NUTRIENT DYNAMICS IN QUEENSLAND SAVANNAS: IMPLICATIONS FOR THE SUSTAINABILITY OF LAND CLEARING FOR PASTURE PRODUCTION

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Abstract

Eucalyptus savannas on low nutrient soils are being extensively cleared in Queensland. In this paper we provide background information relevant to understanding nutrient (particularly nitrogen) dynamics in sub/tropical savanna, and review the available evidence relevant to understanding the potential impact of clearing *Eucalyptus* savanna on nutrient relations. The limited evidence presently available can be used to argue for the extreme positions that: (i) woody vegetation competes with grasses for resources, and tree/shrub clearing improves pasture production, (ii) woody vegetation benefits pasture production. At present, the lack of fundamental knowledge about Australian savanna nutrient relations makes accurate predictions about medium- and long-term effects of clearing on nutrient relations in low nutrient savannas difficult. The future of cleared savannas will differ if herbaceous species maintain all functions that woody vegetation has previously held, or if woody species have functions distinct from those of herbaceous vegetation. Research suggests that savanna soils are susceptible to nitrate leaching, and that trees improve the nutrient status of savanna soils in some situations. The nitrogen capital of cleared savanna is at risk if mobile ions are not captured efficiently by the vegetation, and nitrogen input via N_2 fixation from vegetation and microbiotic crusts is reduced. In order to predict clearing effects on savanna nutrient relations, research should be directed to answering (i) how open or closed nutrient cycles are in natural and cleared savanna, (ii) which functions are performed by savanna constituents such as woody and herbaceous vegetation, native and exotic plant species, termites, and microbiotic crusts in relation to nutrient cycles. In the absence of detailed knowledge about savanna functioning, clearing carries the risk of promoting continuous nutrient depletion.

Key-words: nitrogen, nutrient acquisition, nutrient cycles, savanna, tree clearing, tropical woodland

Introduction

Clearing of tropical forests and savannas for agriculture currently represents the most extensive alteration of land cover on the planet (Erickson and Keller 1997). At present Queensland has one of the highest clearing rates in the world (Glanznig 1995) accounting for over 90% of tree clearing in Australia between 1991-97, at a rate of 446,000 ha per year (Wilson *et al.* 2002 [this Volume]). Woody vegetation clearing (the term "tree clearing" is used here) and associated changes in pasture composition in Australia has long followed the view that "pasture improvement is an article of faith to Australia's farmers and graziers. Its necessity is never questioned; only its relative cost" (Wilson 1968). However, while improved pastures have provided successful grazing systems in parts of southern Australia, less is known about the fate of northern Australian savannas once the woody vegetation has been cleared. In Queensland, recent (1997-1999) tree clearing is occurring mostly in areas of low nutrient *Eucalyptus* dominated savannas (Wilson *et al.* 2002 [this Volume]).

For the nutrient poor *Eucalyptus* woodlands of the Desert Uplands biogeographic region "timber clearing by pulling of the eucalypt woodlands is not recommended" according to a report by the Department of Primary Industries (Western Arid Region Land Use Study 1978). The study cautioned against tree clearing since low soil fertility, low soil moisture levels, and management practices potentially hinder successful pasture maintenance. Once deteriorated, some land types are highly susceptible to erosion and nutrient decline (Western Arid Region Land Use Study 1978). However, the study also suggests that when "properly managed, these lands are stable". There is an obvious need to understand the role of woody and herbaceous

vegetation and other ecosystem components in Australian savannas. As stated by Scanlan *et al.* (1991), "a greater understanding of the interactions of water and nutrients in relation to trees and grass growth is essential if the long-term impacts of modifying woody vegetation structures are to be predicted". It is in the public interest to prevent short-term increases in pasture production at the expense of land deterioration in the medium- and long-term.

However, with the current knowledge it is difficult to predict the effect of clearing on nutrient relations in low nutrient Queensland savannas. Remarkably little research has been carried out to address this issue. Regrettably, no long-term studies exist in Queensland, and no studies have been carried out that encompass a wide range of ecosystem components to identify how nutrient poor savannas function. The assessment of the effects of tree clearing on nutrient relations is particularly problematic because (i) vegetation dynamics are strongly influenced by the irregular rainfall patterns in Queensland (Fensham and Holman 1999), (ii) "clearing" ranges from thinning to complete removal of woody vegetation, (iii) cleared areas often contain woody resprouts which may fulfill a similar function as the previously existing woody vegetation, and (iv) effects of management (e.g. stocking density, fire) and clearing can result in confounding effects (Scanlan *et al.* 1991).

One could argue that the rationale for and against tree clearing for pasture improvement is based on two concepts: (i) that trees and grasses compete for resources, such as nutrients and water, and that clearing woody vegetation will increase pasture production (Scanlan and Burrows 1990); and (ii) that presence of trees benefits herbaceous vegetation and that clearing ultimately results in reduced pasture production (Jackson and Ash 1998). Here we examine the literature to address the question how clearing may affect nutrient relations, particularly nitrogen, in nutrient poor savannas. We speculate about nutrient relations of nutrient poor savanna after clearing, present conceptual models, and suggest research approaches that would aid to rapidly improve our understanding of nutrient poor savannas.

Savanna nutrient relations

Savannas cover approximately one fifth of the land surface of the world, and are "one of the most important, but least studied ecosystems" (Scholes and Walker 1993). Savannas have a complex structure and contain different proportions of woody and herbaceous elements. The relative proportion of woody and herbaceous species in savanna ecosystems is influenced by a suite of abiotic factors, including fire, water and nutrient availability, and biotic factors, particularly herbivores (Burrows 2001, Scholes and Archer 1997). It is important to recognise that savannas are not an intermediate between forests and grasslands. Savannas lack the topsoil organic matter accumulation that typifies grasslands, and the microclimatic amelioration that characterises forests (Scholes and Walker 1993). Herbaceous and woody savanna vegetation cannot be treated separately as interactions between both vegetation components are important for savanna functioning (Scholes and Archer 1997).

Little is known about nutrient dynamics of tropical savannas (Solbrig 1996, Scholes and Archer 1997), and it is therefore difficult to predict the outcome for savanna nutrient relations when natural savanna vegetation is replaced with pasture grasses. Due to the strong link between soil nutrient availability and productivity, the nutrient capital of cleared savannas has to remain stable in order to provide long-term sustainability. Savanna soils typically have a low content of major mineral nutrients, particularly nitrogen and phosphorus (Solbrig 1996). On most continents, savannas occur along a continuum ranging from arid/eutrophic to moist/dystrophic environments (Huntley and Walker 1982). In contrast, in Australian arid and moist climates, savannas are associated with ancient and highly leached soils and they have a lower primary productivity than African and American savannas (Braithwaite 1991). The significantly lower leaf nitrogen content of Australian savanna species compared with African species with similar root specialisations confirms that Australian savannas are the more nutrient depauperate (Schmidt and Stewart, unpublished data).

Nutrient inputs into ecosystems occur via soil weathering, atmospheric nutrient deposition, and N_2 fixation. Nutrients are lost from the system via volatilisation, leaching, soil erosion, and removal of biomass. Soil macrofauna ingestion of litter results mostly in decomposition (oxidisation of organic carbon, reducing C/N and C/P ratios) of organic matter, which is subsequently mineralised by soil microorganisms, transforming organically bound nutrients into low-molecular weight ions (Attiwill and Adams 1993). However, loss of nutrients from litter cannot be interpreted solely as mineralisation since the boundaries between litter and soil organic matter are not clearly defined (Attiwill and Adams 1993).

It has long been debated how "open" or "closed" nutrient cycles are in a given ecosystem, and a range of generalisations has been made for tropical soils. A nutrient cycle is considered "closed" when no significant amounts of nutrients are lost from the ecosystem. Closed nutrient cycles are generally found in ecosystems with strongly leached soils that have a great depth of weathering (> 2 m) (Burnham 1989). In contrast, systems with open nutrient cycles lose substantial amounts of nutrients through leaching, run-off, erosion, or volatilisation. Open cycles are more common in seasonally dry, weakly weathered and/or nutrient-rich soils, for example soils that have received volcanic ash or alluvial depositions (Burnham 1989). Although Australian savannas occur in seasonally dry climates, their association with nutrient-poor and highly weathered ancient soils suggests that closed cycles exist for those nutrients that are not replenished. A general view is that roots in systems with open cycles penetrate deeper soil layers where soil weathering allows nutrient capture, whereas in closed cycle systems roots are concentrated in the surface layers (Bruijnzeel 1989). This view is supported by a Mexican study showing that highly weathered sand contained more roots in the topsoil and stronger retention of numerous soil nutrients than less weathered sand (Kellman 1990). A transition from closed to open nutrient cycles may be promoted if clearing alters nutrient cycling processes and reduces the ability of vegetation to capture nutrients.

Nitrogen cycling in savannas

When characterising nutrient cycles, input, loss, availability and uptake of nutrients have to be considered. The nitrogen cycle is more complex than other nutrient cycles due to the diverse nitrogen transformations that occur (Eviner and Chapin 1997). Nitrogen cycle characteristics important for plant nitrogen acquisition include (i) organic matter decomposition and mineralisation rates, (ii) temporal changes of nitrogen mineralisation (wetting-drying cycles), (iii) soil nitrogen forms, (iv) movement of nitrogen in the soil profile, (v) nitrogen loss via leaching, denitrification, ammonia volatilisation, and erosion, and (vi) nitrogen gains via N_2 fixation and aerial deposition.

Nitrogen is quantitatively the most important nutrient that the majority of plants acquire from the soil accounting for up to 80% of the total ion uptake of roots (Marschner 1995), but parent rock contains only small amounts of nitrogen. Nitrogen typically enters the ecosystem via biological N_2 fixation, where inert N_2 gas is reduced to reactive nitrogen forms, a process performed only by some prokaryotes (cyanobacteria, bacteria). Nitrogen fixing prokaryotes occur on soil surfaces as part of microbiotic crusts, free-living in soils, and in association or symbiosis with plants.

As a general rule, soil nitrogen levels are low in the arid and semi-arid areas of Australia (Beadle 1981, Williams and Raupach 1983). Most nitrogen is thought to be located in the upper few centimeters of the soil where organic matter accumulates and is turned over (Attiwill and Adams 1993). Soil organic matter contained 92% of the total nitrogen pool of a South African savanna (Scholes and Walker 1993), and a similarly high proportion in an Ethiopian savanna (Jensen *et al.* 2001), highlighting the potentially large impact that changes to the soil organic matter pool will have on ecosystem nitrogen relations. Depending on climate and forest type, between 1 and 24% of the soil organic matter pool is mineralised per year (Pfadenhauer 1979, Attiwill and Adams 1993, Connell *et al.* 1995). These mineralisation

estimates, however, do not consider the more recent proposition that plants are not restricted to mineral (inorganic) nitrogen sources, but also use organic forms of nitrogen (Eviner and Chapin 1997).

Soils contain different proportions of soluble nitrogen compounds including complex organic soil nitrogen (e.g. protein, DNA), low molecular weight organic nitrogen (e.g. small peptides, amino acids, urea), and inorganic nitrogen (ammonium, nitrate) (Eviner and Chapin 1997, Schmidt and Stewart 1999). Organic and inorganic forms of soil nitrogen were present in North Australian savanna soil during the dry season (Schmidt and Stewart 1999). In wet Brazilian and Australian savannas (> 1500 mm mean annual rainfall) high rates of nitrogen mineralisation occur during the transition from dry to wet season (Marrs *et al.* 1991, Schmidt *et al.* 1998). While the Brazilian study suggests that ammonium is immobilised rather than nitrified (Marrs *et al.* 1991), in tropical Australian savanna the generation of soil nitrate increases strongly at the onset of the wet season and is sustained during the wet season (Schmidt *et al.* 1998) indicating that savannas differ in their nitrogen cycle characteristics.

Plant nutrient acquisition

Nutrient utilisation among the plant species of a given plant community is competitive as well as complementary, and is related to plant characteristics including physiology, root morphology, specialised roots and associations with microorganisms (Pate 1994, Turnbull *et al.* 1996). The diverse nutrient acquisition strategies of component plant species are likely to be a prerequisite for efficient nutrient cycling in savanna. The dominant trees in Australian savanna belong to the genus *Eucalyptus* (Myrtaceae), which possess ecto- (ECM) or ecto/arbuscular-mycorrhizal (ECM/AM) root fungal partners. Other woody and herbaceous savanna species have AM (arbuscular mycorrhizal associations. *Acacia* and other woody legumes possess ECM/AM or AM associations and potentially N_2 fixing bacterial symbioses. Proteaceous species including common genera *Hakea, Grevillea,* and *Banksia*, do not have fungal associations but possess specialised cluster roots.

Generally, ECM associations are thought to enhance plant access to complex organic nutrient sources, while AM associations considered to be particularly effective in increasing plant access to certain sources of phosphorus and micronutrients (Smith and Read 1997). Similarly, cluster roots exude compounds that dramatically increase the availability of micronutrients and phosphorus (Dinkelaker *et al.* 1995, Neumann and Martinoia 2002). Soil nutrient limitations result in assemblages of dominant trees with distinct nutrient acquisition strategies. In African savanna, N_2 fixing trees dominate savannas poor in nitrogen but comparatively rich in phosphorus, non-N_2 fixing AM trees dominate savannas poor in phosphorus but rich in nitrogen, whereas non-N_2 fixing ECM trees dominate soils poor in both elements (Högberg 1989). The dominance of *Eucalyptus* in Australian tropical savanna is symptomatic of their low N and P status.

The forms of nitrogen present in the soil are important since plants differ in their ability to access different forms of nitrogen. Complex organic nitrogen, such as protein, is not directly available to plants, but plant species with certain ECM associations can access protein via their fungal partners (Read 1991). While all plants are thought to be able to use ammonium as a nitrogen source, nitrate use varies between species (Turnbull *et al.* 1996, Stewart and Schmidt 1999). The complexity of plant nitrogen relations in savanna can be demonstrated in tropical Australian savannas, where plant nitrogen utilisation is related to root associations, physiological attributes, and life strategies. Long-lived *Eucalyptus* species use nitrate as a nitrogen source to a lesser extent than some herbaceous species, exotic weeds and *Ficus* species; while short-lived, fire intolerant *Acacia* species have substantially higher tissue nitrogen contents than most woody savanna species, and an efficient root system to access a wide spectrum of nitrogen sources including ammonium, amino acids, nitrate and atmospheric N_2 (Schmidt *et al.* 1998, Schmidt and Stewart 1998, 1999).

The African grass species *Andropogon gayanus* had a higher ability to acquire nitrogen from Venezuelan savanna soil than the native South American grass *Paspalum plicatulum* (Bilbao and Medina 1990). The efficiency with which the exotic and widespread pasture species buffel grass (*Cenchrus ciliaris*) acquires nutrients may be a key factor allowing it to outcompete native grasses and to invade savanna (Fairfax and Fensham 2000). The ability to fix N_2 allows species to compete in soil where nitrogen limits plant growth, and this ability could contribute to the success of N_2 fixing woody weeds (i.e. prickly acacia, *Acacia nilotica*) to invade nitrogen-impoverished Australian savannas.

A conceptual diagram of savanna nutrient relations (Fig. 1) illustrates that nitrogen and other essential plant macronutrients are concentrated in the upper centimeters of the soil profile due to the accretion of litter and soil organic matter. Termites, soil fauna and microorganisms are involved in decomposition and mineralisation processes. Woody and herbaceous species with diverse root specialisations explore the soil profile and acquire nutrients depending on their ability to access different forms of nitrogen and other nutrients. Nutrient demand, species-specific root structures, root exudation of compounds that enhance the availability of nutrients, as well as microbial root associations and symbioses determine plant nutrient acquisition. For example, trees with ECM associations may short circuit mineralisation processes by accessing complex organic matter, while species with VAM associations are restricted to using nitrogen forms with a low molecularly weight. Cycles of essential plant nutrients that are not replenished are closed, and losses are minimal and the nutrient status of the ecosystem is constant over time. It is conceivable that the nitrogen cycle is open and that some losses of nitrogen occur via leaching of highly mobile nitrate ions. However, nitrogen losses are compensated for by N_2 fixation of leguminous species and microbiotic crusts.
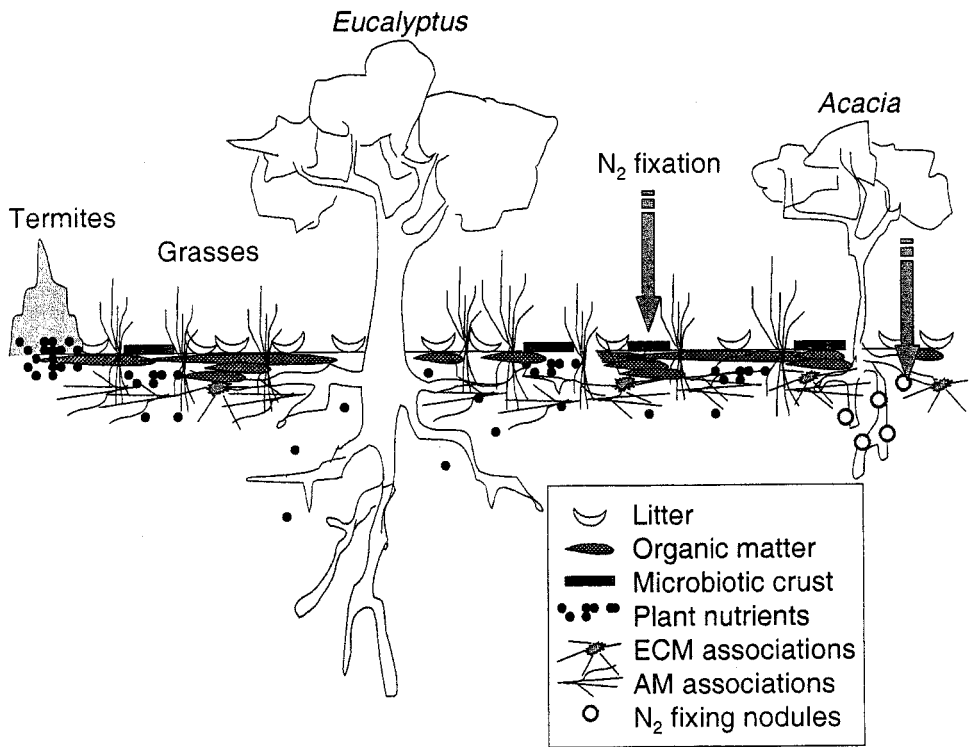
Fig. 1. Conceptual diagram of savanna components. For simplicity, grasses represent all herbaceous vegetation in the diagrams.

Do trees and grasses compete for nutrients?

The effects of trees on soil nutrients have important implications for low nutrient savannas and the long-term viability of cleared savannas. A number of studies suggest that trees have a nutrient and in some cases moisture enhancing effect on soil associated with tree canopies. A higher nutrient and water availability in soil under tree canopies compared to soil outside the canopy has been observed in a diversity of plant communities (Boerner and Koslowsky 1989, Turner et al. 1993, Wilson 1998). Frequently cited explanations for this pattern include the deep root penetration of trees and subsequent nutrient acquisition from the deeper soil profile, their long growth period, capacity for litter accumulation, enhanced aerosol deposition, and the lower soil temperatures under tree canopies (Kellman and Carty 1986, Ernst and Tolsma 1989, Campbell et al. 1994).

In the South African Nylsvley study a large number of savanna components were studied over considerable time. It was shown that soil below the canopy of trees had a higher nutrient content, including total nitrogen, higher organic carbon content, and greater microbial activity than soil outside the canopy (Scholes and Walker 1993). The authors suggested that the improved soil conditions under tree canopies are a consequence of the ability of trees to pump nutrients from the deeper soil to surface layers. Hibbard et al. (2001) found that woody plant establishment in a subtropical savanna caused changes in soil physical and chemical properties, where "islands of fertility" developed in soil associated with woody plants. These islands of fertility had increased levels of carbon, nitrogen and higher rates of nitrogen mineralisation compared to soil associated with herbaceous species (Hibbard et al. 2001). Similarly, soil associated with *Pinus caribaea* canopies in open savanna had increased exchangeable nutrient levels (Kellman and Hudson 1982). Aerosols caught by canopy filtration may contribute substantial amounts of nutrients to neotropical savanna (Kellman and Carty 1986), a suggestion which has not been explored in Australian savannas.

Two Australian studies demonstrate a positive effect of trees on soil nutrient levels. There were significantly higher levels of available phosphorus and exchangeable potassium in the upper soil layers under trees compared with tree gaps within poplar box (*Eucalyptus populnea*) communities in southern Queensland (Ebersohn and Lucas 1965). Similarly, soil nitrate availability was higher in soil under the canopy of trees than in soil outside the canopy in ironbark (*Eucalyptus crebra*) savanna in north Queensland, and this was associated with higher N content of grass foliage (Jackson and Ash 1998).

It has been argued that because grass and tree root distributions overlap, grasses and trees compete for nutrients and water. Belsky's (1994) study in a Kenyan savanna suggested that savanna trees compete more intensively with understorey plants at wetter sites where tree roots were restricted to the crown area, while at drier sites competition was less intense because tree roots are more diffuse, extending beyond the canopy zone into the open grassland. However, presence or absence of roots cannot be used as the sole indicators for plant competition. As discussed above, root specialisations play an important role in the ability of species to access different nutrient pools. Grass species differ strongly in their ability to exploit and retain nitrogen (Busso et al. 2001). The available evidence indicates that the ability to acquire nutrients differs not only between woody and herbaceous species, but also between species with similar growth forms.

Under natural conditions temporal shifts occur between forest and grassland boundaries, but it is unclear how competition for resources is involved in this process. Wilson (1998) pointed out that grasses have a high root:shoot ratio and a high root length:root mass ratio due to overall finer roots compared to trees. This has prompted claims that grasses have a competitive advantage over trees for nutrient and water acquisition, and it has been suggested that, in some situations, grasses outcompete trees for water in surface soils (Walker and

Noy-Meir 1982). It could be argued that because trees and grasses differ with respect to phenology, rooting depth and root associations, different nutrient pools are accessed.

Overall, trees may improve grass growth due to enhanced water and nutrient status, but potentially limit grass growth if conditions of low irradiance exist under the canopy, or through competition for belowground resources. It was therefore concluded that the net result of tree-grass interactions can be either an increase or a decrease in the productivity of grasses under the canopy compared with growth in a treeless areas, depending on the interactions of all factors (Scholes and Walker 1993).

Microbiotic crusts and termites

Microbiotic crusts and termites are discussed here because they are an integral part of Australian savannas and play an important role in nutrient cycling. In general, microbiotic crusts are assortments of non-vascular plants including lichens, mosses, liverworts, algae, fungi, bacteria, and cyanobacteria that colonise the soil surface (Eldridge and Greene 1994), where they can represent up to 70% of the living cover in some semi-arid ecosystems (Belnap *et al.* 1994). Microbiotic crusts buffer against wind and water erosion, increase soil particle aggregation, enhance seedling establishment and survival (Johansen 1993), and improve the nutrient status of soils (Belnap *et al.* 1994). In some systems, microbiotic crusts contribute considerably to ecosystem carbon budgets, with estimates of carbon input ranging between 28 and 350 kg C/ha/a (Evans and Johansen 1999). The ability of cyanobacteria to survive extreme conditions (Smith *et al.* 1990) ensures they are well adapted to the long dry periods associated with many savannas. The cyanobacteria populations within microbiotic crusts make a significant contribution to N_2 fixation. Estimates for N input from N_2 fixation by microbiotic crusts range widely from 0.7 to 100 kg N/ha/a in a range of ecosystems (Evans and Johansen 1999). Vascular plant species grown in crusts with a high proportion of N_2 fixing cyanobacteria had higher concentrations of macronutrients than those not grown in crusts (Belnap *et al.* 1994). The contribution of microbiotic crusts towards nitrogen input is likely to be important in Australian savannas, although quantitative data are currently lacking. Disturbance causes changes in microbiotic crust composition and cover (Evans and Johansen 1999). It needs to be established if changes in microbiotic crust functioning occur in cleared savanna and how such changes affect the nitrogen relations of the resulting ecosystem.

Termite activity strongly affects soil characteristics of savannas (Holt and Coventry 1990). Termites collect clay particles from deep soil layers and combine them with organic matter for nest construction (Menaut *et al.* 1995). Termites continuously redistribute nutrients, organic matter and clay particles in the landscape, and host N_2 fixing microorganisms in their hindgut. Termitaria in an African savanna covered 9% of the area but accounted for a large proportion of total soil nutrients (14% of carbon, 16% of nitrogen, 74, 61 and 47% of exchangeable calcium, potassium, and magnesium, respectively (Menaut *et al.* 1995)). In South American savannas, termite mounds are sinks for nutrients and contain more carbon, nitrogen and phosphorus than adjacent soils (López-Hernández 2001). Substantial microbial activity in mounds resulted in a high proportion of plant available forms of nitrogen and phosphorus (López-Hernández 2001). Termites contribute greatly to organic matter decomposition. Holt and Coventry (1990) claim that savanna termite populations near Townsville possibly contribute up to 20% of the total mineralised carbon. A conservative estimate suggests that mound-building termites in savanna woodland near Charters Towers provide at least 24 kg/ha/a of organic carbon and 1.8 kg nitrogen/ha/a (Holt and Coventry 1990). For other savannas Lüttge (1997) estimated that organic matter mineralisation might be as much as 250 kg/ha/a. However, while there is a considerable body of knowledge on termite effects on savanna nutrient relations in other continents, much less is known about their role in natural and cleared Australian savannas.

Nutrient-water interactions

Strong rainfall seasonality is a major determinant in dry forest and savanna ecosystems which dictates growth periods, plant structure and species composition (Cuevas 1995, Huntley and Walker 1982). Soil nutrient turnover is dependent on adequate soil moisture. In savanna with a pronounced wet season, woody species decouple nitrogen uptake and nitrogen use, taking up nitrogen mainly during the wet season when soil nitrogen availability is high (Schmidt and Stewart 1998). However, in semi-arid savanna with distinct wetting-drying cycles, nutrient availability will be pulsed. Root function in relation to ephemeral nutrient fluxes plays an important role for nutrient capture by plants. During episodes of transient release of nitrogen ions, the uptake capacity of existing roots was more important than production of new roots (Cui and Caldwell 1997).

In deciduous tropical forests, nutrients contained in soil microbes become available during soil drying due to their death (Jaramillo and Sanford 1995). The authors hyphothesised that sudden re-wetting of soil results in further microbe death, so that during soil drying-wetting nutrient release and immobilisation cycles take place. The relationship between plant nutrient uptake and nutrient release cycles has not been studied in Australian savannas. It is also unknown to what degree nitrate and other mobile ions are intercepted and recycled by shallow or deep-rooted species during nutrient pulses.

Savanna trees produce the majority of their fine roots in the upper soil profile (<1m) (Eamus et al. 2002), while a taproot extends down to several metres where soil depth allows. Research in wet tropical savanna in northern Australia has shown that tree water use does not differ strongly between seasons, and that mature trees exploit a large soil volume (Hutley et al. 2000). These authors suggest that trees access most of their water from depths between 2 to 10 m where soil moisture relations are favourable throughout the year (Fensham and Kirkpatrick 1992).

Studies of plant water relations in a diversity of ecosystems have established that "hydraulic lift" occurs, which involves water transport from the deeper soil into the upper soil profile. The deep rooting components of some ecosystems are responsible for substantial hydraulic redistribution of water within the soil profile (Richards and Caldwell 1987, Caldwell et al. 1998). Roots can also distribute water from the surface into the deeper profile, facilitating vertical root growth in dry soils (Burgess et al. 1998). Plant controlled water redistribution in the soil profile has obvious implications for nutrient processes, including organic matter decomposition and mineralisation, nutrient availability in the soil solution, and maintenance of viability of fine roots, which would be important for short "response times" of roots to nutrient pulses (Burgess et al. 1998).

Nutrient relations of cleared savannas

A number of studies have quantified the success of pasture establishment in cleared Australian savannas. However, it is flawed to interpret increased pasture production after tree clearing solely as the result of eliminating competition by woody vegetation. This interpretation does not consider that transient increases in nutrient availability occur after clearing due to nutrient release stored in woody vegetation, for example after burning. Similarly, decaying fine roots contributed significant amounts of available nutrients in dry forests (Cuevas 1995), and decaying fine roots are also a likely nutrient source in cleared savanna. Whether the nutrient status of cleared savannas remains stable over time will depend on nutrient cycle characteristics and the ability of pasture species to access nutrients.

A range of central Queensland woodlands with lower density of woody vegetation had greater herbaceous biomass compared to woodlands with a higher density of woody vegetation (Scanlan and Burrows 1990). In poplar box (*Eucalyptus populnea*) communities, enhanced

pasture production on cleared sites compared to uncleared sites was associated with higher levels of available soil ammonium, nitrate, and water (Tunstall *et al.* 1981). It is likely that a primary cause of enhanced pasture production is the improved access to soil nutrients. After initial increases, pasture production was reduced after several years in both poplar box (Tunstall *et al.* 1981) and brigalow communities (Graham *et al.* 1981), although pasture production in cleared pastures was still higher than in uncleared areas. Pasture performance in cleared areas needs to be determined in the long-term by revisiting older experiments (e.g. Tunstall *et al.* 1981) and monitoring existing experiments over a longer period. The enhancement of soil fertility by trees is proportionately greater in low than high nutrient *Eucalyptus* woodlands (Jackson and Ash 1998, 2001). This may reflect the fact that changes in low nutrient savanna occur more rapidly in nutrient poor systems than in nutrient richer systems. Burrows (1993) emphasised that clearing is only justified if pasture productivity is above pre-clearing levels in the long-term (>10 years), but most studies have only assessed pasture production over much shorter periods.

Long-term sustainability of nutrient relations in cleared savannas may be problematic since some Australian savanna soils have a high potential for nitrogen leaching. Unfertilised pastures on cleared red earth soils near Charters Towers (Queensland) contained approximately 1 and 2 μg NO_3^--N and NH_4^+-N/g soil, respectively, throughout the top metre of the soil profile (Probert and Williams 1986). After addition of nitrogen fertiliser, nitrate and ammonium were detected to a depth of 2 and 0.5 m respectively, indicating their susceptibility to nitrate leaching. The same authors also emphasised that rainfall events that promote leaching are a regular occurrence in the semi-arid tropics (Probert and Williams 1986). In cleared tropical savannas fertilised and sown with pastures near Katherine, Northern Territory, nitrate accumulated in the topsoil during the dry season, and readily leached into the deeper soil profile during the wet season (Wetselaar and Norman 1960). Crops were able to capture only 25-40% of the applied nitrogen since nitrate leaching occurred prior to crop establishment (Wetselaar 1962). While nitrogen fertilisation is not common practice in typical Australian savannas, these studies highlight the potential for leaching of nitrate and other mobile ions from savanna soils.

Only a small proportion of the total soil nutrient pool is considered to be readily plant available, and total soil nitrogen is therefore not a sensitive indicator in the assessment of clearing effects. Graham *et al.* (1981) emphasised that reduced nitrogen availability rather than a reduction in total soil nitrogen content affected pasture production in cleared brigalow. Soil microbes have a preference for ammonium and do not immobilise nitrate as well as ammonium (Attiwill and Adams 1993). If more nitrate is generated in cleared savannas than in uncleared savannas, and the ability of the vegetation and soil organisms for nitrate capture is low, then nitrate loss via leaching is a likely contributing factor for reduced levels of plant available soil nitrogen. The loss of nitrogen may be an important cause of pasture run-down after clearing, which may also result from soil compaction by grazing animals, increased shrub densities, erosion and scalding, fire exclusion, and salinity (Graham *et al.* 1981, Tunstall *et al.* 1981).

Apart from nitrogen, phosphorus is considered to be a major limiting factor for plant productivity in savannas (Högberg 1989). It has been estimated that phosphorus stored in the former woody vegetation in addition to the existing soil phosphorus will support pastures (and removal of phosphorus in animal products) in north-eastern Australia for over 200 years (Burrows 1993). However, phosphorus is often immobilised in soil, for example, as ferro-aluminium complexes. Since plant species differ in their ability to access soil phosphorus (Marschner 1995), it is possible that different pasture species can access soil phosphorus sources to different extents. To assume that phosphorus stored in woody vegetation is available to pasture species (Burrows 1993) may therefore be an oversimplification. It has been shown that cluster rooted species such as Proteaceae are particularly efficient at mobilising phosphorus from soil sources, due to their ability to exude large quantities of
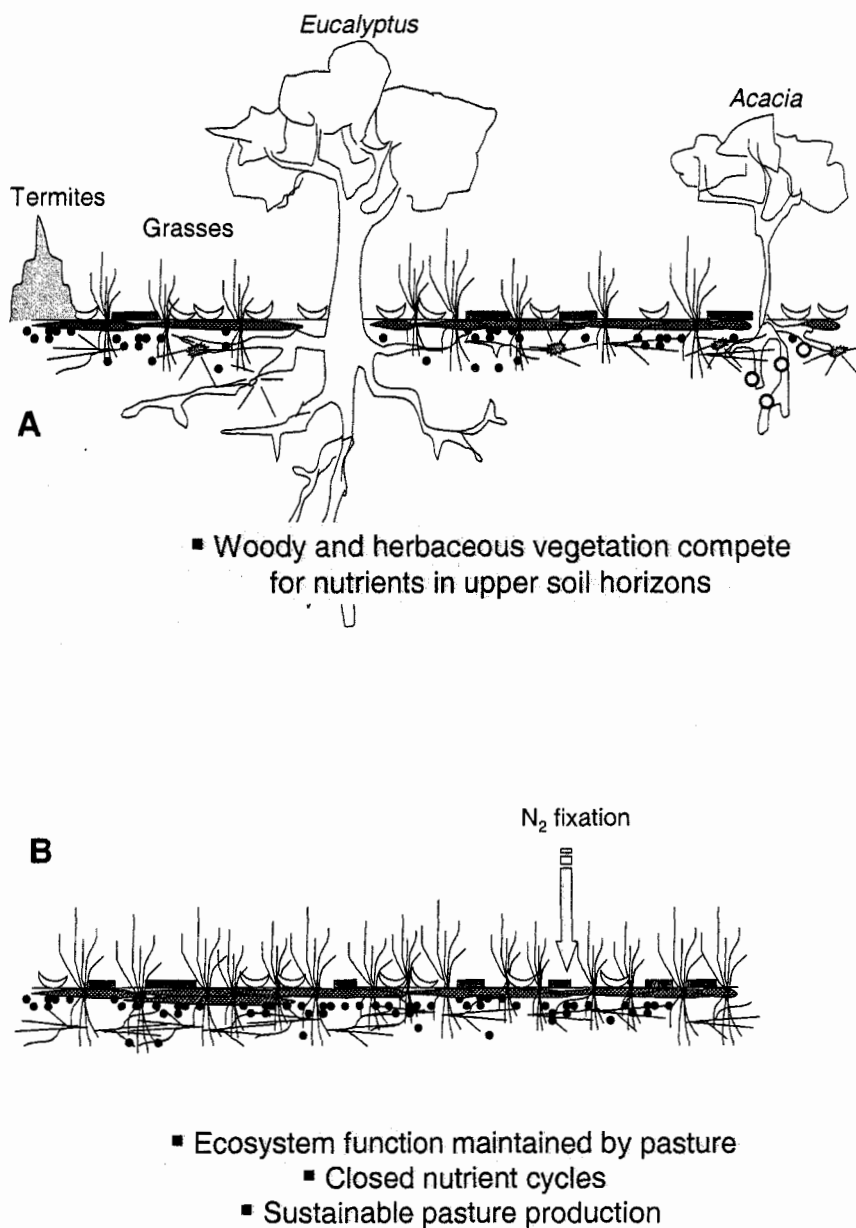
organic acids from their roots (Dinkelaker *et al.* 1995, Neumann and Martinoia 2002). Species that access soil phosphorus efficiently will therefore have an important role in accessing and redistributing soil phosphorus in savanna.

The two scenarios of cleared savanna nutrient relations

Predictions for the future of cleared savannas are that removal of woody vegetation will result in sustainable systems with stable nutrient conditions, or unsustainable systems with decreasing nutrient capital. In the first example (Fig. 2A) nutrient cycles are closed and nutrient decomposition and mineralisation occurs in the upper soil profile, where fine roots of woody and herbaceous species are concentrated and compete for nutrients. An important prerequisite for this scenario is that herbaceous species possess an effective root system that captures nutrients when they become available, thus preventing nutrient losses beyond the root zone. Nutrients stored in the woody vegetation become available after clearing and benefit the growth of herbaceous vegetation (Fig. 2B). Nitrogen input occurs via microbiotic crust and/or pasture legume N_2 fixation to compensate for nitrogen losses via removal of biomass. Cattle replace termites as main herbivores recycling nutrients. This scenario assumes that native and exotic pasture grasses and herbs maintain all functions that woody vegetation has previously held. In this scenario clearing results in a relatively stable system because grasses and trees have similar ecological functions, and loss of trees does not change nutrient cycling processes.
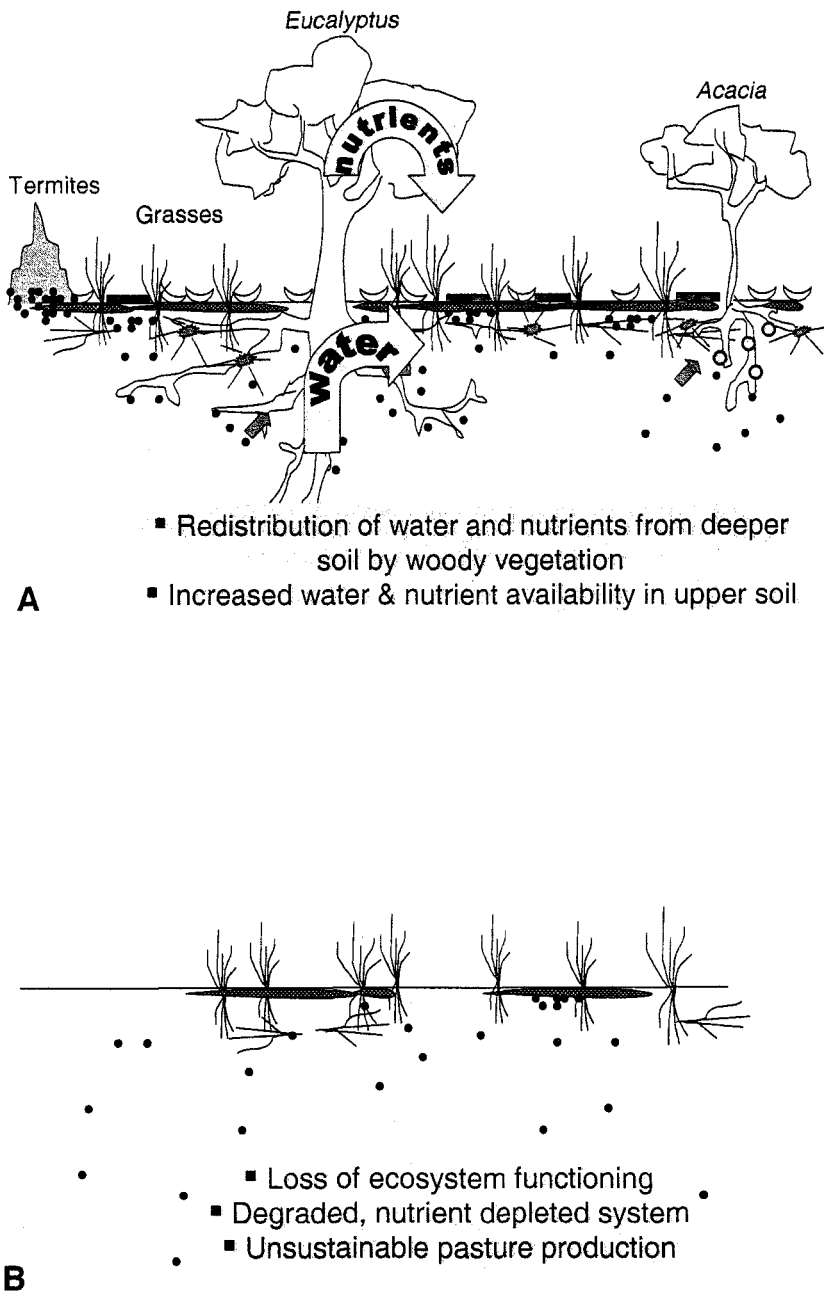
The second scenario (Fig. 3) assumes that woody vegetation has a function for nutrient acquisition and water distribution that is distinct from the role of herbaceous vegetation. This scenario places emphasis on the ability of tree roots to access the deeper soil profile, and to redistribute water and nutrients from the deeper soil profile to the upper soil layers (Fig. 3A). Perennial woody species intercept nutrients that become available during times when herbaceous vegetation does not take up nutrients, for example early in the wet season, or during intermittent rainfall events. Nutrients leach into the deeper soil profile resulting in a net loss of nitrogen and other mobile ions (e.g. potassium). Clearing activities may also damage microbiotic crusts and termites and result in reduced N_2 fixation by microbiotic crusts and organic matter mineralisation by termites. Redistribution of nutrients from deeper soil layers is significantly reduced, and removal of N_2 fixing trees such as *Acacia* species negatively impacts on the long-term nitrogen budget. After clearing, soil evaporation increases as a result of reduced shading of the soil surface by woody vegetation. Water interception and evapotranspiration decrease, leading to increased run-off, nutrient leaching and seasonal watertable ascension (Maass 1995). In the medium- and long-term, open nutrient cycles result in nutrient losses from the system and reduced pasture production (Fig. 3B).

We cannot provide a definitive answer to the question as to which of the two scenarios is the more likely one to occur. Two findings may indicate that clearing low nutrient savannas carries the risk of nutrient depletion: (i) nitrate is easily leached from savanna soil and this process may be enhanced in cleared systems, (ii) trees increase the nutrient status of soil associated with their canopy in some savannas. Whether an open nitrogen cycle, and possibly other nutrient cycles, characterises uncleared and/or cleared savannas has yet to be established. The rate at which nutrients are lost in a cleared system would *inter alia* depend on the condition of the resulting pasture such as initial nutrient status, grazing pressure, and preservation of soil structure. It needs to be established how soil-climate-vegetation components interact with respect to nutrient cycles so that clearing guidelines can be developed for different regions. Useful parameters are required in order to develop nutrient cycling models for Australian savannas. For example, total soil element concentration may not be a good indicator for nutrient relations; instead plant available nutrients (i.e. soluble and weakly bound nutrient fractions) should be measured with spatial and temporal resolution, and in relation to how they are accessed by different plant species. Subsequently, threshold levels for nutrients could be devised as indications for permissible clearing in savannas.

- Woody and herbaceous vegetation compete
  for nutrients in upper soil horizons

- Ecosystem function maintained by pasture
- Closed nutrient cycles
- Sustainable pasture production

Fig. 2. A & B Conceptual diagram of savanna before and after clearing. This scenario assumes that trees and grasses compete for nutrient and water resources in the upper soil horizons (see text for details).

Here we have shown that savanna nutrient relations are determined by complex interactions of biotic and abiotic ecosystem components, and that our knowledge about savanna nutrient relations is extremely limited. With this mind, we conclude that the current clearing of low nutrient savannas in Queensland carries the risk of nutrient depletion. While increases in pasture production may be an initial short-term response to clearing, the success or failure of pastures on cleared low nutrient savannas will become evident in the medium-term future. Evidence is required that demonstrates that resulting pastures are sustainable in the long-term prior to large scale clearing of low nutrient savannas.

* Redistribution of water and nutrients from deeper soil by woody vegetation
* Increased water & nutrient availability in upper soil

A

* Loss of ecosystem functioning
* Degraded, nutrient depleted system
* Unsustainable pasture production

B

Fig. 3. A & B Conceptual diagram of savanna before and after clearing. This scenario assumes that trees have an important function in redistributing water and nutrients in the soil profile (see text for details).

Recommendations for research

A variety of time and cost efficient techniques is available to study savanna nutrient relations, ranging from *in situ* measurements of soluble soil nutrients, comparison of nutrient uptake and transport processes in different species, to stable isotope tracers. Addressing the following key questions would help to understand the role of vegetation components and suitability of pasture species in relation to nutrient relations and understand nutrient cycle characteristics.

- How is the soil organic matter pool affected by clearing?
- Do woody and herbaceous species exploit soil nutrients complementary or competitively?
- Do woody plants capture nutrients from the deeper soil profile, thus recycling nutrients that are otherwise lost from the system?
- Do exotic grasses access nutrients more effectively than native grasses?
- Do deep-rooted exotic grasses such as buffel grass act as surrogate woody plants in relation to nutrient uptake patterns?
- How much nitrogen is lost through run-off, volatilisation or leaching in Australian savanna and gained via N_2 fixation and aerial deposition in natural and cleared savanna?

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