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Tropical savannas: Biomass, plant ecology, and the role of fire and soil on vegetation

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Abstract
Four major themes can be identified over the period 2008–2009: (1) the increasing use, sophistication and resolution of remote sensing techniques and the application of these methods to assessment of biomass, C-balance and biosphere-atmosphere interactions; (2) continued interest in dynamic change processes affecting individual species and plant communities, and the changing proportions of tree, shrub and herbaceous components; (3) the nature, impact and management of fire; and (4) increasing awareness of the importance of soils and soil moisture in shaping the nature and distribution of vegetation, particularly at local scales.

Keywords
biomass, carbon, fire, plant ecology, savannas, soils

I Biomass and carbon balance

The mapping of savanna distributions has been greatly facilitated by advances in remote sensing. This has utilized both optical and microwave sensors, either airborne or satellite-mounted, and offers a rapid overview that is particularly useful at a broad scale. However, at a field scale, although inexpensive and repeated satellite imaging has improved in resolution, it is still limited in detecting fine patterns within savanna vegetation. Some forms of remote sensing, such as the submetre resolution IKONOS and QUICKBIRD satellite sensors, allow individual trees to be recognized; these data are increasingly and freely available via Google earth although the raw data is still costly. So, despite the high resolution permitting analysis of canopy cover and structure, the scenes are currently too expensive for large-scale or regional studies on account of the volume of data generated and the amount of processing required. Discriminating between subtypes of savanna vegetation, even simply looking at structural differences, has proved a taxing undertaking, as demonstrated by Hill *et al.* (2008) in eucalypt savannas. They echo the frequently expressed exasperation of fieldworkers when they say that there is a pressing need to intensify studies calibrating satellite with field measurements, especially given the increasing accuracy and practical usefulness of GPS. In addition to spatial measurement, it has long been clear that temporal surveys at varied time intervals are required, particularly in biomes that are highly dynamic.

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Partly as a result of concerns over climate change and the role of the carbon cycle, a considerable emphasis has been placed recently on biomass and carbon surveys. There have been a number of important large-scale surveys, such as project CarboAfrica (Merbold *et al*., 2009), examining net productivity and emissions from forest degradation and the resulting C-balance. Mitchard *et al*. (2009) used satellite synthetic aperture radar (SAR) to predict above-ground biomass and found a consistent relationship between biomass and backscatter at several widely separated African sites. In sub-Saharan Africa, Bombelli *et al*. (2009) present a summary of current data and underline the importance of savannas in view of their extent, fire regimes and strong interannual NEP variability, as well as their high degree of unpredictability in the overall C-budget. The importance of burning for C-accounting has led to much research on fire detection and impact studies. For example, Roberts *et al*. (2009) used visible and infrared imagers on the Meteosat-8 satellite to assess fires and radiative power over Africa; Vermote *et al*. (2009) used MODIS observations to estimate radiative energy from burning; and Jarlan *et al*. (2008) describe analysis of leaf area indices (LAI) from imaging spectroradiometer products in Mali. The estimation of C-stocks at a landscape scale in Australia using SAR was outlined by Collins *et al*. (2009) and from hyperspectral and multispectral imagery by Guerschman *et al*. (2009). Published allometric data for the principal trees (*Eucalyptus miniata* and *E. tetrodontata*) were used to convert basal area measurements to estimates of above-ground biomass, which were then combined with below-ground biomass data to assess C-stocks. Airborne SAR was also used in a detailed, very high-resolution study in Belize but was not found to give consistent results at this resolution for non-continuous woodland (Viergever *et al*., 2008).

Subsurface C-stocks are much more difficult to estimate, although attempts have been made to relate vegetation data (such as LAI) from field and related sensing techniques to soil C (eg, Wang *et al*., 2009a; 2009c; 2009d). It is also well known that radar data includes information about soil properties and moisture and, although interpreting these data remains experimental, some satellite scatterometer data is promising (Zribi *et al*., 2009). At present there is no real alternative to detailed field study, as shown in the work of Wang and colleagues (Wang *et al*., 2009b) over the Kalahari Transect through investigation of organic C and stable isotope C, or Williams *et al*. (2008) investigating carbon sequestration and biodiversity in a miombo savanna woodland in Mozambique. Maia *et al*. (2009) assessed soil carbon sequestration in western Brazil – a theme taken up in a recent book edited by't Mannetje *et al*. (2008).

II Plants and plant communities

1 Overview

While recent research on savanna plant ecology has extended our understanding of species composition and functioning, it has at the same time increasingly revealed its complexity and dynamic nature. At a broad scale, Sankaran *et al*. (2008) have studied different driver variables regulating the woody cover across African savannas. The variables included mean annual precipitation (MAP), selected soil properties, fire regimes and herbivory across 161 sites. All of these variables were found to be significant albeit at different levels of importance, and together they explained over 70% of the variance. As might be expected, MAP was the most important predictor of woody cover, especially between 200 and 700 mm y^{-1}, but there were complex other interconnections – for instance, between total soil P, clay content and soil N-availability. These intricate relationships suggest that future dynamic change is likely to have interacting and possibly, at times, opposing influences on the tree-grass balance. Controls on above-ground NPP have also been discussed at an intercontinental scale by Buis *et al*. (2009). The respective contributions of woody and herbaceous vegetation to savanna productivity were reported by Lloyd *et al*. (2008) from a study of 22 savannas in Australia, Brazil and Ghana. It was estimated that nearly 60% of the NPP of tropical savannas is attributable to C-4 grasses but that the proportion varies considerably within and between regions. In eastern and southern Africa, the work by Chamaille-Jammes and Fritz (2009) shows that precipitation is less effective in explaining distributions at interannual time periods where limitations other than water constrain plant growth. At a regional scale, Reed *et al*. (2009) attempted to generate a structural vegetation map of the Serengeti and tested the influences of different landscape factors on spatial heterogeneity. Once again there were significant relationships between average rainfall and vegetation diversity (using Simpson's index), but soil moisture, related to a topographic index, was also influential. Their results agree with earlier work showing that the woody cover in savannas, with less than 650 mm y^{-1}, is bounded by the MAP. In addition to the amount and distribution of precipitation, the nutrient content may be extremely significant in influencing plant growth especially in dry savanna sites (Galy-Lacaux *et al*., 2009). The influence of topography and drainage in the Kruger National Park is also shown to affect plant community distribution through links with stream orders (Khomo and Rogers, 2009).

2 Floristic composition

A cornerstone of savanna ecology is sound taxonomy. There have been several useful floristic papers over the review period but they illustrate the problem of comparability since they often use different field and survey techniques. Much recent work has been focused on the Brazilian *cerrados*, such as de Carvalho and Martins (2009), examining tree and shrub communities (20 x 20 m plots) in three disjoint but adjacent regions of Minas Gerais. They came up with 170 species with 103 genera and 46 families, and found that much of the differentiation resulted from differences in soil properties. Further studies by Carvalho *et al*. (in Goias; 2008) generated 79 species and 33 families in 10 20 x 20 m plots, giving one of the richest woody floras in the *cerrado* domain, and in the UEG campus Carvalho and Marques-Alves (2008) studied 30 100 m^2 plots resulting in 46 species over 28 genera in 20 families. Much of the *cerrado* exists today in fragments and studies of these remnants prove very useful for prioritizing conservation (eg, Cabacinha and de Castro, 2009; Carvalho *et al*., 2009). Examples include the study by de Medeiros *et al*. (2008) in Maranhão using plots of 20 x 50 m giving 53 species over 45 genera in 25 families, the work of H.G. Silva *et al*. (2008) in the same state using Point Centred Quarter methods, and Munhoz and Felfili (2008) employing transect-intersect methods to study moist grasslands in central Brazil. These types of study normally quote diversity indices and importance values and can therefore be used to some extent comparatively. Wet grasslands are an important component of *cerrado* landscapes with superficial water tables and hydromorphic soils, described over a year-long study by Cianciarusco and Batalha (2008). The species richness and distribution of semi-arid *caatinga* vegetation of NE Brazil, which is arguably within the woody end of savanna woodland, is described by Santos *et al*. (2008). This research catalogued 225 species from 43 families over 20 phytosociological surveys covering some 36 years. The floristics of a seasonal forest at the forest-savanna ecotone is examined by Pinheiro and Monteiro (2008) in São Paulo state, finding 264 arboreal-shrubby species belonging to 58 families.

3 Structure

Several papers deal with tree, shrub and grass communities. For example, Farruggia (2008) describes the flora of a neotropical savanna near its northern limit in Belize, dominated by graminoids but exhibiting clusters of trees in varying topographic and drainage locations. Hyperseasonal *cerrados* are typically dominated by grasses, and I.A. Silva and Batalha (2008) found reduced species diversity as a result of prolonged waterlogging, while Cianciaruso and Batalha (2009) portrayed distinct species differences between the hyperseasonal and less water-affected seasonal savanna. The scale problem in identifying and explaining grass species distribution is illustrated in northern Australia by Scott *et al*. (2009), where differences in soil moisture are important. The additional problem of invasive grasses crops up all over the savannas, an example being the inhibiting effect of *Melinis minutiflora* on the dynamics of woody plants in Brazil (Hoffman and Haridasan, 2008). The phylogeny of C-4 grasses has been examined by Edwards and Still (2008) in Hawaii, considering physiological attributes of C-4 photosynthesis as well as their evolutionary history. The evolution of C-4 grasslands in Madagascar has been explored by Bond *et al*. (2008) and provides an interesting test case for diversification, given the differences between Madagascan and adjacent African floras. The photosynthetic properties of C-4 plants were examined by Mantlana *et al*. (2008b) in a savanna-wetland mosaic in Botswana. They looked at photosynthetic rates and photosynthesis leaf nutrient relationships, which highlighted the critical availability of phosphorus. The problem of what limits trees in C-4 grasslands is addressed by Bond (2008) in a discussion of the uncertainty in predicting the future of these ecosystems, given the complexity of interacting determinants and the level of detail required to understand processes affecting species distributions. This theme is taken up in a different approach by van der Waal *et al*. (2009), examining how woody seedlings (*Colophospermum mopane*) coexist with herbaceous plants and respond to changes in nutrient availability and water. Bloesch (2008) looked at thicket clumps distributed within the Kagera savanna of East Africa, finding that the thickets have a distinct floristic and structural composition relating in broad terms to the topography and drainage (affecting fire regimes and termite activity). Co-occurrence of tree species in savanna woodland in the *cerrados* was investigated by Silva and Batalha (2009), who tested for phylogenetic or functional structuring. Bieras and Sajo (2009) examined leaf structures of *cerrado* woody plants, and Rossatto and Kolb (2009) show how some savanna trees adapt by producing different dry and wet season leaf types. Tree recruitment and mortality in the Kakadu, in monsoonal northern Australia, was the subject of study by Prior *et al*. (2009), who identified feedback processes that may help to confer long-term stability to the tree components, while Lehmann *et al*. (2009) investigated spatiotemporal variations in the tree cover in the same region, focusing on rainfall, fire frequency and interspecies competition.

A further complication is introduced when considering the influence of herbivores on the structure and composition of tree cover (Riginos and Grace, 2008; Asner *et al*. 2009). The interactions between animals and plants cannot be covered in detail here, but the impact of large herbivores has been known for many years, particularly the influence of elephant populations (Guldemond and van Aarde, 2008). As instances of recent work in the Serengeti, Holdo *et al*. (2009) demonstrate the interaction between fire and browsing/grazing on fuel loads, Sharam *et al*. (2009) show how *Acacia polyacantha* can be introduced in riparian grasslands and shelter incipient tree growth partly by providing a barrier against grazers, and Dobson (2009) discusses the dynamics of the ecosystem from food-web theories.

4 Physiological research

The water economy of savanna plants has long been a source of interest. Goldstein *et al*.

(2008) examined six theories influencing the distinctive anatomical characteristics of neotropical trees in the *cerrado*. They found considerable differences between and within deciduous and evergreen trees and examined the utilization of soil water from different depths, stomatal and functional groups. Seasonal patterns of soil water utilization and environmental controls of transpiration were also examined in the *cerrados* by Bucci *et al*. (2008) across a topographic gradient from *cerradão* (woody savanna) to *campo sujo* (open savanna with scattered shrubs). Stem and leaf hydraulics in adjacent savanna and forest congeneric species pairs were studied by Hao *et al*. (2008), where the success of savanna species was shown to be related to their ability to cope with dry conditions, determined more by leaf than stem hydraulic characteristics and strongly related to phylogeny. Hydraulic lift in neotropical savanna trees was studied by Scholz *et al*. (2008) using measurements of sap flow and stable isotope labelling techniques. Zhang *et al*. (2009) investigated hydraulic architecture and carbon allocation of a dominant neotropical savanna species (*Sclerolobium paniculatum*) and compared taller with smaller individuals to assess mortality. In Botswana, Veenendaal *et al*. (2008) investigated differences in morphological and physiological attributes of the mopane (*Colophospermum mopane*), examining short and tall forms of growth and their relationship to soil water. They showed that growth differences could be related to rooting depth and tree density, and stomatal water regulation was also shown to be distinct. The interactions between grasses and deeply rooted trees and shrubs on the energy and water fluxes of savannas are not well understood and Giambelluca *et al*. (2009) provide data for adjacent *cerrado* sites of different woody density. As might be expected, evapotranspiration reached a minimum at both sites at the end of the dry season, and energy partitioning was strongly affected by differences in LAI. It is suggested that LAI can be used to clarify much of the observed temporal and spatial evapotranspiration variability and to explain differences in woody density. da Rocha *et al*. (2009) looked at seasonal patterns of water vapour and heat flux across the forest-savanna transition with evidence from the network of flux towers of the Large-Scale Biosphere-Atmosphere experiment in Amazonia, and demonstrated how controls over evapotranspiration changed across the gradient with soil moisture playing a more important role in the savanna sites.

5 Models of dynamic change

The savanna biome ranges from grassland to near-continuous cover of trees and the tree-grass ratio is often highly changeable, giving rise to numerous theories explaining trends. Essentially savannas are continuously unstable, shaped by disturbance factors such as irregularity of rainfall, fire and herbivory. The importance of each of these determining factors can change rapidly both spatially and temporally. Furthermore, phases of savanna vegetation may persist for long periods and may then change rapidly to a new form. Such resilience and threshold ideas have been explored in the Kruger National Park by Gillson and Ekblom (2009), using pollen records and nitrogen ($\partial^{15}N$) and fire (charcoal) to understand these transitions. The dynamic nature of savannas has given rise to several groups of theories and models of development from niche separation to ideas on demographic changes, species recruitment and patch dynamics. Many savannas appear to follow a pattern of succession, or even a cyclical pattern, before the sequence is interrupted by disturbance. Recent contributions to this debate include: Meyer *et al*. (2009), assessing the coexistence of trees and favouring patch dynamics theory; Nicholas *et al*. (2009), who demonstrated that sharp boundaries between (mulga) shrubland and (spinifex) grasslands could evolve across diffuse environmental gradients by soil-fire-vegetation feedback loops;

and Riginos *et al*. (2009), who looked at the impact of individual trees and tree cover at a landscape scale. As indicated by Caylor *et al*. (2009), the difficult task of coupling ecological and hydrological spatiotemporal models provides a powerful way of developing more accurate hypotheses of vegetation patterns and processes. Monitoring change over time at an individual tree scale requires long-term observations that have not been widely available, although historical archives of aerial photography can help to locate patterns of plant invasion (Robinson *et al*., 2008). Finally Laris (2008) reminds us that anthropological disturbance has not been well quantified and should be considered in any general hypothesis of grass-tree coexistence. While there have been no new theories that have achieved general acceptance over the past two years, patch dynamics models currently appear to be predominantly in favour.

The highly dynamic forest-savanna boundary continues to attract much attention, supporting the contention that, given a chance in the face of human pressure and fire, the forests are currently expanding as a result of climatic change. One of the clearest transitions is that between gallery forest and grassy or woody savanna subsystems (Silva *et al*., 2008). Isotopic analysis of organic carbon in the soil profile with other plant and soil indicators appears to confirm the known expansion of forest margins into the savanna, and there is some evidence to show that this occurred at least 3000 to 4000 BP based on C-14 analyis. Stable isotope analysis and spectroscopy were employed by Awiti *et al*. (2008) in Kenya, with an emphasis on the changes that occur as forest is converted to cropland. Differences in growth patterns between congeneric forest and savanna trees (Rosatto *et al*., 2009) illustrate the different functional types associated with each environment. This was evident from diameter growth rates, specific leaf area, photosynthesis and various phenological attributes. It is argued that the higher growth rates and denser crowns of the forest enhance shading and promote changes in equilibrium. In central Cameroon, the forest-savanna boundary has been studied over a period from 1986 to 2006 over a 5400 km^2 area using high-resolution images. Most of the area showed a positive increase in forest although there was a small area of decrease (possibly deforestation). The cause is attributed to a reduction in fire damage as the rainfall figures have remained constant over the study period, but increasing atmospheric CO_2 may be altering the competitive balance. In reverse, the impact of human disturbance expanding the savannas at the expense of forest communities has been documented by Ekblom (2008) in Madagascar from pollen and archaeological evidence over the past 600 years. Isolated forest fragments are considered to be at risk in view of their sensitivity to climate change. Deliberate or accidental fires reverse the natural trends and this is shown at the Amazon forest edge by Balch *et al*. (2009), who demonstrate the fire-initiated grass invasions. Hoffman *et al*. (2009) illustrate the role of fire in determining the boundary and analyse the incursions of fire into the forest and the ability of forest trees to withstand burning. Some indicator trees may also indicate the effects of transitions over the past. For instance Duputie *et al*. (2009) focus on manioc (*Manihot esculenta*) and, by using microsatellite locations, they investigated the population genetics of accessions of *M. esculenta* in French Guiana, where the taxon tends to be restricted to coastal savannas or rocky outcrops within the forest. The coastal populations were shown to be strongly differentiated from the inselberg groups and are highly differentiated, whereas the isolated inselberg populations are strikingly homogeneous, supporting the view that they were connected until recently.

III Savannas and fire

1 Overview

Regular or periodic burns characterize savanna landscapes and there is a voluminous literature ranging from the nature of the fires to impacts on vegetation and management or fire policy. There have also been a number of significant texts dealing with savanna fires over the past decades – the most recent, in the period under review, being the compilation edited by Cochrane (2009). This includes broad regional summaries, such as the analysis by Miranda *et al*. (2009) in the *cerrados*, and Gill *et al*. (2009) who assessed fire effects in Australian landscapes, with a gamut of fire regimes (fire intensities, between-fire intervals and timing). A wide-ranging Indian perspective is offered by Vadrevu *et al*. (2008) using a scanning radiometer to assess spatial patterns of fires, and in Namibia MODIS sensors were utilized to predict fire occurrence (Siljander, 2009).

Climatic controls underpin understanding fire regimes as illustrated from a global perspective by van der Werf *et al*. (2008) or Archibald (2008) in Africa, and Pekin *et al*. (2009) in Australia. The long-term potential for fire is treated by Cardoso *et al*. (2008) in a vegetation model developed in Brazil, and long-term experiments on the effects of fire frequency with specific reference to Zimbabwe were investigated by Furley *et al*. (2008). Relationships between fire history, vegetation structure and floristics are assessed in *Banksia* woodlands of SW Australia by Fisher *et al*. (2009), highlighting the influence of burning on plant invasions. The size, frequency and timing of fires clearly affects their impact and these issues are illustrated in two examples from Australia: the work by Yates *et al*. (2008), showing the effect of large fires on flora and fauna; and Elliott *et al*. (2009), also in northern savannas, examining fire frequency in relation to distance from settlements. These and other studies have yielded models describing vegetation, fire and feedbacks (Beckage *et al*., 2009), and feedback models from fire disturbance plus empirical models dealing with the spread and intensity of fires (Higgins *et al*., 2008).

2 Effects of fire on plants and vegetation

The frequency of burning is of considerable concern. In the savannas of the Venezuelan Guyana, Bilbao *et al*. (2009) demonstrate how fires in the Canaima National Park affect not only the wooded areas, transforming them into treeless savannas, but also the hydroelectrical industry and other stakeholders in the Park including the Pemon indigenous communities. A similar story is recounted in Sumatra, where Chokkalingam *et al*. (2009) show some of the effects of fire on the communities utilizing the wetland grasslands, and burn-scar patterns in wetlands of insular SE Asia have been examined by Miettinen and Liew (2009) using high-resolution SPOT-4 images. As savannas are continuously reduced in extent, so the survival of fragments becomes a matter of concern as illustrated in Bahia by Roitman *et al*. (2008), investigating the structural and floristic changes in a *cerrado* reserve surrounded by pine and eucalypt plantations.

Individual species and genera frequently respond differently to fire. At the arid end of the spectrum in the southern Kalahari, for example, Seymour and Huyser (2008) describe investigations of fire on the demography of camelthorn (*Acacia erioloba*), showing the effect of large trees on the potential flammable organic material. A different acacia (*A. sieberiana*) was studied in Uganda's Kidepo National Park by Aleper *et al*. (2008), looking at how this species responds to repeated burning and the importance of burn timing. Seedling dynamics are clearly significant in the survival and recuperation of species after fire, as shown by Dezzeo *et al*. (2008) in southern Venezuela, and by Ikeda *et al*. (2008), who investigated seedbanks following burning and cultivation in a previous *cerrado*-savanna. A widespread *cerrado* tree (*Zanthoxylum rhoifolium*) has been studied by I.A. Silva *et al*. (2009), where resprouting appears to be more important than seedling survival after severe fires; however, de Medeiros and Miranda (2008) could find no relationship between sprouting capacity and species survival at the IBGE ecological reserve, close to Brasília. Resprouting has also been studied in the Lamto reserve, Cote d'Ivoire (Gignoux *et al.*, 2009), indicating that this survival strategy can be heavily constrained by the frequency of disturbance. Pine ecosystems are characteristic of many savannas and have a close relationship to fire incidence and intensity. Neotropical examples are given in Myers (2009), who points out that prescribed fires are not considered by people in these areas as little is understood in detail as to the exact relationship between the plant communities and burning. Analogous insights are offered by Williams (2009) for eucalypt woody savannas across Australia, where seedling recruitment may hold the answer to the survival of species. Sapling survival is the subject of studies by Wigley *et al.* (2009) in an *Acacia karroo*, positing that stored carbon promotes faster stem growth to a height where saplings can escape fire injury, and Schutz *et al.* (2009) analysed the carbon allocation and biomass partitioning of *A. karroo* emphasizing their contribution to species survival against repeated burning and topkill.

It is known that there are multiple aspects to burning and multiple responses in the vegetation. Multiple disturbances on herbaceous plant communities have, for example, been examined by Savadogo *et al.* (2008; 2009) in a Sudanian type of savanna woodland in Burkina Faso. They report on a long-term factorial experiment showing that disturbance regimes affected species abundances over time and were site-specific. Relatively few empirical studies of perennial grasslands have been undertaken, as Zimmermann *et al.* (2008) elaborate, and most of these isolate one or two factors. In a discussion of several contributing factors, fire was found positively to affect seedling emergence, growth flowering and survival, and periodic fires enable the recruitment of new individuals into the population. In the Cape York Peninsula of Australia, Crowley *et al.* (2009) illustrate the role of 'storm burning' and the effect of fires on woody species such as *Melaleuca viridiflora*, paralleled by an invasion of grass species. Fire appears to hold the balance between the structural and compositional components of the savanna. The combined influence of fire and herbivory is particularly noticeable on vegetation structure (with less information available on compositional changes), as shown by: Klop and Prins (2008), studying fire and ungulate diversity in West Africa; Waldram *et al.* (2008), investigating the white rhino in South Africa, described as 'an influential ecosystem engineer'; and Moncrieff *et al.* (2008), examining the synergistic effects of fire and elephants in the Kruger National Park. Levick *et al.* (2009) used airborne remote sensing to map a herbivore-fire exclusion experiment in the same Park, and they highlight the need for information of this nature in conservation and management.

3 Conservation and management

Traditional fire management has been recognized for many years, with well-known advantages and disadvantages, as, for example, Kayapo land management in the Amazon (Woods *et al.*, 2009). Fire suppression, a feature of much modern fire management, has often led to increased fuel load and the risk of an eventual catastrophic fire. Understanding the significance of burn-timing, frequently familiar to indigenous peoples, has also occasionally been lost. Examples of work trying to understand historical land-use methods and allying them to modern practices include Butz (2009), considering the Masai traditions in East Africa, and Vigilante *et al.* (2009), dealing with the aboriginal people of northern Australia. The latter also form part of a study by Franklin *et al.* (2008) comparing different and adjacent land tenure systems. In northern Queensland, Radford *et al.* (2008) recommend the preservation of large trees in riparian habitats through a system of controlled fires of low intensity with early wet season or early dry season burning. One of the effective tools in a modern approach to fire management is the greater understanding of ecological thresholds. In Arnhem Land, Edwards and Russell-Smith (2009) discuss the assembled information for a 24,000 km^2 region where there was a 16-year fire history and LANDSAT-derived mapping of vegetation structure. Drucker and colleagues (2008) evaluated alternative fire management regimes in the Cape York Peninsula. A cautionary note is put forward by Clarke (2008) who points out that fire management proposals are almost invariably angled towards plant communities – which may not always match the needs of fauna. It is evident from these and similar examples from past years that land-use policy needs to consider not only the multiple factors causing change but also the needs of local people and the amalgamation of traditional practice with modern data from remote sensing and from models of possible alternative strategies (see, for example, Kull and Laris, 2009).

IV Soils and soil-plant communities in savannas

The role of physical, chemical and biological soil differences in shaping the pattern and composition of savannas has received less attention than above-ground factors, partly because of the difficulties in obtaining sufficient data. Most information is available in soil surveys, designed for agriculture rather than for ecology. However, this situation is improving and edaphic controls on individual plants and plant communities, along with the converse impacts of vegetation change on soil, are now better understood leading to greater appreciation of vegetation distributions.

The importance of soils in determining the boundaries between savanna and forest or other adjacent ecosystems continues to generate research. Recent investigations focusing on C-changes include gallery forest-savanna boundary studies in central Brazil from C-13 abundance data (L.C.R. Silva *et al*., 2008), and the work of Dümig *et al*. (2008) on C-14 and delta C-13 measurements on *Araucaria* forest expansion over grassland in southern Brazil. In a study of soil aggregates and organic matter linked to N and P additions in India, Tripathi *et al*. (2008) demonstrated a clear difference between savanna and forest systems, and related these properties to actual and potential soil fertility. The boundary between wet savanna and forest in hyperseasonal savannas (with long periods of flooding) is often sharp and Borma *et al*. (2009) show how atmospheric and hydrological controls on Bananal island, Amazonia, have stimulated savanna conditions, linked to very free drainage, within what is mostly floodplain forest.

Subsurface rooting, microbial activity and the activities of meso- and micro-organisms in the soil are known to have marked impact on savannas. The difficulty in obtaining accurate rooting data has limited the evidence available, but Janos *et al*. (2008) have investigated temporal and spatial variations of fine roots in a eucalypt woodland savanna in northern Australia. Fine roots were almost absent from the surface soils during the dry season but proliferated after the onset of the wet season. At the period of maximum abundance, fine roots were distributed throughout 1 m in the profile, unlike other tropical areas where the roots tend to predominate near the surface. The rapid decline in fine roots with the arrival of the dry season suggests that the trees are able to extract from deep roots and thereby constitute a 'dual' system helping to sequester C at depth. Microbial biomass has been studied as its importance to the global C-balance has been increasingly recognized. For instance, Liao and Buotton (2008) studied the changes in biomass-C in grasslands and in invading woodland, increasing from the grasslands to the woodlands, and with time. The woody encroachment affected competitive interactions and nutrient dynamics, improving physical structure and increasing trace gas fluxes. Fungi are very diverse in savannas (see de Castro *et al.*, 2008, in *cerrado*) and are often good indicators of land-use disturbance. Mycorrhizae are notably affected by disturbance, as shown by Tchabi *et al.* (2008) in the Benin savannas of west Africa. In India, Singh *et al.* (2009) have given a comparative account of microbial biomass-N and N-mineralization across forest, grassland and cropland illustrating the role that microbial activity has on soil nutrient status. There have been several publications highlighting the role of ants and termites in savanna ecology. Interrelationships between vegetation structure and the ant fauna has been shown by Vasconcelos *et al.* (2008b) to affect diversity in Amazonian savannas. The fungus-growing ants have been a continual source of interest in view of their redistribution of organic matter and nutrients within the soil system, as witnessed in a *cerrado* habitat in central Brazil (Vasconcelos *et al.*, 2008a). Fires affect this role and resilience to fire has been demonstrated by Parr and Andersen (2008) in northern Australia, and by Sousa-Souto *et al.* (2008) in Brazil. Similarly, termites have a major influence on nutrient availability and on physical transfer of mineral components within the soil, as shown in a study of abundance and diversity in tropical Australia (Dawes-Gromadzki, 2008) or by Obi and Ogunkunle (2009) in the Guinea savanna of Nigeria. The impact of mound-building termites is both visually obvious and pedologically significant. Abe *et al.* (2009) describe the physiochemical and morphological properties of mounds and surrounding soils over a toposequence in Nigeria, and Moe *et al.* (2009) illustrate the contribution of mound termites to the diversity of vegetation in the Mburu National Park, Uganda. The soil-concentrating effect breaks down on the abandonment of mounds and Ruckamp *et al.* (2009) illustrate the subsequent C- and nutrient-leaching in *cerrado* sites. Edaphic factors are further shown to be important for other organisms such as ground beetles in southwest Africa, particularly at local spatial scales (Davis *et al.*, 2008). Gas exchanges may also be affected, as shown by Brummer *et al.* (2009) in Burkina Faso focusing on CH_4 and CO_2 fluxes.

1 South America

The Brazilian *cerrado*s contain over 200 M ha of acid, low-fertility soils, whose adverse properties for agropastoral development inhibited development for many years. These have now been successfully surmounted, such that widespread agriculture exists over much of what was native savanna until 30–40 years ago. Large areas of Colombia, Bolivia, Venezuela and Peru have similar issues. Whereas most of the problems of adverse soils for exotic plants/agricultural crops have been tackled, there is still an obstacle in micronutrient deficiencies in soil (eg, Fageria and Stone, 2008), although flooded soils are able to accumulate micronutrients through their organic and inorganic complexes (Lopez-Hernandez, 2008).

At a landscape scale, the debate between conservationists and developers is exemplified by research in the Brazilian *cerrados*, where a prodigious research output on natural and replacement land systems has been carried out over the past few decades. *Cerrados* are among the most humid of savannas and therefore experience some of the most pronounced weathering and leaching over time, leading to acidic, allic (aluminium-rich) and nutrient-poor soils, though often deep and with good structural qualities. This is revealed in recent publications such as the work of Figueiredo *et al.* (2008), where physical properties and organic matter were studied in a comparison of natural savanna with various types of land-use disturbance. From a range of mostly physical soil properties, it was concluded that disturbance led to a critical change in two major parameters – organic matter and soil moisture storage capacity. These are, in turn, related to seasonal inputs from litterfall (Valenti *et al.*, 2008). Soil structure can also affect seed germination as shown by Bocchese *et al*. (2008). Complementary to this, a study by Neto *et al*. (2009) examined soil carbon and chemical properties over different land-management systems in the widespread Red Latosols (Oxisols) *cerrados*. In a complex set of interactions it was evident, yet again, that maintenance of organic matter was a crucial factor in retaining sufficient nutrients and moisture. In a study of silvopastoral land use derived from woody savanna (*caatinga*) in northeastern Brazil, Wick and Tiessen (2008) show how the organic matter content in the soil of cleared areas is a residual effect from the original native vegetation and, in this property at least, represents a non-sustainable system. In western Mexico, remnant tree effects have also been shown (Galicia and Garcia-Oliva, 2008) to be important for soil C and N stocks. In the Emas National Park in central Brazil, Amorim and Batalha (2008) indicate how aluminium levels and pH can be used to predict species density in herbaceous forms of the *cerrados*, while D.M. Silva and Batalha (2008) studied soils and fire regimes in the same Park. The effects of burning on the micromorphological character of different types of organic matter was examined in research by Kounda-Kiki *et al*. (2008) on tropical inselbergs in French Guiana, suggesting that the cyclic succession of vegetation patches can be inferred from a study of humus profiles. A different form of disturbance has been the widespread introduction of exotic tree species, as shown by L.G. Silva *et al*. (2009), investigating the impact of forest plantations (pine, *Pinus tecunamanii*, eucalyptus, *E. grandis*, and carvoeiro, *Sclerolobium paniculatum*) on physical, chemical and microbiological soil properties. Soil quality diminished with these land-use changes compared with a control, and microbial variables were significantly sensitive to the changes. Biological properties were shown by Carneiro *et al*. (2009) to be among the most strongly affected soil attributes under different forms of land use and tillage. Soil and water losses were reported following the introduction of *Acacia mangium* into the isolated savannas of Roraima in northern Brazil (Barros *et al*., 2009). Plant available water (PAW) is recognized as a principal resource in savanna plant community success and Ferreira *et al*. (2009) demonstrate how the diversity of woody species was related to differences in PAW at a fine spatial scale, and available moisture throughout the soil profile had a marked effect on species composition. Seasonal water variations were also investigated by Quesada *et al*. (2008) in woody savannas with different fire histories. The link between hydromorphic soils and species distribution in wet grasslands (*campo limpo*) is outlined by Munhoz *et al*. (2008), where organic matter and textural classes as well as soil moisture were shown to be significant in determining species distribution. Soil water content was followed over a two-year period near Brasília at sites with a different fire history, and this has suggested a strong coupling of atmospheric water demand and the physiological response of the vegetation.

2 African savannas

Many of the features of soil-plant relationships mentioned above are paralleled in the varied and geographically distinct African savannas. Spatial patterns of surface organic matter and macronutrients are described for southern African savannas along the Kalahari transect (KT) by Okin *et al*. (2008), who pointed to the more heterogeneous character at the dry end of the spectrum. C and N dynamics were investigated along the KT transect by Wang *et al*. (2009a; 2009b). Using a process-based model, the authors showed that there were distinct differences for soil moisture, decomposition and nitrogen mineralization between plots sited below tree canopies compared with those in open grassland. These differences were also more marked at the drier end of the transect, indicating once again that water availability is crucial in determining the pattern and rates of nutrient cycling. In a separate southern African study, Aranibar *et al*. (2008) presented values for N-isotopic abundance along an aridity gradient showing how land use was affecting N-cycling processes.

The main soil properties that have been discussed are, not surprisingly, C, N and P and their interactions with water balance. The Kruger National Park continues to provide a stream of research, such as the response of C-fluxes to water studied by Kutsch *et al*. (2008) using eddy covariance methods, which demonstrated ecosystem respiration changes over a year, related to phenology and soil moisture. In the same area, Coetsee *et al*. (2008) discuss the availability of N under frequent fire pressure and suggest that fire is less damaging than often perceived in mesic environments. Although the variability of savanna productivity as a result of climate is well known (Swemmer and Knapp, 2008), the role of soil nutrients (especially P and N) is less well understood, as shown in the work of Ries and Shugart (2008) in Botswana. Groen *et al*. (2008) looked at burn frequency but also showed that clay content affected tree clustering, which in turn reduced fire impact. Within a study of dynamic changes in the woody species in Mali, Hiernaux *et al*. (2009) also show how differences in texture and soil depth have influenced vegetation structure and density, while d'Annunzio *et al*. (2008) analyse soil organic particle size changes between native savannas and plantations in Congo. Textural differences have not been well identified as determinants in savanna structure and composition and should lead to a better understanding of distributions at a local scale. N-limitations form a frequently addressed topic, illustrated by the work of LeBauer and Treseder (2008) at a global scale comparing savannas with other major biomes, with confirmation that N is the major (or co-major) limiting factor in growth. The well-known effect of P-limitation in tropical soils is considered by Hartshorn *et al*. (2009) also at Kruger, showing that, in these systems, slow and moderate intensity fires can play a valuable role in supplying labile-P. In a plinthitic landscape of Nigeria, Yaro *et al*. (2008) analysed a range of soils over different topographic and drainage sites for extractable micronutrients showing intercorrelations between them and organic matter.

The wet soils of riparian and lower slope sites and floodplains tend to develop analogous hydromorphic characteristics throughout the tropics, and are particularly striking in semi-arid savannas, as illustrated by the N and P accumulation in soils (Jacobs *et al*., 2007) and in related photosynthetic fluxes (Mantlana *et al*., 2008a). In Lamto (Ivory Coast), Boudsocq *et al*. (2009) explain the nitrification-inhibiting nature of wet savannas that contribute to ecosystem fertility and primary production. Many of the African savannas are treeless and Craine *et al*. (2008) have looked at both N and P to try to assess their limiting effects in grasslands within the Kruger National park. The presence of trees within the grassland has often been shown to influence growth beneath the tree canopy and Treydte *et al*. (2008) demonstrate how trees are able to help grass growth by improving nutrient uptake in the wet season and delaying wilting in the dry, while Iponga *et al*. (2009) assessed the impact of the introduced Peruvian pepper tree (*Schinus molle*) in South Africa. The impact of N-fixing trees such as *Acacia auriculiformis* on sandy soils in the Bateke plateau, DR Congo, has been studied by Kasongo *et al*. (2009) comparing the soil fertility changes with an undisturbed savanna and revealing significant increases in organic C, total N, cation exchange capacity and base cations.

3 Australia

Individual species of white cypress pine (*Callitris glaucophylla*) have been shown to have an enriched impact on soils, which is multiplied with the very dense patches that are often encountered (McHenry *et al*., 2009). Extractable P and C, soil moisture and pH decreased away from individual trees with high values observed close to the stems. However, it is argued that from a land-use point of view this improvement, analogous to similar studies throughout the tropics, has to be weighed up against the negative effects of decreased ground cover. The responses of vegetation to P-deficiencies have been analysed in controlled conditions by Ghannoum *et al*. (2008), who look at the photosynthetic sensitivity of four taxonomically related grasses belonging to C-3 and C-4 subtypes. Rossiter-Rachor *et al*. (2008) illustrate the effect that invasive grasses can have on N losses in northern Australia, since the exotic species substantially alter fuel loads and therefore fire regimes. Over a long period this can significantly deplete N and other soil nutrients in an already low fertility environment.

4 Soil properties and land-use and land-management changes

While vegetation changes as a result of land-use alterations are well documented, relatively little information is available on changes in soil quality (Moussa, 2009). Various attempts have been made to identify appropriate indicators from a range of chemical, physical and biological properties and repeatedly the nature, amount and distribution of organic matter has been highlighted as a key factor. In some studies, organic fractions have been the focus, such as Hernandez-Hernandez *et al*. (2008) in Venezuela looking at organic C, light and heavy soil fractions, microbial biomass, basal respiration, humic and fulvic acids and aggregate stability. Although these parameters proved useful in assessing soil change, the effort required to identify such quality indicators is likely to be a restricting factor in wider adoption. San Jose *et al*. (2008) emphasize the usefulness of CO_2 flux patterns in their study of land-use changes in the Orinoco lowlands of Venezuela, while Neto *et al*. (2009) utilize total C and other attributes to discriminate different land uses in Brazilian savannas, and Gomez *et al*. (2008) also looked at soil-C as indicator of the effects of pine plantation introduction in native savannas in Venezuela. In India, Tripathi and Singh (2009) assessed the effects of N and P additions on soil organic matter and aggregate structure. In southeastern Nigeria, Igwe and Agbatah (2008) draw attention to the value of soil textural indicators following different land-use practices, although they also reinforce the importance of soil organic matter changes. Some land-use techniques have long been known to influence soil properties – for example, the improvements resulting from legume crops in the Ivory Coast (Kone *et al*., 2008) or liming to improve soil acidity and allic concentrations (Fageria and Baligar, 2008). Several papers refer to the process of 'savanization' where disturbance to precipitation and water balance, coupled with poor soils, can lead to the replacement of forest by savanna-like vegetation (eg, Senna *et al*., 2009), and this proves to be extremely difficult to reverse.

These publications have added considerably to our knowledge of soil-species relationships and soil-plant community links, soils being both determinants and also responders to vegetation changes. However, nutrient availability is closely related to many other factors, including herbivory and fire as shown by Cech *et al.* (2008). Finally the residual effect of past changes needs to be considered, derived from climatic change, recovery from fire and from past land-use change. Examples of subsequent soil recovery have been tracked in southern Kenya by Muchiru *et al*. (2009).

V Conclusions: Looking ahead

There are many outstanding questions of savanna ecology and biogeography. Among these, the problems of scaling-up from detailed local studies or scaling-down from broad scales remain unresolved; there are still no clear or universally applicable theories that explain processes or dynamic changes satisfactorily, and it may be that there are no ubiquitous generalizations possible from specific case studies; there is still patchy information on insect-plant interactions and the role of microbial organisms, and there are very few long-term studies of temporal change.

Significant advances in recent years seem to be the improvement in resolution, appropriate sensors and usefulness of remote sensing, increasing numbers of surveys offering more detailed and accurate taxonomic data, better information on the role and strategies for dealing with fire, and the new leads being offered by DNA sequencing and tracking together with phylogenetic histories. There are likely to be increasingly accurate global- and continental-scale models, and institutional organizations are taking a major cooperative role in cross-national and expensive projects despite political swings that continue to affect the success of conservation and management strategies.

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