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 (NP) 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 NP in the Neotropics, whereas in African regions, a greater proportion of savanna NP is attributable to woody plants. The relative contribution of C4 grasses in Australian savannas is intermediate between those in the Neotropics and Africa. 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-
tem level against the heavier, naturally occurring 13CO2 molecule versus 12CO2 during photosynthesis (Farquhar et al. 1989, Miranda et al. 1997). The resulting overall difference in vegetation carbon isotopic composition allows use of 13C/12C 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 C4 grasses in savanna (as well as in other ecosystems) complicates the use of 13C/12C 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 C4 grasses is similar to that accompanying air-to-sea CO2 exchange (Lloyd and Farquhar 1994). By contrast, Δ for C3 plants is considerably greater, which allows spatial and temporal variations in atmospheric 13CO2/12CO2 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 C4 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 C4 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 13C/12C ratios were considered for 22 savanna sites in Australia, Brazil and Ghana.

The relative contribution of C4 grasses to the overall ecosystem productivity p4 can be determined as:

\[
p_4 = \frac{\delta_{\text{obs}} - \delta_3}{\delta_4 - \delta_3}, \quad p_3 = 1 - p_4
\]

where δobs is the estimated mean isotopic composition of the surface soil carbon pool (assumed here to be a natural integrator of ecosystem accumulated carbon), δ3 is the ecosystem mean value for C3 (tree) organic matter in the soil, δ4 is the ecosystem mean value for C4 (grass) organic matter and p3 represents the relative contribution of C3 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 p1 and p2 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°48′ S, 131°48′ E), Douglas Daly (13°54′ S, 131°18′ E), Willeroo (15°06′ S, 131°42′ E), Kidman Springs (16°6′ S, 131°54′ E) and Kalkaringi (17°18′ S, 131°48′ 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 Brasilia: 15°48′ S, 49°48′ W) and two near the main highway west of the town of Barreiras in the state of Bahia (12°06′ S, 45°06′ W). Around Brasilia, all sites are characterized by a high rainfall for the savanna region (about 1560 mm year−1) with the Barreiras sites being drier with a mean average rainfall of about 1110 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°36′ N, 1°48′ W), located in an area just north of the savanna–rain forest transition zone. Mean annual rainfall at Mole is around 1070 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° × 0.5° 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 ζ = αC, 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.
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 δ¹³C 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 middle 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 δ¹³C 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-CO₂ scale with an analytical uncertainty of 0.1‰.

Mean plant and soil isotopic compositions and relative contributions of C₃ and C₄

For each of the major vegetation components (C₃ trees, C₃ shrubs, C₄ grasses), the mean foliar δ¹³C was calculated as the arithmetic mean of all species sampled, with the C₄ grass Echinolaena 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 δ¹³C 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 (Trappnell and Langdale-Brown 1972), Chad (Pias 1970), Sudan (Harrison and Jackson 1958), Ghana (Taylor 1952) Central African Republic (Guigonis 1968), Nigeria (Keay 1953), Ethiopia and Somalia (Pichi-Sermolli 1957), Gabon and the Republic of the Congo (Congozavuile); Trochlain and Koechlin 1958), Democratic Republic of the Congo (Congozavuile); Duveigneaud 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 mapable 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° × 0.5° or 1.0° × 1.0° 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):

\[ N_p = 11.0 \Omega - 539 \]  

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

\[ \Omega = \sum_{i=1}^{12} d_i w_i; \quad w_i = \min\left[ \frac{R_i}{E_i}, 1 \right] \]  

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° × 0.5° 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 \( \zeta \) 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 \( \alpha \) was less variable across sites ranging from 0.34 (Brazil) to 0.60 (Australia). Ground shrub and herb \( \zeta \) 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. Wendll and Syagrus comosa (Mart.) Mart. were quite abundant; accounting for about 0.8 of the non-grass ground cover layer.

Grass \( \zeta \) 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 \( \zeta \) 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 (\( \zeta_{w} \) and \( \zeta_{g} \), 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, \( \zeta_{w} \) was greater than about 0.8, whereas \( \zeta_{w} \) was invariably low. For the Barreiras sites (circled in Figure 2), \( \zeta_{w} \) was low (< 0.2) despite \( \zeta_{g} \) 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 \( \zeta_{w} \) and \( \zeta_{g} \) were relatively high.

Carbon isotope measurements

Figures 3a and 3b summarize the foliar δ\(^{13}\)C measurements for non-grass and grass vegetation types, respectively. The δ\(^{13}\)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 δ\(^{13}\)C signatures could be divided into two populations; the chief one having a median δ\(^{13}\)C of ~13.2‰, showing
Table 1. Soil texture and vegetation cover characteristics of the study sites. Terminology follows local sources, namely, Camahan (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 \( (\alpha) \) = the mean proportion of light intercepted by individual canopy crowns; fractional foliar (projected) cover \( (\zeta) \) 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 \( \zeta = \alpha C \).

<table>
<thead>
<tr>
<th>Site</th>
<th>Soil texture</th>
<th>Vegetation cover type</th>
<th>( C )</th>
<th>( \alpha )</th>
<th>Tree + shrub ( \zeta )</th>
<th>Ground shrub + herb ( \zeta )</th>
<th>Total non-grass ( \zeta )</th>
<th>Grass ( \zeta )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Australia</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Annabaroo</td>
<td>Loam</td>
<td>Open forest</td>
<td>0.75</td>
<td>0.45</td>
<td>0.34</td>
<td>0.01</td>
<td>0.35</td>
<td>0.75</td>
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<td>0.68</td>
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<td>0.02</td>
<td>0.39</td>
<td>0.50</td>
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<td>Loam</td>
<td>Low woodland</td>
<td>0.52</td>
<td>0.55</td>
<td>0.29</td>
<td>0.05</td>
<td>0.34</td>
<td>0.67</td>
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<tr>
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<td>Low open forest</td>
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<td>0.30</td>
<td>0.03</td>
<td>0.37</td>
<td>0.52</td>
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<td>Clay</td>
<td>Low open woodland</td>
<td>0.02</td>
<td>0.60</td>
<td>0.01</td>
<td>0.00</td>
<td>0.01</td>
<td>0.95</td>
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<td>0.01</td>
<td>0.01</td>
<td>0.02</td>
<td>0.95</td>
</tr>
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<td>Loam</td>
<td>Low open woodland</td>
<td>0.04</td>
<td>0.50</td>
<td>0.02</td>
<td>0.01</td>
<td>0.03</td>
<td>0.63</td>
</tr>
<tr>
<td>Kidman Springs</td>
<td>Sand</td>
<td>Low woodland</td>
<td>0.37</td>
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<td>0.20</td>
<td>0.00</td>
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<td>Clay</td>
<td>Low open woodland</td>
<td>0.09</td>
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<td>0.04</td>
<td>0.00</td>
<td>0.04</td>
<td>0.63</td>
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<td>Low woodland</td>
<td>0.51</td>
<td>0.45</td>
<td>0.23</td>
<td>0.04</td>
<td>0.27</td>
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<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Barreiras</td>
<td>Sand</td>
<td>Cerrado sensu strictu (aberta)</td>
<td>0.24</td>
<td>0.45</td>
<td>0.11</td>
<td>0.09</td>
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<td>0.10</td>
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<td>0.29</td>
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<td>Rocky, sand</td>
<td>Campo limpo</td>
<td>0.00</td>
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<td>0.00</td>
<td>0.00</td>
<td>0.85</td>
</tr>
<tr>
<td>Brasilia</td>
<td>Loam</td>
<td>Campo sujo</td>
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<td>0.34</td>
<td>0.02</td>
<td>0.04</td>
<td>0.05</td>
<td>0.85</td>
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<td>Loam</td>
<td>Cerradão</td>
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<td>Campo cerrado</td>
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<tr>
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<td>Loam</td>
<td>Cerrado sensu strictu</td>
<td>0.56</td>
<td>0.40</td>
<td>0.25</td>
<td>0.09</td>
<td>0.35</td>
<td>0.34</td>
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<tr>
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<td>Loam</td>
<td>Cerrado denso</td>
<td>0.81</td>
<td>0.39</td>
<td>0.31</td>
<td>0.12</td>
<td>0.43</td>
<td>0.21</td>
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<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Mole</td>
<td>Loam</td>
<td>Grassland</td>
<td>0.01</td>
<td>0.45</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.70</td>
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<td>Sand</td>
<td>Guinea savanna</td>
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<td>0.47</td>
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<td>0.11</td>
<td>0.36</td>
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<tr>
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<td>Sand</td>
<td>Open Guinea savanna</td>
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<td>0.54</td>
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<td>0.22</td>
<td>0.59</td>
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<tr>
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<td>Loam</td>
<td>Tall moist grassland</td>
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<td>0.00</td>
<td>0.00</td>
<td>0.02</td>
<td>0.02</td>
<td>0.85</td>
</tr>
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</table>
the expected dominance of C4 grasses in these subtropical environments (Collatz et al. 1998). In addition, Brazilian plots showed the signature of C3 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 C3 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 \( \phi \):

\[
\phi = \frac{\zeta_w}{\zeta_w + \zeta_g}
\]

(3)

Figure 4 shows variations in C3 and C4 plant foliar \( \delta^{13}C \) as a function of \( \phi \). For the C3 plants, there was a tendency for \( \delta^{13}C \) to become more negative as \( \phi \) 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 C4 grasses. There was no significant correlation between mean annual precipitation and foliar \( \delta^{13}C \) for either C3 or C4 plants (\( P = 0.5 \)).

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:

\[
\delta_{obs} = \delta_3 + \psi + \phi(\delta_3 - \delta_4) + \beta\zeta_w + \gamma E + \alpha_p
\]

(4)

where \( \psi \) and \( \beta \) are fixed effects defining the offsets implicit in Figures 5 and 6, respectively, \( E \) is a variable indicating the presence or absence of \( E. \text{inflexa} \) and \( \alpha_p \) is a random plot effect representing the residual error. Fitted values (± SE) were \( \psi = -1.95 \pm 0.43 \% e \), \( \beta = 5.24 \pm 3.80 \% e \), and \( \gamma = -1.45 \pm 1.25 \% e \). 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:

\[
p_3 = \frac{\delta_{obs} - \delta_4}{\delta_3 - \delta_4}
\]

(5a)
Likewise a rearrangement of Equation 4 less the random error term \(a_i\) gives:

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

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 \(\delta_{obs} = \delta_4 + \psi\). Thus, for pure \(C_4\) grasslands, mean soil \(\delta^{13}C\) 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 \(\beta\) is significant, suggesting that there is an opposing enrichment of \(\delta_{obs}\) dependent on the absolute magnitude of the woody canopy cover. This is in addition to the influence of \(\zeta_w\) on \(\phi\) (Equation 3). (3) Where present, the \(C_3\) grass \(E.\ inflexa\) reduces soil \(\delta^{13}C\) 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) \(\phi\) is numerically equivalent to the (theoretical) \(p_3\). This is because both terms have the same slope, namely \((\delta_{obs} - \delta_4)/(\delta_3 - \delta_4)\). Thus, referring to Equation 3, after taking account of points 1–3 above, the relative proportions in a savanna ecosystem of total foliar...
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 \( \phi \) 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 \( \zeta \) of grasses and trees, as most savanna vegetation classifications measure the abundance of trees in terms of \( \zeta_w \) 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 \( \zeta_w \) 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 \( \zeta_w \), 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 \( \zeta_w > 0.4 \) 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 arbórea densa (dense woodland), arbórea aberta (open woodland), parque (parkland) and gramíneo-lenhoasa (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.

**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 \( \zeta_w \) 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 \( p_1 \approx 1.0, 0.95, 0.85, 0.65 \) and 0.25. Estimates based on these values of the proportions of \( N_p \) contributed by \( C_4 \) grasses in each region (\( p_1 \)) are shown in the two rightmost columns of Table 2. Considering only the three savanna types, \( p_1 \) varies from 0.34 in CnA to 0.84 in NhN with an overall \( N_p \)-weighted mean of 0.59. Overall regional \( p_1 \) (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-
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 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° × 1.0° (about 100 × 100 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,
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 cerradão 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...
of the sites studied, though being in protected areas, most Brasilia 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, \( \phi \), there was an effectively linear relationship between soil \( \delta^{13}C \) and \( \phi \) (Figure 5), which according to our model, suggests a linear relationship between the proportion of ecosystem productivity contributed by trees and \( \phi \). This relationship was only slightly affected by the occasional presence of the C3 grass *Echinolaena inflexa* and suggests that the relative contributions of grasses and trees to the overall productivity of savanna ecosystems may be estimated from \( \phi \). 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 C3 individuals per hectare and the \( \delta^{13}C \) 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 Brasilia), there was no significant correlation between foliar \( \delta^{13}C \) 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 \( \delta^{13}C \) (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 \( \delta^{13}C \) to become more negative as \( \phi \) 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 \( \delta^{13}C \)), 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 \( \delta^{13}C \) of the surface soil carbon pool may not accurately reflect the \( \delta^{13}C \) of input vegetation, with pure grassland surface soil \( \delta^{13}C \) being about 2‰ less than that of overlying vegetation. Such discrepancies have been observed before with the depletion of soil \( \delta^{13}C \) 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 \( \zeta_w \). At least in part, this could be associated with the presence in the soil of carbon derived from decomposed woody plant material; the \( \delta^{13}C \) 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 \( \delta^{13}C \) with soil carbon density across all sites (burned and unburned), again suggesting that C3 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 \( \delta^{13}C \) 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 \( \delta^{13}C \) associated with charcoal production resulting from burning for some C3 grasses, and this may contribute to soil \( \delta^{13}C \) depletion compared with the overlying plant \( \delta^{13}C \) for C4 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 \( \phi \), a ready means of estimating the relative contributions of trees and grasses to savanna ecosystem productivity. Moreover, although \( \phi \) requires the determination of both \( \zeta_w \) and \( \zeta_g \), Figure 8 shows that \( \zeta_w \) itself is a reasonable predictor, because the relationship between \( \zeta_w \) and \( \zeta_g \) is not completely random (Figure 2). Figure 8 thus provides a means to estimate \( \phi \) on the basis of \( \zeta_w \) which is closely related to \( C \). This is because individual tree or shrub \( \alpha \) is quite conservative at about 0.5 for savanna trees (Table 1; Gillison 1994).

When estimated at the continental scale by simply assigning the C4 grass fraction of ecosystem productivity to assigned classes of \( C \), substantial regional variation was predicted. The most striking difference is the low savanna \( p_L \) for African regions as opposed to Australia or the Neotropics (Table 2). Although the high savanna \( p_L \) for both Australia and Northern hemisphere Neotropics can be attributed mainly to a proportionally low amount of woody vegetation being present, the relatively low savanna \( p_L \) for Africa are due to both substantial amounts of open woodland and woodland being present and to these woody 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 \( p_L \) 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 \( p_L \) 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 C4 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, Piase 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, \( \text{C}_4 \) 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 Mojos 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, Cavleler 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 cerradão types tend to occur only on unusually fertile soils (Furley and Ratter 1988, Moriera 2000, Chauis 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 observed 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 (Scholos 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 \( \text{C}_4 \) grass vegetation layer compared with the \( \text{C}_3 \) woody component. Under similar climatic conditions, Santos et al. (2003) estimated for the grassy campo sujo cerrado type a maximum mean \( G_f \) 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 \( \text{C}_4 \) 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\(_4\) 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 (Moleele and Perkins 1998, Henry et al. 2002) or increased atmospheric \( \text{CO}_2 \) 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\(_3\) 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, Acock 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 \( -24.5 \%_{\text{ec}} \); 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, Backéus 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 \( \phi \) 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 (Malaise 1978), better estimates of the magnitude of rates of change of C, \( \phi \) and \( p_4 \) at regional, continental and global scales should become possible.

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