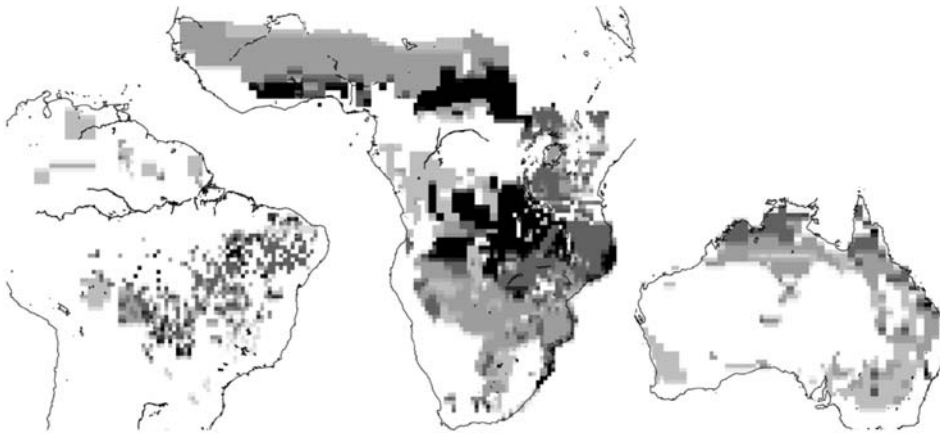


Figure 9. Simulated distribution of tropical savanna woody vegetation cover in South America, mainland Africa and Australia. Shading is in proportion to the tree + shrub canopy cover and ranges from 0.00 on pure grassland (light gray) to 0.65 in closed woodland (black). Even where known to occur, savanna areas in other regions (e.g., Central America, Asia) are not shown as they were not included in this analysis.

no large effect of annual precipitation on vegetation type, although there is a tendency for savanna woodland to dominate over tree savanna where annual precipitation is between 1400 and 1800 mm year⁻¹ (Figure 10c). There is also an increased abundance of grasses where rainfall is high (> 2500 mm year⁻¹) associated largely with high rainfall Nhn areas such as the Rio Branco, Rupinuni and Sipaliwini savannas.

Discussion

Variation in savanna structure

Our study, encompassing 22 sites on three continents, sampled a wide range of savanna types with vastly different proportions of tree versus grass foliage cover (Table 1). This high variation in the relative compositions of woody versus herbaceous vegetation is well documented for savanna vegetation in general (Scholes and Archer 1997) and may be attributable to variations in soil fertility (Goodland and Pollard 1973, Furley and Ratter 1988, Walker and Langridge 1997), soil texture and available rooting depth (Eagleson and Segarra 1985, Williams et al. 1996), soil water availability (Eagleson and Segarra 1985, Williams et al. 1996, Bird et al. 2004), fire history (Eiten 1983, San José and Fariñas 1983, Frost and Robertson 1987, Menaut et al. 1990, Moreira 2000, Roscoe et al. 2000) and grazing intensity (Moleele and Perkins 1998, Burrows et al. 2002). We suspect that all of these factors have contributed, at least to some extent, to the observed variation in the composition of the savannas we investigated. For example, the Australian sites, incorporating the Northern Australian Tropical Transect, were specifically chosen because of known variations in precipitation and soil texture. In contrast, it is likely that many of the variations in savanna structure around Brasília can be accounted for by differences in fire history, fertility or effective rooting depth rather than soil texture or precipitation (Moreira 2000), as exemplified by the presence of the woody cerrado on unusually fertile soils (Chapuis-Lardy et al. 2001, Ruggiero et al. 2002) and the almost treeless campo limpo on a shallow lithosol with an available rooting depth of only about 0.2 m. We do not know the precise fire histories

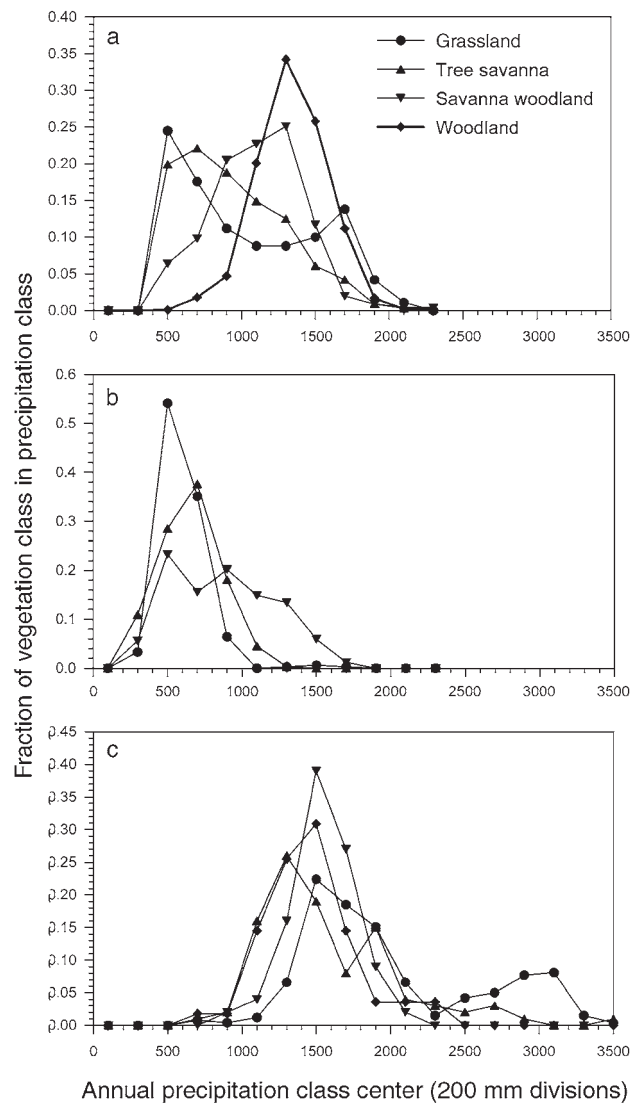


Figure 10. Relative distributions of grassland, tree savanna, savanna woodland and woodland for (a) Africa, (b) Australia and (c) the Neotropics in relation to mean annual rainfall. In all cases, the sum of the fraction of each vegetation class over all precipitation classes is unity.

of the sites studied, though being in protected areas, most Brasília sites would have experienced no burning for at least 10 years. Quite likely, all other sites were exposed to more-or-less natural fire regimes with grazing by either native herbivores or cattle, or both, also having occurred near Barreiras in Brazil as well as in Ghana and Australia in the years immediately before sampling.

The carbon isotope signal

Despite the large differences in underlying soil characteristics, annual precipitation and most likely fire and grazing history, when relative tree dominance was expressed as a fraction of total projected cover, ϕ , there was an effectively linear relationship between soil $\delta^{13}\text{C}$ and ϕ (Figure 5), which according to our model, suggests a linear relationship between the proportion of ecosystem productivity contributed by trees and ϕ . This relationship was only slightly affected by the occasional presence of the C_3 grass *Echinolaena inflexa* and suggests that the relative contributions of grasses and trees to the overall productivity of savanna ecosystems may be estimated from ϕ . This may appear surprising, as one might anticipate that tree effects on grass productivity might be mediated, at least in part, by a reduction in available photon flux penetrating to the ground layer and that an inverse exponential relationship between tree foliage cover and grass productivity would result (Beer-Lambert Law). Such a relationship has been implied from experimental studies where trees have been selectively removed from tropical savannas (Pressland, 1975, Scanlan and Burrows 1990, Burrows et al. 1990). Nevertheless, factors other than light penetration should affect the tree–grass productivity interaction. For example, savanna productivity is generally water limited, at least for part of the year (House and Hall 2001), therefore, as tree foliage cover increases, the amount of water available to the grass layer should decrease with adverse effects on plant productivity. A similar relationship to Figure 5 was observed by Sanaiotti et al. (2000) who, working in savanna areas of the Brazilian Amazon, observed a strong correlation between the number of C_3 individuals per hectare and the $\delta^{13}\text{C}$ of carbon in the surface soil.

Despite the large variations in rainfall experienced across the savannas examined (from about 650 mm at Kidman Springs to about 1450 mm in Brasília), there was no significant correlation between foliar $\delta^{13}\text{C}$ and annual precipitation for either trees or grasses. This is consistent with other work where only at annual precipitations less than around 400 mm are significantly less negative foliar $\delta^{13}\text{C}$ (indicative of a higher intrinsic water use efficiency) observed compared with high rainfall sites (Miller et al. 2001). However, we observed a tendency for foliar $\delta^{13}\text{C}$ to become more negative as ϕ increased, and this relationship was independent of rainfall (Figure 4). Overall, our data indicate that the primary savanna overstory adjustment to changing soil water availability reflects changes in tree and foliage density rather than altered underlying physiological processes. Also, as trees become less abundant, those trees that are present seem to show increasing signs of long-term stress (less negative foliar $\delta^{13}\text{C}$), indirectly suggesting an important role of competition between trees and

grasses for soil water or other factors in influencing the structure of savanna ecosystems (Walter 1971).

The modeled fit of Equation 4 suggests that the mean $\delta^{13}\text{C}$ of the surface soil carbon pool may not accurately reflect the $\delta^{13}\text{C}$ of input vegetation, with pure grassland surface soil $\delta^{13}\text{C}$ being about 2‰ less than that of overlying vegetation. Such discrepancies have been observed before with the depletion of soil $\delta^{13}\text{C}$ being attributed to either a slower mean residence time for more depleted carbon compounds (e.g., lignin) or fractionation during microbial decomposition (Benner et al. 1987, Melillo et al. 1989, Wedin et al. 1995, Schweizer et al. 1999, Santrucková et al. 2000). Our confinement of sampling to the soil surface layer limited confounding problems that may be associated with the enrichment of soil ^{13}C with depth (Wynn et al. 2005). Although our sampling strategy may not have been perfect, an overrepresentation of woody vegetation for predominately grassland areas but with isolated trees cannot account for the relatively large 2‰ offset observed between surface soil organic matter and vegetation.

Our modeling analysis indicated a second offsetting effect dependent on ζ_w . At least in part, this could be associated with the presence in the soil of carbon derived from decomposed woody plant material; the $\delta^{13}\text{C}$ of which tends to be higher than that of foliage from the same tree (Figure 6) and may be relatively resistant to decomposition. Because of differences in carbohydrate chemistry, carbon from these woody organs may have a longer turnover time than foliage, even when partially decomposed and part of the soil carbon pool (Palm et al. 2001).

An additional complication is the likely occurrence of fires in many sample plots, which would likely result in a preferential loss of grass-derived carbon to the atmosphere (Miranda 2002). Nevertheless, when considered in relation to the annual rates of carbon acquisition through photosynthesis, Santos et al. (2003) found that fire-induced losses accounted for only about 20% of campo sujo gross primary productivity (G_p). Moreover, following savanna fires, there can be a general stimulation of savanna G_p which, even in the first year after fire, can all but compensate for the fire-induced carbon losses (Santos et al. 2003).

This means that, as long as the mean fire return time is similar to or longer than the mean foliage residence time, fires will not necessarily reduce inputs to the soil carbon pool. A related factor is that much of the carbon of savanna plants is below ground (De Castro and Kauffmann 1998), suggesting that fire effects on the overall soil carbon balance should be minimal. This is consistent with the results of Roscoe et al. (2000) who found fire frequency had no effect on the magnitude of soil carbon stocks in Brazilian cerrado. In contrast, Bird et al. (2000) found that, in Zimbabwean savanna plots that had been excluded from fire for 50 years, soil organic carbon content was significantly higher than in plots exposed to regular controlled burns over the same period. Differences in long-term fire treatment have, however, been associated with large changes in vegetation cover in the fire protected plots that may have contributed to the increase in soil carbon densities. For instance, fire protected plots had considerably greater woody

tree and shrub cover than those exposed to regular fires. There was also a strong correlation of soil $\delta^{13}\text{C}$ with soil carbon density across all sites (burned and unburned), again suggesting that C_3 carbon derived from woody tissues has a longer mean residence time in the soil than is the case for other plant material. Thus, the greater density of woody plant material in the unburned plot may have increased soil carbon densities independent of differences in fire frequency. Across a wide range of grassland, savanna and forest sites, Bird and Pousai (1997) found a strong relationship between soil $\delta^{13}\text{C}$ and soil carbon densities, suggesting that this may be a widespread effect. Although charcoal residues from fire would be expected to have a longer mean residence time in the soil carbon pool than more refractory carbon compounds, Bird et al. (1999) found that, for a Zimbabwean savanna, refractory carbon decays over a time-scale of decades rather than centuries. Thus, greater charcoal production in more heavily burned sites may not necessarily significantly increase the size of the soil carbon pool above that in unburned sites. Krull et al. (2003) found a significant depletion of $\delta^{13}\text{C}$ associated with charcoal production resulting from burning for some C_4 grasses, and this may contribute to soil $\delta^{13}\text{C}$ depletion compared with the overlying plant $\delta^{13}\text{C}$ for C_4 grassland.

Quasi-global estimate

Despite the many likely differences in site history, soil fertility and savanna structure across the 22 sites surveyed, the simple model outlined in Equation 4 provided a good fit to the data and, via determination of ϕ , a ready means of estimating the relative contributions of trees and grasses to savanna ecosystem productivity. Moreover, although ϕ requires the determination of both ζ_w and ζ_g , Figure 8 shows that ζ_w itself is a reasonable predictor, because the relationship between ζ_w and ζ_g is not completely random (Figure 2). Figure 8 thus provides a means to estimate ϕ on the basis of ζ_w which is closely related to C . This is because individual tree or shrub α is quite conservative at about 0.5 for savanna trees (Table 1; Gillison 1994).

When estimated at the continental scale by simply assigning the C_4 grass fraction of ecosystem productivity to assigned classes of C , substantial regional variation was predicted. The most striking difference is the low savanna p_4 for African regions as opposed to Australia or the Neotropics (Table 2). Although the high savanna p_4 for both Australia and Northern hemisphere Neotropics can be attributed mainly to a proportionally low amount of woodier vegetation being present, the relatively low savanna p_4 for Africa are due to both substantial amounts of open woodland and woodland being present and to these woodier savanna types tending to occur in areas of higher rainfall (Figure 10) and, hence, (generally) higher N_p . This is evident when comparing N_p -weighted versus area-weighted estimates of p_4 for Africa as a whole (0.62 and 0.68, respectively), as is also the case for Australia to a lesser extent (0.70 versus 0.75). By contrast, for Neotropical savannas (Southern and Northern hemispheres combined) both methods of weighting yield the same estimate for savanna p_4 of 0.64.

Large scale patterns

The tendency for woody plant cover to decrease with increasing aridity has been reported before for northern Australia (Williams et al. 1996) and southern Africa (Scholes et al. 2004), and this decrease is clearly unaccompanied by concomitant decreases in grass cover, at least for areas where strongly seasonal rainfall patterns characteristic of savanna-type vegetation are maintained (Wilson et al. 1990, Scholes et al. 2004). This also seems to be the case for West Africa where the well documented decline of woody plant cover as rainfall declines across the Guinea-Sudan-Sahel savanna zones (Chevalier 1933, Lawson 1966, White 1983) results in wooded grassland giving way to a semi-desert grassland in the northern Sahel (Harrison and Jackson 1958, White 1983). However, in our analysis, this pattern is less marked because we accounted for the anthropomorphic transformation of woodland and open woodland into open savanna in much of the West African savanna belt (White 1983, p 106). This can be seen from Table 2 and Figure 9.

The extremely low N_p for grasses in West Africa is associated with the presence of semi-desert grassland on the edge of the Sahara (e.g., Harrison and Jackson 1958), and the presence of this vegetation type in this region reflects the relative dominance of grasses over trees in regions of low but still strongly seasonal rainfall. The overall reason for this relative dominance of grasses in climates of low but strongly seasonal rainfall most likely reflects the intrinsically higher photosynthetic water-use efficiency of C_4 tropical grasses (Black 1973, Ludlow 1976) as well as perhaps their low whole-plant construction and maintenance costs (Orians and Solbrig 1977). Collatz et al. (1998) also noted that tropical grasses occur only in regions where sufficiently high ambient air temperatures and adequate rainfall both occur in the same month(s).

Grasslands occur to a considerable extent in higher rainfall areas, especially in Africa and the Neotropics (Figure 10). Some of these grasslands are natural—a consequence of soil conditions that are adverse for tree growth—for example, heavily textured clay soils that tend to become easily waterlogged but have only a limited water-holding capacity to support plant growth during dry periods (Medina and Silva 1990, Williams et al. 1996). The term “edaphic grassland” is almost endemic in the African biogeographical literature. The grasslands of the Serengeti Plains grow on calcareous soils derived from volcanic ash (Anderson and Talbot 1965), and there is also an extensive grassland area associated with dark, cracking Pleistocene clays around Lake Chad and the upper Nile Basin (Harrison and Jackson 1958, Pias 1970, White 1983). Grasslands also occur naturally within the Congo Basin in areas climatically more suitable for rain forest, for example at valley headwaters (“dambos”) and in areas subjected to seasonal flooding (Vesey-Fitzgerald 1963).

Nevertheless, it is likely that much of the grassland that surrounds the Congo forest in CeA with high predicted N_p (Table 2, Figure 9) is anthropogenic in origin and maintained by fire (Duvigneaud 1952, 1953). Whether this is the case for all higher rainfall grasslands in tropical and subtropical regions is

unclear. For example, Bond et al. (2005) suggest that fire is a key determinant for the existence of extensive grasslands of South Africa, yet there is strong evidence that soil physical and chemical properties may also be important (O'Connor and Bredenkamp 1997). Likewise, the llanos of Venezuela and Colombia are characterized by low densities of woody vegetation but occur in regions with reasonably high rainfall (1100–2000 mm year⁻¹). Although this relatively low density of woody vegetation may be maintained as a consequence of regular fires, it is clear that this extensive high rainfall savanna region occurs as a consequence of an extremely low soil nutrient availability combined with adverse soil physical characteristics (Blydenstein 1967, Sarmiento 1983, Medina and Silva 1990). These savannas are, as put by Beard (1953), “the natural vegetation of senile land-forms.” Thus, because of a prevalence of adverse soil conditions, C₄ grasses contribute to the productivity of these regions to a far greater extent than would be predicted on the basis of prevailing climate.

Even when accounting for the seasonally flooded grasslands of Pantanal and significant areas of seasonally flooded grassland in Venezuela and Colombia as well as the llanos de Moxos in Bolivia (Haase 1992, Hamilton et al. 2004), the relationship between Neotropical woody plant cover and mean annual precipitation differs markedly from that in Australia or Africa (Figure 10). There is a more or less random distribution of the various physiognomic forms of cerrado with variation in annual precipitation (Figures 9 and 10) and a subsequent high savanna p_4 (Table 2).

Accounts of the underlying causes of differences between physiognomic forms of cerrado vegetation have concentrated on the degree to which variations in the density of woody plants is a function of degradation caused by fire and human activity (Rizzini 1963, Bond et al. 2005) as opposed to variations in soil nutrients and texture. On balance, there is little to suggest that burning and other human activities account for large-scale variations in savanna form, although this is no doubt the case under certain circumstances in Brazil as elsewhere (Eiten 1983, Sarmiento 1983, Cavellier et al. 1998, Dezzeo et al. 2004). That factors other than fire are important in determining woodiness of cerrado vegetation is also supported by plant ordination studies across the various cerrado types (Ribeiro and Tabarelli 2002, Miranda et al. 2003) and indicates that soil fertility is a major determinant of woodiness in Brazilian savanna at the landscape scale (Lopes and Cox 1977a, 1977b). For example, it is well established that some woodland cerrado types tend to occur only on unusually fertile soils (Furley and Ratter 1988, Moriera 2000, Chapuis-Lardy et al. 2001), although, whether the grassland cerrado forms such as campo sujo occur because the soils have an exceptionally low nutrient status is less clear (Alvim and Araújo 1952, Askew et al. 1970, Goodland and Pollard 1973, Lopes and Cox 1977a, 1977b, Furley and Ratter 1988, Furley 1992, Ruggiero et al. 2002). Fire frequencies must also be important. However, what is clear is that the Brazilian cerrado occupies an area much of which, on the basis of climate alone, would be expected to be occupied by forests (Bond et al. 2005), and one significant factor accounting for the vegetation actually ob-

served is the infertility of the soil (Montgomery and Askew 1983).

Thus, low soil fertility has predisposed the sustained existence of open savanna vegetation, rather than closed woodland or forest (Sarmiento 1992), with a correspondingly high regional N_p by savanna standards and a high p_4 (Table 2). Significant areas of savanna and patches of heath-like vegetation can also occur naturally as islands surrounded by rain forest within high rainfall areas, and again, unusually adverse physical or chemical conditions, or both, for tree growth seem to be responsible (Beard 1953, Anderson 1981, Brown 1987). A corollary is the thickening of woody vegetation leading to the so-called “relic” forests of West Africa that cover the ruins of ancient villages and graves. Climatically these areas should be savannas (Lamb 1942, Thomas 1942, Keay 1947, 1949, Sobey 1978) and are associated with anthropogenically modified soils of an unusually high fertility. There are also many islands of forest around current settlements in the West Africa forest–savanna transition zone, where fire suppression through animal grazing and early burning may be a factor contributing to the development of these forests (see review by Fairhead and Leach 1996).

Uncertainties in the analysis

Despite complexities at landscape and regional scales, our estimate of a globally averaged savanna p_4 of 0.59 is surprisingly close to an earlier naive guess of 0.50 (Lloyd and Farquhar 1994). Nevertheless, there remain appreciable uncertainties in the current analysis. For example, we have used a relatively simple water balance equation to estimate the N_p weighting factor for all savanna types (Scholes and Hall 1996, House and Hall 2001), and this may introduce significant errors, for example, in seasonally flooded areas and for shallow heavily textured soils with low water-holding capacities. Our formulation also ignores the different photosynthetic and water-use characteristics of the predominantly C₄ grass vegetation layer compared with the C₃ woody component. Under similar climatic conditions, Santos et al. (2003) estimated for the grassy campo sujo cerrado type a maximum mean G_p of around 0.5 mol C m⁻² day⁻¹, which is only slightly higher than the 0.4 mol C m⁻² day⁻¹ estimated for a nearby woodier cerrado denso by Miranda et al. (1997) at the same time of year. This is what one would expect for daily sums because, other things being equal, grassy savannas should show a lesser tendency to light saturation at the highest irradiances (Grace et al. 1998, Santos et al. 2003)—a characteristic of the C₄ photosynthetic pathway (Björkman 1971, Osmond et al. 1980). Nevertheless, on an annual productivity basis, this effect may be partly offset by the greater mean leaf lifetime of trees versus grasses allowing woody vegetation to better utilize any available soil water at the beginning and end of the wet season (Rutherford and Pangos 1982, Sarmiento and Monasterio 1983, Scholes 2003).

We used ground-based maps to make our spatial representation of the various savanna and grassland types (Figure 9) as accurate as possible, and this included incorporation of widespread anthropogenic effects on savanna structure as appropriate (for example in western Africa; White 1983). However,

many of the maps used may reflect the landscape of over 50 years ago, rather than now. Since then, there may have been significant areas of savanna cleared for pasture and cropland in, for example, the cerrado of Brazil (Smith et al. 1999, Sano et al. 2000), western and central Africa (Gornitz and NASA 1985, Yang and Prince 2000) and the northeast of Australia (Henry et al. 2002). In general, a decrease in woody vegetation cover associated with disturbance should result in a higher regional p_4 , as should also be the case with conversion of savanna to pasture, especially given the potentially higher carbon assimilation rates of the latter (Santos et al. 2004). But opposite effects may also be occurring, for example, with the widespread conversion of Brazilian savanna to fields of the C_3 crop plant *Glycine max* (L.) Merr. (soybean; Smith et al. 1999) or as a consequence of secondary thickening of vegetation in response to increased intensity of livestock grazing (Molelele and Perkins 1998, Henry et al. 2002) or increased atmospheric CO_2 concentrations.

Where identified, we excluded agricultural landscapes from our analysis (e.g., Carnahan 1990, IBAMA 1993), but the contribution of C_4 crop plants such as maize is significant on a global scale as is photosynthesis by C_4 grasses in the mixed grasslands of extra-tropical and tropical montane regions (Lloyd and Farquhar 1994, Still et al. 2003). Thus our overall estimate of C_4 plant N_p ($0.58 \text{ Pmol year}^{-1}$) does not represent a true global sum. Our analysis included no C_4 photosynthesis in the thorn-scrub and thicket of many parts of Africa or in the *caatinga* vegetation of north-east Brazil. Although dominated by trees, sometimes in an even impenetrable configuration, these vegetation types are characterized by the presence of grasses, albeit usually at a lesser density than in savannas (Trapnell and Langdale-Brown 1972, Acocks 1988, Schacht et al. 1989). White (1983) describes the grasses in thicket areas as “physiognomically subordinate,” and on the basis of our own limited measurements of soil $\delta^{13}C$ under *caatinga* vegetation (with subordinate grasses present) in the Bahia region of Brazil (about -24.5 ‰ ; Lloyd, Miranda and Bird, unpublished data), we suggest a typical p_4 of about 0.20. A thin layer of grasses may also be present under semi-deciduous forest types, such as for the extensive Chaco areas south of the Amazon (Killeen and Hinz 1992a), but, despite the tropical climate, these grasses tend to be of the C_3 photosynthetic mode (Killeen and Hinz 1992b). Our analysis also omitted relatively minor tropical savanna areas in Central America (Sarmiento 1992) as well as savanna regions in India and South-East Asia, many of which have been derived from dry tropical forest ecosystems (Misra 1983, Stott 1990, Yavada 1990, Backeus 1992). Savannas on islands off the main three continents, including countries such as Papua New Guinea and Madagascar, have also been omitted.

In conclusion, it is hard to define the uncertainty in our overall savanna p_4 estimates because of the relatively crude assignment of the various ϕ to estimated C . Nevertheless, we believe our estimates of p_4 are within 0.1 of the suggested values and that our earlier estimate for a globally averaged savanna p_4 of 0.50 was reasonable. This also provides increased confidence

in a previous global p_4 estimate of 0.21 (Lloyd and Farquhar 1994), quite close also to the 0.23 estimate obtained by Still et al. (2003). Table 2 suggests that the assumption of Fung et al. (1997) of all regional $p_4 = 0.75$ was an overestimate. Likewise, their estimate of a global p_4 of 0.27 is likely too high. We have ascertained that all current global databases of vegetation cover have significant errors in vegetation classifications within and around savanna regions (details available on request). These errors in vegetation cover definition have probably caused as large an error in earlier studies as is the case for any inaccuracies in the assumed p_4 .

Remote sensing technologies such as those being developed and applied by Yang and Prince (1997), DeFries et al. (2000) and Xu et al. (2003) should, in the future, allow global estimates of woody plant and grass vegetation cover in mixed communities. When combined with expanded field studies, especially in under-investigated savanna areas with high N_p , such as the miombo woodlands of Africa (Malaisse 1978), better estimates of the magnitude of rates of change of C , ϕ and p_4 at regional, continental and global scales should become possible.

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References

- Acocks, J.P.H. 1988. Veld types of South Africa. Mem. Bot. Surv. S. Afr. 57:1–146.
- Airy Shaw, H.K. 1947. The vegetation of Angola. J. Ecol. 35:23–48.
- Alvim, P. and W.A. Araújo. 1952. El suelo como factor ecológico en el desarrollo de la vegetación en el centro-oeste del Brasil. Turrialba 2:153–160.
- Anderson, A.B. 1981. White-sand vegetation of Brazilian Amazonia. Biotropica 13:199–210.
- Anderson, G.D. and L.M. Talbot. 1965. Soil factors affecting the distribution of grassland types and their utilization by wild animals on the Serengeti Plains, Tanganyika. J. Ecol. 53:33–56.
- Askew, G.P., D.J. Moffatt, R.F. Montgomery and R.L. Searl. 1970. The interrelationships of soils and vegetation in the savanna-forest boundary of north east Mato Grosso. Geog. J. 136:370–376.
- Backeus, I. 1992. Distribution and vegetation dynamics of humid savannas in Africa and Asia. J. Veg. Sci. 3:345–356.
- Beard, J.S. 1953. The savanna vegetation of northern tropical America. Ecol. Monogr. 23:149–215.
- Benner, R., M.L. Fogel, E.K. Sprague and R.E. Hodson. 1987. Depletion of ^{13}C in lignin and its implications for stable carbon isotope studies. Nature 329:708–710.
- Bird, M.I. and P. Pousai. 1997. Variations of $\delta^{13}C$ in the surface soil organic carbon pool. Global Biogeochem. Cycles 11:313–322.

- Bird, M.I., S.G. Haberle and A.R. Chivas. 1994. Effect of altitude on the carbon-isotope composition of forest and grassland soils from Papua New Guinea. *Global Biogeochem. Cycles* 8:13–22.
- Bird, M.I., C. Moyo, E.M. Veenendaal, J. Lloyd and P. Frost. 1999. Stability of elemental carbon in a savanna soil. *Global Biogeochem. Cycles* 13:923–932.
- Bird, M., E. Veenendaal, C. Moyo, J. Lloyd and P. Frost. 2000. Effect of fire and soil texture on soil carbon in a sub-humid savanna (Matopos, Zimbabwe). *Geoderma* 94:71–90.
- Bird, M.I., E. Veenendaal and J. Lloyd. 2004. Soil carbon inventories and $\delta^{13}\text{C}$ along a moisture gradient in Botswana. *Global Change Biol.* 10:342–349.
- Björkman, O. 1971. Comparative photosynthetic CO_2 exchange in higher plants. *In* Photosynthesis and Photorespiration. Eds. M.D. Hatch, C.B. Osmond and R.D. Slatyer. Wiley-Intersciences, New York, pp 18–32.
- Black, C.C. 1973. Photosynthetic carbon fixation in relation to net CO_2 uptake. *Ann. Rev. Plant Physiol.* 24:253–286.
- Blydenstein, J. 1967. Tropical savanna vegetation of the Llanos of Colombia. *Ecology* 48:1–15.
- Bond, W.J., F.I. Woodward and G.F. Midgley. 2005. The global distribution of ecosystems in a world without fire. *New Phytol.* 165: 525–538.
- Brown, K.S. 1987. Soils and vegetation. *In* Biogeography and Quaternary History in Tropical America. Eds. T.C. Whitmore and G.T. Prance. Clarendon Press, Oxford, pp 19–45.
- Burke, A., W. du Plessis and B. Strohbach. 2002. Vegetation types in Namibia. Supplement to Environmental Atlas of Namibia, Ministry of Environment and Tourism, Windhoek. http://www.dea.met.gov.na/data/Atlas/Atlas_web.htm#4Vegetation.
- Burrows, W.H., J.O. Carter, J.C. Scanlan and E.R. Anderson. 1990. Management of savanna for livestock production in north-east Australia: contrasts across the tree–grass continuum. *J. Biogeogr.* 17:503–512.
- Burrows, W.H., B.K. Henry, P.V. Back et al. 2002. Growth and carbon stock change in eucalypt woodlands in northeast Australia: ecological and greenhouse sink implications. *Global Change Biol.* 8: 769–784.
- Carnahan, J.A. 1990. Atlas of Australian resources. Third Series. Vol. 6, Vegetation. Australian Surveying and Land Information Group, Canberra, Australia, 64 p.
- Cavelier, J., T.M. Aide, C. Santos, A.M. Eusse and J.M. Dupuy. 1998. The savannisation of moist forests in the Sierra Nevada de Santa Marta, Colombia. *J. Biogeogr.* 25:901–912.
- Chapuis-Lardy, L., M. Brossard and H. Quiquampoix. 2001. Assessing organic phosphorus status of Cerrado oxisols (Brazil) using P-31-NMR spectroscopy and phosphomonoesterase activity measurement. *Can. J. Soil Sci.* 81:591–601.
- Chevalier, A. 1933. La territoire géobotanique de l’Afrique tropicale nord-occidentale et ses subdivisions. *Bull. Soc. Bot. Fr.* 80:4–26.
- Collatz, G.J., J.A. Berry and J.S. Clark. 1998. Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: past, present and future. *Oecologia* 114:441–454.
- De Castro, E.A. and J.B. Kauffman. 1998. Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. *J. Trop. Ecol.* 14:263–283.
- DeFries, R., M.C. Hansen and J.R.G. Townshend. 2000. Global continuous fields of vegetation characteristics: a linear mixture model applied to multi-year 8 km AVHRR data. *Int. J. Rem. Sens.* 21: 1389–1414.
- Dezzeno, N., N.E. Chacon, E. Sanoja and G. Picon. 2004. Changes in soil properties and vegetation characteristics along a forest-savanna gradient in southern Venezuela. *For. Ecol. Manage.* 200: 183–193.
- Downton, W.J.S. and E.B. Tregunna. 1968. Carbon dioxide compensation—its relation to photosynthetic carboxylation reactions, systematics of the Gramineae and leaf anatomy. *Can. J. Bot.* 46: 207–215.
- Duvigneaud, P. 1952. La flore et la végétation du Congo méridional. *Leujunia* 16:95–125.
- Duvigneaud, P. 1953. Les formations herbeuses (savanes et steppes) du Congo méridional. *Nat. Belg.* 34:66–75.
- Eagleson, P.S. and R.I. Segarra. 1985. Water limited equilibrium of savanna vegetation systems. *Water Resour. Res.* 21:1483–1493.
- Eiten, G. 1983. Classificação da Vegetação do Brasil. Conselho Nacional de Desenvolvimento Científico e Tecnológico: Brasília, Brazil, 305 p.
- Fairhead, J. and M. Leach. 1996. Misreading the African landscape: society and ecology in a forest–savanna mosaic. Cambridge University Press, Cambridge, 354 p.
- Farquhar, G.D., J.E. Ehleringer and K.T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 40:503–537.
- Frost, P.G.H. and F. Robertson. 1987. The ecological effects of fire in savannas. *In* Determinants of Tropical Savannas. Ed. B.H. Walker. IUBS, Paris, pp 93–140.
- Fung, I., C.B. Field, J.A. Berry et al. 1997. Carbon-13 exchanges between the atmosphere and biosphere. *Global Biogeochem. Cycles* 11:507–533.
- Furley, P.A. 1992. Edaphic changes at the forest–savanna boundary with particular reference to the Neotropics. *In* Nature and Dynamics of Forest–Savanna Boundaries. Eds. P.A. Furley, J. Proctor and J.A. Ratter. Chapman & Hall, London, pp 91–117.
- Furley, P.A. and J.A. Ratter. 1988. Soil resources and plant communities of Central Brazilian cerrado and their development. *J. Biogeogr.* 15:97–108.
- Gillison, A.N. 1994. Woodlands. *In* Australian Vegetation. Ed. R.H. Groves. Cambridge University Press, Cambridge, pp 227–255.
- Gilmour, A.R., R. Thompson and B.R. Cullis. 1995. Average information REML, an efficient algorithm for variance parameter estimation in linear mixed models. *Biometrics* 51:1440–1450.
- Goodland, R.J.A. and R. Pollard. 1973. The Brazilian cerrado vegetation: a fertility gradient. *J. Ecol.* 61:219–224.
- Gornitz, V. and NASA. 1985. A survey of anthropogenic vegetation changes in West Africa during the last century—climatic implications. *Clim. Change* 7:285–325.
- Gossweiler, J. 1939. Carta Fitogeográfica de Angola. Gov. Geral de Angola, Luanda, 242 p.
- Grace, J., J. Lloyd, A.C. Miranda, H. Miranda and J.H. Gash. 1998. Fluxes of carbon dioxide and water vapour over a C_4 pasture in south-western Amazonia (Brazil). *Aust. J. Plant Physiol.* 25: 519–530.
- Guigonis, G. 1968. République Centralafricaine. *In* Conservation of Vegetation in Africa South of the Sahara. Eds. I. Hedberg and O. Hedberg. Acta Phytogeogr. Suec. 54:104–111.
- Haase, R. 1992. Physical and chemical properties of savanna soils in northern Bolivia. *Catena* 19:119–134.
- Hamilton, S.K., S.J. Sippel and J.M. Melack. 2004. Seasonal inundation patterns in two large savanna floodplains of South America: the Llanos de Moxos (Bolivia) and the Llanos del Orinoco (Venezuela and Colombia). *Hydrol. Process.* 18:2103–2116.
- Harrison, M.N. and J.K. Jackson. 1958. Ecological classification of the vegetation of the Sudan. *Forests Bull. Sudan (New series)*, 2:1–45.
- Henry, B.K., T. Danaher, G.M. McKeon and W.H. Burrows. 2002. A review of the potential role of greenhouse gas abatement in native vegetation management in Queensland’s rangelands. *Range. J.* 24:112–132.

- House, J.I. and D.O. Hall. 2001. Productivity of tropical savannas and grasslands. *In* Terrestrial Global Productivity, Eds. J. Roy, B. Saugier and H.A. Mooney. Academic Press, San Diego, pp 363–400.
- Huber, O. 1995. Vegetation. *In* Flora of Venezuelan Guayana: Volume 1, Introduction. Eds. P.E. Berry, B.K. Holst and K. Yatskivych. Missouri Botanical Garden, St. Louis, pp 97–160.
- Huber, O., G. Gharbarran and V.A. Funk. 1995. Preliminary vegetation map of Guyana. Biological Diversity of the Guianas Program, Smithsonian Institution, Washington, DC.
- IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis). 1993. Mapa de Vegetação do Brasil. IBAMA, Rio de Janeiro.
- Keay, R.W.J. 1947. Notes on the vegetation of old Oyo forest reserve. *Farm For.* 8:36–47.
- Keay, R.W.J. 1949. An example of Sudan zone vegetation in Nigeria. *J. Ecol.* 37:335–364.
- Keay, R.W.J. 1953. An outline of Nigerian vegetation, 2nd Edn. Government Printer, Lagos, Nigeria, 52 p.
- Keeling, C.D., S.C. Piper and M. Heimann. 1989. A three-dimensional model of atmospheric CO₂ transport based on observed winds. 4. Mean annual gradients and interannual variations. *In* Aspects of Climate Variability in the Pacific and Western Americas, Vol. 55. Ed. D.H. Peterson. Am. Geophys. Union, Washington, DC, pp 305–363.
- Killeen, T.J. and P.N. Hinz. 1992a. Grasses of the Precambrian Shield region in eastern lowland Bolivia. I. Habitat preferences. *J. Trop. Ecol.* 8:389–407.
- Killeen, T.J. and P.N. Hinz. 1992b. Grasses of the Precambrian Shield region in eastern lowland Bolivia. II. Life-form and C₃–C₄ photosynthetic types. *J. Trop. Ecol.* 8:409–433.
- Klink, C.A. and C.A. Joly. 1989. Identification and distribution of C₃ and C₄ grasses in open and shaded habitats in São Paulo State, Brazil. *Biotropica* 21:30–34.
- Krull, E.S., J.O. Skjemstad, D. Graetz, K. Grice, W. Dunning, G. Cook and J.F. Parr. 2003. ¹³C depleted charcoal from C₄ grasses and the role of occluded carbon in phytoliths. *Org. Geochem.* 34: 1337–1352.
- Lamb, A.F. 1942. The kurmis of northern Nigeria. *Farm For.* 3: 187–192.
- Lawson, G.W. 1966. Plant life in West Africa. Ghana University Press, Accra, Ghana, 150 p.
- Leavitt, S.W. and A. Long. 1982. Evidence for ¹³C/¹²C fractionation between tree leaves and wood. *Nature* 298:742–744.
- Lind, E.M. and M.E.S. Morrison. 1974. East African vegetation. Longman, London, 257 p.
- Lloyd, J. and G.D. Farquhar. 1994. ¹³C discrimination during CO₂ assimilation by the terrestrial biosphere. *Oecologia* 99:201–215.
- Lopes, A.S. and F.R. Cox. 1977a. A survey of the fertility status of surface soils under “Cerrado” vegetation in Brazil. *Soil. Sci. Soc. Am. J.* 41:742–747.
- Lopes, A.S. and F.R. Cox. 1977b. Cerrado vegetation in Brazil: an edaphic gradient. *Agron. J.* 69:828–831.
- Low, A.B. and A.G. Rebio. 1998. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria, South Africa, 85 p.
- Ludlow, M.M. 1976. Ecophysiology of C₄ grasses. *In* Water and Plant Life: Problems and Modern Approaches. Eds. O.L. Lange, L. Kappen and E.-D. Schulze. Springer-Verlag, Berlin, Heidelberg, New York, pp 364–386.
- Malaisse, F. 1978. The Miombo ecosystem. *In* Tropical Forest Ecosystems: A State-of-knowledge Report Prepared by UNESCO/ UNEP/FAO. UNESCO, Paris, pp 589–606.
- Mangenot, G. 1971. Une nouvelle carte de la végétation de la Côte d’Ivoire. *Mitt. Bot. Staatssamml. Münch.* 10:116–121.
- Matthews, E. 1983. Global vegetation and land use: new high-resolution data bases for climate studies. *J. Appl. Meteorol.* 22:474–487.
- Medina, E. and J. Silva. 1990. Savannas of northern South America: a steady state regulated by water–fire interaction on a background of low nutrient availability. *J. Biogeogr.* 17:403–413.
- Medina, E., L.A. Martinelli, E. Barbosa and R.L. Victoria. 1999. Natural abundance of ¹³C in tropical grasses from the INPA, Instituto Nacional de Pesquisas da Amazônia, herbarium. *Rev. Bras. Bot.* 22:44–51.
- Melillo, J.M., J.D. Aber, A.E. Linkens, A. Ricca, B. Fry and K.J. Nadelhoffer. 1989. Carbon and nitrogen dynamics along a decay continuum: plant litter to soil organic matter. *Plant Soil* 115:189–198.
- Menaut, J.C., J. Gignoux, C. Prado and J. Colbert. 1990. Tree community dynamics in a humid savanna of the Cotê-d’Ivoire: modeling the effects of fire and competition with grass and neighbours. *J. Biogeogr.* 17:471–481.
- Miller, J.M., R.J. Williams and G.D. Farquhar. 2001. Carbon isotope discrimination by a sequence of *Eucalyptus* species along a sub-continental rainfall gradient in Australia. *Funct. Ecol.* 15:222–232.
- Miranda, H.S. 2002. The fire factor. *In* The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Eds. O. Paulo and R. Marquis. Colombia University Press, New York, pp 51–68.
- Miranda, A.C., H.S. Miranda, J. Lloyd et al. 1997. Fluxes of carbon, water and energy over Brazilian cerrado, an analysis using eddy covariance and stable isotopes. *Plant Cell Environ.* 20:315–328.
- Miranda, I.S., M.L. Absy and G.H. Rebêlo. 2003. Community structure of woody plants of Roraima savannahs, Brazil. *Plant Ecol.* 164:109–123.
- Misra, R. 1983. Indian savannas. *In* Tropical Savannas. Ecosystems of the World, Vol. 13. Ed. F. Bourlière. Elsevier, Amsterdam, pp 151–166.
- Moleele, N.M. and J.S. Perkins 1998. Encroaching woody plant species and boreholes: is cattle density the main driving factor in the Olifants Drift communal grazing lands, south-eastern Botswana? *J. Arid Environ.* 40:245–253.
- Montgomery, R.F. and G.P. Askew. 1983. Soils of tropical savannas. *In* Ecosystems of the World, Vol. 13. Tropical Savannas. Ed. F. Bourlière. Elsevier, Amsterdam, pp 63–78.
- Moreira, A.G. 2000. Effects of fire protection on savanna structure in Central Brazil. *J. Biogeogr.* 27:1021–1029.
- Mullenders, W. 1955. The phytogeographical elements and groups of the Kaniama District (High Lomani, Belgian Congo) and the analysis of the vegetation. *Webbia* 11:497–517.
- New, M., D. Lister, M. Hulme and I. Makin. 2002. A high-resolution data set of surface climate over global land areas. *Climate Res.* 21:1–25.
- O’Connor, T.G. and G.J. Bredenkamp. 1997. Grassland. *In* Vegetation of Southern Africa. Eds. R.M. Cowling, D.M. Richardson and S.M. Pierce. Cambridge University Press, Cambridge, pp 215–257.
- Orians, G.H. and O.T. Solbrig. 1977. A cost–income model of leaves and roots with special reference to arid and semi-arid areas. *Am. Nat.* 111:677–690.
- Osmond, C.B., O. Björkman and D.J. Anderson. 1980. Physiological processes in plant ecology: toward a synthesis with *Atriplex*. Springer-Verlag, Berlin, New York, 468 p.
- Palm, C.A., C.N. Gachengo, R.J.M. Delve, G. Cadich and K.E. Giller. 2001. Organic inputs for soil fertility management in tropical agroecosystems: application of an organic resources database. *Agric. Ecosys. Environ.* 83:27–42.

- Penridge, L.K. and J. Walker. 1988. The crown gap ratio (*C*) and cover percent: derivation and simulation study. *Aust. J. Ecol.* 13: 109–120.
- Pias, J. 1970. La Végétation du Tchad: ses rapports avec les sols: variations paléobotaniques au Quaternaire. *Travaux et documents de L'ORSTOM* 6. ORSTOM, Paris, 49 p.
- Pichi-Sermolli, R.E.G. 1957. Una carta geobotanica dell'Africa orientale (Eritrea, Etiopia, Somalia). *Webbia* 13:15–132.
- Pratt, D.J., P.J. Greenway and M.D. Gwynne. 1966. A classification of East African rangeland with an appendix of terminology. *J. Appl. Ecol.* 3:369–382.
- Pressland, A.J. 1975. Productivity and management of mulga in south-western Queensland in relation to tree structure and density. *Aust. J. Bot.* 23:965–976.
- Renvoize, S.A. 1984. The Grasses of Bahia. Royal Botanic Gardens, Kew, U.K., 301 p.
- Ribeiro, L.F. and M. Tabarelli. 2002. A structural gradient in cerrado vegetation in Brazil: changes in woody plant density, species richness, life history and plant composition. *J. Trop. Ecol.* 18: 775–794.
- Rizzini, C.T. 1963. A flora do cerrado. Análise florística das savannas centrais. *In* Simpósio Sobre o Cerrado. Ed. M.G. Ferri. University of São Paulo, Brazil, pp 125–177.
- Roscoe, R., P. Buurman, E.J. Velthorst and C.A. Vasconcelos. 2000. Soil organic matter dynamics in density and particle size fractions as revealed by the ¹³C/¹²C isotopic ratio in a Cerrado's oxisol. *Geoderma* 104:185–202.
- Ruggiero, P.G.C., M.A. Batalha, V.R. Pivello and S.T. Meirelles. 2002. Soil-vegetation relationships in cerrado (Brazilian savanna) and semi-deciduous forest, South-eastern Brazil. *Plant Ecol.* 160: 1–16.
- Rutherford, M.C. and M.D. Panagos. 1982. Seasonal woody plant shoot growth in *Burkea africana*–*Ochna pulchra* savanna. *S. Afr. J. Bot.* 1:104–106.
- Sanaiotti, T.M., L.A. Martinelli, R.L. Victoria, S.E. Trumbore and P.B. Carmargo 2000. Past vegetation changes in Amazon savannas determined using carbon isotopes of soil organic matter. *Biotropica* 34:2–16.
- San José, J.J. and M.R. Fariñas. 1983. Changes in tree density and species composition in a protected *Trachypogon* savanna, Venezuela. *Ecology* 64:447–453.
- Sankaran, M., N.P. Hanan, R.J. Scholes et al. 2005. Determinants of woody cover in African savannas. *Nature* 438:846–849.
- Sano, E.E, A.O. Barcellos and H.S. Bezerra. 2000. Assessing the spatial distribution of cultivated pastures in the Brazilian savanna. *Pastur. Tropic.* 22:2–15.
- Santos, A.J.B., G.T. da Silva, H.S. Miranda, A.C. Miranda and J. Lloyd. 2003. Effects of fire on surface carbon, energy and water vapour fluxes over campo sujo savanna in Central Brazil. *Funct. Ecol.* 17:711–719.
- Santos, A.J.B., C.A. Quesada, G.T. Silva, J.F. Maia, H.S. Miranda, A.C. Miranda and J. Lloyd. 2004. High rates of net ecosystem carbon assimilation by *Brachiara* pasture in the Brazilian Cerrado. *Global Change Biol.* 10:877–885.
- Santrucková, H., M.I. Bird and J. Lloyd. 2000. Microbial processes and carbon-isotope fractionation in tropical and temperate grassland soils. *Funct. Ecol.* 14:108–114.
- Sarmiento, G. 1983. The savannas of tropical America. *In* Tropical Savannas. Ecosystems of the World, Vol. 13. Ed. F. Boulière. Elsevier, Amsterdam, pp 245–288.
- Sarmiento, G. 1992. A conceptual model relating environmental factors and vegetation formations in the lowlands of tropical America. *In* Nature and Dynamics of Forest–Savanna Boundaries. Eds. P.A. Furley, J. Proctor and J.A. Ratter. Chapman & Hall, London, pp 583–601.
- Sarmiento, G. and M. Monasterio. 1983. Life-forms and phenology. *In* Tropical Savannas. Ecosystems of the World, Vol. 13. Ed. F. Boulière. Elsevier, Amsterdam, pp 79–108.
- Scanlan, J.C. and W.H. Burrows. 1990. Woody overstorey impact on herbaceous understorey in *Eucalyptus* spp. communities in central Queensland. *Aust. J. Ecol.* 15:191–197.
- Schacht, W.H., R.C.M. Mesquita, J.C. Malechek and R.D. Kirmse. 1989. Response of Caatinga vegetation to decreasing levels of canopy cover. *Pesq. Agropec. Bras.* 24:1421–1426.
- Scholes, R.J. 2003. Convex relationships in ecosystems containing mixtures of trees and grass. *Environ. Res. Econ.* 26:559–574.
- Scholes, R.J. and S.R. Archer. 1997. Tree–grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28:517–544.
- Scholes, R.J. and D.O. Hall. 1996. The carbon budget of tropical savannas, woodlands and grasslands. *In* Global Change: Effects on Coniferous Forests and Grasslands. Eds. A.I. Breymer, D.O. Hall, J.M. Melillo and G.I. Agren (SCOPE 56). Wiley, Chichester, U.K., pp 69–100.
- Scholes, R.J., P.G.H. Frost and Y. Tian. 2004. Canopy structure in savannas along a moisture gradient on Kalahari sands. *Global Change Biol.* 10:292–302.
- Schweizer, M., J. Fear and G. Cadich. 1999. Isotopic ¹³C fractionation during plant residue decomposition and its implications for soil organic matter studies. *Rapid. Comm. Mass Spec.* 13:1284–1290.
- Smith, J., J.V. Cadavid, M. Ayarza, J.L. Pimenta de Aguiar and R. Rosa. 1999. Land use change in soybean production systems in the Brazilian savanna: the role of policy and market conditions. *J. Sust. Agric.* 15:95–117.
- Sobey, D.G. 1978. *Anogeissus* groves on abandoned village sites in the Mole National Park, Ghana. *Biotropica* 10:87–99.
- Still, C.J., J.A. Berry, G.J. Collatz and R.S. DeFries. 2003. Global distribution of C₃ and C₄ vegetation: carbon cycle implications. *Global Biogeochem. Cycles* 17:1006.
- Stott, P. 1990. Stability and stress in the savanna forests of mainland South-East Asia. *J. Biogeogr.* 17:373–383.
- Taylor, C.J. 1952. The vegetation zones of the Gold Coast. *For. Dep. Bull.* 4:1–12.
- ter Steege, H. and G. Zondervan. 2000. A preliminary analysis of large-scale forest inventory data of the Guiana Shield. *In* Plant Diversity in Guyana. Tropenbos Series 18. Ed. H. ter Steege. Tropenbos Foundation, Wageningen, The Netherlands, pp 35–54.
- Thomas, A.S. 1942. A note on the distribution of *Chlorophora excelsa* in Uganda. *Emp. For. J.* 21:42–43.
- Trapnell, C.G. 1953. The soils, vegetation and agriculture of North-Eastern Rhodesia. 2nd Edn. Government Printer, Lusaka, Zambia, 146 p.
- Trapnell, C.G. and J.N. Clothier. 1957. The soils, vegetation and agricultural systems of North-Western Rhodesia. Government Printer, Lusaka, Zambia, 87 p.
- Trapnell, C.G. and I. Langdale-Brown. 1972. Natural vegetation. *In* East Africa: Its Peoples and Resources. Ed. W.T.W. Morgan. Oxford University Press, Oxford, pp 127–140.
- Trochain, J.-L. and J. Koechlin. 1958. Les pâturages naturels du sud de l'AEF. *Bull. Inst. Etudes Centr. Afr.* 15–16:59–83.
- van Langevelde, F., C.A.D.M. van de Vijver, L. Kumar et al. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84:337–350.

- Vesey-Fitzgerald, D.F. 1963. Central African grasslands. *J. Ecol.* 51:243–274.
- Victoria, R.L., F. Fernandes, L.A. Martinelli, M.D.C. Piccolo, P.B. Decamargo and S. Trumbore. 1995. Past vegetation changes in the Brazilian pantanal arboreal grassy savanna ecotone by using carbon isotopes in the soil organic-matter. *Global Change Biol.* 1:165–171.
- Walker, J. and M.S. Hopkins. 1990. Vegetation. *In* Australian Soil and Land Survey Field Handbook. Eds. R.C. McDonald, R.F. Isbell, J.G. Speight, J. Walker and M.S. Hopkins. Inkata Press, Melbourne, Sydney, pp 58–86.
- Walker, B.H. and J.L. Langridge. 1997. Predicting savanna vegetation structure on the basis of plant available moisture (PAM) and plant available nutrients (PAN): a case study from Australia. *J. Biogeogr.* 24:813–825.
- Walker, B.H. and J.-C. Menaut. 1988. Responses of savannas to stress and disturbance. No. 1. Research procedure and experimental design for savanna ecology and management. CSIRO, Melbourne, 122 p.
- Walker, J., P.F. Crapper and L.K. Penridge. 1988. The crown-gap ratio (*C*) and crown cover: the field study. *Aust. J. Ecol.* 13:101–108.
- Walter, H. 1971. Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh, 539 p.
- Wedin, D.A., L.L. Tieszen, B. Dewey and J. Pastor. 1995. Carbon isotope dynamics during grass decomposition and soil organic matter formation. *Ecology* 76:1383–1392.
- White, F. 1983. The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. UNESCO, Paris, 356 p.
- Wild, H. and A. Fernandes. 1967. Vegetation map of the flora Zambesiaca area. M.O. Collins, Salisbury, Rhodesia. With a 71 page Supplement.
- Williams, R.J., G.A. Duff, D.M. Bowman and G.D. Cook. 1996. Variations in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large scale climatic gradient in the Northern Territory, Australia. *J. Biogeogr.* 23: 747–756.
- Wilson, B.A., P.S. Brocklehurst, M.J. Clark and K.J.M. Dickinson. 1990. Vegetation of the Northern Territory, Australia. Conservation Commission of the Northern Territory, Tech. Rep. No. 49, Darwin, Australia, 222 p.
- Wynn, J., M.I. Bird and V.N.L. Wong. 2005. Rayleigh distillation and the depth profile of $^{13}\text{C}/^{12}\text{C}$ ratios of soil organic carbon from soils of disparate texture in Iron Range National Park, Far North Queensland, Australia. *Geochim. Cosmochim. Acta* 69: 1961–1973.
- Xu, B., P. Gong and R. Pu. 2003. Crown closure estimation of oak savannah in a dry season with Landsat TM imagery: comparison of various indices through correlation analysis. *Int. J. Rem. Sens.* 24:1811–1822.
- Yadava, P.S. 1990. Savannas of north-east India. *J. Biogeogr.* 17: 385–394.
- Yang, J. and S.D. Prince. 1997. A theoretical assessment of the relation between woody canopy cover and red reflectance. *Rem Sens. Environ.* 59:428–439.
- Yang, J. and S.D. Prince. 2000. Remote sensing of savanna vegetation changes in eastern Zambia 1972–1989. *Int. J. Rem. Sens.* 21: 301–322.