

Soil organic carbon content at a range of north Australian tropical savannas with contrasting site histories

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Abstract

Soils play an important role in the global carbon cycle, and can be major source or sink of CO₂ depending upon land use, vegetation type and soil management practices. Natural and human impact on soil carbon concentration and storage is poorly understood in native north Australian savanna, yet this represents the largest carbon store in the ecosystem. To gain understanding of possible management impacts on this carbon pool, soil organic carbon (SOC) of the top 1 m of red earth sands and sandy loams common in the region was sampled at 5 sites with different vegetation cover and site history (fire regime and tree removal). SOC was high when compared to other published values for savannas and were more comparable with dry-deciduous tropical forests. Sites sampled in this study represent high rainfall savannas of northern Australia (> 1600 mm annual rainfall) that feature frequent burning (2 in 3 years or more frequent) and a cycle of annual re-growth of tall C₄ grasses that dominate the savanna understorey. These factors may be responsible for the higher than expected SOC levels of the surface soils, despite high respiration rates. Medium term fire exclusion (15-20 years) at one of the sampled sites (Wildlife Park) dramatically reduced the grassy biomass of the understorey. This site had lower SOC levels when compared to the grass dominated and frequently burnt sites, which may be due to a reduction in detrital input to surface (0-30 cm) soil carbon pools. Exclusion of trees also had a significant impact on both the total amount and distribution of soil organic carbon, with tree removal reducing observed SOC at depth (100 cm). Soil carbon content was higher in the wet season than that in the dry season, but this difference was

not statistically significant. Our results indicated that annual cycle of grass growth and wildfire resulted in small carbon accumulation in the upper of the soil, and removal of woody plants resulted in significant carbon losses to recalcitrant, deep soil horizons greater than 80 cm depth.

Key words: carbon cycling, wet-dry tropics, savannas, Australia, fire, tree clearing

Introduction

The amount of carbon (C) in the soils of the world, estimated between 1000-3000 Pg (1Pg=10¹⁵g), constitutes approximately two-thirds of the C in terrestrial ecosystems and is an important component of the global C cycle (Houghton et al., 1987; Jobbagy and Jackson, 2000; Post et al., 1982). In addition to the large size of this pool, soil C has a strong interaction with the atmosphere and responds to change in land cover and land managerial practices (Jobbagy and Jackson, 2000).

The amount and distribution of SOC affects and is affected by plant production (Jobbagy and Jackson, 2000). Numerous important processes in forest ecosystems, such as nutrient cycling, cation exchange capacity and soil water storage are all strongly influenced by SOC. Carbon storage in soils is a dynamic balance between detrital inputs (primarily litter and dead roots) and organic matter outputs in the form of CO₂ efflux from the soil. Generally, in young, rapidly growing forests, the highest rates of C accumulation are observed, whereas in mature forests, C storage in soil approaches a steady state where output nearly equals inputs (Simmons et al., 1996). Cultivation of forestland for agriculture is considered to result in net losses of soil carbon, whereas forest regrowth results in a significant increase in soil carbon content (Thuille et al., 2000).

Globally, the relative distribution of SOC with depth has stronger association with vegetation than ₄ climate, but the opposite is true for

the total amount of SOC (Jobbagy and Jackson, 2000). Changes in the dominant plant life form or community type (e.g. grasses, shrubs or trees) greatly influence soil C content, chemistry and distribution, as plant life forms differ in litter chemistry, patterns of detrital input and rooting depth (Gill and Burke, 1999). In addition, plant life forms typically differ in the depth and distribution of their root systems (Jackson et al., 1996; Nepstad et al., 1994), which influences the amount and distribution of soil C. In a study assessing the amount and distribution of soil C below woody vegetation and grasses, Gill and Burke (1999) reported that there was significantly more soil C beneath woody communities than grass dominated ecosystems and the invasion of grasses into shrub-lands influenced the soil C content of only the upper 30 cm of the soil profile.

Temperature and moisture are two critical environmental factors influencing soil respiration and soil C storage. In general, SOC increases with increasing precipitation, decreasing temperature, and decreasing evapotranspiration / precipitation ratio (Amundson et al., 1989; Jobbagy and Jackson, 2000; Post et al., 1982). Soil organic matter varies inversely with temperature at the landscape scale (Arrouays et al., 1995; Tate, 1992). After reviewing a total of 2696 soil profile data sets from almost every terrestrial biome in the world, Post et al. (1982) reported that warm temperate and dry tropical forests generally had the smallest soil C content, while wet boreal and tropical forests had the largest values.

With structural complexity in tree-grass composition, a history of frequent fires and marked wet and dry seasons and a range of land use pressures, savannas have a potentially dynamic SOC. The

composition and density of trees and grasses in savannas affects both above- and below-ground production, quality of litterfall and vertical root distribution (Belsky, 1994; Priess et al., 1999; Walker et al., 1972), which controls organic C inputs to the soil. Fire can increase or decrease primary production and SOC in savanna ecosystems, depending on fire frequency, intensity and interval time (Anderson et al 2004, Bird et al., 2000). For sites in sub-tropical savanna of Zimbabwe, Bird et al. (2000) observed that reduced fire frequencies resulted in 10% increase in SOC of the top 0-5 cm soil, while higher fire frequencies resulted in a 10% decrease. Total exclusion of fire over a 50-year period resulted in a 40-50 % increase in soil C.

Given the seasonal nature of climate in savanna regions, there is typically a distinct seasonal trend in soil CO₂ efflux, fine root production and litterfall (Chen et al. 2002, Cavelier et al., 1999; Keith et al., 1997; Sundarapandian and Swamy, 1996). Such seasonal patterns of C input to the soil have been observed in the tropical savanna of northern Australia (Chen et al., 2002; 2004) and given the strongly seasonal climate, SOC content could also exhibit seasonal changes despite the inherent stability of SOC. There are few published values of SOC storage in northern Australia and there are no studies examining seasonal changes and differences due to site history. In this paper we hypothesise that *Eucalypt* open-forest savanna, the dominant vegetation of the northern Australia, has greater SOC than a tree-less grassland site, as the former has more detrital inputs (both above- and below- ground) than the latter. Moreover, it is proposed that the vertical distribution of soil C will be different in the two communities. Given the seasonality of climate and detrital input to the soil, the soil C of the upper soil changes with

season. The objectives of the present study, therefore, were to (1) provide values of soil C storage for the wet and dry seasons in this tropical ecosystem, (2) determine the influence of plant form (tree-grass savanna or grassland) on soil C storage and distribution and (3) compare SOC at a site where fire has been excluded to sites with a frequent burning regime.

Materials and methods

Study sites

Five sites of the Darwin region (12⁰30'S, 130⁰45'E), Northern Territory, Australia, were used in this study. These were Humpty Doo, Howard Springs, the Territory Wildlife Park, located approximately 35 km south-east of Darwin. The two other sites, a grassland and an adjacent open forest savanna site were situated on the Gunn Point Peninsula, approximately 30 km to the north of the Howard Springs site. The climate of all sites is similar, wet-dry tropical, with approximate 95% of the 1700 mm annual rainfall occurring during the wet season (November to April) and the dry season (May to October) is characterised by little or no rainfall. Solar radiation and temperature are high year-round. Average maximum and minimum temperatures are 31.8 and 24.8 °C, respectively, in the wet season and 30.5 and 20.0 °C, respectively, in the dry season.

Vegetation of the study region is dominated by *Eucalypt* open-forest and woodland savanna (Fox et al. 2001). *Eucalyptus tetrodonta* and *E. miniata* are the two dominant species occupying the overstorey and they account for approximate 80% of the tree basal area of 8-10 m² ha⁻¹ and

75% of standing biomass of 5.5 kg m^{-2} (O'Grady et al., 2000). Overstorey LAI ranges from 0.6 during the dry season to 1.0 during the wet season (O'Grady et al., 2000). Sub-dominant tree species include *Erythrophyleum chlorostachys*, *Terminalia ferdinandiana*, *Eucalyptus porrecta* and *Eucalyptus bleeseri*. The understorey is dominated by annual grasses such as *Sorghum* spp. and to a lesser extent, perennial grasses, plus semi-deciduous and deciduous small trees and shrubs. The annual grass growth occurs during the wet season, with understorey LAI reaching 1.5 by February-March (Hutley, unpublished data), giving a total seasonal range of LAI in these savannas of 2.5, declining to 0.6 by the dry season. This vegetation type was found at the Howard Springs, Humpty Doo and savanna site at Gunn Point. Savanna vegetation at the fire-excluded Wildlife Park site differed, with higher tree canopy (18 m), lower tree density and greatly reduced occurrence of annual grasses with a higher density of understorey shrub species.

Soils at all sites were typical of the sandy or sandy loam red earths of the Koolpinyah surface (Calder and Day 1982). These soils are extensively weathered and laterised, with low available N and P (total N, <0.1% Schmidt et al. 1998). The A-horizon is well drained and has a massive and earthy structure. These soils are acidic with pH ranging from 5.4 to 6 with little variation with depth (Fogarty et al. 1984). Surface clay content is typically <5% (Calder and Day 1982), with a gradational transition with depth to a sandy loam or sandy clay loam B-horizon. Between 1-2 m depth, a duricrust of low permeability and variable depth is commonly observed which consisted of ferricrete boulders in a matrix of mottled and heavy clays (Hutley et al., 2000). Prominent macropores, often containing tree roots, are found in this layer. Saturated hydraulic

conductivity is high ranging from 0.5 to 1 m d⁻¹ in surface soils (0-50 cm) depth (Kelley 2002). The presence of macropores have a significant impact on patterns of deep drainage, with a large range of drainage fluxes observed (~0 to >3.0 m d⁻¹). High rates would be due to bypass flow through macropores. Surface gravels of up to 20% by volume were observed at all sites except the Wildlife Park site where soils were deeper, more uniform in structure, with little or no gravel present. Soils at the study sites are classified as petroferric red Kandosols (Isbell 1996), which equates to the Ferralsols soil group of the FAO-Unesco (1997) soil classification.

There is an annual cycle of grass growth in these savannas and fire occurrence is frequent, although fires are typically cool by Australia standards (Williams et al., 1998). Except for the Wildlife Park site, where fire has been excluded for approximately 15-20 years, the other Eucalypt open-forest sites are subjected to frequent burning, about two years in every three or more frequent, a typical regime of these savannas (Williams et al., 1999). The grassland site has been maintained in a tree-less state for approximately 15-20 years (Dr. Dave Bowman person comm.) with grass biomass harvested for hay at irregular intervals and was approximately 0.4-0.5 kg m⁻², significantly higher than the grass biomass of surrounding open forest savanna (0.2-0.3 kg m⁻²).

Soil samples were collected using a hand auger. At each site, three plots, 100 - 200 m apart from each other, were chosen for soil sampling. Within each plot, three replicate holes were augured. Soil samples were taken from the augured soil core within each hole at depths of 0-10, 10-20, 20-30, 30-50, 50-80 and 80-100cm, respectively, giving the soil

depth zones as given in Table 1. Soil samples were brought to the laboratory and passed through a < 2 mm sieve, then dried in an oven at 60 °C for 48 hours. After that soil samples were stored in sealed sample jars for preparation for chemical analysis.

In summary, sampling was undertaken at five sites, with three plots at each site randomly selected and three sample holes augured per plot. To express SOC concentration (%) as a mass per area basis (kg m^{-2}), soil bulk density is required. Soil bulk density data for these red earth soils are available at the Howard Springs study site (Dr. Anthony O'Grady, unpublished data). Bulk density samples were collected from 2 soil pits with soil sampled using ring-samplers of known volume (100 cm^3). These two pits were used to sample soils at 40, 60, 90 and 110 cm depths, with between 5 and 3 replicate samples taken for each depth. In addition, for surface soils (0-5 and 5-10 cm), 5 replicate samples were taken at the Howard Springs site, with ring samplers hammered into the soil surface (5 reps per depth) and a known volume of soil extracted. All samples were dried at 105 °C to obtain dry weight.

Soil organic carbon analysis

SOC was determined using an improved Walkley-Black wet digestion method (Heanes, 1984). Approximately 0.5 g air-dry soil samples (particle size < 0.15 mm) were transferred to graduated test tubes with 2 ml of $\text{NK}_2\text{Cr}_2\text{O}_7$ and agitated, with 4 ml of 98% H_2SO_4 gradually added. The test tubes and contents were then heated in an aluminium block at 135 °C for 30 minutes. Tubes were then allowed to cool to room

temperature and adjusted to a final volume of 20 ml using distilled water. Blank solutions were prepared in the same way. The soil suspension was then allowed to settle and then the supernatant was centrifuged at 3000 rpm for 15 minutes. Absorbance of all spun supernatant was then measured at 600 nm and a standard curve constructed of relative absorbency versus organic-C (mg). A series of organic C standard solutions was prepared by dissolving 0.4754 g sucrose in distilled water, dilute to 100 ml and 1 ml of this solution equates to 2 mg organic C. There was a strong relationship between absorbance at 600 nm and the weight of organic carbon.

Results

Soil carbon concentration in three Eucalypt open-forest savanna sites

At the three Eucalypt open-forest savanna sites, soil C concentration decreased from approximately 3.5% at 5 cm depth to approximately 0.4 % at 100 cm depth (Figure 2). The decline in soil C occurred rapidly within the top 30 cm soil depth and then more gradually from 30 to 100 cm depth. Among the three sites, Howard Springs had the highest value of soil C concentration, followed by the Humpty Doo site and then the Wildlife Park site with the lowest value. A significant difference ($p < 0.01$) of soil C concentration (%) occurred in the upper 50 cm soil depth between Howard Springs and Wildlife Park. There were no significant differences in soil C concentration between the three sites below 50 cm soil depth.

The vertical distribution of soil C concentration was similar in both wet and dry seasons at the Eucalypt open-forest sites, although soil C concentration was slightly higher at the end of the wet season (May) than that at the end of the dry season (October) (Figure 1).

Bulk densities of these red earth soils ranged from 1.42 at 5 cm depth to 1.7 g cm⁻³ at 1 m (Figure 2) and were similar to values given in Calder and Day (1982) for red earths of the Darwin region. Using bulk densities and C concentration for each sampled depth, total soil C storages in the top 100 cm of soil for Howard Springs, Humpty Doo and Wildlife Park site for wet season and dry season were given in Table 1 and Table 2, respectively.

Over half of the total organic C was concentrated in the upper 20 cm soil layer and approximately 80% of soil C was found in 0- 50 cm depth in all three Eucalypt open forest sites (Table 1 and Table 2).

To analyze site and seasonal differences specifically, the replicate organic C contents in kg C m⁻² for each sampled soil horizon were used. Each 1 m replicate auger hole at each site was divided into three zones, UPPER (0-20 cm), MID (30-50 cm) and LOWER (80-100 cm). In addition, total SOC in kg C m⁻² for each hole was calculated. Data were arranged in this way for both wet and dry season and analysed as a fixed two-way ANOVA (SITE and SEASON as factors) with depth (UPPER, MID, LOWER) set as a covariate, i.e. SOC varied in a similar fashion with depth at all sites. All data were log transformed to stabilise variances and results are given in Table 3.

The ANOVA showed both site and seasonal differences and *post hoc* comparison of means (Tukey HSD tests) revealed significant differences between Howard Springs and Wildlife Park sites for both the wet ($P < 0.01$) and dry seasons ($P < 0.01$). There were no differences between Howard Springs and Humpty Doo sites, nor differences between Humpty Doo and the Wildlife Park, for either season. To examine site and seasonal differences including soil depth, data were also analysed as a 3 factor fixed design with soil depth as a factor (and not a covariate). In general, this analysis showed few differences between sites and season and soil depth, with the only significant differences being found between Howard Springs and Wildlife Park sites for the MID soil depth during the dry season ($P < 0.039$) and for the LOWER depth zone during the wet season ($P < 0.021$). The use of this design runs the risk of a Type I error as there was a significant interaction and conclusions must be treated with caution. Data used in these statistical analyses are given in Figure 3. Total soil C storage did not change significantly between seasons (Figure 3).

Soil carbon content of the grassland and savanna sites

Figure 4 showed the patterns of soil C concentration (%) with soil depth for the grassland and adjacent open forest savanna at Gunn Point. Soil C concentration was higher in Eucalypt open-forest than in grassland at all depth zones, with differences particularly large at depth (Figure 4). Total SOC at the savanna site was higher than the adjacent grassland site (Table 3, Figure 5a). The difference between the two communities was 6.8 kg m^{-2} , with the mean total SOC $13(\text{kg m}^{-2})$ at the grassland site being

16.1 kg m⁻² and at the adjacent savanna site was 22.9 kg m⁻² (Figure 5a). These means were significantly different (one-way ANOVA, F=17.1, df=15, P < 0.001).

To examine these differences statistically, values were again converted into SOC (kg m⁻²) and again grouped into UPPER, MID and LOWER depth zones (Figure 5b). Two-way ANOVA suggested that the MID (P < 0.029) and LOWER (P < 0.001) soil depths were significantly different.

Discussion

For most ecosystems, SOC represents the most stable C pool. Change to this C pool is generally slow, occurring at decadal to century time-scales and driven by changes in vegetation cover, vegetation type and land use. In savannas, long-term changes in SOC are largely due to changes in fire regime and grazing pressure (Ringrose et al., 1998, Northup and Brown, 1999). In this study, estimates of SOC were undertaken in savanna ecosystems of varying fire history (frequently burnt, Howard Springs, Humpty Doo vs unburnt, Wildlife Park) and structure (grassland vs adjacent open forest savanna). By examining such a set of sites, the range of the soil C pool can be established and can be incorporated into a savanna C balance (e.g. Chen et al. 2003).

Generally savannas have a low SOC content when compared to tropical forest or temperate grasslands (Montgomery and Askew, 1983; Scholes and Hall, 1996). However, values of 14SOC at the sites sampled in this

study were higher than those typically found in savannas. The organic C concentration of surface soils (0-10 cm depth) had a mean of approximately 3.5% and in general were higher than the limited data available for soils of the humid savannas in the Darwin region. For surface soils (0-10 cm), Fogarty et al. (1984) gave values ranging from 1.2% to 3.5% SOC for soils from 0-10 cm depth for a number of red earth soil types supporting *E. tetradonta* and *E. miniata* open-forest, as sampled in this study. They also reported a value of 4.2% for a massive grey earth, higher than values found in this study, although these soils tend to be waterlogged during the wet season and supported a dense covering of grass and sedge growth which may account for the SOC being higher than that of the well drained red earths. However, it is unlikely that waterlogging is the cause of high SOC values as reported for the red earth soils of the current study, as these soils are well drained. Ponding has been observed during monsoonal downpours but waterlogging is short-lived (hours) and excess water drains away. Calder and Day (1982) also reported values of 2.4 % for surface soils of a red earth of the Douglas-Daly region of the Northern Territory (150 km south of the present study sites, receiving a lower annual rainfall of approximately 1300 mm). Values of SOC (%) at depth (> 50 cm) in the present study were also higher than those given by Fogarty et al. (1984).

SOC tends to be more than three-quarters of the total ecosystem C stocks in woodlands and savannas (Scholes and Hall, 1996). The SOC density in these *Eucalypt* open forest savannas ($15 \pm 3.3 \text{ kg C m}^{-2}$) was higher than the global savanna mean ($5.7 \pm 4.6 \text{ kg C m}^{-2}$) but was similar to the mean for tropical woodlands ($11.8 \pm 5.4 \text{ kg C m}^{-2}$) as given by Scholes and Hall (1996). The high levels of SOC of these savannas may reflect the

high below-ground C allocation and productivity, mainly due to fine root growth during the wet season. At the Howard Springs site, below-ground biomass allocation was 57% of total vegetation biomass, a high value for woody dominated ecosystems (Chen et al 2003). Despite high year to year variation in annual rainfall (Taylor and Tulloch, 1985, Cook and Heerdegen 2001), grass growth in the understorey and the large annual flushing of fine roots in these savanna (Chen et al 2004) occurs every year and represents a significant sequestration of carbon, both above- and below- ground (approximately $0.6 \text{ kg C m}^{-2} \text{ y}^{-1}$). While above-ground grass biomass is lost to fire, the annual below-ground biomass is not fire affected and this results in detrital accumulation in excess of soil respiration. At the Howard Springs and Wildlife Park sites, measurements of litterfall and net root production have been made (Chen et al., 2003; 2004) plus estimates of soil respiration (Chen et al., 2002). During the study period of 1999 to 2001, C inputs to the soil via litterfall and root production less losses due to soil respiration resulted in a net soil C exchange of $0.07 \text{ kg C m}^{-2} \text{ y}^{-1}$, suggesting a small annual net accumulation of SOC. The significant woody component of these savannas (evergreen trees to 16 m in height, 700 trees per ha) includes deep rooted evergreen trees that are able to contribute to the SOC pool, especially at depth (1 m, Figure 4). Sites used by Scholes and Hall (1996) to derive global mean savanna SOC tend to have lower rainfall than those of this study, which have a wet season rainfall in excess of 1600 mm. Soil C reported in this study therefore represents a measure of SOC in one of the wetter savanna sites in the world.

Site differences - tree removal

Savanna vegetation of sites examined in this study has different structure (presence/absence of trees and grass), due to differing fire history or past tree removal. Although the amount of SOC at the grassland site was within the range of SOC of the other three sites (Howard Springs, Humpty Doo and Wildlife Park), the value of the grassland site is significantly lower (ANOVA, $F = 17.1$, $df = 15$, $P < 0.01$) than that of the adjacent Eucalypt open forest savanna. This suggests that the presence of trees results in an increase of SOC, which is consistent with the finding of Gill and Burke (1999). They reported that there was significantly more organic C stored in soils beneath woody plants than beneath grass-dominated sites in the semi-arid savannas of Texas and Utah, USA. This 30% increase in SOC in the tree-grass savanna of Gunn Point is attributable to increases in C input to the soil from grass plus tree litterfall, root production and turnover from the deep-rooted evergreen trees.

Site differences - fire exclusion

The amounts of SOC at the Humpty Doo and Wildlife Park sites were approximately 80% and 64% of that at Howard Springs, respectively (Table 1 and Table 2), and differences between Howard Springs and the Wildlife Park sites were statistically different (Table 3). Soil organic content at Humpty Doo was lower than that at the Howard Springs site, possible due to lower stand density at Humpty Doo, although these differences were not statistically significant.

The significant differences in SOC between the Howard Springs and Wildlife Park are likely to be due to fire history, as the Wildlife Park has had fire excluded for more than 15 17years, whereas savanna at the

Howard Springs site is burnt approximately twice every 3 years. Little is known of the impacts of fire on SOC pools in tropical savanna (Bird et al., 2000). Most studies suggest frequent fire reduces soil C pools over time (decadal to century time scales), through changes to above-ground vegetation dynamics, their detrital inputs to the SOC pool and root biomass. Fire reduction favours woody re-growth and thickening while increased fire frequency favours a grass-dominated savanna. Fire can also influence soil microbial populations, inorganic and organic nutrient levels (especially nitrogen cycling, Andersson et al. 2004) and can alter soil hydraulic properties (Poth et al., 1995). Daly et al. (2000) simulated root distributions of tree-grass systems and the influence of fire and found that shallow-rooted grasses resulted in smaller soil C pools over the long term. Bird et al. (2000) examined fire impacts on SOC in sub-tropical savanna of Zimbabwe and found a 40-50 % increase in soil C in 50-year-old fire exclusion plots. However, decreases of only 10% were observed in plots where the fire frequency had been reduced rather than fire excluded.

In contrast to the studies cited above, exclusion of fire for 15 years or more from the Wildlife Park significantly reduced the SOC when compared with the frequently burnt Howard Springs site. This difference in sites was apparent during both the wet season and dry season. The exclusion of fire at the Wildlife Park also reduced the annual grass biomass to almost zero and increased woody shrubs in the understorey. When compared to trees, grasses tend to have a shallow rooting system (Jackson et al. 1996), which reduces the vertical SOC distribution (Trumbore, 2000). Detrital input from shallow rooted grasses (0-30 cm) can be inferred from the higher SOC levels of the upper soil zone of

the burnt site (Howard Springs) compared to the Wildlife Park (ANOVA $F=5.28$, $df=12$, $P < 0.021$).

Considering the entire soil profile, the complete removal of trees at the Gunn Point sites resulted in a 30 % decline in total SOC, with the soil C content of the adjacent savanna (22.9 kg m^{-2}) being significantly higher than the grassland site (16.1 kg m^{-2}). While removal of trees from these savanna has reduced SOC, removal of annual grasses via fire exclusion has also reduced SOC, at least of the upper soil horizons (0-50 cm). In humid tropical savannas of northern Australia, the high temperatures and non-limiting available soil water during the growing season results in high annual primary production for grass and fine roots, and the grass dominated understorey makes a large contribution to upper soil organic pools, despite losses due to the impact of fire and high decomposition and respiration rates (Chen et al., 2002). The cycle of fire and vigorous annual grass re-growth may cause an accumulation of organic C in the soil as primary production of tropical grasses can increase by about 20% in the season after a fire (Scholes and Hall, 1996). However, such increases may only be observed in the upper soil horizons (0- 30 cm), as reduced tree cover will tend to decrease deep recalcitrant soil C pools (Boutton et al., 1999). Such a trend has been observed in this study, with the amount of SOC at depth (80 - 100 cm) at the grassland site (2.5 kg C m^{-2}) being significantly lower than that observed at any of the treed-savanna sites ($3-7 \text{ kg C m}^{-2}$).

Seasonal differences in soil organic carbon

In this study a small difference of 19SOC content (about 10%) was

observed between wet and dry season sampling. Reduced late-dry season SOC (October) would represent cumulative losses from respiration following the low below-ground productivity of the previous 4 to 5 months (June to September). However this seasonal difference was not statistically different (Table 3). Sampling occurred within a single year and large changes to the total soil C were not expected, given the fact that the net flux to the soil C pool is small relative to the total pool size. In fact, on an annual basis, when inputs from root detritus and litterfall minus soil respiration are considered, there was a small net increase to the total soil C pool in these savannas of $0.07 \text{ kg C m}^{-2} \text{ y}^{-1}$, although this change is very small relative to the total soil C pool of 15.1 kg C m^{-2} . Further sampling over a number of wet-dry cycles at a larger number of sites would be required to more thoroughly examine the hypothesis that given the frequent disturbance and seasonal climate, SOC is variable on a short-term basis in this ecosystem.

Conclusions

We have presented SOC data for a tropical ecosystem subjected to frequent fire with a strongly seasonal climate. These savanna ecosystems are a mosaic of vegetation types due to differing soils, subtle drainage patterns and fire histories. To provide a mean value of SOC store for this ecosystem requires a degree of spatial sampling. We have therefore sampled at savanna sites that represent extremes of this range in terms of site histories (no fire to frequent fire, tree-grass savanna to grassland) to examine the range of values that occur in this

environment and what impact such factors may have on soil C. The role of tree cover and fire frequency were found to have major impacts on SOC. The annual growth cycle of the C₄ grasses also made a large contribution to SOC of the upper soil horizons, despite losses due to fire and high decomposition and respiration rates.

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Table 1. The vertical distribution of soil carbon storage (kg m^{-2}) at three *Eucalypt* open forest sites in Northern Australia at the end of the wet season (May).

Soil depth (cm)	Howard Springs		Humpty Doo		Wildlife Park	
	Amount	%	Amount	%	Amount	%

0-10	5.3	26.8	4.9	30.8	4	31.7
10-20	3.9	19.7	2.4	15.1	2.2	17.5
20-30	2.8	14.1	1.8	11.3	1.5	11.9
30-50	3.5	17.7	3.0	18.9	2.5	19.8
50-80	2.8	14.1	2.3	14.5	1.5	11.9
80-100	1.5	7.6	1.5	9.4	0.9	7.1
Total	19.8	100.0	15.9	100.0	12.6	100.0

Table 2. The vertical distribution of soil carbon storage (kg m^{-2}) at three *Eucalypt* open forest sites in Northern Australia at the end of the dry season (October).

Soil depth (cm)	Howard Springs		Humpty Doo		Wildlife Park	
	Amount	%	Amount	%	Amount	%
0-10	5.4	30.7	5	36.5	3.7	33.3
10-20	3.1	17.6	2	14.6	2.1	18.9
20-30	2.5	14.2	1.5	10.9	1.2	10.8
30-50	2.9	16.5	1.5	10.9	1.7	15.3
50-80	1.9	10.8	2.2	16.1	1.5	13.5
80-100	1.8	10.2	1.5	10.9	0.9	8.1
Total	17.6	100.0	13.7	100.0	11.1	100.0

Table 3. Two-way fixed ANOVA for SOC for Howard Springs, Humpty Doo and Wildlife Park sites. In this analysis, depth was set as a covariate.

	df Effect	MS Effect	F	p-level
Site	2	1.184	23.54	0.000
Season	1	0.310	6.15	0.017
Site * Season	2	0.003	0.06	0.946
Error	47	0.050		

Table 4. SOC storage (kg m^{-2}) in *Eucalypt* open forest and grassland in tropical Northern Australia.

Soil depth (cm)	<i>Eucalypt</i> open-forest		Grassland	
	Amount	%	Amount	%
0-5	3.1	13.5	2.8	17.4
5-10	2.0	8.7	1.9	11.8
10-20	3.6	15.7	3.0	18.6
20-30	2.7	11.8	2.3	14.3
30-50	4.5	19.7	3.6	22.4
50-80	4.2	18.3	1.6	9.9
80-100	2.8	12.2	0.9	5.6
Total	22.9	100.0	16.1	100.0

Figure 1. Distribution of soil carbon concentration (%) along the soil profile at the three sites used: (a) at the end of wet season, (b) at the end of dry season. The error bars represent the standard deviation of the mean.

Figure 2. Distribution of soil bulk density along the soil profile at northern Australia. The error bars represent the standard deviation of the mean.

Figure 3. (a) Seasonal and site differences in mean SOC (kg m^{-2}) and (b) and (c) coarse distribution of SOC with depth for sampling during the wet and dry seasons, respectively. The error bars represent the standard deviation of the mean.

Figure 4. Comparison of soil carbon concentration vertical distributions for the *Eucalypt* open-forest savanna and grassland sites. The error bars represent the standard deviation of the mean.

Figure 5. (a) Site means and standard deviations for the grassland and adjacent savanna sites at Gunn Point. The coarse distribution of soil organic carbon for the two sites is given in (b).

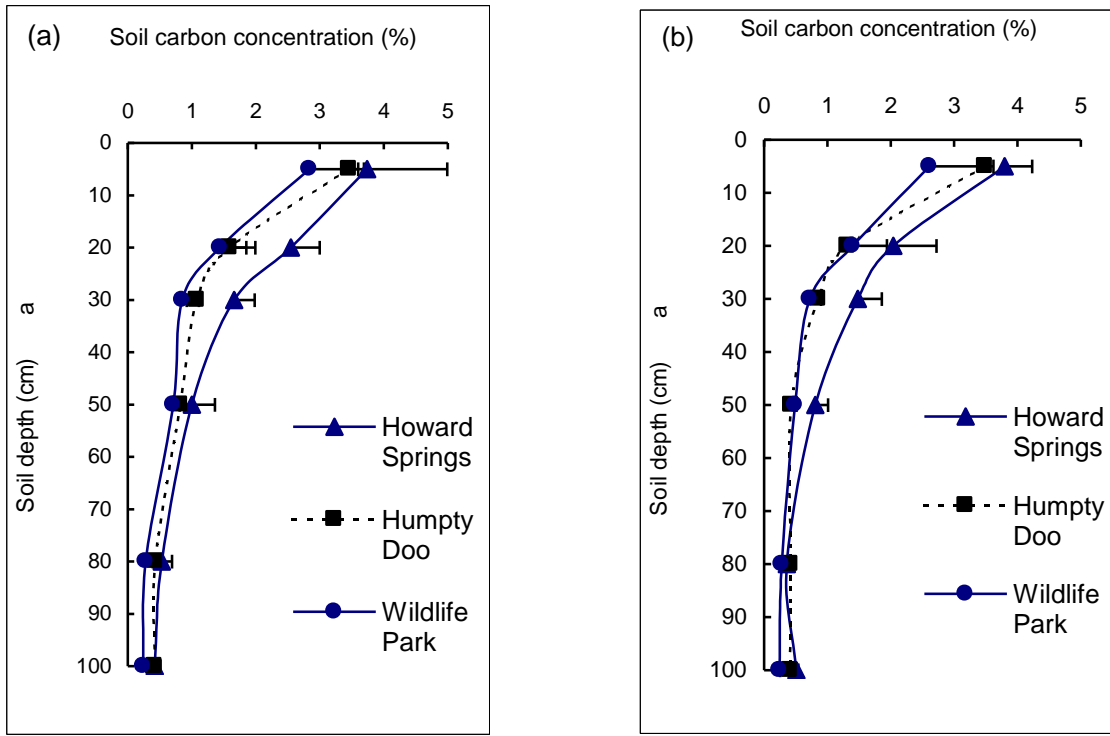


Figure 1. Distribution of soil carbon concentration (%) along the soil profile at the three sites used: (a) at the end of wet season, (b) at the end of dry season. The error bars represent the standard deviation of the mean.

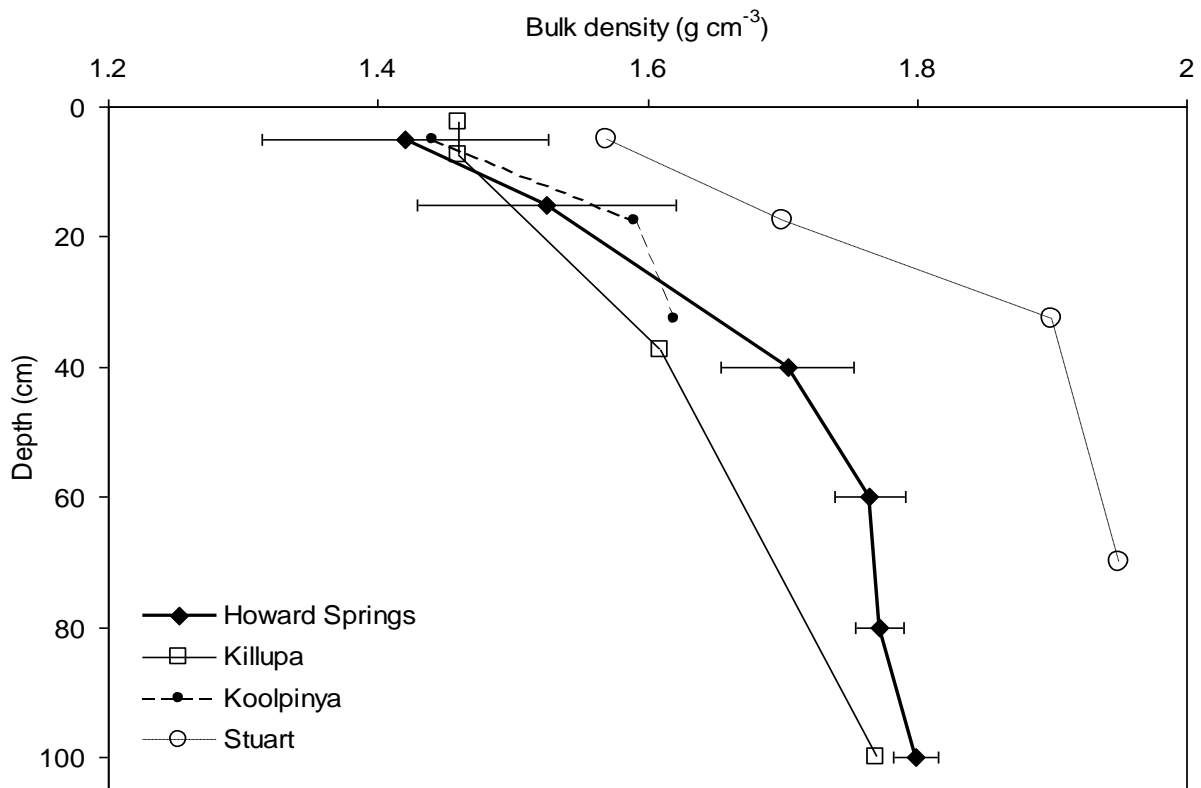


Figure 2. Distribution of soil bulk density with depth for red earth soil at the Howard Springs site. Error bars are the standard deviation of the mean. Comparative data are also given for typical red earth soils of the Koolpinyah surface, 'Killupa', 'Koolpinyah' and 'Stuart' soil types as described by Calder and Day (1982).

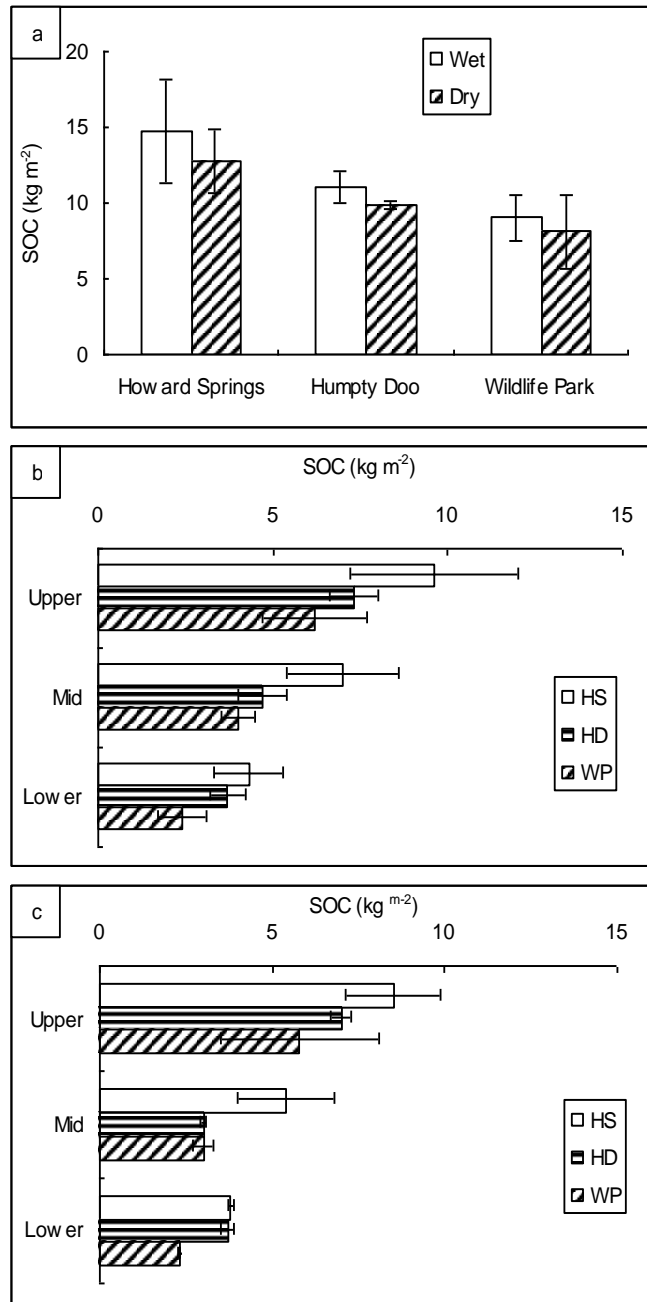


Figure 3. (a) Seasonal and site differences in mean SOC (kg m⁻²) and (b) and (c) coarse distribution (UPPER, MID and LOWER) of SOC with depth for sampling during the wet and dry seasons, respectively. The error bars represent the standard deviation of the mean.

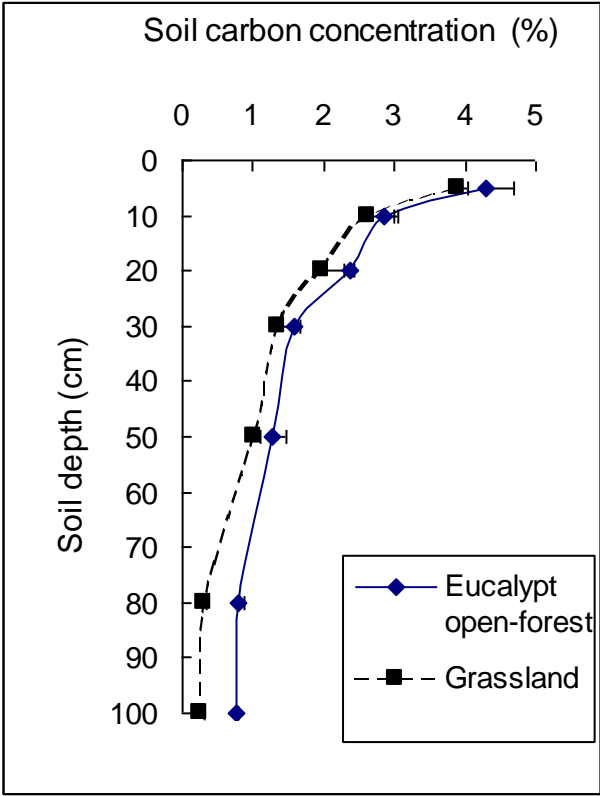


Figure 4. Comparison of soil carbon concentration vertical distributions for the *Eucalypt* open-forest savanna and grassland sites. The error bars represent the standard deviation of the mean.

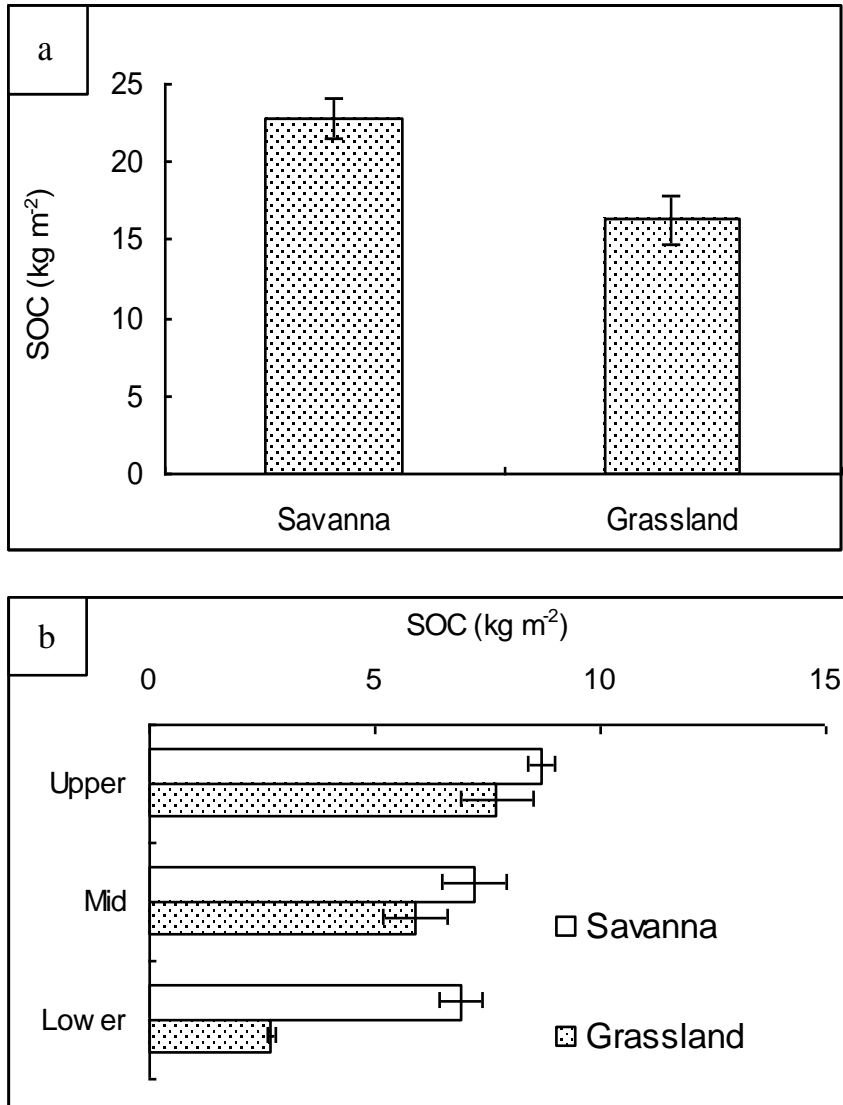


Figure 5. (a) Site means and standard deviations for the grassland and adjacent savanna sites at Gunn Point. The vertical distribution of soil organic carbon for the two sites is given in (b). The error bars represent the standard deviation of the mean.