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Carbon cycle processes in tropical savannas of far north Queensland, Australia

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Thesis submitted for the degree of

DOCTOR OF PHILOSOPHY

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and the Centre for Tropical Environmental and Sustainability Science

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Statement on the contribution of others

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Additional contributions to each chapter are stated at the beginning of each chapter.

Abstract

Tropical savannas represent a diverse range of heterogenous ecosystems that play an important role in the global carbon cycle as they occupy approximately one fifth of the land surface. Despite their significance, there remains a paucity of studies that quantify the carbon stocks and fluxes of these dynamic ecosystems, particularly within Australia (Chapter 1). This study contributes to the field of tropical savanna carbon cycle dynamics by quantifying the carbon stocks and fluxes at three study sites in northern Queensland and placing them in the context of climate change and the global carbon cycle.

Chapter 2 presents a review of the ecology and carbon dynamics of tropical savannas. The chapter addresses uncertainty regarding the definition and extent of tropical savannas, and the state of knowledge surrounding the drivers behind the extent of tropical savannas. In particular, stochastic disturbances such as fire play a crucial role in these ecosystems. Tropical savannas are also unique in that they consist of a mix of distinct and competing vegetation in the form of trees and grasses, that generally utilise contrasting photosynthetic strategies. As these photosynthetic pathways respond differently to atmospheric CO₂ and temperature, how these ecosystems will respond to climate change is also a matter of some uncertainty.

Chapter 3 presents a detailed description of the three sites used in this study; two of the sites (Davies Creek and Koombooloomba) are located near the rainforest-savanna boundary in a high rainfall zone (mean annual precipitation (MAP) ~ 1500mm) while the third site (Brooklyn Station) is both more arid (MAP ~900mm) and more seasonal.

In Chapter 4, aboveground biomass (AGB) and aboveground net primary productivity (ANPP) is quantified using an inventory-based assessment. These sites are some of the more densely wooded tropical savannas in Australia and basal area remained unchanged at all sites over the sample interval. While the carbon stocks in the AGB (40, 75, and 87 t C ha⁻¹ for Brooklyn Station, Davies Creek, and

Koombooloomba, respectively) were dominated by the tree component, the grassy understorey was a significant contributor to ANPP (4.1, 5.1, and 9.2 t C ha⁻¹ y⁻¹ for Brooklyn Station, Davies Creek, and Koombooloomba, respectively) at all sites, consisting of almost three quarters of the total. The woody carbon stock was sensitive to disturbance with high mortality at two sites attributed to damage caused by fire and Tropical Cyclone (TC) Yasi. These results highlight the sensitivity of the carbon storage potential of tropical savannas to stochastic disturbance and their vulnerability to substantial shifts in both structure and composition as a result of climate change.

Chapter 5 presents data on soil carbon and nitrogen, as well as their stable isotopes. Soil carbon stocks (0-30cm) were 114 ± 25, 41 ± 14, and 38 ± 19 t C ha⁻¹ at Koombooloomba, Davies Creek, and Brooklyn Station, respectively. The carbon isotopes were used to partition the soil carbon into C₃ and C₄ sources; the grassy understorey contributed approximately half of the soil carbon at two of the sites (Brooklyn Station and Koombooloomba), but contributed only 27% at the third site. Soil carbon displayed a high level of spatial arrangement at the two wettest sites with higher soil carbon in areas adjacent to trees, but not at the driest site and redistribution of carbon inputs by termites may be responsible. Although considerable quantities of soil carbon are stored at these sites for now, climate change may result in vegetation shifts, changes to fire regimes, and exacerbated erosion that could result in the loss of soil carbon from these sites.

Chapter 6 provides the most comprehensive dataset of soil respiration in tropical savannas in Australia. Soil respiration was measured monthly for two years at the three sites. Soil respiration was temporally controlled by temperature and moisture availability, with high respiration rates (~4-8 μmol m⁻² s⁻¹) during the wet season (November - April) when plant growth is high, and low respiration rates (~1-4 μmol m⁻² s⁻¹) during the dry season (May - October) when plant growth slows. Soil respiration was spatially variable and controlled by proximity to woody vegetation with high soil respiration rates near trees and low soil respiration rates in open areas dominated by grasses. Soil respiration in these tropical savanna environments is thus both temporally and spatially heterogeneous suggesting that more complex models may be required to accurately estimate the soil respiration in such systems.

In Chapter 7, an experimental drought was created at Davies Creek over two years in order to examine the effects of drought on soil respiration and soil chemistry. The drought successfully reduced soil moisture without impacting significantly on other environmental variables. The drought delayed the growing season of the grasses in

the first year and killed them in the second year. Soil respiration was correspondingly reduced in the first wet season and then increased in the second wet season, likely as a result of these changes to plant biomass availability. Higher soil carbon in the drought experiment suggests that there were additional carbon inputs, presumably due to the death of the grass and subsequent recolonisation of the soil by neighbouring grasses. Extended droughts could see shifts in species and ecosystems potentially accompanied by an increase in soil respiration before ecosystem stability is reached.

This study presents the first comprehensive assessment of carbon cycle dynamics in tropical savannas in Queensland. Furthermore, this is the first study in Australia to examine transition zone savannas that occur at the rainforest-savanna boundary and the first study in Australia to attempt to simulate drought in tropical savannas.

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Terms and Abbreviations

aboveground net primary productivity (ANPP) The rate at which plants assimilate carbon as aboveground biomass gains

aboveground biomass (AGB) All components of plant biomass that occur above the soil including trunk, stems, leaves, *etc.* (*i.e.* all components except roots)

Akaike's information criterion (AIC) A measure of the relative quality of statistical models for a given set of data

alternative stable states (ASS) Ecological theory that postulates two stable ecosystems (such as a forest and savanna) may both occupy the same climatic envelope and that stability is maintained by the presence or absence of fire

Australian Wildlife Conservancy (AWC) Australian nature conservation charity that owns and operates a large number of sanctuaries including the property where the Brooklyn Station field site used in this study is located

belowground biomass (BGB) All components of plant biomass that occur below the soil including fine and coarse roots, root boles, *etc.*

C:N ratio The ratio of carbon to nitrogen in a sample

carbon use efficiency (CUE) The ratio of NPP to GPP

Commonwealth Scientific and Industrial Research Organisation (CSIRO)
The federal government agency for scientific research in Australia. Its chief role is to improve the economic and social performance of industry, for the benefit of the community

diameter at breast height (dbh) The diameter of a tree trunk at breast height (defined as 1.3m)

dry season The cooler period from May to October during which rainfall tends to be low

El Niño Southern Oscillation (ENSO) An irregular cycle in wind speeds and sea surface temperatures over the tropical eastern Pacific Ocean that is influential in driving weather patterns in the southern hemisphere

generalised additive mixed model (GAMM)

Great Dividing Range (GDR) Australia's largest mountain range that runs in a north-south direction along the eastern edge of the continent

gross primary productivity (GPP) The amount of carbon that plants uptake from the atmosphere; this represents the balance between carbon fixed during photosynthesis and carbon that is respired during photorespiration

interquartile range (IQR) The range between the first and third quartiles

mean annual temperature (MAT)

mean annual precipitation (MAP)

net biome productivity (NBP) The rate at which carbon is assimilated as plant biomass at the biome (ecosystem) scale; includes all gains and losses associated with GPP, respiration, decomposition as well as stochastic events such as fire

net ecosystem exchange (NEE) The rate at which carbon is assimilated as plant biomass at the ecosystem scale; includes all gains and losses associated with GPP, respiration and decomposition but typically may not include stochastic losses such as fire. Synonymous with net ecosystem productivity (NEP) although NEE is more commonly used when fluxes are measured from gas exchange rates (for example, using eddy covariance techniques)

net ecosystem productivity (NEP) The rate at which carbon is assimilated as plant biomass at the ecosystem scale; includes all gains and losses associated with GPP, respiration and decomposition but typically may not include stochastic losses such as fire. Synonymous with net ecosystem exchange (NEE) although NEP is more commonly used when fluxes are measured from carbon stock changes (for example, using inventory-based techniques)

net primary productivity (NPP) The rate at which plants assimilate carbon as biomass gains. Represents the balance between GPP and respiration

Northern Australia Tropical Transect (NATT) Part of a global network of sub continental-scale transects that traverse the world's major biomes, under the auspices of the United Nation's International Geosphere-Biosphere Programme

sea surface temperature (SST) Anomalous seas surface temperatures are used to define phases of oscillations such as ENSO

soil organic carbon (SOC) The organic portion of the soil carbon, as distinct from the inorganic portion or the total soil carbon. In many soils there is no inorganic carbon content and so soil organic carbon and soil carbon may be used interchangeably

Tropical Biomes in Transition (TROBIT) Research project examining the role of tropical biome transitions in affecting the magnitude and rate of future climate change

Tropical Cyclone (TC) Low pressure weather systems that form over warm tropical waters and have gale force winds near the centre. Comparable to hurricanes, typhoons, tornados, *etc.*

wet season The warmer period from November to April during which most of the rainfall occurs

Wet Tropics World Heritage Area (WTWHA)

Chapter 1

Introduction

The climate is changing; 2016 was the hottest year globally for the 3rd consecutive year. Global temperatures are now 1.1°C above the pre-industrial average and 16 out of the 17 hottest years on record have occurred since 2000 (WMO, 2017). The effects of climate change are becoming more evident, with extreme weather events occurring around the world including serious drought across southern Africa, above-average hurricane activity in the eastern north Pacific and Atlantic, minimum recorded Arctic and Antarctic sea ice extent, and record temperatures across all continents (NOAA, 2017). Furthermore, in recent decades we have started to see regime shifts in long term climate drivers such as the El Niño Southern Oscillation (ENSO). In 2009-2010, there was an El Niño event that marked record breaking warm sea surface temperature (SST) in the central Pacific. This was followed by the fastest transition on record, to the strongest La Niña event in 8 decades (Boening et al., 2012; Kim et al., 2011).

What is not yet apparent is the effect that climate change will have on the terrestrial carbon cycle. In 2011 there was a 30% anomaly in the terrestrial carbon sink associated with this rapid phase change in the ENSO due to above average plant growth associated with higher rainfall, predominantly due to ecosystems in the southern hemisphere and especially those in tropical and subtropical regions (Bastos et al., 2013; Poulter et al., 2014). 60% of the anomaly in the carbon sink was due to above average net primary productivity (NPP) in Australia alone (Detmers et al., 2015). However, less than five years later, those plants have died back after sustained drought and all the biomass gains have been negated (Ma et al., 2016).

As climate change begins to take its toll, it is imperative that we are able to accurately predict not only how our climate will change under elevated atmospheric CO₂, but also how those climate changes will impact the terrestrial carbon cycle. For this, we need high quality field data on carbon stocks and fluxes of terrestrial ecosystems as well as an understanding of the processes that drive the cycling of carbon through the various pools within terrestrial ecosystems.

The size and diversity of Australia’s ecosystems means there are large gaps in our knowledge of carbon stocks and fluxes across substantial portions of the country. For example, the Australian terrestrial carbon budget published by Haverd et al. (2013a) modelled carbon stocks and fluxes at the national scale using a variety of data sources. These included the 12 OzFlux sites with a distinct lack of above-ground biomass (AGB), litter and soil data from the tropics (Haverd et al., 2013b). Furthermore, our understanding of why carbon is cycled the way it is is even less well understood. Especially in the case of tropical savannas there is a dynamic balance between the trees and the grasses and yet there remains very little work on the relative contribution of each to the productivity of the ecosystem (although see Moore et al. (2015) for a recent contribution from the Northern Territory).

In particular, a lack of soil carbon data is causing large variation and model bias in model projections of the terrestrial carbon sink. As a result, improving spatial coverage of soil carbon data and improving soil carbon projections is of a high priority for earth system modelling (Luo et al., 2016). In Australia, most soil carbon data is for a narrow agricultural strip in the southeast of the country. This means there is a paucity of soil carbon measurements across most of the continent. The variation in the productivity of trees and grasses in the savannas means that soil carbon is extremely variable at relatively small spatial scales. This poses some concerns regarding the suitability of traditional random sampling designs; indeed this is a subject that has been debated extensively (see for example, Chappell et al. (2013) and Allen et al. (2010b)). Despite the sampling challenges that heterogenous vegetation present, the contrasting physiology of trees and tropical grasses means that tropical savannas provide a unique opportunity to examine the cycling of soil carbon in more detail. And yet, this opportunity has also remained largely unexploited (although see Wynn et al. (2006a)).

Finally, soil respiration remains one of the most poorly understood components of the carbon cycle despite being the largest terrestrial flux of carbon to the atmosphere, being an order of magnitude higher than annual fossil fuel emissions (Marland et al., 2007; Schlesinger and Andrews, 2000). This uncertainty is due

principally to the difficulty in accurately sampling not only spatial variability but also substantial temporal variability. Furthermore, as an integration of multiple processes, soil respiration can be difficult to interpret and incorporate into mathematical models. A particular challenge in this area is the upscaling of soil respiration measurements to the plot scale, with most studies simply using the mean of measurements (Phillips et al., 2016). Additionally, describing the relationship between soil respiration and abiotic drivers is critical for modelling the response of soil respiration to climate change. As global temperatures increase, a large release of carbon from the soil would be catastrophic for climate change (Bond-Lamberty and Thomson, 2010b). Notwithstanding, a consensus has yet to be reached on the exact nature of the response of soil respiration to anticipated climatic warming. There is evidence to suggest that both plant (Atkin and Tjoelker, 2003) and microbial communities (Karhu et al., 2014) acclimatise to increased temperatures with the temperature sensitivity of soil respiration decreasing above a threshold of $\sim 25^{\circ}\text{C}$ (Carey et al., 2016). Also of particular concern in tropical savannas are changes to precipitation patterns and extended periods of drought that may be exacerbated by vegetation shifts (Tietjen et al., 2017). Although the global dataset of soil respiration studies is increasing (Bond-Lamberty and Thomson, 2014), there remains a paucity of prior studies of soil respiration in Australian tropical savannas (Chen et al., 2002; Holt et al., 1990; Livesley et al., 2011) and no attempts have been made to simulate or understand the impacts of drought conditions on savanna soil respiration.

This thesis aims to address some of these data gaps and contribute to the field of knowledge on carbon cycling in tropical savannas by quantifying aspects of the carbon cycle at three tropical savanna sites in northern Queensland and placing these results in the context of global carbon cycling and climate change. Chapter 2 provides some background on the ecology of tropical savannas and their role within the carbon cycle in more detail. Chapter 3 describes the three study sites used in the study in terms of their soils, vegetation and climate. Chapter 4 aims to assess the aboveground biomass and productivity of the three tropical savanna sites. Chapter 5 aims to inform our understanding of soil organic matter cycling in tropical savannas by comparing soil carbon, nitrogen, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with soil characteristics. Chapter 6 aims to quantify temporal and spatial variation in soil CO_2 flux in terms of climate drivers and tree/grass abundance and presents a model for up-scaling of point measurements to the plot level. Chapter 7 builds upon Chapter 6 by manipulating water availability at one of the sites to disentangle some of the complexity surrounding the influence of soil moisture on soil respiration. Chapter 8 provides a synthesis of the research and general conclusions.

Chapter 2

Ecology and carbon dynamics of tropical savannas

Statement of contribution

Conceptualised by Kalu Davies and Michael Bird.

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2.1 Abstract

Tropical savannas consist of a diverse range of ecosystems and they are globally important both economically and ecologically, supporting ~40-50% of the world's cropland and pasture as well as maintaining high biodiversity. Within Australia, tropical savannas include some of the more intact ecosystems in a landscape that has been drastically changed over the past two centuries. Comprised of a mix of trees and grasses, tropical savannas encompass characteristics of both forests and grasslands and yet are facilitated by a dynamic relationship with disturbance vectors (particularly fire) that is unique to savannas. In addition, the competition between these distinct life forms results in a complex competition for resources. Although tropical savannas store less carbon than forests, their global extent is so great that they store ~15% of the world's carbon stocks, the majority of which is stored in the soil. Tropical savannas also account for ~25% of global net primary productivity (NPP) and ~60% of the world's fire emissions. The high level of disturbance, dominantly through fire and drought mean that carbon stored in biomass is vulnerable to loss, however the high rate of productivity means that given appropriate management there is potential to rapidly replace those losses. Nonetheless, as atmospheric CO₂ levels continue to increase, there is considerable uncertainty as to how climate change will affect these ecosystems. In addition to changing the frequency and intensity of disturbances, increased CO₂ will likely favour the growth of trees by removing the competitive advantage currently enjoyed by tropical grasses that utilise the C₄ photosynthetic pathway. These changes will potentially shift the tree/grass balance and trigger a suite of feedback cycles that will have serious ramifications for the global carbon cycle.

2.2 Tropical savannas

The Oxford dictionary defines savanna as 'a grassy plain in tropical and subtropical regions, with few trees', however in practice the term encompasses a much wider range of ecosystems. Most authors agree that the term excludes closed-canopy ecosystems but beyond this demarcation there are many variations. The most widely used classification suggests a mixed tree/grass system (for example, Bond and Midgley (2012); House et al. (2003); Ratnam et al. (2011); Scholes and Archer (1997)) although even this vague definition is not entirely accepted. Some authors insist on the presence of grasses, irrespective of a woody component (Grace

et al., 2006), whilst still others require that the grasses follow the C_4 photosynthetic pathway (Lehmann et al., 2011) and C_4 grasses tend to dominate in tropical savannas (Ehleringer et al., 1997). Others maintain that savannas must include a tree or shrub layer (Bond, 2008) while others refer to both grasslands and savanna as ‘savannas’ (Scurlock and Hall, 1998).

Compounding this confusion is the development of a classification system that is applicable on a global scale, with some savanna environments unique to a particular continent (such as the Brazilian *cerrado*). Recently, Torello-Raventos et al. (2013) have suggested a classification system where the term ‘savanna’ is included as a prefix or suffix for all vegetation types with at least 10% herbaceous cover and 5-70% woody canopy cover (Figure 2.1). Irrespective of the classification system used, the ‘tropical’ qualifier generally refers to those ecosystems that lie within between the Tropic of Cancer and the Tropic of Capricorn (Sanderson, 1999). Within this range of latitudes, annual rainfall can vary significantly but generally occurs with pronounced seasonality such that the majority falls during the summer months and is commonly associated with monsoon systems (Feng et al., 2013; Rohr et al., 2016; Sankaran et al., 2005; Scholes and Archer, 1997; Staver et al., 2011a). This delineation can be equally arbitrary and ‘tropical’ may also be defined by a climatic envelope such as that defined by the Köppen-Geiger climate classification system (Peel et al., 2007).

2.2.1 Significance of tropical savannas

As a result of the ambiguity in savanna classification, assessments of the global extent of these ecosystems vary (Parr et al., 2014). They are generally considered, however, to make up between one fifth and one sixth of the land surface (Figure 2.2), covering large areas of tropical Africa, South America, Australia, and to a lesser extent, Asia (Grace et al., 2006; Scurlock and Hall, 1998). Although traditionally regarded as less productive than tropical forests, tropical savannas account for approximately 25% of gross primary productivity (GPP) of all terrestrial vegetation (Beer et al., 2010). Furthermore, grasslands and savannas support a large and increasing proportion of the world’s population through the provision of 38% of global cropland and 48% of global pasture (Monfreda et al., 2008; Ramankutty et al., 2008). Demand for increased food production has led to the conversion of large areas of natural savanna to cropland (Willcock et al., 2016). For example, more than 50% of the 2 million km² of Brazilian *cerrado* has been transformed for human use, mainly supporting pasture

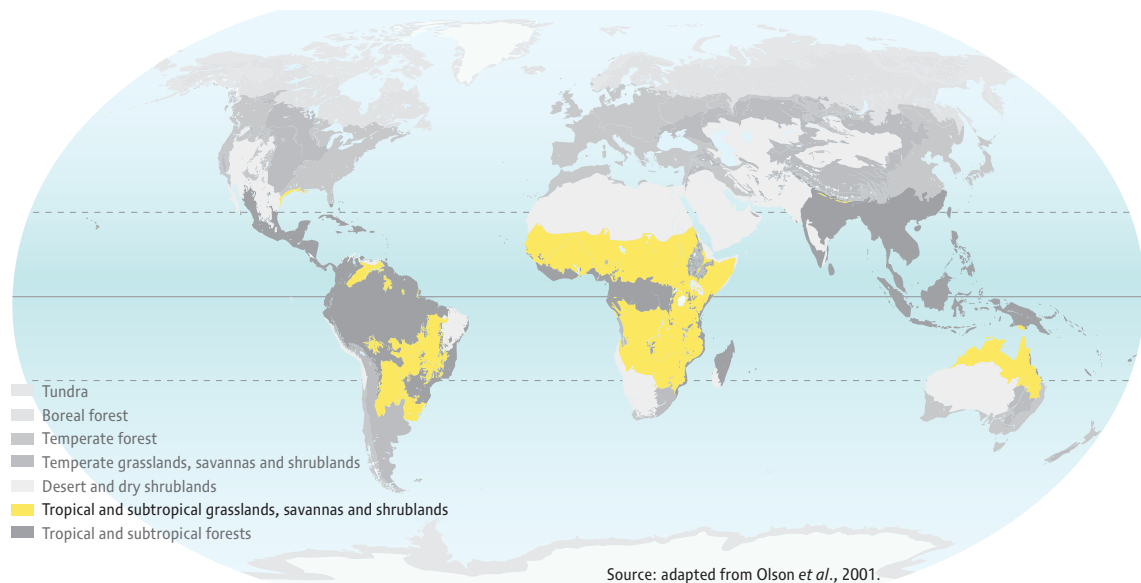


Figure 2.2: Major biomes of the world. Source: Adapted from Olson et al. (2001) by Riccardo Pravettoni, Unet ecosystem productivity (NEP)/GRID-Arendal downloaded from http://www.grida.no/graphicslib/detail/savannas-and-tropical-grasslands_5bca

and cash crops (Klink and Machado, 2005). Furthermore, the majority of the world's tropical pastoral land (65%) occurs in tropical savannas in Africa, with a large part of the remainder occurring in South America, Asia and other developing countries (except the 9% that occurs in Australia (Reid et al., 2004)). The majority of farming in these developing countries is subsistence based. Overgrazing and subsequent degradation of significant areas of land has been attributed to population, economic and climatic pressures (Conant, 2010; Stringer et al., 2012). Nonetheless, the highest rates of overgrazing occur within Australia (Conant and Paustian, 2002).

In addition to supporting a substantial portion of the world's food sources, tropical grasslands and savannas are also a rich source of global biodiversity. In comparison to tropical forests, tropical savannas feature sparsely in the list of the world's top 'biodiversity hotspots' compiled by Myers et al. (2000), with one listing out of the 25. However, tropical savannas have been studied much less than tropical forests, both in terms of endemism and remaining area, both metrics used to quantify biodiversity (Bond and Parr, 2010). Arguably the most iconic of the tropical savannas are those found in Africa, such as the Serengeti-Mara ecosystem which hosts the largest migration of ungulates in the world (as well as the carnivores that prey on them) and is habitat to several well known endangered and vulnerable species such as the black rhinoceros, African elephant, cheetah, and African wild dog (IUCN, 2016; Sinclair

et al., 2007; Stoner et al., 2007).

Although now bereft of most, if not all, of their large fauna, tropical savannas also support a high diversity of smaller mammals, birds, reptiles, invertebrates and plants. The Brazilian *cerrado* is the second largest biome in South America with almost half of the 10 000 species of vascular plants and 10% of the vertebrate species being endemic and comprising 1.5% and 0.4% of global total species respectively (Cardoso da Silva and Bates, 2002; Myers et al., 2000). Often overlooked are the highly diverse savanna ecosystems of Madagascar (Bond et al., 2008) and India (Kodandapani et al., 2004; Sankaran, 2009) although this is due in part to dispute over the classification of ‘savanna’ (Bond, 2008; Bond and Parr, 2010; Parr et al., 2014).

2.2.2 Australian savannas

Unlike savannas elsewhere in the world, most Australian savannas are sparsely populated, supporting less than 5% of the Australian population (Williams et al., 1996) and, in comparison to the rest of Australia, are considered relatively ecologically intact (Burbidge et al., 2008). Australian savannas occupy 25-30% of the land surface (Chen et al., 2003; Cook et al., 2010) occurring across the northern parts of Western Australia, the Northern Territory and Queensland. Australian savannas are unusual in that the tree layer tends to be dominated by evergreens such as *Eucalyptus* species, although genera that dominate in other savannas such as *Acacia* and *Terminalia* also occur (Bond et al., 2012; Bowman et al., 2010). Semi-arid regions in Australia accounted for almost 60% of the 2011 global carbon sink anomaly on account of above average NPP due to atypically high annual rainfall (Cleverly et al., 2016; Poulter et al., 2014). In terms of the predicted climate for northern Australia in the second half of the 21st century, which will be hotter with more seasonal rainfall (Hughes, 2003), it is perhaps more significant that all the additional biomass gains have since diminished as a result of drought induced tree death followed by the subsequent loss of carbon from the system due to decomposition and fire (Ma et al., 2016).

Livestock grazing of cattle and, to a lesser extent, sheep occurs throughout most of the savanna region (Russell-Smith and Yates, 2007). Unsustainable management practices have resulted in widespread degradation (McAlpine et al., 2009) and invasion by exotic species (Setterfield et al., 2010). Traditionally, Australian savannas were managed by indigenous populations using a fire regime consisting of small, low

intensity fires resulting in a patchy mosaic of burned areas, whilst contemporary fire regimes consist of much larger and more intense fires, including non-anthropogenic wildfires (Parr and Andersen, 2006; Russell-Smith et al., 2003; Yates et al., 2008; Yibarbuk et al., 2001). The change in fire regime, coupled with overgrazing, has resulted in substantial changes to the landscape including biodiversity loss (Andersen et al., 2012b; Bowman, 1998), changes to species composition (Bond et al., 2012), tree demography (Lehmann et al., 2009a; Murphy et al., 2010; Prior et al., 2010; Werner et al., 2006), tree/grass balance (Beringer et al., 2004; Hoffman et al., 2012), and soil properties (Russell-Smith et al., 2003).

The savanna communities of the Northern Territory in Australia have more than twice the levels of plant endemism (14.6%) than occurs within the rainforest ecosystems in this area (Woinarski et al., 2006). Other areas of high biodiversity and endemism occur within the savanna communities of Cape York Peninsula in Queensland and the Kimberley of Western Australia, with tropical savanna communities comprising one third of the top 12 areas of plant species richness and endemism in Australia (Crisp et al., 2001).

2.3 Controls on the extent of savannas

On a global scale, the extent of woody vegetation tends to be correlated with mean annual precipitation (MAP) or some derivative thereof relating to moisture availability. Extremely low MAP usually results in deserts and extremely high MAP supports forests, with savannas tending to dominate the intermediate niche (Lloyd et al., 2008; Ratnam et al., 2011; Sankaran et al., 2005; Staver et al., 2011a). For example, Lehmann et al. (2011) found that C_4 savannas were most likely to occur in areas where MAP ranged from ~500-2000 mm, although this differed markedly between continents (see also Lehmann et al. (2014, 2009b) but *c.f.* Veenendaal et al. (2014)). Furthermore, the seasonality of rainfall can play a significant role with more pronounced seasonality leading to a higher probability that savanna is the established vegetation (Good and Caylor, 2011).

Despite these general trends, there are many exceptions on global, continental, regional and local scales with closed-canopy systems occurring within savanna-dominated regions and vice versa (Bowman, 2000; Lloyd et al., 2008; Russell-Smith et al., 2004). Furthermore, there is a need to understand how trees and grasses can coexist without one out-competing and ultimately excluding the other, given

they are such very different life-forms. A number of explanations and models have been proposed to explain the coexistence of trees and grass. These can be broadly classified as ‘bottom-up’ (resource) or ‘top-down’ (disturbance) controls, although a combination of these factors is likely to be involved (Bond, 2008). In addition, the relative importance of these mechanisms will differ across environmental gradients such that resources are more likely to limit plant growth in arid savanna systems while disturbance is likely to be more important in mesic savanna systems (Bond et al., 2012; Gardner, 2006; Sankaran et al., 2004; Werner and Prior, 2013).

2.3.1 Resource controls

Resource controls are primarily orientated around climate and soils as they relate specifically to water and nutrients; low precipitation, prolonged dry seasons, soil parent material, organic matter content, extent of weathering, soil texture, and depth all affect the amount of water and nutrients that are retained and available to plants (Bond, 2008; Scholes, 1990; Williams et al., 1996). Light can also become an important resource as different physiologies of plants, not only between trees and grasses but also between species within these broad groups, leads to different responses to resource limitations (Lloyd et al., 2008). These limitations may result in competition for resources, with one strategy resulting in more success than another (for example, Pinno and Wilson (2013); Riginos (2009)). Alternatively, different strategies may result in the occupation of separate resource niches such that different plants ameliorate conditions for each other (for example, Moustakas et al. (2013); Weltzin and Coughenour (1990)).

Water

Closed-canopy forest tree species are considered more vulnerable to water-stress as they have a lower root:shoot ratio with a higher allocation to fine roots at shallow depths. As rainfall becomes more erratic, intermittent dry periods may favour the establishment of savanna tree species that allocate more resources to the growth of coarse roots and are able to access water at greater depths (Hoffmann et al., 2004b; Pinno and Wilson, 2013). Quick growing grasses are also able to capitalise on low levels of soil moisture more efficiently than slow growing woody vegetation that require sustained moisture levels for seedling establishment and recruitment (for example, Higgins et al. (2000)). Furthermore, C_4 grasses are able to out-compete C_3 grasses

in open areas with high temperatures owing to water use advantages conferred by their photosynthetic pathway (Bond (2008) and references therein).

In addition to the size and frequency of precipitation events, the soil water balance also varies according to the rate of evaporation and the depth and texture of soil. Generally speaking, deep soils and clay-textured soils have a higher water holding capacity and may be associated with increased woody cover in mesic savannas (for example, Ruggiero et al. (2002); Van Langevelde et al. (2003)). In contrast, within arid savannas with coarse textured soils, infiltration is rapid while runoff and evaporation is low, which can result in higher soil moisture at depth. This results in the ‘inverse texture effect’ (Noy-Meir, 1973), where coarse textured soils support a higher density of vegetation and support taller vegetation than clay textured soils (for example, MacGregor and O’Connor (2002); Williams et al. (1996)). Several studies have found this may indeed be the case for arid savannas of Africa, however other controls such as nutrient availability and disturbance may be more influential in mesic savannas (Bucini and Hanan, 2007; Sankaran et al., 2005, 2008; Staver et al., 2011a; Strickland et al., 2016).

In contrast to other continents, the woody biomass in savannas of Australia appear to be more tightly constrained by water availability across the precipitation spectrum (Eamus, 2003; Fensham et al., 2005; Williams et al., 1996). Differences in rooting architecture, rooting depth, and xylem matric potential have been cited as factors that may influence the degree of constraint on woody biomass imposed by water availability (Fensham and Fairfax, 2007; Rice et al., 2004).

Nutrients

Tropical ecosystems are often characterised by highly weathered, nutrient poor soils (with areas of higher soil fertility occurring beneath forests (Bond (2010) and references therein)) and nutrient availability has been shown to limit productivity in more mesic savannas (Lloyd et al., 2008; Murphy and Bowman, 2012). The higher root:shoot ratio of savanna vegetation gives savanna species a competitive advantage over forests in nutrient depleted soils, however root:shoot ratios also tend to be negatively correlated with MAP such that the effects of soil moisture and nutrient availability are frequently compounded (Mokany et al., 2006). Differences in soil parent material aside, woody species expansion into savannas can improve soil fertility and increase total soil carbon, soil organic carbon (SOC), potassium, total nitrogen, and nitrogen mineralisation and turnover (for example Blaser et al.

(2014); Hibbard et al. (2001); Pellegrini et al. (2014); Ruggiero et al. (2002)) leading to positive feedback loops which make causality in plant community composition difficult to infer (Don et al., 2011). However, Jackson et al. (2002) conducted a global analysis and concluded this was only the case at arid sites and that sites above approximately 400 mm MAP displayed a decrease in both SOC and nitrogen with an increase in woody vegetation.

The effect of nutrient heterogeneity within savanna ecosystems is equally problematic and highly variable with experimental studies involving the addition of fertilisers to savanna plots yielding mixed results. For example, Ries and Shugart (2008) found an increase in biomass when fertilisers were added to grasses in Botswana but O'Halloran et al. (2009) found no such increase at their study site (also in Botswana), even in wetter years. Some studies have concluded that trees and grass differ in their nutrient limitations, with grasses more likely to be limited by nitrogen and trees by phosphorus (Nardoto et al., 2006; Sankaran et al., 2008; van der Waal et al., 2011). In contrast, other studies maintain that the trees and grasses are in direct competition with each other (February and Higgins, 2010; Riginos, 2009).

As woody expansion can affect the fertility of soil at the landscape scale, so too can individual trees which create 'islands of fertility' within their immediate vicinity, increasing soil carbon (Bird et al., 2000), nitrogen (Coetsee et al., 2010), phosphorus (Holdo et al., 2012), moisture (Ludwig et al., 2004; Potts et al., 2010), leaf litter (Wang et al., 2009) and bulk density (Wang et al., 2007). Some authors have reported that these differences may be responsible for increased grass biomass beneath tree canopies (Weltzin and Coughenour, 1990) although others have concluded this is only the case for drier sites with MAP ≤ 550 mm (Moustakas et al., 2013). In addition, the scale at which nutrients become available can also be important; for example van der Waal et al. (2011) found that trees benefit from fertiliser applied at a coarse spatial scale while grasses displayed no preference. Similarly, the timing, intensity, and frequency of precipitation events can influence the temporal availability of nitrogen and phosphorus (Austin et al. (2004a) and references therein).

Light and Temperature

The effects of light as a resource can be difficult to separate from the effects of both moisture and temperature; shade reduces temperature, which in turn reduces evaporation resulting in higher soil moisture. Such microclimates beneath savanna

trees can permit rainforest species to establish in the understorey. Once established, their greater investment in structural tissues such as woody stems enables them to intercept incident radiation before the understorey of grasses and herbs and thus outcompete them (Geiger et al., 2011; Veenendaal et al., 2014). Plants that utilise the C_4 photosynthetic pathway are particularly disadvantaged as they have an inferior ability to utilise short sun flecks, as found at ground level in a forest (Sage and Kubien, 2003). In contrast, the formation of hot and dry microclimates will favour C_4 plants as C_3 plants have approximately half the water use efficiency as their C_4 counterparts (Sage and Kubien, 2003) and the quantum yield (light use efficiency) of C_3 plants decreases with increasing temperature (Ehleringer et al., 1997). Although grasses tend to be warm climate specialists (Edwards and Smith, 2010), hot and dry conditions particularly favour C_4 grasses, which tend to dominate biomes at minimum growing season temperatures $>28^{\circ}\text{C}$ (Ehleringer et al., 1997).

2.3.2 Disturbance controls

Tropical savannas are characterised by a high incidence of disturbance by fires, herbivory, droughts, windstorms and floods, all of which affect the tree/grass balance (for example, Bond (2008); February et al. (2013); Wilson and Bowman (1987)). Fire is arguably the most important disturbance with most savannas being burnt every few years, if not annually, although there is a large variation in the timing and intensity of these fires, modulated by the impacts of other disturbances (for example, Higgins et al. (2000); Williams et al. (2003)). Herbivory is also a characteristic feature of tropical savannas, whether it be grazing by introduced species such as cattle (for example, Petty et al. (2007)), native species (Murphy and Bowman, 2007) or macroinvertebrates such as termites and ants (Andersen and Lonsdale, 1990).

The seasonality of rainfall in savanna ecosystems means that prolonged dry periods are common and many savanna species have developed unique adaptations to moisture stresses (Fensham and Fairfax, 2007). Similarly, tropical monsoonal rainfall can lead to periods of inundation that may occur with annual regularity (Sarmiento and Pinillos, 2001). Less frequently, these typical seasonal fluctuations may extend into unusually long periods of drought that can lead to significant and abrupt changes to the ecosystem (Fensham et al., 2015; Rice et al., 2004). Additionally, floods may also occur in association with cyclones that result in increased litterfall, woody debris and tree death due to strong winds and this too can have significant ramifications

for the local fire regime (Cook and Goyens, 2008).

The alternative stable states (ASS) theory postulates that savanna and forest ecosystems may both exist within a set of climate conditions and that ecosystem stability is maintained by the facilitation of fire by the savanna and the exclusion of fire by the forest (Staal and Flores, 2015). Evidence for the existence of ASS is generally in the form of abrupt changes in vegetation, with little, if any, ecotonal boundary such that contrasting ecosystems are essentially occupying the same environmental niche. In contrast, a monostable system would change along a continuum and only one ecosystem occurs in each environmental niche (Staver et al., 2011b). Such abrupt vegetation changes are common in the Wet Tropics of north Queensland, prompting the suggestion that these ecosystems exhibit ASS (Warman and Moles, 2009). However, there is some controversy as to whether ASS exist in the tropical forest/savanna systems, with other studies reporting that the observed changes are not considered abrupt if the middle and lower strata of woody vegetation is also considered (Veenendaal et al., 2014). Furthermore, abiotic factors such as soil are often cited as the reason for abrupt transitions (Lloyd and Veenendaal, 2016) although despite the novelty of these transition ecosystems, there remains a lack of detailed studies on the soils of these ecosystems (although see Veenendaal et al. (2014)). While the ASS theory specifically relates to the role of fire in determining ecosystem extent, all disturbances have the potential to behave in a similar fashion.

Fire

One of the most popular theories relating to the distribution of forest and savanna ecosystems is that the extent of each is mediated by fire. In the absence of fire, forest species can expand into neighbouring savannas and may make up a significant component of the understorey, particularly where savanna trees are approaching canopy closure (Geiger et al., 2011; Veenendaal et al., 2014). Fires result in a high mortality rate for juvenile trees (Balch et al., 2013; Hoffman et al., 2012; Werner and Prior, 2013), whilst grass retains a competitive advantage due to its ability to regenerate quickly. Similarly, savanna trees are able to establish and survive via a number of adaptations to fire including larger seed size and bark thickness as well as modifications including epicormic re-sprouting and underground rhizomes (Bond and Midgley, 2012; Hoffmann, 2000; Lawes et al., 2011). The grass in savannas then forms a highly flammable understorey, which, coupled with prolonged dry periods,

allows sufficient curing of the fuel load. This ensures that savannas will burn at least every few years (Bond, 2008; Hoffmann et al., 2012), forming a positive feedback loop that can be considered a ‘landscape fire trap’ (Lindenmayer et al., 2011). This theory is supported by a number of fire exclusion experiments that indicate fire is required to maintain the savanna vegetation structure and composition (Geiger et al., 2011; Swaine et al., 1992; Williams et al., 1999; Woinarski et al., 2004).

Within ‘stable’ savannas, fire intensity and frequency continues to have a dramatic impact on the tree/grass balance. The presence of even low levels of grass can lead to a positive feedback loop leading to the establishment of savanna, and similarly the presence of invasive grasses can lead to fires of greater intensity that significantly reduce canopy and understorey cover as well as species diversity (Brooks et al., 2010; Hoffman et al., 2012; Setterfield et al., 2010). As this process favours the reestablishment of the invasive grasses, a positive feedback loop is established known as the ‘grass-fire cycle’ (D’Antonio and Vitousek, 1992). Similarly, the frequency of fires can restrict the survival of seedlings and delay the recruitment of adult trees, resulting in demographic bottlenecks (Bond et al., 2012; Gardner, 2006; Werner and Prior, 2013).

Changes in fire intensity and frequency can also occur as a result of changes to management practices. For example, indigenous burning practices in Australia are comprised of small-scale, low intensity fires that created a ‘patch mosaic’ style of habitat (Bowman et al., 2004; Fensham, 1997; Yibarbuk et al., 2001) and are widely considered to have shaped the evolution of the native flora and fauna (Bliege Bird et al., 2008; Bowman, 1998; Brook and Bowman, 2006; Kershaw, 1994; Wyrwoll and Notaro, 2014). Since European settlement, burning regimes have shifted to large-scale fires of higher intensity (Russell-Smith et al., 2003; Yates et al., 2008) with negative consequences for biodiversity (Andersen et al., 2012b; McKenzie et al., 2007; Murphy and Bowman, 2007; Short and Smith, 1994; Woinarski et al., 2004), although the extent of these consequences remains a controversial issue (for example, Parr and Andersen (2006); Sakaguchi et al. (2013)).

Herbivory

The effects of herbivory on the tree/grass balance are dependent on animal size, density and feeding strategy, which are inextricably linked with the effects of fire and may vary considerably within and between continents (Midgley et al., 2010; Van Langevelde et al., 2003). For example, grazing of savannas in northern Australia

by cattle has led to a reduction in grass biomass that results in a reduction of fuel load and fire intensity, in turn favouring the establishment of woody plants and unpalatable herbs and forbs (Sharp and Whittaker, 2003). Similarly, the removal or reduction of grazers has been associated with increased mortality of juvenile trees, presumably as a result of increased grass biomass increasing resource competition as well as fire intensity (Petty et al., 2007; Werner, 2005; Werner et al., 2006), although this hypothesis is not supported by all studies in the field (Bowman et al., 2008; Lehmann et al., 2008).

In contrast, the presence of large browsers in African savannas can produce the opposite result; whilst fire is the most likely driver for the conversion of woodland to savanna, the browsing of seedlings by elephants (Dublin et al., 1990) and antelope (Mills and Fey, 2005) has been sufficient to restrict tree recruitment and prevent the regeneration of woodland. Similarly, Holdo (2007) modelled the interaction of fire, frost and elephant browsing and concluded that elephant browsing was the most crucial determinant of vegetation structure. In addition, activities such as horning by wildebeest have also been reported to reduce woody cover and may result in the conversion of savanna to treeless grassland (Estes et al., 2008). As well as landscape scale vegetation changes, large herbivores can also affect the tree/grass balance at a more local scale. For example, browsers can reduce leaf density and biomass as well as the height of shrubs and trees (Augustine and McNaughton, 2004; Dharani et al., 2009; Staver et al., 2009) and trampling by animals can increase seedling mortality as well as affect soil compaction and water infiltration (Cumming and Cumming, 2003; Hobbs and Searle, 2005; Midgley et al., 2010).

In addition to mammalian herbivores, the impact of invertebrate fauna is often overlooked even though they may comprise the most important consumers within tropical savannas (Andersen and Lonsdale, 1990). For example, tree-piping termites in Australia have been found to reduce tree growth and survival, with mortality likely to be further exacerbated by fire and cyclones (Werner and Prior, 2007). Furthermore, seed predation by ants is reported to increase following fire, further reducing seedling recruitment in two species of *Eucalyptus* and *Acacia* (Setterfield, 2002), although post-dispersal seed removal may also facilitate dispersion if the seeds are left intact and stored in appropriate microsites (Vander Wall et al., 2005).

Drought

The annual dry season that is characteristic of tropical savannas is an important disturbance determining the extent of tropical savannas. Forest species typically have variable but generally poor tolerance to prolonged dry periods, with drought susceptibility determining both the forest extent and within-forest species distribution (Engelbrecht et al., 2007). In more mesic environments, this can represent the primary determinant of the extent of savannas (Good and Caylor, 2011; Hutley et al., 2011; Wilson and Bowman, 1994) with forest contractions associated with periods of drought (Gonzalez, 2001). Some savanna trees (such as *Eucalyptus* sp.) tend to have superior water transport efficiency and storage capacity (Bucci et al., 2004), and they are able to continue to assimilate carbon throughout the dry season (Beringer et al., 2007). Savanna grasses are similarly adapted to cope with water stress; annual grasses ‘escape’ water stress by completing their reproductive cycle within the growing season while perennial grasses ‘avoid’ water stress via adaptations to leaf traits and rooting architecture that minimise water loss and maximise water gain (Ludlow, 1980).

Despite these adaptations, prolonged drought is associated with extensive tree mortality (Allen et al., 2010a; Fensham et al., 2009; Meir et al., 2015; Steinkamp and Hickler, 2015; Viljoen, 1995) and may reduce the occurrence of the dominant species (Fensham et al., 2015; MacGregor and O’Connor, 2002) or facilitate community composition changes by affecting specific species (Rice et al., 2004). In addition, prolonged drought may lead to significant changes to understorey vegetation (O’Connor, 1998), especially in association with grazing (O’Connor, 1995). This in turn may trigger a number of feedbacks that can lead to desertification. For instance, reduced vegetation cover reduces infiltration, increasing runoff and erosion that further reduces soil moisture levels and vegetative cover (Reichstein et al., 2013a). Furthermore, reduced vegetation reduces transpiration and can reduce precipitation on a regional scale, exacerbating the effect of the drought (Foden et al. 2007). These effects may be further compounded by more intense fires as a result of increased fuel loads and prolonged curing periods (Fensham et al. 2003).

Wind

Damage from windstorms can lead to substantial damage to tropical ecosystems, particularly within the non-equatorial tropics where tropical cyclones and hurri-

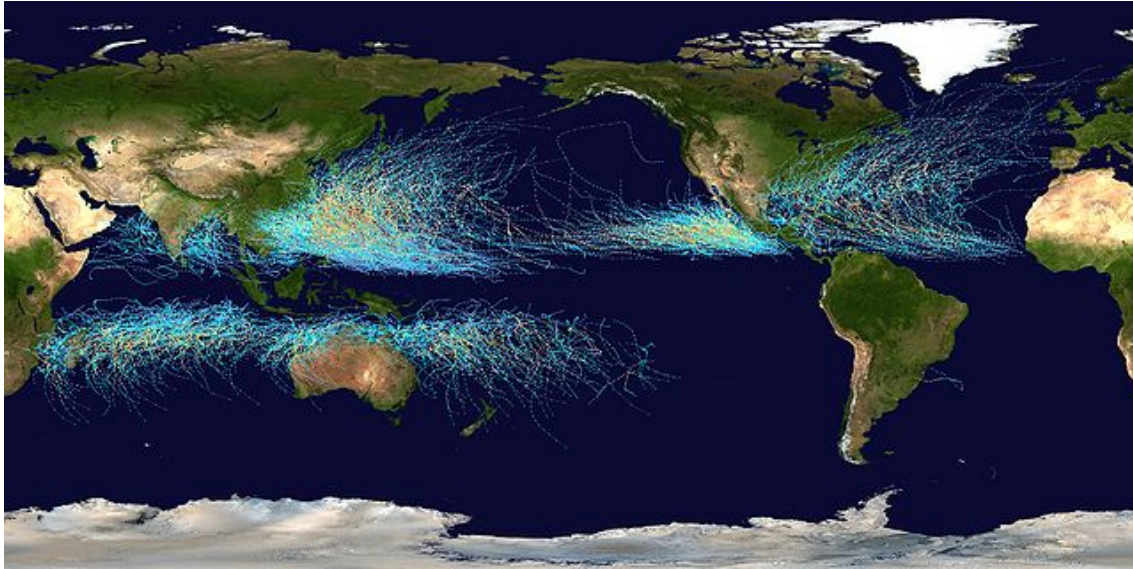


Figure 2.3: Global tropical cyclone tracks. Source: Background image from NASA, this version downloaded from http://commons.wikimedia.org/wiki/File:Global_tropical_cyclone_tracks-edit2.jpg

canes commonly occur (Figure 2.3). Strong winds cause defoliation and branch loss that results in increased litterfall and coarse woody debris, but unlike prevailing winds that favour a single direction, these windstorms involve winds from multiple directions over a short period that can result in significant shearing forces that snap, twist or even uproot entire trees, leading to considerable increases in fuel loads (Cook and Goyens, 2008; Lugo, 2008). Tropical rainforests are frequently moist enough to facilitate rapid decomposition of this debris, however, the increase in canopy openness can increase desiccation and allow fire to penetrate (Bowman and Panton, 1994; Grove et al., 2000). This is particularly the case in fragmented forests as strong winds can result in tree mortality up to 500 m from the forest edge (Laurance and Curran, 2008) and fire frequency increases with proximity to the forest edge (Cochrane and Laurance, 2002). Once fire has penetrated a forest, it is possible to trigger a feedback loop resulting in forest contraction or a complete conversion to savanna (Bowman and Panton (1994) and references therein). There is also evidence to suggest that savannas may be more resistant to severe windstorms than forests (Cook and Goyens, 2008), as the vigorous resprouting that occurs following fire damage forms a convenient ‘exaptation’ (*sensu* Gould and Vrba (1982)) to defoliation from wind. For example, Franklin et al. (2010) recorded re-sprouting rates of >60% following tornado damage to savanna trees in Kakadu National Park in the Northern Territory of Australia and reported mortality rates of 0-4% among trees that resprouted.

To date, most research on tropical storms has focused on the impact of windthrow on tropical forests, as north Australia comprises the only major savanna biome that experiences frequent tropical cyclones (Hutley et al., 2013). Of the cyclones that cross the coast in Australia, more have crossed on the west coast than the more densely populated east coast (Haig et al., 2014). Northern Australia also has a particularly low population density and post-cyclone damage assessments tend to focus on human impacts. The east coast area has the highest population density and also has a strip of rainforest along the coast associated with the Great Dividing Range (GDR) so consequently research in this area has focused on the impacts of cyclones on the rainforests of the Wet Tropics World Heritage Area (WTWHA) in north Queensland (see for example Turton (2008)).

Nonetheless, cyclones represent a significant disturbance to savanna ecosystem function at both short- and long-term time scales. For example, Hutley et al. (2013) calculated fuel loads of up to 30 Mg biomass ha⁻¹ after Tropical Cyclone Monica crossed the north coast of Australia in 2006 with an estimated loss of 51.2 Mt CO₂-e (CO₂ equivalent) from the system as a result. Cook and Goyens (2008) measured tree damage after the same cyclone and reported up to 77% of trees uprooted and up to 85% defoliation. Nonetheless, GPP returned to pre-cyclone levels within 4 years. Furthermore, intact canopies can restrict recruitment such that wind disturbance may be reflected in the size demographics of woody vegetation (Hutley and Beringer 2010).

Flood

Seasonal flooding is a characteristic feature of some savannas, occurring in association with the summer rains. Inundation decreases oxygen diffusion in soils and leads to a state of hypoxia which then decreases root aerobic respiration, restricting the plant's ability to assimilate carbon (Parolin and Wittmann, 2010), a phenomenon that may occur within a few hours of inundation (Baruch, 1994). This results in impaired growth as well as reduced biomass, root length and stomatal conductance (Lopez and Kursar, 2003) and can result in the formation of tree rings that are often absent from tropical trees (Worbes, 2002). Adaptations to periods of prolonged inundation are highly variable and surprisingly widespread amongst tropical forest genera (Lopez and Kursar, 1999; Pimenta et al., 2010) with seasonally flooded forests occurring in South America, Africa and Asia (Parolin and Wittmann, 2010). As such, flooding in itself does not appear to be a determinant of the extent of

savanna, but rather a determinant of the type of savanna, with zonation of species according to levels of inundation recorded in floodplains of Amazonia, Africa, and Australia (Bowman and McDonough, 1991; Franklin et al., 2007; Medina and Motta, 1990; Parolin and Wittmann, 2010).

Flood adaptations in understorey plants are similarly species specific; for example, Oosterheld and McNaughton (1991) compared flood responses of Serengeti grasses and found that while all species grew taller under flooded conditions, two of the species were able to develop new root systems above the soil level. In contrast to seasonal inundation, flash floods may present a more significant disturbance if large quantities of vegetation and soil are removed but other species may benefit from the deposition of new soil (Franklin et al., 2007; Parsons et al., 2006). As such, the impacts of floods are highly variable and frequently species specific but are likely to determine vegetation structure in conjunction with other disturbances such as grazing (Oosterheld and McNaughton, 1991), fire (Franklin et al., 2007) or drought (Lopez and Kursar, 2003).

2.4 The global terrestrial carbon cycle and tropical savannas

The global carbon cycle consists of complex exchanges between the atmosphere, hydrosphere, and biosphere with the stocks of carbon therein, namely plant biomass and SOC. Photosynthesis is the primary process by which carbon enters terrestrial ecosystems from the atmosphere but there are a number of processes by which it returns including leaf, stem, and root respiration, decomposition, and soil emissions (collectively termed ecosystem respiration), as well as losses due to burning, land-use change, and agriculture (Figure 2.4). Tropical savannas form a major component of the global carbon cycle as a result of their large extent (Grace et al., 2006). Globally, approximately 15% of the world's soil carbon stocks (345 Gt C) are found in tropical savannas and the biome is the second largest contributor to soil carbon stocks at 1-3m depth after tropical forests (Jobbágy and Jackson, 2000). Furthermore, they contribute approximately 25% to global terrestrial gross primary productivity (Beer et al., 2010) and up to 60% of global fire emissions (Van der Werf et al., 2010).

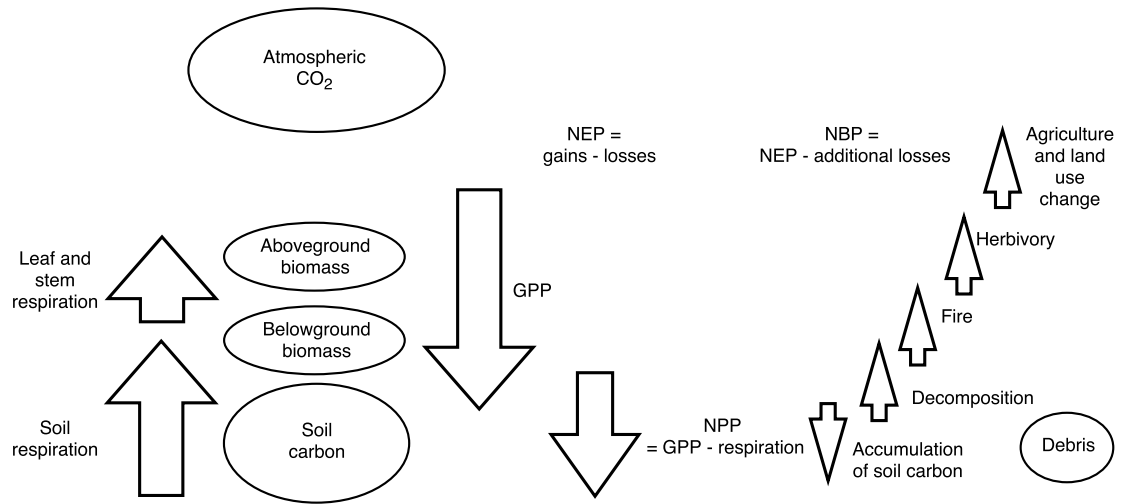


Figure 2.4: The terrestrial carbon cycle with stocks in the circles and fluxes in the arrows. Net Primary Productivity (NPP) is the balance between gains due to Gross Primary Productivity (GPP) and losses due to respiration. At the ecosystem scale, additional fluxes may be considered to estimate the Net Ecosystem Productivity (NEP). Finally, losses that become apparent over longer time scales such as land use change and fire may be considered in the estimation of Net Biome Productivity NBP. Adapted from Bloom et al. (2016).

2.4.1 Carbon stocks

Carbon stocks can be broadly classified as aboveground biomass (AGB), which includes trees, shrubs, grasses, and herbs; belowground biomass (BGB) consisting of plant roots, corms, and rhizomes; and SOC. Biomass may be further divided into living and dead components and dead components may be further divided into coarse woody debris (CWD) and leaf litter (Figure 2.4). For modelling purposes, it becomes necessary to further divide components based on turnover times. For example, soil carbon may be divided into labile and recalcitrant pools, plant biomass may be divided into trees and grass, and tree biomass may be further divided into leaves, twigs, branches and stems.

The structural diversity of tropical savannas is such that there is a great range in reported carbon stocks for these environments. For example, total AGB varied more than five-fold along a 5km transect in Mozambique (Woollen et al., 2012) while Saiz et al. (2012) found SOC varied as much as eight-fold across a precipitation gradient in West Africa. Globally, carbon stocks of tropical savannas are even more variable; for example AGB varies more than 245-fold (Table 2.1) while SOC can vary as much as 1000-fold (Table 2.2). Further compounding this variability is the difficulty in accurately measuring belowground components. For example, Mokany

et al. (2006) calculated that global carbon stocks have been underestimated by approximately 46 Pg C as a result of the under-estimation of roots in tropical savannas and grasslands.

2.4.2 Carbon fluxes

The exchange of carbon between the terrestrial biosphere and atmosphere is complex and begins at the plant scale with GPP, which is carbon assimilated during photosynthesis (Figure 2.4). NPP forms the balance between GPP minus autotrophic respiration losses resulting from growth and maintenance respiration of plant stems and roots (Woodwell and Whittaker, 1968). NPP is traditionally calculated using changes in biomass, with the most common method utilising changes in peak aboveground live biomass as the productivity indicator (Scurlock et al., 2002). Issues associated with this method include a failure to adequately account for belowground dynamics, resulting in up to a five-fold under-estimation of productivity in grasslands (Long et al., 1989). Furthermore, few methods include decomposition dynamics (for example, Silva et al. (2016), Mackensen et al. (2003), Liu et al. (2015)). Despite these limitations, NPP calculated in this fashion can provide a good estimation of the rank of productivity between sites and provides an indication of the variability between sites (Scurlock et al., 2002). For example, a review by Grace et al. (2006) found NPP in tropical savannas varied by as much as 1.4 to 22.8 t C ha⁻¹ y⁻¹ and was strongly seasonal with high inter-annual variability.

While NPP tells us about the exchange of carbon at the vegetation level, net ecosystem productivity (NEP) describes the balance of NPP minus losses from heterotrophic respiration such as herbivory and decomposition, including soil respiration (Buchmann and Schulze, 1999; Woodwell and Whittaker, 1968). Carbon emissions from soil form the second largest ecosystem flux after gross photosynthesis (Raich and Schlesinger, 1992) but this flux consists of both autotrophic plant respiration and heterotrophic decomposition respiration with biologically distinct pathways that are difficult to differentiate (Kuzyakov, 2006). The use of micrometeorological technology such as eddy covariance (Moncrieff et al., 1997) enables the direct measurement of CO₂ fluxes above vegetation, termed net ecosystem exchange (NEE). These measurements essentially comprise the NEP of an ecosystem plus contributions from any sources or sinks of inorganic carbon, which are often negligible (Lovett et al., 2006). There are limitations to this method however, including the need to extrapolate data in order to partition the NEE into assimilation and

respiration components (Reichstein et al., 2005).

The productivity of an ecosystem is important when considering if that ecosystem is a net source or sink for carbon. However, caution must be exercised when using NEP or NEE as an indication of the potential for net ecosystem carbon accumulation (Lovett et al., 2006; Randerson et al., 2002), as this may not include non-respiratory losses such as fire. To this end, Schulze and Heimann (1998) propose the term net biome productivity (NBP) to describe the carbon balance after further losses to the system as a result of disturbance. For example, Beringer et al. (2007) calculated the annual NEP of an Australian tropical savanna to be $-4.3 \text{ t C ha}^{-1} \text{ y}^{-1}$, but after accounting for additional direct and indirect losses due to fire the estimated NBP was $-2.0 \text{ t C ha}^{-1} \text{ y}^{-1}$ (Table 2.3).

Table 2.1: Aboveground carbon stocks in tropical savannas (t C ha^{-1}) adapted from Grace et al., 2006 and published data. A range of values indicates multiple sites were included in the study.

Location	Trees	Grass	Total AGB	Litter	Reference
Australia (QLD)	33.6 - 40.6				Burrows et al. (2000)
Australia (NT)	17.7 - 41.2	0.7 - 1.5	19.4 - 47.3	0.8 - 1.4	Chen et al. (2003)
Australia (NT)	12.4 - 57.5				Cook et al. (2005)
Africa (Ethiopia)	15.2 - 93.7	4.7 - 14.9	15 - 49		Michelsen et al. (2004)
Africa (Mozambique)	0.8 - 38.4	0.7 - 2.6	8.4 - 42.2	0.1 - 4.5	Woollen et al. (2012)
South America (Brazil)	1.7 - 12.9	6.0 - 10.4	5.5 - 24.9 ^a	0.6 - 3.8	de Castro and Kauffman (1998)
South America (Brazil)	0.5 - 3.64	2.3 - 3.7	2.8 - 7.3	0.0 - 0.2	Barbosa and Fearnside (2005)
South America (Brazil)	0.2 - 10.1	0.6 - 0.8	0.8 - 10.4		San José et al. (2008)
South America (Venezuela)	0.2 - 4.6	2.1 - 4.5	2.3 - 7.9		San José et al. (1998)
Asia (India)	10.6 - 39.0	5.7 - 7.1	17.7 - 44.7		Pandey and Singh (1992)

^a Total AGB includes woody debris

Table 2.2: Belowground carbon stocks in tropical savannas (t C ha^{-1}) adapted from Grace et al., 2006 and published data. Sample depth (in m) is given in parentheses. A range of values indicates multiple sites were included in the study.

Location	Total BGB	SOC	Reference
Australia (NT)	11.1 - 80.9 (2)		Eamus et al. (2002)
Australia (NT)	5.4 - 39.6 (2)	111.5 - 198.9 (1)	Chen et al. (2003)
Africa (Zimbabwe)		3.5-19.9 (0.05)	Bird et al. (2000)
Africa (Ethiopia)		238 - 1275 (1)	Michelsen et al. (2004)
Africa (Mozambique)		5.8 - 86.2 (0.3)	Woollen et al. (2012)
Africa (West Africa)		1.2 - 9.1 (0.05)	Saiz et al. (2012)
		4.3 - 35 (0.3)	
		7.6 - 50.1 (0.5)	
		11.6 - 74.2 (1)	
		15.8 - 98.2 (1.5)	
South America (Brazil)	16.3 - 52.9 (2)		de Castro and Kauffman (1998)
South America (Brazil)	0.8 - 2.2 (0.3)	15.4 - 36.0 (0.3)	San José et al. (2008)
South America (Venezuela)	1.7 - 2.8 (0.3)	66.4 - 96.1 (0.3)	San José et al. (1998)
Asia (India)	6.4 - 16.8 (0.5)		Pandey and Singh (1992)

Table 2.3: Net primary productivity (NPP), soil respiration (R_{soil}), tree biomass increment (B_{tree}), grass biomass increment (B_{grass}), net ecosystem productivity (NEP), net ecosystem exchange (NEE) and net biome productivity (NBP) of tropical savannas ($\text{t C ha}^{-1} \text{ y}^{-1}$), assuming that biomass is 50% carbon (Schlesinger, 1997). Negative values indicate a carbon sink. * R_{soil} is conventionally reported in units of $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and has been converted for ease of comparison by applying a conversion factor of 3.79

Location	NPP	R_{soil}^*	B_{tree}	B_{grass}	NEP/NEE	NBP	Reference
Australia (NT)					-2.8 ^a		Eamus et al. (2001)
Australia (NT)		8.3 - 20.3 ^b					Chen et al. (2002)
Australia (NT)	-11.0 ^c		-1.6 ^c	-0.5 ^c	-3.8 ^c		Chen et al. (2003)
Australia (NT)					-3.6 ^a	-2.0 ^{ad}	Beringer et al. (2007)
Australia (NT)		10.2 - 31.5 ^b					Richards et al. (2012)
Australia (NT)					-2.6 ^a		Eamus et al. (2013b)
Africa (Botswana)					0.12 ^a		Veenendaal et al. (2004)
Africa (Burkina Faso)					-28.0 - -3.0 ^{ae}	-1.79 - 4.29 ^{ad}	Brummer et al. 2008
Africa (Burkina Faso)		3.86 - 5.82 ^f					Brümmer et al. (2009)
Africa (Senegal)		5.76					Delon et al. (2016)
Africa (Senegal)					-2.29 ^a		Tagesson et al. (2016)
Africa (South Africa)					-1.38 - 1.55 ^a	1.15 ^{aeg}	Archibald et al. (2009)
Africa (South Africa)					-85 - 139 ^a		Räsänen et al. (2016)
North America (Panama)		26.9 - 35.2 ^h					Pendall et al. (2010)

continued

Location	NPP	R _{soil} [*]	B _{tree}	B _{grass}	NEP/NEE	NBP	Reference
South America (Brazil)		10 - 15 ^f					Davidson et al. (2000)
South America (Brazil)					0.1 ^a		da Rocha et al. (2002)
South America (Brazil)		6.1 - 23.9 ^b					de Pinto et al. (2002)
South America (Brazil)		1.0 - 6.5 ^b					Fernandes et al. (2002)
South America (Brazil)					-4.56 ^a	-1.44 ^{ad}	Santos et al. (2003)
South America (Brazil)		24					Salimon et al. (2004)
South America (Brazil)	-1.63 ^c	17.4	-0.007 ^c	-1.62 ^c	-0.06 ^a		San José et al. (2008)
	-1.69 ^a						
	-1.77 ^c	20.5	-0.80 ^c	-0.96 ^c	-1.16 ^a		
	-1.81 ^a						
	-3.86 ^c	19.7	-3.65 ^c	-0.02 ^c	-1.39 ^a		
	-4.02						

^a Measured using eddy covariance

^b Range represents mean of dry and wet season

^c Measured using harvest method

^d Includes losses from fire

^e Range represents multiple years

^f Range indicates annual totals of two consecutive years

^g Includes losses from fire and herbivory

^h Includes a range of measurements within a single year (*c.f.* seasonal means)

2.4.3 Disturbance variability

One of the major limitations associated with accounting for losses due to disturbance is the frequency and magnitude of the disturbance concerned. For example, Hutley et al. (2013) calculated a loss of 51.2 Mt CO₂-e as a result of Tropical Cyclone Monica, a category 5 cyclone that made landfall in the Northern Territory of Australia in 2006. They calculated that damage from the storm equated to a loss of 2% of GPP when integrated over the calculated return interval of 500 years. However, Cook and Nicholls (2009) estimated an uncertainty of 90% associated with this return interval due to sampling and methodological errors in statistical analysis. Further compounding this uncertainty is the short temporal range of modern meteorological data, with estimates based on palaeoclimatic data suggesting that the current level of cyclone activity in Australia is in fact at an unprecedented low (Haig et al., 2014).

Carbon losses due to fire can produce similar conundrums. For example, an accurate measure of the consumed fuel load is required, which can vary significantly depending on climatic inter-annual variability as well as the fire-free interval. Furthermore, the resulting intensity of the fire has indirect impacts via mortality and loss of productivity of recovering vegetation. As such, losses due to fire require continuous monitoring over a sufficient time interval to capture this variability before they can be sensibly represented as an annual flux (see for example, Beringer et al. (2007); Cook et al. (2005); Lehmann et al. (2008); Williams et al. (2004); Williamson et al. (2016)).

To this end, it can be more sensible to express disturbance losses as a ‘committed flux’ (*sensu* Fearnside (1997)) rather than an annual flux, though this can thwart global comparisons, as the two methods are not comparable (Ramankutty et al., 2007). This method is commonly utilised to describe changes in soil carbon stocks as a result of land use change that may take years or decades to reach a new equilibrium. For example, Don et al. (2011) reported the committed flux of SOC losses of 12-32 t C ha⁻¹ as a result of the conversion of ‘primary forest’ (includes natural savannas and rangelands) and a gain of up to 7 t C ha⁻¹ as a result of conversion to managed pastures.

2.5 Climate change and tropical savannas

The complex nature of tropical savanna ecosystems renders them particularly susceptible to the effects of climate change; changes to MAP, seasonality of MAP or mean annual temperature (MAT) will influence the vegetation balance and can result in significant changes to ecosystems (Lehmann et al., 2011; Moncrieff et al., 2016; Staver et al., 2011a). In addition, these changes are likely to be associated with changes to the disturbance regime, with stochastic events such as windstorms, droughts, and floods predicted to change not only in frequency but also in intensity under a warming climate (Reichstein et al., 2013a). The fertilisation effects of increasing atmospheric CO₂ and increased N deposition complicate the situation (Bond and Midgley, 2000; Sage and Kubien, 2003; Stevens et al., 2017), with complexity further compounded by the interaction with changes to fire and other management regimes (Bond and Midgley, 2012; Bradstock, 2010). Furthermore, C₃ and C₄ plants will respond differently to these changes. In order to understand why, it is useful to examine the origin of the C₄ photosynthetic pathway.

2.5.1 Atmospheric CO₂ and the evolution of C₄ photosynthesis

The C₄ photosynthetic pathway is present in only 3% of all land plants and yet they contribute approximately 18% to global productivity including some major food plants for both humans and livestock (Ehleringer et al., 1997; Sage, 2004). C₄ photosynthesis present in approximately 50% of grass species is an alternative to the more ancient C₃ pathway that first evolved among the grasses approximately 24-35 million years ago and has independently evolved at least 45 times, predominantly in tropical lineages (Sage, 2004). Grasses in general are predisposed to C₄ evolution, as they are warm climate specialists (Edwards and Smith, 2010). C₃ photosynthesis tends to be favoured except at the high temperatures characteristic of tropical latitudes under low levels of atmospheric CO₂. Under elevated levels of atmospheric CO₂ however, C₃ photosynthesis becomes more competitive at high temperatures (Cerling et al., 1997). A global expansion of C₄ ecosystems occurred approximately 7-5 million years ago, coinciding with a decrease in atmospheric CO₂ although causality in this relationship remains controversial (Bond and Midgley, 2012; Cerling et al., 1997; Sage, 2004). Furthermore, the significant expansion of C₄ grasslands coincided with significant changes to mammalian fauna and there is

evidence to suggest that this too was driven by low atmospheric CO₂ (Cerling et al., 1998). Consequently, as atmospheric levels of CO₂ continue to rise, there is growing interest in the fate of C₄ dominated ecosystems in a warmer, higher CO₂ world where they may lose their competitive advantage.

2.5.2 Atmosphere, weather and community composition

High levels of atmospheric CO₂ (>500 ppm) tend to favour C₃ vegetation except at very high temperatures (Cerling et al., 1997; Xu et al., 2013) and there is evidence to suggest that forests may replace tropical savannas as woody C₃ vegetation outcompetes C₄ grasses (Ainsworth and Long, 2005; Bond and Parr, 2010). Bond et al. (2003) further postulate that high levels of CO₂, in conjunction with fire, will favour woody expansion at the expense of all grasses. This is because juvenile tree growth rate increases with increasing CO₂, thus increasing the number of juveniles that reach a fire resistant height (see also Shanahan et al. (2016)). In addition, atmospheric N deposition is increasing globally and the higher N use efficiency of C₄ plants could lead to eutrophication, further favouring C₃ plants (Bond and Midgley, 2000; Sage and Kubien, 2003). Alternatively, this effect may favour C₃ understorey plants that then outcompete seedlings of woody plants (Sankaran et al., 2004). Despite the advantage that C₃ plants enjoy at high CO₂ levels, C₄ plants have also responded favourably to CO₂ fertilisation experiments and both C₃ and C₄ plants acclimate to high levels of CO₂, particularly in nutrient poor soils (Sage and Kubien, 2003; Wand et al., 1999).

As a result of rising atmospheric CO₂, the average global temperature is increasing and prevailing weather conditions are also expected to change (IPCC, 2013; Karl and Trenberth, 2003). In particular, the inter-annual variability of seasonal rainfall in the tropics has been increasing over the past century. Consequently, the arrival, duration, and intensity of rainfall is becoming increasingly unpredictable (Feng et al., 2013), the incidence of large-scale droughts is increasing (Zhao and Running, 2010), and the impact of these droughts on semi-arid systems is driving global variability in the carbon cycle (Huang et al., 2016). The implications of these changes are difficult to predict, as ecosystem responses are variable and driven by multiple feedbacks, both positive and negative (Figure 2.5) but they are likely to lead to significant shifts in the composition and phenology of savanna ecosystems (Tietjen et al., 2017; Walther et al., 2002).

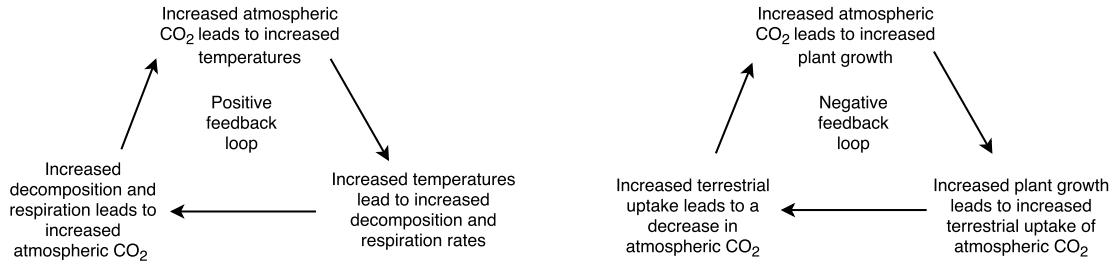


Figure 2.5: Examples of potential positive (left) and negative (right) feedback loops in the terrestrial carbon cycle. Simplified from Cox et al. (2000) and Huntingford et al. (2013), however see Brien et al. (2015).

Some changes are likely to be gradual; for example, while increased CO₂ is likely to increase woody plant density in tropical savannas (Lu et al., 2016), increased seasonality of precipitation and MAT may be associated with an expansion of tropical grasslands into subtropical and temperate latitudes (Bond and Midgley, 2000). In contrast, some shifts may be more abrupt; for example, increases in droughts or tropical storms can lead to sudden high tree mortality. If dry periods are sufficient to allow curing times for fuel loads then high intensity fires could devastate regeneration and reinforce a sustained change in the dominant vegetation in a region (Ahlström et al., 2015; Bradstock, 2010; McAlpine et al., 2009). These changes will have profound implications for the carbon cycle as large-scale losses of carbon from biomass and soils have the potential to quickly and drastically increase atmospheric CO₂ beyond the scope of human intervention.

2.6 Conclusion

Tropical savannas include a wide range of ecosystems from woodlands and shrublands through to grasslands and everything in between. They are important globally as a major source of pastoral land and support a substantial portion of the world's population, in addition to being an important source of biodiversity. Unfortunately, population pressures have resulted in the conversion of large areas of savanna to cropping and pasture, frequently leading to degradation due to overgrazing, particularly in Australia. In addition to anthropogenic influences altering the nature of tropical savannas, these systems are also highly seasonal and prone to disturbance, which adds to their complexity and dynamic nature. These factors combine to frequently obfuscate the mechanisms driving the extent of tropical savanna ecosystems. The vast extent of tropical savannas means that they play an important role in the

global carbon cycle, storing a large amount of carbon (particularly in soil carbon) and contributing substantially to the fluxes of GPP and respiration. Tropical savannas are sparsely studied and generally poorly understood; how they will respond to complex climate changes including increased atmospheric CO₂, altered precipitation patterns and alterations in intensity and frequency of disturbances remains to be seen.

Chapter 3

Description of study sites

Statement of contribution

Conceptualised by Kalu Davies.

Written by Kalu Davies.

Edited by Kalu Davies and Michael Bird with advice from Michael Liddell.

3.1 Abstract

The study was conducted at three 1 ha plots in the wet-dry tropics of Far North Queensland, Australia. The area can be broadly divided into two distinct bioregions with the Wet Tropics dominated by rainforest to the east and the Einasleigh Uplands dominated by savanna to the west. The study sites are all located near rainforest/savanna boundaries and represent some of the wetter tropical savanna types. Brooklyn Station is the hottest, driest and most seasonal of the sites located on alluvial sediments of the Mitchell River floodplain overlying metamorphic bedrock. The grassy understorey consists of C₄ native perennial grasses and the invasive annual species *Themeda quadrivalvis* (grader grass). Davies Creek is located on shallow gravelly soils of granitic origin with a sparse shrub layer and grassy understorey of C₄ perennial grasses. Koombooloomba is the coolest and wettest of the sites with a dense secondary canopy of *Allocasuarina torulosa* growing on deep soils of basaltic origin. The grassy understorey consists of a mix of perennial C₃ and C₄ grasses with considerable *Lantana camara* invasion.

3.2 Regional context

As it does for much of the eastern seaboard of Australia, the Great Dividing Range escarpment runs roughly parallel to the coast in a north-south direction through the study region. The escarpment itself is composed primarily of metamorphic rocks of the Hodgkinson Formation and granitic intrusions, with alluvial fans and storm surge sediments overlying ancient mangrove muds on the coastal side. To the west of the escarpment are the broad plateaus of the Atherton and Carbine Tablelands extending from 400 m to 1000 m above sea-level (Nott, 2003). The climate of the region is wet/dry monsoonal with a wet season from November to April and a dry season from May to October. Winter rain primarily occurs as a result of orographic uplift associated with the Great Dividing Range, which has led to the formation of two distinct bioregions in the area: the Wet Tropics on the eastern side, dominated by rainforest and the Einasleigh Uplands on the western side that are dominated by savannas (Figure 3.1; QLD Herbarium, 2014).

Two of the study sites (Koombooloomba and Davies Creek) are located adjacent to rainforest/savanna boundaries, while the third site is located approximately 10km from the nearest rainforest (Figure 3.1). Mean annual precipitation increases, and

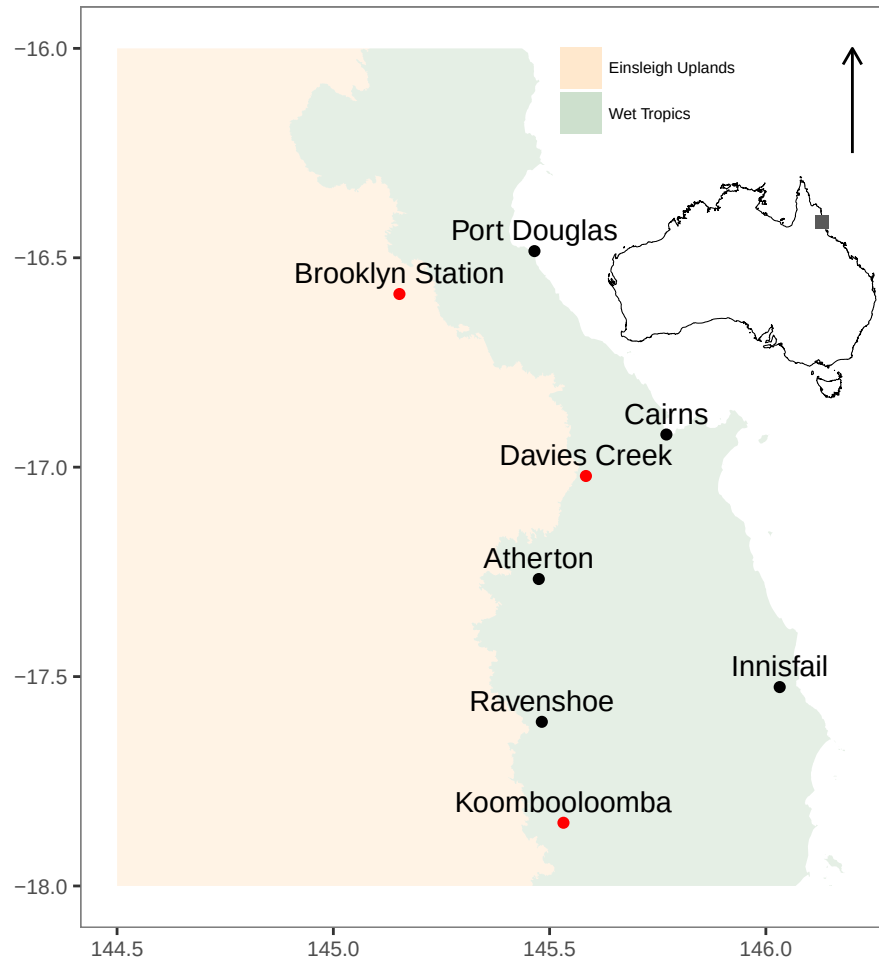


Figure 3.1: Location of study sites (●) within the greater Cairns region in relation to the biogeographic regions of the area and local towns (●). The Wet Tropics (green shading) to the east is dominated by rainforest and the Einasleigh Uplands (orange shading) to the west is dominated by savanna.

seasonality of precipitation decreases, with proximity to the rainforest boundary. In addition, mean annual temperature decreases with altitude such that Koombooloomba is the coolest, wettest site, while Brooklyn Station is the hottest, driest, and most seasonal of the sites (Figure 3.2). A full description of the sites is given in the following sections with a brief summary of the site characteristics in (Table 3.1).

The Brooklyn Station site is within a permanent site established as part of the Terrestrial Ecosystem Research Network (TERN) and the Koombooloomba and Davies

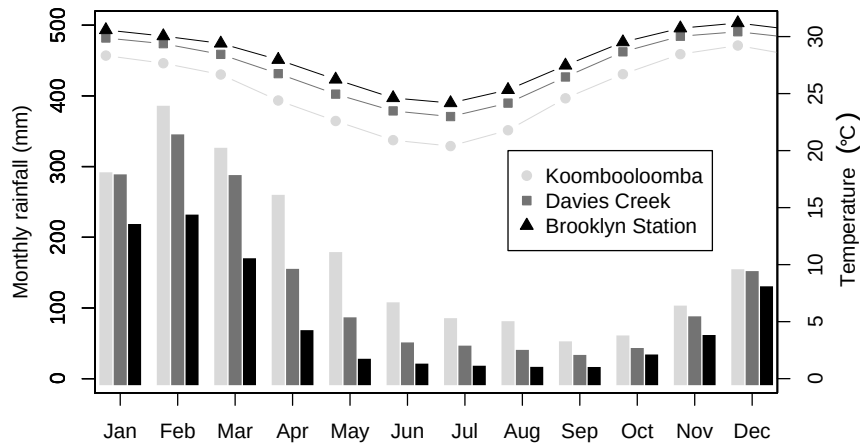


Figure 3.2: Mean monthly rainfall (left side y-axis; vertical bars) and maximum temperature (right side y-axis; points) for the Koombooloomba, Davies Creek and Brooklyn Station study sites. Data sourced from the Australian Water Availability Project (AWAP; www.bom.gov.au/jsp/awap/) and was extracted using the SDMTTools package (VanDerWal et al., 2014) for R (www.R-project.org).

Creek sites are within permanent 1 ha plots established as part of the Tropical Biomes in Transition (TROBIT) project (Torello-Raventos et al., 2013; Veenendaal et al., 2014).

Table 3.1: Main characteristics of the study sites

Site	Brooklyn Station	Davies Creek	Koombooloomba
Savanna classification ^a	Long-grassed woodland savanna	Tall woodland savanna	Tall woodland savanna
Mean annual precipitation (mm)	906	1460	1430
Height above sea level (m)	365	671	848
Soil parent material	Alluvium and metamorphics	Granite	Basalt
Soil classification ^b	Sodosol	Tenosol	Ferrosol

^a (Torello-Raventos et al., 2013)

^b (Isbell, 2016)

3.3 Brooklyn Station

Brooklyn station is located within the Brooklyn Nature Reserve operated by the Australian Wildlife Conservancy and is approximately 120 km from Cairns at 16.586°S, 145.155°E (Figure 3.1).

3.3.1 Climate and vegetation

This site has the most pronounced seasonality of the three sites in this study, receiving 90% of the mean annual precipitation (MAP) during the wet season (Figure 3.2). Although winter rainfall does occur, the median precipitation during the dry season is 0 mm.

Brooklyn Station is a long-grassed woodland savanna (Torello-Raventos et al., 2013) that is locally classified as Regional Ecosystem 9.3.3 (open woodland on alluvial flats, levees and plains of the Einasleigh Uplands bioregion; QLD Herbarium (2016)). The overstorey is dominated by *Eucalyptus cullenii* with a sparse shrub layer and a seasonally dense grass layer consisting of native perennials and invasive annuals (Table 3.2). The dominant grass species, *Themeda quadrivalis* (grader grass), grows to heights of over 2m during the wet season (Plate 3.1) and completely senesces in the dry season (Plate 3.2).

3.3.2 Soils

The lithology of the site is metamorphic overlain by a dense clay floodplain with occasional rocky layers, clay lenses and perched aquifers and the soil is classified as a Sodosol (Isbell, 2016). The alluvial sediments are dominated by clay and silt particles that cause the soils to crack during the dry season (Plate 3.3) and become waterlogged during the wet season (Plate 3.4).

3.3.3 Disturbance

The site is inaccessible during the wet season due to flooding, surface ponding and inundation (Plate 3.4). In addition, the site is burnt approximately every 2 years (NAFI, 2014). The site was burnt in a medium intensity fire in May 2011, which



Plate 3.1: Brooklyn Station during the late wet season (March 2012)



Plate 3.2: Brooklyn Station during the late dry season (November 2010)

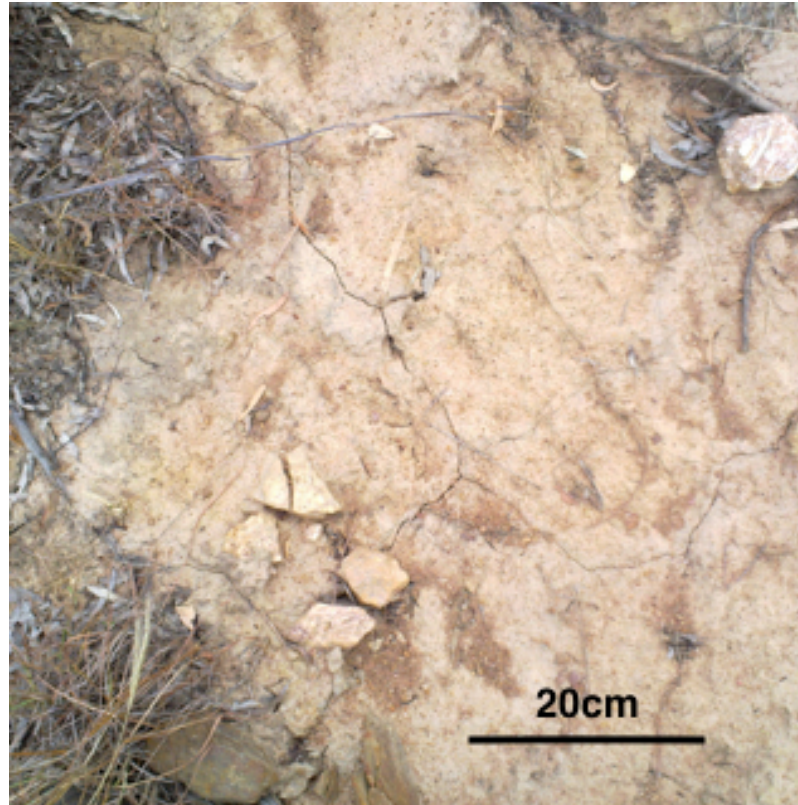


Plate 3.3: Cracking clay during the dry season at Brooklyn Station)

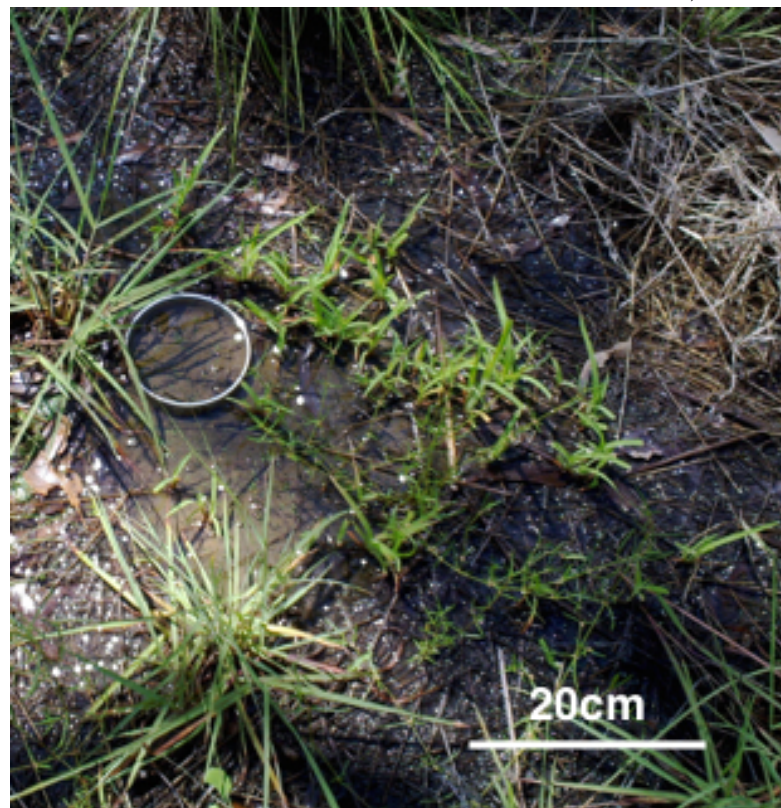


Plate 3.4: Surface ponding at Brooklyn Station during the wet season



Plate 3.5: Medium intensity burn at Brooklyn Station in May 2011

resulted in complete crown scorching to a height of over 4m and ~90% of groundcover burnt (Plate 3.5). Feral pigs also occasionally disturb the site.

Table 3.2: Species composition of the Brooklyn Station site. All species identified by Rigel Jensen (Australian Wildlife Conservancy). Common names retrieved from the Atlas of Living Australia (www.bie.ala.org.au) and scientific names follow the Australian Plant Census naming conventions.

Strata	Scientific name	Common name
Dominant tree species	<i>Eucalyptus cullenii</i> Cambage	Cullen's ironbark
	<i>Eucalyptus chlorophylla</i> Brooker & Done	Greenleaf box
Dominant grass species	<i>Heteropogon contortus</i> (L.) P. Beauv. ex Roem. & Schult.	Black spear grass
	<i>Chrysopogon fallax</i> S.T.Blake	Golden beardgrass
	<i>Bothriochloa decipiens</i> var. <i>decipiens</i>	
	<i>Paspalidium constrictum</i> (Domin) C.E.Hubb	Box grass
	<i>Fimbristylis dichotoma</i> (L.) Vahl.	Common fringe-rush
	<i>Eragrostis leptostachya</i> (R.Br.) Steud.	Love grass
	<i>Cyperus fulvus</i> R.Br.	Sticky sedge
	<i>Cyperus distans</i> L.f.	
	<i>Scleria brownii</i> Kunth	
	<i>Themeda triandra</i> Forssk.	Kangaroo grass
Subdominant tree species	<i>Grevillea striata</i> R.Br.	Beef oak
	<i>Petalostigma pubescens</i> Domin	Quinine bush
	<i>Terminalia subacroptera</i> Domin	

continued

Strata	Scientific name	Common name
Subdominant understorey	<i>Acmella grandiflora</i> var. <i>brachyglossa</i> (Benth.) R.K.Jansen	
	<i>Brunoniella acaulis</i> ssp. <i>acaulis</i>	
	<i>Carissa spinarum</i> L. (also <i>Carissa lanceolata</i> R.Br.)	Bush plum, Conkerberry
	<i>Clerodendrum floribundum</i> R.Br.	Lolly bush
	<i>Commelina lanceolata</i> R.Br.	
	<i>Cyanthillium cinereum</i> (L.) H.Rob.	Ironweed
	<i>Emilia sonchifolia</i> (L.) DC.	Red tasselflower, purple sow thistle
	<i>Epaltes australis</i> Less.	Epaltes
	<i>Flueggea virosa</i> ssp. <i>Melanthesoides</i> (F.Muell.) G.L.Webster	Snowball bush
	<i>Galactia tenuiflora</i> var. <i>macrantha</i> Domin	
	<i>Grewia retusifolia</i> Kurz	Dog's nuts, dysentery bush
	<i>Murdannia graminea</i> (R.Br.) G.Bruckn.	Grass lily
	<i>Neptunia gracilis</i> f. <i>glandulosa</i> Windler	
	<i>Ocimum americanum</i> var. <i>americanum</i>	
	<i>Rostellularia adscendens</i> ssp. <i>clementii</i> (Domin) R.M.Barker	
	<i>Typhonium angustilobum</i> F.Muell.	Fire lily
	<i>Urarian lagopodioides</i> (L.) Desv. ex DC.	
Invasive species	<i>Themeda quadrivalis</i> (L.) Kuntze	Grader grass
	<i>Cenchrus ciliaris</i> L.	African buffel grass
	<i>Cryptostegia grandiflora</i> R.Br.	Rubber vine

continued

Strata	Scientific name	Common name
	<i>Sporobolus fertilis</i> (Steud.) Clayton	Rat-tail grass
	<i>Stachytarpheta cayennensis</i> (Rich.) Vahl	Cayenne snakeweed
	<i>Stylosanthes humilis</i> Kunth	Townsville lucerne
	<i>Stylosanthes scabra</i> Vogel	

3.4 Davies Creek

The Davies Creek site is located within the Dinden National Park (adjacent to Davies Creek National Park) on the Lamb Range approximately 22km southwest of Cairns at 17.021°S, 145.584°E (Figure 3.1).

3.4.1 Climate and vegetation

MAP is approximately 1500 mm (Table 3.1) of which ~60% falls during the wettest quarter (January to March). The site is moderately seasonal with ~17% of the MAP falling during the driest six months (November to April; Figure 3.2) and rain events during the driest quarter are not uncommon.

Vegetation at Davies Creek is a tall woodland savanna (Torello-Raventos et al., 2013) and is locally classified as Regional Ecosystem 7.12.34 (open woodland to open forest on dry uplands on granite of the Wet Tropics bioregion). This is one of the more common ecosystems across the Atherton tablelands (QLD Herbarium, 2016). The overstorey is dominated by *Eucalyptus acmenoides*, *E. tereticornis*, *Corymbia calrksoniana* and *C. citriodora* with a sparse understorey of shrubs, grasses and herbs (Table 3.3). The grassy layer is dominated by the perennial grass *Themeda triandra*, which has a peak growing season during the wet season (Plate 3.6) and partially senesces during the dry season (Plate 3.7).

3.4.2 Soils

The lithology of the area consists of coarse porphyritic biotite granite that formed during the early Permian (Willmott and Trezise, 1989). The soils at the site consist of gravelly grey-brown to yellow-grey sandy loams to approximately 1m with granite rock outcrops common near hill crests (QLD DPI, 1997) that are classified as Tenosols (Isbell, 2016). The gravelly soils have low organic matter and water holding capacity, and may become hydrophobic after extended dry periods.

3.4.3 Disturbance

The site is located within a National Park so it is actively managed with low levels of invasive plant species and is burnt approximately every 4 years (NAFI, 2014). A low



Plate 3.6: Davies Creek during the wet season (February 2011)



Plate 3.7: Davies Creek during the dry season (September 2011)

intensity fire occurred at Davies Creek at the beginning of the study that resulted in scorching to a height of approximately 1.4m (Plate 3.8)) and left approximately 70% of the groundcover at the site burned or charred (Figure 3.3). The area had previously been used for cattle grazing, which ceased 10 years prior to this study.



Plate 3.8: Low intensity burn at Davies Creek in August 2010 with a scorch height of approximately 1.4m and partial combustion of the grass and litter layer.

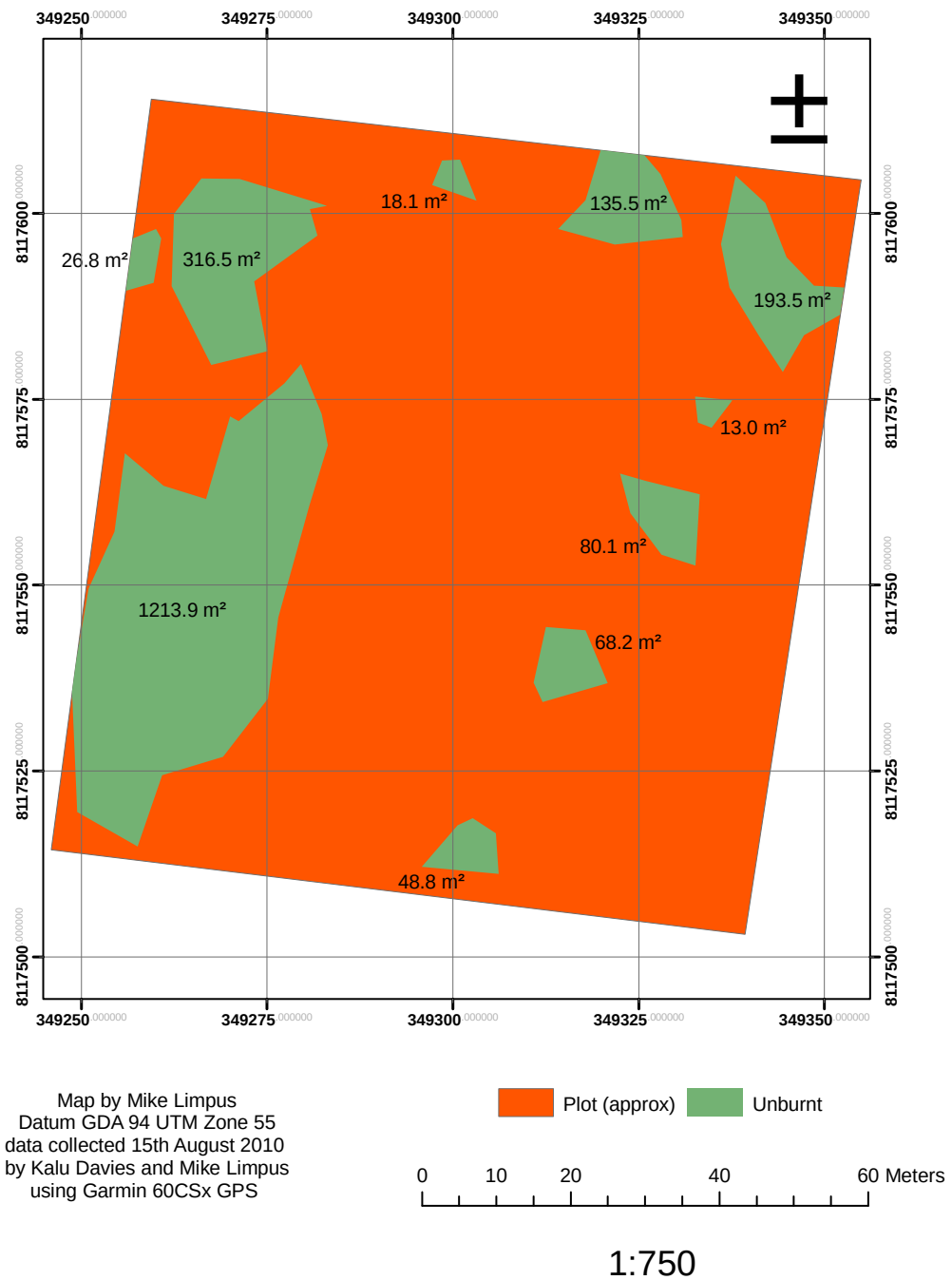


Figure 3.3: Map of burnt and unburnt areas at Davies Creek following a low intensity burn July 2010. Map by M. Limpus, used with permission.

Table 3.3: Species composition of the Davies Creek site. Tree species identified by Jeanette Kemp (Australian Wildlife Conservancy); other species identified by Andrew Ford (CSIRO). Common names retrieved from the Atlas of Living Australia (www.bie.ala.org.au) and scientific names follow the Australian Plant Census naming conventions.

Strata	Scientific name	Common name
Dominant tree species	<i>Eucalyptus acmenoides</i> Schau. (also <i>Eucalyptus portuensis</i> K.D.Hill)	White mahogany, broad leaved stringy-bark
	<i>Eucalyptus tereticornis</i> Sm.	Forest red gum
	<i>Corymbia citriodora</i> (Hook.) K.D.Hill & L.A.S.Johnson	Lemon-scented gum
	<i>Corymbia clarksoniana</i> (D.J.Carr & S.G.M.Carr) K.D.Hill & L.A.S.Johnson	Clarksons bloodwood
Dominant grass species	<i>Themeda triandra</i> Forssk.	Kangaroo grass
	<i>Heteropogon triticeus</i> (R.Br.) Stapf ex Craib	Giant speargrass
	<i>Mnesithea rottboellioides</i> (R.Br.) de Koning & Sosef.	
Subdominant tree species	<i>Eucalyptus crebra</i> F.Muell. (also <i>Eucalyptus drepanophylla</i> F.Muell. ex Benth.)	Grey ironbark
	<i>Eucalyptus petrensis</i> Brooker & Hopper	
	<i>Melaleuca viridiflora</i> Sol. Ex Gaertn	Broad leaved paperbark
	<i>Lophostemon suaveolens</i> (Sol. ex Gaertn.) Peter G.Wilson & J.T.Waterh.	Swamp turpentine
	<i>Planchonia careya</i> (F.Muell.) R.Knuth	Cocky apple

continued

Strata	Scientific name	Common name
Understorey species (grasses, herbs, shrubs)	<i>Grevillea glauca</i> Banks & Sol. ex Knight	Bushman's clothes peg
	<i>Acacia flavescens</i> A.Cunn. ex Benth.	Red wattle
	<i>Acacia calyculata</i> A.Cunn. ex Benth	
	<i>Aristolochia meridionalis</i> E.M.Ross (also <i>Aristolochia pubera</i> R.Br.)	
	<i>Breynia oblongifolia</i> Mull.Arg.	Coffee Bush
	<i>Crotalaria medicaginea</i> Lam.	Trefoil rattlepod
	<i>Crotalaria montana</i> K.Heyne ex Roth	
	<i>Curculigo ensifolia</i> var. <i>ensifolia</i>	
	<i>Cyanthillium cinereum</i> (L.) H.Rob	Ironweed
	<i>Desmodium rhytidophyllum</i> F.Muell. ex Benth.	
	<i>Eremochloa bimaclata</i> Hack.	Poverty grass
	<i>Flemingia parviflora</i> Benth	
	<i>Glycine cyrtoloba</i> Tindale	
	<i>Hibbertia longifolia</i> F.Muell.	Arsenic plant
	<i>Hybanthus enncaspermus</i> orth. var. F.Muell.	
	<i>Indigofera pratensis</i> F.Muell.	Forest indigo
	<i>Persoonia falcate</i> R.Br.	Booral
	<i>Pteridium esculentum</i> (G.Forst.) Cockayne	Bracken
	<i>Pteridium revolutum</i> (Blume) Nakai	Hairy bracken
	<i>Pycnospora lutescens</i> (Poir.) Schindl.	

continued

Strata	Scientific name	Common name
	<i>Wahlenbergia gracilis</i> (G.Forst.) A.DC.	Australian bluebell
	<i>Zornia muriculata</i> ssp. <i>muriculata</i>	
Invasive species	<i>Praxelis clematidea</i> R.M.King & H.Rob	Praxelis
	<i>Stylosanthes humilis</i> Kunth	Townsville lucerne

3.5 Koombooloomba

Koombooloomba is located within the Koombooloomba State Forest approximately 120km south-southwest of Cairns at 18.849°S, 145.532°E (Figure 3.1).

3.5.1 Climate and vegetation

The MAP is ~1500 mm of which approximately half falls during the wettest quarter (January to March). Koombooloomba has the highest elevation and is the coolest of the sites. It is also the least seasonal, with approximately 25% of MAP occurring during the dry season (Figure 3.2). Koombooloomba vegetation consists of a tall woodland savanna (Torello-Raventos et al., 2013) that is locally classified as Regional Ecosystem 7.8.7 (open forest and associated grasslands predominantly on basalt uplands of the Wet Tropics bioregion). This ecosystem type is confined to the soils that developed on the Atherton basalt group and is currently classified as endangered due to weed invasion (QLD Herbarium, 2016). The overstorey consists of *Corymbia intermedia* and *Eucalyptus tereticornis* with a dense secondary canopy of *Allocasuarina torulosa*. The understorey is a dense mix of shrubs, grasses, herbs and sedges (Plates 3.9 and 3.10) including the invasive species *Lantana camara* (full species list in Table 3.2). The grass layer only partially senesces and the site may remain green throughout the dry season during wetter years.

3.5.2 Soils

The lithology of the area is basanite, hawaiite and alkali basalt with minor pyroclastic deposits that formed as part of the Atherton basalt group during the Miocene to Holocene (QLD DME, 1997). The resulting Ferrosols (Isbell, 2016) consist of an A horizon of approximately 10 cm of red clay loam with a light to medium clay B horizon to depths of over 1.5 m with ferromanganiferous nodules throughout (QLD DPI, 1992).

3.5.3 Disturbance

The Koombooloomba site has not burnt in the study period 2009-2014 (NAFI, 2014), although high levels of charcoal in the soil indicate that it has burnt in the past,



Plate 3.9: Koombooloomba during the wet season (January 2011)



Plate 3.10: Koombooloomba during the dry season (October 2011)

presumably in December 1990 when a wildfire burnt approximately 5000 ha in the region (QPWS, 2016). The site was, however, damaged by Tropical Cyclone (TC) Yasi in February 2010 and potentially also by TC Larry that passed nearby in 2006 (Figure 3.4). TC Yasi resulted in substantial crown damage, defoliation and minor tree death (Plate 3.11) as well as significant weed invasion (Plate 3.12), with access to the site blocked for 3 months. Additionally, the site is located within state forest and is regularly traversed by vagrant cattle. These cattle frequently destroyed litter traps (Plate 3.13) and disturbed soil collars resulting in a reduction in sample size for those experiments at this site. This ecosystem is also under threat as a result of severe weed invasion, particularly *Lantana camara*, with large areas of the plot heavily infested.



Plate 3.11: Cyclone associated tree death and post cyclone weed invasion at Koombooloomba following TC Yasi in 2010.

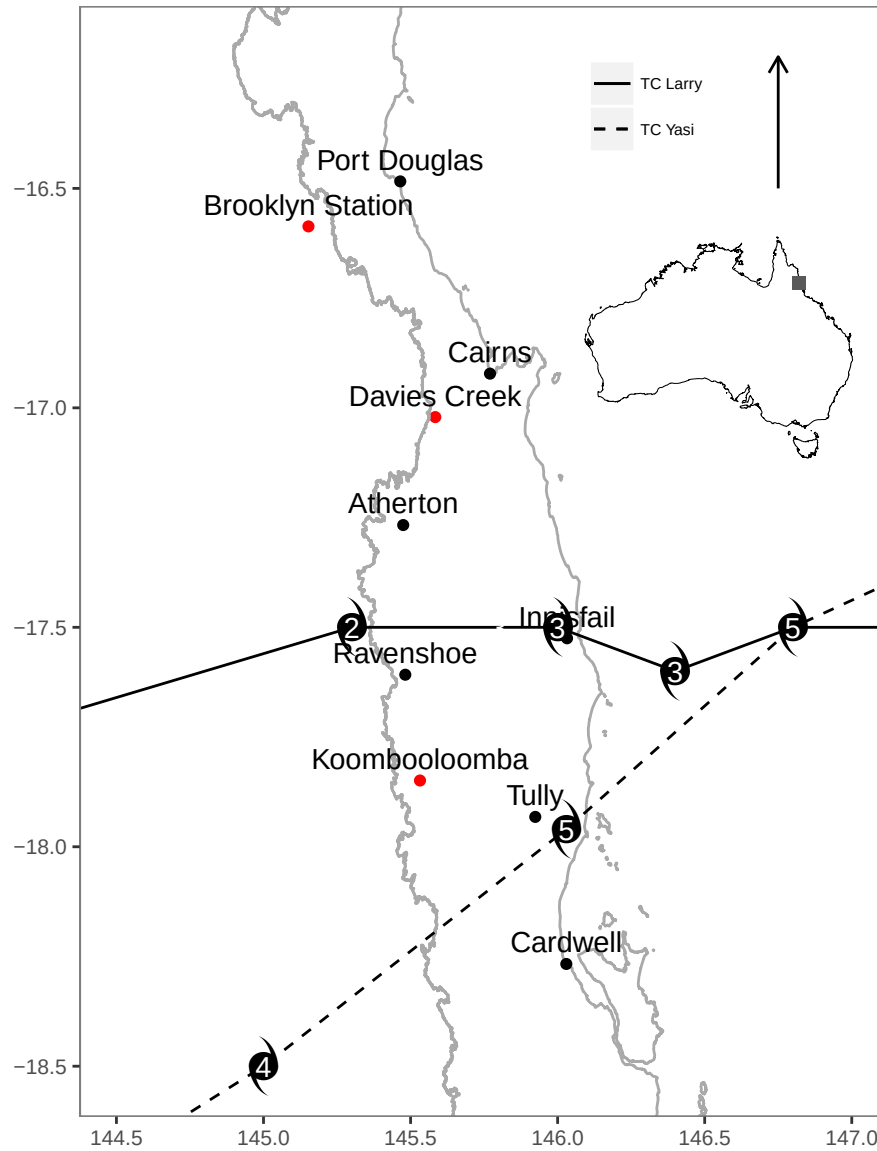


Figure 3.4: Map showing the cyclone tracks for TC Larry in 2006 (solid line) and TC Yasi in 2010 (dashed line) in relation to the study sites (●) and local towns (●). Cyclone intensity categories (scale 1:5) are shown on each track. Source: The Australian Tropical Cyclone Database (www.bom.gov.au/cyclone/history/)



Plate 3.12: Weed infestation at Koombooloomba after TC Yasi in 2010. Broad leaved weeds dominated the understorey for over 6 months following the cyclone.



Plate 3.13: Damanged equipment, trampled vegetation, and cow paths at Koombooloomba.

Table 3.4: Species composition of the Koombooloomba site. Tree species identified by Jeanette Kemp (Australian Wildlife Conservancy (AWC)); other species identified by Andrew Ford (Commonwealth Scientific and Industrial Research Organisation (CSIRO)). Common names retrieved from the Atlas of Living Australia (www.bie.ala.org.au) and scientific names follow the Australian Plant Census naming conventions.

Strata	Scientific name	Common name
Dominant tree species	<i>Eucalyptus tereticornis</i> Sm.	Forest red gum
	<i>Corymbia intermedia</i> (R.T.Baker) K.D.Hill & L.A.S.Johnson	Pink bloodwood
	<i>Allocasuarina torulosa</i> (Aiton) L.A.S.Johnson.	Baker's oak, forest she oak
Dominant grass species	<i>Dichelachne rara</i> (R.Br.) Vickery.	
	<i>Imperata cylindrica</i> (L.) P.Beauv.	Blady grass
	<i>Cymbopogon refractus</i> (R.Br.) A.Camus	Barb wire grass
	<i>Digitaria diminuta</i> Hughes (also <i>Digitaria orbata</i> Hughes)	
	<i>Mnesithea rottboellioides</i> (R.Br.) de Koning & Sosef.	
	<i>Themeda triandra</i> Forssk.	Kangaroo grass
Subdominant tree species	<i>Melaleuca viridiflora</i> Sol. Ex Gaertn	Broad leaved paperbark
	<i>Lophostemon suaveolens</i>	Swamp turpentine
	<i>Acacia</i> sp.	Wattle
	<i>Rhodomyrtus trineura</i> (F.Muell) Benth.	
	<i>Mallotus philippensis</i> (Lam.) Mull.Arg	Kamala
	<i>Polyscias elegans</i> (C.Moore & F.Muell.) Harms	Black pencil cedar

continued

Strata	Scientific name	Common name
Understorey species (grasses, herbs, shrubs)	<i>Axonopus compressus</i> (Sw.) P.Beauv.	Broad leaved carpet grass
	<i>Centella asiatica</i> (L.) Urb.	Gotu cola, Indian pennywort
	<i>Conyza canadensis</i> (L.) Cronquist	Canadian fleabane
	<i>Desmodium varians</i> (Labill.) G.Don	Slender tick trefoil
	<i>Dianella caerulea</i> Sims	Blue berry lily
	<i>Hybanthus stellarioides</i> (Domin) P.I.Forst.	
	<i>Hydracotyle hirta</i> R.Br. ex A.Rich.	Hairy pennywort
	<i>Lomandra longifolia</i> Labill.	Long leaved matrush
	<i>Oplismenus burmannii</i> (Retz.) P.Beauv.	
	<i>Paspalum paniculatum</i> L.	Russell River grass
	<i>Rhodamnia</i> sp. Jack	
	<i>Richardia brasiliensis</i> Gomes	Mexican clover
	<i>Rostellularia adscendens</i> ssp. <i>adscendens</i>	
	<i>Rubus rosifolius</i>	Native raspberry
	<i>Sida rhombifolia</i> L.	Paddy's lucerne
Invasive species	<i>Triumfetta rhomboidea</i> Jacq.	Chinese Burr
	<i>Praxelis clematidea</i> R.M.King and H.Rob	Praxelis
	<i>Lantana camara</i> L.	Common lantana

Chapter 4

Aboveground biomass and productivity in three tropical savanna sites

Statement of contribution

Conceptualised by Kalu Davies, Michael Bird and Jon Lloyd.

Written by Kalu Davies.

Field work: Koombooloomba and Davies Creek plot establishment as part of the Tropical Biomes in Transition (TROBIT) consortium with funding from the UK Natural Environment Research Council administered by the University of Leeds. Field assistance from Jon Lloyd, Michael Bird, Gustavo Saiz, and others. Botanical identifications by Andrew Ford and Jeanette Kemp. Brooklyn Station plot establishment by Kalu Davies, Rigel Jensen and Michael Limpus, botanical identifications by Rigel Jensen. Koomooloomba and Davies Creek recensus by Jon Lloyd, Michael Bird, Kalu Davies, Samuel Reiseger, Marc Jacobs and others with funding from Oliver Phillips. Brooklyn Station recensus by Samuel Reiseger and Amy Beavan. All other fieldwork by Kalu Davies with assistance from Michael Limpus, Amy Beavan, Penny King, Marcin Skladaneic and others.

Data analysis and interpretation by Kalu Davies and Jon Lloyd with advice from Michael Bird and Michael Liddell.

Edited by Kalu Davies, Michael Bird and Michael Liddell with advice from Paul Nelson.

4.1 Abstract

Despite the significance of tropical savannas to terrestrial net primary productivity (NPP) and the global carbon cycle, there remains a paucity of inventory-based estimates of biomass and carbon stocks. In this study, all trees greater than 10 cm diameter at breast height (dbh) were measured within a 1 ha plot at each of three tropical savanna sites and all trees were re-measured three to four years later. In addition, litterfall was collected over a two-year period and grass biomass was destructively harvested over a 12 month period. These savannas are some of the more densely wooded savannas in Australia, with basal area largely constrained by water availability. Basal area remained constant at all sites over the study period, although this did not reflect the dynamic nature of the biomass changes where growth was negated by mortality in all but one site. The grassy understory contributed ~50% of the aboveground net primary productivity (ANPP) at all sites (4.1, 5.1, and 9.2 t C ha⁻¹ y⁻¹ at Brooklyn Station, Davies Creek and Koombooloomba, respectively) while accounting for <10% of the aboveground carbon stock, however the results were similarly highly dependent on the method chosen, with alternative methods yielding differences of up to 400%. The woody carbon stock (37, 70, and 78 t C ha⁻¹ at Brooklyn Station, Davies Creek and Koombooloomba, respectively) was highly sensitive to disturbance with Tropical Cyclone (TC) Yasi resulting in high mortality at Koombooloomba and frequent fire resulting in high mortality and low growth rates at Brooklyn Station. Davies Creek remained disturbance free during the study period and was the only site to have positive carbon gains in woody biomass. These results highlight the sensitivity of the carbon storage potential of tropical savannas to stochastic disturbance and their vulnerability to substantial shifts in both structure and composition as a result of climate change.

4.2 Introduction

Tropical savannas occupy approximately 20% of the global land surface (Grace et al., 2006) and approximately 30% of the land surface in Australia (Cook et al., 2010). They are characterised by spatially heterogeneous vegetation consisting of trees and shrubs that utilise the C₃ photosynthetic pathway and grassy understorey plants that largely utilise the C₄ photosynthetic pathway (Bond and Midgley, 2012; House et al., 2003). These plant forms respond differently to the highly seasonal precipitation typical of tropical savannas, resulting in significant temporal variation in carbon

cycle processes (Chen et al., 2003; Moore et al., 2015). In addition, there is a large range in the productivity of tropical savannas between and within sites (Lloyd et al., 2008), further compounded by high levels of disturbance of varying intensities and frequencies (Andersen et al., 2012a; Hutley et al., 2013; Russell-Smith et al., 2003). For example, tropical savannas have been estimated to account for only 30% of terrestrial NPP (Grace et al., 2006), yet they are responsible for up to 60% of global fire emissions (van der Werf and Randerson, 2010). As a result of these complexities, management practices may determine if a savanna ecosystem operates as a carbon source or sink (Beringer et al., 2007).

In addition to management practices, the source/sink potential of tropical savannas is also highly vulnerable to perturbations in environmental factors. For example, increases in precipitation or seasonality in precipitation that lead to increases in fuel loads or curing time can increase fire intensity (Bradstock, 2010). Furthermore, disturbances such as tropical cyclones lead to significant carbon losses (Hutley et al., 2013), that are similarly beyond the control of land owners/managers. As atmospheric CO₂ concentrations and average global temperatures continue to rise (Hartmann et al., 2013), climatic extremes such as droughts and storms are increasing (Feng et al., 2013; Zhao and Running, 2010) and these events are decreasing global terrestrial uptake of atmospheric CO₂ (Reichstein et al., 2013a). When combined with their large extent, the potential exists for these ecosystems to sequester and store appreciable quantities of carbon (Cook et al., 2010; Dean et al., 2012).

The carbon storage potential of tropical savannas lies largely within the soil carbon and woody biomass components of the ecosystem as frequent fires generally consume the grassy understorey biomass. Despite the significance of savannas, there remains a paucity of studies that provide inventory-based biomass estimates for tropical savannas in Australia. The majority of studies have been concentrated in the Northern Territory (for example Chen et al. (2003); Cook et al. (2005), although see Burrows et al. (2000) for estimates in Queensland and Alchin et al. (2010) for estimates in Western Australia). This study aims to assess the aboveground biomass (AGB) and ANPP of three tropical savanna areas in the tropics of northern Queensland. Specifically, this study will address the following research questions:

1. How much carbon is stored in AGB at these sites?
2. What is the ANPP at these sites?
3. What influences the contribution of trees and grasses to carbon stocks and ANPP?

4.3 Methods

4.3.1 Site description

The study was conducted at the Koombooloomba, Davies Creek, and Brooklyn Station sites that are described in detail in Chapter 3. A brief summary of relevant characteristics is given in Table 4.1.

Table 4.1: Characteristics of study sites

	Brooklyn Station	Davies Creek	Koombooloomba
Location	16.586°S, 145.155°E	17.027°S, 145.585°E	17.786°S, 145.546°E
Mean annual precipitation (mm)	906	1460	1430
Mean monthly maximum temperature (°C)	24-31	23-30	20-29
Savanna classification ^a	Long-grassed woodland savanna	Tall woodland savanna	Tall woodland savanna
Height above sea level (m)	365	671	848
Tree density (stems ha ⁻¹) (>10 cm dbh)	173	273	273

^a Torello-Raventos et al. (2013)

4.3.2 Tree stand structure and biomass estimation using allometric relationships

All trees greater than 10 cm dbh were measured within a square 1 ha area. The plot was further subdivided into 25 subplots of 20 m x 20 m and the individual trees were assigned x-y coordinates based on visual estimation. Davies Creek and Koombooloomba were measured in April of 2009 (t_1) and April 2013 (t_2) while Brooklyn Station was measured in June of 2010 (t_1) and July 2013 (t_2). For the (t_2)

measurements, ‘recruits’ were classed as individual trees that had moved into the >10 cm dbh size class range while ‘mortality’ was visually assessed as individuals with a lack of living foliage or bark. Individual stems that were classified as dead at t_2 were considered to reduce the stand AGB by an amount equivalent to tree biomass at t_1 .

Although the same operators were used where possible, the Davies Creek and Koombooloomba sites were established and re-measured as part of a larger project where such details were beyond our control. In a comparison of measurements between different operators, the mode deviation between measurements was 1 mm. In addition, there is a ± 1 mm instrument error associated with the dbh measuring tape. Combining these errors, the individual dbh tape measurements are considered accurate to ± 2 mm.

The AGB of the tree layer was estimated by applying allometric relationships to the tree stand data at each site. Allometric regression equations are used to relate tree biomass to an easily measured parameter such as stem diameter by harvesting (and potentially excavating) and then weighing trees of a range of size classes. Published equations for a given site may not be applicable beyond the range of that site and generalised equations should therefore be used with caution. The allometric equation applied to the tree stand data in this study is

$$\ln(AGB) = 2.5243 \times \ln(dbh) - 2.3046$$

where AGB = (kg biomass tree⁻¹) and dbh = diameter (cm) at breast height (1.3m). This equation developed by Williams et al. (2005) is the most comprehensive generalised equation that has been developed in tropical northern Australia and this has been applied to all genera. Additional allometric equations developed by Williams et al. (2005) include tree height as a parameter but this resulted in an improvement to the model of only 5% and so tree height was not included in this study. Published and unpublished data from 220 individuals of 14 species (of which approximately 90% were *Eucalyptus* sp.) across 11 sites in the Northern Territory, Queensland, and northern New South Wales were included in the study where rainfall ranged from ~350-1700 mm y⁻¹ and basal area ranged from ~4-16 m² ha⁻¹. Despite many environmental similarities with the sites used to develop this equation, none of the 20 species of tree that occur at the sites used in this study co-occur at sites that were harvested. Furthermore, Koombooloomba sits at the upper end of the climatic and productivity range over which the equations were developed with a mean annual

rainfall of 1500 mm and a basal area of 17 m² ha⁻¹.

The standard errors of the estimated parameters were used to estimate the uncertainties in the use of the allometric model using a bootstrap approach. A normal distribution with a mean equivalent to the parameter estimate and a standard deviation equivalent to the standard error of the parameter was used to randomly generate new parameter estimates. These parameters were applied to the tree stand data in order to generate a range of plot level estimates of the carbon stock contained in the aboveground woody biomass. A random error was also applied to the tree stand data to simulate measurement error of 2 mm per diameter measurement. Each simulation was run 10000 times. This approach was also used to estimate uncertainty associated with the woody component of ANPP. Where differences between tree biomass are reported, the differences were calculated within a single simulation such that the same parameter estimates were applied to each set of tree stand data before the difference was calculated. Additional sources of uncertainty beyond the scope of this study include variation in woody tissue density and variation in tree form.

4.3.3 Grass biomass and productivity

Grass biomass was measured by monthly destructive harvest of all sub-canopy grassy plants within two randomly selected 1 m² quadrats (Chen et al., 2003), from March 2011 until June 2012. Initially, only total biomass was measured, however from August 2011 the samples were separated into living and senesced components. The total biomass (for each component) was weighed and then a subsample (~10%) was weighed and oven dried at 60°C. Two samples are likely to be insufficient to describe the variation in the grass biomass but it was not possible to collect additional samples on account of the intensive labour required to separate the biomass into the components. Hence the grass biomass results should be viewed as a rough estimate only. Grass litterfall was not measured *per se*, but is approximated by the dead component of the monthly changes in biomass.

A variety of methods were utilised for calculating grass productivity with a full review of the assumptions and limitations associated with each described by Singh et al. (1975), Long et al. (1989) and Scurlock et al. (2002). A summary of the methods is given in Table 4.2 *sensu* Scurlock et al. (2002). Methods (4) and (5) involve the partitioning of harvested grass into living and dead components however this data was only available for 11 months. Hence the partitioning of the total biomass

for the first month that was not measured was estimated using the partitioning that was measured in the following month. In addition, access to the Koombooloomba and Brooklyn Station sites was blocked in February of 2012 due to cyclone damage and flooding, respectively and so biomass for this month was estimated using the average of the month prior and the month following.

Table 4.2: Summary of harvest methods for assessing NPP of sub-canopy vegetation (adapted from Scurlock et al. (2002))

			Method	Assumptions
(1)	Peak live biomass		Maximum above-ground living biomass	Standing dead matter and litter is carried over from previous year, death in current year is negligible and live biomass from previous year is negligible.
(2)	Peak standing biomass		Maximum above-ground living and dead biomass	Standing dead matter is formed by death in current year decomposition in current year is negligible and no living or dead biomass is carried over from previous year
(3)	Δ Live biomass		Maximum minus minimum living biomass	As for method (1) except that living biomass from previous year is excluded
(4)	Incremental sum of live biomass		Sum of positive increments in living biomass	Simultaneous growth and death do not occur and NPP cannot be negative
(5)	Incremental sum of live and dead biomass		Sum of positive increments in living and dead biomass	Simultaneous growth, death, and decomposition do not occur and NPP cannot be negative.

4.3.4 Litter

Litterfall was collected throughout the study period (August 2010 to June 2012) from circular mesh traps (0.25 m²) attached to metal stakes of 100 cm height to keep them off the ground and minimise grass litter from entering the trap. Grass litter that

entered the traps was removed. The traps were emptied approximately monthly and dried at 60°C (Chen et al., 2003). Although the litter traps were emptied as frequently as possible, there is potential for some loss due to litter decomposition, particularly during the wet season. Therefore, the litterfall estimates should be seen as a conservative estimate. The total mass was divided by the number of days between collections to give $\text{g C m}^{-2} \text{ day}^{-1}$. A total of 12 litter traps per site were randomly located either near trees (beneath the approximate mid-point of the canopy cover, termed ‘tree’; $n = 6$) or away from trees (at the approximate mid-point between two trees, termed ‘grass’; $n = 6$). Litterfall included leaves, flowers, fruits, bark and stems $< 2 \text{ mm}$ diameter and these components were not separated. If grass entered the trap, it was discarded.

Differences between litterfall trap locations were analysed using repeated measures ANOVA; initial analysis indicated differences between the savanna sites, so each site was treated separately. Where the analysis indicated different main effects in different time periods, the ANOVA was run separately for each time period. The litterfall biomass was log transformed to meet the assumptions of the ANOVA however the descriptive summary statistics for the litterfall analyses are presented as the median and interquartile range of each group (*i.e.* ‘tree’ or ‘grass’), as this is appropriate for skewed data. All statistical analyses were performed using R v.1.14.2 Software (R Development Core Team, 2012; www.r-project.org).

4.4 Results

4.4.1 Carbon stocks in biomass

Basal area remained roughly stable at all sites with no meaningful changes at any site. Koombooloomba exhibited the highest increase with basal area increasing from 17.0 ± 0.2 to $17.5 \pm 0.2 \text{ m}^2 \text{ ha}^{-1}$ while Davies Creek increased from 16.5 ± 0.2 to $16.9 \pm 0.2 \text{ m}^2 \text{ ha}^{-1}$ over a 4 year interval. Brooklyn Station showed a small decrease from 9.7 ± 0.1 to $9.5 \pm 0.1 \text{ m}^2 \text{ ha}^{-1}$ over a 3-year interval. Similarly, aboveground woody carbon stocks did not vary greatly between t_1 and t_2 (Table 4.3). Aboveground biomass increased slightly at Davies Creek and decreased slightly at Brooklyn Station and Koombooloomba. Mortality was highest at Koombooloomba with a loss of 7.6% of total basal area ($n = 27$), however this was offset by the highest recruitment rate of 6.7% of basal area ($n = 108$). Davies Creek experienced

low mortality and recruitment at 0.4% ($n = 3$) and 0.7% ($n = 7$) of basal area, respectively. Brooklyn Creek had the lowest recruitment at 0.1% of basal area ($n = 1$) although mortality at this site was 5.5% of basal area ($n = 8$). Large trees (dbh >40 cm) were present at all sites accounting for 30% ($n = 15$), 40% ($n = 31$), and 60% ($n = 39$) of the basal area at Brooklyn Station, Davies Creek, and Koombooloomba, respectively (Figure 4.1). Maximum dbh recorded was >80 cm at all sites. The frequency distribution of stem size classes at Koombooloomba displays a classic ‘reverse-J’ or negative exponential relationship, while Davies Creek is more closely approximated by a bimodal distribution. Multiple peaks are also evident at the Brooklyn Station site.

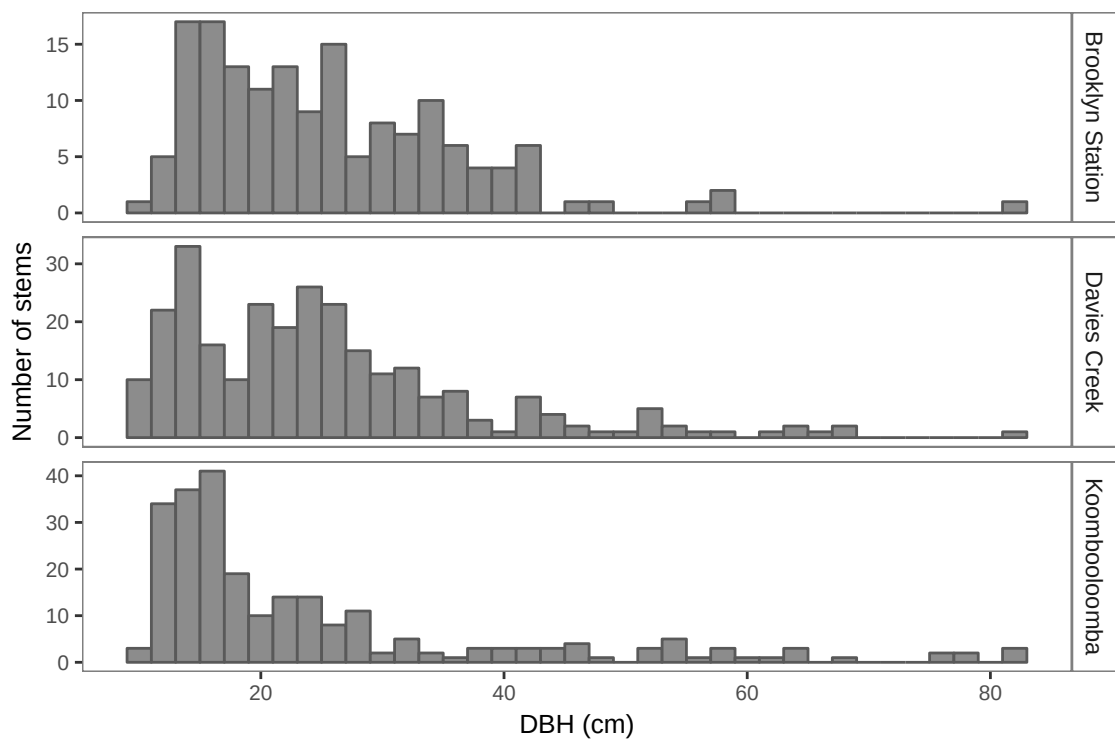


Figure 4.1: Size class distribution of dbh for 2013 in 5 cm increments (note the different scales on the y-axis)

Aboveground grass biomass was higher in the wet season (after January) than it was at the end of the dry season (Figure 4.2). At Brooklyn Station, a fire consumed all the grass biomass at the commencement of the measurement period and initial biomass remained low until the onset of the wet season at which time the living component increased rapidly for a period of 2-3 months, followed thereafter by a marked increase in the senesced component. Increases in the senesced component occurred more gradually at the other sites and the seasonality was less distinct. The annual mean grass biomass for each site was 9.0, 4.5, and 2.7 t C ha⁻¹ for

Koombooloomba, Davies Creek, and Brooklyn Station, respectively. Of this, mean living biomass accounted for 50%, 42%, and 70% of the total for each site.

Table 4.3: Living aboveground carbon stocks of tree stand data. Values given are the mean $\pm$ s.d. of 10000 simulations.

Site	Standing live biomass (t_1)	Standing live biomass (t_2)
Brooklyn Station	38 ± 4	37 ± 4
Davies Creek	68 ± 8	70 ± 8
Koombooloomba	79 ± 9	78 ± 9

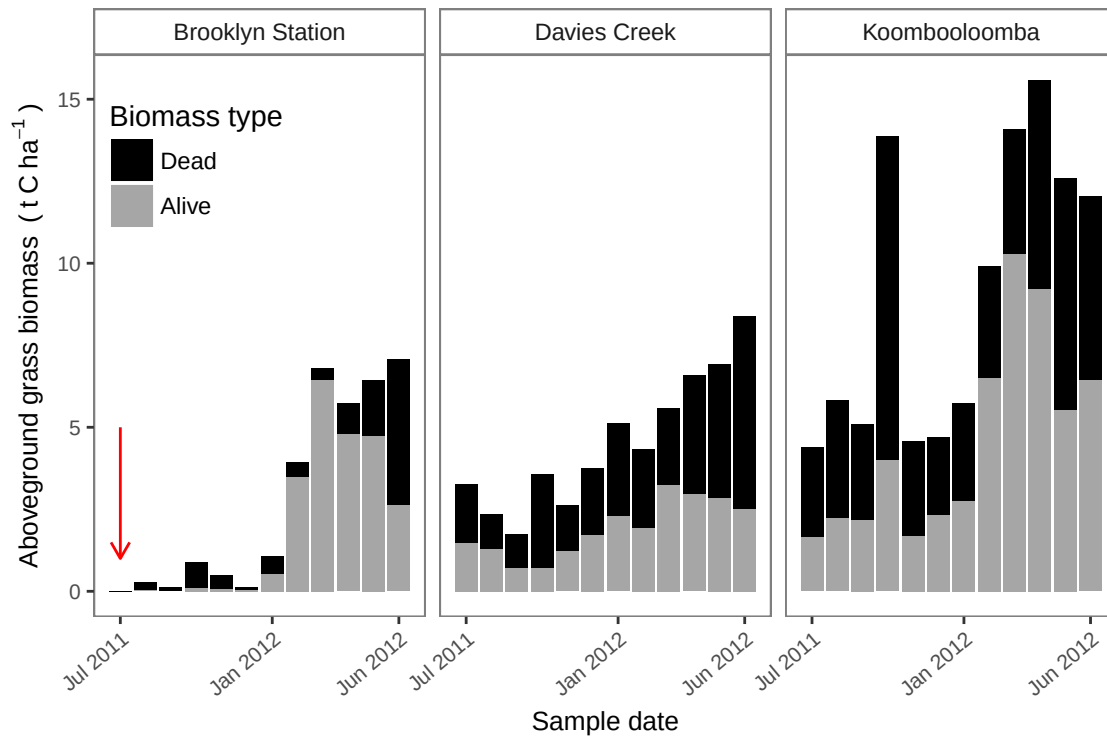


Figure 4.2: Aboveground grass biomass in living and dead components for each sample date. Values are the mean of two samples and the red arrow at Brooklyn Station indicates when the site was burnt.

4.4.2 Aboveground productivity

Stem increment rates were highly variable and differences between sites, species and size classes were not significant. Nonetheless, there were some apparent trends. For example, mean stem increment rates ($\pm$ s.d.) at Davies Creek and Brooklyn Station were 1.4 ± 3.7 mm y^{-1} and 1.9 ± 2.3 mm y^{-1} , respectively, but stem increment rates were considerably higher at Koombooloomba, averaging 3.6 ± 4.8 mm y^{-1} . This was largely due to rapid growth among the *A. torulosa*, and in particular the smaller trees (10 - 20 cm dbh size class) where mean stem increment rates peaked at 6.0 ± 4.1 mm y^{-1} . There were also minor reductions in dbh observed among the very large trees, particularly at Koombooloomba. Growth increment in existing stems accounted for the majority of the woody ANPP at Davies Creek and Brooklyn Station, while new recruits accounted for the majority of the woody ANPP at Koombooloomba (Table 4.4). Mortality exceeded recruitment at all sites and the AGB loss exceeded the AGB gain at all sites except Davies Creek.

Table 4.4: Aboveground woody productivity (t C ha $^{-1}$ y $^{-1}$) of the three sites assuming biomass is 50% carbon (Schlesinger, 1997). Values given are the mean $\pm$ s.d. of 10000 simulations.

Site	Growth increment	New recruits	Mortality
Brooklyn Station	0.5 ± 0.1	0.0 ± 0.0	0.7 ± 0.1
Davies Creek	0.6 ± 0.1	0.0 ± 0.0	0.1 ± 0.0
Koombooloomba	0.4 ± 0.1	0.6 ± 0.1	1.2 ± 0.1

Litterfall was significantly different between sites ($F_{(2,15)} = 7.5$, $p = 0.006$) and Tukey's test was used to confirm that all sites were different to each other. Litterfall was higher in the first year than the second year for all sites, but differences were only significant for Koombooloomba ($F_{(1,11)} = 9.73$, $p = 0.0098$). Median litterfall rates tended to be higher in the wet season for Davies Creek and Koombooloomba but not for Brooklyn Station, and higher at tree locations for Brooklyn Station and Koombooloomba but not for Davies Creek (Table 4.5), although differences were not significant. Monthly litterfall rates at Brooklyn Station were slightly higher in traps located beneath trees ('tree') than in traps located between trees ('grass'), with the exception of the 3 months following the fire, where the pattern was reversed, but

even then results were not significant (Figure 4.3) Similarly, there was no significant difference between trap locations at Davies Creek. In contrast, monthly litterfall rates at Koombooloomba were significantly higher ($F_{(1,9)} = 20.2$, $p = 0.0015$) in tree locations during the first 6 months of the study period, prior to the passage of TC Yasi. After this time there were no longer significant differences between the trap locations ($F_{(1,11)} = 2.95$, $p = 0.11$).

Table 4.5: Median litterfall rates ($\text{t C ha}^{-1} \text{ y}^{-1}$) for collection zones, season, sample year and study for the three sites. Values in brackets are the interquartile range.

	Brooklyn Station	Davies Creek	Koombooloomba
Tree	0.6 (0.3 - 0.9)	1.2 (0.7 - 1.8)	1.3 (0.8 - 2.4)
Grass	0.4 (0.2 - 0.7)	1.5 (0.8 - 2.1)	0.5 (0.3 - 0.9)
Dry season	0.5 (0.3 - 0.9)	1.0 (0.6 - 1.5)	0.8 (0.4 - 1.4)
Wet season	0.4 (0.2 - 0.8)	1.7 (1.2 - 2.4)	0.9 (0.4 - 1.8)
Annual site total (2010 - 2011)	0.6 (0.4 - 0.9)	1.5 (1.0 - 2.2)	1.1 (0.5 - 2.6)
Annual site total (2011 - 2012)	0.4 (0.2 - 0.7)	1.2 (0.6 - 1.8)	0.8 (0.4 - 1.1)

Aboveground grass productivity was highest at Koombooloomba, irrespective of which method was used (Table 4.6). Method (5) yielded the highest productivity at all sites. Brooklyn Station was the lowest utilising method (2) and Davies Creek was the lowest according to all other methods.

4.4.3 The contribution of trees and grasses to stocks and productivity

Total AGB carbon stocks (woody AGB + grass AGB) for each site were 41, 76, and 88 t C ha^{-1} for Brooklyn Station, Davies Creek, and Koombooloomba, respectively. Of this total, the grass contributes 7%, 6%, and 10% at Brooklyn Station, Davies Creek and Koombooloomba, respectively. The total ANPP for each site is shown in Table 4.7. Of this total, the grass contributes 73% at Brooklyn Station, 63% at Davies Creek, and 78% at Koombooloomba.

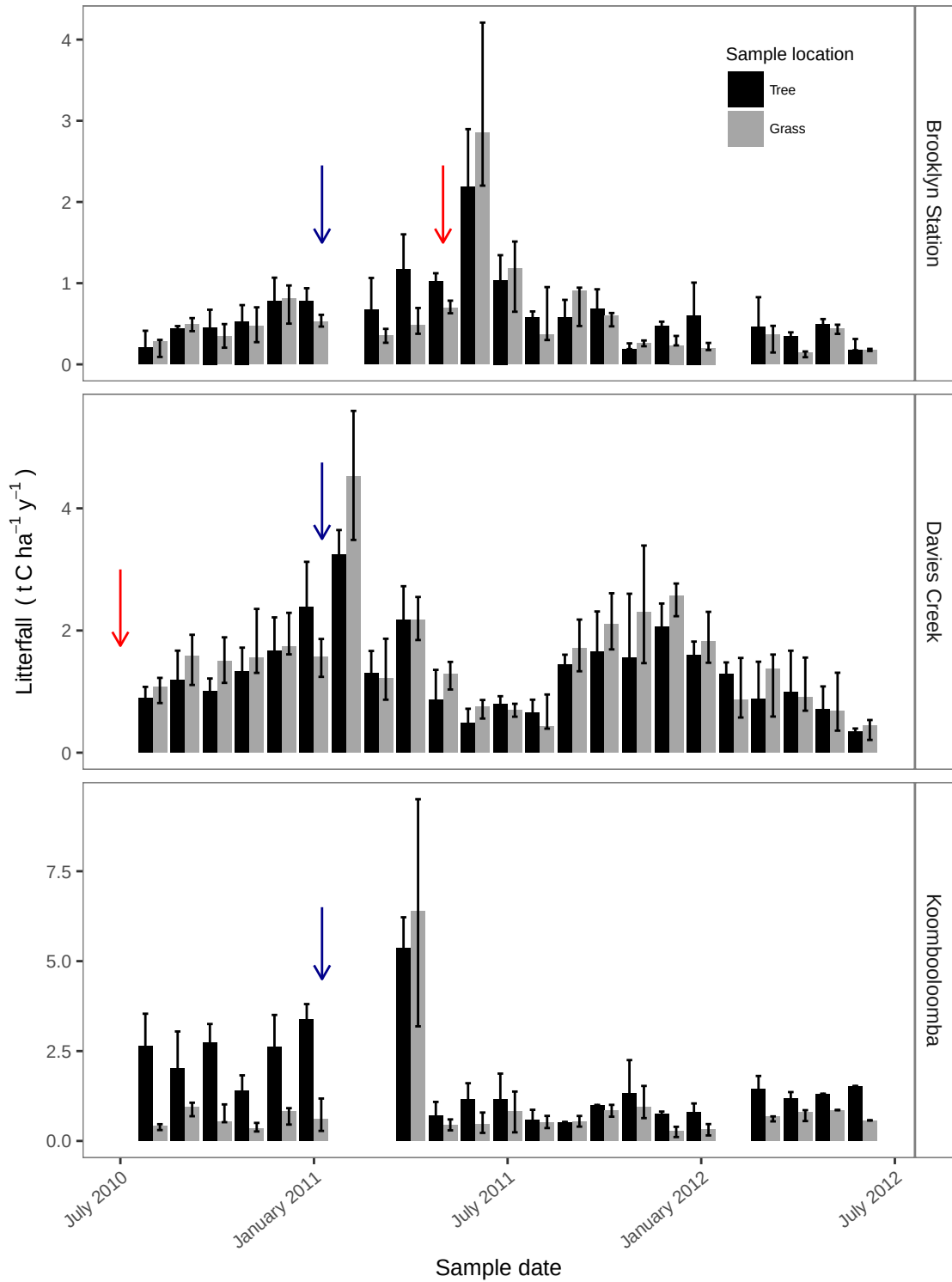


Figure 4.3: Mean monthly litterfall rates between tree ($n = 6$) and grass ($n = 6$) trap locations at each study site. Error bars are mean $\pm$ s.d. TC Yasi is marked with blue arrows and red arrows indicate fire at Brooklyn Station and Davies Creek. Note the different scales on the y-axes. Gaps in the data indicate access to the site was blocked.

Table 4.6: Aboveground productivity of grassy understorey ($\text{t C ha}^{-1} \text{ y}^{-1}$) of the three sites using a range of methods and assuming biomass is 50% carbon (Schlesinger, 1997)

Method	Brooklyn Station	Davies Creek	Koombooloomba
(1) Peak live biomass	1.2	0.8	2.6
(2) Peak standing biomass	1.8	2.1	3.9
(3) Δ Live biomass	1.2	0.6	2.1
(4) Incremental sum of live biomass	1.6	1.1	3.4
(5) Incremental sum of live and dead biomass	3.0	3.2	7.2

Table 4.7: Aboveground net primary productivity ($\text{t C ha}^{-1} \text{ y}^{-1}$) estimates for the three sites.

	Brooklyn Station	Davies Creek	Koombooloomba
Woody biomass increment (growth + recruitment; ΔB_{tree})	0.5	0.6	1.0
Litterfall (ΔB_{litter})	0.6	1.3	1.0
Grassy biomass increment (ΔB_{grass})	3.0	3.2	7.2
Aboveground NPP ($\Delta B_{tree} + \Delta B_{litter}$ $+ \Delta B_{grass}$)	4.1	5.1	9.2

4.5 Discussion

4.5.1 Aboveground carbon stocks

Woody biomass

Koombooloomba and Davies Creek represent examples of some of the more densely wooded savannas found within Australia, with basal areas of 17.5 ± 0.2 and $16.7 \pm 0.2 \text{ m}^2 \text{ ha}^{-1}$, respectively. For example, Burrows et al. (2002) reported basal area for 57 savanna sites throughout Queensland of which only four had a basal area of greater than $16 \text{ m}^2 \text{ ha}^{-1}$, and none had a basal area greater than $18 \text{ m}^2 \text{ ha}^{-1}$. Similarly, Williams et al. (1996) assessed the variation in vegetation structure along a precipitation gradient in the Northern Territory utilising 940 quadrats that encompassed 40 savanna types and the maximum basal area reported did not exceed $13 \text{ m}^2 \text{ ha}^{-1}$.

Russell-Smith et al. (2003) reported basal area of $18.5 \text{ m}^2 \text{ ha}^{-1}$ in a *Eucalyptus* dominated open forest site but this only occurred in plots where fire had been largely excluded for over 20 years. Similarly, Prior et al. (2004) reported a basal area of $17 \text{ m}^2 \text{ ha}^{-1}$ in a *Eucalyptus* open forest, although fire had also been excluded at this site. Bowman et al. (2008) reports a range of basal areas of $4.8 - 31.5 \text{ m}^2 \text{ ha}^{-1}$ for sites located within Arnhem Land although this area is under semi-traditional Aboriginal management and has a considerably lower fire frequency and fire intensity than other areas of Australian savanna. In contrast, Brooklyn Station has a basal area of $9.5 \pm 0.1 \text{ m}^2 \text{ ha}^{-1}$, which is only slightly above the average of the sites reported in Burrows et al. (2002) and is similar to a variety of sites in the Northern Territory including $9.7 \text{ m}^2 \text{ ha}^{-1}$ (Hutley and Beringer, 2010) and $8 - 10 \text{ m}^2 \text{ ha}^{-1}$ (O'Grady et al., 2000) near Howard Springs, and $10 \text{ m}^2 \text{ ha}^{-1}$ (Cook et al., 2005) near Kapalga.

As suggested by the high basal area, the Koombooloomba and Davies Creek sites in this study also contain some of the highest carbon stocks of woody AGB for tropical savannas in Australia. Tree AGB stocks for the Northern Territory range from $12.4 - 57.5 \text{ t C ha}^{-1}$ Cook et al. (2005) as compared to 78.6 and 69.8 t C ha^{-1} for Koombooloomba and Davies Creek, respectively (Table 4.3). They are comparable to other densely wooded savannas throughout the world, for example, Michelsen et al. (2004) reported woody AGB stocks of $56.4 - 93.7 \text{ t C ha}^{-1}$ for dry woodlands in Ethiopia. In addition, Miranda et al. (2014) reviewed biomass studies for 170

sites in the Brazilian *cerrado* and reported woody AGB of up to 80 t C ha⁻¹.

In contrast, Brooklyn Station is fairly typical for intermediate savannas in both Australian and globally. Tree AGB stock at this site is 38.2 t C ha⁻¹, which is similar to values of 33.6 - 40.6 t C ha⁻¹ for Queensland (Burrows et al., 2002) and 17.7 - 41.2 t C ha⁻¹ for the Northern Territory (Chen et al., 2003). Other studies have reported carbon stocks of 36.6 t C ha⁻¹ for a wooded grassland in Ethiopia (Michelsen et al., 2004) and 39.0 t C ha⁻¹ for a dry tropical savanna in India (Pandey and Singh, 1992). Similarly, the review by Miranda et al. (2014) gives the mean woody biomass stock for 'forestlands' (as opposed to grasslands or shrublands) as 39.8 t C ha⁻¹.

Grass biomass

Grass AGB carbon stocks averaged 2.7, 4.5, and 9.0 t C ha⁻¹ for Brooklyn Station, Davies Creek, and Koombooloomba, respectively. Similar to issues associated with tree allometry, the method of calculating aboveground grass biomass has a variety of limitations. These are detailed in Scurlock et al. (2002) and the main points are summarised in Table 4.2. The grass AGB carbon stocks in this study are substantially higher than the annual mean of 1.0 t C ha⁻¹ reported by Chen et al. (2003) for a tropical savanna in the Northern Territory and are comparable to the 4.7 - 16.9 t C ha⁻¹ reported by Michelsen et al. (2004) for four tropical savannas in Ethiopia. While invasive African grasses are present at Brooklyn Station, they are not at the other two sites.

Further comparisons of 'grass' biomass are hampered by variations in the component of the understorey that are measured. For example, Rossiter et al. (2003) reported average fuel loads of 0.3 t C ha⁻¹ and 1.4 t C ha⁻¹ for native savannas and invaded savannas in the Northern Territory. Similarly, Kauffman et al. (1994) reported fuel loads of 3.5 to 5.0 t C ha⁻¹ for *cerrado* tropical savannas in Brazil although it is not clear if either study included live biomass in their estimates, or if these estimates equate to peak standing biomass, or if they include tree derived litter. Averaged over the sample year, dead grass AGB was 30%, 58%, and 49% of the total grass AGB at Brooklyn Station, Davies Creek, and Koombooloomba, respectively. The low proportion of dead grass AGB at Brooklyn Station reflects the fire that removed the grassy layer prior to the commencement of sampling. Nevertheless, the grass AGB at this site is dominated by the annual grader grass and this species would normally completely senesce within a 12 month period.

4.5.2 Aboveground productivity

Tree growth

Woody biomass increment was 0.5, 0.6, and 0.4 t C ha⁻¹ y⁻¹ for Brooklyn Station, Davies Creek, and Koombooloomba, respectively, which is comparable to reported values for other Australian savannas. For example, Burrows et al. (2002) and Cook et al. (2005) both reported a woody biomass increment of 0.5 t C ha⁻¹ for Queensland and the Northern Territory, respectively. In contrast, Chen et al. (2003) reported annual woody biomass increments of 1.6 t C ha⁻¹ for tropical savannas in the Northern Territory, which is considerably higher than the results in this study. The savanna site used by Chen et al. (2003) has a higher rainfall than the sites in this study, with a mean annual precipitation (MAP) of 1700 mm as compared to 900 mm for Brooklyn Station and 1500 mm for Davies Creek and Koombooloomba.

The individual stem diameter increment rates presented in this study differ between sites and in some cases species and/or size. The most evident of these is the stem increment of *A. casuarina* at Koombooloomba, which varies considerably with size, reaching a peak of 5.6 mm y⁻¹ within the 10-20 cm dbh trees and then dropping off as size increases, eventually resulting in a slightly negative growth rate. The high stem increment rate of the *A. casuarina* is consistent with rapid recruitment to the canopy as a result of defoliation due to cyclone damage (Cook et al., 2005), however the trend was not evident in the other species at the site. Conversely, all large trees (>40 cm dbh) displayed negative stem increments, irrespective of species. There is a tendency to attribute ‘shrinking trees’ to measurement error and it must be emphasised that the stem diameter growth rates presented here are associated with a high degree of uncertainty that is equivalent to or greater than the estimate itself.

Nevertheless, negative stem diameter increment rates have been reported in other studies although these are usually associated with water use (Pastur et al., 2007). For example, Worbes (1999) reported that tropical rainforest trees were observed to shrink during the dry season in association with a reduction in stem water content. Similarly, Gerhardt and Todd (2009) reported seasonal shrinkage in a dry forest in Zimbabwe, although they reported that smaller trees tended to shrink more than larger trees and Burgan (1971) reported that shrinking and swelling of bark influenced variations in the diameter of *Eucalyptus robusta*. Koombooloomba and Davies Creek were both measured at the end of the wet season (April) on both occasions so

typical seasonal water availability is unlikely to have led to the observed decreases. However, the 2010-2011 wet season was the wettest ever recorded in Australia on account of the extreme La Niña event and all the species that displayed negative stem diameter increment rates have thick fibrous or corky bark so this may have been a factor.

In contrast, Boaler (1963) measured stem diameter on a weekly basis for the African savanna tree *Pterocarpus angolensis* and reported that stem diameter increments were not consistently related to rainfall. All individuals displayed a negative stem diameter increment after the onset of the wet season and the authors postulated that this may have been associated with the production of new leaves, shoots and flowers. As *P. angolensis* is a deciduous species, while the *Allocasuarina* sp. and *Eucalyptus* sp. are evergreen, this seasonal allocation of resources may not be so pronounced in the Australian context. Nevertheless, it is also possible that the larger trees suffered such significant crown loss as a result of TC Yasi that they are drawing on stem reserves to facilitate resprouting (Cook and Goyens, 2008; Cook et al., 2005).

The stem increment rates observed at Brooklyn Station ranged from 1.5 to 2.6, with a mean of 1.9 mm y⁻¹. These rates are fairly typical of Australian savannas; for example, Cook et al. (2005) reports growth rates of six savanna species that range from 1.2 - 2.4 mm y⁻¹. The fact that growth rates are typical (and not unusually low) in itself is actually surprising as Brooklyn Station has burnt on average every 2 years for the last 13 years. The fires are usually lit in May, which is considered an early dry season fire, but the fires appear to be of a moderate intensity. This is based upon complete canopy scorching, which Williams et al. (1998) found to be an adequate predictor for the Byram fire-line intensity. Using the same fire intensity classification, Murphy and Bowman (2007) found that a severe fire every two years was sufficient to reduce mean stem increment rates from 1.7 mm y⁻¹ to approximately 0.6 mm y⁻¹.

In contrast, stem increment rates at Davies Creek were highly variable, ranging from 3.7 mm y⁻¹ for *E. citriodora* to a 0.8 mm y⁻¹ decrease for *E. tereticornis*. While these results are more variable than those reported by Cook et al. (2005), they are within the range of 0.4 -16 mm y⁻¹ reported by Prior et al. (2004) for savanna types near Darwin. In contrast to Koombooloomba, Davies Creek did not sustain any appreciable damage as a result of TC Yasi. Similarly, it is unlikely that seasonal water use is responsible for the observed decrease in the larger *E. tereticornis*. Given the observed decrease was so small, measurement error and/or the fibrous nature of the bark is the most probable explanation.

Tree recruitment

Productivity due to recruitment of new trees to the >10 cm dbh cohort was negligible at both Brooklyn Station and Davies Creek (Table 4.7). Fire is often proposed as the disturbance vector that prevents the recruitment of saplings into the tree layer, forming a recruitment bottleneck (Bond et al., 2012; Lawes et al., 2011; Prior et al., 2010; Russell-Smith et al., 2003). This may be the case for Brooklyn Station where recruitment was non-existent and the site is frequently burnt. In contrast, Davies Creek is burnt much less frequently and in much lower intensity fires and yet there is no recruitment at this site either. Nevertheless, Murphy et al. (2015) contend that the *Eucalyptus* species that dominate the Australian savannas are remarkably tolerant to a range of fire frequencies and intensities and are able to grow through the ‘fire trap’.

In contrast to fire, which tends to result in higher mortality among small trees and juveniles (Bond et al., 2012), cyclone damage is generally more significant among the medium to large size classes (Cook and Goyens, 2008) and the abrupt canopy removal can provide the conditions for rapid recruitment. This may explain the high levels of recruitment at Koombooloomba, where new recruits exceeded productivity due to tree growth. Periods of rapid recruitment are reflected in the size demographics of the woody vegetation (for example, Hutley and Beringer (2010)). Figure 4.4 shows the size class distribution for the three sites and by assuming a growth rate of 2 mm y⁻¹ (Hutley and Beringer, 2010) it is possible to convert size to age and hence date of recruitment.

Caution must be exercised when applying generic stem diameter increment rates across sites as they can be highly variable, as they are in this study. Stem diameter increment rates have been shown to vary with fire frequency (Murphy and Bowman, 2007), season (Prior et al., 2004), slope, and presence of buffalo (Werner, 2005). In addition, species and size may or may not influence stem diameter increment rates with multiple trends typically reported for a single study (for example, Cook et al. (2005, 2006)).

Taking account of these limitations, both Brooklyn Station and Davies Creek display noticeable peaks in the size class that corresponds to recruitment towards the end of the 1800s. Historical records indicate that a severe tropical cyclone devastated the settlements of Cairns in 1878 (Anon., 1878) and Port Douglas/Mossman in 1911 (Anon., 1911) and palaeo-records suggest a spike in cyclone activity in the area around 1890 (Haig et al., 2014). In addition, although the pattern is almost

indiscernible at the scale presented, there is a similar peak at the Koombooloomba site around the same time.

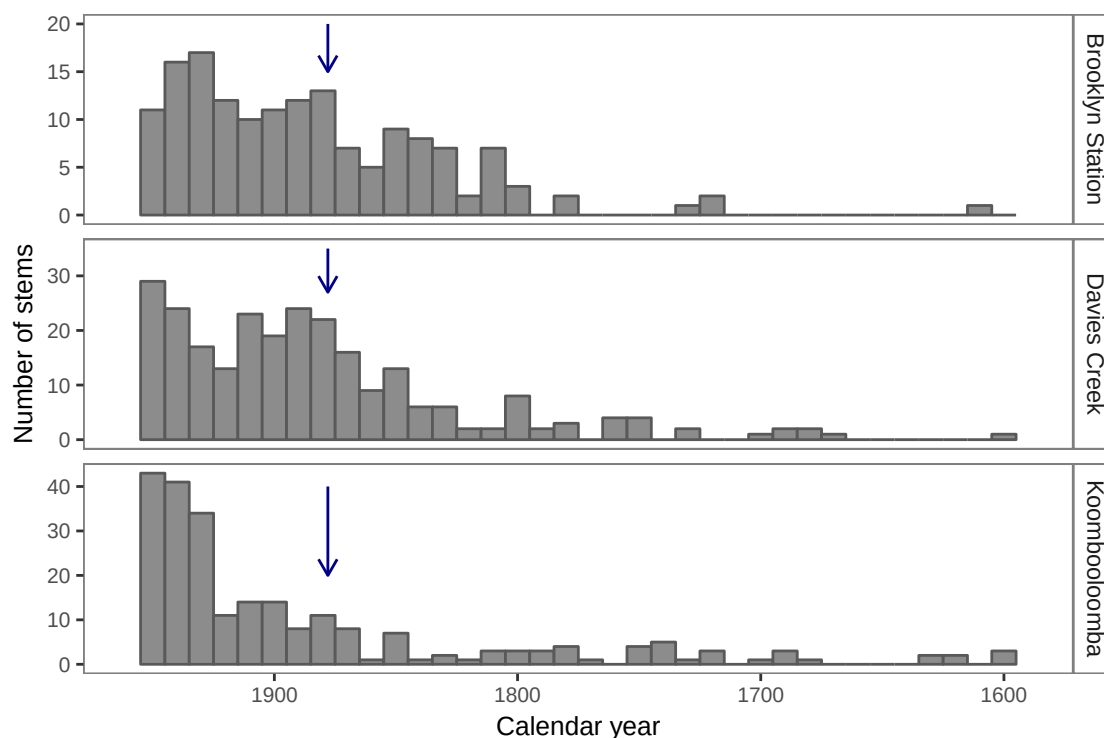


Figure 4.4: Tree size classes converted to age by assuming mean stem diameter increment of 2 mm y^{-1} (Hutley and Beringer, 2010) and converted to date of recruitment by subtracting age from 2013. The blue arrow indicates a spike in cyclone activity commencing in 1880.

Litterfall

The canopy scorching as a result of the fire resulted in a substantial increase in litterfall at Brooklyn Station. Mean litterfall rates increased over three-fold during the first sampling period after the fire from $0.85 \text{ t C ha}^{-1} \text{ y}^{-1}$ to $2.80 \text{ t C ha}^{-1} \text{ y}^{-1}$ and continued to remain high during the next sampling period at $1.25 \text{ t C ha}^{-1} \text{ y}^{-1}$ before returning to pre-fire levels after three months (Figure 4.3). Litterfall was almost 50% higher in grass areas after the fire, in contrast to increased litterfall from the cyclone which was 2 - 3 times higher in tree regions. There was an increase in litterfall rates following TC Yasi at all sites, however the effect was most pronounced at Koombooloomba where the site was visibly devastated.

Litterfall was generally higher during the wet season at Koombooloomba and Davies Creek although this effect was enhanced by leaf drop following the cyclone. Litterfall

rates were higher during the dry season at Brooklyn Station, although similarly this was due to leaf drop following the fire at the beginning of the dry season. Litterfall rates at Koombooloomba were significantly higher in the canopy traps up until TC Yasi occurred. As a result of the cyclone, one study tree was completely felled, another was snapped off at 2m, and the remainder ($n = 12$) suffered substantial canopy defoliation and removal. The litterfall following the cyclone was not significantly different between the canopy and inter-canopy litter traps and it is possible that the driving force behind this change was wind. The *A. casuarina* leaf litter is comprised of elongated needles and in combination with a dense canopy, there is presumably minimal air flow available to distribute the litter around the site. Following the extensive canopy removal, more wind may have been able to facilitate litter distribution. This is somewhat supported by the litterfall rates at the other sites where the canopy is much more open and the *Eucalyptus* spp. leaves catch more wind.

Grass productivity

The grass ANPP (Table 4.6) was highly seasonal at all sites with maximum biomass (both living and dead components) occurring during the wet season and minimum biomass occurring during the dry season (or following fire, in the case of Brooklyn Station). Method (5) yielded the highest values at all sites followed by (2), (4), (1) and (3). Methods (1) and (3) yielded identical results for Brooklyn Station as the site had burnt prior to the commencement of grass harvest; thus any living (or dead) matter from the previous year was excluded, irrespective of whether that was inherent in the method or not. Generally speaking, methods (1) to (4) gave estimates of biomass that were 20-60% lower than those calculated using method (5). The implementation of a consistent method in savanna studies is hampered by the large variation in sampling effort between the methods.

Grass ANPP at all sites was considerably higher than the grass ANPP of 0.5 t C ha⁻¹ reported by Chen et al. (2003) for a tropical savanna in the Northern Territory. Koombooloomba yielded the highest values for grass ANPP irrespective of which method was used. Bowman et al. (2007) reports grass productivity values of 1.1 - 2.2 t C ha⁻¹ for savanna sites across the Northern Territory and Kimberley region of Western Australia and Rossiter et al. (2003) reports grass productivity values of 1.3 - 2.0 t C ha⁻¹ for native grasses in the Darwin area. Assuming the authors used method (2), Koombooloomba is considerably higher than this range (3.9 t C

ha⁻¹), while Davies Creek (2.1 t C ha⁻¹) and Brooklyn Station (1.8 t C ha⁻¹) are more comparable. The Davies Creek and Koombooloomba sites are transitional savannas, which are quite different from the ‘typical’ savanna found in most of northern Australia, and this is potentially why the grass ANPP at these sites is so much higher. On the other hand, although Brooklyn Station is arguably more ‘typical’, the grass ANPP is still higher than expected and this is likely due to the presence of quick growing and productive invasive grasses.

4.5.3 The contribution of trees and grasses to stocks and productivity

Factors affecting the contribution of trees

The carbon storage capacity of these sites (as far as AGB is concerned) is largely controlled by the woody component, which contributes >90% to the total biomass carbon stock for the plot at all sites. This is due partly to the fact that the mortality of the grasses is high with the annual senesced component between 45 and 55% of the total productivity (Table 4.6). Furthermore, the grassy understorey is preferentially consumed by fire. The high basal area and woody AGB for the Koombooloomba and Davies Creek sites is not surprising as woody cover tends to increase with increasing MAP, both within Australia (Eamus, 2003; Williams et al., 1996) and globally (Lehmann et al., 2011; Staver et al., 2011a), although the rate of increase tends to drop off above a MAP of 2000 mm (Eamus, 2003).

The MAP for the Koombooloomba and Davies Creek sites is ~1500 mm, of which approximately 1000 mm falls in the wettest quarter at both sites (Figure 3.2). By comparison, the wettest site included in Burrows et al. (2002) reported mean rainfall for the wettest quarter as 800 mm and similarly, MAP reported by Williams et al. (1996) and Russell-Smith et al. (2003) did not exceed 1800 mm and 1500 mm, respectively. Brooklyn Station also receives a relatively high rainfall in the wettest quarter (~700 mm) although the seasonality is much more pronounced at this site, with the wettest quarter accounting for >75% of the MAP of 900 mm (as opposed to 50% and 60% for Koombooloomba and Davies Creek, respectively). In addition, >90% of the MAP falls between November and April (as opposed to 74% and 83% for Koombooloomba and Davies Creek, respectively). Furthermore, all the sites experience a dry season of ~8 months (number of months where mean rainfall <10% of annual rainfall) and under these conditions, forest closure has not been observed

to occur in either Africa, Australia or South America (Staver et al., 2011a).

Sankaran et al. (2005) reported that above a MAP of 650 mm, African savannas were ‘unstable’ as there was sufficient precipitation for canopy closure and some form of disturbance such as fire or herbivory is required to maintain the savanna ecosystem. While there are feral cattle at the Koombooloomba site, they are not present at high densities and it is unclear if they impose a level of disturbance sufficient to prevent canopy closure. In addition, while there is evidence of the site having burnt in the past with sizeable (>2 mm) pieces of charcoal within the surface soils (0-30 cm), the site has not burnt in the last 13 years (NAFI, 2014) although it was likely burnt in a large wildfire in the area in 1990 (QPWS, 2016). Nonetheless, the site was significantly disturbed by TC Yasi in 2010 (Plate 3.11), and most probably TC Larry in 2006 (Figure 3.4), and this likely presents a disturbance sufficient to prevent canopy closure. In contrast, Davies Creek (while not subject to any appreciable mammalian grazing pressures or cyclone damage) is burnt regularly, approximately every three years (three planned burns in 2005, 2007, 2010 and one unplanned burn in 2013; QPWS (2016)). Similarly, Brooklyn Station has been burnt on average every two years for the past 13 years (NAFI, 2014) and up until recently was also subject to cattle grazing.

An alternative climate index to seasonality or MAP is effective rainfall. This is estimated by subtracting the potential evapo-transpiration from the MAP to provide an estimate of moisture available to the ecosystem. Parr et al. (2014) employed this approach to compare tree stand structure across savanna sites in Australia, Africa and South America. Figure 4.5 shows the position of the sites in this study relative to the Australian savannas. Brooklyn Station falls almost exactly on the regression line, highlighting the role that moisture availability has on tree stand structure, while Koombooloomba and Davies Creek are somewhat more densely vegetated than the equation predicts.

Although basal area and carbon stocks (of biomass) are able to be mathematically related, they are not exactly the same thing. Liedloff and Cook (2007) used modelling techniques to demonstrate that the scaling factors between basal area (which relates to water use) and tree biomass differ, such that different stands using the same amount of water can have different biomass. Ultimately this means that the carbon stock of a tropical savanna can be maximised, without the use of additional water, by the preservation of the large trees as these hold disproportionately more carbon. Furthermore, the rate at which trees accumulate carbon also increases with tree size (Stephenson et al., 2014).

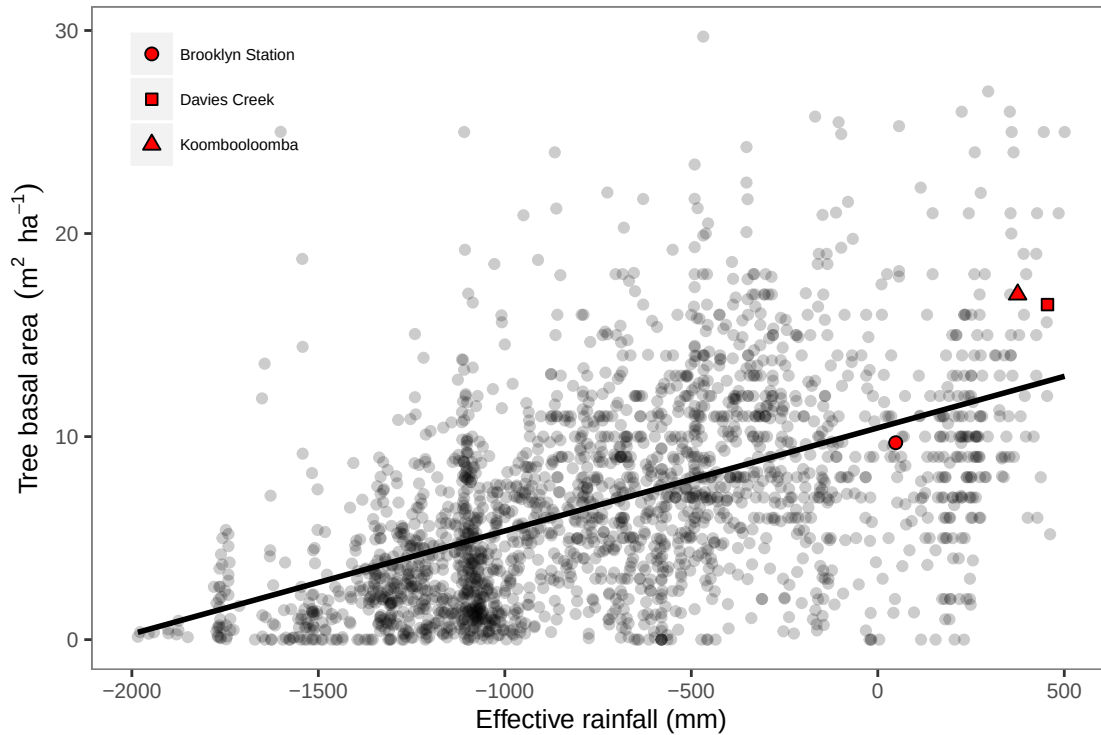


Figure 4.5: Basal area vs effective rainfall for Australian savannas (Lehmann et al., 2014) and this study. Effective rainfall calculated as the balance between mean annual precipitation and potential evapo-transpiration. Weather data for this study sourced from the Australian Government Bureau of Meteorology. Available online at <http://www.bom.gov.au/climate/data/>

Factors affecting the contribution of grass

The grassy understorey was a significant contributor to ANPP, exceeding contributions by woody growth, recruitment, and litterfall (Table 4.7). Utilising method (5), the grassy contribution to ANPP is 73% at Brooklyn Station, 63% at Davies Creek, and 78% at Koombooloomba. By comparison, Chen et al. (2003) estimated that the grassy understorey contributed 15% to ANPP at a tropical savanna in the Northern Territory. Further studies at the same site by Moore et al. (2015) attributed 32% of the net ecosystem productivity (NEP) to the understorey using eddy covariance measurements. The savanna site used in those studies has a higher MAP (1700 mm) than the sites in this study (900 - 1500 mm), but the woody AGB and ANPP is comparable to that of Brooklyn Station.

Unlike woody AGB and ANPP, grass AGB and ANPP does not tend to be tightly constrained by rainfall (Bowman et al., 2007). Instead grass biomass is highly dependent upon management strategies, particularly fire regime. For example, large and

frequent fires favour the establishment of more flammable annual grasses over perennial grasses and the timing of fires can also influence this balance (Bowman et al., 2007). In addition, a number of invasive annual grasses have managed to proliferate throughout large parts of Australia (see Setterfield et al. (2010) and references in Bowman et al. (2007)). These grasses cure late in the season and are generally not affected by low intensity early dry season fires, instead promoting the occurrence of high intensity late season fires. These fires can significantly reduce canopy cover and understorey cover, as a consequence favouring the reestablishment of the invasive grasses.

This positive feedback loop is known as the ‘grass-fire cycle’ (D’Antonio and Vitousek, 1992). For example, the standing biomass of the invasive species Gamba grass (*Andropogon gayanus*) at a study site in the Northern Territory was up to seven times that of native perennial grasses in the same area, resulting in fuel loads capable of supporting fires eight times more intense (Rossiter et al., 2003). A similar phenomenon may be occurring at Brooklyn Station as the site suffers considerable invasion of grader grass (*Themeda quadrivalis*). This annual grass grows to >2m and has a thick bushy flower that is extremely flammable, even early in the dry season. Fuel loads were approximately 3.1 t C ha⁻¹ prior to the fire in 2011 that resulted in complete canopy scorching and the peak standing biomass had returned to 1.8 t C ha⁻¹ within 9 months of the fire (Figure 4.2).

A strong relationship between rainfall and wet season ANPP of the herbaceous layer was reported by Augustine et al. (2003) for a variety of tropical savannas in Kenya. Certainly there is a trend between the sites in this study, with the high woody AGB at Koombooloomba associated with the highest grass ANPP and high rainfall, and the lowest woody AGB at Brooklyn Station was associated with the lowest grass ANPP and lowest rainfall (Table 4.3 and Figure 4.2). This trend is unusual because as rainfall increases and woody biomass increases, grassy biomass is often observed to decrease as the grasses are progressively shaded out by the trees (for example, Michelsen et al. (2004)). Notwithstanding, this trend is dependent on the anomalously high grass ANPP estimates at Koombooloomba, which can be explained by a number of factors. Firstly, the canopy cover (particularly the large, overstorey *Eucalyptus* sp.) has been substantially reduced due to cyclone damage, which has decoupled the relationship between basal area and leaf area index (and hence shade). Secondly, leguminous trees such as *Allocasuarina torrulosa* have been shown to facilitate grassy understorey growth rather than compete with it (Mazía et al., 2016).

Furthermore, although the high woody biomass at Davies Creek was similar to that of Koombooloomba and the MAP is also comparable for these two sites. However, the peak grass biomass at Davies Creek was only approximately half that of Koombooloomba and more comparable to that at Brooklyn Station which is substantially drier. This is likely due to differences in soil, which is much more fertile at Koombooloomba and likely able to support more grass, particularly during the dry season (Figure 4.2). These differences are also potentially exacerbated by the prevailing disturbance regime; the low intensity fires at Davies Creek favour the combustion of the grasses and leave the trees almost entirely unscathed. In comparison, the defoliation of the canopy at Koombooloomba as a result of TC Yasi not only damaged the trees in preference to the grasses, but also allowed a lot more light to penetrate the understorey, thus favouring the proliferation of the grasses.

4.5.4 Implications for climate change and the global carbon cycle

Across sites, although woody ANPP was high, mortality was also high with gains in woody biomass increment and recruitment frequently matched by losses in mortality in this study (Table 4.4). Woody AGB decreased by $0.8 \pm 0.2 \text{ t C ha}^{-1}$ at Brooklyn Station and $0.9 \pm 0.3 \text{ t C ha}^{-1}$ at Koombooloomba while woody AGB increased by $2.1 \pm 0.3 \text{ t C ha}^{-1}$ at Davies Creek. The dynamics of this net change were different for each site, with high recruitment, low growth, and high mortality at Brooklyn Station. Woody biomass gain was largely driven by growth rather than recruitment or mortality at Davies Creek, while at Koombooloomba growth, recruitment, and mortality were all high.

High growth at all sites is likely a reflection of high rainfall, particularly during the wet season of 2010-2011 due to above average rainfall associated with an extreme La Niña event (Detmers et al., 2015). Biomass gains associated with extreme weather events tend to be short lived and elsewhere in Australia such unusual biomass gains have since been lost due to subsequent drought (Ma et al., 2016). At Davies Creek a 3.3% increase in AGB was almost entirely due to tree growth and was associated with a 2.3% increase in basal area, suggesting that the stand has increased its water use (Liedloff and Cook, 2007). If such water supply is no longer available under the altered precipitation regimes of a changing climate (Feng et al., 2013; Trenberth, 2011) then drought can lead to widespread tree death (Fensham et al., 2015) not only undoing the sequestration of the biomass but also undermining the

storage capacity of the ecosystem. Similarly, increases in the length of seasonal droughts may lead to a proliferation of grass-dominated savannas at the expense of tree-dominated savannas (Allen et al., 2010a; Chen et al., 2013; Steinkamp and Hickler, 2015; Zhang et al., 2014a) and a continued reduction in carbon stocks, with additional implications for biodiversity.

It is also possible that high growth is associated with a long-term woody thickening trend as has been reported for other tropical savannas in Australia (Beringer et al., 2007; Burrows et al., 2002; Sharp and Whittaker, 2003) although this was not supported by Murphy et al. (2014). Increases in the abundance of woody vegetation have been attributed to CO₂ fertilisation, which favours the growth of trees over herbaceous species (Ainsworth and Long, 2005). Bond and Midgley (2000) further suggests that CO₂ fertilisation accelerates the growth of juvenile trees, increasing the proportion that survive topkill from fire. This mechanism would result in high recruitment, which certainly occurs at Koombooloomba, but this is not evident at the other sites.

High mortality at both Brooklyn Station and Koombooloomba was likely due to disturbances at both sites. For example, there were two medium intensity fires at Brooklyn Station during the census period; the first in June 2011 and the second in June 2013. Frequent fires have been shown to preferentially kill large trees with hollows (Werner and Prior, 2007) and reduce growth rates (Murphy et al., 2010), with high mortality and reduced growth rates also evident at the Brooklyn Station site in this study (Table 4.4). This leads to a reduction in stand biomass. Paradoxically, a subsequent reduction in fire frequency and/or intensity may favour the establishment of a large number of small trees (Hoffman et al., 2012; Williams et al., 1999) at the expense of large trees, also resulting in a reduction in stand biomass (Murphy et al., 2015). Alternatively, the biomass may remain (relatively) constant while the species composition changes. For example, this is potentially occurring at the Koombooloomba site where the large old *Eucalyptus* trees appear to be declining, concurrent with a rapid recruitment of *A. torulosa* individuals following approximately 25 years of fire absence.

High mortality at Koombooloomba was mostly due to cyclone damage from TC Yasi which crossed the Queensland coast in February 2011 (Figure 3.4) with broken or uprooted trees accounting for at least 55% of the mortality at the site (Plate 3.11), which was the highest out of the study sites (8.5% of basal area). This mortality was minimal in comparison to that of TC Monica that crossed the Northern Territory coast in 2006 (77% of trees uprooted), however based on the relationship between

tree damage and wind speed formulated by Cook and Goyens (2008), it is possible that the Koombooloomba site would still have experienced wind gusts of 70-100 km h⁻¹. This would be sufficient to cause widespread canopy removal from defoliation, which can in turn lead to increasing basal area (Cook et al., 2006). In addition, TC Larry also passed close by to the site in 2006, and may well have resulted in similar damage to the site on that occasion (Figure 3.4).

The level of disturbance wrought by cyclone damage has been estimated to be similar in magnitude to fire (Cook and Goyens, 2008) and when combined with fire and seasonal drought, can lead to irreversible shifts in vegetation communities. With a decrease in the frequency but an increase in the intensity of storms (Frank et al., 2015; Haig et al., 2014), this type of disturbance may become more common and we may see a reduction in the standing biomass of coastal savannas. Furthermore, with an increase in the seasonality of precipitation (Feng et al., 2013; Fischer et al., 2013; Trenberth, 2011), we may also see an expansion of mesic savannas such as Koombooloomba and Davies Creek at the expense of neighbouring rainforest ecosystems.

4.6 Conclusions

Carbon stocks at all sites were dominated by the woody tree layer, with the grasses making a small and transient contribution. All the savanna sites presented in this study are fairly densely wooded in terms of Australian savannas, particularly Koombooloomba and Davies Creek. While basal area appears largely determined by climatic factors such as water availability, standing biomass (and therefore carbon stock) is largely determined by the demographics of the tree population and the presence of large trees. The grassy understory at all sites was a highly dynamic component of the ecosystem, contributing 60-80% of the ANPP although it comprised <10% of the aboveground carbon stock. The choice of methodology for the quantification of the grass production and biomass yielded results that differed by up to 400% between methods. Litterfall constituted a substantial portion of the tree derived ANPP at all sites. Litterfall rates were seasonal, with higher rates during the wet season and there was no spatial arrangement in litterfall between ‘tree’ and ‘grass’ litter traps. Litterfall rates were also sensitive to disturbance, with higher rates following fire or cyclone. Both Koombooloomba and Brooklyn Station were highly disturbed during the study period (by TC Yasi and prescribed fires, respectively) and both sites suffered a decrease in live carbon stocks, which we have

attributed to these disturbances. In contrast, Davies Creek was undisturbed during the study period and was the only site to accumulate carbon in aboveground live biomass during the study period. These results support previous findings that the carbon storage potential of biomass in tropical savannas is highly sensitive to stochastic disturbance and are vulnerable to substantial shifts in both structure and composition as a result of climate change.

Chapter 5

Soil carbon, nitrogen and stable isotopes in three tropical savanna sites

Statement of contribution

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Written by Kalu Davies.

Fieldwork by Kalu Davies with assistance from Michael Limpus, Amy Beavan and Sebastian Robinson-Arrow.

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Data analysis and interpretation by Kalu Davies with advice from Michael Bird, Paul Nelson and Jon Lloyd.

Edited by Kalu Davies and Michael Bird with advice from Paul Nelson and Michael Liddell.

5.1 Abstract

Soil carbon represents a significant pool in the global carbon cycle and may store the largest portion of carbon within tropical savanna ecosystems. This study presents data on soil carbon and nitrogen for three tropical savanna sites in far north Queensland and associated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The sites were located on contrasting soil types and encompassed a precipitation gradient ranging from 900 - 2000 mm year⁻¹. The two wetter sites are dominated by a perennial grassy understorey, with annual grasses at the third, drier site. Soil carbon stocks (0-30 cm) were 114 ± 25 , 41 ± 14 , and 38 ± 19 t C ha⁻¹ at the three sites and broadly corresponded to the magnitude of aboveground net primary productivity (ANPP) recorded at the sites. Soil carbon and nitrogen displayed a high degree of spatial organisation at two of the sites and $\delta^{13}\text{C}$ values indicate that this is due to spatial patterns in the input of soil carbon from C₃ and C₄ sources. The third site did not display these spatial patterns. Soil carbon and nitrogen contents and C:N ratio decreased, and $\delta^{13}\text{C}$ increased, with increasing soil depth at all sites, congruent with relatively higher inputs at the soil surface and a higher degree of carbon mineralisation by microbial organisms in the deeper soil layers. Mean $\delta^{13}\text{C}$ (weighted by carbon stock) for 0-30cm soil depth was -19.8, -24.2, and -20.0 ‰ at Brooklyn Station, Davies Creek, and Koombooloomba, respectively. Contributions of C₃ and C₄ vegetation to the soil carbon pool were approximately equal at two of the sites, but contributions of C₃ vegetation to soil carbon were 78% at the third site. Although considerable quantities of soil carbon are stored at these sites at present, climate change may result in vegetation shifts, changes to fire regimes, and exacerbated erosion, resulting in the loss of soil carbon from these sites.

5.2 Introduction

The characteristic heterogeneity in savanna vegetation (Torello-Raventos et al., 2013; Veenendaal et al., 2014) also extends to heterogeneity in vegetation inputs, microclimate, and soil properties. Previous studies have reported differences in soil carbon (Bird et al., 2000), nitrogen (Coetsee et al., 2010), moisture, leaf litter (Wang et al., 2009), bulk density (Wang et al., 2007), surface soil chemistry (Amiotti et al., 2000), decomposition rates, and root production (February et al., 2013) in areas adjacent to trees as compared to areas remote from trees. Such differences tend to lead to more favourable soil conditions around trees, with ‘islands of fertility’ forming around the

woody vegetation (Sankaran et al., 2004; Scholes and Archer, 1997).

Soil organic carbon (SOC) forms as a result of organic inputs derived from plant litter (leaves, stems, flowers, etc.), root exudates and sloughs (dead root cells shed during root growth), as well as microbial biomass. All these inputs tend to be higher near trees as opposed to away from trees in grassy areas (Bird et al., 2004; Eldridge and Wong, 2005; Hibbard et al., 2001; Kuzyakov et al., 2000a; Mcelhinny et al., 2010). In addition, trees provide roosts and shade for both animals and humans, resulting in a higher local input of animal remains and faeces (Cerling et al., 2011; Dean et al., 1999; Eldridge and Rath, 2002). This higher SOC can in turn result in lower bulk density and higher moisture retention, which may in turn lead to higher microbial activity and higher microbial biomass.

Trees and tropical grasses contribute different types of carbon to the soil carbon pool. Trees utilise the C_3 photosynthetic pathway while tropical grasses usually utilise the C_4 photosynthetic pathway, named for the number of carbons in the intermediate carbon compound that is fixed from the atmosphere in the photosynthetic process (Farquhar and Ehleringer, 1989; Hobbie and Werner, 2004). The two photosynthetic pathways fractionate the isotopes of carbon to differing degrees and as a result, C_3 carbon tends to have a low average $\delta^{13}C$ value of $\sim -27\text{‰}$, compared to C_4 grasses which tend to exhibit an average $\delta^{13}C$ value of $\sim -14\text{‰}$ (Krull et al., 2007). Naturally occurring stable carbon isotopes have been extensively utilised as a natural tracer to record changes in vegetation over time such as the conversion of a savanna (C_4 dominated) to a forest (C_3 dominated) or *vice versa* (Bird and Cali, 1998; Cerling et al., 1997; Krull et al., 2005). In addition, they provide a tool for examining the contributions of these contrasting vegetation to soil carbon (Saiz et al., 2015a) and ecosystem productivity (Lloyd et al., 2008). They may also provide useful insights into the cycling of carbon as a result of land use change or management practices (Traoré et al., 2015; Zatta et al., 2013).

There are many processes that affect the $\delta^{13}C$ value of soil carbon. For example, when microorganisms metabolise organic matter, the carbon is fractionated and the light ^{12}C is preferentially respired, resulting in the $\delta^{13}C$ enrichment of the remaining soil carbon. Alternatively, microorganisms may display a preference for $\delta^{13}C$ -rich compounds that are rich in energy such as sugars, leaving the remaining soil carbon relatively $\delta^{13}C$ depleted (Blagodatskaya et al., 2011; Šantrůčková et al., 2000). Furthermore, processes such as combustion, leading to the formation of charcoal, may decrease the $\delta^{13}C$ value of the char relative to the plant biomass (Saiz et al., 2015b) and the soil matrix may also preferentially preserve some forms of carbon

over others, resulting in further potential modifications to the $\delta^{13}\text{C}$ value of soil carbon (Wynn and Bird, 2007). Finally, time also plays a role, as atmospheric changes to CO_2 composition through the addition of low- $\delta^{13}\text{C}$ fossil fuel-derived carbon have gradually decreased the $\delta^{13}\text{C}$ values in biomass relative to times past (Friedli et al., 1986).

In contrast to soil carbon, soil nitrogen production is a much more complex process. Firstly, inorganic carbon is of little consequence to the terrestrial carbon cycle as it is fairly inert and often absent from many soil types. In contrast, nitrogen cycles through organic and inorganic forms and different states of reactivity. Atmospheric nitrogen is fixed to NH_4^+ before being assimilated as organic nitrogen by cyanobacteria or symbioses between vascular plants and bacteria. These form soluble bioavailable organic molecules that are part of plant and microbe biomass (Vitousek et al., 2002). Organic nitrogen enters the soil nitrogen pool via plant and microbe biomass and is mineralised when it is converted from organic to inorganic forms (NO_3^- , NO_2^- , NH_4^+) during the decomposition process (Parton et al., 2007). In addition, nitrogen may also add to the soil pool via direct atmospheric deposition (Reay et al., 2008). Inorganic forms are then removed from the soil pool by assimilation into plant tissues or they may be lost from the system via leaching and denitrification. Naturally occurring nitrogen isotopes can be a useful tool to inform our understanding of ecosystem processes. For example, $\delta^{15}\text{N}$ values can provide an integrated assessment of water availability (Handley et al., 1999), as well as information on how tightly nitrogen is conserved within an ecosystem, given that enrichment of the soil pool occurs when more nitrogen is lost due gas loss or leaching relative to turnover (Craine et al., 2015; Robinson, 2001; Soper et al., 2014).

This study compares soil carbon, nitrogen, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with soil characteristics between three tropical savanna sites in far north Queensland. The aim of the study is to inform our understanding of soil organic matter cycling that may occur at these sites and place these sites in the wider context of tropical savannas within Australia and globally. Specifically, this study will address the following research questions:

1. How much carbon is stored in the soil and how is that influenced by nitrogen and soil characteristics?
2. How do soil carbon, nitrogen and their stable isotopes vary in space and what influences this variation?
3. What is the relative contribution of trees and grasses to the soil carbon pool?

5.3 Methods

This study was conducted at Brooklyn Station, Davies Creek and Koombooloomba study sites that are described in detail in Chapter 3. A brief summary of relevant characteristics is provided in Table 5.1.

Table 5.1: Main characteristics of the study sites

Site	Brooklyn Station	Davies Creek	Koombooloomba
Mean annual precipitation (mm)	906	1460	1430
Mean annual maximum temperature ($^{\circ}\text{C}$)	32	28	29
Soil parent material	Alluvium	Granite	Basalt
Soil classification	Sodosol	Tenosol	Ferrosol
C_3 aboveground net primary productivity ($\text{t C ha}^{-1} \text{ y}^{-1}$)	1.1	1.9	2.1
C_4 aboveground net primary productivity ($\text{t C ha}^{-1} \text{ y}^{-1}$)	3	2.4	6

5.3.1 Experimental design

At each site, sampling was stratified based on proximity to trees and grouped according to canopy cover. These groups were: adjacent to the tree trunk (termed ‘tree’), at the mid-point of tree canopy cover (termed ‘mid-canopy’), at the edge of the canopy cover or drip line (termed ‘drip line’), and in the open grassy areas equidistant from the nearest trees (termed ‘grass’). The average distance from the nearest tree of each group of measurements is given in Table 5.2

Table 5.2: Distance from the nearest tree (in m) of each group of measuring points. Values shown are mean $\pm$ s.d.

Site	Tree	Mid-canopy	Drip line	Grass
Koombooloomba	0.28 ± 0.12	2.01 ± 0.40	3.64 ± 0.62	6.50 ± 0.65
Davies Creek	0.22 ± 0.14	2.16 ± 0.53	4.36 ± 1.08	6.25 ± 1.80
Brooklyn Station	0.24 ± 0.09	2.08 ± 0.54	3.71 ± 0.91	6.87 ± 2.96

The measurement locations were arranged in transects running from tree to tree as shown in Figure 5.1. There were seven such measurement transects at each of the Brooklyn Station and Koombooloomba sites to give a total of 49 samples at each site and eight measurement transects at Davies Creek to give a total of 56 samples.

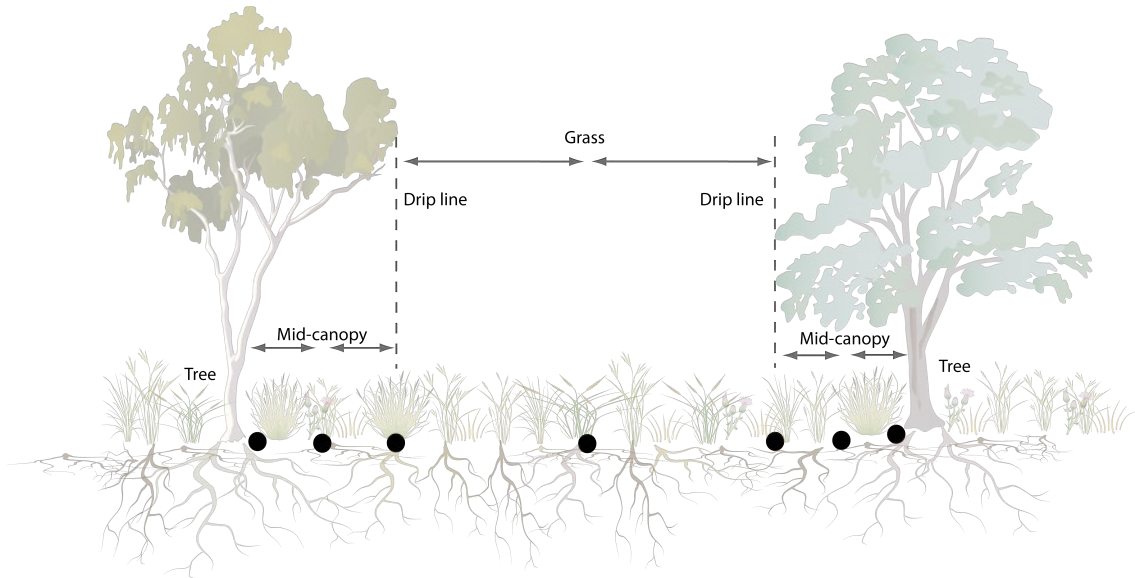


Figure 5.1: Diagram of sampling locations (•) arranged between trees with samples adjacent to the tree trunk ('tree'), mid point of canopy cover ('mid-canopy'), at the edge of the canopy cover or drip line ('drip line') and equidistant between the trees ('grass').

5.3.2 Soil sampling and analysis

Soil sampling was conducted using a manual soil corer at all sites. Additionally, a subset of sampling locations ($n = 6$) at Brooklyn Station were sampled using a vehicle mounted hydraulic soil corer (Christie Engineering, NSW, AU). At each sampling location, vegetation and litter was removed prior to sampling. At all sites, hand

samples were taken to a depth of 30 cm. The 0-5 cm increment was kept separate from the remainder of the core, while the cores at Brooklyn Station were taken to a depth of 1m. The samples were weighed, oven dried at 60°C and then sieved to 2 mm using a powered soil grinder (Humboldt, IL, USA). A weighed subsample of the <2 mm component was further dried at 105°C to determine bulk density of the soil core. Additional subsamples of the <2 mm component were (i) bulked for particle size distribution analysis and (ii) milled using a ring mill (Rocklabs Ltd, NZ) before analysis for total carbon, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and total nitrogen using an elemental analyser (Costech, CA, USA) and isotope ratio mass spectrometer (Thermo Delta V plus, Bremen, Germany).

5.3.3 Statistical analysis

All statistical analyses were performed using R v.3.2.0 Software (R Development Core Team, 2014; www.r-project.org). Differences between sites for soil analyses were assessed using ANOVA and differences (if applicable) were identified using Tukey's honest significant difference test. The relationships between dependent and independent variables were described using linear regression. Soil carbon, nitrogen, and C:N ratios were log transformed to meet the assumptions of both the ANOVA and the linear regression.

Soil carbon stocks were estimated by multiplying the carbon abundance by the bulk density for each soil depth layer and then adding the stocks from each soil layer to give the total soil carbon stock. Where a significant relationship between proximity to woody vegetation and carbon content exists, this relationship was used to map the spatial arrangement of soil carbon stocks at the plot scale. The 1 ha study plots were divided into 10000 1m x 1m cells and the distance to the nearest tree calculated. This enabled the model to be applied to the entire plot by using these distances as input variables for the 'predict' function. Plot level $\delta^{13}\text{C}$ values for each site were estimated by taking the mean of all samples for each depth, weighted by the carbon content.

5.4 Results

5.4.1 Soil characteristics

Bulk density (0-30 cm) differed significantly between sites ($F_{(1,80)} = 259.1$, $p < 0.001$) and Tukey's test was used to confirm that the savanna sites were different to each other. Mean ($\pm$ s.d.) bulk density (0-30 cm) at each site was 1.27 ± 0.15 , 1.06 ± 0.15 , and 0.67 ± 0.09 g cm⁻³ for Brooklyn Station, Davies Creek, and Koombooloomba, respectively. Bulk density did not differ between sample depths (0-5 cm versus 5-30 cm) at any of the sites and did not differ between sampling locations at Brooklyn Station or Davies Creek, but the bulk densities of the 'tree' sample locations at Koombooloomba were significantly lower than the other sample locations ($F_{(1,26)} = 5.688$, $p = 0.025$).

Soil texture (0-5 cm) varied between the sites, with Brooklyn Station dominated by silt and fine sand while Koombooloomba was principally composed of fine sand and Davies Creek was mainly coarse sand with less fine sand (Table 5.3).

Table 5.3: Particle size distribution for soils sampled from the three sites. Samples consisted of bulked soil (0-5 cm).

Site	Clay (%) ($<2\mu\text{m}$)	Silt (%) ($2\text{-}20\mu\text{m}$)	Fine sand (%) ($20\text{ - }200\mu\text{m}$)	Coarse sand (%) ($>200\mu\text{m}$)
Brooklyn Station	1	36	41	22
Davies Creek	<1	14	28	57
Koombooloomba	6	16	64	14

5.4.2 Soil carbon, nitrogen, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$

Soil carbon content was highest at Koombooloomba with a mean of 5.2% (0-30 cm) compared to 1.0% for Brooklyn Station and 1.2% for Davies Creek (Figure 5.2). At all sites, the surface soils (0-5 cm) had more than twice the carbon abundance of subsurface soils (5-30 cm). $\delta^{13}\text{C}$ values for the surface soils (0-5 cm) ranged from -22.4 to -17.7‰ for Brooklyn Station, -27.2 to -21.0‰ at Davies Creek, and

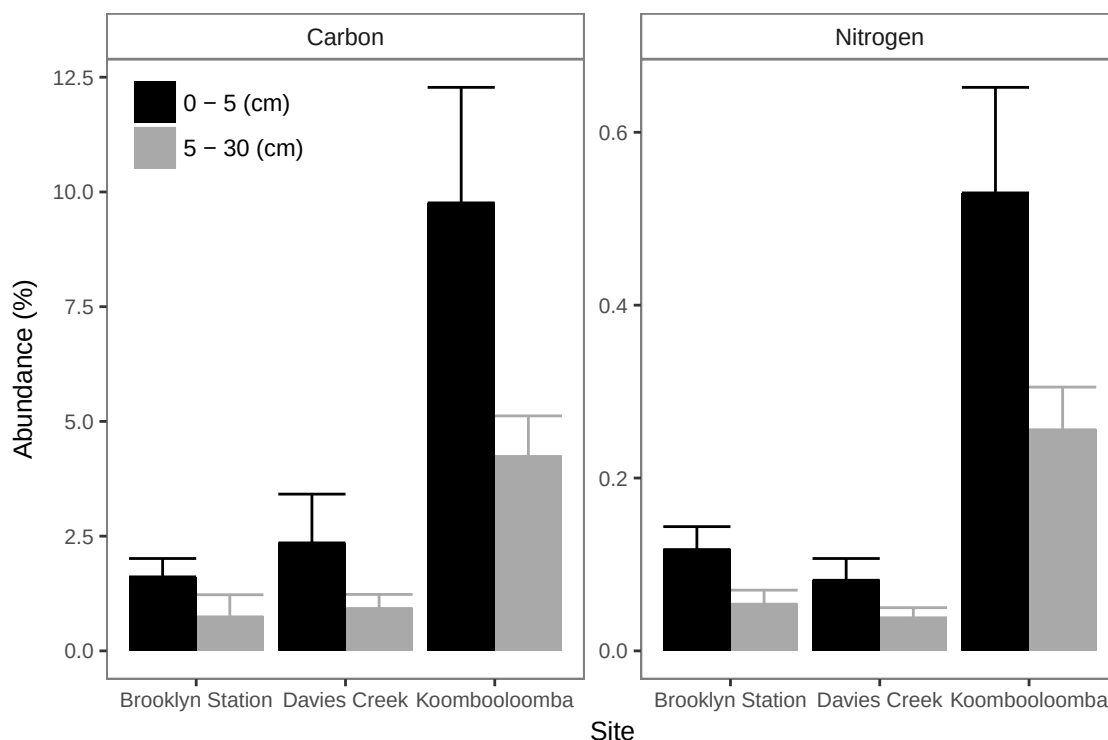


Figure 5.2: Soil carbon (left) and soil nitrogen (right) abundance (%) at the three study sites for 0-5 cm and 5-30 cm depths. Bars are mean $\pm$ standard deviation

-25.7 to -19.1‰ at Koombooloomba. The subsurface soils (5-30 cm) were relatively enriched in $\delta^{13}\text{C}$ in comparison to the surface soils and ranged from -23.7 to -15.9‰ at Brooklyn Station, -25.8 to -20.5‰ at Davies Creek, and -21.3 to -17.4‰ at Koombooloomba. In addition, the deeper samples from Brooklyn Station (30-100 cm) ranged from -21.2 to -16.9‰.

The same abrupt decrease in abundance with increasing depth was evident for nitrogen at all sites (Figure 5.2). $\delta^{15}\text{N}$ values in the surface soils (0-5 cm) ranged from +5.0 to +7.5‰ for Brooklyn Station and +6.4 to +0.4‰ at Davies Creek. The subsurface soils (5-30 cm) ranged from +5.8 to +7.5‰ for Brooklyn Station and +2.6 to +6.9‰ for Davies Creek. Data for Koombooloomba is not available.

C:N ratios also differed significantly between sites and depths ($F_{(2,308)} = 28$, $p < 0.001$) with the highest values for all depths at Davies Creek and the lowest at Brooklyn Station. C:N ratios were highest in the surface soils (0-5 cm) and decreased with depth at all sites (Table 5.4). C:N ratios tended to be slightly higher adjacent to trees, but the differences were not significant.

5.4.3 Spatial variation in soil carbon, nitrogen, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$

Soil carbon decreased with increased distance from trees such that a combination of depth and distance to tree explained 64% of the variation at Davies Creek ($F_{(2,108)} = 99.05$, $p < 0.001$) and 83% of the variation at Koombbooloomba ($F_{(2,93)}=239.4$, $p < 0.001$). At Brooklyn Station however, soil carbon was significantly related only to depth ($F_{(2,101)}=99.48$, $p < 0.001$) with depth alone explaining 66% of the variation (Figure 5.3).

Table 5.4: Mean C:N ratios ($\pm$ s.d.) for differing sample depths at each site

Soil depth	Brooklyn Station	Davies Creek	Koombbooloomba
0-5 cm	13.8 ± 1.3	28.2 ± 6.6	18.6 ± 2.7
5-30 cm	12.9 ± 3.7	24.3 ± 4.6	16.7 ± 2.1
30-100 cm	9.7 ± 2.2	NA	NA

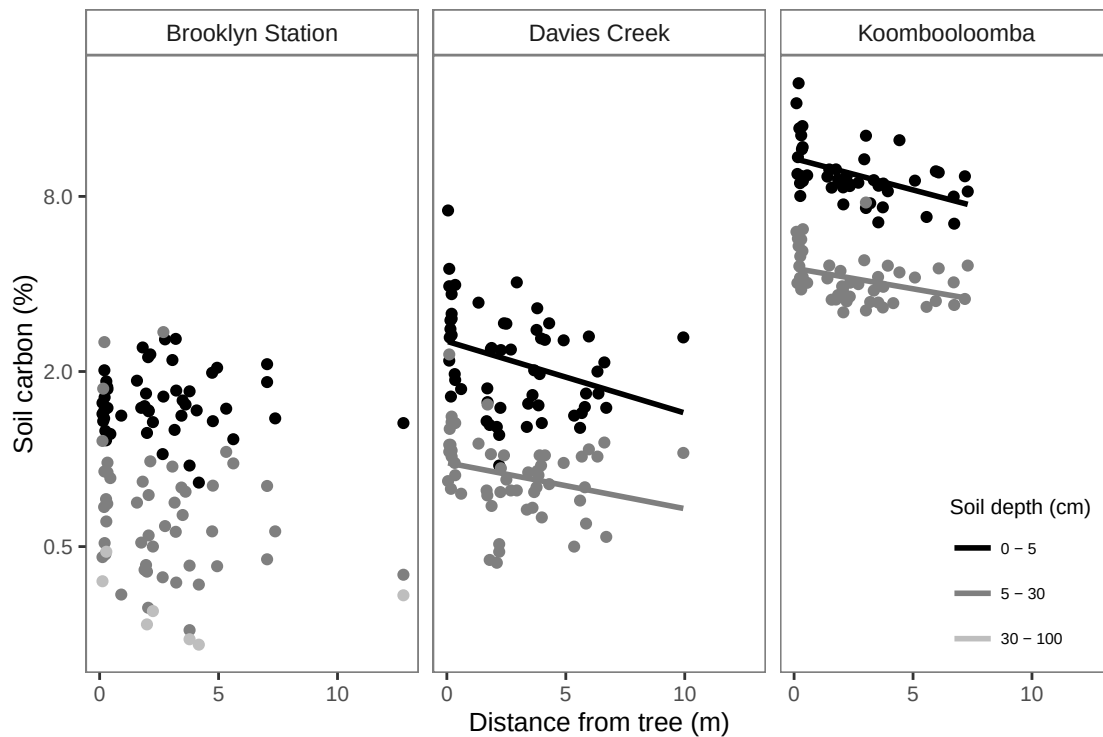


Figure 5.3: Variation in soil carbon abundance with distance to the nearest tree. Soil carbon is presented on a logarithmic scale. Lines shown are significant at $p < 0.001$.

$\delta^{13}\text{C}$ values were also related to proximity to trees with, $\delta^{13}\text{C}$ increasing with increasing distance from trees. $\delta^{13}\text{C}$ values also became less negative with increasing soil depth (Figure 5.4). These relationships were significant, with soil depth and distance to the nearest tree explaining 41% and 46% of the variation at Davies Creek ($F_{(2,109)} = 39.74$, $p < 0.001$) and Koombooloomba ($F_{(2,93)} = 42.49$, $p < 0.001$), respectively. The relationship was weaker at Brooklyn Station, with soil depth and distance explaining only 9% of the variation in $\delta^{13}\text{C}$ ($F_{(2,101)} = 6.529$, $p < 0.05$).

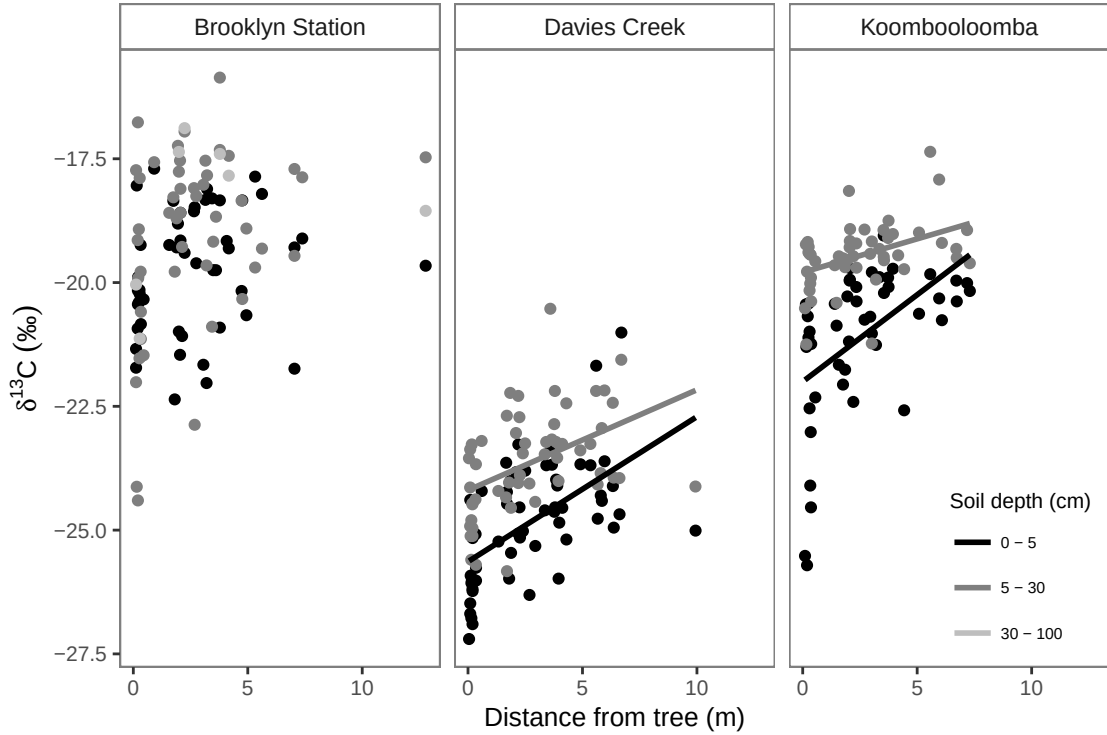


Figure 5.4: Variation in $\delta^{13}\text{C}$ (‰) values with distance to the nearest tree (m). Lines shown are significant at $p < 0.001$.

Soil carbon was also closely related to the $\delta^{13}\text{C}$ value, with higher carbon abundance associated with lower $\delta^{13}\text{C}$ values (Figure 5.5). This trend was consistent across all sites with $\delta^{13}\text{C}$ and distance to the nearest tree explaining 90%, 72%, and 82% of the variation in soil carbon at Koombooloomba ($F_{(2,93)} = 439.3$, $p < 0.001$), Davies Creek ($F_{(2,108)} = 141.1$, $p < 0.001$), and Brooklyn Station ($F_{(3,157)} = 157$, $p < 0.001$), respectively.

Spatial patterns in the soil nitrogen abundance and $\delta^{15}\text{N}$ values were similar to those observed for total carbon (data not shown). The combination of depth and distance from trees explained 73% of the variation in soil nitrogen at Davies Creek ($F_{(2,109)} = 155.3$, $p < 0.001$) and 82% of the variation at Koombooloomba ($F_{(2,93)} = 219.2$, $p < 0.001$). At Brooklyn Station, only depth was significant, explaining 72% of the

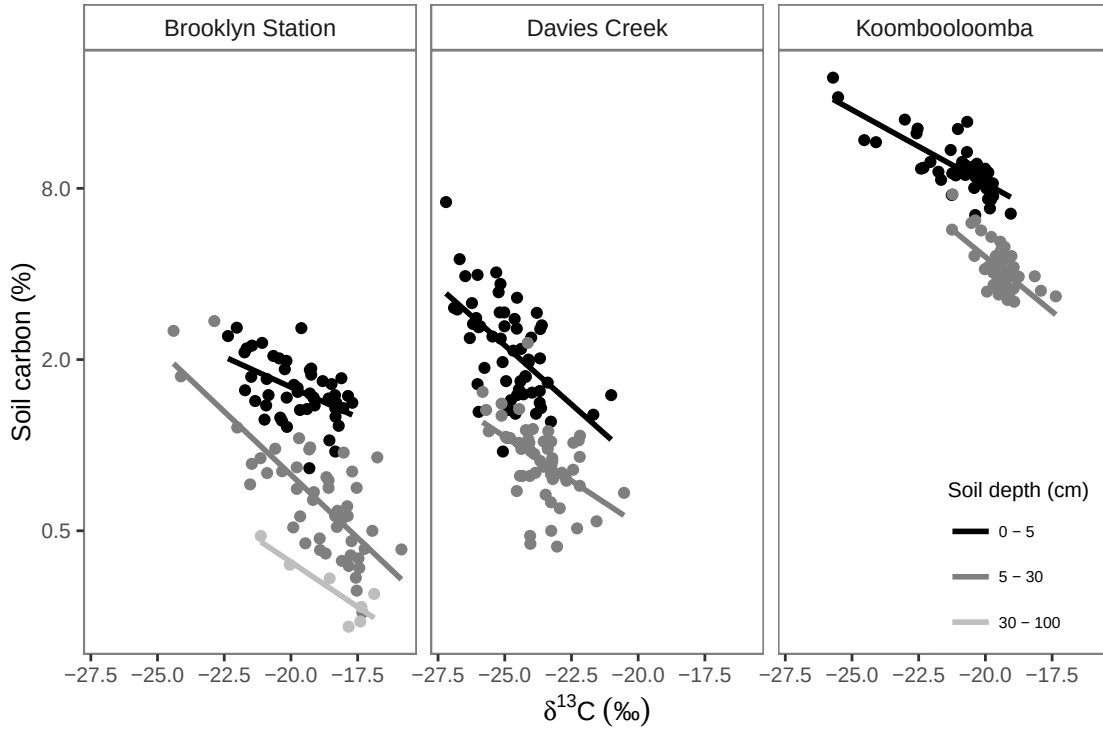


Figure 5.5: Correlation between soil carbon (%) and $\delta^{13}\text{C}$ values (‰). Soil carbon is presented on a logarithmic scale. Lines shown are significant at $p < 0.001$.

variation in the soil nitrogen ($F_{(2,55)} = 75.7$, $p < 0.001$).

There was a correlation between $\delta^{15}\text{N}$ values and distance to the nearest tree at Davies Creek ($F_{(2,109)} = 70.7$, $p < 0.001$, $R^2 = 0.57$; data not shown), but there was no such trend at Brooklyn Station and the data was not available for Koombooloomba.

There was a close relationship between $\delta^{15}\text{N}$ and soil nitrogen abundance at Davies Creek ($F_{(2,109)} = 180.2$, $p < 0.001$, $R^2 = 0.76$, data not shown) but there was no significant trend at Brooklyn Station and the data was unavailable for Koombooloomba.

5.4.4 Plot level SOC stocks and $\delta^{13}\text{C}$

The strong correlation between soil carbon and proximity to trees at Davies Creek and Koombooloomba enabled the soil carbon stock to be mapped for each 1m^2 cell in the study plot by multiplying the carbon abundance by the bulk density and soil depth (Figure 5.6). This also enabled the soil carbon stock to be upscaled to plot level, taking the systematic spatial variation into account. The total soil carbon

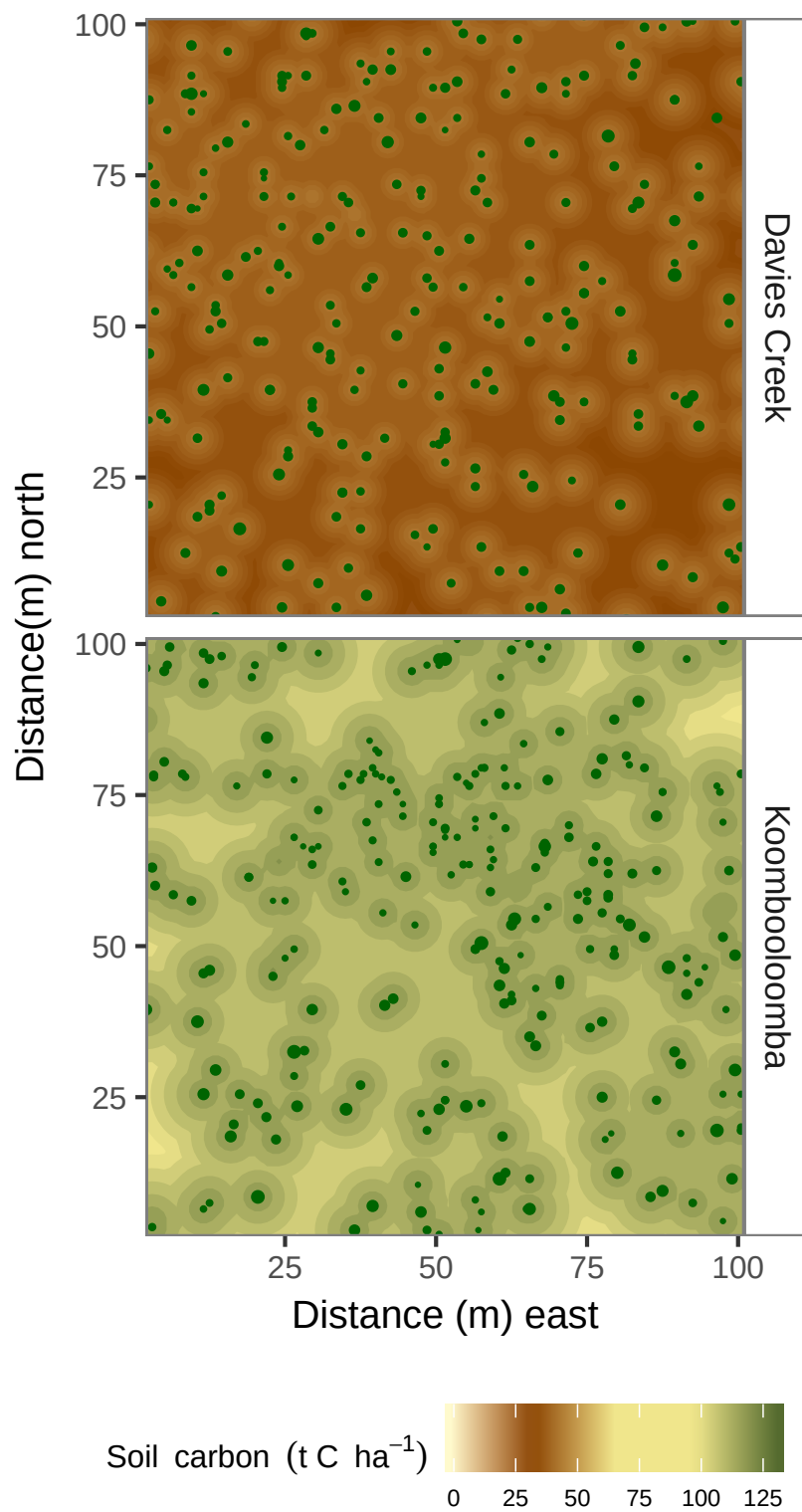


Figure 5.6: Soil carbon stocks for Davies Creek (top) and Koombooloomba (bottom) in the 0-30 cm soil depth for the study plot. Individual trees within the plot are indicated by green circles (●) with size proportional to dbh.

stock (0-30 cm) for each study plot (*i.e.* the sum of the modelled soil carbon stock for each cell) at Koombooloomba was $113 \pm 4 \text{ t C ha}^{-1}$ and the soil carbon stock at Davies Creek was $39 \pm 3 \text{ t C ha}^{-1}$ (mean $\pm$ s.d.). Modelled soil carbon stocks for each grid cell within the plot ranged from 97 - 121t C ha⁻¹ at Koombooloomba and 29 - 45t C ha⁻¹ at Davies Creek. As there was no clear spatial relationship between soil carbon and the trees at Brooklyn Station, it was not possible to map the soil carbon for this site. By comparison, the mean ($\pm$ s.d.) soil carbon stock (without incorporating spatial variation) was 114 ± 25 , 41 ± 14 , and $38 \pm 19 \text{ t C ha}^{-1}$ for Koombooloomba, Davies Creek, and Brooklyn Station, respectively.

Similarly, the correlation between $\delta^{13}\text{C}$ and proximity to trees at Davies Creek and Koombooloomba enabled the $\delta^{13}\text{C}$ to be mapped for each 1m² cell in the study plot in a similar fashion (Figure 5.7). In this case, the model predicts the $\delta^{13}\text{C}$ for each soil depth in each cell. Therefore, to integrate the $\delta^{13}\text{C}$ over the 0-30 cm soil depth, the $\delta^{13}\text{C}$ for each soil depth is weighted by the soil carbon stock for each soil depth before being averaged for each cell. The modelled $\delta^{13}\text{C}$ for the 0-30 cm soil depth was $-19.7 \pm 0.6 \text{ ‰}$ at Koombooloomba and $-23.9 \pm 0.4 \text{ ‰}$ at Davies Creek (mean $\pm$ s.d.).

By comparison, the mean ($\pm$ s.d) of the $\delta^{13}\text{C}$ (weighted by carbon stock but without incorporating spatial variation) for 0-30 cm soil depth is $-19.8 \pm 2.1 \text{ ‰}$ at Brooklyn Station, $-24.2 \pm 1.3 \text{ ‰}$ at Davies Creek, and $-20.0 \pm 1.3 \text{ ‰}$ at Koombooloomba. Additionally, the mean $\delta^{13}\text{C}$ (weighted by carbon content) for each study site and sample depth is shown in Table 5.5. Brooklyn Station was the highest, closely followed by Koombooloomba, while Davies Creek was substantially lower and this trend was evident at all sample depths.

Table 5.5: $\delta^{13}\text{C}$ (‰) values (weighted by soil carbon content) for each sample depth at each site (mean $\pm$ s.d)

Sample depth	Brooklyn Station	Davies Creek	Koombooloomba
0-5 cm	-19.9 ± 1.3	-25.1 ± 1.2	-21.4 ± 1.5
5-30 cm	-19.9 ± 1.8	-23.8 ± 1.0	-19.5 ± 0.7
0-100 cm	-18.8 ± 1.6	NA	NA

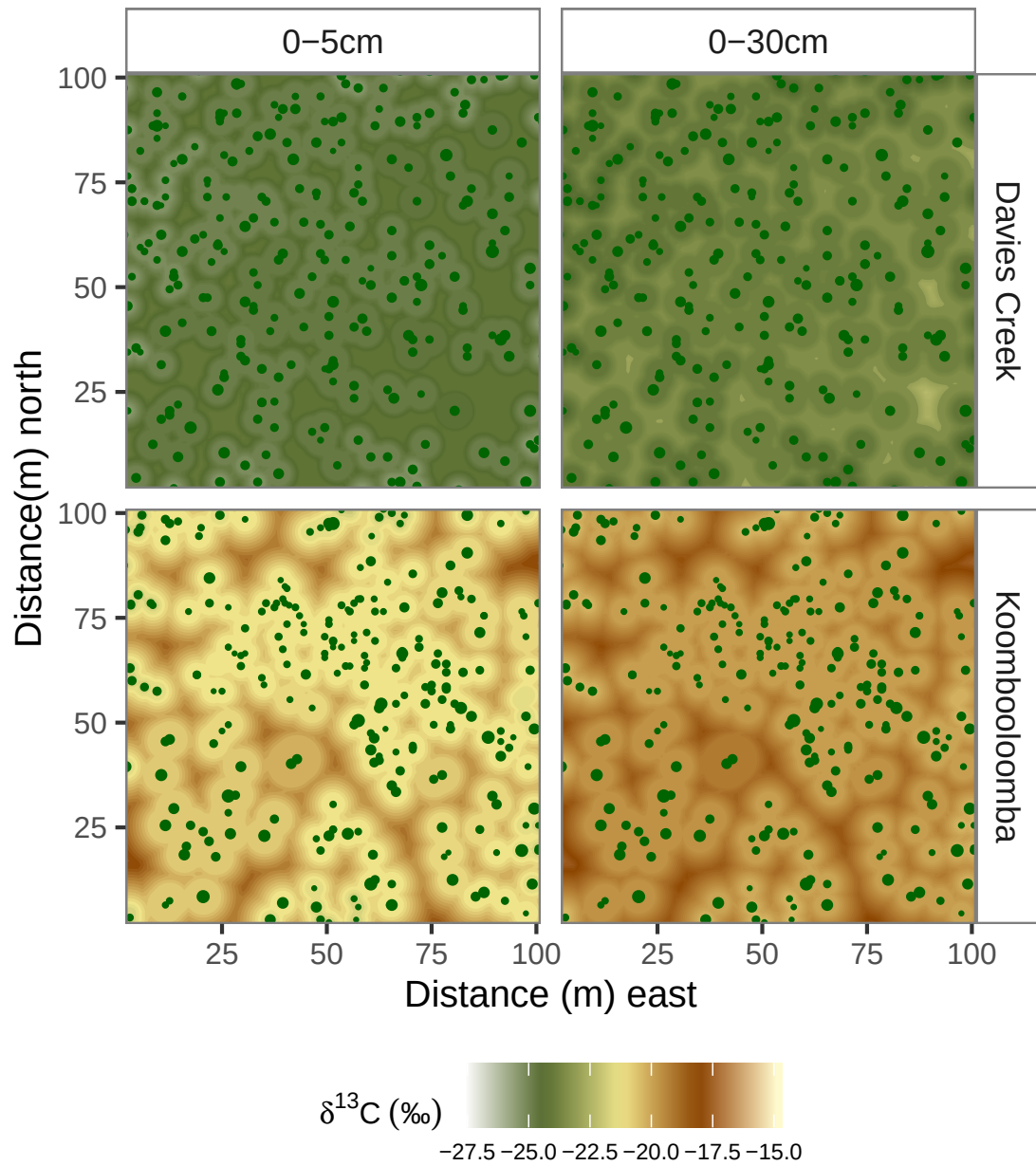


Figure 5.7: $\delta^{13}\text{C}$ for Davies Creek (top) and Koombooloomba (bottom) in the 0–5 cm soil depth (left) and 0–30 cm soil depth (right) for the study plot. Individual trees within the plot are indicated by green circles (●) with size proportional to dbh.

5.5 Discussion

5.5.1 Carbon stocks and the cycling of soil carbon

The soil carbon stocks from these study sites are highly variable and Koombooloomba represents some of the highest soil carbon stocks in northern Australian savannas. Although the results presented here ($\sim 121 \text{ t C ha}^{-1}$; Figure 5.6) are lower than previous measures from this site (182 t C ha^{-1} ; TROBIT, Unpubl. data), they are still among the highest in northern Australia. For example, soil carbon stocks of 176 t C ha^{-1} (5-30 cm) have been reported for a savanna nearby in the Wet Tropics (TROBIT, Unpubl. data) and Richards et al. (2012) reported stocks of $\sim 90 \text{ t C ha}^{-1}$ (5-30 cm) for very high rainfall savannas of the Tiwi Islands, Northern Territory. The soil carbon stocks at Davies Creek and Brooklyn Station ($\sim 40 \text{ t C ha}^{-1}$) are much more typical of Australian environments. For example, Viscarra Rossel et al. (2014) modelled soil carbon stocks (0-30 cm) across Australia and reported stocks of $30\text{-}50 \text{ t C ha}^{-1}$ (0-30 cm) for the tropical savannas with stocks of up to 120 t C ha^{-1} (0-30 cm) for the Wet Tropics. Similarly, stocks of $30\text{-}50 \text{ t C ha}^{-1}$ (0-30 cm) have been reported for savannas in the Tiwi Islands and Darwin region of the Northern Territory (Richards et al. (2012) and Chen et al. (2005), respectively) as well as coastal savannas in south eastern Queensland (Wynn et al., 2006b).

Soil carbon stocks represent the balance between inputs from plant productivity and losses from decomposition and so soil carbon stocks tend to be higher in areas of high rainfall where moisture is sufficient to support more plant growth (Stockmann et al., 2013). For example, Figure 5.8 shows previous studies on soil carbon in the tropical savannas of Australia and the relationship between soil carbon stocks and mean annual precipitation (MAP). The predictive value of the climatic constraint to soil carbon accumulation can be improved by taking into account evaporation and/or seasonality of rainfall such that some index of moisture availability *per se* is a better predictor of soil carbon than mean annual precipitation alone. Unfortunately, most studies use differing metrics and do not report enough information to calculate such metrics independently of the study.

Nonetheless, there are many studies that have reported some constraint of moisture in tropical savannas including in Africa (Alam et al., 2013; Aranibar et al., 2004; Saiz et al., 2012) and South America (González-Roglich et al., 2014). The association between higher moisture availability, higher plant production, and higher

soil carbon content is not exclusive to tropical savannas; for example, Wynn et al. (2006b) reported a similar trend in across Australia and Amundson (2001) reported a similar trend for soil carbon globally. Although decomposition is linked to moisture availability, it is also constrained by temperature. Consequently, soil carbon will accumulate more in cool, wet environments than in warm, wet environments (Stockmann et al., 2013).

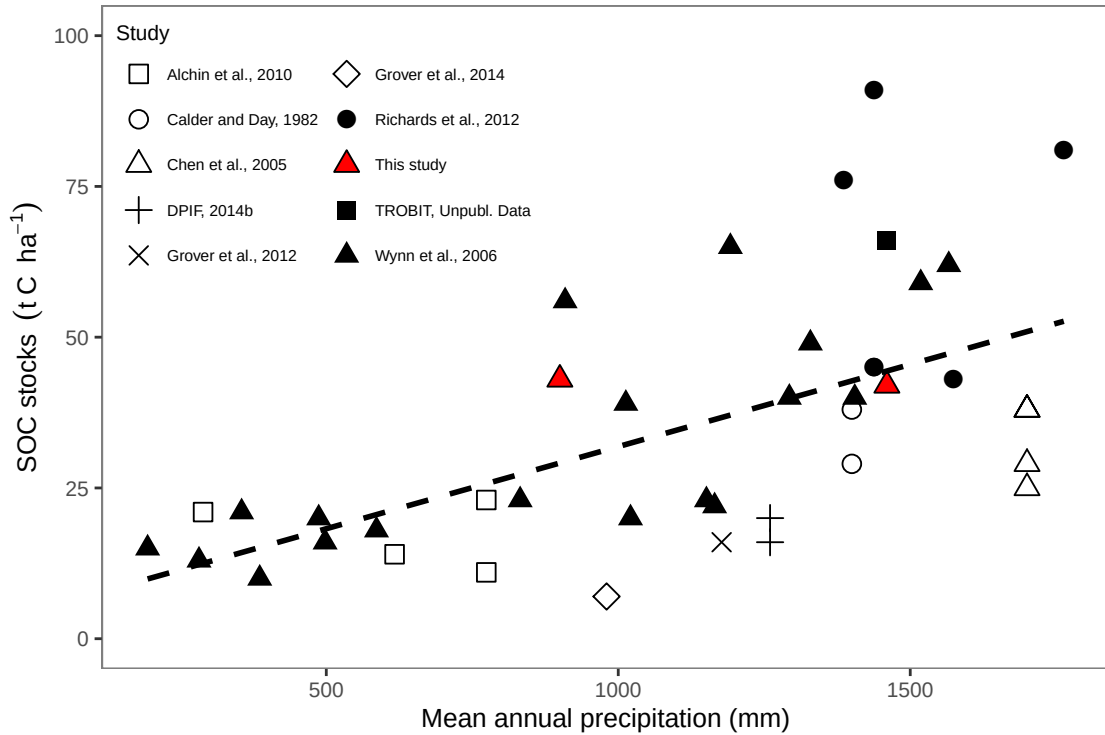


Figure 5.8: Previous studies on SOC stocks in northern Australian tropical savannas and the mean annual precipitation of those sites. SOC stocks are on a logarithmic scale.

In addition to climate, edaphic controls also influence the accumulation of soil carbon, with finer textured soils storing more soil carbon than coarse textured soils (Bird et al., 2000; Saiz et al., 2012). This is partly due to the fact that fine textured soils retain more moisture than coarse textured soils, although clay particles also physically and chemically protect soil carbon from decomposition (Schmidt et al. 2011). This trend is observable in this study as sites with the fine textured soils (Brooklyn Station and especially Koombooloomba) have soil carbon stocks that are higher than predicted by the general MAP trend (Figure 5.8).

Microbes are the primary agent of the decomposition of organic matter, although in arid environments photo-degradation may also contribute significantly (Austin and Vivanco 2006). As the carbon in organic matter is mineralised, a portion is assimilated into the microbial biomass while the remainder is respired as CO₂. Mi-

crobes require nitrogen for this process and so the initial stages of decomposition are closely associated with the C:N ratio of litter and the chemical composition of the litter, with high C:N ratios considered an indicator of ‘poor quality’ litter (Enrquez et al. 1993). At C:N ratios above ~20-25, microbial activity tends to be limited by nitrogen availability while below this value nitrogen is usually released as mineral N.

The C:N ratios in this study varied considerably and range from ~13 at Brooklyn Station and ~17 at Koombooloomba, up to ~28 at Davies Creek for the surface soils (Table 5.4). Other C:N ratios reported for tropical savannas range from 8-20 in the Kalahari desert (Aranibar et al., 2004), 10-20 in West Africa (Saiz et al., 2015a) and 15-22 in Brazil (Lilienfein et al., 2003; Nardoto and Bustamante, 2003) so Brooklyn Station and Koombooloomba are fairly typical, despite 10-fold differences in the absolute abundance of both C and N at each site. Davies Creek however, is considerably higher than the highest C:N ratio reported for other savannas and the other sites included in this study. This could be due to the coarse texture of the shallow soil at Davies Creek as fungi tend to dominate over bacteria in sandy soils. Soil C:N ratios tend to equilibrate at values intermediate to those of the plant inputs and the microbial inputs, with fungi having the higher C:N ratio (Hassink et al., 1993).

Furthermore, the disparity in the C:N ratios could be due to differences in the nitrogen input to the system. For example, Koombooloomba is dominated by *Allocasuarina torulosa*, a species that is known to fix nitrogen. While the C:N ratios of plant biomass were not measured in this study, previous studies in Australia have shown that nitrogen fixing *Acacia* have a lower C:N ratio than the non-nitrogen fixing *Eucalyptus*, particularly in the root biomass (Wang et al., 2004). In addition, the grassy understorey at Brooklyn Station is dominated by annual grasses that completely senesce during the dry season while Davies Creek is dominated by perennial grasses. Information specifically relating to nutrient cycling in these grasses is unavailable, however it is possible that the perennial grasses retain much of their nitrogen prior to senescence, while the annual grasses contribute their entire biomass stock to the soil nitrogen pool when they senesce. This is consistent with a study by Abbadie et al. (1992) who reported that two species of perennial grasses in West Africa sourced ~65% of their nitrogen needs from the recycling of recently deceased roots. In addition, the fire intensity at Davies Creek is considerably lower than that at Brooklyn Station and as a result, considerably more of the aboveground grass biomass (and therefore nitrogen) is retained within the system.

Alternatively, Brooklyn Station is the driest study site and the soils of arid regions tend to have lower a C:N ratio, as the nitrogen is not utilised to the full extent due to water limitations. Consequently, it is then lost from the system as a result of leaching or denitrification (Aranibar et al., 2004). However, a recent study by Soper et al. (2014) on the North Australian Tropical Transect supported findings from previous studies that $\delta^{15}\text{N}$ abundance tends to increase with aridity as a result of ‘leakier’ nitrogen cycles; that is, a decoupling of nitrogen availability and plant demand that results in nitrogen being lost from the system (Aranibar et al., 2004; Austin et al., 2004b). The $\delta^{15}\text{N}$ values for Davies Creek and Brooklyn Station are both between $\sim+5$ and $+7\text{‰}$, which is consistent with the ‘leakiest’ of savannas in their study. Thus it is unlikely that the contrast in C:N ratios between these two sites is due to differences in nitrogen losses and more probable that it is due to differences in nitrogen additions.

5.5.2 Spatial variation in SOC and $\delta^{13}\text{C}$

There is a high degree of spatial organisation in the soil carbon at both Davies Creek and Koombooloomba with higher soil carbon found adjacent to trees (Figure 5.3), a trend that has been reported in other studies (for example, Bird et al. (2000); Dintwe et al. (2014); Saiz et al. (2012); Wang et al. (2009); Woollen et al. (2012); Wynn et al. (2006b)). In addition, higher soil carbon values are closely associated with lower $\delta^{13}\text{C}$ values (Figure 5.5), suggesting that the higher carbon is C_3 (*i.e.* tree) in origin with $\delta^{13}\text{C}$ -depleted carbon deposited adjacent to trees (Figure 5.4). This is similar to results reported by Bird et al. (2000), Bird et al. (2004) and Saiz et al. (2015a) for studies in Africa.

Trees may locally enhance soil carbon over grass-dominated areas due to increased input of carbon from roots, *i.e.* root turnover. However, there are a number of other ways that soil carbon may be locally increased including enhanced rhizodeposition, hydraulic redistribution, and increased litter inputs. Rhizodeposition involves the sloughing of root cap cells, secretion of mucilage, excretion of organic compounds, and senescence of the root epidermis (including root hairs). Collectively, rhizodeposition may contribute carbon to the soil equivalent to approximately 17% of the root biomass, the majority of which is sourced from the excretion of organic compounds (Nguyen, 2003; Rasse et al., 2005). Rhizodeposition may also result in a ‘priming’ effect that can accelerate the decomposition and metabolism of pre-existing soil carbon (Kuzyakov et al., 2000a). The bacterial cells and fungal hyphae then be-

come additional carbon substrates for consumption by other microbes or macrofauna (Singh and Gupta, 1977) that can alter the moisture retention of the soil, while the digging activity of increased macrofauna may in turn decrease bulk density (Wang et al., 2009), creating islands of fertility around savanna trees.

Hydraulic redistribution occurs when the trees have a more extensive rooting system than the grasses and are able to access water in one part of the soil and redistribute it to roots that may be located in a dry part of the soil. This has the effect of hydrating the rhizosphere and creating a favourable microclimate for microbial activity and fine roots (Neumann and Cardon, 2012), which enhances rhizodeposition and increases decomposition (Aanderud and Richards, 2009) as well as nitrogen uptake (Armas et al., 2011). There was no spatial variation in soil moisture at these sites (see Chapter 6) so it is unlikely that this was a significant process at these sites.

Soil carbon may also be higher near trees as a result of tree litter inputs, which may exceed those of grasses. For example, Mlambo and Nyathi (2007) reported that both total litterfall and standing litter was at least five times greater beneath large trees as opposed to intercanopy spaces in a southern African savanna and this resulted in higher carbon abundance in the soils beneath. Similar results have also been reported for temperate savannas in Australia (Mcelhinny et al., 2010; Travers and Eldridge, 2015). In contrast, in this study there was no difference in litterfall between traps located beneath trees and those located away from trees at any of the sites in this study (see Chapter 4). Nevertheless, there may be additional inputs in the form of twigs and bark that are not dispersed by wind, which were not measured in this study that do lead to enhanced litter inputs beneath trees. Similarly, litter inputs from grasses may be reduced as a result of fire or grazing, whilst litter inputs from trees (in the form of sticks and branches) may be preferentially preserved in the form of charcoal (Wynn and Bird, 2008). Many wood eating termites will preferentially locate under tree canopies (Braithwaite et al., 1988) and mound building termites prefer the thermal protection of tree canopy from midday sun (Jacklyn, 1992). This can also contribute to spatial relocation of organic matter and soil carbon.

In contrast to the Koombooloomba and Davies Creek sites, Brooklyn Station was the only site not to display any spatial arrangement in soil carbon distribution (Figure 5.3) although there was a very weak association with the $\delta^{13}\text{C}$ (Figure 5.4). The studies by Wang et al. (2009) and Dintwe et al. (2014) reported that spatial patterns of soil carbon were most pronounced at their drier sites and disappeared entirely at the wetter sites. However, Brooklyn Station is the driest site included in this study with the lowest basal area and productivity (Chapter 4). There is potential at this

site for organic matter to be redistributed after initial delivery to the soil surface as the site floods most years. However, if this were the case then it should only be the surface soils that are affected, which is not the case. Furthermore, there is a strong relationship between the soil carbon abundance and the $\delta^{13}\text{C}$ (Figure 5.5), suggesting that the trees do produce more carbon but it isn't necessarily produced near the trees. The soil at this site is quite heterogeneous with clay lenses and perched aquifers and it may be that the tree roots have spread laterally in search of resources as opposed to vertically. Alternatively, there are a large number of termites at Brooklyn Station that are not present at the other sites and it is probable that this has resulted in substantial lateral variation of organic inputs and soil particles.

Koombooloomba and Davies Creek also displayed spatial variation in the soil nitrogen but there was no such pattern at Brooklyn Station. Stubbs and Pyke (2005) reported that spatial distribution of nitrogen tended to increase with increasing aridity; again, this contrasts to this study as Brooklyn Station is the driest of the sites and displays no spatial variation. Spatial patterns in soil nitrogen have been reported in other studies, for example Richards et al. (2012) reported higher soil nitrogen in all forms beneath tree canopies as opposed to inter-canopy spaces. They suggested that factors such as superior quality of fine roots (lower C:N ratio) and more litter accumulation could be contributing factors. However, there was no spatial variation in C:N ratio of the bulk soil in this study and in addition there is no spatial variation in the litterfall (Chapter 4).

Additional reasons for spatial arrangement of soil include higher quality litter - a parameter not measured in this study - and factors that contribute to changes in microbial communities and biomass such as rooting depth and architecture and hydraulic redistribution. Aranibar et al. (2004) also suggested that spatial variation could occur as a result of widespread shallow lateral roots taking up the nitrogen and transporting it back to the plant, thus leaving the inter-plant spaces depleted. In addition, $\delta^{15}\text{N}$ value and soil nitrogen are closely related at Davies Creek but not at Brooklyn Station. Nitrogen losses due to gas flux tend to exert an $\delta^{15}\text{N}$ enrichment fractionation of 28 - 60‰ (Robinson, 2001), which could suggest that more nitrogen has been lost to gaseous evolution in the inter-tree spaces at Davies Creek, but not at Brooklyn Station.

As well as lateral variation, soil carbon content also tends to decrease with depth (Figure 5.2), a trend observed in other studies (for example, Chen et al. (2005); Saiz et al. (2012); Saraiva et al. (2014)). This is partly due to variation in carbon inputs; for example, plant litter and combustion products are added at the soil surface and

fine plant roots tend to be more concentrated at the soil surface (February and Higgins, 2010). In addition, microbial biomass is more concentrated at the soil surface where fresh inputs are more easily metabolised. As such, the surface soil carbon pool tends to turn over fairly quickly relative to the subsurface pool, which tends to consist of older, more stabilised carbon (Jobbágy and Jackson, 2000). As carbon inputs are decomposed, the C:N ratio tends to decrease as the carbon is mineralised and the limitation to microbial activity shifts from nitrogen to carbon (Enríquez et al., 1993; Wang et al., 2004). This can result in a decrease in the C:N ratio of the bulk soil with increasing depth, a trend that is evident at all sites (Table 5.4).

In addition to a decrease in bulk soil carbon, the $\delta^{13}\text{C}$ value of the soil carbon tends to increase with depth. At the plot level, this equates to an increase of 1.9‰ at Koombooloomba and 1.3‰ at Davies Creek between the surface soils (0-5 cm) and the subsurface soils (5-30 cm). There is no such difference at Brooklyn Station over the same sample interval and this could be associated with vertical mixing of organic matter as a result of cracking clays at the site or vertical mixing due to faunal activities. However, there is a 1.1‰ decrease between the 0-5 cm samples and the 0 - 100 cm samples (Table 5.5) at Brooklyn Station.

Typically, vertical trends in $\delta^{13}\text{C}$ are due to a number of factors. These include changes in the atmospheric $\delta^{13}\text{C}$ due to the burning of fossil fuels that has resulted in a decrease in the atmospheric $\delta^{13}\text{C}$ value known as the terrestrial Suess effect (Friedli et al., 1986). As a result, older (and deeper) soil carbon may be enriched by up to a maximum of 1.5‰ as it retains the ‘signature’ of the older atmosphere (Bird et al., 1996; Wynn and Bird, 2008). Furthermore, root biomass tends to have a higher $\delta^{13}\text{C}$ value than leaf biomass (at the plant scale), which could result in more $\delta^{13}\text{C}$ -enriched carbon inputs deeper in the soil profile compared to relatively $\delta^{13}\text{C}$ -depleted carbon inputs to the soil surface (Wynn et al. 2006). Finally, as the soil carbon becomes progressively more decomposed, kinetic fractionation by microbial respiration results in the $\delta^{13}\text{C}$ -enrichment of the remaining soil carbon, which can also result in higher $\delta^{13}\text{C}$ values with depth (Šantrůčková et al., 2000; Wynn et al., 2005).

5.5.3 Relative contribution of C₃ and C₄ vegetation inputs to soil carbon

The relative contribution of C₄ vegetation to the soil carbon pool can be estimated by:

$$\%C_4 = \frac{(\delta_{sample} - \delta_{C3})}{(\delta_{C4} - \delta_{C3})} \times 100$$

where δ_{sample} is the $\delta^{13}\text{C}$ value of the soil sample, δ_{C4} is the average $\delta^{13}\text{C}$ value of the C₄ organic matter in the soil and δ_{C3} is the average $\delta^{13}\text{C}$ value of the C₃ organic matter in the soil (Boutton et al., 1999; Lloyd et al., 2008). Although $\delta^{13}\text{C}$ values for the organic matter were not measured in this study, they can be approximated from the literature.

A study by Lloyd et al. (2008) reported foliar $\delta^{13}\text{C}$ values for C₄ vegetation across a range of tropical savannas with a median value for Australian vegetation of $\sim -12.5\text{‰}$ with no significant difference between leaves, stems or roots. In addition, foliar $\delta^{13}\text{C}$ measurements are available for the dominant C₄ vegetation at the Davies Creek and Koombooloomba sites (TROBIT, Unpubl. data). Averaged across all species sampled, C₄ vegetation has a foliar $\delta^{13}\text{C}$ value of -12.3‰ at both sites.

C₃ vegetation from Australia was reported to have a median value of $\sim -28\text{‰}$ with an enrichment of $\sim 0\text{--}2\text{‰}$ for branch and trunk components (Lloyd et al., 2008). C₃ roots are reported to have an enrichment of $\sim 1\text{--}3\text{‰}$ relative to foliar components (Hobbie and Werner 2004; Cernusak et al. 2009). This is similar to post-photosynthetic fractionation between plant organs reported by other authors. For example, a review by (Badeck et al., 2005) reported that woody stems were enriched by an average of 1.91‰ while roots are enriched by an average of 0.91‰ . In addition, foliar $\delta^{13}\text{C}$ measurements are available for the dominant C₃ vegetation at the Davies Creek and Koombooloomba sites (TROBIT, Unpubl. data). Averaged across all species sampled C₃ leaves are -29.2‰ at Davies Creek and -29.0‰ at Koombooloomba.

The average $\delta^{13}\text{C}$ of the C₃ contribution to the soil organic matter will depend not only on foliar input but also input from roots, which could be considerable. For example, Chen et al. (2003) reported that carbon allocation belowground was three times higher than carbon allocation aboveground for a tropical savanna in the Northern Territory. Most significantly, litterfall of $0.9 \text{ t C ha}^{-1} \text{ y}^{-1}$ was matched by fine root production of $7.0 \text{ t C ha}^{-1} \text{ y}^{-1}$ in that study. If we assume this is a typical ratio of foliar to fine root input then we can estimate that the litterfall rates of 0.6,

1.3, and 1.0 t C ha⁻¹ y⁻¹ at Brooklyn Station, Davies Creek and Koombooloomba respectively are associated with fine root production of 4.6, 10.1, and 7.8 t C ha⁻¹ y⁻¹. This in turn gives an average $\delta^{13}\text{C}$ for the C₃ organic matter of -26.2‰ for Brooklyn Station, -27.4‰ for Davies Creek, and -27.2‰ for Koombooloomba (using foliar values from TROBIT, Unpubl. data for Davies Creek and Koombooloomba, foliar values from Lloyd et al. (2008) for Brooklyn Station, and assuming an enrichment of 2.0‰ for root biomass for all sites).

However, litterfall at Davies Creek and Koombooloomba was noticeably increased after TC Yasi and similarly, litterfall at Brooklyn Station was noticeably increased after the fire (Figure 4.3). Consequently, the litterfall rates may not be typical and may not be the best predictor of fine root input. The study by Chen et al. (2003) also reported that the woody biomass increment of 1.6 t C ha⁻¹ y⁻¹ was matched by fine root production of 7.0 t C ha⁻¹ y⁻¹. If we assume this is a typical ratio between woody biomass increment and fine root production then we can estimate that woody biomass increment of 0.5, 0.6, and 1.0 at Brooklyn Station, Davies Creek and Koombooloomba respectively (Table 4.7) is associated with a fine root production of 2.2, 2.6, and 4.4 t C ha⁻¹ y⁻¹. This in turn gives an average $\delta^{13}\text{C}$ for the C₃ organic matter of -26.4‰ at Brooklyn Station, -27.8‰ for Davies Creek, and -27.4‰ at Koombooloomba (using foliar values from TROBIT, Unpubl. data, for Davies Creek and Koombooloomba, foliar values from Lloyd et al. (2008) for Brooklyn Station, and assuming an enrichment of 2.0‰ for root biomass for all sites).

Using the %C₄ equation described by Boutton et al. (1999) and Lloyd et al. (2008), we can estimate the contribution of C₄ vegetation to the soil carbon in the surface soil (0-5 cm). The values used for each site and the estimated contribution of C₄ vegetation are summarised in Table 5.6. The relative contribution of the trees and grasses to soil carbon at Brooklyn Station and Koombooloomba are both approximately half and half, but the contribution of trees to soil carbon at Davies Creek is almost 80%. By comparison, the contribution of C₄ vegetation to ANPP (Chapter 4) is 73% at Brooklyn Station, 63% at Davies Creek, and 78% at Koombooloomba (Table 4.7).

Table 5.6: $\delta^{13}\text{C}$ values used to calculate the contribution of C_3 and C_4 vegetation to soil carbon (0-5 cm) at each site

Site	$\delta^{13}\text{C}_{\text{sample}}$ (‰)	$\delta^{13}\text{C}_{\text{C}_3}$ (‰)	$\delta^{13}\text{C}_{\text{C}_4}$ (‰)	C_4 contribution to soil carbon (%)
Brooklyn Station	-19.9	-26.4	-12.5	50
Davies Creek	-25.1	-27.8	-12.3	22
Koombooloomba	-21.4	-27.4	-12.3	43

Furthermore, if we weight the $\delta^{13}\text{C}$ by the productivity of each component we can estimate the average $\delta^{13}\text{C}$ of both C_3 and C_4 inputs to the soil (*i.e.* not just the average tree contribution). At Brooklyn Station the grass contributed an ANPP of $3.0 \text{ t C ha}^{-1} \text{ y}^{-1}$ at a $\delta^{13}\text{C}$ of -12.5‰ and litterfall contributed $0.6 \text{ t C ha}^{-1} \text{ y}^{-1}$ at a $\delta^{13}\text{C}$ of -28.0‰ . This gives an average aboveground $\delta^{13}\text{C}$ input to the soil of -15.1‰ . If we include input from tree roots of $2.2 \text{ t C ha}^{-1} \text{ y}^{-1}$ at a $\delta^{13}\text{C}$ of -26.0 then the average $\delta^{13}\text{C}$ input is -19.2‰ as compared to -19.9‰ measured in the actual sample.

Similarly, at Davies Creek the grass contributed an ANPP of $3.2 \text{ t C ha}^{-1} \text{ y}^{-1}$ at a $\delta^{13}\text{C}$ of -12.3‰ and litterfall contributed $1.3 \text{ t C ha}^{-1} \text{ y}^{-1}$ at a $\delta^{13}\text{C}$ of -29.2‰ . This gives an average aboveground $\delta^{13}\text{C}$ input to the soil of -17.2‰ . If we include input from tree roots of $2.6 \text{ t C ha}^{-1} \text{ y}^{-1}$ at a $\delta^{13}\text{C}$ of -27.2 then the average $\delta^{13}\text{C}$ input is -20.9‰ as compared to -25.1‰ measured in the actual sample.

Finally, at Koombooloomba the grass contributed an ANPP of $7.2 \text{ t C ha}^{-1} \text{ y}^{-1}$ at a $\delta^{13}\text{C}$ of -12.3‰ and litterfall contributed $1.0 \text{ t C ha}^{-1} \text{ y}^{-1}$ at a $\delta^{13}\text{C}$ of -29.2‰ . This gives an average aboveground $\delta^{13}\text{C}$ input to the soil of -14.3‰ . If we include input from tree roots of $4.4 \text{ t C ha}^{-1} \text{ y}^{-1}$ at a $\delta^{13}\text{C}$ of -28.2 then the average $\delta^{13}\text{C}$ input is -18.8‰ as compared to -21.4‰ measured in the actual sample.

There are several shortcomings with the above approach: firstly, data from Chen et al. (2003) used to estimate root production may not be applicable to these sites. Notwithstanding differences between the sites used in this study, the site used by Chen et al. (2003) has a higher MAP than any of the sites in this study and the grass productivity at the sites in this study are an order of magnitude greater on occasion. Secondly, the above approach does not include inputs from grass roots

when considering the average $\delta^{13}\text{C}$ input to the soil. This may be less important for the sites dominated by perennial grasses that rely on a persistent root stock to resprout (although root turnover still occurs), but the annual grasses at Brooklyn Station could be expected to contribute root mass to the soil carbon pool when the grasses senesce. Furthermore, the fine root production reported by Chen et al. (2003) includes fine root production of both trees and grasses. In the above examples, this productivity has been attributed entirely to trees, but as has previously been discussed, the contribution by grass roots at these sites could be considerable given the ANPP of the grass. This is particularly the case for Brooklyn Station where the annual grasses completely senesce.

Both Koombooloomba and Davies Creek have an estimated average aboveground $\delta^{13}\text{C}$ input to the soil that is enriched relative to the average $\delta^{13}\text{C}$ of the soil (Table 5.6). This could be related to different decomposition rates of the soil carbon, as soil carbon derived from C_4 plants (i.e. grasses) tends to decompose faster than soil carbon derived from C_3 sources (i.e. trees) leaving samples relatively enriched (Wynn and Bird, 2007, 2008). C_4 plant roots have also been shown to have a negative priming effect in C_3 dominated soils when compared to C_3 plant roots in C_4 dominated soils (Fu and Cheng 2002), which may further accelerate the decomposition of grass carbon relative to tree carbon. This is consistent with the lower $\delta^{13}\text{C}$ values observed near trees (Figure 5.4) and also the correlation between high soil carbon and low $\delta^{13}\text{C}$ values (Figure 5.5) observed at all sites in this study. According to the study by Wynn and Bird (2008), this spatial variability in the $\delta^{13}\text{C}$ values tends to be more pronounced in drier ecosystems. In contrast however, the wetter sites in this study (Davies Creek and Koombooloomba) have a much greater difference in mean $\delta^{13}\text{C}$ values between tree and grass sampling locations than the drier site, Brooklyn Station (1.8‰ and 2.2‰ as opposed to 0.6‰ respectively).

Soil texture can also influence $\delta^{13}\text{C}$, with higher values in finer textured soils (Bird and Pousai 1997; Bird et al. 2003; Wynn et al. 2005). This trend is apparent in this study where the two sites with finer textured soils (Brooklyn Station and Koombooloomba) have a markedly higher range of $\delta^{13}\text{C}$ values (~-22 to -18‰) than the site with the coarser textured soils (Davies Creek) where the $\delta^{13}\text{C}$ values range from ~ -27 to -22‰. However, this does not explain the disparity between the $\delta^{13}\text{C}$ of biomass input and the $\delta^{13}\text{C}$ of the soil. Indeed, what is potentially more interesting is that there is no such disparity at Brooklyn Station as multiple processes would be expected to alter the $\delta^{13}\text{C}$ of the biomass input as has been previously discussed. One potential explanation is that the contribution of the grass roots at this site

is considerable (relative to the other two sites). As previously mentioned, there is a large amount of annual grasses at this site that may contribute a considerable amount of root biomass to the soil carbon pool. Furthermore, invasive annual grasses have been reported to have a higher belowground allocation and a higher root density in surface soils when compared to native perennial grasses in a subtropical grassland in Texas (Wilsey and Polley, 2006). Both of these factors would increase the average $\delta^{13}\text{C}$ of the biomass input.

Brooklyn Station and Koombooloomba tend to have similar contributions of C_4 vegetation (%) to both ANPP and soil carbon (Table 5.6). This is somewhat surprising given the large differences between the two sites in productivity (Table 4.7) and tree density (Figure 4.1). One of the things that distinguishes Davies Creek from the other two sites is the soil texture (Table 5.3). The finer soil texture at Koombooloomba and Brooklyn Station could give the grasses an advantage over the trees by storing more water in the shallow soil layers if the grass roots are concentrated in the shallow layers with the trees exploiting the deeper layers (Hoffmann et al., 2004a; Pinno and Wilson, 2013). However, this contrasts with results by Ruggiero et al. (2002) and Van Langevelde et al. (2003) who reported that finer textured soils supported increased woody cover. Furthermore, the preservation potential of C_4 soil carbon is likely to be low at Davies creek due to the coarse texture of the soil because C_4 derived carbon has been shown to degrade faster than C_3 derived carbon in the absence of protection mechanisms such as the association with fine particles. The combination of this lack of ability to protect soil carbon, in combination with the preferential removal of grass biomass by fire, could explain the particularly low levels of C_4 derived soil carbon at Davies Creek.

5.5.4 Implications for climate change and the global carbon cycle

While carbon stored in soil is generally considered ‘stable’ over short to medium time frames, there is a growing fear that increased atmospheric CO_2 will lead to warming-accelerated decomposition of soil carbon. This would, in turn, contribute more CO_2 to the atmosphere, forming a positive feedback effect (Davidson and Janssens, 2006; Jenkinson et al., 1991). Unfortunately, there is no consensus on how much warming will impact on soil carbon stocks with variable results from laboratory and field studies and a lack of long term studies (Conant et al., 2011; Giardina and Ryan, 2000; von Lützow and Kögel-Knabner, 2009). For sites such as Koombooloomba

and Brooklyn Station, at least half of the carbon stocks at these sites is in the surface soils (5-30 cm) so any substantial loss of carbon from the surface soils would also substantially reduce the carbon storage. Furthermore, the soil carbon stocks at Koombooloomba are among the highest in the world for tropical savannas and even a small change to this stock would result in considerable emissions of carbon from the soil.

Alternatively, there is also the potential for increases in atmospheric CO₂ to lead to increases in plant biomass and productivity, particularly those that utilise the C₃ photosynthetic pathway (Ainsworth and Long, 2005). This CO₂ fertilisation effect would also result in increased carbon inputs to the soil. If these inputs exceeded losses due to decomposition then it would lead to an increase in soil carbon (Heimann and Reichstein, 2008). The tree growth increment at the Davies Creek site was slightly higher than the other sites (Table 4.4, see Chapter 4 for details). Furthermore, the soil carbon at Davies Creek is derived mostly from trees, with 76-90% of the soil carbon C₃ in origin. Thus it is possible that CO₂ fertilisation may be increasing the soil carbon at this site. However, the soil carbon stock at Davies Creek is accurately predicted by the long term MAP (Figure 5.8), suggesting that there has not been an unusual increase in the soil carbon at this site.

The capacity for ecosystems to produce more biomass as a result of CO₂ fertilisation is also potentially limited by nitrogen availability (Reich et al., 2006a). For example, modelling by Thornton et al. (2007) suggests that the global terrestrial carbon uptake response to CO₂ fertilisation is reduced by 74% by coupling the nitrogen cycle to the carbon cycle. Nitrogen limitation is likely to be an issue at the Davies Creek site as the C:N ratio of the surface soils is very high (~28, Table 5.4), suggesting that nitrogen is already limiting at this site. In contrast, the soils at Koombooloomba had nitrogen abundances five times that of the other two sites (Figure 5.2), likely as a result of nitrogen fixing species at the site.

At all sites, especially Davies Creek, the trees contribute the majority of the carbon to the soil carbon pool. This means that the soil carbon stock is also vulnerable to any changes in the tree-grass balance due to climate change as discussed in Chapter 4. In particular, changes to precipitation patterns and increases in the length, severity, and frequency of droughts (Feng et al., 2013; Reichstein et al., 2013b) that may result in widespread tree death (Anderegg et al., 2012; Arndt et al., 2015; Fensham et al., 2015) will result in not only the short term loss of the carbon stock in the biomass as it decomposes or burns, but also the mid to long term loss of the soil carbon. Similarly, the damage from TC Yasi resulted in widespread tree

death at Koombooloomba and with changes to the frequency and intensity of storms and cyclones (Frank et al., 2015; Haig et al., 2014) we could see changes to the soil carbon stock as a result.

One of the many confounding factors affecting the stability of soil carbon is the effect of fire. Frequent fire has been shown to reduce soil carbon in tropical savannas in Africa (Bird et al., 2000; Coetsee et al., 2010) although this contrasts with results by Dai et al. (2006) who found no effect of fire on soil carbon at a savanna site in southern Brazil. There is no experimental evidence to confirm or refute that fire affects soil carbon in Australia although modelling suggests that any response in tropical savannas would take up to 100 years (Richards et al., 2011). Fire management remains a controversial issue in Australia as debate continues over what constituted indigenous management practices in the past and whether they are still applicable in modern climate conditions (Bird et al., 2012; Bradstock et al., 2012; Russell-Smith et al., 2013).

One impact of climate change that has received rather too little attention is erosion. Erosion is a serious issue in tropical savannas with seasonal droughts and high rainfall creating ideal conditions for water erosion. Prolonged dry periods also leave the soil vulnerable to wind erosion (Webb et al., 2006) and both can be severely exacerbated by prolonged mismanagement such as overstocking (Dean et al., 2012) or intense fires (Edwards et al., 2015). Soil carbon tends to be concentrated in surface layers, so the loss of surface soils leads to a preferential loss of soil carbon from the system. In addition, wind eroded particles are also enriched in carbon relative to the remaining soil (Webb et al., 2012). The loss of the surface soil also exposes the subsurface soils and makes them more susceptible to erosion, which may result in a positive feedback loop. Soil erosion is of particular concern at Brooklyn Station where rill and gully erosion are widespread.

Soil erosion can also be exacerbated by the timing of fires. For example, the fire at Brooklyn Station in June 2011 left the soil essentially bare for 5-6 months before the grass began to appreciably regrow (Figure 4.2). This is similar to results reported by Townsend and Douglas (2000) who reported that fires lit late in the dry season resulted in increased amounts of bare ground and increased susceptibility to erosion in an Australian tropical savanna in the Northern Territory. Climate change can impact upon fire regime by influencing the amount and curing time of fuel loads and it is imperative that management efforts prevent large and intense wildfires.

5.6 Conclusions

The soil carbon stocks at Koombooloomba represent some of the highest stocks in northern Australia, while those at Davies Creek and Brooklyn Station are more typical. Soil nitrogen content was low at Davies Creek and Brooklyn Station but high at Koombooloomba. The production of soil carbon is largely governed by plant productivity and as such, is closely related to available moisture and soil fertility such as water and nutrient retention. In warm environments, the preservation of soil carbon is largely determined by clay content. Soil carbon and nitrogen display a high level of spatial organisation at both the Koombooloomba and Davies Creek sites and similar spatial patterns in $\delta^{13}\text{C}$ confirm that this is due to spatial patterns in the input of carbon from C_3 and C_4 sources. The Brooklyn Station site displayed the lowest spatial organisation of soil carbon and nitrogen, presumably due to redistribution of soil by termites. Soil carbon and nitrogen also decrease with increasing depth. This is likely due to a combination of higher inputs at the soil surface as well as increased decomposition of soil carbon at depth. An increase in the C:N ratio and $\delta^{13}\text{C}$ supports the hypothesis that carbon has been increasingly metabolised by microbial organisms at depth. At the Koombooloomba and Brooklyn Station sites, the C_4 vegetation contributes up to half of the carbon found in the soil while at Davies Creek the contribution is approximately half that, reflecting similar patterns in ANPP. These soil carbon stocks are potentially vulnerable to climate change as a result of a combination of factors including changes to precipitation and fire regimes, as well as increased erosion.

Chapter 6

Controls on soil respiration at three tropical savanna sites

Statement of contribution

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6.1 Abstract

Soil respiration represents the second largest flux in the terrestrial carbon cycle after gross primary productivity (GPP), but studies in tropical savannas remain particularly underrepresented in global research. We present two years of monthly soil respiration measurements from three tropical savanna sites in far north Queensland. The sites were located on contrasting soil types and encompassed a precipitation gradient ranging from 900 - 2000 mm year⁻¹. The two wetter sites are dominated by a perennial grassy understorey, with annual grasses at the third, drier site. The measurements were undertaken with the aim of partitioning variability in soil respiration in terms of climate and tree/grass distribution. Measurement locations were stratified based on proximity to trees and, for analysis, grouped according to their position relative to the tree canopy. At all sites, soil respiration rates were consistently higher during the wet season and lower during the dry season although the relative influence of soil temperature and moisture differed between sites. At all sites, respiration rates were consistently higher at tree locations, with measurements close to trees (<0.5m) ~1.5-2 times greater than measurements remote (>6m) from trees. The magnitude of the difference between tree and grass locations was variable between sites and across seasons (dry season > wet season). The seasonality of fluxes was highest in the open areas dominated by grasses at all sites. Mean annual soil-derived CO₂ carbon export for the three sites was 8.0, 11.2 and 12.6 t C ha⁻¹ y⁻¹ and broadly reflected patterns of aboveground net primary productivity (ANPP). Although this study presents only two years of data, variation between the two years of data was approximately 15% at all sites, reflecting a combination of inter-annual variability in rainfall and the effects of disturbance such as fire. Soil respiration in these tropical savanna environments is thus both temporally and spatially heterogeneous suggesting that more complex models may be required to accurately estimate the soil respiration in such systems.

6.2 Introduction

Soil respiration comprises one of the largest carbon fluxes between the terrestrial biosphere and the atmosphere. At 98 Pg of carbon per annum (Bond-Lamberty and Thomson, 2010b), the flux represents over ten times the quantity of carbon that is emitted from the combustion of fossil fuels (Grace, 2004; Schlesinger and Andrews, 2000). Soil respiration can be classified as either plant or non-plant produced, with

these fluxes derived from five biologically distinct pathways. Plant-derived or ‘autotrophic’ CO₂ includes respiration from plant roots, as well as associated mycorrhizae and the CO₂ derived from the priming effect of root exudates. Non-plant-derived heterotrophic sources of CO₂ are derived from the decomposition of plant matter and soil organic matter (SOM) by soil microbes that are not part of the rhizosphere (Kuzyakov, 2006). A sixth component can also play a significant role - respiratory CO₂ from other soil organisms, especially termites and ants (Risch et al., 2012).

The different pathways of CO₂ efflux from the soil potentially respond in different ways to different drivers. As with most biological processes, respiration rates are greatest at optimum values of temperature and moisture, while extremes generally act as retardants (Davidson et al., 2000; Lloyd and Taylor, 1994). For example, extremely low temperatures (<5°C) can affect respiratory functions by inhibiting enzyme activity or function (Atkin and Tjoelker, 2003), as well as limiting microbial diffusion and substrate use (Mikan et al., 2002). Extremely high temperatures may interfere with adenylates and substrate supply (Atkin and Tjoelker, 2003). Soil respiration processes tend to follow an exponential increase with soil temperature between these two extremes (Lloyd and Taylor, 1994). Notwithstanding, the temperature sensitivity of both autotrophic respiration and heterotrophic respiration rates (*i.e.* the decomposition of soil carbon) has repeatedly been demonstrated to be variable Davidson and Janssens (2006); Davidson et al. (2006) and there is evidence to suggest that both plant and non-plant sources of soil respiration may in fact acclimate to increased temperatures as a result of climate change (Conant et al., 2011; Giardina and Ryan, 2000; von Lützow and Kögel-Knabner, 2009).

Confounding the elucidation of the temperature response of soil respiration in arid environments, is the influence of soil moisture. Moderate levels of soil moisture are required for all processes of soil respiration, but similarly extreme values will act as retardants. Extremely high values can retard autotrophic respiration by limiting the diffusivity of gases through the saturated pore spaces in the soil, preventing conventional respiratory processes that only occur under aerobic conditions. This may also restrict the transport of soil CO₂ to the soil surface (Kiese and Butterbach-Bahl, 2002; Ryan and Law, 2005). Very low levels of soil moisture can restrict stomatal conductance and limit the supply of photosynthates, as well as restricting microbial diffusion through the soil (Austin et al., 2004b; Huxman et al., 2004). Autotrophic and heterotrophic sources of respiration respond differently to changes in soil moisture. For example, plant-sourced soil CO₂ is limited by the supply of

photosynthates, such that there are lags in response time and responses may not be sensitive to small and/or short term perturbations in the environment (Kuzyakov and Gavrichkova 2010; Tang et al. 2005), whereas microbial sources of soil CO₂ can respond rapidly to the smallest of changes in moisture or temperature (Carbone et al., 2011; Thomas et al., 2011), releasing a ‘pulse’ of CO₂, a phenomenon known as the Birch effect (Birch, 1958).

Tropical savannas are characteristically heterogeneous in nature, consisting of scattered trees and a grassy understory. Such ecosystems tend to occupy regions with highly seasonal rainfall and are often prone to frequent disturbances such as fire, drought, floods and (in some cases) cyclones (Hutley et al., 2013). Heterogeneity at local scales also extends to soil properties, particularly chemical properties such as soil carbon and nitrogen (Chapter 5). In addition, the generally uneven distribution of rainfall creates pronounced periods where water shortages and excesses are both commonplace. Not only are trees and grasses adapted differently to these conditions (O’Grady et al., 1999), but inter-species variability in adaptations also exists (Fensham and Fairfax, 2007) and this likely creates further complexity in patterns of soil respiration rates (Bond-Lamberty and Thomson, 2010a).

Despite these complexities, or perhaps because of them, many studies in savannas have neglected spatial variation, or only mentioned such complications in passing (see for example, Butler et al. (2011); Chen et al. (2003); Makhado and Scholes (2011); Michelsen et al. (2004); Savadogo et al. (2012)). The major disadvantage of this simplification is that when results are scaled up to plot or landscape level, the potential for amplification of errors associated with single or few measurements increases dramatically (Grace et al., 2006). Confounding the quantification of these errors is the paucity of studies in tropical savannas in general. In the Global Database of Soil Respiration Data (V 3.0, current to 2014,), tropical savannas and grasslands make up just 1.6% of over 5000 records. Tropical savannas alone make up just 0.4% of the total (Bond-Lamberty and Thomson, 2014), and yet tropical savannas cover one sixth (17%) of the global land surface (Grace et al., 2006).

As levels of atmospheric CO₂ rise along with global temperature there are concerns that this could lead to increases in soil respiration, a phenomenon that has already been observed (Bond-Lamberty and Thomson, 2014). This could be the beginning of a positive feedback resulting in even higher atmospheric CO₂, thereby compounding the effects of global warming (IPCC, 2013). On the other hand, as anthropogenic carbon emissions continue to increase, this has created growing interest in the potential for soil carbon sequestration in a range of ecosystems (Conant and Paustian,

2002; Powlson et al., 2011; Williams et al., 2004). Due to their size and extent, tropical savannas currently represent a carbon sink of approximately 0.39 Pg C y^{-1} (Grace et al., 2006). There is potential, through changes to management practices, to increase the magnitude of this sink, but accurate estimates of stocks and fluxes are required to confidently inform management decisions and verify sequestration (Wise et al., 2009). This study aims to quantify variation in soil respiration in terms of climate drivers and tree/grass abundance and presents a model for up-scaling of point measurements to the plot level for three savanna locations in northern Queensland. Specifically, this study will address the following research questions:

1. How does soil respiration vary temporally and how is this influenced by soil temperature and moisture?
2. How does soil respiration vary in space and how is this influenced by the tree/grass balance?
3. How much carbon is emitted from the soil at these sites and how is this affected by the method of calculation?

6.3 Methods

The study was conducted at the three study sites (Koombooloomba, Davies Creek, and Brooklyn Station) that are described in detail in Chapter 3. Table 6.1 summarises the main characteristics of the study sites and the key findings from Chapter 4 and Chapter 5.

6.3.1 Experimental design

At each site, sampling was stratified, based on proximity to trees and grouped for analysis according to canopy cover in the same fashion as described in Chapter 5. Briefly, these groups were: adjacent to the tree trunk (termed ‘tree’), at the mid-point of tree canopy cover (termed ‘mid-canopy’), at the edge of the canopy cover or drip line (termed ‘drip line’), and in the open grassy areas equidistant from the nearest trees (termed ‘grass’; Figure 6.1).

The measurement locations were arranged in transects running from tree to tree with the mean distance from the nearest tree of each measurement group presented in Table 6.2. A total of 49 measurements (7 transects) per month were taken at

Koombooloomba ($n = 969$) and Brooklyn Station ($n = 1075$) with 56 measurements (8 transects) taken at Davies Creek prior to October 2011, after which 42 measurements (6 transects) were taken ($n = 1208$).

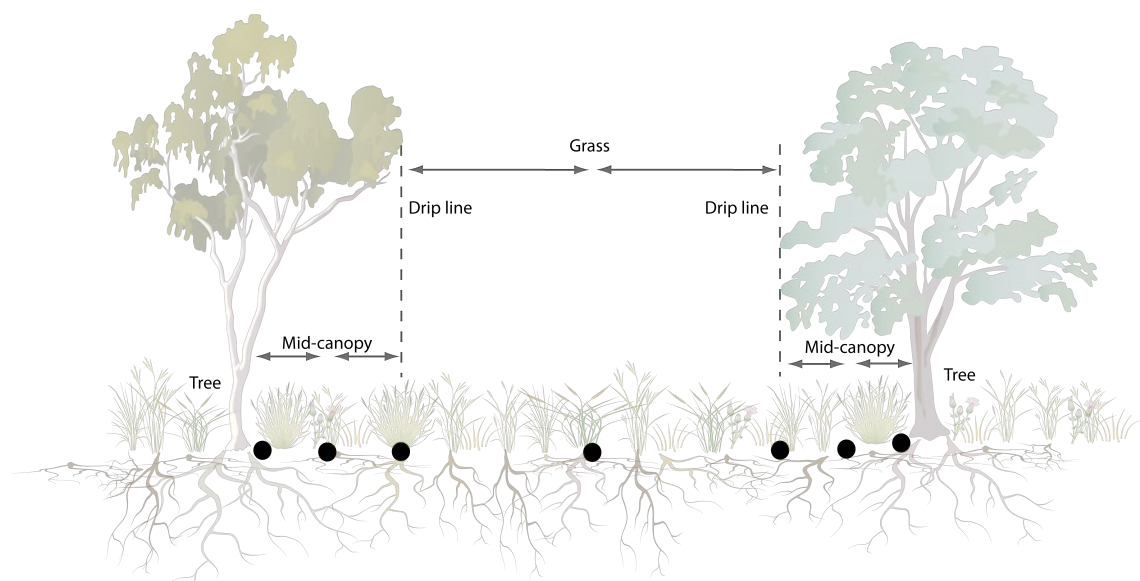


Figure 6.1: Diagram of sampling locations (•) arranged between trees with samples adjacent to the tree trunk ('tree'), mid point of canopy cover ('mid-canopy'), at the edge of the canopy cover or drip line ('drip line') and equidistant between the trees ('grass').

Table 6.1: Main characteristics of study sites. Effective rainfall is calculated as the balance between mean annual precipitation (MAP) and potential evapotranspiration (PET); aboveground net primary productivity (ANPP) and aboveground biomass (AGB; see Chapter 4 for details).

	Brooklyn Station	Davies Creek	Koombooloomba
Savanna classification ^a	Long-grassed woodland savanna	Tall woodland savanna	Tall woodland savanna
Effective rainfall (MAP- PET; mm)	858	1055	1055
ANPP (t C ha ⁻¹ y ⁻¹)	4	5	9
Woody AGB carbon stock (t C ha ⁻¹)	37	70	78
Soil carbon (t C ha ⁻¹)	38	41	114

^a Torello-Raventos et al. (2013)

Table 6.2: Distance from the nearest tree (in m) of each group of measuring points. Values shown are mean $\pm$ standard deviation

Site	Tree	Mid-canopy	Drip line	Grass
Koombooloomba	0.28 $\pm$ 0.12	2.01 $\pm$ 0.40	3.64 $\pm$ 0.62	6.50 $\pm$ 0.65
Davies Creek	0.22 $\pm$ 0.14	2.16 $\pm$ 0.53	4.36 $\pm$ 1.08	6.25 $\pm$ 1.80
Brooklyn Station	0.24 $\pm$ 0.09	2.08 $\pm$ 0.54	3.71 $\pm$ 0.91	6.87 $\pm$ 2.96

6.3.2 Soil respiration measurement

Soil respiration was measured on a monthly basis from July 2010 until June 2012 using a Licor-8100 portable infrared gas analyser (LI-COR inc, Lincoln, NE, USA) connected to a 10 cm diameter closed survey chamber (volume 854.2 cm³) . To ensure repeatability of measurements, stainless steel collars (10 cm inside diameter) were inserted into the soil at least 48 hours prior to the first measurement and remained in place throughout the experiment. Stainless steel was used in place of the traditional PVC in order to withstand fire. The collars were 2.5 cm in length and were inserted approximately 1.5 cm into the soil (headspace volume 78.5 cm³). The area inside each collar was kept free of live vegetation by clipping at the soil surface at least 30 minutes prior to the first measurement. Litter that fell within the collar was left in place and litter that was partially within the collar was similarly clipped prior to measurement so that the portion of litter within the collar remained. Measurements occurred over two minutes. All measurements were taken between 9am and 1pm and collars were measured in the same order at each visit to minimise the effects of diel variation.

6.3.3 Environmental variables

Soil moisture was measured approximately 5 cm from each collar following the completion of the soil respiration measurement using a Theta-Probe soil moisture sensor at 10 cm depth (type ML2X) prior to October 2011, after which date soil moisture was measured using a Hydrosense II soil moisture sensor (Campbell Scientific) at a depth of 0-12cm. Although both soil moisture sensors utilise time-domain reflectometry, the functional lifespan of the two devices did not overlap and so it was

not possible to calibrate the two sensors. For this reason, only measurements taken using the Hydrosense II have been included in the analyses. The volumetric water content was converted to water filled pore space (wfps) using the equation:

$$wfps = \left(\frac{\theta}{1 - (\rho B_{soil} - \rho B_{quartz})} \right)$$

where θ = volumetric water content (%), ρB_{soil} = bulk density of soil (g cm^{-3}) and ρB_{quartz} = the bulk density of quartz (2.65 g cm^{-3}). Soil temperature was measured at 10 cm depth approximately 5 cm from each collar using a soil temperature probe (type E thermocouple) connected to the auxiliary sensor port of the Licor. Air temperature ($^{\circ}\text{C}$) was measured inside the Licor chamber during the efflux measurement using the Licor-8100 sensor.

6.3.4 Statistical analysis

All statistical analyses were performed using R v. 3.2.2 Software (R Core Team (2016); www.r-project.org). Differences in the mean soil respiration rates between sites was assessed using one-way analysis of variance (ANOVA); differences were significant at $p < 0.001$ so subsequent analyses were performed on each of the three sites individually. The same process was applied to soil characteristics and analyses were performed on individual sites unless otherwise indicated. The relationship between soil characteristics and proximity to woody vegetation was assessed using linear regression.

A generalised additive mixed model (GAMM) was fitted to the soil respiration data using the ‘mgcv’ R-package (Wood, 2011). GAMMs permit the incorporation of both linear and non-linear (smoother) fixed-effect predictor variables as well as random-effects to accommodate spatial autocorrelation and repeated measures (Wood, 2006). Our models (Table 6.3) used time (day of the study) and distance to the nearest tree as independent predictor variables of soil respiration that were smoothed using a thin plate regression spline. The specified model included an autoregressive covariance structure, which recognised that proximate observations were more correlated in time and space than those that were more distant in time and space. The model also allowed for heterogeneous variance of the distance to the nearest tree, as soil respiration fluxes were more variable closer to the trees (`corAR1and VarIdent`, package ‘nlme’).

The performance of the models was assessed by comparing predicted fluxes with observed fluxes (Figure 6.4) and checked for bias using standard visual techniques as described by (Zuur et al., 2009). It is worth noting that the thin plate regression spline is scale dependent (Wood, 2003); our model uses distance to the nearest tree in cm and time in days, but the model will produce a different result if different units are used in the fit as this changes the relative weightings of the input variables. Alternative models were fitted using different scales and also comparing different variance and covariance structures with the best model selected on the basis of diagnostic plots, distribution of residuals and Akaike’s information criterion (AIC) (Akaike, 1976).

Table 6.3: Models for the three study sites and characteristics. F-values, significance test p -values and estimated degrees of freedom (edf) are given for the explanatory variables. The adjusted R^2 , number of observations (n) and AIC (Akaike’s Information Criterion) are also shown.

Model		Brooklyn Station	Davies Creek	Koombooloomba
Intercept	t	51.51	58.1	58.99
	$Pr(> t)$	< 0.001	< 0.001	< 0.001
	Estimate	1.45	1.75	1.88
Distance, Time	F	220.3	59.25	55.64
	p	< 0.001	< 0.001	< 0.001
	edf	28.56	26.21	22.01
n		1075	1208	969
R^2 -adj		0.787	0.477	0.52
AIC		422.4	51	66.9

Each of the 1 ha study plots were divided into 10000 1m x 1m cells and the distance to the nearest tree calculated. This enabled the model to be applied to the entire plot by using these distances and time (defined as days from study commencement on July 10th 2010) as input variables for the ‘predict’ function for the purposes of up-scaling observations over the study period to estimate the plot level soil CO₂ export. The uncertainty associated with these estimates was ascertained using a bootstrap approach. Bootstrap samples were created by sampling (with replacement) from the soil respiration dataset on a per sampling location basis. That is,

if a sampling location was selected for inclusion in the bootstrap sample, then each monthly measurement for that sampling location was included. The GAMM was then refitted to the new data set with new coefficients, and the new model was used to upscale the observations over the study period and estimate the plot level soil CO₂ export. This process was repeated 1000 times for each site as the simulations were computationally expensive.

6.4 Results

6.4.1 Temporal patterns of soil respiration and environmental variables

Soil respiration rates were significantly higher during the wet seasons at all sites, coinciding with the periods of highest temperature and soil moisture (Figure 6.2). For all study sites, soil moisture was highest during the 2010-2011 wet season and lowest during the 2011 dry season. Soil temperature was highest during the 2011-2012 wet season.

Brooklyn Station displayed the most significant temporal variation in soil respiration with both the minimum ($<0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$) and maximum ($15.3 \mu\text{mol m}^{-2} \text{s}^{-1}$) fluxes recorded over the entire study occurring at this site. Generally, mean soil respiration rates were high ($>4 \mu\text{mol m}^{-2} \text{s}^{-1}$) during the wet season and low ($1\text{-}2 \mu\text{mol m}^{-2} \text{s}^{-1}$) during the dry season. Soil moisture was also the most seasonal at Brooklyn Station with mean values of $\sim 2\text{-}10\%$ wfps during the dry season and mean values of $>20\%$ wfps during the wet season, culminating in periods of local inundation during February of both wet seasons. These periods of inundation were associated with low soil respiration rates similar in magnitude to dry season fluxes. Brooklyn Station was the hottest of the sites with an overall mean soil temperature of 30°C . Mean soil temperatures ranged from $25\text{-}33^\circ\text{C}$ with the exception of September 2010 where soil temperature averaged 41°C on the day of measurement.

Individual soil respiration measurements at Davies Creek ranged from $<1.0\text{-}11.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ with mean fluxes of $\sim 1\text{-}4 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the dry season and $\sim 4\text{-}7 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the wet season. Davies Creek displayed the least seasonality in soil moisture with mean values of $<10\%$ wfps during the dry season, increasing to $\sim 20\%$ during the wet season. Individual soil moisture measurements ranged from

<1-33% wfps and mean soil temperature ranged from 18-31°C with an overall mean of 25°C.

Koombooloomba was the most productive of the sites with higher rainfall matched by higher biomass and higher soil respiration rates. Individual soil respiration measurements ranged from <0.3-14.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ throughout the study with means of 2-4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the dry season and 4-8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the wet season. The lowest mean soil respiration rates at Koombooloomba were measured during the driest month (September 2011) but otherwise periods of high moisture tended to coincide with high temperature and high fluxes, and vice versa. Mean soil moisture at Koombooloomba ranged from ~30-50% wfps during the wet season and ~25-30% wfps during the dry season. The exception to this was September 2011 where mean soil moisture was 15% wfps and individual measurements were as low as 6% wfps. Mean soil temperature was lowest at Koombooloomba ranging from 16-25°C with an overall mean of 21°C.

6.4.2 Spatial patterns of soil respiration and environmental variables

Mean soil respiration rates were higher closer to trees at all sites (Figure 6.3) irrespective of season and this was not associated with similar trends in either soil moisture or soil temperature (data not shown). Average soil respiration adjacent to trees was 1.4-1.8 times greater than soil respiration remote from trees for Brooklyn Station, 1.5-1.8 times greater for Davies Creek, and 1.9-2.1 times greater for Koombooloomba (wet and dry seasons, respectively). At Koombooloomba, the decrease in fluxes away from trees was relatively gradual. However, this decrease was more abrupt at Davies Creek and Brooklyn Station, with soil respiration rates dropping sharply approximately 1.5m from the base of the tree and only minimal further decreases as distance from the tree increased.

Spatial variation in soil respiration was consistent throughout the study; *i.e.* individual measurement locations that yielded high fluxes continued to yield high fluxes and *vice versa* throughout. The exception to this trend occurred at Brooklyn Station in March 2011. On this occasion, soil respiration rates measured at intermediate locations were higher than soil respiration rates from either tree or grass locations. This visit coincided with high temperatures and soil moisture towards the end of the wet (growing) season and the pattern is heavily influenced by exceptionally high

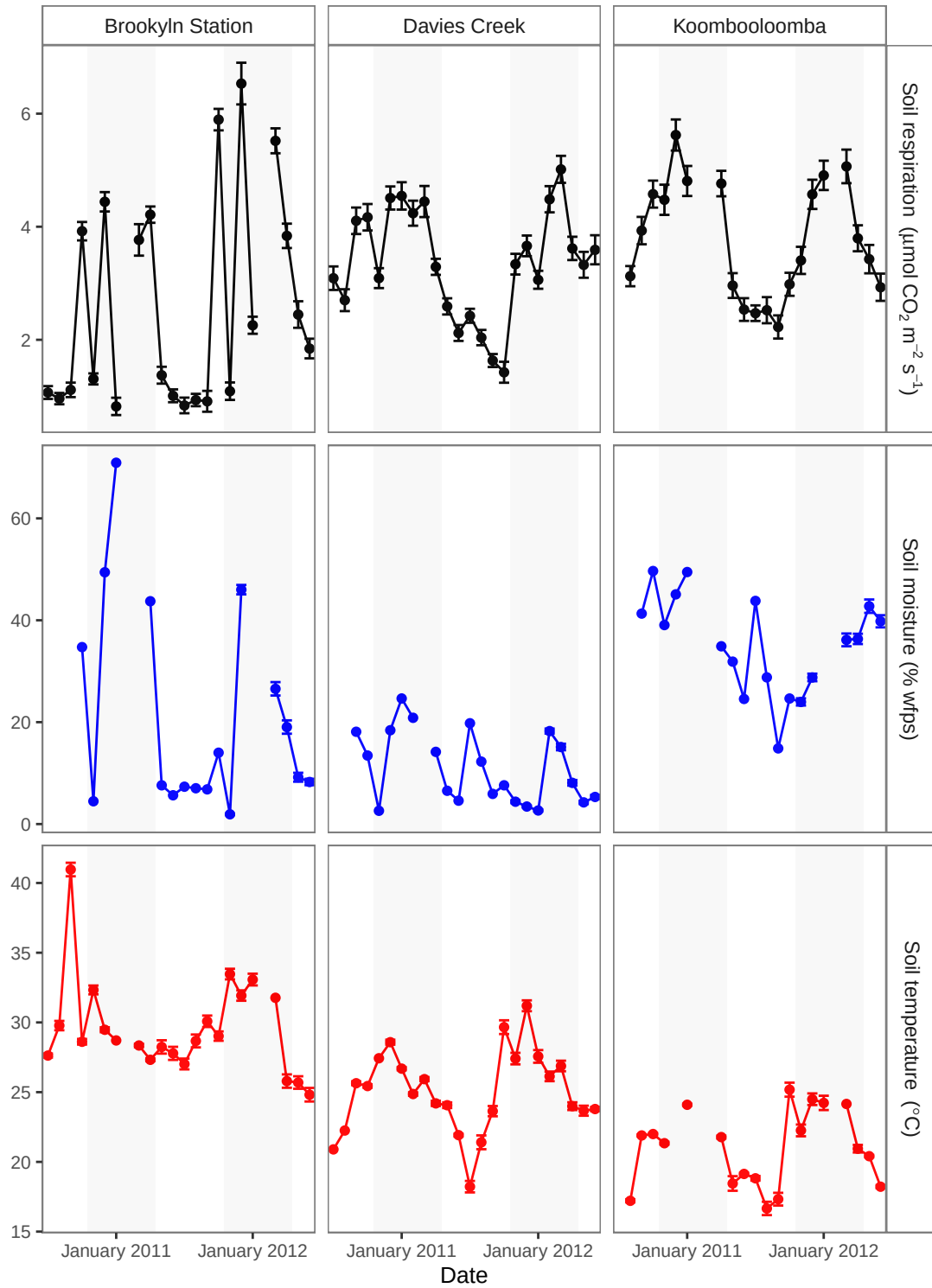


Figure 6.2: Mean soil respiration ($\bullet$), soil moisture ($\bullet$) and soil temperature ($\bullet$) for the three study sites over the two-year study period from July 2010 to June 2012, measured monthly. The wet season (November to April) is shaded in grey for clarity. Gaps in data are due to blocked access to site or instrument malfunction.

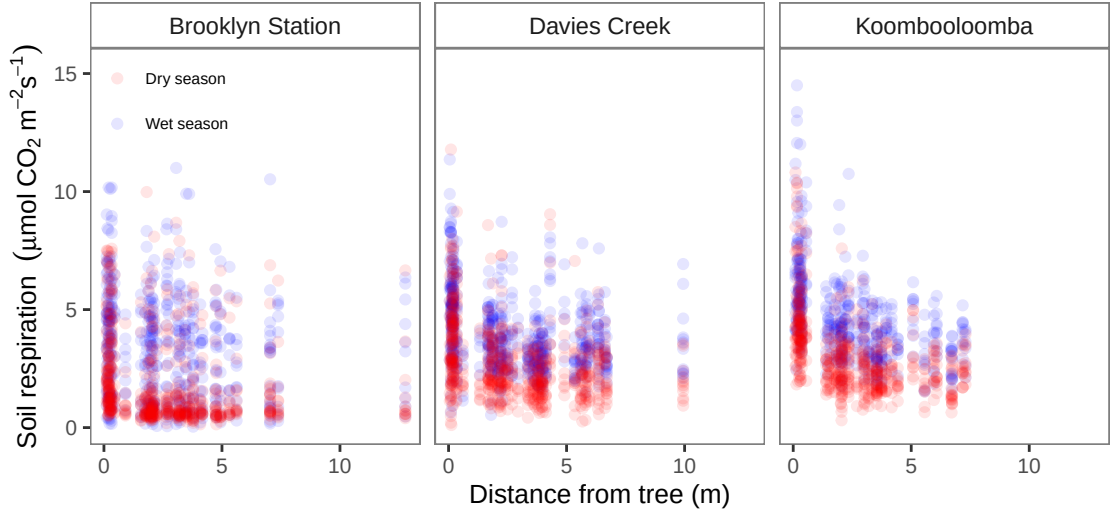


Figure 6.3: Soil respiration and distance from the nearest tree for Brooklyn Station (left), Davies Creek (middle), and Koombooloomba (right). Points are coloured to indicate wet season (November to April; $\bullet$) and dry season (May to October: $\bullet$).

soil respiration rates from only a few intermediate locations ($n = 5$).

6.4.3 Model performance and outcomes

Our models (Table 6.3) used time (day of the study) and distance to the nearest tree as independent predictor variables of soil respiration that were smoothed using a thin plate regression spline. Figure 6.4 shows the model predicted fluxes against the observed fluxes for each site. While the model is a good predictor of low and intermediate fluxes, it tends to truncate the predictions at a maximum flux that is often several $\mu\text{mol m}^{-2} \text{ s}^{-1}$ lower than the observed flux. As this only occurs with extreme data points, and there are very few of those ($\sim 1\%$ of the data points), the influence of this bias is likely to be very small.

Figure 6.5 shows the thin plate regression spline smoother for the time predictor variable used in the model. The lines show a smoothed temporal trend in the soil fluxes with different lines representing sample locations at different distances from trees. The distance smoother (Figure 6.6) generally has a fairly constant slope throughout the year and thus the effect of distance on the temporal smoother is an adjustment in magnitude, rather than shape. The exception to this trend is Brooklyn Station, where the distance smoother has a moderately different slope and intercept depending on the time of the year.

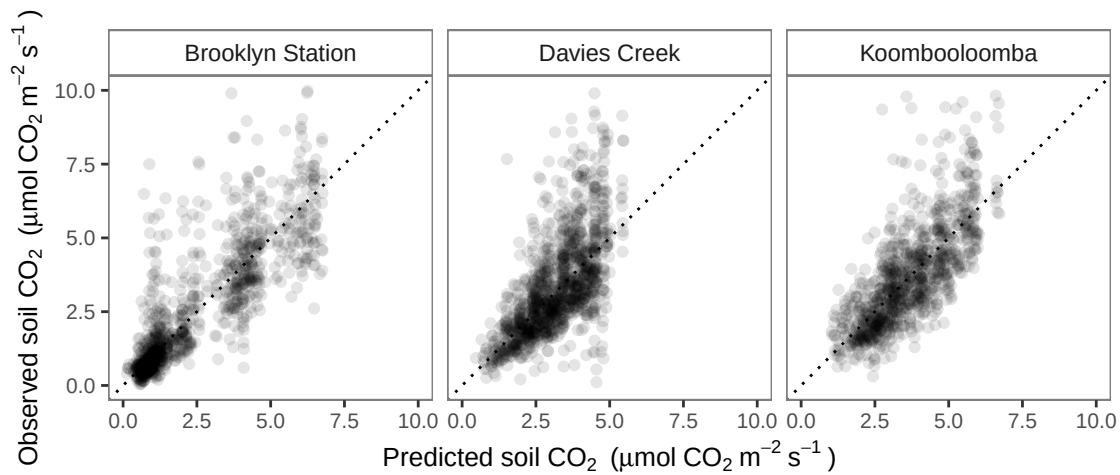


Figure 6.4: Observed soil respiration and predicted soil respiration for the three study sites.

6.4.4 Modelled soil CO₂ export at the plot level

The modelled annual soil-derived carbon export was 8.2 ± 0.7 , 11.7 ± 0.8 , and 12.8 ± 0.9 t C ha⁻¹ y⁻¹ Brooklyn Station, Davies Creek, and Koombooloomba, respectively (mean $\pm$ s.d. of 1000 simulations). The contributions of each sample year and season to the mean soil-derived carbon export are summarised in Table 6.4. Carbon export as CO₂ from the soil was biased towards the wet season with wet season fluxes accounting for ~60-65% of the total annual soil-derived CO₂ export. There was also some variation between the study years with higher fluxes in the first year for both Davies Creek and Koombooloomba. In contrast, the reverse was true for Brooklyn Station with a 25% increase in the second study year. Generally the seasonal contribution to total soil CO₂ export remained consistent, despite the total annual flux differing between years.

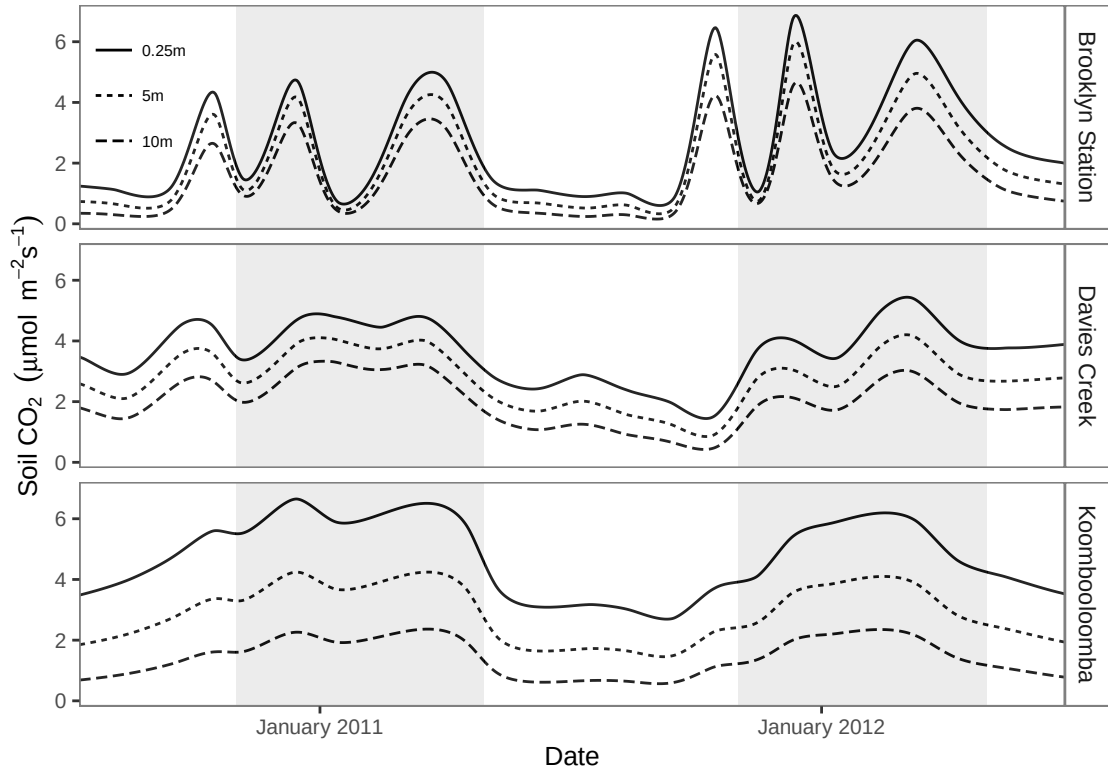


Figure 6.5: The thin plate regression spline smoother for the time predictor variable (day of the study) used in the GAMM. Lines shown are the time smoothers for sampling locations at varying distances from the tree: 0.25m (solid line), 5m (dotted line), and 10 m (dashed line). The wet season (November to April) is shaded in grey for clarity.

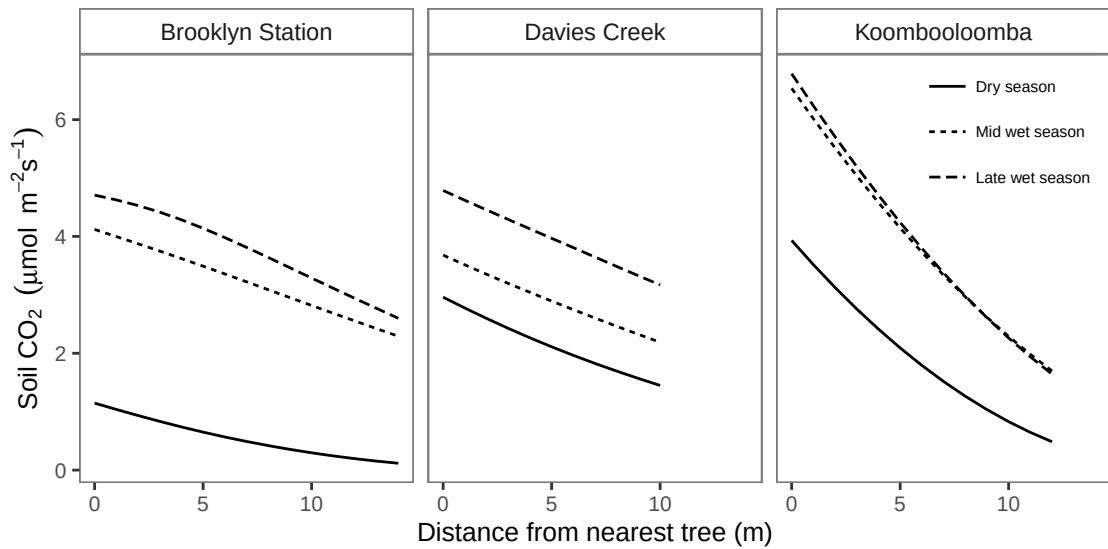


Figure 6.6: The thin plate regression spline smoother for the distance predictor variable (distance to the nearest tree) used in the GAMM. Lines shown are examples of smoothers for different times of the year: July 2010, dry season (solid line), December 2010, mid wet season (dotted line), and March 2011, late wet season (dashed line).

Table 6.4: Mean soil-derived carbon export for each site ($\text{t C ha}^{-1} \text{ y}^{-1}$ or season^{-1}) based on the GAMM estimates. Values given for the mean annual export are the mean and s.d. of 1000 simulations.

Site		Wet season (Nov - Apr)	Dry Season (May - Oct)	Annual
Brooklyn Station	2010-2011	4.7	2.3	7.0
	2011-2012	6.3	3.3	9.6
	Mean	5.5	2.8	8.2 ± 0.7
Davies Creek	2010-2011	7.2	5.3	12.6
	2011-2012	6.7	4.2	10.9
	Mean	6.9	4.8	11.7 ± 0.8
Koombooloomba	2010-2011	8.4	5.3	13.8
	2011-2012	7.5	4.4	11.9
	Mean	8.0	4.9	12.8 ± 0.9

The spatial distribution of the soil-derived carbon export is shown in Figure 6.7. Areas adjacent to trees comprised the highest fluxes but total export was dominated by grassy areas as these areas constituted the largest component of the study sites in terms of area.

6.5 Discussion

6.5.1 Soil respiration as a function of soil temperature and water content

Soil respiration was highly seasonal at all sites and high fluxes corresponded to seasonal highs of both soil temperatures and moisture. This pattern is typical of tropical savannas globally where biological activity is at its peak during the wet season and may become limited by water availability during the dry season. For example, Chen et al. (2002) measured soil respiration rates at an Australian tropical savanna in the Northern Territory and reported that soil respiration during the wet

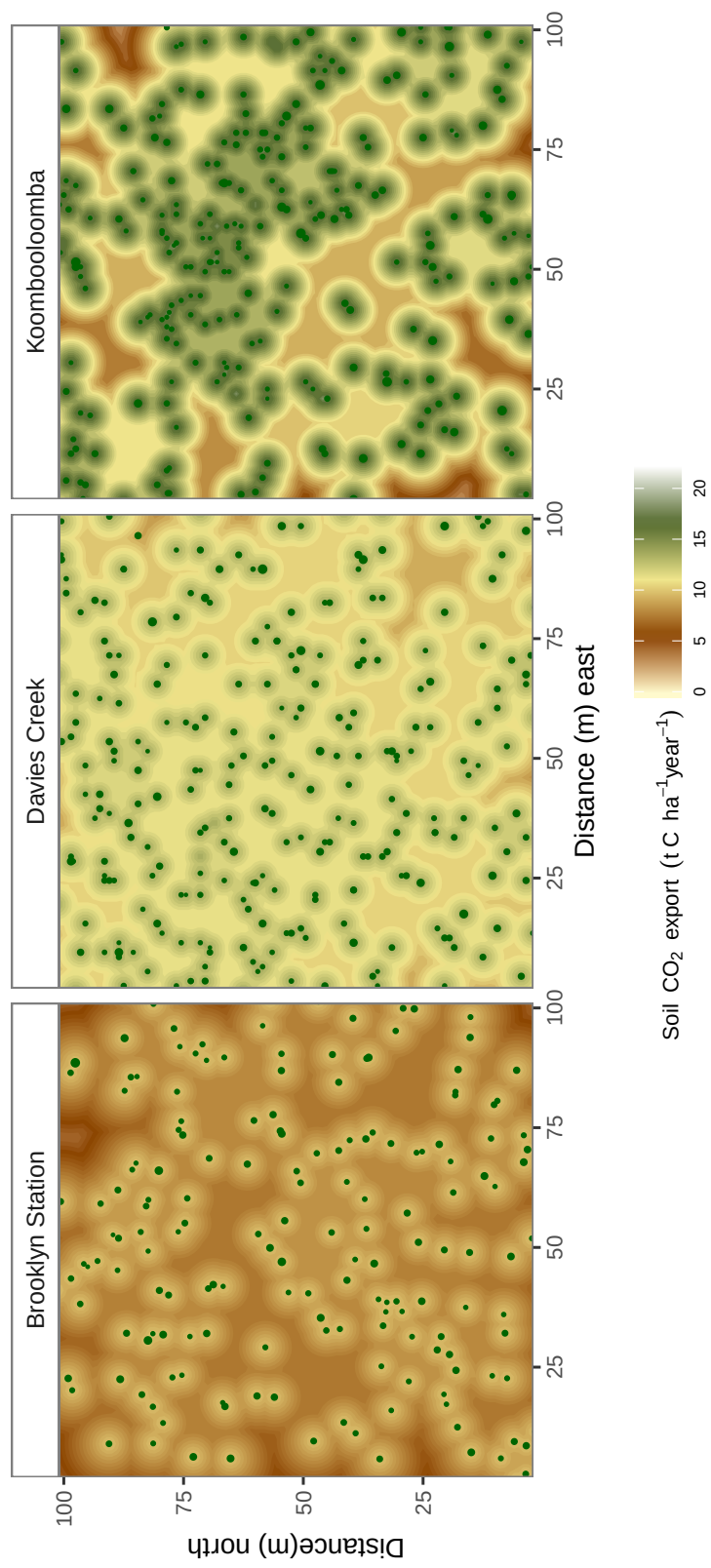


Figure 6.7: Soil-derived CO_2 export for Brooklyn Station (left), Davies Creek (middle), and Koombbooloomba (right). Individual trees within the plot are indicated by green circles ($\bullet$) with size proportional to dbh.

season was approximately three times greater than during the dry season. Similar results have been reported for other tropical savannas in Australia (Holt et al., 1990; Livesley et al., 2011) as well as those in Africa (Caquet et al., 2012; Makhado and Scholes, 2011; Thomas, 2012) and the Americas (Butler et al., 2011; de Pinto et al., 2002; Pendall et al., 2010).

At higher temperatures, soil respiration increases due to an increase in reaction rates, soil diffusivity and plant growth (Singh and Gupta, 1977; Zhou et al., 2006) as well as microbial decomposition (Frey et al., 2013). The relationship between soil respiration and soil temperature can be described by an exponential function of the form:

$$R = R_{20}e^{E_0(\frac{1}{T_{20}-T_0}-\frac{1}{T_{soil}-T_0})}$$

where R = soil respiration rate, R_{20} = the soil respiration rate at 20°C, T_{soil} = the soil temperature (K), and E_0 and T_0 are fitted parameters (Lloyd and Taylor, 1994). This function was fitted to the soil respiration data and the remaining variation was examined with regard to soil moisture (Figure 6.8). The relationship shown in this equation was sufficient to describe the relationship between soil respiration and soil temperature at Koombooloomba, with soil moisture failing to explain any additional variation. In contrast, there was a slight but significant trend at Davies Creek for the R_{20} rate to increase with increased soil moisture. At Brooklyn Station however, there was a conspicuous relationship with soil respiration rising sharply up to a soil moisture of ~15% wfps, beyond which there was a marked reduction in the rate of increase.

Temperature was one of the first drivers of soil respiration to be identified, primarily due to the high density of studies conducted in temperate climates that are typically cold and not water-limited (Singh and Gupta, 1977). Temperatures in tropical ecosystems tend to be more stable. Consequently temperature is rarely identified as a driving variable in isolation of other factors (particularly soil moisture) in seasonal ecosystems. For example, Maggs and Hewett (1990) measured soil respiration in the neighbouring forests of the Wet Tropics at Lake Eacham. Their study site experiences a higher and less seasonal mean annual precipitation (MAP) and is located on the same soil type as the Koombooloomba site. They reported that low soil moisture resulted in lower soil respiration during the dry season and remained a significant factor controlling soil respiration rates throughout the wet season, and as such, temperature was only a significant determinant during the wet season. Their findings

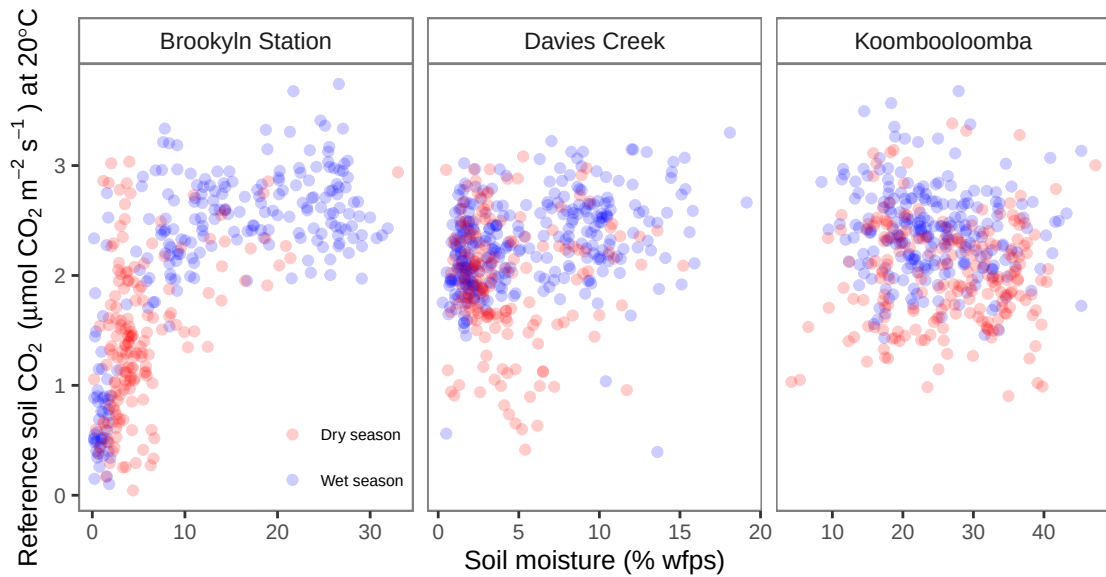


Figure 6.8: Reference soil respiration at 20°C and soil moisture at the three study sites. Points are coloured to indicate wet season (November to April; ●) and dry season (May to October: ●).

are likely influenced by the fact that rainfall was slightly below average during both years of their measurements. This contrasts to this study, which coincided with one of the strongest La Niña events on record, which is associated with the wettest 24 months in Australia since 1900 (BOM, 2012; Figure 6.9).

Similarly, Kiese and Butterbach-Bahl (2002) measured soil respiration in a rainforest adjacent to the Davies Creek site and reported that soil temperature was not at all significant in determining soil respiration rates. The soil type at Davies Creek is very shallow and gravelly, with a very low water holding capacity and has formed on the same geological unit as the soil type of the study site reported by Kiese and Butterbach-Bahl (2002). Nonetheless, the area experienced some above-average rainfalls during the field campaigns by Kiese and Butterbach-Bahl (2002) who also reported that soil moisture contents were on occasion high enough to retard the soil respiration. Despite high rainfalls at the Davies Creek site, such high soil moisture values (50-60% wfps) were never recorded. This could be accounted for by site differences; the site in Kiese and Butterbach-Bahl (2002) study probably has higher levels of soil carbon/organic matter and is somewhat lower on the hill than Davies Creek, which has very shallow and coarse soils.

Many savanna species, including *Eucalyptus* spp., have efficient water transport and storage mechanisms meaning they are able to continue to assimilate carbon throughout periods of water shortage (Beringer et al., 2007; Bucci et al., 2004; Cernusak

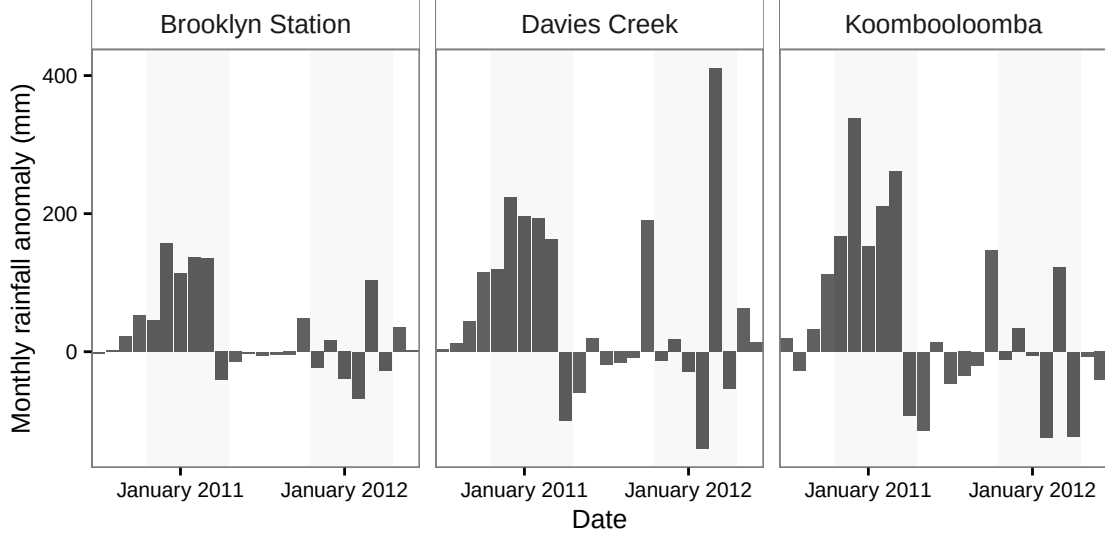


Figure 6.9: Deviation of monthly rainfall from long term average throughout the study period. The wet season (November to April) is shaded in grey for clarity.

et al., 2006). For example, Moore et al. (2015) reported that almost 80% of the GPP of the grassy understorey in an Australian tropical savanna occurred during the wet season as compared to only 54% of the GPP of the trees. Thus, it may not be appropriate to compare this study to results obtained in rainforest environments, despite the close proximity of the study sites and comparable soil types. Nevertheless, soil moisture has been identified as a limiting resource in many seasonal vegetation communities around the world ranging from rainforests to dry forests and other rainforest-savanna boundary vegetation types. For example, Valentini et al. (2008) reported water availability was the primary driver of soil respiration in ‘transitional forests’ (Brazilian *cerrado*). Similarly, Adachi et al. (2006) reported that temperature was only identifiable as a driver of soil respiration during the wet season in a ‘dry evergreen forest’ in Thailand.

The relationship between soil moisture and soil respiration at Brooklyn Station at a reference temperature of 20°C can be expressed by the following equation:

$$R_{20} = R_{max}(1 - e(\alpha(wfps - z)))$$

where R_{20} = the reference soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at 20°C, $wfps$ = water filled pore space (%), $R_{max} = 2.75 \mu\text{mol m}^{-2} \text{ s}^{-1}$, $\alpha = -0.07$ and $z = -3.65$. What this relationship does not capture is the fact that at extremely high values, soil moisture reduces soil respiration. During February of both years of the study, the soil at

Brooklyn Station became saturated (*i.e.* inundated) at which point soil respiration rates were comparable in magnitude to dry season fluxes. Unfortunately, equipment malfunction means that no soil moisture data was collected on the two occasions where inundation was visually observed, which may have helped to constrain the threshold at which this process occurs.

Several studies have reported that soil respiration is retarded by high levels of soil moisture, including Kiese and Butterbach-Bahl (2002), Brümmer et al. (2009), Johnson et al. (2013) and Wood et al. (2013). Inundation of the pore space in soil decreases gas diffusivity, restricting the emission of CO₂ that is already present in the soil and also leads to a state of hypoxia that restricts root respiration, reducing CO₂ production in the soil (Parolin and Wittmann, 2010), and this may occur within a few hours of inundation (Baruch, 1994). Adaptations to prolonged inundation are surprisingly widespread among tropical plant genera, for example Oosterheld and McNaughton (1991) reported that two species of Serengeti grasses were able to develop new root systems above the soil. Unfortunately, the saturated soil restricted further access to Brooklyn Station for 6-8 weeks in both study years. This prevented the collection of data that might either support or refute the operation of such a phenomenon at this site, an issue reported in other tropical savanna studies (Chen et al., 2002).

6.5.2 Soil respiration as a function of tree-grass abundance

Environmental factors exert a strong influence over the temporal pattern of soil respiration, but the spatial variability is largely governed by the distribution of trees and grasses. In this study, there were higher soil respiration rates adjacent to trees at all sites (Figure 6.3), with the exception of one visit at Brooklyn Station (March 2011). There are a number of mechanisms by which this may occur that can be broadly grouped as biological (root density, plant allocation) that primarily affect autotrophic respiration and chemical (soil carbon and nitrogen, hydraulic redistribution, litter inputs) that primarily affect heterotrophic respiration, as well as physical (changes to soil structure) that affect both sources of respiration.

Biological influences

Higher soil respiration rates may be due to a higher density of root biomass, thus contributing higher densities of root respiration. For example, Xu et al. (2011) found that fine root biomass exponentially decreased with increased distance from trees, and similarly Mordelet et al. (1997) found higher fine root biomass in areas beneath tree canopies as opposed to open areas away from canopies. However, those results contrast with the findings of February and Higgins (2010) who reported no such trend at two tropical savanna sites in South Africa. Similarly, Eamus et al. (2002) also reported that fine root biomass did not vary with distance to trees at a tropical savanna site in northern Australia and Epron et al. (2004) reported the same for a *Eucalyptus* plantation in the Congo.

Australian savanna trees do not tend to shade out grasses, and understory taxa can often be found growing right up to the base of the tree trunk. The roots are generally not partitioned into their respective sources in reported studies, and proximity is an unreliable proxy for origin. For example, February and Higgins (2010) examined vertical root distribution at two savannas in South Africa. They found that grass root biomass exceeded tree root biomass both beneath trees and between trees at their arid site, a trend that continued to a depth of 60 cm. In contrast, tree roots exceeded grass roots at the mesic site they examined at all depths to 60 cm with the exception of the surface soils (0-10 cm) that were sampled between the trees.

The grass species at Brooklyn Station are dominated by annual species that completely senesce; thus the autotrophic respiration measured during the dry season at this site is arguably solely of tree origin. If this is indeed the case then the gradient in soil fluxes observed at this site must be at least partly caused by a gradient in tree root respiration. Of course, one cannot decisively attribute dry season fluxes to purely tree autotrophic respiration as this neglects the contribution of heterotrophic respiration. For example, Tang et al. (2005) measured soil fluxes near trees and in grassy gaps in a Mediterranean oak savanna. They concluded that soil fluxes from the grassy gaps following the senescence of the grass constituted the heterotrophic component of total soil respiration. Nonetheless, the trees in the study by Tang et al. (2005) were much more widely spaced than at Brooklyn Station (~40 m as opposed to ~25m) and it is indeed possible that tree roots had not colonised these gaps, which is unlikely to be the case in this study.

Although the tree component presents a greater store of carbon in terms of biomass, the grass component can equal or exceed the tree component in terms of productivity.

For example, the grasses at these study sites tend to have a higher net primary productivity (NPP) than the trees, at least for the aboveground component (Table 4.7; see Chapter 4 for details). Furthermore, the grasses may also exceed the trees in photosynthetic capacity. For example, Beringer et al. (2007) partitioned GPP into tree and grass derived sources across two years at a tropical savanna site in the Northern Territory. They reported a tree GPP of 8.5-8.6 t C ha⁻¹ y⁻¹ and a grass GPP of 8.5-10.2 t C ha⁻¹ y⁻¹. In contrast, further studies conducted at the same site have partitioned carbon fluxes using eddy covariance towers located at different heights within the savanna and reported that the grasses contributed only 32% or 7.2 t C ha⁻¹ y⁻¹ to the total GPP of 22.6 t C ha⁻¹ y⁻¹ (Moore et al., 2015). As a result, all that one can definitively state is that due to their higher biomass gains the grasses cannot be assumed to have lower respiratory losses.

Chemical influences

Plants can also affect soil CO₂ production via an effect on heterotrophic respiration, by providing additional substrate and nutrient supply. At Davies Creek and Koombooloomba, higher soil respiration rates near trees could be partially explained by higher levels of soil nitrogen (Chapter 5), a trend that has been reported in other studies (Stubbs and Pyke, 2005). Nitrogen is often cited as the primary nutrient limiting productivity in savanna ecosystems (Bustamante et al., 2006; Devi Kanniah et al., 2010; Higgins et al., 2015; Schimel and Bennett, 2004) although fertilisation experiments in tropical savannas have reported conflicting results (Ludwig et al., 2001; O'Halloran et al., 2009). Nitrogen is required by soil organisms during the decomposition process and microsite variation in nitrogen, particularly labile forms of nitrogen, can result in spatial variation in the heterotrophic component of soil respiration. Furthermore, if such microsite patches of nutrient are large enough, they may also promote localised growth of plant roots and mycorrhizae, facilitating increased autotrophic respiration (Austin et al., 2004b).

In addition to higher soil nitrogen, there was also higher soil carbon in areas adjacent to trees at the Koombooloomba and Davies Creek sites (Chapter 5). Higher levels of soil carbon provide more potential substrate for microbial (heterotrophic) respiration. This is consistent with other studies that have reported similar influences of soil carbon on soil respiration rates ranging from the plant scale (Maestre and Cortina, 2003; Stoyan et al., 2000) to plot and landscape scales (Martin et al., 2009; McCulley et al., 2004; Webster et al., 2009). The association with higher soil

carbon and more depleted $\delta^{13}\text{C}$ (Chapter 5) suggests that the additional carbon is C_3 in origin (*i.e.* from the trees as opposed to the grass). Trees may enhance soil carbon over grasses in a number of ways including enhanced rhizodeposition, hydraulic redistribution and increased local litter inputs.

Rhizodeposition involves the sloughing of root cap cells, secretion of mucilage, excretion of organic compounds and senescence of the root epidermis (including root hairs). Collectively, rhizodeposition may contribute carbon to the soil equivalent to approximately 17% of the root biomass, the majority of which is sourced from the excretion of organic compounds (Nguyen, 2003). Furthermore, root cell sloughing, exudation and turnover provide as much carbon as root biomass and remains in the soil due to a combination of chemical recalcitrance, physical protection and physio-chemical protection (Rasse et al., 2005). Rhizodeposition may also result in a ‘priming’ effect that can accelerate the decomposition and metabolism of pre-existing soil carbon (Kuzyakov et al., 2000b). The bacterial cells and fungal hyphae then become additional carbon substrates for consumption by other microbes or fauna, which in turn also deposit organic matter in the form of faeces and bodily remains (Singh and Gupta, 1977). This in turn can alter the bulk density and moisture retention of the soil (Wang et al., 2009), creating islands of fertility around savanna trees.

Jin et al. (2008) reported that proximity to trees in a semiarid woodland in Mongolia was also associated with higher soil respiration, higher microbial biomass, and higher soil moisture content. They concluded that the effect of the woody vegetation was primarily to facilitate microbial respiration by the hydraulic redistribution of deeper moisture sources, as they found no relationship between root biomass and proximity to trees. Proximity to woody vegetation was not associated with higher soil moisture at any of our sites; indeed the opposite was true for the Koombooloomba site. Microbial biomass was not measured in this study, but it is entirely possible that there are spatial differences in the heterotrophic contributions to soil respiration.

Litter inputs can also result in higher soil fluxes. For example, Epron et al. (2004) examined spatial variation in soil respiration in a *Eucalyptus* plantation in the Congo and found higher emissions adjacent to woody vegetation. However, they concluded that the influence of the trees was not due to higher soil carbon but was instead controlled by greater litter inputs, which is not the case at any of the sites in this study (Chapter 4). Nevertheless, there may be additional inputs in the form of sticks and bark, which were not measured in this study but are more likely to be deposited directly below the trees than leaves. Furthermore, soil carbon derived from C_4 plants

(*i.e.* grasses) tends to decompose faster than soil carbon derived from C_3 sources (*i.e.* trees) such that carbon may accumulate around trees (Wynn and Bird, 2007). In addition, C_4 plant roots have been shown to have a negative priming effect in C_3 dominated soils when compared to C_3 plant roots in C_4 dominated soils (Fu et al., 2002), which may further accelerate the decomposition of grass carbon in open areas and retard the decomposition of tree carbon in proximity to trees.

It is worth noting that the spatial variation in soil respiration, soil carbon and nitrogen at Koombooloomba and Davies Creek was very high, making the influences of heterotrophic and autotrophic contributions to soil respiration difficult to disentangle. In contrast, while Brooklyn Station showed a high degree of spatial variation in the soil fluxes, this was not associated with similar spatial variation in the soil carbon and nitrogen (Chapter 5). The spatial variation in soil respiration at Brooklyn Station was most pronounced during the dry season, when heterotrophic respiration is likely to be at its lowest, suggesting that these fluxes were dominantly autotrophic and of tree origin. Wet season fluxes tended to be less spatially distinct, although this likely reflects a (relatively) uniform contribution from heterotrophic respiration as well as a similarly uniform contribution from grass-sourced autotrophic respiration.

Physical influences

Finally, spatial differences in the physical characteristics of the soil may result in preferential diffusion pathways. For example, Fang et al. (1998) reported spatial variation of soil respiration in a pine plantation was related to soil porosity. Similarly, Brito et al. (2009) identified macro-porosity as one of the factors determining spatial variation in soil respiration in a sugarcane plantation and highlighted the importance of pore size distribution. Furthermore, Novara et al. (2012) reported a negative correlation between soil compaction and soil respiration; soil with a bulk density of 1.1 g cm^{-3} respired 32% more CO_2 than a soil with a bulk density of 1.5 g cm^{-3} . This is consistent with the results of this study, where the site with the lowest soil bulk density (Koombooloomba) had the highest soil respiration and the soil with the highest bulk density (Brooklyn Station) had the lowest soil respiration. In addition, all sites had lower soil bulk density near trees.

6.5.3 Up-scaling of point measurements to plot level and soil CO₂ export

Modelled soil-derived CO₂ export averaged 8.2 ± 0.7 , 11.7 ± 0.8 , and 12.8 ± 0.9 t C ha⁻¹ y⁻¹ for Brooklyn Station, Davies Creek, and Koombooloomba, respectively (Table 6.4). By comparison, the mean measured fluxes for each site were 9.7 ± 8.4 , 12.8 ± 6.5 , and 14.2 ± 7.2 t C ha⁻¹ y⁻¹ for Brooklyn Station, Davies Creek, and Koombooloomba, respectively. Carbon export was approximately 25% lower using the GAMM estimates as compared to taking the mean of the measurements and this is likely due to sampling bias. Two trees are required to measure one gap in between, but the reality of the savanna is that it is a continuous system that actually has much more area in gaps than in trees.

The disparity between these two results highlights the need for careful sampling when dealing with such heterogeneous environments in order to avoid under- or over-estimating carbon stocks and export. Despite the fact that fluxes from near trees were typically double those of the grassy gaps, they did not contribute disproportionately to the total plot flux. This is due to the fact that the higher fluxes drop off very quickly away from the tree. As such, the proportion of the plot area that has these much higher fluxes is quite low. For example, discounting cells that were within 1m of a tree constituted <10% of the plot area and only resulted in a reduction in the mean plot soil flux of ~2%. Similarly, a power analysis suggests that the plot mean can be estimated to within 15% of the plot mean by simple random sampling using as few as 20 samples at the $\alpha = 0.05$ significance level (Figure 6.10).

Comparisons between ‘tropical savannas’ can be difficult to make on account of the high level of diversity between these ecosystems and because the vegetation community plays a large role in driving soil respiration (Metcalf et al., 2011). For example, annual soil fluxes of 1.0 - 28.8 t C ha⁻¹ y⁻¹ have been reported for tropical savannas in Brazil (Fernandes et al. (2002) and Valentini et al. (2008), respectively). In comparison to soil respiration studies from tropical savannas and grasslands included in the Global Database of Soil Respiration (GDSR V. 3.0, Bond-Lamberty and Thomson (2014)), the sites in this study are at the lower end of the scale (Figure 6.11).

This is especially true of Brooklyn Station which is lower than ~70% of the studies. This is actually somewhat surprising given the high ANPP and aboveground biomass

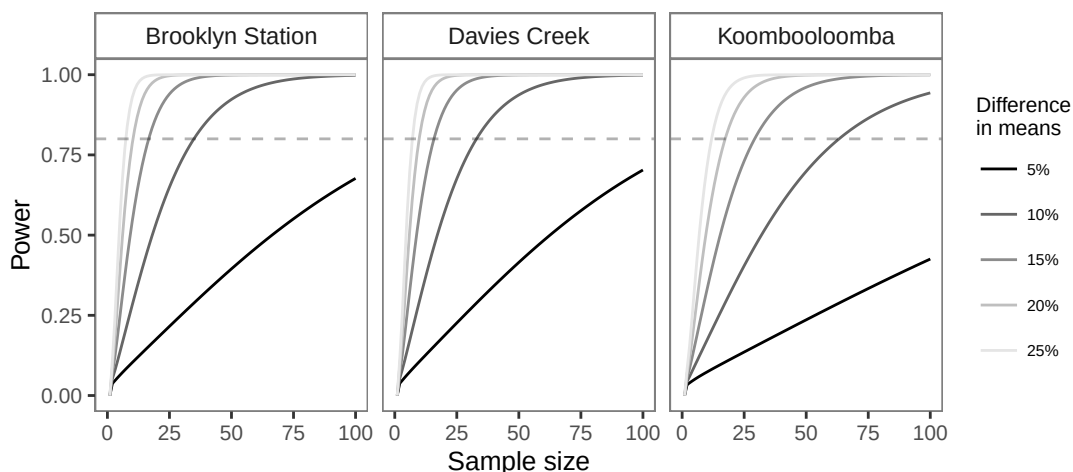


Figure 6.10: Power analysis of the number of samples required to estimate the plot mean within 5, 10, 15, 20, and 25% of the mean at the $\alpha = 0.05$ significance level and $b = 0.8$ (indicated by the dashed line).

(AGB) of the sites (Chapter 4) and, in the case of Koombooloomba, the high soil carbon (Chapter 5). Unfortunately, very few tropical savanna or grassland studies in the GDSR include AGB or ANPP and so a direct comparison is not possible. Nevertheless, the few studies in the GDSR that include soil carbon are similar to the sites in this study, *i.e.* Brooklyn Station and Davies Creek have comparable soil carbon contents to a group of sites with low soil carbon and Koombooloomba is comparable to a cluster of study sites with very high soil carbon.

An alternative possibility is that other studies have over-estimated the soil-derived carbon flux by failing to take spatial variability into account. As previously mentioned, the modelled plot level carbon flux is ~25% higher than the mean of the samples. Utilising the sample mean would place the soil-derived carbon flux for these study sites at an ‘average’ position for their respective climatic envelopes. Nonetheless, the soil-derived CO₂ exports in this study are similar to values reported for other Australian savannas in the Northern Territory, for example 14.3 t C ha⁻¹ y⁻¹ (Chen et al., 2002), 7.7 - 17.3 t C ha⁻¹ y⁻¹ (burnt and unburnt, respectively (Richards et al., 2012)) and 6.4 - 14.4 t C ha⁻¹ y⁻¹ (unburnt and burnt, respectively (Livesley et al., 2011)).

The seasonality of soil CO₂ export was slightly less pronounced than what has been reported for other Australian tropical savannas. For example, Chen et al. (2002) reported that soil respiration during the dry season in the Northern Territory constituted 30% of the total as compared to 32-34% for Brooklyn Station, 38-42% for Davies Creek, and 36-38% for Koombooloomba. The most pronounced difference

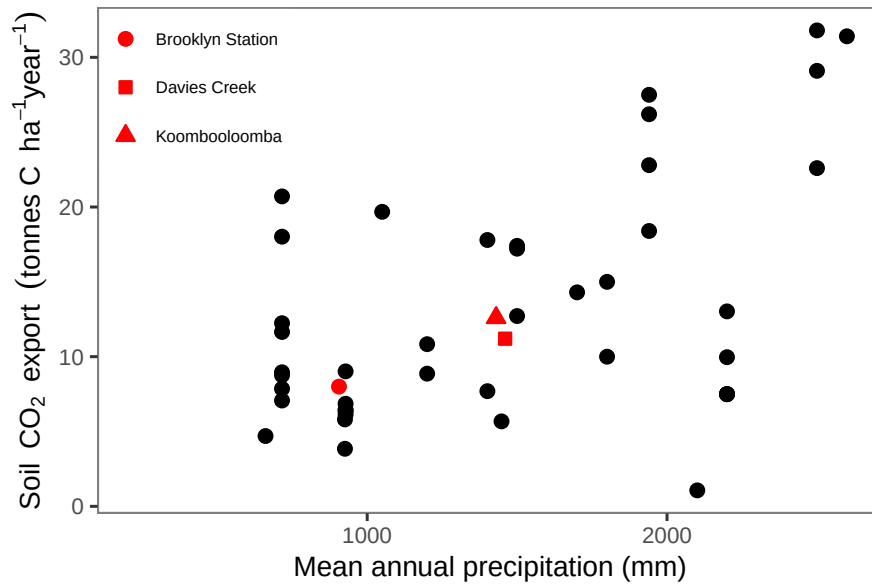


Figure 6.11: Annual soil-derived carbon export for Brooklyn Station (●), Davies Creek (■) and Koombooloomba (▲) and mean annual precipitation in comparison to other soil respiration studies • in tropical grasslands and savannas (Bond-Lamberty and Thomson, 2014)

between the sites used in this study and the savannas of the Northern Territory is the seasonality of precipitation and consequently the seasonality of vegetation growth. While approximately 95% of the annual rainfall falls during the summer months in the Northern Territory, the sites in this study are heavily affected by orographic rainfall that occurs throughout the year and as such, the winter rainfall can account for up to 35% of the annual total. As a result, there is a large amount of overlap between ‘wet season’ and ‘dry season’ moisture values, whereas the temperature differences are more distinct (Figure 6.2).

This also highlights issues associated with delineating the tropical climate into two distinctly different seasons when many more may be applicable. For example, recent work on documenting Indigenous ecological knowledge in Australia has identified the substantial variation in seasons across northern Australia with local groups identifying up to 13 different seasons, not all of which occur every year (Woodward et al., 2012).

In contrast to the other two sites, Brooklyn Station has much more distinct seasons and low soil moisture demonstrably constrained soil respiration at Brooklyn Station, irrespective of high soil temperatures (Figure 6.2). Nonetheless, rainfall outside of the dry season ‘limits’ does occur and even small rainfall events at the end of the dry season have a disproportionate influence on soil respiration. These responses are

likely microbial in nature, as these organisms can lie dormant throughout prolonged dry periods and quickly capitalise on short-term moisture availability and rapidly metabolise carbon substrates that have accumulated during the dry season. Similarly, any delay in the onset of the wet season rains will also introduce deviations from the seasonal norms as plants tend to require somewhat more sustained water availability in order to start their growing season.

6.5.4 Implications for climate change and the global carbon cycle

One of the most serious risks associated with climate change and the terrestrial carbon cycle is the possibility of warming accelerated decomposition of soil carbon, *i.e.* a net increase in heterotrophic respiration resulting in a net flux of carbon from the soil to the atmosphere (Davidson and Janssens, 2006; Rustad et al., 2000). Global soil respiration was estimated to be $98 \pm 12 \text{ Pg C y}^{-1}$ in 2008 (Bond-Lamberty and Thomson, 2010b), which is an order of magnitude greater than anthropogenic emissions from fossil fuels. Thus, even small increases in this rate will release large quantities of CO_2 to the atmosphere and accelerate global warming (Cox et al., 2000; Heimann and Reichstein, 2008). Global soil respiration increased by $\sim 0.1\% \text{ y}^{-1}$ between 1989 and 2008 and was correlated to an increase in temperature (Bond-Lamberty and Thomson, 2010b). However, it remains unclear if this constitutes a response to the increased temperature or a response to higher carbon inputs to the soil.

Increases in autotrophic respiration may be associated with, and therefore offset by, increases in GPP and NPP. In this study, Koombooloomba had the highest ANPP ($9.2 \text{ t C ha}^{-1} \text{ y}^{-1}$, Table 4.7) and was also associated with the highest soil respiration ($12.8 \text{ t C ha}^{-1} \text{ y}^{-1}$). Similarly, Brooklyn Station had the lowest ANPP ($4.1 \text{ t C ha}^{-1} \text{ y}^{-1}$, Table 4.7) and was also associated with the lowest soil respiration ($8.2 \text{ t C ha}^{-1} \text{ y}^{-1}$). In contrast, Davies Creek also had a low ANPP ($5.1 \text{ t C ha}^{-1} \text{ y}^{-1}$, Table 4.7), but it had high soil respiration. Autotrophic soil respiration depends on carbon assimilated during photosynthesis and heterotrophic soil respiration depends upon plant tissue substrates and, as such, both components of respiration should be constrained by GPP.

If the ratio of NPP to GPP or the carbon use efficiency (CUE) is constant then respiration should also be proportional to NPP when integrated over long timescales.

This is certainly a widely held belief regarding forests (DeLucia et al., 2007), but there is somewhat less research available regarding tropical savannas. Eddy covariance studies from a tropical savanna in the Northern Territory suggest that this is not the case at this site over time intervals of 2-4 years (Beringer et al., 2007; Moore et al., 2015). Furthermore, modelling studies by Zhang et al. (2014b) suggest that in fact CUE is linked to environmental variables and is thus vulnerable to climate change. They reported a decrease in the global CUE due to decreasing NPP and stable GPP, suggesting that respiration is increasing.

A contrasting perspective is that respiration is proportional to biomass in the same way that respiration scales to body size in animals (Reich et al., 2006b), in which case CUE will vary. In this study, the relative differences in soil respiration between sites were more closely associated with carbon stocks than they were with ANPP with the ratio of respiration to carbon stocks 0.22 for Brooklyn Station and 0.16 for both Davies Creek and Koombooloomba. Nevertheless, this is a simplification that does not take into account a number of omissions. Firstly, the estimates of ANPP do not include belowground productivity which could be up to three times the ANPP (Chen et al., 2003). Secondly, soil respiration includes heterotrophic respiration as well as autotrophic respiration, which may constitute 10-90% of total soil respiration (Hanson et al., 2000), although 50% is more probable (Chen et al., 2003). Finally, soil respiration, or even the autotrophic component of soil respiration, does not include leaf and stem respiration and this may represent approximately 25% of total soil respiration (Moore et al., 2015).

Inter-annual variability of soil respiration in seasonal ecosystems is often accounted for by inter-annual variability in precipitation, with above-average rainfall leading to above-average biomass production (Archibald et al., 2009; Hovenden et al., 2014; Rohr et al., 2013). A large source of inter-annual variation in precipitation (particularly in Australia) is driven by the El Niño Southern Oscillation (ENSO). The ENSO has three phases: El Niño, neutral and La Niña. Typically, El Niño events are associated with below average precipitation in northern and eastern Australia and a net source of carbon from terrestrial ecosystems. In contrast, La Niña events are associated with the reverse (Jones, 2001). For example, one of the strongest La Niña events on record occurred in 2010-2011 (Boening et al., 2012) and was associated with record increases in precipitation and plant productivity such that vegetation growth in Australia was responsible for approximately 60% of the global carbon sink anomaly for that year (Detmers et al., 2015; Poulter et al., 2014). In this study, carbon export was higher during the first study year (2010-2011) at both

Davies Creek and Koombooloomba, although the opposite was true for Brooklyn Station (Table 6.4). The influence of the ENSO on soil respiration has also been reported for Central America. For example, Schwendenmann et al. (2003) reported El Niño drought effects on soil respiration as indicated by restrictions on microbial activity and peaks in fine root mortality in neotropical rainforest, Costa Rica.

At Brooklyn Station however, higher than average precipitation during the 2010-2011 wet season did not result in correspondingly higher soil respiration. Rather, the soil respiration appeared to be more influenced by the fire at Brooklyn Station in July 2011 and the subsequent influence on moisture availability and substrate availability. During both measurement years the same pattern occurred at Brooklyn Station; early rains in October sparked high soil respiration rates, but a lack of rain in November and rising temperatures saw a return to dry season conditions and low soil respiration. This was followed by rainfall in December that continued until late March, which was accompanied by an abrupt and sustained increase in soil moisture during which time, soil respiration remained high. The most pronounced difference between the two study years relates to the soil moisture/soil respiration dynamics at the end of the wet season. There was a sharp transition between periods of high and low soil moisture/soil respiration during the first study year (Figure 6.2) that was followed by a more gradual return to dry season conditions in the second study year and this was not related to patterns of rainfall (Figure 6.9).

This discrepancy is likely due to the fire at the end of the 2010-2011 wet season at Brooklyn, which eliminated the thick layer of senesced grass and thereby increased evaporation. As a result, the soil column dried sooner than it would otherwise have and this may have restricted heterotrophic respiration. Furthermore, fire has been observed to immediately reduce soil respiration due to a combination of high temperatures damaging metabolic processes in both plants and microorganisms and also due to a reduction in organic matter as a result of fuel consumption (Andersson et al., 2004; Castaldi et al., 2010; Savadogo et al., 2012). Similarly, by eliminating the thick senesced grass cover, fire facilitates the rapid regeneration of the grassy understorey the following wet season, resulting in higher contributions of root respiration during the second wet season.

In addition, ash and other fire products provide an easily colonised substrate for soil microfauna (Andersson et al., 2004) and fires enhance litterfall (Chapter 4), resulting in more inputs to the soil. The same pattern was reported by Livesley et al. (2011) who reported that fire resulted in an immediate reduction of soil respiration, but this was followed by an increase in soil respiration the following wet season, in comparison

to a neighbouring unburnt plot. This resulted in a higher soil CO₂ export from the burnt plot with annual soil fluxes from burnt and unburnt savanna of 14.4 and 12.1 t C ha⁻¹ y⁻¹ respectively. This contrasts with results by Richards et al. (2012) who reported that a burnt savanna showed a negligible increase in soil respiration the following wet season, compared to an unburnt savanna where soil respiration increased three-fold. The study site used by Richards et al. (2012) was subject to annual burns for 6 years prior to the study. While Livesley et al. (2011) did not report the full fire history of their study site they did conclude that prolonged annual burning regimes were required to significantly reduce soil CO₂ export. Both authors agreed that this phenomenon is facilitated by a reduction in plant productivity and a consequential reduction in root respiration.

The close association between respiration and plant productivity means that soil respiration is also sensitive to climate change induced changes as a result of shifts in the dominant vegetation and/or ecosystem. For example, Raich and Tufekciogul (2000) reported that forest stands had ~20% higher soil respiration than comparable grasslands on the same soil type. Furthermore, a review by Metcalfe et al. (2011) suggests that shifts in the dominant species towards rapidly growing species with nutrient rich litter would provide yet another positive feedback to climate change. Thus, impacts of climate change including increased temperature, changes to precipitation, and changes to the frequency and intensity of stochastic events such as storms and fire that effect plant productivity and biomass as discussed in Chapter 4, will also impact upon soil respiration. Unfortunately, the relative magnitude and importance of each of these impacts remains too complex to be disentangled at present.

6.6 Conclusions

Soil respiration reflected the seasonal nature of tropical savannas, with higher fluxes during the wet season and lower fluxes during the dry season. This was ultimately constrained by climatic limitations to biological processes, *i.e.* plant production and microbial decomposition. The relative influence of temperature and water differed between the sites, with temperature being the dominating driving force at Koombooloomba and soil moisture being the dominating driving force at Brooklyn Station, while Davies Creek tended to be moderated by both. The primary spatial determinant of soil respiration was the proximity to nearby trees. The presence of woody vegetation alters autotrophic respiration through changes to root density

and variations in allocation patterns between trees and grasses, as well as soil chemical properties such as soil carbon and nitrogen abundance that alter the location of heterotrophic respiration. The presence of trees also alters the soil structure and provides preferential diffusion pathways for all sources of soil CO₂. While the GAMM generally provided an unbiased estimate of soil respiration, it performed poorly at extreme values of soil fluxes although the overall influence of this bias on soil flux estimates is likely to be low. Nonetheless, the modelled estimates here are lower than expected for these sites, which could be an artefact of the model bias or could represent a sampling bias inherent in studies that fail to take the spatial variation of savanna vegetation into account. The soil -derived CO₂ carbon export of 8.2, 11.7, and 12.8 t C ha⁻¹ y⁻¹ for Brooklyn Station, Davies Creek, and Koombooloomba, respectively appears to be linked to the AGB of each of these sites as opposed to the productivity. However, inter-annual variability in soil respiration does appear to be influenced by inter-annual variability in precipitation (and therefore productivity). This reinforces the hypothesis that climate determines temporal trends while vegetation determines spatial trends at both the seasonal/plot scales and annual/ecosystem scales. Plot level soil CO₂ export is influenced by both climate and disturbance and as such is likely to be significantly altered by global warming.

Chapter 7

The influence of simulated drought on soil respiration and soil chemistry at a tropical savanna site

Statement of contribution

Conceptualised by Kalu Davies and Michael Bird.

Written by Kalu Davies.

Fieldwork by Kalu Davies with assistance from Michael Limpus, Samuel Reiseger and Raziel Rasmus-Retara.

Data analysis and interpretation by Kalu Davies with advice from Paul Nelson and Michael Bird.

Edited by Kalu Davies and Michael Bird with advice from Michael Liddell and Paul Nelson.

7.1 Abstract

Increasing atmospheric greenhouse gas concentrations lead to changes in the hydrological cycle, with the tropics likely to experience an increase in the seasonality of rainfall. Of further concern is a general drying trend in the Southern Hemisphere as well as a more active and intense monsoon. The effects of drought on soil respiration in tropical savannas remain largely unstudied. In this study, two clear vinyl tents were placed over sections of a tropical savanna in Queensland and soil respiration was compared to nearby control locations for two years. The drought tents were successful in reducing the soil moisture (mean of 3.6%) compared to the control (mean of 11.6%) but did not affect soil temperature or relative humidity at the soil surface and had a variable impact on soil respiration rates. Soil CO₂ export from the drought treatment was reduced in the first wet season relative to the control, but the opposite was true for the second wet season. Nonetheless, cumulative soil respiration in the drought treatment was reduced by 0.8 t C ha⁻¹ over the course of the experiment, as compared to the control. Reduced soil respiration in the drought treatment may have been associated with a delay to the growing season of the grass as a result of the reduction in soil moisture. Higher soil carbon in the drought tents (mean of 70 t C ha⁻¹) compared to the control (mean of 47 t C ha⁻¹) suggest that there were additional inputs to the soil carbon pool, presumably due to the death of the grass in the the second year of the experiment. The death of the grass also coincided with increased soil respiration in the drought tent during the second wet season. Furthermore, soil respiration, normalised to the carbon content of the soil, was lower in the drought treatment. Extrapolating from these results, we could see shifts in species and ecosystems as a result of extended droughts, potentially accompanied by an increase in soil respiration before ecosystem stability is reached.

7.2 Introduction

Increasing atmospheric greenhouse gas concentrations lead to higher average global temperatures, higher evaporation rates and more water vapour in the atmosphere (Wentz et al., 2007). This in turn will lead to changes in the hydrological cycle, with an increase in rainfall in some areas and a decrease in rainfall in others (Fischer et al., 2013; Karl and Trenberth, 2003). In the tropics, these changes are expected to result in an increase in the seasonality of rainfall with changes to the timing, duration and magnitude of rainfall events (Feng et al., 2013). Of further concern is a general

drying trend in the Southern Hemisphere that has led to a reduction in net primary productivity (NPP) and an increase in severe regional droughts during the period 2000 - 2009 (Zhao and Running, 2010). While summer rainfall in northern Australia is reported to have increased in the 50 years since 1952 (Smith, 2004), this increase is associated with a more active and intense monsoon (Evans et al. 2014) resulting in a higher frequency of intense rainfall events, as well as longer dry seasons (Shi et al., 2008). Furthermore, summer rainfall has decreased in northeast Australia over the same time period (Li et al., 2012) with an associated increase in drought that is projected to continue into the future under a range of climate scenarios (Makuei et al., 2013; Mpelasoka et al., 2008).

Tropical savannas are naturally seasonal by nature and experience prolonged seasonally dry periods as a matter of course. As a result, the vegetation of these regions has evolved methods of adapting to low moisture conditions. For example, some *Eucalyptus* species are able store and transport water more efficiently than other tree species by accessing water both from deep subsoil layers and the capillary fringe of the water table (Hutley et al., 2000). Consequently, they are able to continue to assimilate carbon throughout the dry season (Beringer et al., 2007; Bucci et al., 2004; Moore et al., 2015). Grasses that use the C₄ photosynthetic pathway are similarly adapted to warm environments as a result of their leaf traits and root architecture which offer a competitive advantage in high temperature/low moisture environments (Cerling et al., 1997; Edwards and Smith, 2010; Ludlow, 1980).

Nonetheless, inter-annual variation in both gross primary productivity (GPP) and NPP tends to be dominated by inter-annual variation in precipitation and the occurrence of drought (Chen et al., 2013; Kanniah et al., 2013), particularly in the arid and semi-arid areas (Cleverly et al., 2016; Huang et al., 2016). For example, almost 60% of the 2011 global carbon sink anomaly was accounted for by above average NPP in northern and central Australia as a result of above average rainfall (Poulter et al., 2014). Similarly, prolonged below average rainfall can result in tree mortality that converts forests into savannas and savannas into deserts (Allen et al., 2010a; Anadón et al., 2014; Gonzalez, 2001) through substantial changes to the prevailing fire regime (Scheiter et al., 2014). These processes can result in these ecosystems becoming a substantial carbon source to the atmosphere (Grace et al., 2014).

Under current climatic conditions, Australian savannas act as a weak carbon sink (Beringer et al., 2007; Moore et al., 2015), but this is sensitive to changes in management including fire frequency and intensity, grazing pressures and the impact of invasive species (Cook et al., 2010; Dean et al., 2012; Hunt, 2014). Soil respi-

ration is the dominant flux by which carbon is returned to the atmosphere and while autotrophic (plant-derived) respiration tends to be coupled with photosynthesis and large scale precipitation patterns (Williams et al., 2009), heterotrophic respiration is much more sensitive to short-lived and/or small precipitation events (Fierer and Schimel, 2002; Huxman et al., 2004). During the dry season low soil moisture restricts microbial function and decreases microbial biomass (Butler et al., 2011) resulting in labile carbon and inorganic nitrogen accumulating in/on the soil as a result of inputs such as litterfall, root senescence, disruption of soil aggregates, and microbial death (Austin et al. (2004b) and references therein).

The carbon storage capacity of tropical savannas lies largely belowground, with up to 70% of the carbon stock present in the form of plant roots and soil carbon (Chen et al., 2003). Conceptually, arid savanna ecosystems should benefit from more extreme precipitation events as deep infiltration increases, but more mesic savanna systems are likely to suffer moisture stress more often with an increase in precipitation variability (Knapp et al., 2008). Although plant death will decrease autotrophic respiration, it also results in increased substrate for microbial decomposition, leading to a temporary increase in heterotrophic respiration. In addition, increased temperatures could lead to the decomposition of existing soil carbon stocks, resulting in a positive feedback loop that will further exacerbate warming (Bird et al., 1999; Davidson et al., 2006).

The importance of drought as a modulator of the global carbon cycle rose to prominence following the 2003 heat wave and drought in Europe that reversed four years of net ecosystem carbon accumulation. This has triggered an increase in studies examining the effects of simulated drought on temperate grasslands (Burri et al., 2015), subtropical grasslands (Hoover et al., 2016), mediterranean savannas (Pereira et al., 2007), and tropical rainforests (Cleveland et al., 2010; Davidson et al., 2004; Zhang et al., 2015), with excellent syntheses provided by Vicca et al. (2014) and Estiarte et al. (2016). However, no published attempts have been made to characterise the influence of drought in tropical savannas, despite evidence that droughts are severely affecting these ecosystems (Eamus et al., 2013a; Fensham et al., 2015; Rice et al., 2004).

This study aims to disentangle some of the complexity surrounding the influence of soil moisture on soil respiration in an Australian tropical savanna through the implementation of a closed shelter drought experiment over two years. Specifically, this study will address the following research questions:

1. What is the effect of reducing soil moisture (simulating drought) on soil respiration?
2. What effect does simulated drought have on soil carbon and soil chemistry?
3. What effect does simulated drought have on carbon export?

7.3 Methods

The experiment was conducted at the Davies Creek site that is described in detail in Chapter 3.

7.3.1 Experimental design

This experiment was conducted on a subset of the measurements detailed in Chapter 5 and follows the same sampling design. Briefly, this consists of a series of transects between adjacent trees with seven soil collars positioned on each transect. Four of the total number of transects available were used for this experiment with drought tents placed over two of the transects and the other two acting as a control. The collar positions are grouped according to proximity to the tree and the canopy cover above the soil. These groups were: ‘tree’ (adjacent to the tree trunk), ‘mid-canopy’ (positioned below the middle of the tree canopy), ‘dripline’ (at the edge of the canopy) and ‘grass’ (equidistant from each tree). The ‘tree’ groups were not included in this study as they were deemed too close to the edge of the drought tent to be sufficiently influenced by the presence of the tent and the ‘tree’ measurements were similarly discarded from the control transects. This issue arises because the tent is attached to the tree and does not sit flush against the trunk. This places the ‘tree’ sampling locations at the edge of the tent and subject to more rainfall, as well as higher flow down the outside of the stem during rain events, than the other sampling locations in the drought treatment.

In September 2011 (at the end of the dry season), two rainfall reduction tents were established at the Davies Creek site over two of the transects. Each shelter encompassed the gap between trees, sheltering an area 2 m wide by 12-14m long. The eaves of the shelters were 0.3 m above the ground and the ridge height was 1 m, allowing free flow of local air. The shelters were constructed out of clear, 1 mm, UV-transparent vinyl with gaps every 1-2 m to allow air movement and to enable

some precipitation to enter the tents (Figure 7.1). Each tent contained 5 stainless steel collars arranged in a line between the trees, commencing at least 1 m from the end of the tent. An additional 10 collars similarly arranged between trees in two transects, formed the non-droughted control.



Plate 7.1: One of the drought tents.

7.3.2 Soil respiration and environmental variables

Soil respiration and environmental variables (soil temperature, soil moisture, relative humidity and air temperature) were measured throughout the experiment. Soil respiration was measured using a LiCor-8100 portable infrared gas analyser (LiCor, Inc., Lincoln, NE, USA) connected to a 10 cm closed survey chamber and measurements were made every 1-5 weeks from November 2011 until June 2013. In order to avoid systematic bias as a result of diurnal variation in soil respiration, the measurements were alternated between the two treatments. In addition, relative humidity (%) at the soil surface, is also recorded by the LiCor-8100 at the time of the CO₂ measurement.

Soil moisture was measured approximately 5 cm away from each collar following the CO₂ efflux measurement using a Hydrosense II soil moisture sensor (Campbell

Scientific, Inc., North Logan, UT, USA) at a depth of 0-12 cm. The volumetric water content was converted to water filled pore space (wfps) using the equation:

$$wfps = \frac{\theta}{(1 - (\frac{\rho B_{soil}}{\rho B_{quartz}}))}$$

where θ = volumetric water content (%), ρB_{soil} = bulk density of soil (g cm^{-3}) and ρB_{quartz} = the bulk density of quartz (2.65 g cm^{-3}). Soil temperature was measured at 10 cm depth approximately 5 cm from each collar using a soil temperature probe (type E) connected to the auxiliary sensor port of the Licor.

Furthermore, dataloggers (XR5-SE; Pace Scientific, NC, USA) were installed at the site approximately 50 m from the experiment for recording rainfall (rainfall sensor RS-100; Pace Scientific) under the canopy and soil moisture (soil moisture sensor Echo EC-10; Degagon, WA, USA) at 10 and 30 cm soil depths at half-hourly intervals. Further details are described in (Zimmermann et al., 2015).

7.3.3 Soil sampling and analysis

In June 2013, following completion of the experiment, the soil within each collar was sampled for analysis of C and N content as well as $\delta^{13}\text{C}$ as detailed in Chapter 5. In addition, the soils were also analysed for pH, electrical conductivity (EC), effective cation exchange capacity (ECEC), exchangeable cations (Na^+ , K^+ , Ca^{2+} , Mg^{2+}), $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$ and Colwell P by Analytical Research Laboratories (Napier, New Zealand). Soil pH was measured in H_2O and 0.01 M CaCl_2 using a pH meter and 1:2.5 soil weight: extractant volume ratio. The EC was determined by a conductivity meter on 1:2.5 soil: water suspension. Exchangeable cations were determined using 1 M ammonium acetate extraction buffered at pH 7 for 30 minutes and atomic absorption analysis and ECEC was calculated as the sum of the exchangeable cations (Rayment et al., 1992). Soil $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ were determined colorimetrically by an automated photometer using 1 M KCl extraction method (Rayment and Lyons, 2011) and phosphorus was determined according to Colwell (1963).

In order to ascertain root biomass, a 2m x 1m trench located between the treatments was excavated to 5 cm depth and all the soil was collected. This was passed through a 5mm sieve to remove large roots and clumped grass roots. These roots were washed and sorted into size classes: fine roots ($<2 \text{ mm}$), coarse roots ($>2 \text{ mm}$), grass rhizomes and organic debris. The remaining soil was washed and all organic

material floated out. The remaining mixture was passed through a 2 mm sieve. A subsample of the fine material was separated by hand into very fine roots and other debris. All samples were oven dried at 60°C to a constant mass.

7.4 Results

7.4.1 The influence of drought on soil respiration

Averaged across the entire study period, soil respiration was higher and relative humidity at the soil surface was lower in measurements taken beneath the drought tents ($n = 305$) as compared to the control ($n = 308$) and differences were significant ($p = 0.05$). Soil temperature was equal between the two treatments during the soil respiration measurements but there was a significant ($p < 0.001$) decrease in soil moisture beneath the drought tents (Table 7.1). Air temperature as measured during the respiration measurements did not differ between treatments (data not shown).

Immediately following the emplacement of the drought tents, there was an abrupt decrease in the average soil respiration in the drought treatments of approximately $1 \mu\text{mol m}^2 \text{s}^{-1}$ of CO_2 (Figure 7.1). This difference continued from October 2011 through the wet season to February 2012, after which time soil respiration began to increase in the drought treatments relative to the control, becoming substantially higher during March and April of 2012. After this time, soil respiration was equal between the treatments until the following wet season. While lower average soil respiration was measured in the drought tents in January 2012, soil respiration rates rose sharply during the following months and remained substantially higher in the drought treatments for the remainder of the experiment (until April 2013).

In contrast to the CO_2 measurements, the emplacement of the drought tents resulted in an immediate increase in soil temperature of 2-3 °C (Figure 7.1). Following February 2012, the soil temperatures were equal between the two treatments with the exception of a few isolated occasions: April 2012 (late wet season) and December 2012 (early wet season) where soil temperature was lower in the drought treatment, and June 2012 (mid dry season) where the reverse was true. Differences were $< 3^\circ\text{C}$ with the exception of June 2012 when average soil temperature was 4.5°C higher in the drought treatment.

Table 7.1: Soil respiration, temperature, moisture, and relative humidity of air throughout the study for the drought treatment and the control. Values are mean $\pm$ s.d. Significant differences between treatments are denoted by * ($p = 0.05$) and ** ($p < 0.001$.)

	Control	Drought
Soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	$2.6 \pm 0.1^*$	$2.8 \pm 0.1^*$
Soil temperature ($^{\circ}\text{C}$)	25.0 ± 0.2	25.2 ± 0.2
Soil moisture (% wfps)	$11.6 \pm 0.5^{**}$	$3.6 \pm 0.2^{**}$
Relative humidity (%)	$66.4 \pm 1.1^*$	$62.7 \pm 1.1^*$

The emplacement of the drought tents occurred at the end of the dry season when soils were already dry and as such, there was no immediate substantial decrease in soil moisture in the drought tent as compared to the control (Figure 7.1). Following the onset of the summer rains (January - February 2012), soil moisture in the control spiked sharply and was generally $>10\%$ wfps while soil moisture in the drought tents remained $<10\%$ wfps for the duration of the wet season. The exception to this occurred in late March 2012 when mean soil moisture in the drought tent peaked at 13% wfps, the highest moisture content recorded in the drought tent during the experiment. Soil moisture was equal between the two treatments from September - December 2012, remaining $<2\%$ wfps in both treatments. Following the onset of the second wet season (January - February 2013), soil moisture in the control rose sharply and differences between the two treatments were similar to the first wet season such that the control tended to $>10\%$ wfps and the drought tended to be $<10\%$ wfps.

In contrast to soil moisture, there was not such a noticeable difference in relative humidity between the two treatments. When measurements were not equal, the drought tents had a lower humidity and this was consistent throughout the experiment. The maximum difference between the treatments was measured in September 2012, when humidity was 2% higher in the control as compared to the drought treatment.

Although biomass was not measured within the drought tents so as not to disturb the experiment, grass biomass was visually estimated as equivalent between the two treatments at the beginning of the experiment, at which time the grasses were

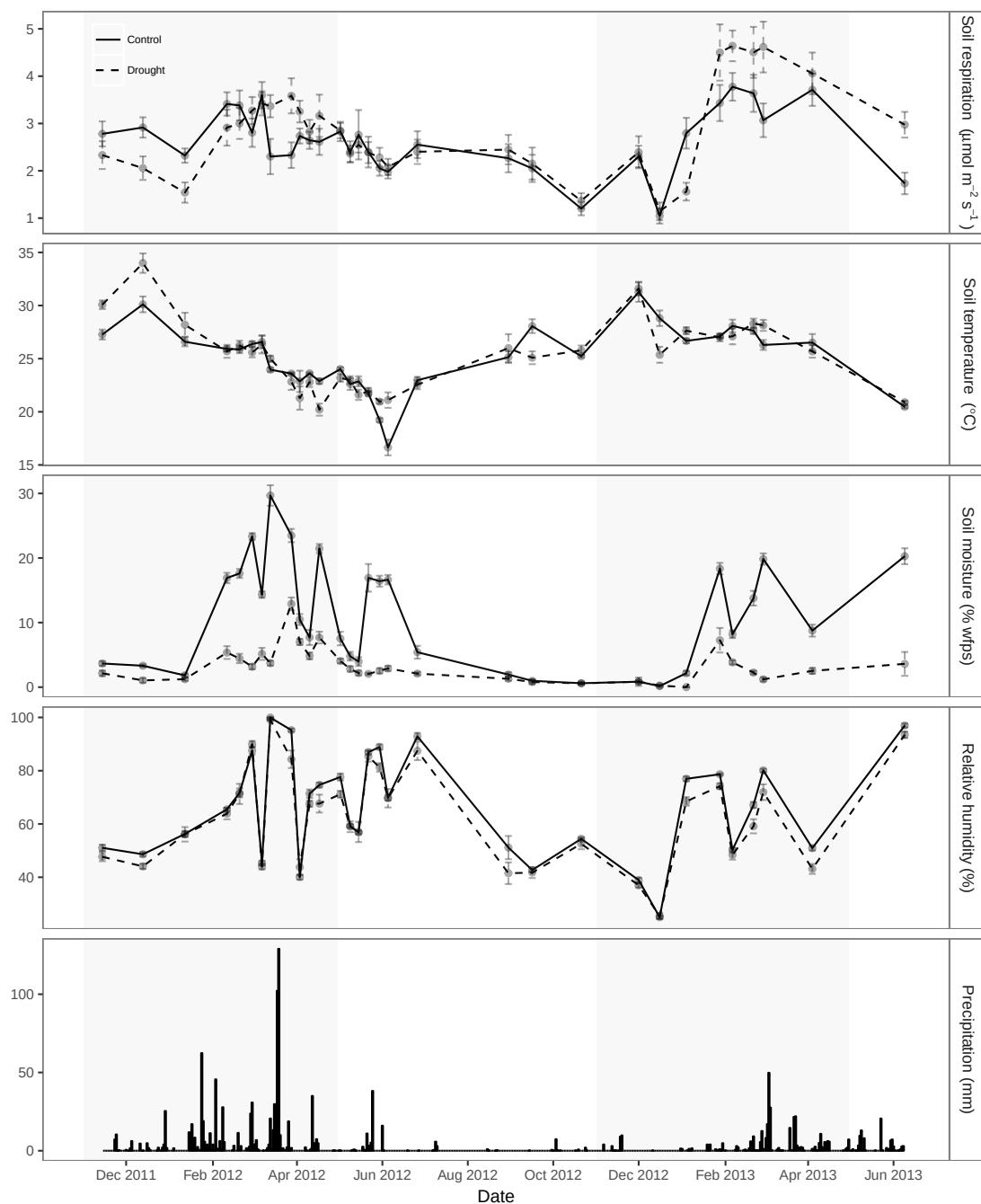


Figure 7.1: Soil respiration, temperature, moisture, relative humidity at the soil surface, and precipitation for measurements beneath the drought tent (dashed line) and the control (solid line) for the duration of the drought tent experiment. Wet season (November to April) is shaded for clarity.

largely senesced. During the first wet season, the grass in the drought tent re-sprouted as normal, albeit 2-3 weeks later than the control, and the grass in both treatments senesced during the following dry season. In contrast, during the second wet season, the grass in the drought treatment did not regrow and continued to senesce to apparent total plant death (Plate 7.2).



Plate 7.2: One of the drought tents showing the dead grass

7.4.2 Soil chemistry

Soil carbon, $\delta^{13}\text{C}$, C:N ratio and Colwell phosphorus for surface soils (0-5 cm depth) and subsurface soils (5-30 cm depth) are shown in Figure 7.2 for both the drought treatment and control, sampled at the end of the experiment. Soil carbon was significantly higher in surface soils (0-5 cm depth) than subsurface soils (5-30 cm depth) for both the drought and the control ($p < 0.001$). Soil carbon was also significantly higher in the control than in the drought treatment ($p = 0.01$) and this was consistent across both depths. $\delta^{13}\text{C}$ value was significantly lower in the surface soils ($p = 0.01$) and significantly lower in the drought treatment ($p = 0.05$). The C:N ratio is significantly higher in the surface soils of the control, but the subsurface control soils are comparable to the surface and subsurface soils of the drought treatment ($p = 0.05$). Phosphorus was significantly higher in the surface soils for both

treatments ($p = 0.001$) and tended to be higher in the drought treatment for the surface soils only, though differences were not significant. There was no discernible difference in phosphorus between treatments for the subsurface soils.

Soil nitrogen, $\delta^{15}\text{N}$, NH_4^+ and NO_3^- for surface soils (0-5 cm depth) and subsurface soils (5-30 cm depth) are shown in Figure 7.3. Soil nitrogen was significantly higher in surface soils (0-5 cm depth) than subsurface soils (5-30 cm depth) for both the drought and the control ($p < 0.001$). Soil nitrogen was also significantly higher in the control than in the drought treatment ($p = 0.05$) and this was consistent across both depths. The $\delta^{15}\text{N}$ values displayed greater within-treatment variation than between-treatment variation, but this trend only holds for the surface soils. All soils were more enriched in $\delta^{15}\text{N}$ at depth than the surface soils. At depth, the drought soils had consistently more depleted $\delta^{15}\text{N}$ values than the control soils. $\text{NH}_4^+\text{-N}$ was consistently higher in the surface soils in the drought treatment, but the same could not be said for soils at depth and there were no discernible differences in $\text{NO}_3^-\text{-N}$ in either surface or subsurface soils.

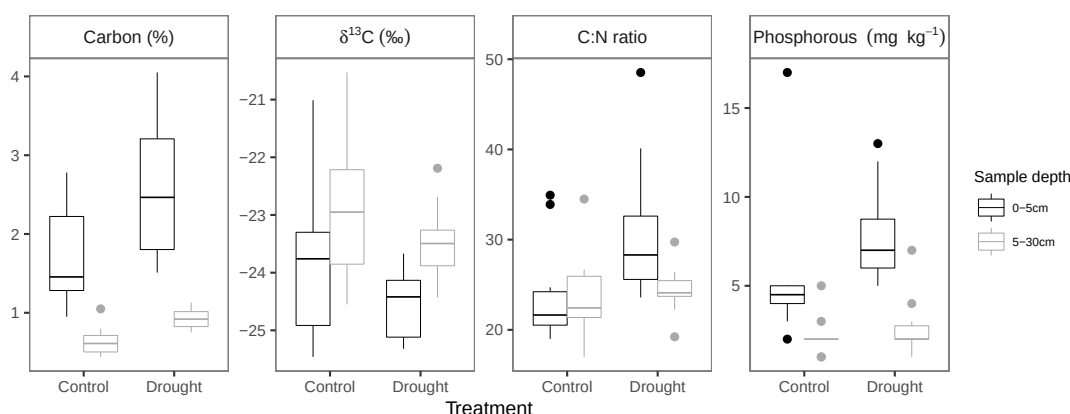


Figure 7.2: Soil carbon, $\delta^{13}\text{C}$, C:N ratio, and Colwell phosphorus for the control and drought treatments at 0-5 cm sample depth (black) and 5-30 cm sample depths (grey). Boxes indicate the interquartile range (IQR) of the data, hinge indicates the median value and the whiskers extend to 1.5 times the IQR. Values beyond the whiskers are plotted as outliers.

Soil pH, effective cation exchange capacity (ECEC), and exchangeable cations (EC) are shown in Figure 7.4 for the surface soils (0-5 cm depth) and subsurface soils (5-30 cm depth). There was no significant difference in pH between sample depths or treatments although pH tended to be slightly lower in the drought soils and slightly lower in the surface soils. Both ECEC and EC were significantly higher in surface soils as opposed to subsurface soils ($p = 0.001$). In addition, EC was significantly higher in the drought treatment for the surface soils ($p = 0.01$) although there was

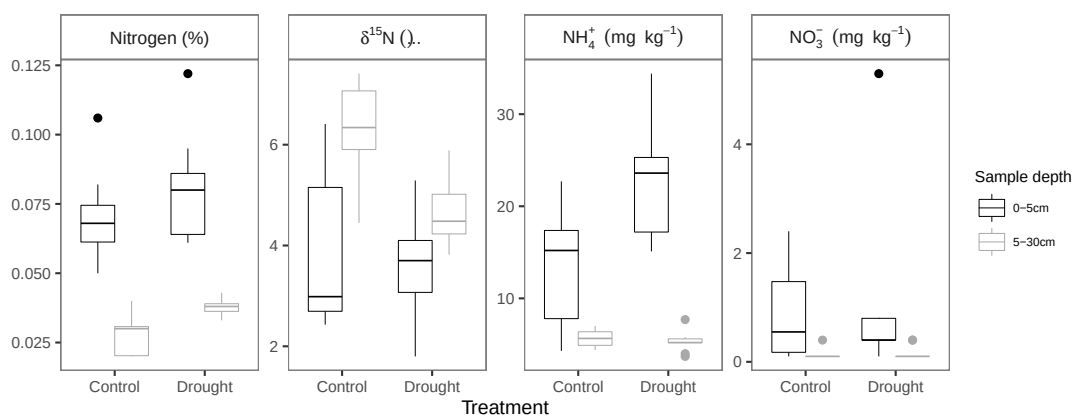


Figure 7.3: Soil nitrogen, $\delta^{15}\text{N}$, NH_4^+ , and NO_3^- for the control and drought treatments at 0-5 cm sample depth (black) and 5-30 cm sample depths (grey). Boxes indicate the interquartile range (IQR) of the data, hinge indicates the median value and the whiskers extend to 1.5 time the IQR. Values beyond the whiskers are plotted as outliers.

no discernible difference in the subsurface soils.

Exchangeable cations (Ca^{2+} , Mg^{2+} , K^+ and Na^+) are shown in Figure 7.5 for the surface soils (0-5 cm) and subsurface soils (5-30 cm). Sodium and potassium were both significantly higher in the drought treatments and significantly higher in the surface soils ($p = 0.001$). Calcium and magnesium were both significantly higher in the surface soils ($p = 0.001$) but there was no significant difference between treatments.

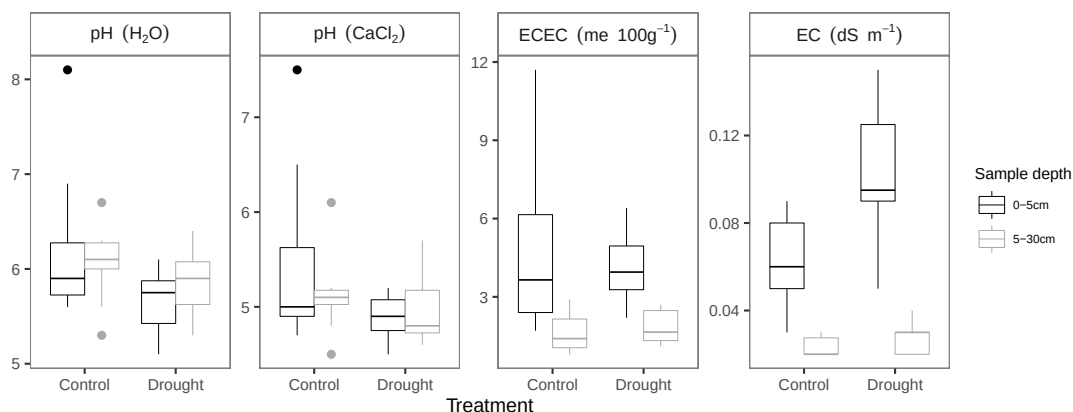


Figure 7.4: pH (H_2O), pH (CaCl_2), ECEC and EC for the control and drought treatments at 0-5 cm sample depth (black) and 5-30 cm sample depths (grey). Boxes indicate the interquartile range (IQR) of the data, hinge indicates the median value and the whiskers extend to 1.5 time the IQR. Values beyond the whiskers are plotted as outliers.

The excavation of the top 5 cm soil from 2m^2 determined that the soil contained 20 g m^{-2} of very fine roots, 50 g m^{-2} of fine roots, 90 g m^{-2} of grass rhizomes, 25 g m^{-2}

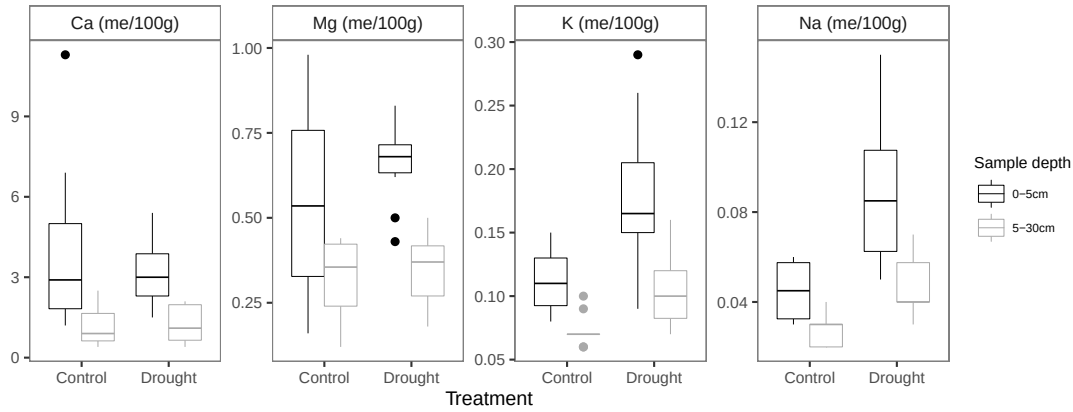


Figure 7.5: Exchangeable cations Ca^{2+} , Mg^{2+} , K^{+} and Na^{+} for the control and drought treatments at 0-5 cm sample depth (black) and 5-30 cm sample depths (grey). Boxes indicate the interquartile range (IQR) of the data, hinge indicates the median value and the whiskers extend to 1.5 time the IQR. Values beyond the whiskers are plotted as outliers.

of coarse roots and 6.5 g m^{-2} of litter and stems.

The soil moisture profile at the site weather station for 10 cm and 30 cm soil depths is shown in Figure 7.6.

7.5 Discussion

7.5.1 The impact of the drought tents on environmental variables

Over the course of the study, the emplacement of the drought tents did not affect soil temperature but resulted in a substantial and sustained decrease in soil moisture (Figure 7.1), particularly during the wet season, thus the main control variable in the experiment was successfully implemented. Soil moisture during the 2011 dry season was $8 \pm 7\%$ wfps in the control and $2 \pm 1\%$ wfps in the drought (mean $\pm$ s.d.). The drought tents did not negate wet season moisture entirely, with mean measurements as high as 13% wfps and individual measurements as high as 20% wfps compared to 30% wfps and 40% wfps respectively in the control. Soil moisture in the control averaged $14 \pm 9\%$ wfps during the 2011-2012 wet season and $10 \pm 7\%$ wfps during the 2012-2013 wet season (mean $\pm$ s.d.), which is consistent with higher rainfall during the 2011-2012 wet season as compared to the 2012-2013 wet season (Figure 6.9, see Chapter 6 for details). In contrast, soil moisture in the drought tent

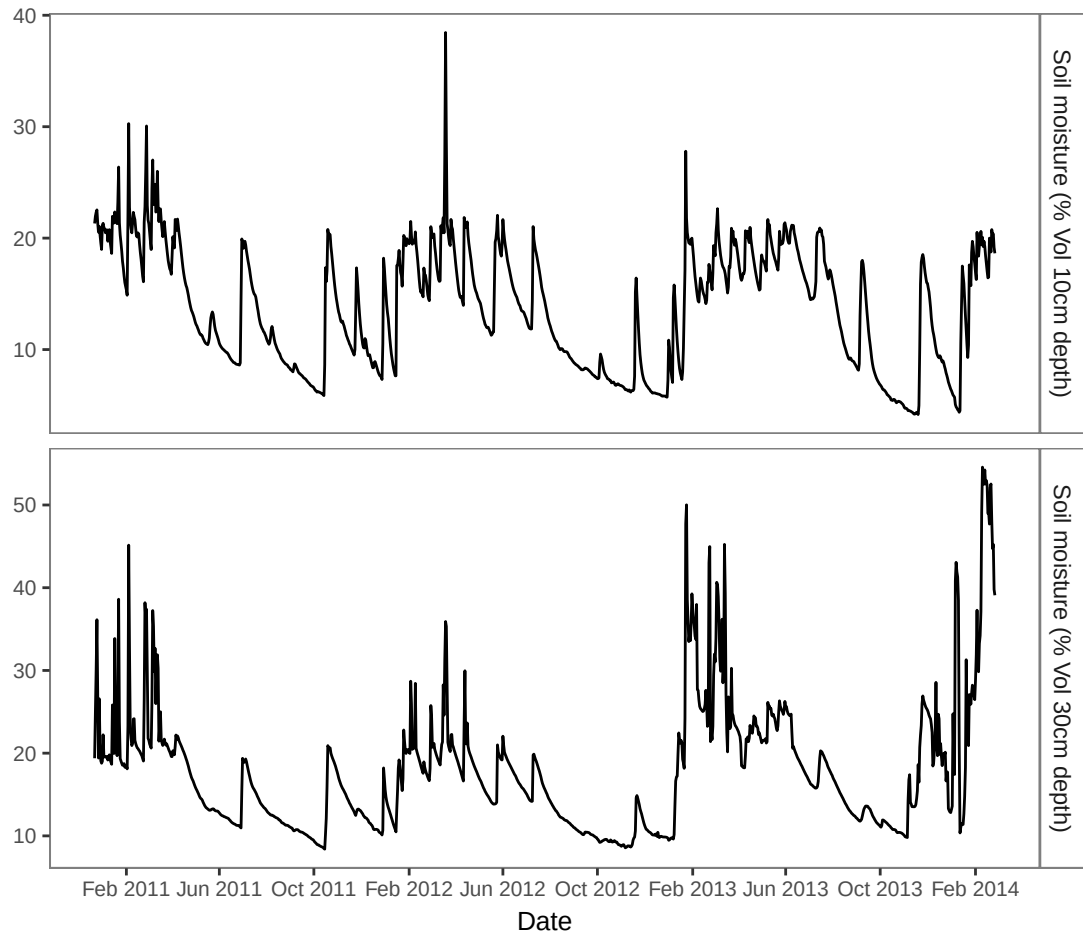


Figure 7.6: Comparison of volumetric soil moisture at 10 cm depth (top) and volumetric soil moisture at 30 cm depth (bottom) as recorded by an onsite weather station at the Davies Creek site.

averaged $2 \pm 1\%$ wfps during the 2011-2012 wet season and $5 \pm 4\%$ wfps during the 2012-2013 wet season (mean $\pm$ s.d.).

Despite the substantial reduction in soil moisture during the 2011-2012 wet season, the grass in the drought treatment regrew during the 2011 dry season. This is to be expected because savanna grasses are adapted to growth in low moisture conditions. For example, transpiration in *T. triandra* is not affected until soil potential falls below -2.0MPa (Snyman, 1994) and photosynthesis does not cease until soil potential drops below -6.0MPa (Snyman et al. (2013) and references therein). In a sandy soil such as that at Davies Creek, this broadly corresponds to a soil moisture content of $\sim 7\%$ wfps (Hodnett and Tomasella, 2002). In this study, soil moisture did not consistently drop below these values until late into the 2011 dry season (Figure 7.1). Similarly, a review by Unger and Jongen (2014) concluded that a reduction in rainfall had less impact on productivity and soil respiration in mesic savannas

compared to arid savannas at the ecosystem level.

Although soil moisture appeared to be very low throughout the dry season, it is possible that the measured soil water content at 12cm depth was not an accurate representation of plant available water. Plant available water is a function of the water potential of the soil over time as the moisture moves through the root zone and is difficult to predict using a single index (Walker and Langridge, 1997). As the drought tents had no impact on relative humidity, with humidity in both treatments closely tracking the soil moisture of the control, this suggests that surface moisture as a result of dew would also be present in both treatments. However, this level of moisture is unlikely to percolate to the depth of the soil moisture sensor and will instead be intercepted by shallow roots as well as lost to evaporation.

Furthermore, it is possible that rainfall events rapidly infiltrate through the coarse soil and are stored at deeper, yet plant available, soil depths. This is consistent with the inverse texture hypothesis (Noy-Meir, 1973). For example, Danckwerts and Stuart Hill (1988) reported that drought induced mortality of *T. triandra* was lower on sandy soils as a result of increased infiltration. In their study, *T. triandra* was reported to have twice the density of roots at depths of 20-40 cm than other grasses at the site and consequently rainfall that infiltrated to this depth would be preferentially available to this species. It is possible that such a phenomenon occurred at the Davies Creek site as the soil moisture at 30 cm was consistently higher than soil moisture at 10 cm as measured by an onsite weather station (Figure 7.6) further suggesting that surface soil moisture may not be indicative of plant available water.

Nonetheless, following the 2011 dry season, the grasses within the drought tent fully senesced and did not resprout with the onset of the wet season. The grasses at Davies Creek are dominated by the perennial tussock grasses kangaroo grass (*Themeda triandra* Forssk.) and giant spear grass (*Heteropogon triticeus* (R.Br.)). Although both dominant grass species are adapted to seasonal rainfall, they are not drought specialists. For example, several experiments have shown that drought makes *T. triandra* more susceptible to grazing death (Mott et al., 1992; Stokes et al., 2005). Furthermore, *H. triticeus* reportedly prefers fine textured soils and only grows in sandy soils in high rainfall areas such as Davies Creek (Hooker 2010). *T. triandra* is not drought resistant (Snyman et al. (2013) and references therein) and has become locally extinct in subtropical pastures after severe drought (McKeon et al. (1990) and references therein). Thus, it is probable that while the grasses were able to survive a single season of reduced water availability, they were not able to persist

into the second season of reduced water availability.

7.5.2 The influence of drought on soil carbon and soil chemistry

The soil samples taken at the completion of the experiment (Figure 7.2) showed higher soil carbon within the drought tent (mean of 70 t C ha⁻¹) as compared to the control (mean of 47 t C ha⁻¹). The fine root biomass in the top 5 cm of soil equates to ~350 t C ha⁻¹ (assuming that biomass is 50% carbon) although February et al. (2013) reported that grasses including *H. triticeus* contribute disproportionate amounts of carbon and nitrogen to soil relative to root biomass so the true value could be somewhat higher. Thus, it is possible that the discrepancy in soil carbon between the treatments is at least partially explained by the death of the grass roots within the drought tent. The drought tent reduced the moisture enough to kill the grass within the tent that had already sustained one reduced wet season, but as the wet season progressed and moisture increased, roots of the neighbouring grasses that were still alive were able to colonise the soil, as was proposed by Hamerlynck et al. (2013).

In addition to higher soil carbon, the soil samples from the drought tents also had higher C:N ratios than those from the control (Figure 7.2). This suggests that there is an augmented level of ‘fresh’ carbon in these soils as organic matter that has been subject to extensive microbial metabolism will have a lower C:N ratio approximating that of microbial biomass (Enríquez et al., 1993; Wang et al., 2004). Given that the drought tents excluded the addition of fresh tree-sourced leaf litter, this suggests that the ‘fresh’ carbon must be from dead grass roots.

Soil nitrogen was also higher in the drought treatment compared to the control and this was consistent across both sample depths (Figure 7.3). This also suggests that fresh inputs to the organic matter pool were sourced from roots, as the influence of grass leaf and stem matter would only be evident in the surface layers. In contrast, there was also higher NH₄⁺-N, but only in the surface soils, indicating that heterotrophic decomposition of the grass litter had commenced (Austin and Vivanco, 2006). Interestingly, the $\delta^{15}\text{N}$ was higher in the control (Figure 7.3). In general, $\delta^{15}\text{N}$ tends to increase with aridity as water availability limits the utilisation of available nitrogen, but in this case, the results are consistent with more constant moisture availability in the drought treatment and higher soil moisture variability

in the control (Figure 7.1). Erratic water availability tends to decouple nitrogen availability and plant demand (Austin and Vivanco, 2006), requiring tighter cycling of nitrogen when compared with the drought treatment where more nitrogen would be required to decompose the extra soil carbon (Aranibar et al. (2004); Soper et al. (2014) and Chapter 5).

There were also higher concentrations of Na^+ and K^+ in the soils in the drought tent. This is potentially due to higher inputs and/or decreased uptake as a result of the dead grass. Plants absorb more K^+ than any other mineral but Na^+ can also be beneficial in low doses, particularly in C_4 plants (Gattward et al., 2012). EC was also higher in the drought treatment, likely due to the influence of the K^+ and Na^+ . The slightly lower pH in the drought soils likely also contributed to the elevated EC in the drought soils. In contrast, there was no difference in Ca^{2+} or Mg^{2+} between the treatments.

7.5.3 The influence of drought on soil respiration

The simulated drought was assumed not to have affected tree-derived soil respiration in this study. Trees use water more efficiently during the dry season, transpire more (O’Grady et al., 1999), and continue to assimilate carbon during dry season (Beringer et al., 2007). Furthermore, the trees would be expected to have a wide area of roots that would be able to access soil moisture from well beyond the limits of the drought tent and are therefore unlikely to be meaningfully affected.

The effect of soil moisture on soil respiration was variable. Broadly speaking, the soil respiration tracked both soil moisture and soil temperature inasmuch as periods of high flux coincided with the warm, wet summer months, which is consistent with the results of Chapter 5. However, there was no correlation between soil respiration and soil moisture content for the control and only a weak correlation between soil respiration and soil moisture content in the drought ($R^2 = 0.08$, $p < 0.001$). This was consistent even if the data were considered season by season.

Compared to the control, soil respiration was initially lower in the drought tent but it was higher towards the end of both wet seasons and was the same during the dry season. Although the start of the experiment coincided with the beginning of the wet season, appreciable rainfall did not fall until approximately February 2012. During this time the soil moisture was very low in both the drought and the control (although it was slightly lower in the drought tent) and soil respiration was lower in

the drought treatment. Reduced soil respiration due to drought has been reported by Balogh et al. (2016) for a temperate grassland in Hungary. They reported that autotrophic respiration decreased in response to a decrease in photosynthetic inputs but heterotrophic respiration decreased by a lesser amount, suggesting that the heterotrophic component of soil respiration is not as sensitive to low soil moisture. Similarly, Pereira et al. (2007) reported a greater reduction in GPP than ecosystem respiration associated with drought, leading to a decrease in the strength of the carbon sink in a mediterranean savanna.

Following the onset of the rains, soil respiration spiked in both the control and the drought, despite the fact that soil moisture was substantially reduced in the drought treatment. Soil respiration in the drought tent continued to increase at the end of the 2011-2012 wet season after soil respiration in the control and soil moisture in both treatments had dropped off. This additional increase in soil respiration in the drought treatment at the end of the 2011-2012 wet season (Figure 7.1) could be related to changes in the growing season of the grasses. The dominant grasses at Davies Creek are perennial and continue to grow throughout the year although growth rates are at their highest during the summer months. Following first monsoonal rains, starches from the roots and corm are mobilised and used to produce new leaves (Snyman et al. (2013) and references therein). This period of rapid biomass accumulation starts in approximately October (Chapter 4) and corresponds to an increase in respiration (Chapter 6). It is possible that the delay in significant wetting of the soil in the drought treatment could have delayed the growing season of the grasses. As a result, the grass may still have been undergoing a period of rapid biomass accumulation in the drought tent some weeks after the grasses in the control had stabilised their growth rates. This is consistent with results reported by Scott et al. (2009) for a mesquite savanna in Arizona, North America. The authors reported higher than typical respiration fluxes following unusually dry conditions during the spring, which they suggest was due to unusually high monsoonal growth, following greater down-regulation during the prolonged dry period.

Furthermore, although soil water content fluctuated in both treatments, the wetting events in the drought treatments were substantially muted in comparison to the control and could have resulted in a higher metabolism of heterotrophic sources of soil respiration. For example, leading up to this time (*i.e.* during the 2011-2012 wet season), the soil in the control remained moist (albeit variably moist), whereas the soil in the drought tent had undergone drying and wetting cycles. The wetting of soils stimulates microbial growth that facilitates rapid C and N mineralization. As

the soil dries, the microbial biomass decreases as a result of microbial death, with the dead microbial biomass then rapidly decomposed by surviving microbes during a subsequent wetting event. As a result, wet-dry cycles can lead to a higher rate of C and net N mineralization from the soil compared to a soil that has remained continuously moist (Austin et al., 2004b), and this may have been the case early in this experiment.

Notwithstanding these periods of higher flux in the drought tent during the 2011-2012 wet season, cumulative seasonal carbon loss from the soil was 4.5 t C ha⁻¹ in the control and 4.1 t C ha⁻¹ in the drought treatments, a reduction of 8%. Other simulated drought studies have reported a 25% reduction due to drought for a subtropical prairie grassland (Hoover et al., 2016) and a 10-13% reduction due to drought for a temperate grassland (Burri et al., 2015). The reduction in cumulative carbon loss due to drought is likely to be low in this study as the drought tents are small and therefore limited in their realm of influence.

In contrast to the 2011-2012 wet season, the 2012-2013 wet season was associated with the most pronounced deviation in soil respiration between the two treatments. At this time, soil respiration was approximately 30% higher in the drought tents compared to the control and this continued throughout the 2012-2013 wet season until the completion of the experiment in June 2013. This resulted in a cumulative seasonal carbon loss from the soil of 3.8 t C ha⁻¹ in the control as compared to 4.3 t C ha⁻¹ in the drought, an increase of 14%. This period coincided with the demise of the grass within the drought tents (Plate 7.2) and so this increase in soil respiration is likely associated with a substantial increase in heterotrophic respiration as microbes metabolised the newly available labile carbon added by the fine roots and leaf matter of the dead grass.

Alternatively, this observed increase in soil respiration in the drought tent could be a function of neighbouring grasses (not in the drought tents) colonising newly available soil resources left by the death of the grasses within the drought tents. This effect is likely to be particularly significant in this study, due to the close proximity of plants not affected by the drought. Similar results were reported for a subtropical monsoon grassland in North America following periods of natural drought. In that study, soil respiration was closely related to the health of surviving plants, potentially due to recovery and growth of roots. Ecosystem respiration was also higher following drought years than non-drought years and this was unrelated to precipitation. Furthermore, ecosystem respiration following drought periods was not coupled to ecosystem photosynthesis, suggesting heterotrophic sources were responsible for

the additional respiratory fluxes (Hamerlynck et al., 2013).

Soil respiration normalised to the soil carbon (*i.e.* soil respiration relative to the amount of carbon available at the completion of the experiment) was substantially reduced in the drought tents relative to the control (Figure 7.7). Assuming that the relatively higher carbon was sourced from additional dead fine roots, this is to be expected, as decomposition of the dead roots will occur in stages, with only the most labile fraction supplying suitable substrate for metabolism over such a short timeframe. Nonetheless, there was higher soil soil CO₂ export from the drought treatment over the course of the experiment, with a total cumulative carbon loss of 16.7 t C ha⁻¹ as compared to 15.9 t C ha⁻¹ from beneath the control.

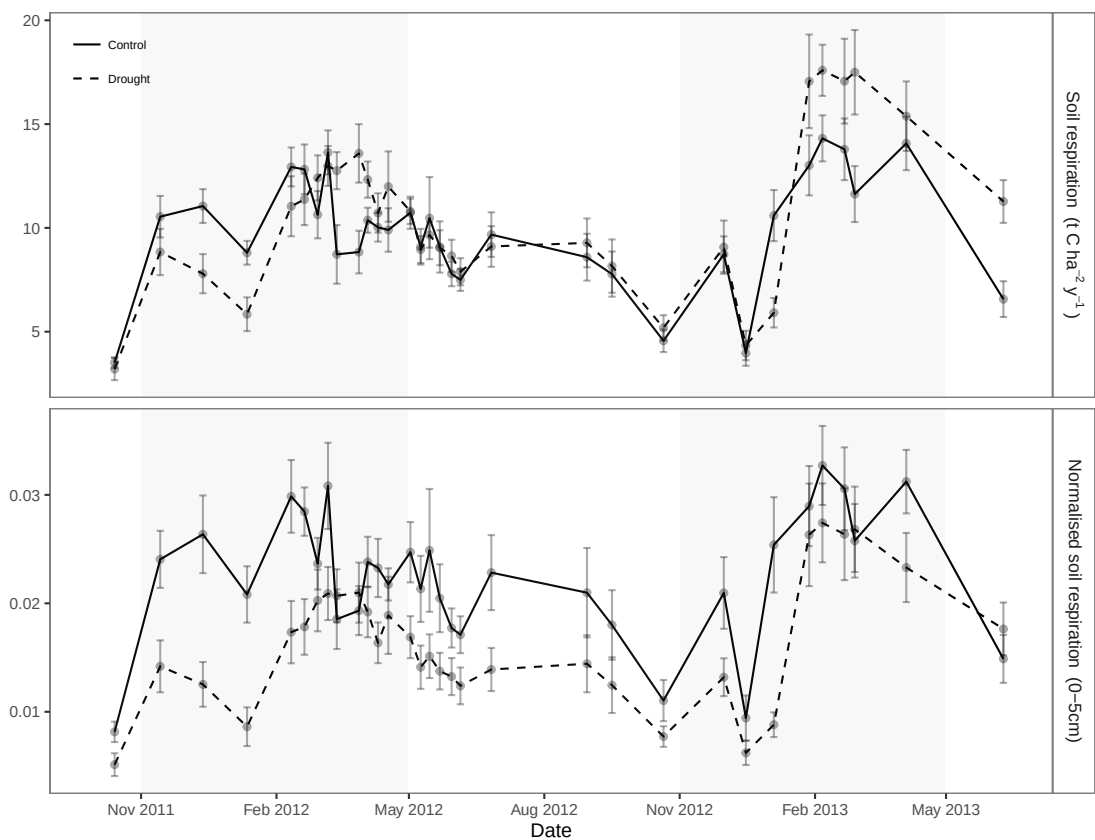


Figure 7.7: Comparison of measured drought soil respiration (top) and normalised drought soil respiration (bottom).

7.5.4 Implications for climate change and the global carbon cycle

Climate change is expected to result in substantial changes to the hydrological cycle and precipitation patterns (Feng et al., 2013; Fischer et al., 2013), although exactly what those changes will be, and how ecosystems will respond, remains a matter for some debate (Ahlström et al., 2015; Li et al., 2012; Sippel et al., 2016; Smith, 2004). Nonetheless, it is evident that droughts are having a substantial impact upon the terrestrial carbon cycle within Australia (Cleverly et al., 2016), the wider tropics (Rohr et al., 2016), and globally (Huang et al., 2016). While the most evident result of drought is tree mortality, which has been observed both globally (Allen et al., 2010a; Anderegg et al., 2012; Eamus et al., 2013a; Meir et al., 2015; Steinkamp and Hickler, 2015) and within Australia (Dwyer et al., 2010; Evans and Lyons, 2013; Fensham et al., 2015), the results from this study show that the grassy component of this tropical savanna site is also vulnerable to sustained drought.

Grass death due to drought may also be exacerbated due to elevated CO₂ as the C₄ photosynthetic pathway loses its competitive advantage at CO₂ levels >500ppm (except under very high temperatures) and therefore C₄ grass could be partly replaced by C₃ plants (Cerling et al., 1997; Xu et al., 2013). In particular, *H. triticeus* reacts poorly to elevated CO₂, especially after fire (Tooth and Leishman, 2014) and prefers early season fire (lower intensity) and higher fire frequency (Williams et al., 2003). Furthermore, both *H. triticeus* and *T. triandra* were outcompeted by invasive grass species (both C₃ and C₄ species) following burning under elevated CO₂ in a glasshouse experiment (Tooth and Leishman, 2013). These types of species shifts may also have implications for animals; for example, *H. triticeus* is food plant for native granivorous parrots and finches and *T. triandra* leaves are the main component in the diet of many Australian herbivores (Hooker, 2011).

Furthermore, changes to the species composition of the grasses can have implications for fire regimes, and *vice versa*. For example, combinations of drought, fire and/or over-grazing can result in a decline in *T. triandra*, which is associated with a decline in grazing value and species richness (Snyman et al., 2013). In the Northern Territory, the replacement of native grasses with the invasive African species Gamba grass (*Andropogon gayanus*) has resulted in substantial changes to the ecosystem as a result of changes to fire regime. Gamba grass has a very high biomass and cures late in the season, facilitating intense fires that cause widespread tree death (Rossiter et al., 2003; Setterfield et al., 2010). This in turn favours the estab-

ishment of grasses, resulting in a ‘landscape fire trap’ (Lindenmayer et al., 2011) known as the grass-fire cycle (D’Antonio and Vitousek, 1992). The replacement of native grasses by invasive grasses has also been reported for tropical savannas in Venezuela (Baruch and Fernández, 1993), Brazil (Hoffmann and Haridasan, 2008) and Botswana (Van der Putten et al., 2007), as well as subtropical savannas in the U.S. (Hamerlynck et al., 2013), resulting in changes to nutrient cycling, tree death and adverse plant-pathogen interactions.

In addition to changing the species composition of the grass component, drought may also lead to complete ecosystem transitions. For example, following the mortality of the grass, the standing biomass can protect the soil and act as mulch to increase the soil water content, leading to increased recruitment of shrub seedlings, thus facilitating a transition from grassland to savanna (de Dios et al., 2014; Wilson, 2014). More commonly, drought will lead to mortality of trees and a subsequent increase in fire frequency, which can result in the expansion of savanna ecosystems at the expense of forests (Anderegg et al., 2012). In contrast, Zeeman et al. (2014) reported that severe drought did not reverse woody plant encroachment in Australia and this may be due to the prevalence of *Eucalyptus* species in Australian savannas as they are well adapted to surviving drought (Arndt et al., 2015; Booth et al., 2015; Drake et al., 2014). For example, leaf scale physiological properties do not change with latitude on the NATT transect, as plants compensate for reductions in precipitation by changing structure (Hutley et al., 2011). Nonetheless, the length of the dry season is more important than total rainfall in determining tree height and biomass stocks, and trees in regions with higher mean annual precipitation (MAP) or less seasonal rainfall tend to become taller (Cook et al., 2015).

Changes to phenology may also occur as changes to the timing of precipitation affect the timing and magnitude of flower and fruit production as well as tiller development (Zeppel et al., 2013). In this study, the drought treatment may have caused a delay in the growing season of the grasses and this has implications for geochemical cycling. For example, *T. triandra* has lower nitrogen and phosphorus in foliage at the beginning of wet season and *H. triticeus* has higher nitrogen and phosphorus at the end of the wet season (Hendricksen et al., 1992). Similarly, the two species also have different flowering times and changes to this will affect nutrient cycling and food availability (Hooker, 2011). In this study, there were differences in soil chemistry (soil nitrogen and $\delta^{15}\text{N}$, Figure 7.3; Na^+ and K^+ , Figure 7.5) between the drought treatment and the control that suggest changes to nutrient use and nitrogen cycling have occurred.

The simulated drought in this study was also associated with changes to soil carbon cycling with higher soil carbon in the drought treatment as compared to the control (Figure 7.2). Initially, the drought was associated with a decrease in soil respiration, and this is consistent with other studies. For example, Borken et al. (2006) reported that drought decreased soil respiration in a temperate forest by decreasing heterotrophic breakdown of soil organic matter. Similarly, other studies have shown an increase in soil respiration with temperature and a decrease with drought in both Europe (Barba Ferrer, 2015; Emmett et al., 2004) and North America (Suseela and Dukes, 2013). In addition, Pereira et al. (2007) reported that GPP decreases more than ecosystem respiration during drought periods in a mediterranean savanna, resulting in a net decrease in carbon accumulation.

In this study, following the death of the grass, the soil respiration rate increased in the drought treatment, resulting in a higher soil CO₂ export from the drought treatment. Thus, this increase in soil carbon is likely to be temporary, resulting in a net loss of carbon from the ecosystem. The increased soil CO₂ export from the drought treatments is assumed to be due to a temporary increase in the heterotrophic component of soil respiration (that exceeds the decrease in the autotrophic component of soil respiration). This has been reported in other studies, for example, Yuste et al. (2012) reported that soil respiration and soil bacterial communities increased under dead trees as a result of drought-induced mortality in a Mediterranean ecosystem. Similarly, Balogh et al. (2016) reported that the autotrophic component of soil respiration was more sensitive to drought and that the relative contribution of heterotrophic respiration increased during drought periods in a temperate grassland.

7.6 Conclusions

The drought tents applied to two transects at Davies Creek were successful in significantly reducing the soil moisture and this was associated with a decrease in soil respiration during the 2011-2012 wet season, followed by an increase in soil respiration during the 2012-2013 wet season. The initial decrease was probably due to a delay in the growing season of the grass during the 2011-2012 wet season that led to a decrease in autotrophic respiration, followed by the death of the grass in the 2011 dry season that led to an increase in heterotrophic respiration. The higher soil carbon in the drought treatment suggests that there was an additional input of carbon as a result of the drought, presumably due to the death of the grass within the

drought treatment and subsequent incorporation into the soil carbon pool. Higher soil nitrogen and C:N ratios in the drought tent also suggest that the higher carbon present was due to 'fresh' carbon inputs, while higher Na^+ and K^+ in the drought treatment suggest that changes to nutrient cycling have occurred as a result of the drought. However, many of these changes may be temporary and long-term experiments are required to determine steady state conditions. Extended droughts will likely lead to shifts in species composition, or perhaps even complete ecosystem shifts. Such changes will likely be accompanied by net loss of carbon from the ecosystem.

Chapter 8

Synthesis and conclusions

Statement of contribution

Conceptualised by Kalu Davies.

Written by Kalu Davies.

Edited by Kalu Davies with advice from Michael Bird, Michael Liddell, and Paul Nelson.

8.1 Objectives of the research

The principal aim of this thesis was to contribute to our understanding of carbon cycling in tropical savannas by quantifying aspects of the carbon cycle at three tropical savanna sites in northern Queensland and placing these results in the context of global carbon cycling and climate change. Although there has been a considerable increase in studies on carbon cycling in tropical savannas in Australia in recent years (for example, the Northern Australia Tropical Transect (NATT), (Hutley et al., 2011)), these studies have focused exclusively on savannas in the Northern Territory, and this study provides the first comprehensive assessment of carbon cycle dynamics in tropical savannas in Queensland. Furthermore, no previous study has been in a position to examine the carbon cycle dynamics of transition zone savannas that occur at the rainforest-savanna boundary and this study presents the only work on these unique ecosystems in Australia.

The first aim of the thesis was to assess the aboveground biomass (AGB) and above-ground net primary productivity (ANPP) of the three sites and to examine the relative contributions of trees and grasses to carbon stocks and fluxes (Chapter 4). The second aim was to inform our understanding of soil organic matter cycling by comparing soil carbon, nitrogen, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with soil characteristics, and to examine the contribution of trees and grasses to soil carbon stocks at the plot level (Chapter 5). The third aim was to quantify temporal and spatial variation in soil respiration in terms of climate drivers and tree/grass abundance, and to present a modelling framework for up-scaling of point measurements to the plot level (Chapter 6). The fourth aim was to examine the impact of drought, focusing on the relationship between soil respiration and soil moisture in more detail (Chapter 7).

The first aim was achieved using an inventory approach whereby each component of biomass was quantified individually using a combination of destructive harvest and allometric techniques. The change in AGB over time was then used as an estimate of ANPP (Chapter 4). The second aim was achieved using a spatially stratified approach to soil sampling that enabled soil carbon and nitrogen to be modelled as a function of woody vegetation cover. The stable carbon isotopes also enabled the separate contribution of trees and grasses to the soil carbon pool to be modelled, both in terms of aboveground inputs to the soil as well as in terms of the carbon currently in the soil (Chapter 5). The third aim was achieved by monitoring soil respiration and soil environmental variables on a monthly basis over a two year period. The same spatially stratified approach was used to quantify the spatial

variation in soil respiration in terms of proximity to woody vegetation (Chapter 6). The fourth aim was achieved by comparing the differences in soil respiration and environmental variables between a simulated drought and a nearby control (Chapter 7).

8.2 Outcomes of the research

8.2.1 Carbon cycling in tropical savannas of northern Queensland

This study has quantified stocks and fluxes of the terrestrial carbon cycle at three tropical savanna sites in Queensland. A summary of these stocks and fluxes is shown in Figure 8.1 with those not measured in this study derived from the literature (Chen et al., 2003; Moore et al., 2015). These results have provided an insight into the key differences in carbon cycling between these sites. Tree biomass dominated AGB at all sites and generally, stocks and fluxes varied two- to three-fold between sites. The carbon stock at Brooklyn Station was equally distributed between biomass (41 t C ha^{-1}) and soil carbon (38 t C ha^{-1}), while the stock at Davies Creek was dominated by biomass (70 t C ha^{-1} as compared to 39 t C ha^{-1} in the soil) and the stock at Koombooloomba was dominated by soil carbon (113 t C ha^{-1} as compared to 78 t C ha^{-1} in the biomass). Similarly, at Brooklyn Station and Davies Creek, soil respiration ($8.2 \text{ t C ha}^{-1} \text{ y}^{-1}$ and $11.7 \text{ t C ha}^{-1} \text{ y}^{-1}$, respectively) was double ANPP ($4.1 \text{ t C ha}^{-1} \text{ y}^{-1}$ and $5.1 \text{ t C ha}^{-1} \text{ y}^{-1}$, respectively), whereas at Koombooloomba soil respiration ($12.8 \text{ t C ha}^{-1} \text{ y}^{-1}$) was only 40% higher than ANPP ($9.2 \text{ t C ha}^{-1} \text{ y}^{-1}$).

All stocks and fluxes were highest at the wettest site (Koombooloomba) and were lowest at the driest site (Brooklyn Station), reflecting the importance of water availability in constraining the biomass and productivity of plants. This, in turn, is critical to how, and how much, carbon is cycled through the ecosystem. At Davies Creek, C_3 sources of carbon were a particularly important component of the carbon storage, comprising 92% of the total storage in soil carbon and AGB. At Brooklyn Station and Koombooloomba, ~70% of the carbon storage is tree-derived. The influence of the trees was also reflected in spatial patterns of soil carbon and $\delta^{13}\text{C}$ at Davies Creek and Koombooloomba (Chapter 5), and spatial patterns in soil respiration at all sites (Chapter 6), with higher carbon and CO_2 effluxes adjacent to trees. The

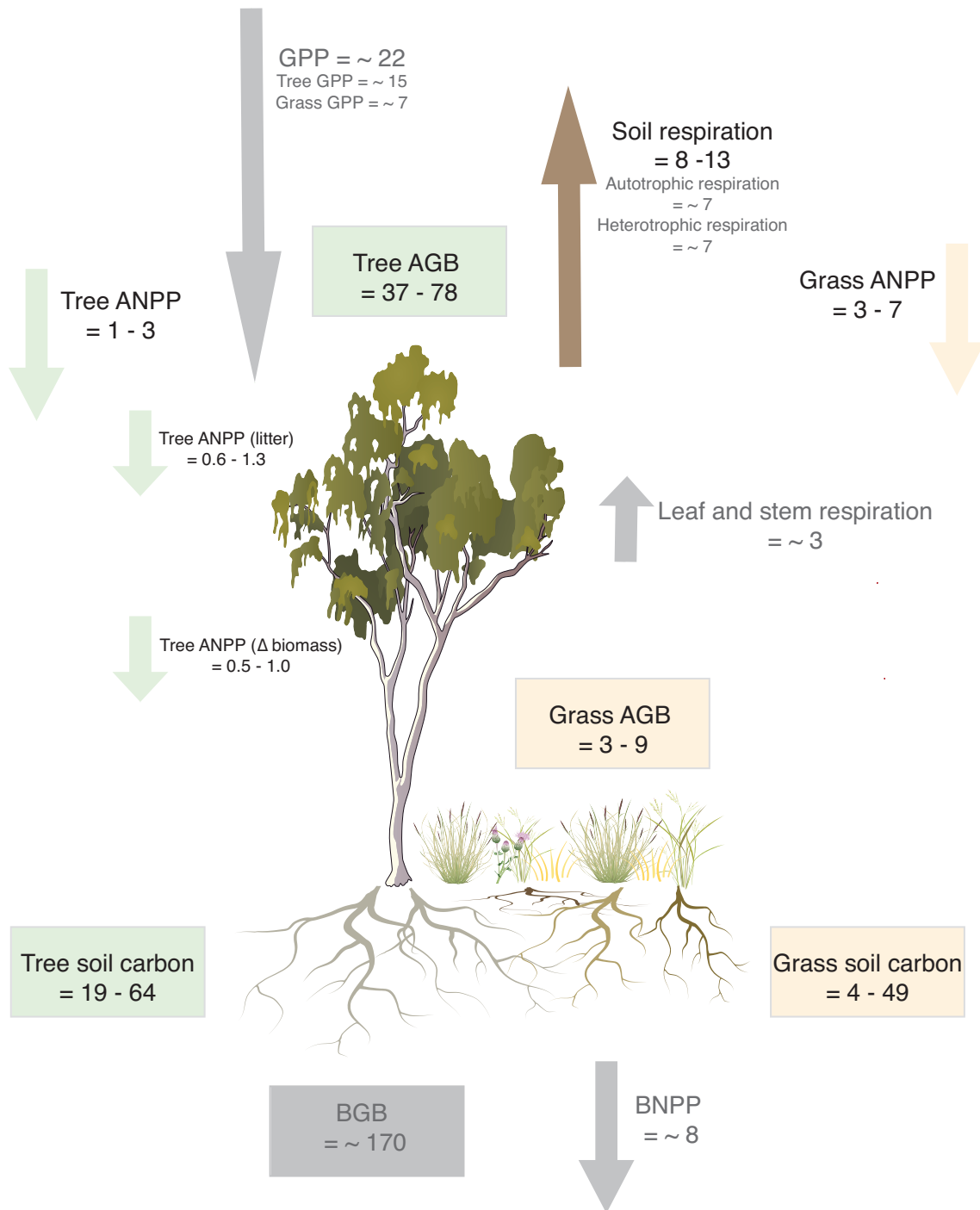


Figure 8.1: Summary of carbon stocks (t C ha⁻¹) and fluxes (t C ha⁻¹ y⁻¹) determined for the three sites in this study and partitioned by tree (green shading) and grass (orange shading) sources where possible (non-partitioned sources are indicated in brown). Fluxes of carbon are indicated by shaded arrows and carbon stocks are indicated by shaded boxes. AGB, aboveground biomass; ANPP, aboveground net primary productivity; BGB, belowground biomass; BNPP, belowground net primary productivity; GPP, gross primary productivity. Stocks and fluxes not determined by this study were sourced from the literature (Chen et al., 2003; Moore et al., 2015) and are indicated in grey. Small font indicates that a stock or flux is a component of a larger stock or flux.

tree component also dominated ANPP (Chapter 4) at Davies Creek (63%), although this was not the case for Brooklyn Station (27%) or Koombooloomba (22%).

These results also highlight some key differences between the sites in this study and those on the NATT in the Northern Territory. For example, relative to the mean annual precipitation (MAP) of each site, the sites in this study have considerably higher woody biomass (Chapter 4). Both Davies Creek and Koombooloomba have a MAP of ~1500 mm and yet the woody carbon stock (of 70 and 78 t C ha⁻¹, respectively) is five-fold greater than the woody carbon stock of 14 t C ha⁻¹ reported for Adelaide River (MAP 1460 mm) and more than double the woody carbon stock of 31 t C ha⁻¹ reported for Howard Springs (MAP 1714mm). Similarly, Brooklyn Station has a MAP of ~900 mm and a woody carbon stock of 37 t C ha⁻¹, more than double the woody carbon stock of 13 t C ha⁻¹ reported for Dry River (MAP 850 mm).

Furthermore, there are also differences in the relative contributions of trees and grasses to ANPP and soil carbon between the sites in this study and those on the NATT in the Northern Territory. For example, Chen et al. (2003) reported that C₃ vegetation contributed 83% of the ANPP at Howard Springs (MAP 1714mm). All the sites in this study had a considerably lower C₃ contribution to ANPP than reported by Chen et al. (2003), particularly Koombooloomba (22% of ANPP was C₃ in origin). In addition, the C₃ contribution to soil carbon was considerably higher at Davies Creek (78%), and somewhat lower at Brooklyn Station (50%) and Koombooloomba (57%), than the average of 70% reported by Lloyd et al. (2008) for savanna sites on the NATT.

Prior to this study, there was only one tropical savanna site in the Northern Territory (Howard Springs) for which measurements of biomass carbon, soil carbon and soil respiration exist (Chen et al., 2002). While the value of the OzFlux sites (Beringer et al., 2016) in the NATT cannot be discounted, the eddy covariance technique estimates total ecosystem respiration, and manual chamber measurements are still required to partition ecosystem respiration into its components (Hutley et al., 2005). Furthermore, this study comprises the largest dataset of soil respiration (Chapter 6) in Australia (compared to published studies (Bond-Lamberty and Thomson, 2014)) and the first attempt to examine soil respiration under simulated drought conditions in tropical savannas in Australia (Chapter 7).

8.2.2 Global carbon cycling and climate change

Many of the stocks and fluxes measured in this study were highly sensitive to disturbance, such as high tree mortality after Tropical Cyclone (TC) Yasi or increased litterfall following a fire. These disturbances are characteristic of tropical savannas, although there is concern that disturbances may become more frequent and/or more severe as the climate changes into the future. A summary of these changes, and how the associated disturbance might influence the terrestrial carbon cycle in tropical savannas, is shown in Figure 8.2. Although there is some consensus regarding the general direction of the change (*i.e.* carbon entering or leaving the ecosystem), there remains considerable uncertainty regarding the magnitude of the change.

Initially, CO₂ fertilisation is expected to lead to an increase in C₃ vegetation (Ainsworth and Long, 2005); given the dominance of C₃ sources of carbon at Davies Creek (63% of ANPP, Chapter 4 and 78% of soil carbon, Chapter 5) this may already be occurring and may explain the observed biomass increase and/or it may cause an increase in the carbon stocks in the future. CO₂ fertilisation may also accelerate the growth rate of juvenile trees and increase the proportion that survive topkill from fire (Bond and Midgley, 2000). This will, in turn, lead to increased inputs to the soil. If these inputs exceed losses due to decomposition then it may lead to an increase in soil carbon (Heimann and Reichstein, 2008). Nevertheless, there are limitations to the capacity for ecosystems to produce more biomass as a result of CO₂ fertilisation, such as nitrogen availability (Reich et al., 2006a; Thornton et al., 2007). Nitrogen availability limits growth in many savannas and is likely to limit productivity at both Davies Creek and Brooklyn Station as the levels at these sites are very low (Chapter 5). Furthermore, the effects of CO₂ fertilisation may be short lived as both C₃ and C₄ vegetation have been shown to acclimate to high levels of CO₂, particularly in nutrient poor soils (Sage and Kubien, 2003; Wand et al., 1999), which are common in the tropical savannas of Australia (Wilson et al., 2009).

Tropical cyclones are relatively rare in tropical savannas (Hutley et al., 2013) but their effects can be devastating (Cook and Goyens, 2008) and they are projected to increase in intensity as the climate changes in the future (Frank et al., 2015; Haig et al., 2014). The strong winds associated with tropical cyclones lead to extensive tree damage and death. This was evident at Koombooloomba where at least half of the tree mortality was due to broken or uprooted trees following TC Yasi in 2011 (Chapter 4). In addition, the extensive tree defoliation was followed by a rapid increase in understorey biomass and an increase in broad leaved weeds, which then

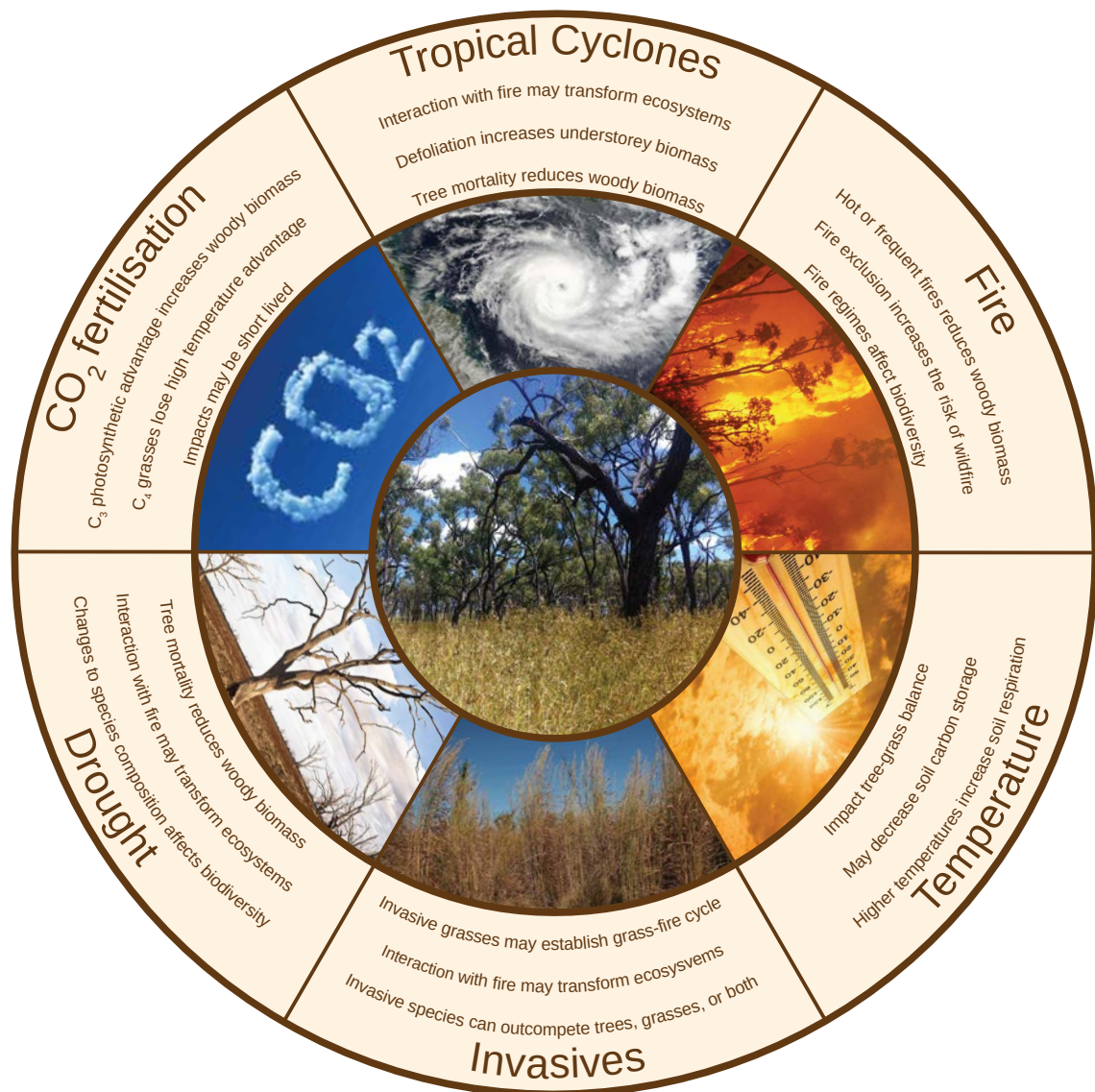


Figure 8.2: Summary of potential changes to the terrestrial carbon cycle in tropical savannas as a result of climate change. This includes the the effects of CO₂ fertilisation, changes to the frequency and magnitude of storms or tropical cyclones, increases in fire frequency or intensity, increases in temperature, the role of invasive species, and the effects of drought.

senesced during the following dry season. This understorey biomass, in addition to broken branches and trunks of trees, can represent a significant flux of carbon to the atmosphere as it decays (Hutley et al., 2013). Furthermore, it also creates an unusually high fuel load and associated fire risk that could precipitate abrupt (and possibly permanent) changes to ecosystem composition and/or structure (Bowman and Panton, 1994). However, in the absence of fire, defoliation from cyclone damage may also facilitate the accelerated growth of seedlings and saplings, resulting in a period of rapid recruitment (Hutley and Beringer, 2010), which was also evident at

Koombooloomba.

Although fires are a characteristic feature of most tropical savannas, their timing, frequency, and magnitude ultimately determines the nature of the effects. Fires that are too hot or too frequent can reduce woody biomass and thus reduce carbon storage in biomass. This appears to be the case at Brooklyn Station where low recruitment and tree mortality has been attributed to fire damage (Chapter 4). Fires that are too frequent or intense can lead to a reduction in woody biomass as mature trees are unable to recover during the short intervals and small saplings and seedlings cannot grow to a fire-proof height during the short interval between fires (Bond et al., 2012; Lawes et al., 2011; Werner and Prior, 2013). Given the importance of the C_3 contribution to soil carbon at these sites (Chapter 5), a reduction in woody biomass will likely lead to a reduction in soil carbon storage. Nevertheless, fire exclusion can increase woody biomass and may increase the risk of catastrophic wildfires (Townsend and Douglas, 2004). The timing of fires is also important; fires late in the dry season tend to be hotter as fuel loads have had longer to cure. The timing of fires can also have ramifications for food supply. In combination, these effects also have substantial implications for biodiversity (Andersen et al., 2012b; Bliege Bird et al., 2008; Parr and Andersen, 2006; Woinarski et al., 2004).

Climate change resulting in higher temperatures may lead to increases in soil respiration. In this study, soil respiration was positively related to temperature (Chapter 6). This is particularly critical if it leads to an increase in the decomposition of carbon already in the soil. There is evidence that soil respiration is increasing as temperature increases (Bond-Lamberty and Thomson, 2010b) but the mechanism behind this change remains an issue for debate. If increases to soil respiration are driven by an increase in productivity, then the two fluxes may essentially cancel each other out. On the other hand, if increased temperatures accelerate the decomposition of existing soil carbon, then a positive feedback loop could establish, further accelerating climate change (Frey et al., 2013; von Lützow and Kögel-Knabner, 2009). For tropical savanna sites such as Brooklyn Station and (especially) Koombooloomba, the soil carbon represents the majority of the carbon storage at these sites (Chapter 5) so any substantial loss from the soil would be detrimental to the carbon storage capacity of these ecosystems. Furthermore, increases to temperature could influence the tree-grass balance. C_4 vegetation tends to have a photosynthetic competitive advantage over C_3 vegetation at higher temperatures. However, this advantage disappears when high temperatures are combined with elevated CO_2 (Cerling et al., 1997; Sage, 2004) and there are concerns regarding the fate of C_4 dominated ecosys-

tems in a warmer, higher CO₂ world (Sage and Kubien, 2003).

Invasive species already pose a threat to tropical savannas, particularly those in Australia, with invasive species (both plant and animal) resulting in widespread damage to both trees and grasses (Bowman et al., 2008; Brooks et al., 2010; McKenzie et al., 2007; Sharp and Whittaker, 2003). In particular, the establishment of invasive grasses can interact with fire in a process known as the ‘grass-fire cycle’ (D’Antonio and Vitousek, 1992). This occurs where introduced grass species accumulate higher fuel loads as a result of higher biomass and earlier curing times. The increased fuel load leads to a fire that is hotter in intensity, which leads to high tree mortality, which in turn favours the proliferation of the grass species and perpetuates the production of high fuel loads. This phenomenon has been well documented in the Northern Territory where the invasive grass species Gamba grass (*Andropogon gayanus*) has led to the complete conversion of tropical savannas to treeless grasslands (Brooks et al., 2010; Rossiter et al., 2003; Setterfield et al., 2010). This may also be occurring at Brooklyn Station where the invasive grass species grader grass (*Themeda quadrivalvis*) is widespread and forms a high fuel load in comparison to the native grasses (Chapter 4). The loss of the trees from the ecosystem may, in turn, lead to a reduction in soil carbon, given the influence of C₃ vegetation on soil carbon storage at these sites (Chapter 5). Furthermore, the combination of elevated atmospheric CO₂ and fire has been experimentally shown to increase the competitive advantage of exotic grasses over native grasses in an Australian tropical savanna (Tooth and Leishman, 2014).

Finally, reduced precipitation and/or increased seasonality of precipitation is expected to lead to a decrease in vegetation biomass as a result of mortality to both trees (Allen et al., 2010a; Eamus et al., 2013a) and grasses (Chapter 7). Changes to species composition of both trees and grasses will have implications for the interaction with fire (Rossiter et al., 2003; Setterfield et al., 2010), as well as implications for biodiversity (Brooks et al., 2010; Hooker, 2011; Snyman et al., 2013). In addition, changes in the tree/grass balance as a result of changes to precipitation patterns will also impact upon the soil carbon. Given the dominance of C₃-derived soil carbon (especially at Davies Creek), an increase in grass biomass is likely to lead to a reduction in soil carbon over time (Chapter 5). The results of this study also suggest that as biomass is reduced, soil respiration will reduce in the long term but may increase in the short term as plant mortality results in further inputs to the soil (Chapter 7).

8.3 Limitations of the research

There are a number of limitations to the assessment of biomass and productivity in this study (Chapter 4). Firstly, the tree census was conducted over a short time interval of three years for Brooklyn Station and four years for both Davies Creek and Koombooloomba. This resulted in a high degree of uncertainty in the assessment of growth increment because it was similar in magnitude to the error of measurement. Secondly, the grass biomass estimates were uncertain because of the small number of replicates. Thirdly, both the grass and tree biomass and productivity was estimated over only a short time interval (three or four years for the trees and 12 months for the grass) and this period may not be representative of average conditions. Indeed, this measurement interval (2009-2013) coincided with a severe La Niña phase (Boening et al., 2012) with unusual and above average rainfall and productivity (Bastos et al., 2013).

Similarly, the La Niña event is likely to have also impacted upon soil respiration and thus those results may also not be typical of the long-term average (Chapter 6). For example, soil moisture did not appear to constrain soil respiration at Koombooloomba. However, this was during anomalously high rainfall and it may be the case that under ‘average’ conditions, soil moisture is a constraint. Furthermore, although the model of soil respiration was useful for interpolating the measurements and upscaling the soil CO₂ export to the plot level, it lacked any predictive power based on environmental variables. This was because soil moisture was not sampled at the same frequency as the soil respiration due to instrument failure. Restricting the dataset to those values for which soil moisture was available would have reduced the size of the dataset considerably and thereby compromised the temporal extent.

Finally, the simulated drought experiment (Chapter 7) only consisted of two rain exclusion shelters with multiple sampling locations beneath each shelter. This experiment could be substantially improved with more replication and additional microclimate data.

8.4 Directions for future research

The establishment of permanent plots with high quality data provides a unique opportunity to support further research. Furthermore, one of the limitations of this

study is arguably its most useful feature. The majority of the sampling was conducted in 2010-2012 which encompassed a period of highly atypical weather (Figure 6.9). Therefore, while this study may not have captured steady state conditions, it provides an interesting wet ‘end-member’ comparison to any future work that might be carried out on these sites. For example, a re-census in the coming years could compare a short time span of extreme wet weather to a short time span of extreme dry weather. Similarly, future research on soil respiration at these sites could provide valuable insight into the medium-term impact of extreme weather events on soil respiration.

Finally, emerging technology such as cavity ring-down spectroscopy (Picarro, Santa Clara, CA, USA) enables the calculation of the $\delta^{13}\text{C}$ value of soil respiration in the field. This, in turn, enables the soil respiration to be partitioned into C_3 and C_4 sources. Unfortunately, the current generation of equipment is sensitive to being transported and a number of technical difficulties prevented the use of a Picarro on site in this study. A method of batch analysis was developed by Munksgaard et al. (2013) that enables the soil CO_2 to be collected remote from the device. However, this relies upon relatively high rates of soil respiration, which were not present at the time of sampling. Further exploration of the $\delta^{13}\text{C}$ value of soil respiration, coupled with the results of this study, would provide a comprehensive assessment of the cycling of carbon within the trees and grasses within these ecosystems and provide invaluable insight into how the carbon dynamics might change under future climates.

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