Soil respiration and ecosystem carbon flux in semi-arid woodlands: Effect of season, precipitation and wildfire

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Qiaoqi Sun

School of Biological Sciences,

The University of Adelaide

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Dedicated to my mom and dad

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Abstract

Carbon exchange in arid and semi-arid ecosystems of the world has recently been highlighted because the areal extent of these ecosystems significantly influences the global carbon cycle. More information about the drivers of carbon fluxes in these ecosystems is required to advance our understanding of the contribution of dry ecosystems to the global carbon budget. Research on ecosystem carbon flux and soil respiration in semiarid to arid ecosystems is lacking relative to the more commonly researched temperate and well-watered systems.

This thesis aims to determine carbon fluxes in example semi-arid woodlands of southern Australia. As is typical of woodlands in rainfall limited environments, the study sites were characterised by vegetation patches interspersed by open areas with little or no vegetation. A primary focus of the research was to characterise the response of soil respiration in the patches to temperature and rainfall with the aim of improving carbon exchange estimates in these ecosystems. The occurrence of a wildfire at one of the sites provided the opportunity to measure carbon flux response to this event which is also a common, but infrequent ecosystem response driver.

Two types of woodlands in South Australia under similar climatic condition were investigated: mallee woodland and floodplain woodland. Mallee woodland was dominated by *Eucalyptus dumosa*, *E. incrassata*, *E. oleosa* and *E. socialis*. Floodplain woodland was dominated by *Eucalyptus camaldulensis* and *E. largiflorens*. In January 2014, a wildfire severely damaged the mallee woodland around an eddy covariance flux tower, burning trees and spinifex and consuming aboveground bark and leaf litter. The eddy covariance flux data was used to calculate net ecosystem productivity (NEP), gross primary productivity (GPP) and ecosystem respiration (Reco) in the mallee woodland. Soil respiration rates were measured in-situ each month under trees and in inter-canopy areas in the two woodlands.

Before the fire, the mallee woodland was a net carbon sink, sequestering 81 g C m^{-2} yr^{-1} in 2013, but became a net carbon source after the fire (- 88 g C m^{-2} yr^{-1}, data from May 2014 – April 2015). Reco and GPP declined by about 35% and 65%, respectively, after the fire. Net carbon uptake resumed 12 to 15 months after the fire with NEP approaching values similar to those before the fire.

Soil respiration was significantly higher under tree canopies (1.5 µmol CO_2 m^{-2} s^{-1}) than in inter-canopy areas (0.9 µmol CO_2 m^{-2} s^{-1}). Soil organic C and microbial biomass C were higher under canopy than inter canopy. Soil respiration (R_{soil}, µmol CO_2 m^{-2} s^{-1}) was mainly driven by soil water content (SWC) and thus magnitude and distribution of rainfall, but was not influenced by the wildfire. Temperature (T, °C) influenced R_{soil} only when SWC (volumetric ratio) was not limiting in both patches. The relationships established for R_{soil} were - inter-canopy: $R_{soil} = 1.79 – 0.08T – 31.82SWC + 2.38T*SWC$, $F_{3, 8} = 8.38$, $p < 0.01$ and under canopy: $R_{soil} = 3.06 – 0.12 T – 46.96SWC + 3.43T*SWC$, $F_{3, 8} = 19.53$, $p < 0.001$. Accounting for differences in area, soil respiration from inter-canopy and under canopy contributed 51 and 32% to total ecosystem respiration with the remaining 17% assigned to autotrophic respiration from aboveground vegetation.

The semi-arid climate of the mallee region is characterized by long dry periods that are interrupted by rainfall events differing in magnitude. The net ecosystem carbon exchanges to single large rainfall events were examined using eddy covariance data from the mallee woodland. Three large rainfall events with similar magnitude (35-55 mm), but contrasting previous rainfall were chosen. NEP, Reco and GPP rates 28 days prior to, and 35 days after the three central rainfall events were used. These system scale observations were complemented with 48h soil respiration measures from a water manipulation experiment (30 mm rainfall simulation) at small plot scale in the field following a long dry period (only 4.8 mm rainfall input in 45 days). Changes in ecosystem carbon fluxes responding to the central rainfall event depended on previous rainfall patterns. After 4 weeks with several medium to large rainfall events, the central rainfall event had little effect on NEP, Reco and GPP. In contrast, a large rainfall event following 4 weeks with very little rainfall induced a decrease in NEP and an increase in Reco for about 3 weeks. The strong increase in Reco after the central rainfall event can, at least partly, be explained by an increase (a "pulse") in soil respiration upon rewetting. GPP rates did not respond to any of three rainfall events.

In a semi-arid floodplain woodland, monthly in-situ soil respiration was higher under tree canopies (5.0 µmol CO_2 m^{-2} s^{-1}) than inter-canopy (2.3 µmol CO_2 m^{-2} s^{-1}), and also had higher soil organic C content. Five days of rainfall (total of 62 mm) in summer (air temperature ca. 23°C) increased soil respiration rates by 70-85% four days after the last rainfall event when compared to rates before the rainfall. Soil respiration rates remained high over the following two months with no rain, although soil water content in the top soil (0-5 cm) was very low. This suggests that in the months following the rain period, roots and associated microbial activity in the moist subsoil were the major contributors to soil respiration. On the other hand, a single rainfall event of similar magnitude in autumn (air temperature ca. 17°C) did not increase soil respiration compared to the previous dry period although top soil water content was three times higher. Therefore, soil respiration in this ecosystem is influenced by a complex interaction between rainfall amount, soil temperature as well as, possibly, distribution of the rainfall.

Soil respiration rates in the floodplain were generally higher than those in the Mallee and also those recorded in other floodplain studies with forests, woodlands, grasses or shrubs. While the respiration rates recorded in this study are at the upper end of those reported from other studies. While the floodplain setting in this experiment was in a semi-arid environment, the location with respect to the free water in the adjacent river resulted in a water table within 2 m of the soil surface. The soil profile below 30 cm will generally remain moist from capillary

upflow from the water table. In this generally warm environment, carbon turnover will be high, while total carbon in the soil will be low, as measured.

Two laboratory incubation experiments were conducted to understand the response of respiration and nutrient availability to drying and rewetting [first experiment], and to labile carbon as it may be released as root exudates [second experiment] in soil from the mallee woodland. Soils (top 0 - 30 cm) were collected from under tree canopies, under shrubs or in inter-canopy areas in unburnt and burnt locations, four months after the wildfire. In the first experiment, the soils were exposed to two water content treatments: constantly moist (CM) and drying and rewetting (DRW). In CM, soils were incubated at 80% of maximum water holding capacity (WHC) for 19 days. In DRW, soils were dried for four days, kept dry for another five days, then rewet to 80% WHC and maintained at this water content until day 19. Soil respiration decreased during drying and was very low in the dry period; rewetting induced a respiration pulse. Compared to soil under shrubs and in inter-canopy areas, cumulative respiration per g soil in CM and DRW was greater under tree canopy, but lower when expressed per g of organic matter content (TOC). TOC, available P, and microbial biomass C (MBC), but not available N were greater under tree canopy than in inter-canopy areas. Wildfire reduced TOC and MBC concentrations only under tree canopies, but had little effect on available N and P concentrations. Wildfire also decreased the pulse of respiration per g TOC in inter-canopy areas and under shrubs. In the second experiment, the soils were incubated at 80% WHC for 24 days without or with addition of 5 g C kg^{-1} as glucose. TOC, MBC and microbial biomass P (MBP) and available N and P were measured at the start of the experiment; soil respiration was measured continuously. Soil TOC, MBC, N and P availability and cumulative respiration were greater under trees than in inter-canopy areas. Fire decreased TOC and cumulative respiration only under trees and had little effect on available N, MBC and MBP concentrations. The greater increase in cumulative respiration by glucose addition under shrubs and in open areas compared to under trees and, in a given patch, greater in burnt than unburnt soils, indicate lower availability of native organic carbon.

In conclusion, this thesis showed that net ecosystem productivity in the mallee woodland was strongly influenced by rainfall and wildfire, with net carbon uptake of the ecosystem beginning approximately one year after the fire. On the other hand, soil respiration in this woodland was not influenced by wildfire and instead was related to soil water content and temperature. Moreover, the previous rainfall pattern determined response of net ecosystem carbon exchange to a single large rainfall event, which should be considered in carbon model development. The observations from the floodplain site indicate that riparian areas adjacent to river systems are highly likely to be have high annual soil respiration rates, especially in warmer environments and therefore have an influence on regional and global carbon cycles that is greater than would be expected based on climate and area alone.

Declaration

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List of publications

Sun, Q., Meyer, W.S., Koerber, G.R. and Marschner, P., 2015. Response of respiration and nutrient availability to drying and rewetting in soil from a semi-arid woodland depends on vegetation patch and a recent wildfire. Biogeosciences. 12, 5093-5101.

Sun, Q., Meyer, W.S., Koerber, G.R. and Marschner, P., 2016. A wildfire event influences ecosystem carbon fluxes but not soil respiration in a semi-arid woodland. Agricultural and Forest Meteorology. 226-227, 57-66.

Chapter 1

Introduction and literature review

1. Plants and soil in semi-arid ecosystems

Arid and semi-arid areas have a mean annual precipitation less than 600 mm and potential evapotranspiration that exceeds precipitation (Nielsen and Ball, 2015). These dry ecosystems occupy 47% of the world's land area, support more than 38% of the global human population and contain approximately 16% of the world's total soil organic carbon to 1m depth (Lal, 2004a; Reynolds et al., 2007). Global carbon cycling is vital to the survival of all ecosystems and people, influences climate change but is also affected by it. The biogeochemical cycle of carbon is driven by primary production, respiration and decomposition in the terrestrial biosphere (Finzi et al., 2011). Due to their global extent, arid and semiarid regions play an important role in sequestering carbon and potentially mitigate the accelerated global warming (Lal, 2004a). Recent studies showed that higher carbon turnover rates in semi-arid ecosystems are important drivers of global carbon cycle inter-annual variability (Poulter et al., 2014; Ahlstrom et al., 2015).

In arid to semi-arid ecosystems, biological and physical processes are constrained by total annual precipitation (e.g., Weltzin et al., 2003a; Noy-Meir, 1973; Beer et al., 2010). Plants are often adapted to water deficiency by developing deep and extensive root systems that are capable of accessing available water from deep soil (e.g., Sardans and Peñuelas, 2013). For example, roots of native mallee trees (*Eucalyptus pileta* and *E. eremophila*) in southern Australia have been found at 28 m depth (Nulsen et al., 1986). These adapted species also use water conservatively (Meyer et al., 2015). Burgess (2006) also showed that deep-rooted Eucalyptus species (*E. wandoo*) were mainly reliant on antecedent soil water and therefore did not quickly respond to large precipitation events. In a semiarid monsoon climate in southwestern US, shrubs preferentially allocate photosynthate to deep roots when conditions near the surface are unfavourable (Breecker et al., 2012). Another case study in an ecosystem dominated by drought-tolerant Juniperus monosperma trees, showed that the carbon isotope ratio of ecosystem respiration ($\delta^{13}C_R$) responded to precipitation, triggering a switch between autotrophic and heterotrophic $\delta^{13}C_R$ dominance as water content in deep and surface soil changed (Shim et al., 2011b). This adaptation indicates that plants and ecosystem carbon turnover in semi-arid regions may respond to precipitation and available soil water differently compared to plants in temperate regions. In general, the response could also be limited by the low soil nutrient availability in semi-arid to arid ecosystems including many regions of Australia (e.g., Orians and Milewski, 2007).

Woodlands in semi-arid regions are often characterised by “clumped” vegetation separated by large open areas with little or no plant growth (Tongway and Ludwig, 1994), also referred to as a “patchy” vegetation arrangement. This patchy distribution of plants results in significant differences in microclimate and soil properties; the well-documented “islands of fertility” and hotspots of microbial activity (e.g., Austin et al., 2004; Goberna et al., 2007).

Soil organic carbon pools, as an important component of global carbon, provide the energy essential for biological processes and maintenance of soil water holding capacity, nutrients, and soil structural stability (Baldock, 2007). Almagro et al. (2009) outline the effect of patchy distribution of plants on soil organic carbon dynamics through multiple pathways: (1) altering the soil water regime, through the interception of precipitation and the extraction of soil water via transpiration; (2) influencing soil microclimate and structure; (3) providing the carbon source to decomposer micro-organisms through both litter quantity and quality; and (4) root or rhizosphere respiration.

2. Soil respiration in semi-arid ecosystems

2.1 Definition and sources of soil respiration

Soil respiration is defined as CO_2 released from soil to the atmosphere via the combined activity of (1) roots (root or autotrophic respiration), and (2) micro- and macro-organisms decomposing litter and organic matter in soil (heterotrophic respiration) (Hogberg et al., 2005). It is one of the most important components of global carbon cycle and the largest contributor to ecosystem respiration (Bond-Lamberty et al., 2004; Valentini et al., 2000). Approximately 10% of atmospheric CO_2 passes through soil each year (Raich and Schlesinger, 1992; Raich and Potter, 1995; Stockmann et al., 2013). Annual global CO_2 flux from soils is estimated to be 64 -76.5 Petagrams of carbon per year and the soil organic carbon pool to 1 m depth stores approximately 30 tons/ha in arid climates (Lal, 2004b).

2.2 Biotic and abiotic factors influencing on soil respiration rates

Vast quantities of organic carbon in the form of roots and decomposed organic matter are stored in soils and the balance between the storage of organic carbon compounds and their release to the atmosphere are strongly affected by physical, chemical and biological processes (Johnston et al., 2004). Soil organic carbon balance is determined by photosynthesis and respiration (Valentini et al., 2000). The characteristics of the vegetation, its litter and debris strongly influence soil respiration (McCulley et al., 2007), e.g. ecosystems with different dominate plant species induce significantly different soil respiration rates, even in ecosystems that are geographically adjacent (Lai et al., 2012). Vegetation may also affect soil respiration by influencing the soil microclimate (Raich and Tufekcioglu, 2000). A study in a semi-arid shrubland in the Great Basin of US found that different vegetation types affect C mineralization primarily through modification of soil water content and, secondarily, the amount of labile C (Norton et al., 2012). Productivity, defined as plant dry matter per unit area, may be more important than temperature for soil and ecosystem respiration in undisturbed European forests (Janssens et al., 2001). This may be due to root respiration being constrained by the allocation of photosynthates to the roots, which is coupled to productivity. It may also be because the largest fraction of heterotrophic soil respiration originates from decomposition of leaves and fine roots, the availability of which also depends on primary productivity. Asensio et al. (2007) found that soil respiration rates in a Mediterranean holm oak forest followed a similar seasonal pattern as photosynthetic activity. The heterogeneity of vegetation coverage induces spatial variation in soil respiration as shown in a study in an oak-grass savanna ecosystem with higher soil respiration under trees compared to that in the open areas (Tang and Baldocchi, 2005). In semi-arid shrublands, soil respiration was greater beneath mesquite canopies than inter-canopy areas (Potts et al., 2008). In contrast, in a semi-arid steppe ecosystem, soil respiration rates measured under bare soil were significantly higher than those measured under plants when soil temperature was greater than 20 °C (Rey et al., 2011).

Soil organic carbon contributes a major flux of CO_2 from terrestrial areas and can act as a feedback to climatic change (Suseela et al., 2012). Soil organic carbon decreases with rainfall and is positively correlated with soil respiration in Mediterranean and desert ecosystems (Talmon et al., 2011). Sponseller (2007) demonstrated that soil CO_2 efflux was more closely related to organic matter content of surface soils than to rainfall amount. Knorr et al. (2005) suggested that non-labile soil organic carbon is more sensitive to temperature than labile organic carbon, implying that long-term negative feedback of soil organic carbon sequestration in a warming world may be even stronger than predicted by global models due to unequal sensitivity of different forms of soil organic carbon.

There are many other abiotic influences that affect soil respiration rates. They range from soil properties, land management and natural disturbances like wildfires. Lai et al. (2012)

suggested that in a typical arid region, a weak positive correlation exists between soil respiration and soil pH or soil carbon organic content. Soil texture was also a major influence on organic matter dynamics in arid grasslands (Parton et al., 1987), which may further affect soil respiration rates. Fine-textured soils tend to have higher water-holding capacity and C and N pools than coarse-textured soils (Austin et al., 2004). The cycling of carbon is also linked with landscape modification (De Deyn et al., 2008). Wildfires, as a consequence of climate change, damage aboveground living plants and consume surface organic materials. The effect of wildfires and pre-scribed fires on soil respiration and net ecosystem carbon exchange will be discussed in section 2.4.

2.3 Rainfall and air temperature as drivers of soil respiration

Different environmental variables and ecological processes may control soil respiration rate and hence terrestrial carbon cycling in different ecosystems in the same climatic zone (Sharkhuu et al., 2013). However, on a global scale, soil respiration rates are positively correlated with mean annual air temperature and mean annual rainfall (Raich and Schlesinger, 1992; Raich and Potter, 1995) which is confirmed by multiple studies (e.g.,Grunzweig et al., 2003). Therefore temperature and rainfall significantly influence the terrestrial carbon balance especially in areas that have limited rainfall i.e. arid and semi-arid regions (Weltzin et al., 2003a; Collins et al., 2008; Correia et al., 2012).

Rainfall regimes influence nutrient cycling and net ecosystem productivities more than any other environmental factor (Weltzin et al., 2003a). For example, rainfall amount and seasonal distribution significantly influence above-and below-ground net primary production and vegetation structure (e.g.,Byrne et al., 2013; Talmon et al., 2011), which will in turn, affect soil organic carbon content. Field data from Ruiz Sinoga et al. (2012) across a climatic gradient indicated that the soil organic carbon pool in semi-arid Mediterranean climate decreased with decreasing rainfall. When soil water content was low due to drought, soil respiration was shown to decrease by 3%–29% in shrublands across a European climate gradient (Emmett et al., 2004).

The size and duration of soil respiration response to rainfall varies with sequence and size of the rainfall event. Schwinning and Sala (2004) found that small rainfall events trigger a small number of relatively minor ecological events, including soil respiration, while larger rainfall events are likely to affect the capacity for carbon sequestration from increased leaf growth in semi-arid to arid regions. Warm season water addition from fog-drip and rainfall following extended dry periods may induce pulses of soil respiration (Carbone et al., 2011). Carbone et al. (2011) also showed that heterotrophic soil respiration and autotrophic (root) respiration responded differently to available water in a pine forest ecosystem with a Mediterranean-type climate. Heterotrophic respiration increased within hours, whereas root respiration responded more slowly over days. Soil respiration increased significantly and immediately after experimental rewetting treatment in semiarid ecosystems, but generally returned to background levels within days (Sponseller, 2007; Lee et al., 2004). In forest soils, rainfall can induce a flush of decomposition of the surface litter (Lee et al., 2004). Another case illustrated that over 5 days after rainfall, soil respiration induced a 21% increase in ecosystem respiration compared to pre-event steady state trajectory of carbon loss (Jenerette et al., 2008).

In semi-arid and arid ecosystems, surface soil water content and soil temperature (0-10 cm or 0-30 cm) follow changes in rainfall regime and air temperature. In general, soil water content influences soil respiration in ecosystems with annual precipitation between 300 and 4700 mm and distinct dry periods (e.g. Jha and Mohapatra, 2011; Rey et al., 2011; Correia et al., 2012;

Kiese and Butterbach-Bahl, 2002; Jin et al., 2009b; Jin et al., 2009a). However, few studies have been carried out in semi-arid woodlands with < 300 mm rainfall (Bond-Lamberty and Thomson, 2014). The seasonal pattern of soil respiration cannot be explained by temperature alone, but seems to be mostly explained by the combination of soil water content and temperature (Tang and Baldocchi, 2005). Soil respiration follows a seasonal pattern with a maximum occurring during a period of high water content and temperature and a minimum associated with low soil water availability at which time respiration was independent of temperature (Carlyle and Than, 1988). Some studies also found that the controlling influence of soil water content and temperature on soil respiration can change with soil water content being more important during dry, warm seasons or periods (e.g., Conant et al., 2004; Tedeschi et al., 2006). Others reported a threshold for soil water content or temperature for soil respiration. For example, Almagro et al. (2009) found that under a Mediterranean climate soil respiration was largely controlled by soil temperature above a soil water content threshold value of 10% volumetric water content (VWC) at 0 – 15 cm depth in a forest and an olive grove, and above 15% VWC for an abandoned field. However, below those thresholds soil respiration was controlled only by soil water content. In a semi-arid steppe ecosystem, soil water content controlled soil respiration when soil temperatures were above 20 °C and constrained the response to temperature when the temperature was below 20 °C (Rey et al., 2011). Soil respiration in a coppice oak forest in Central Italy was highly correlated with temperature during winter and during spring and autumn whenever VWC was above 20% (Rey et al., 2002). In a study conducted in an arid region, seasonal variations in soil respiration were well explained by soil surface temperature but not by soil temperature or soil water content at 10-cm depth (Lai et al., 2012). All of the above indicates that while soil temperature and soil water content are major influencers of soil respiration, the extent of control and with what thresh-holds are not clear, especially for low rainfall ecosystems.

2.4 Overview of soil respiration rates in global woodland type ecosystems

Soil respiration has been studied since 1927 (Vargas et al., 2011). Bond-Lamberty and Thomson (2010) introduced a global soil respiration database that contains data from 818 studies with over 3300 records, from 1961 to 2007. The database showed that soil respiration has been studied in various ecosystems, particularly in temperate climate areas but much less in semi-arid to arid regions (Bond-Lamberty and Thomson, 2014).

Here, I briefly summarize studies of soil respiration in woodlands (Table 1) (literature collected in May 2016). Soil respiration rates were reported in woodlands with a wide range of dominate species and annual rainfall from about 300 mm to > 1500 mm. In these woodland ecosystems, more in-situ soil respiration measurements were conducted under a Mediterranean climate than any other type of climate, mainly at sites with annual rainfall > 600 mm. More than half of these studies included in-situ sampling for 12 months or longer. But data on soil respiration from Mediterranean woodlands with low annual rainfall is limited. There were two studies carried out in a Eucalyptus shrub association (Mallee woodland) that reported very similar soil respiration rates – that by Galbally et al. (2010) in 1990 and by Sun et al. (2016) in 2015. The latter is presented in Chapter 5.

Four soil respiration estimation methods have been reported in recent literature including in-situ continuous measurements with soil chambers or gas wells, isotope approaches (^{13}C and ^{14}C), indirect estimates by laboratory incubation and model based simulation (e.g.,Kato et al., 2013; Vargas et al., 2011). The method selection depends on research focus, budget and specific conditions (e.g., Myklebust et al., 2008).

Table 1 Summary of in-situ soil respiration studies from world woodland ecosystems (MAP – Mean annual precipitation; MAT – Mean annual temperature; Research period only considered real time in-situ measurement).

Biome	**Country**	**Dominate species**	**MAP (mm)**	**MAT (°C)**	**Research period (months)**	**Soil respiration (g C m^{-2} d^{-1})**	**Reference**
Mediterranean	Catalonia	*Quercus ilex, Phillyrea latifolia*	685	12	5	2.07 - 2.62	(Asensio et al., 2007)
Mediterranean	Italy	*Quercus cerris*	755	14	14	4.15	(Tedeschi et al., 2006)
Mediterranean	Italy	*Arbutus unedo*	729	13	24	3.17	(Cotrufo et al., 2011)
Mediterranean	Portugal	*Quercus suber*	669	15.5	14	0.13 - 1.57	(Shvaleva et al., 2011)
Mediterranean	Portugal	*Quercus suber*	608	15.9	6	2.8	(Correia et al., 2012)
Mediterranean	Portugal	*Quercus suber*	680	15.9	19	0.41 - 1.55	(Shvaleva et al., 2014)
Mediterranean	Spain	*Pinus halepensis*	370	15.5	2	1.45 - 3.32	(Almagro et al., 2013)
Mediterranean	Spain	*Alnus glutinosa, Populus nigra*	872	12	4	0.18 - 1.75	(Chang et al., 2014)
Mediterranean	USA	*Quercus douglasii*	559	16.3	18	1.34	(Tang and Baldocchi, 2005)
Semi-arid	Australia	*Acacia aneura*	290	-	1	0.84 - 0.92	(Tongway and Ludwig, 1996)
Semi-arid	Australia	*Eucalyptus*	211	17.5	5	1.14	(Galbally et al., 2010)
Semi-arid	Australia	*Eucalyptus*	242	18.3	12	1.10	(Sun et al., 2016)
Semi-arid	China	*Ulmus pumila*	387	2.1	3	1.96-4.78	(Jin et al., 2009a)
Semi-arid	USA	*Pinus ponderosa*	550	14.5	12	1.82	(Irvine et al., 2007)
Subtropical	China	*Schima crenata, Castanopsis sclerophylla, Cinnamonum camphora*	1533	17	12	1.17	(Fan et al., 2015)
Subtropical	China	-	1577	16.8	27	0.40	(Iqbal et al., 2008)
Subtropical	USA	*Prosopis glandulosa*	716	22.4	24	2.04	(McCulley et al., 2004)
Temperate	Australia	*Eucalyptus marginata*	760	-	7	1.21	(Livesley et al., 2009)
Temperate	Australia	*Pinus radiata*	760	-	7	0.84	(Livesley et al., 2009)
Temperate	Australia	*Eucalyptus globulus*	760	-	8	0.99	(Livesley et al., 2009)

Temperate	China	*Pinus sylvestris, Larix principis*	450.1	-1.4	24	1.27	(Wang et al., 2013)
Temperate	USA	*Juniper virginiana*	835	13	14	1.46	(Smith and Johnson, 2004)
Tropical	Australia	*Eucalyptus and Melaleuca*	850	26	12	1.04	(Holt et al., 1990)
Tropical	Brasil	*Cerrado Sensu stricto*	1322	5 - 35	14	4.98	(Rocha et al., 2002)

3. Rainfall as an important driver of ecosystem carbon flux in semi-arid ecosystems

Net ecosystem exchange (NEE) is the net uptake or release of carbon by terrestrial ecosystems, and the difference between gross primary productivity (GPP) and ecosystem respiration (Reco). Net ecosystem exchange is influenced by multiple abiotic and biotic factors (e.g., Morales et al., 2005; Beer et al., 2010; Eamus et al., 2013) and amongst these factors, rainfall amount, frequency and timing are the most important determinants of NEE in dry ecosystems (Weltzin et al., 2003a; Noy-Meir, 1973; Wohlfahrt et al., 2008). Gross primary production and ecosystem respiration are also strongly coupled with rainfall in semi-arid woodlands (Shim et al., 2011a; Cleverly et al., 2013). In 2010-2011, extensive rainfall in many drier areas of the southern hemisphere caused global terrestrial ecosystems to be a net carbon sink (Poulter et al., 2014). Variations in rainfall and temperature regimes in semi-arid ecosystems has also been shown to be the dominant controller of inner-annual variability of terrestrial CO_2 uptake (Ahlstrom et al., 2015).

On the other hand, high temperature and thus evapotranspiration with limited water input can reduce plant growth, and eventually induce dieback (e.g. 97% of the individual trees died during an extended drought in the US (Shim et al., 2011a)). Moreover, long term drought could result in increased decomposition of the large aboveground carbon store from dead trees and thereby influence the balance of soil CO_2 uptake and loss (Williams et al., 2010).

Drought reduces gross primary production and ecosystem respiration which contributes to inter-annual variability in terrestrial carbon sequestration (Pereira et al., 2007).

Jongen et al. (2013) emphasised that large rainfall events can increase water content in deep soil layers that can then alter the carbon balance in Mediterranean woodlands. However, Wohlfahrt et al. (2008) found that in an arid grassland even small amounts of rain after drought can result in an initial pulse of CO_2 to the atmosphere, temporarily reducing NEE or even causing it to switch from a net sink to a net CO_2 source (Wohlfahrt et al., 2008). But this pulse in ecosystem respiration (Reco) is usually short-lived in grasslands (Ma et al., 2012). When the soil profile is wetted to depth from rainfall, vegetation will grow, it's species composition may change and some plants may access temporary or persistent water tables (Ehleringer et al., 1991; Williams et al., 2006). Quantifying the effect of rainfall events on ecosystem carbon cycle is critically important, but recent studies have been carried out only in grass- and shrub-lands which commonly have shallow roots. The effect of large rainfall events on NEE, Reco and GPP from a deep-root (woodland type) ecosystem will be discussed in Chapter 5.

Native woodlands in semi-arid regions may be substantial carbon sinks when seasonal rainfall conditions are favourable (e.g., Thomas et al., 2011; Eamus et al., 2013; Pereira et al., 2007). However, human-induced land use change or natural events like wildfires may change woodland ecosystems from a net carbon sink to a net source (e.g., Sun et al., 2016). The recovery to net carbon uptake (sequestration) depends on intensity of the disturbance and may last from months to more than a decade (e.g., Dore et al., 2012; Iwata et al., 2011).

4. Effect of wildfires on ecosystem and soil carbon fluxes

4.1 Fire effect on ecosystems and soils

Wildfires, often following long periods with little or no rainfall and high temperatures in semi-arid ecosystems, can significantly alter aboveground and belowground biological processes and may influence the global C balance (Flannigan et al., 2009). Fires induce a flush of CO_2 emission from combustion and can damage or kill tree canopies and above ground parts of other plants (e.g. shrubs and grasses) which reduces the capacity of photosynthetic CO_2 fixation (Sommers et al., 2014). Aboveground accumulated plant litter and organic carbon in the upper top soil can also be consumed by wildfire. There is a body of literature on the effects of wildfires on soil properties which is summarized in review articles (e.g., Bento-Gonçalves et al., 2012; Shakesby, 2011). Predicting the influence of fire regimes is likely to become increasingly important as the climate becomes drier (Noble et al., 1996) in some regions of the world.

4.2 Soil respiration and ecosystem carbon flux post-fire

The effects of fire increase with fire severity, which is positively correlated with fuel load (e.g. Molina and Llinares, 2001; Bradstock and Auld, 1995; Wright and Clarke, 2008). Soil respiration rate declined linearly with increasing number of fires and increasing total fuel load in semi-arid woodlands (Tongway and Hodgkinson, 1992). Low intensity fuel reduction burns on the other hand may have no cumulative negative effect on soil respiration (Fest et al., 2015). The influence of fire is therefore vegetation type- and site-specific. In water-limited ecosystems, fire has been shown to have no effect (e.g., Livesley et al., 2011; Sun et al., 2016), reduce (e.g., Richards et al., 2012; Vargas et al., 2012) or even increase soil respiration rates (e.g., Tufekcioglu et al., 2010; Fest et al., 2015).

Due to the reduction in photosynthesis through burning or damaging of leaves, fire is likely to reduce carbon dioxide uptake and turn the affected ecosystem into a net carbon source, as many case studies showed (e.g., Irvine et al., 2007; Dore et al., 2012; Gough et al., 2007). However, Moore et al. (2001) modelled that annual burning in a semi-arid rangeland dominated by Mulga (*Acacia aneura*) caused it to become a small net sink because fire induced a post-fire thickening of the Mulga stands. A Eucalyptus dominated woodland on the other hand, became a net carbon source after fire and resumed net carbon uptake 12-15 months post-fire (Sun et al., 2016). This emphasises the importance of vegetation and climate which not only influences fire intensity, but also plant response after fire.

5. Research aim of the thesis

In the future, frequency and intensity of long-term drought, heat-waves, extreme rainfall events and wildfires are likely to increase in arid and semi-arid regions of Australia and globally (IPCC, 2014; Hughes, 2003; Murphy and Timbal, 2008; Taschetto and England, 2009). Wildfire alters biological activity and carbon fluxes. The frequency of fire in southern Australia is likely to increase as the climate warms and dries (CSIRO and Bureau of Meteorology, 2015) and this will affect Australian dry ecosystems like Mallee communities (Noble et al., 1996). Plants, soils and microbes in dry ecosystems have adapted to water deficiency and survive through long-term drought (e.g., Sardans and Peñuelas, 2013). With these survival attributes, carbon accumulation and turnover in dry ecosystems may differ from other ecosystems for example under temperate climate, where extensive research has been conducted. The aim of this thesis is to contribute to the understanding of carbon flux in semi-arid woodlands and specifically the effect of rainfall and fire on ecosystem carbon flux and soil respiration.

In order to achieve the research aim, a field study was conducted at Calperum Station (34.04° S, 140.71° E), located adjacent to the Chowilla floodplain of the River Murray near Renmark in South Australia. The area is classified as semi-arid with median rainfall of 242 mm and an annual average of 41 rain days. The mean maximum and minimum air temperatures are 24.9 and 9.6 °C (data recorded from 1996 to 2014, from http://www.bom.gov.au/). Two woodlands in this area were selected due to differences in topography, vegetation communities and accessibility of those trees to Murray River water. The first site was Mallee woodland which is a patchy eucalypt-shrub association. The second woodland was located on the River Murray floodplain. Detailed descriptions of plant and soil are given in chapters 4 and 6.

6. Organization of the thesis

Chapter 1 has systematically reviewed the literature to understand the current status of soil respiration and ecosystem carbon flux research in semi-arid ecosystems. Also this chapter aims to identify potential environmental drivers of these fluxes and confirm research questions.

Chapter 2 was published in Biogeosciences. This chapter assessed the response of respiration and nutrient availability to drying and rewetting (a rainfall event simulation) in semi-arid mallee woodland that was recently subject to a wildfire.

Chapter 3 focuses on another important aspect in these nutrient-poor ecosystems: the response of soil microbial activities to addition of available C (as glucose). It has been submitted as a research article to Journal of Soil Science and Plant Nutrition. The experiments in Chapters 2 and 3 were conducted in the laboratory using soil collected from different patches (under tree and shrub canopies and inter-canopy areas).

Chapter 4 was published in Agricultural and Forest Meteorology. This chapter quantifies the influence of patches and a recent wildfire on soil respiration in a semi-arid mallee woodland on sandy soil; explores the relationship between soil water content, temperature and soil respiration; and assesses the effect of fire on ecosystem respiration (Reco), gross primary productivity (GPP) and net ecosystem productivity (NEP) by comparing pre- (during 2013) and post-fire (up to July 2015) data. Soil respiration was measured also in-situ over a 12 month period.

Chapter 5 was submitted to Agriculture, Ecosystems & Environment as a research article. This chapter examines the effect of previous rainfall patterns on responses of ecosystem carbon fluxes to a large rainfall event in the mallee woodland, using eddy covariance data.

Chapter 6 was submitted to Austral Ecology as a research article. This research was conducted in the semi-arid floodplain woodland which has been infrequently flooded due to river management. The chapter quantifies soil respiration rates under tree canopies and from adjacent bare soil in-situ. Moreover, the chapter illustrates the response of soil respiration rates to rainfall events.

Chapter 7 summarizes the research findings and gives recommendations for future research.

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Chapter 2

Response of respiration and nutrient availability to drying and rewetting in soil from a semi-arid woodland depends on vegetation patch and a recent wildfire

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Principal Author

Name of Principal Author (Candidate)	Qiaoqi Sun		
Contribution to the Paper	Experimental development, data collection, analysis and manuscript writing.		
Overall percentage (%)	80		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	02/02/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above); ii. permission is granted for the candidate in include the publication in the thesis; and iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Wayne S. Meyer		
Contribution to the Paper	Supervised experimental design and completion of the work, data interpretation and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	02/02/2017

Name of Co-Author	Georgia R. Koerber		
Contribution to the Paper	Assisted field sample collection and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	02/02/2017

Name of Co-Author	Petra Marschner		
Contribution to the Paper	Supervised experimental design and completion of the work, data interpretation and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	06/02/2017

Abstract

Semi-arid woodlands, which are characterised by patchy vegetation interspersed with bare, open areas, are frequently exposed to wildfire. During summer, long dry periods are occasionally interrupted by rainfall events. It is well-known that rewetting of dry soil induces a flush of respiration. However, the magnitude of the flush may differ between vegetation patches and open areas because of different organic matter content which could be further modulated by wildfire. Soils were collected from under trees, under shrubs or in open areas in unburnt and burnt sandy Mallee woodland, where part of the woodland experienced a wildfire which destroyed or damaged most of the aboveground plant parts four months before sampling. In an incubation experiment, the soils were exposed to two moisture treatments: constantly moist (CM) and drying and rewetting (DRW). In CM, soils were incubated at 80% of maximum water holding capacity (WHC) for 19 days; In DRW, soils were dried for four days, kept dry for another five days, then rewet to 80% WHC and maintained at this water content until day 19. Soil respiration decreased during drying and was very low in the dry period; rewetting induced a respiration flush. Compared to soil under shrubs and in open areas, cumulative respiration per g soil in CM and DRW was greater under trees, but lower when expressed per g TOC. Organic matter content, available P, and microbial biomass C, but not available N were greater under trees than in open areas. Wildfire decreased the flush of respiration per g TOC in the open areas and under shrubs, and reduced TOC and MBC concentrations only under trees, but had little effect on available N and P concentrations. We conclude that the impact wildfire and DRW events on nutrient cycling differ among vegetation patches of a native semiarid woodland which is related to organic matter amount and availability.

1. Introduction

Semi-arid woodlands are wide-spread in regions with Mediterranean climate where in summer, long dry periods are occasionally interrupted by heavy rainfall events. Rewetting of dry soil induces a flush of respiration which has been explained by increased substrate availability due to death of part of the microbial biomass, release of osmolytes accumulated during the dry period and exposure of previously occluded organic matter (Fierer and Schimel, 2002; Navarro-Garcia et al., 2012; Kim et al., 2012; Borken and Matzner, 2009; Birch, 1958). In dry ecosystems, the respiration pulse upon rewetting may contribute a significant proportion of the total annual CO_2 flux from surface soils (Fierer and Schimel, 2003; Jarvis et al., 2007).

The size of the rewetting flush is determined by concentration, availability and distribution of organic carbon (e.g., Butterly et al., 2010; Franzluebbers et al., 2000) and soil water content before rewetting (e.g., Xu et al., 2004; Chowdhury et al., 2011). In semi-arid woodlands, vegetation cover is highly variable with large patches of bare ground between vegetation patches, resulting in large spatial variations in C, N and P concentrations (e.g., Lal, 2004a; Schlesinger and Pilmanis, 1998). Generally soils under vegetation canopies have higher organic C content than interspaces because of the greater C input (White et al., 2009).

Semi-arid woodlands are frequently exposed to fire which changes not only vegetation structure and communities but also soil properties such as reducing soil organic matter content and increasing recalcitrance of the remaining organic matter (Fernandez et al., 1999; Hatten and Zabowski, 2009). These changes in soil organic matter content and recalcitrance could also influence the response of respiration to drying and rewetting.

The aim of this study was to determine the effect of a recent wildfire on response of soil respiration and microbial biomass in soils from different vegetation patches of a semi-arid woodland on nutrient-poor sandy soil. We hypothesised that (i) the flush of respiration after rewetting will be greater in patches with greater TOC concentration, and (ii) burning will reduce soil respiration in all patches irrespective of moisture treatment.

2. Materials and methods

2.1 Site description and soil sampling

The study site was at Calperum Station, next to the Chowilla floodplain of the River Murray near Renmark in the western part of the Murray Basin in south-eastern Australia. This area is the largest (over one million hectares), continuous remnant of Mallee habitat in Australia (Nulsen et al., 1986).The Mallee woodland is a shrub-eucalypt association, including woodlands of four dominant eucalypt species (*Eucalyptus dumosa*, *E. incrassata*, *E. oleosa* and *E. socialis*) and extensive shrublands of spinifex (*Triodia basedowii*).

The area is semi-arid with 251 mm mean annual rainfall and a mean air temperature of 25 °C (data accessed from http://www.bom.gov.au/). Air temperatures of > 40°C or higher are common in summer. The sandy soil (2% clay, 4% silt and 94% sand) has a a bulk density of 1.6 g cm^{-3} in 0-30 cm depth, and is classified as Tenosol in the Australian Soil classification (Isbell, 2002), and as Aridisol in the US Soil Taxonomy (Soil Survey Staff, 1996). A recent wildfire (from 15th to 19th Jan. 2014) burnt part of the woodland. The fuel load for fires in this ecosystem is primarily the spinifex grass clumps and the bark and leaf litter on the soil surface. Due to high temperature, low humidity and high winds in mid-January, the wildfire rapidly consumed the ground based fuel and spread into the Mallee tree canopies. Foliage on the trees was either burnt completely or killed by the high temperatures. Instruments, located up to 10 m from the ground on a flux tower at the site were destroyed by the radiant heat.

Four months after the fire, two locations were sampled: unburnt (34°0'48.78" S, 140°35'33.65" E) and burnt Mallee (34°0'6.34" S, 140°35'14.99" E) woodland which are about 2 km apart from each other. During the four months after the fire, the daily maximum temperatures remained > 30°C with occasional light (< 3mm) rainfall events. Within each location, after removal of the litter layer, soil from 0 to 30 cm depth was collected underneath patches of eucalyptus (hereafter referred to as “tree”) and patches of spinifex (referred to as “shrub”), as well as from open areas between vegetation patches (referred to as “open”). The open areas were completely bare patches without litter or living plants aboveground. Within burnt and unburnt Mallee, three transects > 50 metres apart from each other were randomly selected. Three samples underneath trees, shrubs and in open areas were taken along each transect. The three samples from a given patch were then combined, mixed and sieved to < 2 mm and air-dried at 30 °C. The composite sample was subsampled to give the four replicates in the experiment. In this semi-arid region with high summer temperatures and little annual rainfall on sandy, rapidly draining soils, top soils are air-dry most of the time.

2.2 Experimental design and methods

The air-dried soil was pre-incubated for 14 days at 25 °C at 80 % of water holding capacity (WHC) to reactivate the microbes at the beginning of the experiment. During pre-incubation soil respiration rate was stable after 10 days (data not shown). The water content of 80% WHC was chosen because in a preliminary experiment with different water contents, cumulative soil respiration after 10 days was maximal at 80% of WHC (unpublished data).

After pre-incubation, 25 g dry weight equivalent of pre-incubated soil were packed into PVC cores (37 mm ID × 50 mm height) with a nylon mesh bottom (0.75 µm, Australian Filter Specialists) and then were subjected to either constantly moist (CM) or drying-rewetting

(DRW) treatments. Soil height in the cores was adjusted to achieve the field soil bulk density. Then the cores were transferred to 250 ml glass jars (Ball® Half Pint Wide Mouth Jars, Jarden Corporation) fitted with gas-tight lids which had stainless steel septum ports with rubber septa to allow sampling of headspace.

Half of the cores was maintained at 80% WHC throughout the experiment. The other half of the soil cores were dried within four days (< 0.03 g water per g soil), then kept dry for the next five days, and then rewetted to 80% WHC after which they were maintained at this water content until the end of the experiment (day 19). Within the drying period of four days, the water content gradually decreased but then remained stable. The experiment was stopped when the respiration rate after rewetting was stable for at least two days. To induce rapid drying, a cotton pouch (60 × 60 mm) containing 8 g self-indicating silica gel (BDH Chemical, England) was added to each jar and changed daily until the end of drying period. The silica gel remained in the jars during the dry period. For regenerating of the silica, the pouches were dried at 75 °C overnight. After removal of the silica pouches on day 9, the soil was rewet to 80% of WHC by adding reverse osmosis (RO) water added slowly in a circular motion to ensure uniform wetting. To minimise water loss from the soil in the constantly moist treatment or after rewetting, vials with 7 ml of reverse osmosis (RO) water were placed into the jars. There were 48 cores (two locations, three patches, two moisture treatments and four replicates).

Soil respiration was measured daily. Soil pH and total organic C was measured in air-dried soils. Microbial biomass C, available N and P were measured at the start (after pre-incubation) and the end of the experiment (day 19).

Maximum water holding capacity (WHC) was measured using a sintered glass funnel connected to a 100 cm water column (ψ_m= -10 kPa). The soils were placed in rings in the sintered glass funnel, thoroughly wetted, covered and allowed to drain for > 48 h after which gravimetric water content was determined (Wilke, 2005). Soil pH was measured in a 1:5 soil : water suspension after 1 h end-over-end shaking at 25 °C (Rayment and Higginson, 1992). Total organic carbon (TOC) content was measured by wet oxidation (Walkley and Black, 1934). Soil respiration was quantified using a Servomex 1450 infrared gas analyser (Servomex Group, Crowborough, England), as described by Setia et al. (2011). After each measurement, the jars were opened to refresh the headspace in the jars using a fan to maximise air exchange. Known amounts of CO_2 were injected into empty glass jars of similar volume to establish a linear regression between CO_2 concentration and detector reading. Cumulative respiration expressed per g soil is strongly influenced by TOC content. To estimate organic C decomposability, we expressed soil respiration rate and cumulative respiration per g TOC. Available N (nitrate + ammonium) was determined after 1 h of mixing the soil sample in an end-over-end shaker with 2 M KCl at 1:5 soil: extractant ratio. Nitrate N was measured based on the method modified by Miranda et al. (2001) and ammonium N concentration as described in Forster (1995). Available P was determined by the anion exchange resin method (Kouno et al., 1995). Microbial biomass C (MBC) was measured by fumigation-extraction (Vance et al., 1987). Fumigated and un-fumigated samples were extracted with 0.5 M K_2SO_4 solution at a 1:4 soil: extractant ratio. After filtering through Whatman filter paper No. 42, the organic C concentration of the extracts was determined by titration with 0.033 M acidified $(NH_4)_2 Fe (SO_4)_2.6H_2O$ after dichromate oxidation (Anderson and Ingram, 1993). Microbial biomass carbon was calculated by subtracting the organic C concentration of fumigated from un-fumigated samples and multiplying the difference by 2.64 (Vance et al., 1987).

2.3 Statistical analysis

Two-way analysis of variance (ANOVA) with post-hoc Tukey test was used to determine effects of patch (under shrubs, in open areas and under trees) × burning (unburnt and burnt) on soil pH, total organic C content, and MBC and available nutrient concentrations after pre-incubation (0-day). Data was also analysed by three-way ANOVA to determine effects of patch (under shrubs, in open areas and under trees), burning (unburnt and burnt) and moisture treatment (constantly moist or dry-rewet) and their interactions on respiration rate on day 1 after rewetting and for the following data from day 19 (end of the experiment): cumulative respiration per soil/g TOC, soil MBC and available nutrients. All statistical analyses were carried out with R software (R development Core Team, 2014). Significance was set at $p < 0.05$.

3. Results

3.1 Soil properties

In the unburnt soils, the pH was higher under shrubs than under trees or in the open areas whereas the reverse was true in burnt soils (Table 1). Burning had no consistent effect on soil pH. Compared to unburnt soils, the pH in the burnt Mallee was lower under shrubs, higher under trees and had no effect in open areas. Soil water holding capacity was greatest under trees of unburnt Mallee, but differed little among other patches. Total organic C (TOC) content was higher under trees than in open areas or under shrubs. The difference in TOC content between soil under trees and the other two patches was greater in unburnt Mallee (more than five-fold) than in burnt soils (about two-fold). Burning reduced the TOC content under trees by 50%, but doubled it in the open areas and had no effect under shrubs.

3.2 Respiration

Respiration rate per g TOC decreased within one to three days after the onset of the drying period and then remained low until rewetting (Figure 1). Rewetting of dry soil induced a flush of respiration with rates higher than the constantly moist soils for two days. After this flush, respiration rates were similar in dry-rewet and constantly moist soils.

The respiration rate per g TOC on the first day after rewetting was two to five-fold higher than it was in constantly moist soils (Table 2 and Table A1). For both unburnt and burnt Mallee, the increase in respiration rate per g TOC after rewetting compared to the constantly moist soil was greater under shrubs and in open areas (two-three fold) than under trees (two-fold). Respiration rates in the constantly moist soil were similar in unburnt and burnt Mallee, but the respiration rate on the first day after rewetting was significantly lower (by 40-90%) in open areas and under shrubs of burnt than unburnt Mallee.

Cumulative respiration per g soil on day 19 was greater under trees than in the other two patches (Figure 2, Table A1). Drying and rewetting had little effect on cumulative respiration per g soil except under trees of unburnt Mallee where it was significantly higher in CM than DRW (by 30%). Burning significantly reduced cumulative respiration under trees in both CM and DRW, but had no effect in the other patches.

Cumulative respiration per g TOC on day 19 was not significantly influenced by soil moisture regime (Figure 2, Table A1). In both CM and DRW, cumulative respiration per g TOC was greatest in open areas of unburnt Mallee but differed little among other patches.

Burning reduced cumulative respiration per g TOC only in open areas and only in CM (by about 40%).

3.3 Microbial biomass C

The MBC concentration was higher under trees than under shrubs and in open areas (Figure 3, Table A1). Burning decreased MBC concentrations on day 0 under trees by about 50% compared to unburnt Mallee, increased MBC concentrations in open areas three-fold, but had no effect on MBC concentration under shrubs.

In general, the MBC concentration at the end of the experiment was similar in CM and DRW except under trees in both unburnt and burnt Mallee where it was about 40% higher in DRW than CM. Burning only influenced the MBC concentration under trees of both CM and DRW soils, reducing it by about 60%.

3.4 Nutrient availability

The available N concentration decreased from the start to the end of the experiment (Figure 3). The available N concentration did not differ among patches and was not affected by fire or moisture regime. (Figure 3, Table A1).

The available P concentration was two to three-fold higher under trees than under shrubs and in open areas (Figure 3, Table A1). It was about three times lower in burnt than unburnt soils, particularly under trees, but did not differ between CM and DRW.

4. Discussion

This study showed that the effect of drying and rewetting differed among vegetation patches and open areas in a native semi-arid woodland. Expressed per g TOC, the flush of respiration upon rewetting and cumulative respiration was greater in open areas or under shrubs than under trees. The recent wildfire reduced TOC and MBC concentrations and cumulative respiration only under trees.

4.1 Initial soil properties (patch and fire effect)

Concentrations of total organic C, MBC and available nutrients in Mallee are generally low compared to Australian agricultural soils (Hazelton and Murphy, 2007; Butterly et al., 2010), which indicates that this ecosystem is nutrient limited. This is likely due to the dry climate and low nutrient and water retention capacity of sandy Mallee soils (Nulsen et al., 1986; Macumber, 1990).

The greater TOC and MBC concentration under trees compared to the other patches (Table 1 and Figure 3), is mainly due to greater organic C input by trees (e.g., Gallardo and Schlesinger, 1992; Jobbagy and Jackson, 2000; White et al., 2009; De Deyn et al., 2008). The three-fold higher available P concentrations under trees than other patches is in agreement with previous studies (e.g., Facelli and Brock, 2000; Casals et al., 2014) and can be explained by the greater litter input and translocation of P by roots from deeper soil horizons or surrounding area.

Burning reduced TOC and MBC concentrations only under trees by about 50%, whereas burning increased TOC and MBC in open areas. A positive correlation between TOC and MBC concentration is well-known (e.g., Banu et al., 2004; Kaiser et al., 1992; Gallardo and

Schlesinger, 1992). The loss of TOC under trees can be explained by volatilisation of OC during the fire (Hernandez et al., 1997). It is likely that the temperature during the fire was higher under trees than in the other patches since fire intensity is enhanced by high fuel load, that is organic matter content (Ursino, 2014). The increase of TOC concentration in burnt compared to unburnt open areas can be explained by wind or water erosion after the fire. Burning reduced available P concentrations in all patches, but not available N concentrations. This is not related to TOC loss with fire because that occurred only under trees. The decrease in available P concentrations may be due binding of P to the charred OC (Bock et al., 2015; Laird et al., 2010).

4.2 Effect of patch, fire and moisture in the incubation experiment

Cumulative respiration in the CM treatment was greater under trees than in the other patches when expressed by per g soil, but lower when expressed per g TOC (Figure 2). The greater cumulative respiration per g soil under trees is due to the higher TOC content under trees (Table 1) which is consistent with previous studies and can be explained by litter fall (Gallardo and Schlesinger, 1992; Wang et al., 2003). However, the lower cumulative respiration expressed per g TOC indicates that organic C under trees was less decomposable than in the other patches (Figure 2). This may be due to the nature of the eucalyptus leaves which have a thick waxy cutin layer and are therefore hydrophobic and contain compounds that inhibit microbial activity (Canhoto and Graça, 1996; Borken and Matzner, 2009).

Cumulative respiration per g soil in DRW and CM was greater under trees than under shrubs and in open areas (Figure 2) and this was also true for the flush of respiration upon rewetting (data not shown). This confirms the first hypothesis (the flush of respiration after rewetting will be greater in patches with greater TOC concentration). However, the hypothesis is not supported when respiration is expressed per g TOC because the flush of respiration per g TOC was greater in open areas and under shrubs than under trees (Figure 1 and Table 2). This supports the argument that OC availability is lower under trees. The flush of respiration after rewetting has been shown to be positively correlated with OC content (Butterly et al., 2010), but particularly the active organic C (Franzluebbers et al., 2000). The latter and our results indicate the importance of OC availability and decomposability for the respiration flush.

Burning reduced the flush of respiration per g TOC in the open areas and under shrubs which suggests that burning reduced OC decomposability (Figure 1 and Table 2). However, this was not the case under trees. The fire may have reduced OC decomposability under shrubs and in open areas through charring (Guerrero et al., 2005; Hatten and Zabowski, 2009). The low decomposability of OC under trees was apparently not further decreased by burning. We reject the second hypothesis (burning will reduce soil respiration in all patches irrespective of moisture treatment) because burning reduced cumulative respiration per g soil only under trees and cumulative respiration per g TOC only in open areas (Figure 2).

Although a respiration flush occurred upon rewetting, the effect of DRW on cumulative respiration compared to CM was inconsistent ranging from no effect to a reduction (Figure 2, Table 3). The former indicates that the flush of respiration upon rewetting can compensate for the low respiration during the dry period (Birch, 1958; Chowdhury et al., 2011; Borken and Matzner, 2009). However, the lower cumulative respiration in DRW compared to CM shows that this is not always the case.

DRW also had little effect on MBC concentration and no effect on N and P availability at the end of the experiment. At the end of the experiment (day 19), the MBC concentration differed between CM and DRW only under trees in the unburnt areas and the moisture treatment. It is possible that these parameters differed between DRW and CM just after rewetting. For example, Butterly et al. (2011) showed a short flush of available P after rewetting. However, after two days, available P concentrations did not differ between DRW and CM.

5. Conclusion

The small and transient effect of DRW on the measured parameters suggests that DRW events will have little impact on nutrient cycling in the semi-arid woodland. Similarly, burning only had a limited effect on nutrient availability and soil respiration. This may be due to the low nutrient availability in the sandy Mallee soils. To better understand the role of DRW and burning on soil C flux at an ecosystem scale, field measurements are required which account for the relative sizes and therefore contributions of the different patches.

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Table 1 Properties of unburnt and burnt Mallee soils under shrubs, trees or in open areas (mean, n=4 for pH and TOC values, n=2 for water capacity data). For pH and TOC, different letters indicate significant differences for the burning x patch interaction at $p < 0.05$.

Soil property	Unburnt Mallee			Burnt Mallee		
	Shrub	**Open**	**Tree**	**Shrub**	**Open**	**Tree**
$pH_{1:5}$	9.6^{a}	8.7^{b}	8.8^{b}	7.8^{c}	9.2^{ab}	9.5^{a}
Maximum water holding capacity (g water g^{-1} soil)	0.06	0.06	0.09	0.05	0.06	0.06
Total Organic C (mg C g^{-1} soil)	2.00^{cd}	1.11^{e}	10.45^{a}	1.71^{de}	2.46^{c}	4.66^{b}

Table 2 Soil respiration rate per g TOC and hour on day 1 after rewetting and that under constantly moist treatment (mean ± standard error, n=4). Different letters indicate significant differences at $p < 0.05$ for the three-way interaction patch x burning x moisture treatment.

Patch	Soil respiration rate (mg CO_2-C g^{-1} TOC h^{-1})			
	Unburnt		Burnt	
	1st Day after rewetting	Constantly Moist	1st Day after rewetting	Constantly Moist
Shrub	0.43 ± 0.01^{b}	0.10 ± 0.01^{de}	0.29 ± 0.01^{c}	0.06 ± 0.01^{e}
Open	0.55 ± 0.06^{a}	0.17 ± 0.04^{de}	0.28 ± 0.01^{c}	0.10 ± 0.01^{de}
Tree	0.14 ± 0.00^{de}	0.08 ± 0.00^{e}	0.20 ± 0.01^{cd}	0.08 ± 0.01^{e}

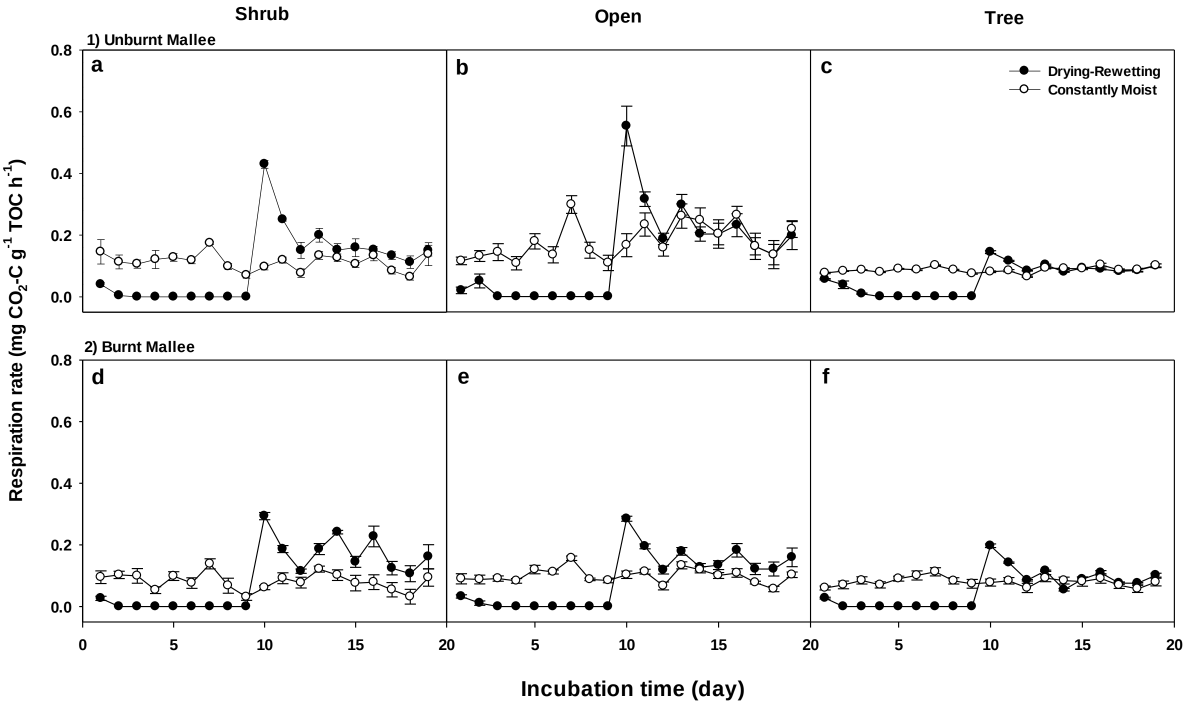

Figure 1 Soil respiration rate per g TOC in soil from under shrubs (a, d), in open areas (b, e) and under trees (c, f) and of unburnt (a-c) and burnt (d-f) Mallee woodlands under constantly moist and dry-rewetting treatments (mean ± standard error, n=4).

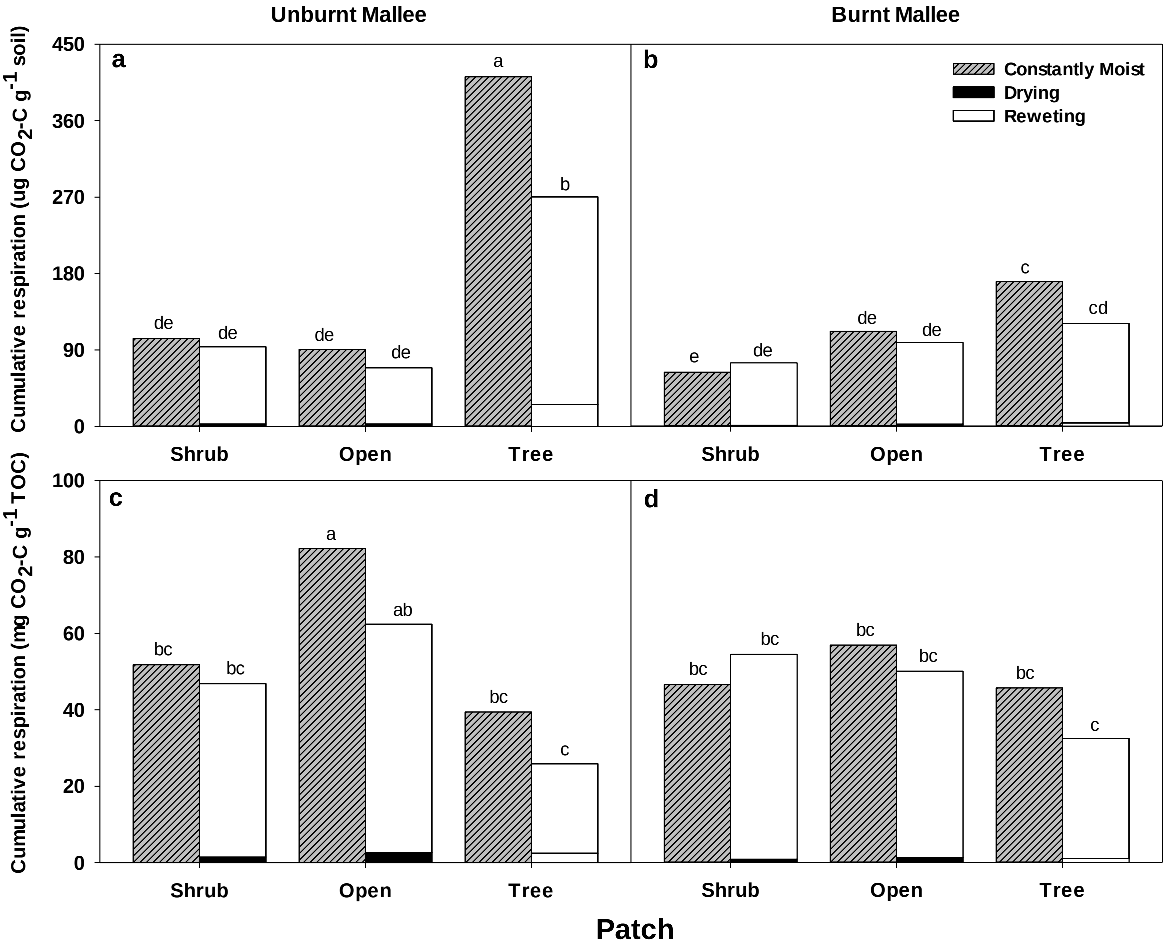

Figure 2 Cumulative respiration per g soil (a and b) and per g TOC (c and d) in constantly moist (CM) and dry-rewetting (DRW) (9-day dry and 10-day moist) soils from unburnt (a, c) and burnt (b, d) Mallee under shrubs, in open areas and under trees (mean, n=4).

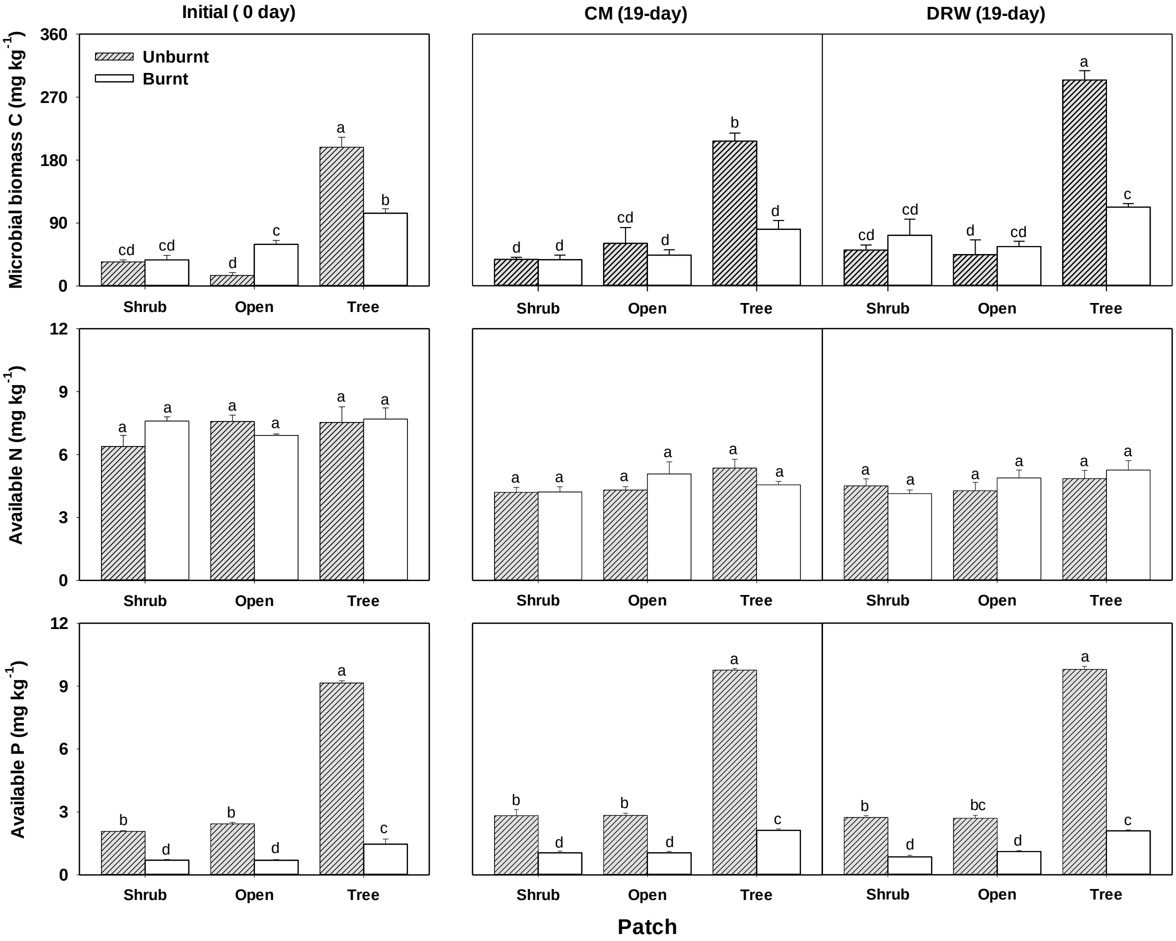

Figure 3 Soil microbial biomass C, available N and P in soil under shrubs, trees or in open areas of unburnt and burnt Mallee woodlands at the start (initial) and end of the experiment in constantly moist – CM and dry-rewetting – DRW treatments (mean ± standard error, n=4). Different letters indicate significant differences for the three-way interaction burning x patch x moisture treatment interaction at $p < 0.05$.

Supplementary Material

Table A1 Outputs of Two-Way or Three-Way Analysis of Variance (ANOVA) analyses of effects of burning (unburnt and burnt), patch (under shrubs, in open areas and under trees) and treatments (constantly moist or dry-rewet) on cumulative respiration per soil, cumulative respiration per g TOC, soil respiration rate on day 1 after rewetting soil, ratio of cumulative respiration per g TOC in DRW to that in CM treatment, microbial biomass C and available N and P (0 day and 19 day).

	Burning	**Patch**	**Treatment**	**Burning × Patch**	**Burning × Treatment**	**Patch × Treatment**	**Burning × Patch × Treatment**
	p	**p**	**p**	**p**	**p**	**p**	**p**
Soil respiration rate on day 1 after rewetting	< 0.001	< 0.001	< 0.001	< 0.001	0.004	< 0.001	0.002
Cumulative respiration per soil on day 19	< 0.001	< 0.001	< 0.001	< 0.001	0.003	< 0.001	0.021
Cumulative respiration per g TOC on day 19	< 0.001	< 0.001	0.015	0.002	0.136	0.158	0.746
pH	0.028	0.008	-	< 0.001	-	-	-
Total organic C	< 0.001	< 0.001	-	< 0.001	-	-	-
Microbial biomass C							
0 Day	0.020	< 0.001	-	< 0.001	-	-	-
19 Day	< 0.001	< 0.001	0.001	< 0.001	0.909	0.011	0.064
Available N							
0 Day	0.538	0.412	-	0.150	-	-	-
19 Day	0.604	0.019	0.891	0.138	0.595	0.882	0.238
Available P							
0 Day	< 0.001	< 0.001	-	< 0.001	-	-	-
19 Day	< 0.001	< 0.001	0.401	< 0.001	0.939	0.690	0.649

Chapter 3

Response of microbial activity to labile C addition in sandy soil from semi-arid woodland is influenced by vegetation patch and wildfire

Statement of Authorship

Title of Paper	Response of microbial activity to labile C addition in sandy soil from semi-arid woodland is influenced by vegetation patch and wildfire
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Principal Author

Name of Principal Author (Candidate)	Qiaoqi Sun		
Contribution to the Paper	Experimental development, data collection, analysis and manuscript writing.		
Overall percentage (%)	80		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	02/02/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above); ii. permission is granted for the candidate in include the publication in the thesis; and iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Wayne S. Meyer		
Contribution to the Paper	Supervised experimental design and completion of the work, data interpretation and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	02/02/2017

Name of Co-Author	Georgia R. Koerber		
Contribution to the Paper	Assisted field sample collection and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	02/02/2017

Name of Co-Author	Petra Marschner		
Contribution to the Paper	Supervised experimental design and completion of the work, data interpretation and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	06/02/2017

Abstract

Nutrient cycling in semi-arid woodlands is likely to be influenced by patchy vegetation, wildfire and the supply of easily available organic C, e.g. root exudates. The study assessed the effect of wildfire and vegetation patch on response of microbial activity to labile C addition in soil from a semi-arid Eucalyptus woodland. Two sites were studied: one unburnt and the other exposed to wildfire four-month before sampling. Top soil (0 – 30 cm) from under trees, under shrubs or in open areas from each site was air-dried and sieved to < 2 mm. The soils were incubated at 80% of maximum water holding capacity for 24 days without or with addition of 5 g C kg^{-1} as glucose. Soil organic carbon (TOC), microbial biomass C, N and P availability and cumulative respiration were greater under trees than in open areas**.** Fire decreased TOC and cumulative respiration only under trees and had little effect on available N, microbial biomass C and P concentrations. The greater increase in cumulative respiration by glucose addition under shrubs and in open areas compared to under trees and, in a given patch, greater in burnt than unburnt soils, indicate lower availability of native organic carbon.

Keywords: Cumulative respiration; Glucose; Microbial biomass; Semi-arid woodland; Vegetation patch; Wildfire

1. Introduction

Semi-arid woodlands are characterised by vegetation patches, often created by single plants, surrounded by open areas with sparse or no vegetation (Tongway and Ludwig, 1994). Consequently, microclimate and soil properties, as well as quantity and quality of plant residues entering the soil vary among vegetation patches and between patches and open areas (e.g., Sardans and Peñuelas, 2013). These variables also strongly influence organic C content, microbial activity and growth (Gallardo and Schlesinger, 1992). Therefore semi-arid woodlands and other semi-arid vegetation types are not only characterised by patchy vegetation, but also by hotspots of microbial activity (Goberna et al., 2007).

In southern Australia, large semi-arid areas on predominantly sandy soils are covered by mallee vegetation that consists of patches of *Eucalyptus* spp. or spinifex (*Triodia basedowii*) interspersed by open areas. Increased duration and severity of drought or infrequent rainfall events are likely to increase risk of wildfire in dry regions (IPCC, 2014). Fire effects increase with fire severity, which is positively correlated with fuel load (Wright and Clarke, 2008). Fuel load and therefore fire intensity are likely to be highly spatially variable in the patchy semi-arid woodlands. The direct consequences of fire are loss of foliage and organic matter aboveground and in the top few centimetres of the soil (e.g. Certini, 2005) and may also influence other soil properties such as nutrient availability (e.g., nitrogen (Wan et al., 2001)). The effect of fire on biological soil properties has been studied in the past, but mainly in temperate and Mediterranean regions with higher annual rainfall than in the semi-arid woodlands in southern Australia (e.g., Boerner et al., 2008). In these studies, fire altered soil microbial community composition, enzyme and soil respiration. However, it remains unclear if fire effects differ among patches with distinct differences in the amount of litter and standing biomass, as typical in semi-arid woodlands. A better understanding of the effect of fire is important because in south-eastern Australia and other semi-arid areas around the world, wildfire frequency and intensity are predicted to increase in a future drier climate (Head et al., 2014). Recently, we reported that the effect that wildfire and drying-rewetting (DRW) events had on nutrient cycling differ among vegetation patches of a native semiarid woodland is related to organic matter amount and availability (Sun et al., 2015).

Many Australian native plants from these areas are adapted to fire and regrow after fire, e.g. from lignotubers of eucalyptus species (Clarke et al., 2015). Root growth and exudation will be initially reduced by burning, but are likely to resume after regrowth of eucalyptus and native grasses. Root exudates are an important source of available C for soil microbes (Bertin et al., 2003). A large proportion of soil organic matter has a complex composition and often low accessibility due to binding to soil particles and occlusion within aggregates (Baldock, 2007). Therefore availability of soil organic matter to soil microbes is limited, which explains the increase in soil respiration after the addition of labile C (Hoyle et al., 2008). We suggest that the increase in soil respiration and microbial biomass induced by labile C is related to native organic C availability, being greater if native organic matter availability is low compared to a soil with higher availability of native organic matter.

The aims of this experiment were to (i) assess the effect of wildfire in the patchy vegetation of the semi-arid woodland on soil properties, and (ii) determine the response of soil respiration and microbial biomass C to addition of labile organic C. The first hypothesis is that the effect of a recent wildfire on the soil organic matter, nutrient availability, microbial biomass and activity differs among patches, and is greater under trees compared to soil under shrubs or in open areas. This is based on the assumption that fire intensity is greater under trees because organic matter content and therefore fuel load are greater than under shrubs and in open areas. The second hypothesis is that the increase in soil respiration after addition of labile C (glucose) is greater in soils with low native organic matter content or availability. This is based on the assumption that microbial activity is limited by available substrates.

2. Materials and methods

2.1 Study site and soil sampling

The study site and soil sampling are as described in Sun et al. (2015). The study site was a semi-arid woodland on Calperum Station, located adjacent to the River Murray near Renmark in South Australia. The mallee woodland in the study area consists of shrub-eucalypt associations and forms the western part of the Murray Basin. The area is semi-arid with 251 mm mean annual rainfall and a mean air temperature of 25 °C (data accessed from http://www.bom.gov.au/). Vegetation in the mallee woodland includes four dominant *Eucalyptus* species (*E.dumosa*, *E. incrassata*, *E. oleosa* and *E. socialis*) and extensive shrublands of spinifex (*Triodia basedowii*). Imagery recorded by an unmanned aircraft (about 1 ha area at 0.01 m resolution) showed that approximately 25% of the area is under eucalypt tree canopies and 25% covered by spinifex (Sun et al., 2016). The sandy soil (2% clay, 5% silt and 93% sand, at 0-30 cm depth) has a bulk density of ~1.6 g cm^{-3}.

After about two weeks of daytime temperatures of > 35 °C, an extensive area of the semi-arid woodland was burnt from 15 to 19 January 2014, four months before the soils were collected for this study (mid May 2015). According to the Country Fire Service, South Australia, the fire affected about 5.3×10^4 hectares of semi-arid woodland. The wildfire had high intensity because it consumed spinifex clumps, bark and leaf litter in the soil O horizon and spread into the tree canopies burning the foliage. Although large areas were affected by the fire, small and isolated locations of woodlands remained unburnt due to discontinuous distribution of trees, shrubs and litter. During the four months after the fire, it was warm to hot and remained mainly dry. Although the total amount of rainfall in this period was 80 mm, this was concentrated in a few rainfall events, the largest in February with 42 mm.

Soil collection was as described in Sun et al. (2015). Briefly, soil was collected from two sites: unburnt (34°0'48.78" S, 140°35'33.65" E) and burnt mallee (34°0'6.34" S, 140°35'14.99" E). The two woodland sites were about 2 km apart. Within each site, after removal of the litter layer, soil (0-30 cm) was collected under patches of eucalypt trees (hereafter referred to as “tree”) and patches of spinifex (referred to as “shrub”), as well as from open areas between vegetation patches (referred to as “open”) which had no litter or living plants aboveground. In each sampling site, three transects > 50 m apart from each other were randomly selected. Several soil samples (> 3) were taken and then pooled to give one composite sample per site and patch. The soil was sieved to < 2 mm and air-dried at 30 °C. In the study area, top soils are air-dry for most of the year. Soil from the top 30 cm was collected because root and microbial densities are higher in this layer than in deeper soil and microbes are more likely to encounter root exudates.

2.2 Experimental design

A preliminary experiment was carried out to determine the optimal water content for soil respiration. The soils were incubated at 40 to 80% of maximum water holding capacity (WHC), at 10% intervals. Cumulative soil respiration measured after 10 days was maximal at 80% of WHC (data not shown). Before starting the experiment, the air-dried soil was pre-incubated for 14 days at 25 °C at 40% of WHC to reactivate the microbes. During the pre-incubation soil respiration rates were stable after 12 days (data not shown).

After pre-incubation, 5 g glucose C kg^{-1} soil was added as solution (10 ml kg^{-1}) and mixed thoroughly into the soil. The non-amended soils received the same amount of water and mixed in a similar manner. Addition of glucose solution or water increased the water content to 80% of WHC. Twenty grams dry weight equivalent of pre-incubated soil with and without glucose was packed into PVC cores (37 mm inner diameter × 50 mm height) with a nylon mesh (0.75 μm, Australian Filter Specialists) at the bottom. Soil height in the cores was adjusted to achieve field soil bulk density. Then the soil cores were transferred to 250 ml glass jars (Ball® Half Pint Wide Mouth Jars, Jarden Corporation) fitted with gas-tight lids. The lids had stainless steel septum ports with rubber septa to allow sampling of the headspace. To minimise water loss from the soil, vials with 7 ml of reverse osmosis (RO) water were placed in the jars. There were 48 cores (two sites, three patches, two C treatments (with and without glucose amendment) and four replicates).

Soil respiration was measured daily until the end of experiment (24 days). Microbial biomass P and available N and P were measured after pre-incubation. Microbial biomass C was measured after pre-incubation and at the end of the experiment.

2.3 Methods

Water holding capacity (WHC) was measured using a sintered glass funnel connected to a 100 cm water column (ψ_m= -10 kPa). The soils were placed in rings on a sintered glass funnel, thoroughly wetted, covered and allowed to drain for over 48 h before determining gravimetric water content (Wilke, 2005). Soil pH and EC were measured in a 1:5 soil : water suspension after 1 h end-over-end shaking at 25 °C (Rayment and Higginson, 1992). Total organic carbon (TOC) content was determined by wet oxidation (Walkley and Black, 1934). Soil particulate organic C (POC) and mineral associated organic C (MaOC) were isolated following Cambardella & Elliott (1992), then organic matter was measured as described for TOC. They are expressed in percentage of OC recovered. Available N (nitrate and ammonium) was determined after 1 h end-over-end shaker with 2M KCl at 1:5 soil extractant ratio. Nitrate N was measured based on the method modified by Miranda et al. (2001) and ammonium N as described in Forster (1995). Available P and microbial P were determined by the anion exchange resin method (Kouno et al., 1995). Microbial biomass C (MBC) was measured by fumigation-extraction (Vance et al., 1987). Fumigated and un-fumigated samples were extracted with 0.5 M K_2SO_4 solution at a 1:4 soil to extractant ratio. After filtering through Whatman filter paper No. 42, the organic C concentration of the extracts was determined by titration with 0.033 M acidified $(NH_4)_2 Fe (SO_4)_2.6H_2O$ after dichromate oxidation (Anderson and Ingram, 1993). Microbial biomass carbon was calculated by subtracting the organic C concentration of fumigated from un-fumigated samples and multiplying the difference by 2.64 (Vance et al., 1987).

Soil respiration (CO_2 release) was quantified by using a Servomex 1450 infrared gas analyser (Servomex Group, Crowborough, England); for a detailed description see Setia et al. (2011) and Elmajdoub and Marschner (2015). After each measurement, the jars were opened to refresh the headspace in the jars using a fan to maximise air exchange. Known concentrations of CO_2 were injected into empty glass jars of similar volume to establish a linear regression between CO_2 concentration and detector reading. Glucose induced cumulative respiration was calculated by dividing cumulative respiration of glucose-amended soil by that of non-amended soil.

2.4 Statistical analysis

Two-way analysis of variance (ANOVA) with a post-hoc Tukey test was used to determine effects of burning (unburnt and burnt) and patch (open, shrub and tree) on soil properties at the start of the experiment and on the ratio of cumulative respiration (amended/non-amended) on day 24. Cumulative respiration and MBC on day 24 were also analysed by three-way ANOVA with a post-hoc Tukey test to determine effects of burning, patch and glucose treatment (without or with glucose). General linear regression was used to determine the relationship between the ratio of glucose induced cumulative respiration to that in un-amended soil and total organic C and MBC. All statistical analyses were carried out with R software (R development Core Team, 2014). Significance was set at $p<0.05$.

3. Results

3.1 Soil properties

As reported in Sun et al. (2015), the soil pH ranged from 7.5 to 9 (Tables 1, 2). In unburnt soils, the pH was highest under shrubs and lowest in open areas. In burnt soils, the pH under shrubs was lower than under trees and in open areas. Burning had no consistent effect on soil pH. Compared to the unburnt soils, burning significantly reduced the pH under shrubs, increased it in open areas, but had no effect under trees. All soils were non-saline ($EC_{1:5} < 0.4$ dS m^{-1}) (Table 1). Burning did not influence EC under trees, but reduced it under shrubs and increased it in open areas.

Total organic C (TOC) content was generally low (< 1%), but higher under trees than under shrubs and in open areas before and after the wildfire (Table 1, 2). Fire reduced TOC content by 50% under trees, but doubled it in open areas and had no effect on TOC content under shrubs. Differences in TOC content among patches were smaller in burnt than in unburnt areas. In the unburnt area, the TOC content under trees was nearly 10-fold higher than in open areas whereas in the burnt area, the TOC content was only about 2-fold higher under trees. The proportion of recovered organic C as particulate organic C (POC) in unburnt soils was greatest under trees, but in burnt it was greatest under shrubs. The reverse was true for the proportion as mineral associated organic carbon (MaOC). The effect of burning on TOC content and proportion as POC and MaOC was inconsistent. Burning nearly doubled the proportion of POC under shrubs, but had no effect under trees and in open areas. Correspondingly, the proportion of MaOC under shrubs was halved by burning.

Available N concentrations after pre-incubation did not differ among patches and was not influenced by fire (Table 1, 2). The available P concentration was highest under trees in both unburnt and burnt soils (Table 1). Burning reduced available P concentrations one to three-fold in all three patches. In unburnt soil, the available P concentration was similar under shrubs and in open areas, but in burnt soil it was lower under shrubs.

The MBC and MBP concentrations after pre-incubation were highest under trees (Tables 1, 2). Burning reduced MBC concentration only in open areas. Compared to unburnt soils, the MBP concentration in burnt soils was higher in open areas, lower under shrubs and not different under trees.

3.2 Soil respiration

Cumulative respiration was significantly higher in glucose-amended soils compared to un-amended soils (Figure 1, Table 3). Without glucose, cumulative respiration in unburnt soils was higher under trees than under shrubs or in open areas, but in burnt soils cumulative respiration under trees was only higher under shrubs (Figure 1a). Burning reduced cumulative respiration under trees and shrubs, but not in open areas. In glucose amended soils, cumulative respiration was highest under trees in both burnt and unburnt soils (Figure 1b). Burning reduced cumulative respiration in amended soils under trees, but increased it in open areas and had no effect under shrubs.

The ratio of glucose-induced cumulative respiration to cumulative respiration in the non-amended soil was greater in burnt than in unburnt soils and smallest under trees (Tables 2, 4). In unburnt soils, the ratio was higher in open areas than under shrubs whereas the reverse was true in burnt soils. The ratio was negatively correlated with TOC content ($F_{1, 22} = 11.92$, $r^2 = 0.35$, $p < 0.01$) and MBC concentration ($F_{1, 22} = 4.40$, $r^2 = 0.17$, $p < 0.05$).

3.3 Microbial biomass C after incubation

Glucose addition increased MBC concentration after 24 days by 20-60 % compared to non-amended soils (Figure 2, Table 3). For a given patch there were no significant differences in MBC concentration between unburnt and burnt mallee soils. In the non-amended soils, the MBC concentration was greater under trees than under shrubs or in open areas. In glucose amended soils, the MBC concentration was higher under trees than under shrubs. But compared to open areas, the MBC concentration under trees was only higher in burnt soils.

4. Discussion

This study showed that in the semi-arid woodland, microbial biomass and activity, organic C content and nutrient availability differed between vegetation patches and bare soils, but the effect of the recent fire on the measured parameters was small. The increase in cumulative respiration after addition of labile organic carbon differed between patches and was influenced by fire.

Our first hypothesis (the recent wildfire reduces organic matter content, nutrient availability and microbial biomass and activity compared to an adjacent non-burnt site, particularly under trees) was based on the loss of organic matter and nutrients via volatilisation during the fire and wind and water erosion after the fire. However the hypothesis can only be partly confirmed.

The TOC content was greater under trees than under shrubs or in open areas before and after the wildfire (Table 1). This can be explained by the greater organic C input by trees than in open areas which have no or only sparse ephemeral plant cover (Jobbagy and Jackson, 2000; White et al., 2009). The high proportion of POC under trees indicates that most of the organic C was in form of loose plant material. Compared to unburnt soils, burning reduced TOC content and cumulative respiration under trees, but had no effect on cumulative respiration in open areas or under shrubs in non-amended soils (Figure 1). Organic matter is the energy and nutrient source of soil microbes (Gallardo and Schlesinger, 1992; Cortez et al., 2014), therefore in non-amended soils, burning also reduced cumulative respiration under trees.

On the other hand, burning increased TOC content in open areas. This increase in TOC is likely because open areas can receive organic matter from vegetated areas through wind and water erosion, which would be greater after fire than in the unburnt areas (Shakesby, 2011). Input of organic matter from adjacent areas (i.e. tree and shrub patches) by wind and water erosion may also explain why there were no consistent differences in percentage POC, MaOC and MBP concentrations between patches (Table 1). Differences in MBP concentrations were more likely due to the inconsistent fire effect on soil organic matter content which is an important source of P for microbes (Alamgir and Marschner, 2016). Phosphorus does not volatilise during fire (Certini, 2005). However, fire reduced available P concentrations by about 60% compared to unburnt soils. This may be due to binding of available P to charred OC (Laird et al., 2010).

Wildfire did not influence available N or MBC concentrations at the start of the experiment except for a lower MBC concentration in open areas in burnt soils (Table 1). Patches also did not differ in available N or MBC concentration. The lack of fire and patch effect on measured parameters may be due to the generally low nutrient availability in the sandy soils where, even in the absence of fire, nutrient cycling is limited (Orians and Milewski, 2007).

In agreement with previous studies (e.g., Hoyle et al., 2008), glucose addition increased soil respiration up to 20-fold (Figure 1, Table 4). The large increase in respiration after addition of easily available organic C suggests that low availability of native organic C limits microbial activity. The low availability of soil organic matter can be explained by its complex structure and binding to soil particles and occlusion within aggregates which reduces accessibility (Baldock, 2007). The proportion of the latter is indicated by mineral associated OC which ranged between 23 and 58% of organic C recovered.

This study confirmed our second hypothesis [the increase in soil respiration after addition of labile C (glucose) is greater in soils with low native organic matter content and availability] because the ratio of glucose induced cumulative respiration to that in un-amended soil was greater under shrubs and in open areas than under trees and, for a given patch, greater in burnt than unburnt soils. And the ratio was negatively correlated with TOC content. The greater ratio of glucose induced cumulative respiration to that in un-amended soil in burnt compared to unburnt soils may be due to the lower organic C content in the former. But the ratio was also higher under shrubs where the organic C content did not differ between burnt and unburnt soils. This suggests that organic C was less available in burnt soils which may be due to charring by the fire. Charred organic C is poorly decomposable (Kuzyakov et al., 2009). In the field, fresh root growth during regrowth after fire would provide a source of available C through root exudates, particularly under trees and shrubs with possibly greater exudation than in unburnt soils where the root system consists predominantly of older roots (Bardgett et al., 2005).

5. Conclusion

This study showed that in semiarid mallee woodlands, only the presence of trees increased TOC content, available P, MBP and MBC concentrations compared to open areas, whereas the presence of shrubs had little effect. This may be due to the inherent low fertility of the soils in this area and wind and water erosion which limits the expression of patches. The effect of fire on the measured parameters differed among patches, but was generally small. In future studies, soils at different distance from trees could be investigated to better understand the extent of the patch effect. The responses of soils from different patches to addition of available C was related to TOC content, being greater in soils with low TOC content and also greater in burnt soils suggesting lower availability of charred organic matter.

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Table 1 Properties of soils from unburnt and burnt semi-arid woodland in open areas or under shrubs and trees or (mean ± standard error, n=4). Different letters in columns indicate significant differences at $p<0.05$ (from Sun et al. 2015).

Site	**Patch**	**pH$_{1:5}$**	**EC**	**Total Organic C**	**POC**	**MaOC**	**Available N**	**Available P**	**Microbial biomass C**	**Microbial biomass P**
			(dS m^{-1})	**(%)**	**(%)[1]**		**(mg kg^{-1})**			
Unburnt mallee	**Open**	7.41 ± 0.09^{c}	0.01 ± 0.00^{d}	0.11 ± 0.01^{e}	42.2 ± 5.23^{c}	57.8 ± 5.2^{a}	3.8 ± 0.2^{ab}	2.7 ± 0.1^{bc}	89.7 ± 8.0^{a}	0.3 ± 0.1^{c}
	Shrub	9.03 ± 0.02^{a}	0.09 ± 0.00^{a}	0.20 ± 0.01^{d}	46. 9 ± 5.8^{bc}	53.1 ± 5.8^{ab}	3.1 ± 0.2^{b}	2.8 ± 0.1^{b}	71.6 ± 28.6^{ab}	1.0 ± 0.0^{b}
	Tree	8.67 ± 0.03^{b}	0.07 ± 0.00^{b}	1.04 ± 0.01^{a}	63.8 ± 2.7^{ab}	36.2 ± 2.7^{bc}	4. 5 ± 0. 5^{ab}	5.4 ± 0.1^{a}	98. 9 ± 9.6^{a}	1. 6 ± 0.2^{a}
Burnt mallee	**Open**	8.68 ± 0.02^{b}	0.07 ± 0.00^{c}	0.25 ± 0.01^{c}	42.6 ± 3.1^{c}	57.4 ± 3.1^{a}	4.8 ± 0.3^{a}	1.7 ± 0.1^{d}	5.5 ± 1.1^{b}	1.0 ± 0.1^{b}
	Shrub	7.51 ± 0.06^{c}	0.02 ± 0.00^{d}	0.17 ± 0.01^{d}	77.3 ± 1.1^{a}	22.8 ± 1.1^{c}	4.4 ± 0.3^{ab}	1.1 ± 0.1^{e}	43.0 ± 11.2^{ab}	0.6 ± 0.0^{c}
	Tree	8.72 ± 0.01^{b}	0.07 ± 0.00^{b}	0.47 ± 0.01^{b}	53.9 ± 2.6^{bc}	46.1 ± 2.6^{ab}	4.5 ± 0.5^{ab}	2.5 ± 0.1^{c}	85.2 ± 26.3^{a}	1.5 ± 0.1^{a}

[1] percentage of recovered organic C.

POC – Particulate organic C; MaOC – mineral associated organic C.

Table 2 Outputs of two-away analysis of variance analyses (ANOVA) of effects of burning (unburnt and burnt) and patch (open, shrub, and tree) on soil properties at the start of the experiment and on ratio of cumulative respiration (amended/non-amended) on day 24.

	Burning	**Patch**	**Burning × Patch**
	p		
pH	0.11	<0.001	<0.001
EC	<0.001	<0.001	<0.001
Total organic C	< 0.001	< 0.001	< 0.001
POC	0.04	< 0.001	< 0.001
MaOC	0.04	< 0.001	< 0.001
Available N	0.01	0.08	0.14
Available P	< 0.001	< 0.001	< 0.001
Microbial biomass P	0.27	< 0.001	< 0.001
Microbial biomass C	0.01	0.05	0.13
Ratio of cumulative respiration (amended/non-amended)	< 0.001	< 0.001	< 0.001

Table 3 Outputs of three-way analysis of variance analyses (ANOVA) of effects of burning (unburnt and burnt), patch (open, shrub, and tree) and amendment (without or with glucose) on cumulative respiration and microbial biomass C on day-24.

	Burning	**Patch**	**Treatment**	**Burning × Patch**	**Burning × Treatment**	**Patch × Treatment**	**Burning × Patch × Treatment**
	p						
Microbial biomass C	0.25	< 0.001	< 0.01	0.42	0.92	0.11	0.13
Cumulative respiration	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.51

Table 4 Ratio of cumulative respiration of amended to non-amended soils from unburnt and burnt semi-arid woodland in open areas or under shrubs and trees (mean ± standard error, n=4). Different letters indicate significant differences at $p<0.05$.

Site	**Patch**	**Ratio of cumulative respiration (amended/non-amended)**
Unburnt mallee	Open	8.7 ± 0.2^{c}
	Shrub	7.6 ± 0.3^{d}
	Tree	3.6 ± 0.2^{e}
Burnt mallee	Open	10.3 ± 0.1^{b}
	Shrub	20.1 ± 1.0^{a}
	Tree	7.9 ± 0.4^{cd}

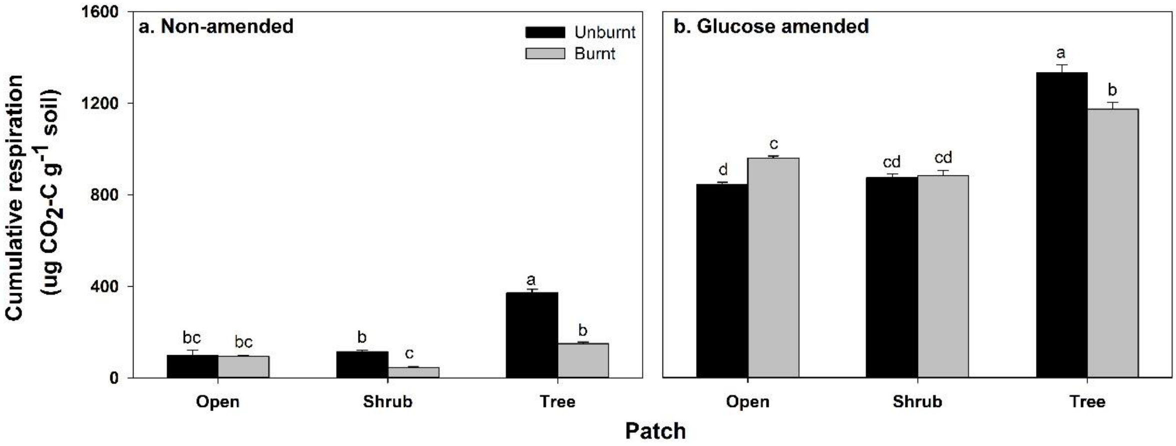

Figure 1 Cumulative respiration on day 24 in non-amended (a) and glucose amended soils (b) from unburnt and burnt semi-arid woodland in open areas or under shrubs and trees (mean ± standard error, n=4). Within each graph, columns with different letters are significantly different at $p<0.05$.

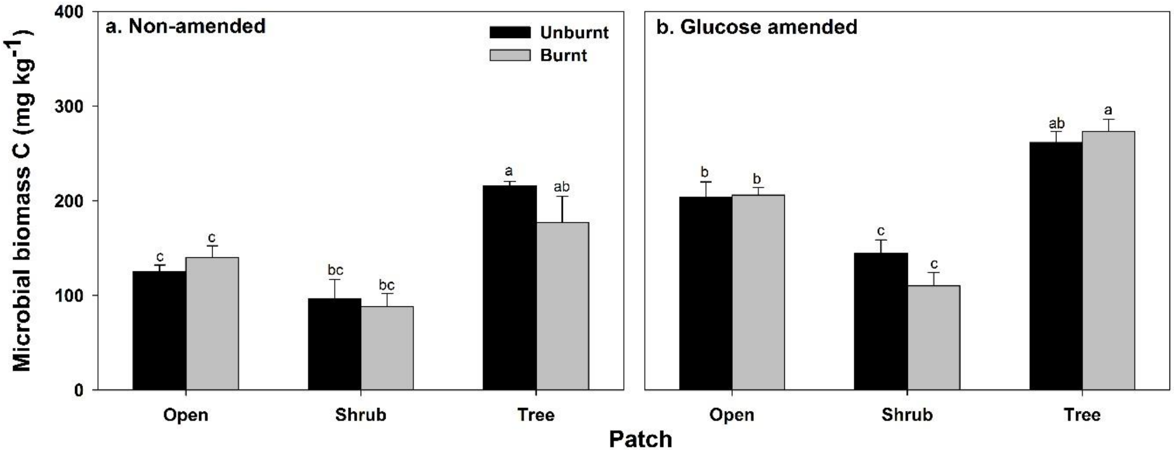

Figure 2 Microbial biomass carbon (MBC) (mean ± standard error, n=4) in non-amended (a) and glucose amended soils (b) from unburnt and burnt semi-arid woodland in open areas or under shrubs and trees on day 24 (mean ± standard error, n=4). Within each graph, columns with different letters are significant different at $p<0.05$.

Chapter 4

A wildfire event influences ecosystem carbon fluxes but not soil respiration in a semi-arid woodland

Statement of Authorship

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Principal Author

Name of Principal Author (Candidate)	Qiaoqi Sun		
Contribution to the Paper	Experimental development, data collection, analysis and manuscript writing.		
Overall percentage (%)	80		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	02/02/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above); ii. permission is granted for the candidate in include the publication in the thesis; and iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Wayne S. Meyer		
Contribution to the Paper	Supervised experimental design and completion of the work, data interpretation and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	02/02/2017

Name of Co-Author	Georgia R. Koerber		
Contribution to the Paper	Assisted field sample collection and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	02/02/2017

Name of Co-Author	Petra Marschner		
Contribution to the Paper	Supervised experimental design and completion of the work, data interpretation and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	06/02/2017

Abstract

The importance of arid and semi-arid ecosystems for global net carbon uptake has recently been highlighted. More information about the drivers of carbon fluxes in these ecosystems is required to advance our understanding of the contribution of dry ecosystems to the global carbon budget. In this study, eddy covariance flux data was used to calculate net ecosystem productivity (NEP), gross primary productivity (GPP) and ecosystem respiration (Reco) in a semi-arid woodland on sandy soil. In January 2014 a wildfire severely damaged the area around the flux tower, burning trees and spinifex and consuming aboveground bark and leaf litter. The flux tower recorded data for one year before the fire (January – December 2013) and more than one year after the fire (May 2014 – July 2015). Soil respiration was measured in-situ monthly after the fire (July 2014 – June 2015), in burnt and unburnt areas under *Eucalyptus* tree canopy and inter-canopy representing 25 and 75% of the area, respectively. Before the fire the ecosystem was a net carbon sink, sequestering 81 g C m^{-2} yr^{-1} in 2013, but became a carbon source after the fire (- 88 g C m^{-2} yr^{-1}, data from May 2014 – July 2015). Reco and GPP declined by about 35% and 65%, respectively, after the fire. Net carbon uptake resumed 12 to 15 months after the fire with NEP approaching values similar to those before the fire. Soil respiration was significantly higher under tree canopies (1.5 µmol CO_2 m^{-2} s^{-1}) than in inter-canopy areas (0.9 µmol CO_2 m^{-2} s^{-1}). Soil respiration was mainly driven by soil water content and thus magnitude and distribution of precipitation, but was not influenced by the wildfire. Accounting for differences in area, soil respiration from inter-canopy and under canopy contributed 51 and 32% to total ecosystem respiration implying that 17% was from aboveground vegetation. It can be concluded that carbon flux in this semi-arid woodland was strongly influenced by precipitation and wildfire, with net carbon uptake of the ecosystem beginning approximately one year after the fire.

Keywords: ecosystem carbon flux, eddy covariance, precipitation, semi-arid woodland, soil respiration, wildfire

1. Introduction

Arid and semi-arid regions occupy more than a third of the world's land area. Plant growth and hence carbon exchange are generally slow in these regions, but due to their extensive area semi-arid environments play an important role in global C fluxes (Lal, 2004a; Reynolds et al., 2007). It has been suggested that large areas in Australia's semi-arid regions may act as substantial carbon sinks (Haverd et al., 2013) when seasonal precipitation conditions are favourable. Indeed, in 2010-2011, extensive precipitation in many of the drier areas of the southern hemisphere caused terrestrial ecosystems to be net carbon sinks, with about 60% of this uptake attributed to Australian ecosystems (Poulter et al., 2014; Haverd et al., 2016).

With global warming the frequency and intensity of long-term drought, heat-waves and wildfires are likely to increase in the dry regions of Australia (Hughes, 2003; Murphy and Timbal, 2008; Taschetto and England, 2009) and globally (IPCC, 2014). It is well-known that temperature and precipitation are the main drivers of the terrestrial carbon exchange (Collins et al., 2008; Weltzin et al., 2003a; Wu et al., 2011; Austin et al., 2004), particularly in semi-arid ecosystems (Talmon et al., 2011; Valentini et al., 2000; Heisler-White et al., 2008). Variations in precipitation and temperature regimes in semi-arid ecosystems has also been shown to be the dominant controller of trend and inner-annual variability of the land CO_2 uptake (Ahlstrom et al., 2015).

Soil respiration is the second largest carbon flux of the global carbon cycle (Raich et al., 2002; Raich and Potter, 1995) and plays an important role in ecosystem respiration which also includes autotrophic respiration (Janssens et al., 2001). Soil water content, which is influenced by precipitation patterns, influences soil respiration in ecosystems with annual precipitation between 300 and 4700 mm and distinct dry periods (e.g. Jha and Mohapatra, 2011; Rey et al., 2011; Correia et al., 2012; Kiese and Butterbach-Bahl, 2002; Jin et al., 2009b; Jin et al., 2009a). However, few studies have been carried out in semi-arid woodlands with < 300 mm rainfall (Bond-Lamberty and Thomson, 2014). Given the global extent of semi-arid and arid ecosystems, more information about drivers of soil respiration in these ecosystems is needed.

Wildfires, commonly occurring after long-term drought and high temperatures in semi-arid ecosystems, strongly affect aboveground and belowground biological processes and thus influence global C balance (Flannigan et al., 2009). Fire induces a flush of CO_2 emission from combustion, and can damage or kill tree canopies and other aboveground green plants (e.g., shrubs and grasses) which will reduce the capacity of photosynthetic fixation of CO_2 (e.g., Sommers et al., 2014). The impact of wildfires on ecosystems depends on fire intensity and fuel load (Flannigan et al., 2009). Accumulated surface plant litter and organic carbon in the top soil are most likely to be consumed by wildfires, which can reduce soil respiration (Trumbore and Czimczik, 2008; Richards et al., 2012).

Woodlands in semi-arid areas are often characterised by “clumped” vegetation separated by large open areas with little or no plant growth (Tongway and Ludwig, 1994), also referred to as “patchy” vegetation arrangement. The endemic plants are adapted to variable and scarce available water by growing slowly even after precipitation, water use is conservative and growth can be sustained for long periods (e.g. Nulsen et al., 1986; Morton et al., 2011; O'Grady et al., 2009; Turner, 1986). This persistence is supported by deep roots accessing water in a large root zone volume of soil. Many plants in these woodlands are also adapted to fire (Orians and Milewski, 2007; Balston and Williams, 2014) and fire intensity is highly variable in these patchy ecosystems because of uneven distribution of flammable resources. It is therefore to be expected that carbon accumulation and turnover in semi-arid woodlands will respond to precipitation and fire differently than in temperate forests. Quantification of ecosystem C uptake and release in response to precipitation and fire in semi-arid woodlands is needed.

The study described here addresses this knowledge gap. It was conducted in a semi-arid woodland (‘the Mallee’) in South Australia characterised by patchy vegetation on sandy soils with a dry Mediterranean climate. Part of the site was burned by a wildfire in January 2014 after more than 10 days with day time temperatures of > 35 °C. The aims of this study were to: (i) determine the influence of patches and a recent wildfire on soil respiration in a semi-arid Eucalyptus woodland on sandy soil; (ii) determine the relationship between soil water content, temperature and soil respiration; and (iii) assess the effect of fire on ecosystem respiration (Reco), gross primary productivity (GPP) and net ecosystem productivity (NEP) by comparing pre- (during 2013) and post-fire (up to July 2015) data. We hypothesised that: (i) soil respiration in the semi-arid Eucalyptus woodland is higher under tree canopies and significantly reduced by a recent wildfire; (ii) variations in soil water content influence the magnitude of soil respiration; and (iii) wildfire will strongly influence woodland Reco and GPP, and the ecosystem will be a net carbon source post-fire.

2. Materials and methods

2.1 Site description

This study site was at Calperum Station (34.04° S, 140.71° E), located adjacent to the Chowilla floodplain of the River Murray near Renmark in South Australia. The area is classified as semi-arid with mean rainfall of 251 mm and an annual average of 41 rain days. The mean maximum and minimum air temperatures are 24.9 and 9.6 °C (data recorded from 1996 to 2014, from http://www.bom.gov.au/).

The mallee woodland is a patchy eucalypt-shrub association. The area around Calperum and surrounding properties contain over one million hectares of mallee habitat, that is the largest continuous remnant of this vegetation association in Australia (Nulsen et al., 1986). The tree vegetation is dominated by four multi-stemmed eucalypt species (*Eucalyptus dumosa*, *E. incrassata*, *E. oleosa* and *E. socialis*) with sparse leaf canopies between 3 to 5 metres aboveground. The understory, often in the space between trees, is mainly spinifex (*Triodia basedowii*) that grows in spreading clumps to a height of ca. 0.7 metres. The rest of the ground surface is largely bare with occasional and limited coverage by ephemeral grasses. Imagery recorded by an unmanned aircraft (about 1 ha area at 0.01 m resolution) showed that approximately 25% of the area is under eucalyptus canopies. Monthly estimates of leaf area index (LAI) based on below canopy images during May to December 2013 showed that LAI varied between 0.44 and 0.67, with a mean value of 0.54 ± 0.03. Based on the period from August 2014 to July 2015 the estimated annual litter fall without fire was 960 ± 195 g m^{-2}.

A wildfire (from 15th to 19th Jan. 2014) burnt part of the woodland. It burnt the spinifex and spread into the Eucalyptus tree canopies. Aboveground bark and leaf litter were consumed. Based on MODIS satellite imagery (2 × 250 m), monthly mean normalised difference vegetation index (NDVI) was nearly halved right after the fire but approached similar values as pre-fire in late March 2015. The fire affected about 5.3×10^4 hectares of mallee woodland, according to the Country Fire Service, South Australia. Field instruments, located up to 10 m from the ground on the eddy covariance flux tower at the site were destroyed by the radiant heat. However, due to gaps in distribution of trees and spinifex typical of arid and semi-arid areas (Gill, 1997) and small topographic variations, isolated areas of woodland were not damaged by fire, ranging in size from < 1 hectare to > 10 hectares.

The alkaline sandy soil (94% sand, 4% silt and 2% clay) at the study site is classified as a Tenosol in the Australian Soil Classification (Isbell, 2002), and as an Aridisol in the US Soil Taxonomy (Soil Survey Staff, 1996). At 0-30 cm depth the soil had a bulk density of 1.6 g cm^{-3} (Sun et al., 2015), was non-saline ($EC_{1:5} < 0.4$ dS m^{-1}) and a $pH_{1:5}$ of 8.3. Soil (KCl 40) extractable S concentration in this layer ranged from 1.0 to 6.5 mg kg^{-1} and Skene K from 59 to188 mg kg^{-1}. Total organic C, total N and percentage of carbonate measured in the 10 cm layers to 30 cm are given in Table 1.

2.2 Soil respiration measurement

Two locations were selected: one in the burnt (34.00° S, 140.58° E) and the other in an unburnt area (34.01° S, 140.59° E) approximately 2 km apart. The whole area is flat and dominated by differences between patches under trees and in the open. We assumed that spatial variability in soil respiration was small. Within each location, two distinct patches were sampled: underneath eucalypt tree canopies (referred to as “under canopy”) and between canopies (referred to as “inter-canopy”). The inter-canopy patches were located adjacent to spinifex but had bare soil without litter or living plants aboveground.

Five PVC collars (20 cm diameter and 20 cm height) were inserted to a depth of about 15 cm into the ground at each location and patch in late March 2014, two months after the wildfire and three months before measurements commenced. The five soil collars per patch were randomly placed, 2-5 metres apart from each other and remained undisturbed throughout the experiment. Any seedlings that germinated inside the collars were carefully removed minimising surface disturbance.

Soil respiration was measured each month from July 2014 to June 2015 (total 12 sampling campaigns) with a manual chamber connected to an infra-red gas analyser (LI-8100, *LI-COR* Inc., Lincoln, Nebraska, USA). All measurements were conducted between 10:30 am and 14:30 pm. The chamber was placed over the PVC soil collars and each measurement took approximately three minutes. At the same time, soil temperature (LI-8100-203 Soil Temperature Thermistor) and soil water content (LI-8100-204 Soil Moisture Probe) in 0-5 cm depth were recorded immediately next to soil collars.

2.3 Eddy covariance measurement and data processing

A 20 m high eddy covariance (EC) tower (34.00° S, 140.59° E) was erected in June 2010 to measure fluxes of CO_2, H_2O, and energy. The flux tower is part of the Terrestrial Ecosystem Research Network's (TERN) OzFlux, Australian Supersite Network programmes (Karan et al., 2013) and the global FLUXNET (http://fluxnet.ornl.gov/). The footprint of the EC tower covers ca. 34 hectares (Meyer et al., 2015); this area was burnt during the wildfire. Detailed description of the instrumentation can be found in Meyer et al. (2015). Briefly, measurements of three-dimensional wind speed (CSAT3 sonic anemometer, Campbell Scientific Inc., Logan, UT, USA), virtual temperature (CSAT3), as well as air water vapour density and CO_2 density using an open-path IRGA (*LI-COR* LI7500, *LI-COR* Biosciences, Lincoln, NE, USA), were recorded at a frequency of 10 Hz.

Auxiliary observations of solar irradiance, air temperature, vapour pressure deficit and rainfall, soil temperature and soil water content were also collected concurrently. Incident solar irradiance was observed from a four component radiometer that was positioned at a height of 20 m (CNR4, Kipp and Zonen, Delft, the Netherlands). Vapour pressure deficit was determined as the difference between atmospheric vapour pressure (kPa) and saturation vapour pressure at air temperature (HMP45C, Vaisala, Helsinki, Finland) at a height of 2 m. An additional pyranometer (*LI-COR* LI2003S, *LI-COR* Biosciences, Lincoln, NE, USA) was mounted at 20 m and cup anemometers and wind direction sensors (RM Young, Traverse City MI, USA) at 2.0 and 8.6 m. Onsite rainfall (CS7000, Hydrologic services, Warwick, NSW, Australia) was measured with the tipping bucket gauge (0.2 mm resolution) mounted on a stand of height 0.65 m in a tree-free area 8 m from the tower. Soil temperature and water content sensors (CS650, Campbell Scientific, Townsville, Australia) were placed 10 metres away from the tower base in bare soil (inter-canopy) or beneath eucalypt canopies (under canopy) with multiple depths, ranging from 0.1 m to 1.8 m. Data from CS650 sensors at 0.1 m depth provided a continuous record of volumetric soil water content from the two patches. Output from the sensors was validated with monthly comparison of manually collected soil water content samples (in 0.1 m segments up to 0.3 m) in an adjacent area. The PVC collars for measuring soil respiration in burnt mallee were within 200 metres from the tower base.

Covariances were computed every 30 min to generate fluxes following standard OzFlux QA/QC correction procedures (Calperum Tech, 2013; Eamus et al., 2013; Cleverly et al., 2013) and cross-checked with methods described in Thomas *et al.* (2011). Removal of latent energy flux and sensible heat flux spikes, gap filling, night-time flux filtering (where solar radiation < 20 W m^{-2}) and friction coefficient threshold determination were carried out as described in Reichstein *et al*. (2005) and Thomas *et al*. (2011), using the add-on package 'REddyProc' (Reichstein and Moffat, 2015) in R program (R development Core Team, 2014). A friction coefficient threshold was then calculated and set to 0.29 m s^{-1}, 0.28 m s^{-1} and 0.43 m s^{-1} for the years 2013, 2014 and 2015 respectively based on temperature, air pressure, humidity, and wind speed in the given year.

The flux tower directly measured net ecosystem exchange of CO_2 (NEE), and NEE was partitioned into gross primary productivity (GPP) and ecosystem respiration (Reco). Net ecosystem productivity (NEP) was calculated as: NEP = -NEE, that is, NEP = GPP - Reco. Thus positive NEP values indicate net C sequestration; while negative NEP values show a net C loss from the ecosystem. Daily average measurements, monthly total and annual carbon sum of NEP, GPP and ecosystem respiration were calculated. The wildfire in January 2014 destroyed most in-situ equipment. Operation of the instrumentation resumed in April 2014. Therefore, no data is available from January to April 2014.

2.4 Data analysis

Multivariate analysis of variance with repeated measures was used to analyse the effects of wildfire (burnt and unburnt), patch (under canopy and inter-canopy), month and their interactions on in-situ soil respiration, soil water content (0-5 cm) and soil temperature (0-5 cm) in the R statistical computing program. Significance was set at $p < 0.05$. If the interaction term was significant, soil respiration data from each location and patch were compared separately to detect monthly differences using a post hoc Tukey test.

A general linear model in R was used to determine relationships between soil respiration, soil temperature and soil water content at 0-10 cm depth from burnt areas. Soil respiration observations from three replicates of the five per patch (the training group), collected at each sampling date, were randomly selected and averaged. Average soil temperature and water content at 0-10 cm recorded from 10:00 am – 15:00 pm by the tower sensors at the sampling dates were used as explanatory variables. Soil temperature and soil water content at 0-10 cm were used rather than 0-5 cm because soil respiration could then be modelled using data continuously collected from the tower. Since soil respiration differed significantly between under canopy and inter-canopy, soil respiration rates from the two patches were modelled separately. The relative importance of explanatory variables (soil temperature, soil water content and their interaction) was compared by a further analysis in an add-on package 'relaimpo' (Gromping, 2006) in R. Soil respiration from different patches was simulated at half-hour intervals, then averaged and presented at daily intervals. Gaps in soil temperature or soil water content data due to sensor failure were excluded from the continuously modelled soil respiration dataset. Monthly soil respiration rates were added to calculate annual soil respiration.

The modelled data of a given day were then compared with the observed dataset (average values from the two remaining replicates – the test group) using the method proposed by Smith et al. (1997). Briefly, Student's t test was used to determine if there was a significant difference between observed and simulated values; the correlation coefficient (r) was calculated to assess how well the shape of the simulation matched that of the observed data (see Equation 1). Root mean square error (RMSE), model efficiency (EF) and the coefficient of determination (CD) were calculated to evaluate model performance.

$$r = \frac{\sum_{i=1}^{n} [(Oi - \bar{O}) \times (Pi - \dot{P})]}{[(\sum_{i=1}^{n}(Oi - \bar{O})^2) \times (\sum_{i=1}^{n}(Pi - \dot{P})^2)]^{\frac{1}{2}}} \quad \textit{(Eqn 1)}$$

where O_i are the observed values, P_i are the modelled values, $\bar{O}$ is the mean of the observed data, $\dot{P}$ is the mean of the modelled data, and n is the number of paired values.

Single factor repeated measures ANOVA was used to compare NEP, GPP and Reco from May to July pre-fire (2013) and post-fire (2015) in R with fire as the independent variable. Average soil respiration for the area was calculated based on the proportion of the area under canopies (25%) and inter-canopy (75%). This value was used to determine the contribution of total soil respiration to ecosystem respiration.

3. Results

3.1 Environmental conditions

During the study period, the mean daily air temperature was 18.3 °C, with a minimum 6.2 °C in July 2014 and a maximum of 36.8 °C in February 2015 (Fig. 1a). Annual rainfall was 228 mm in 2013, 212 mm in 2014, and 168 mm for 1st January - 31st July of 2015. During the measurement period (July 2014 – June 2015), two dry periods of over 70 days occurred with little (< 1 mm) or no rainfall, from early September to mid November 2014 and from early

February to end of March 2015. Rainfall was variable with occasional heavy falls in summer (December to March) and more evenly distributed during winter (May-September).

Soil temperatures at 0-10 cm depth fluctuated strongly associated with air temperature (Fig. 1b). The soil temperature at 0-5 cm depth was higher inter-canopy than under canopy (Fig. 2).

There were no consistent differences in soil water content at 0-10 cm depth between inter-canopy and under canopy before the fire (Fig.1c). The highest soil water contents inter-canopy coincided with rainfall events whereas the water content under canopy remained stable. After the fire, the water content was usually lower under canopy than inter-canopy and the highest water contents in both patches followed rainfall events.

Neither soil temperature at 0-5 cm nor soil water content at 0-5 cm were affected by the preceding wildfire ($p = 0.528$ and 0.074 respectively, Table S1), but they differed significantly between patches and varied over time ($p < 0.01$) (Fig. 2).

3.2 In-situ soil respiration dynamics and modelling

Monthly measured soil respiration significantly differed between patches ($p < 0.001$) and varied over time ($p < 0.001$), but was not affected by the wildfire ($p = 0.233$) (Fig. 2 and Table S1). There was also a significant interaction between month and wildfire/patch on soil respiration rates ($p < 0.001$).

Soil respiration rates were 25% to 132% higher under canopy than inter-canopy, with a mean value of 1.53 and 0.90 μmol CO_2 m^{-2} s^{-1}, respectively. They were greatest in January 2015, measured a week after 70.2 mm of rain when they were about two-fold greater than the rates in October 2014 or March 2015 when soil temperatures were similar. During the rest of the year, soil respiration rates changed little, ranging from 1.10 to 2.18 µmol CO_2 m^{-2} s^{-1} under canopy and from 0.67 to 1.34 µmol CO_2 m^{-2} s^{-1} inter-canopy.

Soil respiration was little affected by soil temperature at 0-5 cm depth alone. Instead, soil temperature (T, °C) and soil water content (SWC, volumetric ratio) at 0-10 cm as well as their interaction influenced soil respiration in both patches (Fig. 3 and Table S2):

Inter-canopy: Soil respiration = 1.79 – (0.08 × T) – (31.82 × SWC) + (2.38 × T × SWC) ($F_{3,8} = 8.38$, $p < 0.01$, adj.$R^2 = 0.67$);

Under canopy: Soil respiration = 3.06 – (0.12 × T) – (46.96 × SWC) + (3.43 × T × SWC) ($F_{3,8} = 19.53$, $p < 0.001$, adj.$R^2 = 0.83$).

According to the relative importance analysis, soil water content was the primary controller of soil respiration whereas soil temperature was a modifier influencing soil respiration only when the soil was sufficiently moist. When the soil was dry in October 2014 and March 2015, soil respiration rates were similar even though soil temperature was higher in October (29.8 °C) than in March (23.8 °C). The influence of temperature in moist soil is evident in the two-fold higher soil respiration under canopy in January 2015 compared to August 2014. Soil water content was similar at the two dates, but soil temperature was 30.0 °C in January 2015 compared with 17.2 °C in August 2014.

Simulated daily soil respiration matched in-situ observations on the same day (Student's t test: $t = 0.15$, $df = 42$, $p = 0.88$), with a correlation coefficient (r) of 0.85 (Fig. 4a). RMSE showed that the average error of model simulation was 8.5%, and both EF (0.71) and CD (1.07) indicated that the modelled data simulated measured data very well.

3.3 Net ecosystem productivity, gross primary productivity, ecosystem respiration and simulated soil respiration

Figure 4 shows daily mean CO_2 flux rates for NEP, GPP and ecosystem respiration derived from the eddy covariance measures and the measured and simulated soil respiration flux rates. High flux rates were often associated with the rainfall events shown in Fig. 1a.

NEP did not show a seasonal pattern from January 2013 to July 2015 (Fig. S1). In the first three months of 2013, the ecosystem was a net source of carbon. During this time there were only six rain days of which four had less than 1 mm, but one day had 55.4 mm (27th February 2013). The response to this rainfall was not apparent until April, more than a month after the event when the ecosystem became a carbon sink until December 2013. Carbon was sequestered in both the winter (May – July 2013) and summer seasons (October – December 2013). The semi-arid woodland sequestered a total of 81 g C m^{-2} yr^{-1} before the wildfire (in January 2014), but then became a net source of CO_2 until April 2015 with a carbon loss of about 88 g C m^{-2} yr^{-1}. This estimate does not include the large C loss that occurred during the fire and after the fire until instrumentation was restored. From May 2014 to April 2015, daily NEP values (Fig. 4b) and total soil respiration (Fig. 4a) were inversely related (correlation coefficient: $r = 0.49$, $F_{1,363} = 111.8$, $p < 0.001$). The ecosystem became a net carbon sink from April 2015 (15 months after the wildfire) onwards, with NEP in May and July similar to that in 2013 ($F = 1.33$, $p = 0.369$), although rainfall was lower in 2015 (Table 2).

High values of ecosystem respiration coincided with those of soil respiration (Fig. 4 and S1) which, in turn, were associated with rainfall in the warm to hot temperatures during summer. In 2013, the contribution of soil respiration (320.5 g C m^{-2} yr^{-1}) to ecosystem respiration (387 g C m^{-2} yr^{-1}) was 83% with 51% and 32% from inter-canopy and under canopy respiration, respectively. Fire resulted in a decrease by 35% in annual ecosystem respiration and by 65% in GPP for 15 months.

Before the wildfire (in 2013) the average GPP flux rate was 1.24 µmol CO_2 m^{-2} s^{-1}, with a maximum of 2.42 µmol CO_2 m^{-2} s^{-1}. It was much lower when measurements resumed after the wildfire (Fig. 4 and Fig. S1). Following rainfall in January 2015 (69 mm) and April (65 mm) GPP flux rates increased, but each event was followed by a dry period during which GPP flux rates declined. For example, during the dry 70-day period from 14th January to late March 2015 with little or no rain GPP decreased from 1.43 µmol CO_2 m^{-2} s^{-1} to 0.00 µmol CO_2 m^{-2} s^{-1}. Following the first winter rain in April, GPP reached a maximum of 2.49 µmol CO_2 m^{-2} s^{-1} in late May 2015 to reach monthly GPP similar to that in 2013 ($F = 0.003$, $p = 0.963$) (Table 2).

4. Discussion

This study showed that both ecosystem and soil respiration in the semi-arid woodland were influenced by rainfall and fire influenced ecosystem carbon fluxes. On an annual basis, ecosystem respiration and GPP declined about 35% and 65%, respectively, after the fire, and the ecosystem changed from a carbon sink to a net carbon source. The onset of net carbon uptake occurred 12 to 15 months after the fire with NEP approaching similar values as before the fire. Soil respiration was strongly influenced by soil water content, altered by the magnitude and distribution of rainfall, but the wildfire effect was small. Soil respiration rates were higher under canopy than inter-canopy. However, fluctuations in ecosystem respiration were likely driven by changes in soil respiration from inter-canopy because the inter-canopy area was greater than that under canopy and soil water content fluctuated more than under canopy.

4.1 Soil respiration

In-situ soil respiration was 25 - 132% higher under canopy than inter-canopy which can be explained by the presence of roots and the greater organic carbon inputs from litterfall of *Eucalyptus* trees compared to inter-canopy patches with no or very sparse plant cover. Organic C input enhances heterotrophic soil respiration (Gallardo and Schlesinger, 1992; De Deyn et al., 2008; Raich and Schlesinger, 1992) (Fig. 2 and Table 1). Root density is likely to be greater under canopy than in inter-canopy areas which will contribute to soil CO_2 release through autotrophic respiration. In native forest ecosystems at least 30% of soil respiration is thought to be from autotrophic respiration (Raich and Tufekcioglu, 2000; Tang and Baldocchi, 2005).

The average soil respiration rate was about 1.06 µmol CO_2 m^{-2} s^{-1}, which is in agreement with other studies in semi-arid or arid ecosystems (e.g. Rey et al., 2011; Lai et al., 2012; Tang and Baldocchi, 2005) and similar to previous measurement in this mallee woodland (1.10 µmol CO_2 m^{-2} s^{-1}) conducted more than 25 years ago (Galbally et al., 2010).

In water-limited ecosystems, fire has been shown to reduce (e.g. Vargas et al., 2012), increase (e.g. Fest et al., 2015) or have no effect on soil respiration (e.g. Tufekcioglu et al., 2010). These variable effects indicate that the influence of fire is vegetation type- and site-specific. In our study, the wildfire event had no effect on soil respiration (Fig. 2 and Table S1). There are several possible reasons for this. Firstly, mineralization rate is generally low in the old and nutrient-poor Australian soils compared to nutrient-richer ecosystems (Bahn et al., 2010; Bond-Lamberty and Thomson, 2014). Secondly, fire may kill roots in the top soil and a proportion of roots may die due to lack of C input from the shoot following the loss of leaves. Dead roots can provide an energy source for surviving microbes compensating for the lower autotrophic respiration (Irvine et al., 2007). Thirdly, new leaves appeared 3-4 months after the fire. Assimilation by new leaves would stimulate new root growth. Therefore, our first hypothesis can only be partially confirmed because soil respiration was higher under tree canopies than inter-canopies, but the recent wildfire had no effect on soil respiration.

The second hypothesis that variations in soil water content influence the magnitude of soil respiration can be confirmed. In this study, soil water content was the main driver of soil respiration and temperature became a modulator. This is in agreement with semi-arid and arid ecosystems with annual rainfall < 300 mm (e.g., Rey et al., 2011; Vargas et al., 2012). However, the two studies by Rey et al. and Vargas et al. were conducted in grass-dominated ecosystems whereas this investigation was carried out in a patchy woodland. Vargas *et al.* (2012) studied soil respiration for 3 months in the summer monsoon seasons. The present study provides a comprehensive picture of soil respiration in semi-arid ecosystems because it includes periods without rainfall interrupted by occasional high rainfall events as well as periods with frequent rainfall. The present study also differs from that of Rey *et al.* (2011) because the soil in the area they studied had a sand content of 60% compared to the very sandy soil in the mallee study site (94%). Therefore the soil in the study of Rey *et al.* (2011) can be expected to have greater water holding capacity than our soil. In the present study, temperature influenced soil respiration only when soil water content was not limiting. For example, soil respiration rate was two-fold higher in January 2015 than in August 2014 at similar high water content (approximately 0.1 v/v) but higher temperature in January. In moister and colder ecosystems, temperature has been shown to be the main driver of soil respiration (Raich et al., 2002).

The effect of rainfall on soil water content differed between patches pre-fire, but not post-fire (Fig. 1). Before fire (in 2013), soil water content at 10 cm depth fluctuated less under canopy than inter-canopy which can be explained by canopy and soil surface litter interception

(Breshears et al., 1997; Owens et al., 2006) and differences in soil surface evaporation. Therefore, soil respiration from inter-canopy varied more than under canopy (Fig. 4). After the wildfire completely removed foliage and surface litter, soil water content differed little between the two patches.

4.2 Ecosystem carbon flux

Similar to soil respiration, NEP and GPP were strongly influenced by rainfall and soil water content (Fig. 4). This is in agreement with other studies not only in semi-arid and arid ecosystems (e.g. Cleverly et al., 2013; Wohlfahrt et al., 2008), but also in high rainfall biomes. A meta-analysis of more than 85 field studies concluded that increased precipitation generally stimulated both ecosystem respiration and photosynthesis and led to an overall increase in net C uptake (Wu et al., 2011).

In 2013, during which rainfall was similar to the long-term average, total C sequestration in this semi-arid woodland was 81 g C m^{-2} yr^{-1} (Table 2). In 2011, the ecosystem received 510 mm rainfall (almost double that of 2013) and sequestered 190 g C m^{-2} yr^{-1} (unpublished data). Thomas et al. (2011) summarized 17 ecosystem C flux studies from temperate or semi deciduous woodlands across the globe. Based on their study, the NEP found here was similar to that in a broadleaf deciduous woodland in the UK (130 g C m^{-2} yr^{-1}) and a warm temperate mixed forest in Japan (90 g C m^{-2} yr^{-1}), but generally lower than in the other ecosystems. NEP in this study is comparable to that in a semi-arid shrubland (77 g C m^{-2} yr^{-1}; (Jia et al., 2014)), but only one third of the NEP in an arid-zone *Acacia* savanna woodland (258 g C m^{-2} yr^{-1}; (Eamus et al., 2013)). GPP in this semi-arid woodland is only 25-30% of that in other woodlands (Thomas et al., 2011), likely due to low annual rainfall, low soil water holding capacity and vegetation type. The low NEP in this study can also be explained by the low nutrient availability of the sandy soil in the Mallee and more generally in Australian soils which limits plant growth (Sardans and Peñuelas, 2013; Lambers et al., 2010; Orians and Milewski, 2007).

After the wildfire, the woodland became a net carbon source which confirms our third hypothesis that ecosystem carbon fluxes and the capacity of sequestering carbon are influenced by the fire. The wildfire either destroyed or damaged most foliage resulting in a decrease of photosynthesis. It took more than 12 months after fire for the ecosystem to recover as indicated by NEP and GPP approaching pre-fire values (Table 2). Native vegetation in southern Australia is well adapted to fire and many species are able to regrow after a fire from protected buds (above or below ground), or from seeds in woody fruits in the canopy seed bank (Balston and Williams, 2014). The eucalypt species in the Mallee regrow from epicormic buds in the bark or lignotubers (Gill, 1997). In the study area, foliage from lignotubers appeared 3 to 4 months after fire. GPP flux rates increased slowly from then on, but maximum monthly total GPP in 2014 only reached minimum values of 2013 (Fig. 4). In previous studies, the time for recovery of ecosystem carbon sequestration rates from fire ranged from one year (low intensity fires) to more than a decade (stand-replacing fire) (e.g. Dore et al., 2012; Gough et al., 2007; Iwata et al., 2011; Starr et al., 2015).

In 2013, soil respiration accounted for 83% of ecosystem respiration. This is slightly more than the average value of 18 European forests where the contribution was 69% (Janssens et al., 2001). Ecosystem respiration was more closely related to inter-canopy than to under canopy respiration probably because of the larger proportion of inter-canopy area (ca. 75% of total area). Another factor may be the greater fluctuation in soil water content and thus soil respiration of inter-canopy patches which coincided with changes in ecosystem respiration. In semi-arid or arid ecosystems, episodic rainfall events can induce peaks in soil respiration and increase the contribution from soil respiration to net ecosystem exchange, as observed by Ma *et al.* (2012) and Unger *et al.* (2012). After the wildfire, apparent ecosystem respiration was lower than total soil respiration. Similar results were found in other studies where ecosystem respiration based on the eddy covariance (EC) technique was compared to chamber based respiration measurement. For example, Speckman et al. (2015) showed that eddy covariance fluxes were lower than chamber estimates of ecosystem respiration (60% lower in 2005, and 32% in 2011), in a subalpine forest where bark beetles killed or infested 85% of the aboveground respiring biomass. These authors summarized 24 studies that also reported that EC estimates of ecosystem respiration were lower than chamber estimates. In the present study this discrepancy may be due to at least two factors. Firstly, uptake of CO_2 released from the soil is likely to be enhanced after the fire because of fast growth of new leaves and smaller distance between new grown leaves and the soil than pre-fire which will decrease eddy covariance fluxes. Secondly, uncertainties exist in soil respiration simulation, EC instrument error and carbon flux partitioning.

5. Conclusion

This study showed that precipitation and therefore soil water content is a major driver of soil and ecosystem processes in semi-arid woodlands. This is the first study on net ecosystem productivity, gross primary productivity and ecosystem respiration shortly after a wildfire event in a semi-arid ecosystem. By also including separate soil respiration measurements in different patches, this study provides a comprehensive picture of the response of semi-arid woodlands to precipitation and fire. The wildfire event influenced aboveground (canopy) more than belowground processes. However, our results may be specific to this study because wildfire intensity and thus effect are highly variable. Further studies on ecosystem carbon fluxes before and after wildfires are required to develop future carbon and vegetation models on regional or global scale.

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Table 1 A survey of soil properties of unburnt and burnt Mallee woodland under canopy and inter-canopy. Soils were sampled one month before wildfire (December 2013) and four months after the fire (May 2014) (n=1).

Location	**Patch relative to canopy**	**Depth (cm)**	**Total Organic Carbon (%)**	**Total Nitrogen (%)**	**Carbonate (%)**
Pre-fire					
	Inter	0-10	0.44	0.03	0.26
		10-20	0.40	0.04	0.24
		20-30	0.35	0.03	0.30
	Under	0-10	1.02	0.07	0.26
		10-20	0.62	0.05	0.24
		20-30	0.61	0.05	0.26
Post-fire					
Burnt	Inter	0-10	0.43	0.04	0.24
		10-20	0.47	0.04	0.52
		20-30	0.39	0.02	0.64
	Under	0-10	0.52	0.04	0.60
		10-20	0.48	0.04	0.30
		20-30	0.40	0.03	1.28
Unburnt	Inter	0-10	0.66	0.04	0.24
		10-20	0.49	0.05	0.48
		20-30	0.42	0.03	0.28
	Under	0-10	0.78	0.06	0.22
		10-20	0.60	0.04	0.24
		20-30	0.51	0.04	0.24

Table 2 Monthly mean temperature, total rainfall, net ecosystem productivity (NEP), gross primary productivity (GPP), ecosystem respiration (Reco) and simulated soil respiration from May to July and average per three-month for inter-canopy and under canopy of semi-arid mallee woodland (Southern hemisphere winter) in 2013-2015.

	2013				**2014**				**2015**			
	Prefire				**4-6 months after fire**				**16-19 months after fire**			
	May	**Jun**	**July**	**Avg.**	**May**	**Jun**	**July**	**Avg.**	**May**	**Jun**	**July**	**Avg.**
Mean temperature (°C)	14	11	11	12	16	12	11	13	14	11	10	12
Monthly total rainfall (mm)	35	32	24	31	28	14	5	16	10	18	6	11
NEP (g C m^{-2})	5	7	15	9	-19	-16	-11	-15	18	13	12	14
GPP (g C m^{-2})	34	36	38	36	2	2	8	4	46	32	29	36
Reco (g C m^{-2})	29	30	22	27	21	18	19	19	27	20	17	21
Rsoil - inter-canopy (g C m^{-2})	27	18	23	23	30	26	28	28	27	26	28	27
Rsoil - under canopy (g C m^{-2})	45	46	47	46	54	42	43	46	48	42	45	45

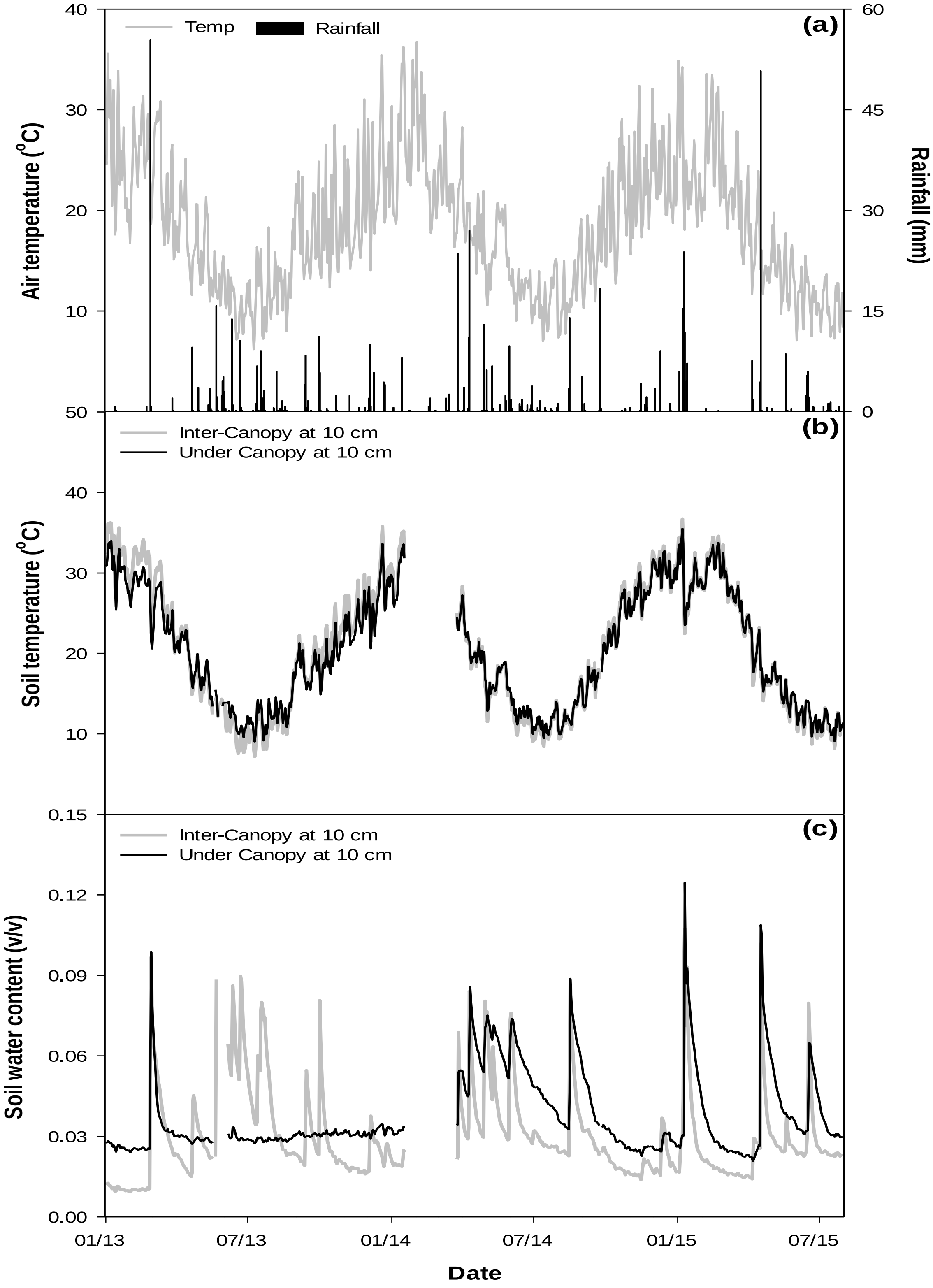

Fig. 1. (a) Daily air temperature and total rainfall amount, (b) soil temperature at 0-10 cm depth, and (c) volumetric soil water content (for inter-canopy and under canopy) of mallee woodland at Calperum Station (34.00°S, 140.59°E) from January 2013 to August 2015.

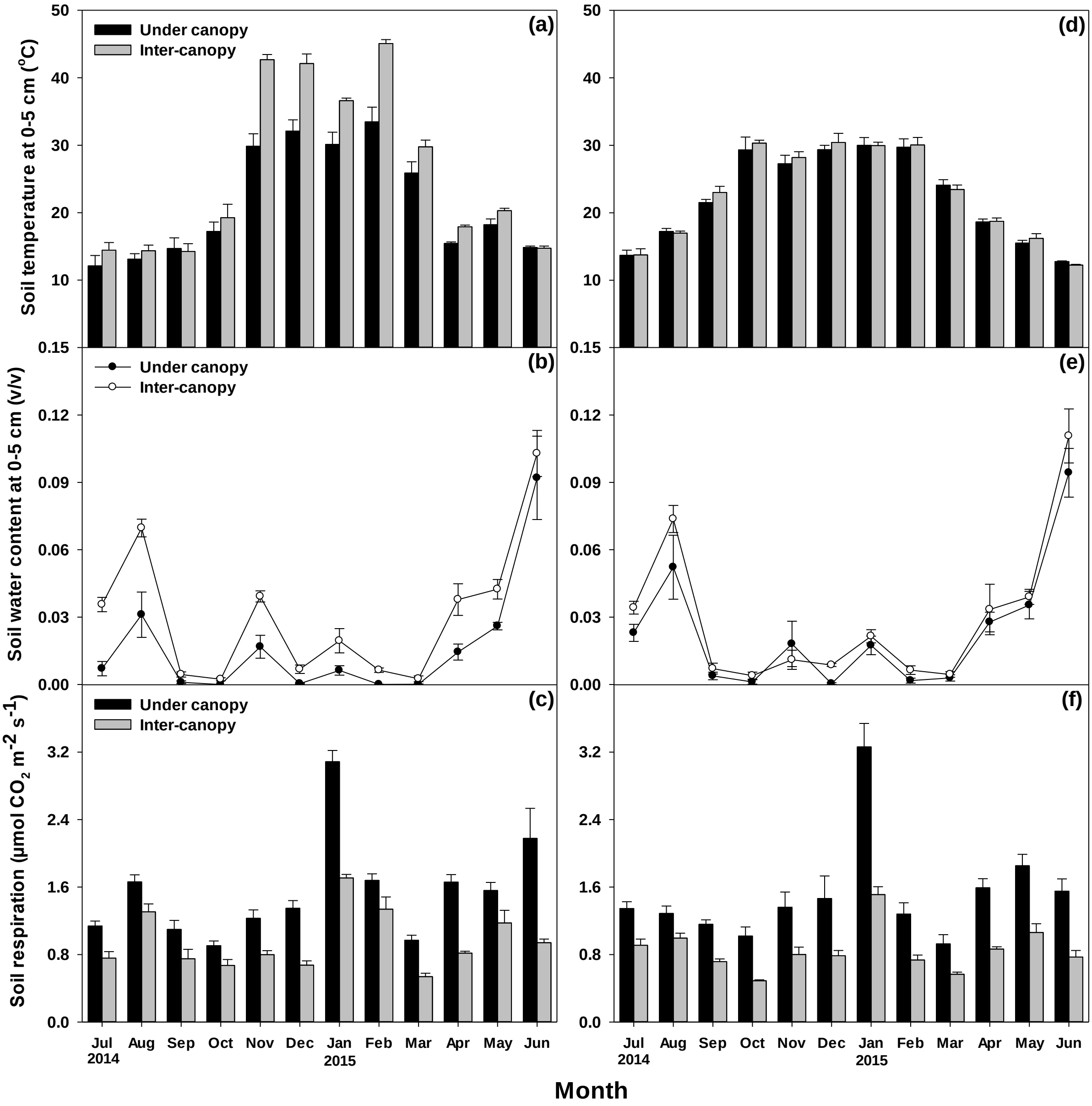

Fig. 2. Monthly measured soil temperature (°C) **(a, d)**, soil water content (v/v) **(b, e)** in 0-5 cm depth, and soil respiration rates (μmol CO_2 m^{-2} s^{-1}) **(c, f)** under canopy and inter-canopy in unburnt **(a-c)** and burnt **(d-f)** mallee woodland from July 2014 to Jun 2015 (mean ± standard error, n=5).

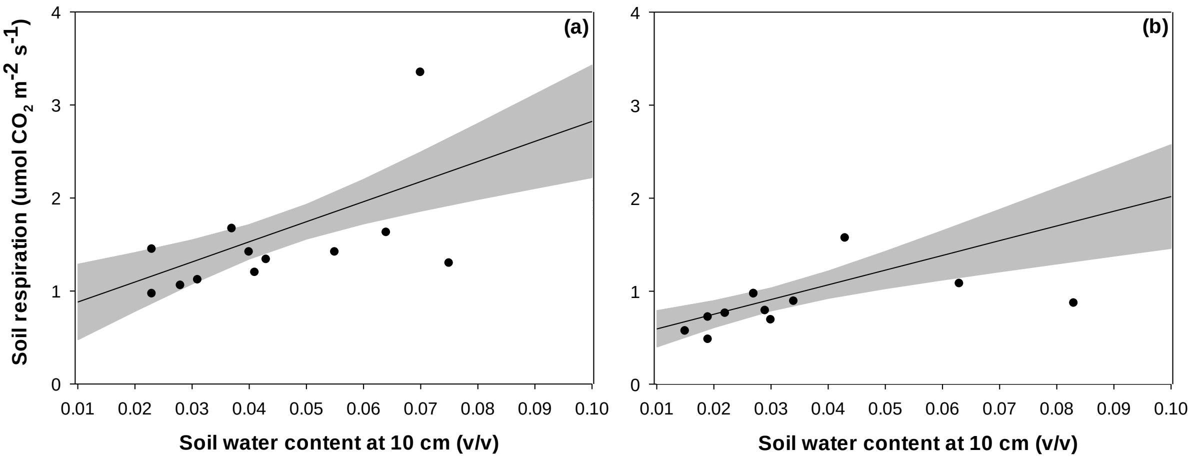

Fig. 3. Relationship between soil respiration and soil water content at 10 cm depth (a) under canopy and (b) inter-canopy of mallee woodland (95% Confident Interval in grey). Soil temperature is standardized to a mean value of 20 °C. Dots indicate raw data for performing linear regression models.

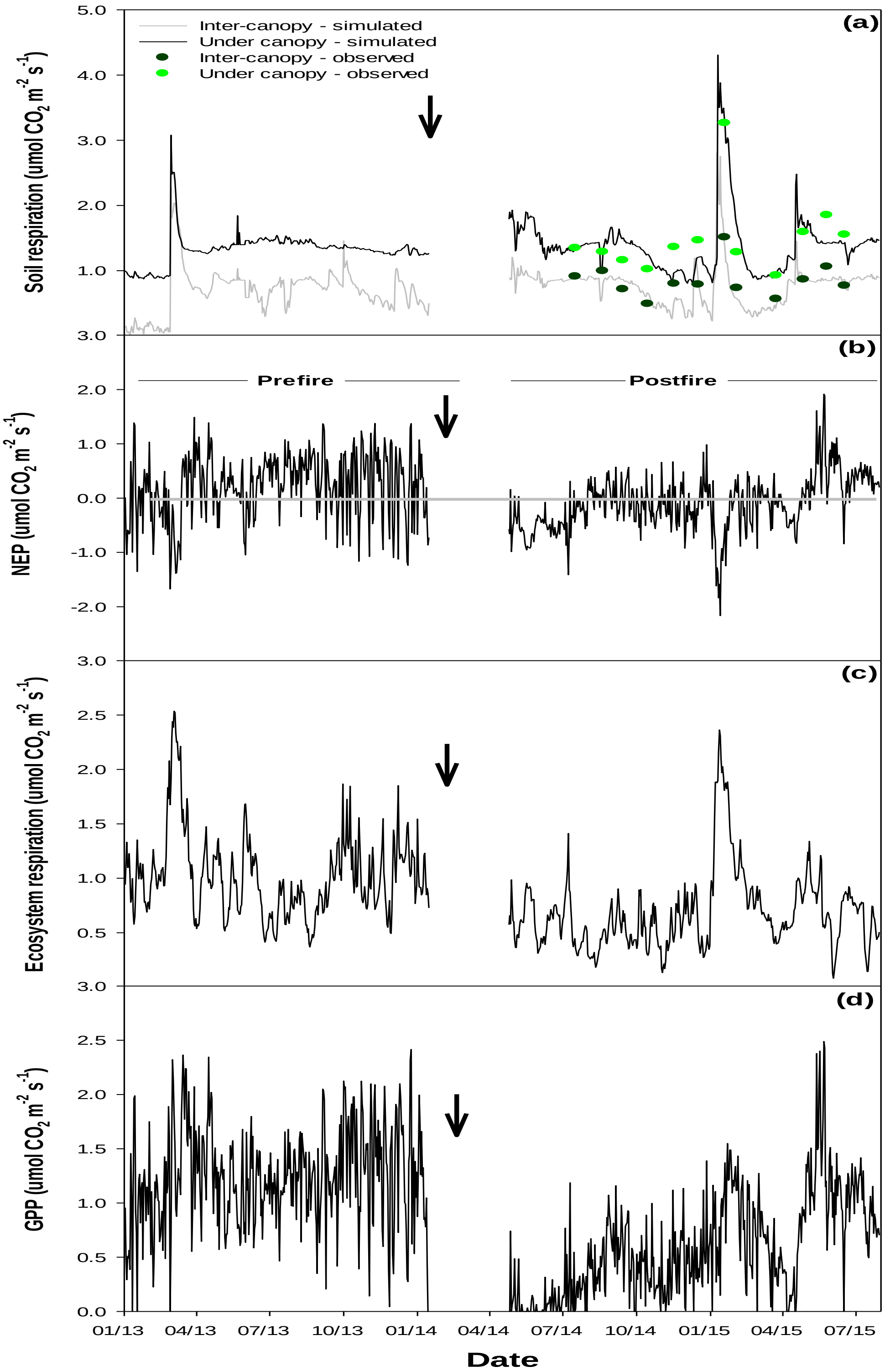

Fig. 4. (a) Daily average values of observed and simulated soil respiration from two patches (Inter-canopy and under canopy), (b) net ecosystem productivity (NEP), (c) ecosystem respiration and (d) gross primary productivity (GPP) of mallee woodland from January 2013 to August 2015. The solid grey line in (b) indicates NEP=0. Arrow indicates occurrence of the wildfire.

Supplementary Material

Table S1 Repeated measures ANOVA outputs of analyses of effects of wildfire (burnt and unburnt), patch (under or inter-canopy), month and their interactions on soil respiration, temperature (0-5 cm) and water content (0-5 cm).

Explanatory variables	**ndf**	**ddf**	**Soil respiration**		**Soil temperature (0-5 cm)**		**Soil water content (0-5 cm)**	
			F	**p**	**F**	**p**	**F**	**p**
wildfire	1	16	1.54	0.233	0.42	0.528	3.65	0.074
patch	1	16	122.00	<.0001	8.80	0.009	34.07	<.0001
month	11	176	67.18	<.0001	350.56	<.0001	110.52	<.0001
wildfire × patch	1	16	0.40	0.534	5.88	0.028	2.37	0.144
wildfire × month	11	176	4.36	<.0001	52.37	<.0001	0.59	0.837
patch × month	11	176	11.64	<.0001	5.95	<.0001	2.14	0.020
wildfire × patch × month	11	176	1.33	0.210	5.36	<.0001	0.61	0.819

ndf, numerator degrees of freedom; ddf, denominator degrees of freedom.

Table S2 Final model for predicting soil respiration with soil temperature (T, 0-10 cm), and volumetric soil water content (SWC, 0-10 cm) for inter-canopy and under canopy in burnt mallee woodland.

Patch relative to canopy	**Explanatory variables**	**Estimate**	**SE**	**t value**	**Pr(>|t|)**	**adj.R^2**
Inter	Intercept	1.79	0.39	4.65	0.002	0.67
	T	-0.07	0.02	-3.48	0.008	
	SWC	-31.82	9.69	-3.28	0.011	
	T × SWC	2.38	0.57	4.20	0.003	
Under	Intercept	3.06	0.84	3.64	0.007	0.83
	T	-0.12	0.04	-3.22	0.012	
	SWC	-46.96	15.71	-2.99	0.017	
	T × SWC	3.43	0.72	4.77	0.001	

‘×’ indicates interaction between explanatory variables; adj.R^2 – adjusted coefficient of determination

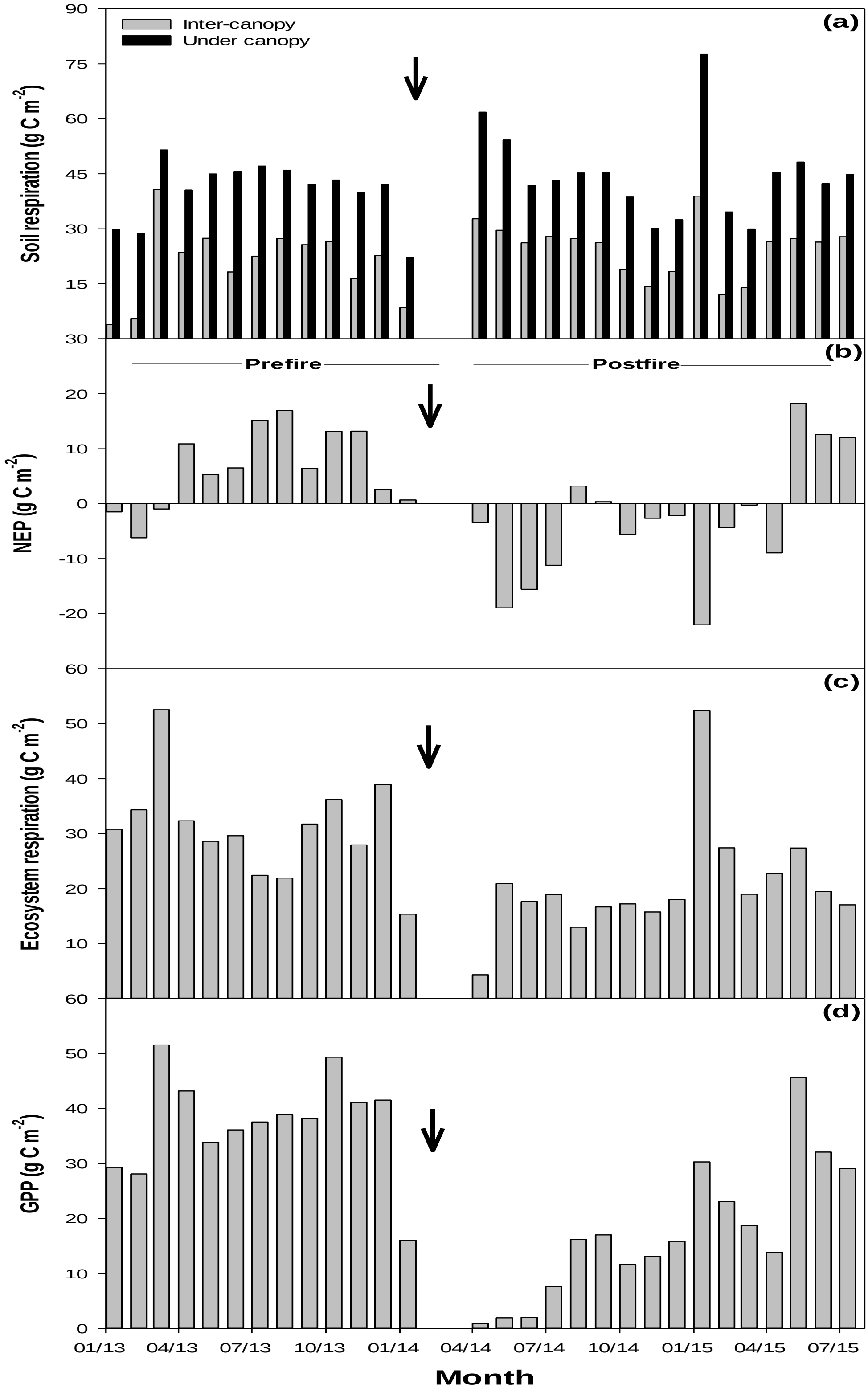

Fig. S1. (a) Monthly total soil respiration for inter-canopy and under canopy, (b) net ecosystem productivity (NEP), (c) partitioned ecosystem respiration and (d) gross primary productivity (GPP) of burnt mallee woodland from January 2013 to July 2015; before and after a wildfire in January 2014. Arrow indicates occurrence of the wildfire.

Chapter 5

Response of net ecosystem carbon exchange to a large rainfall event depends on previous rainfall pattern in a semi-arid woodland

Statement of Authorship

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Principal Author

Name of Principal Author (Candidate)	Qiaoqi Sun		
Contribution to the Paper	Experimental development, data collection, analysis and manuscript writing.		
Overall percentage (%)	80		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	02/02/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above); ii. permission is granted for the candidate in include the publication in the thesis; and iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Wayne S. Meyer		
Contribution to the Paper	Supervised experimental design and completion of the work, data interpretation and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	02/02/2017

Name of Co-Author	Georgia R. Koerber		
Contribution to the Paper	Assisted field sample collection and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	02/02/2017

Name of Co-Author	Petra Marschner		
Contribution to the Paper	Supervised experimental design and completion of the work, data interpretation and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature		Date	06/02/2017

Abstract

Semi-arid climate is characterized by long dry periods which are interrupted by rainfall events differing in magnitude. The effect of these rainfall events on ecosystem carbon fluxes has been studied in semi-arid grass-lands and shrub-lands, but data for woodlands is lacking. In this study net ecosystem productivity (NEP), partitioned ecosystem respiration (Reco) and gross primary productivity (GPP) from a semi-arid eucalyptus woodland were measured using eddy covariance data. Three natural large rainfall events with similar magnitude (35-55 mm), but contrasting previous rainfall patterns were chosen. NEP, Reco and GPP rates 28 days prior to and 35 days after the three central rainfall events were used. A water addition experiment (30 mm rainfall simulation) was conducted in the field following a long dry period (only 4.8 mm rainfall input in 45 days), to measure soil respiration after rewetting. Changes in ecosystem carbon fluxes to the central rainfall event depended on previous rainfall patterns. GPP rates were not affected by the three rainfall events. After four weeks with several medium to large rainfall events, the central rainfall event had little effect on Reco. In contrast, a large rainfall event following four weeks with very little rainfall induced an increase in Reco for about three weeks and thus a decrease in NEP. The strong increase in Reco after the central rainfall event can, at least partly, be explained by an increase in soil respiration upon rewetting. Heterotrophic soil respiration usually decreases rapidly after rewetting. The sustained higher Reco could be due to respiration by roots in the moist deeper soil layers. We conclude that the previous rainfall should be considered when interpreting the response of ecosystem C fluxes to rainfall events.

Keywords: ecosystem carbon flux, eddy covariance, prolonged dry period, rainfall size, soil respiration, semi-arid woodland

1. Introduction

In arid and semi-arid ecosystems, rainfall constrains biological and physical processes (Weltzin et al., 2003b; Noy-Meir, 1973; Beer et al., 2010). On the other hand, extensive and large rainfall across these ecosystems can have a global effect on the trend and inner-annual variability of terrestrial CO_2 uptake (Ahlstrom et al., 2015). Recent climate models project that large rainfall events and extended dry periods will become more frequent (Fischer et al., 2013; IPCC, 2014; Hughes, 2003). Hence there is increased interest in quantifying the C flux response of arid and semi-arid ecosystems.

Many studies suggest that both rainfall amount and frequency are important controllers of ecosystem processes in dry regions (e.g., Huxman et al., 2004) because a significant rainfall event after an extended dry period can lead to rapid nutrient mineralization and a pulse of CO_2 evolution (Austin et al., 2004; Collins et al., 2008; Kim et al., 2012; Nielsen and Ball, 2015). The magnitude of this pulse of CO_2 from soil respiration following rewetting of dry soil has been shown to be dependent on the frequency of previous dry-wet cycles (e.g., Shi and Marschner, 2014; Fierer et al., 2003). Pulses of CO_2 from soil respiration following large rainfall events are therefore commonly observed, but the following effect on ecosystem C fluxes is not clear. In grass- or shrub-lands, some studies showed that large rainfall events increase plant productivity and net ecosystem C uptake (e.g., Parton et al., 2012; Guo et al., 2015; Thomey et al., 2011; Heisler-White et al., 2008); while others reported a net ecosystem C release after rainfall events (e.g., Liu et al., 2013; Huang et al., 2015; Snyder et al., 2004; López-Ballesteros et al., 2016; Wohlfahrt et al., 2008). The C flux response of semi-arid woodlands has not been comprehensively studied (Zeppel et al., 2014) and it is therefore uncertain whether large rainfall events will induce net C uptake or net loss in these ecosystems.

Trees in semi-arid woodlands often have very deep roots (e.g., Nulsen et al., 1986) and use water conservatively (e.g., Meyer et al., 2015) relative to shallow-rooted, annual plants such as grasses and may therefore respond differently to sequences of long dry periods and large rainfall events. Understanding the responses of semi-arid woodlands to drying and wetting is important in projecting ecosystem C flux change, particularly as climate is predicted to become drier in many regions of the world.

The aim of this study was to quantify the effect of previous rainfall patterns on responses of ecosystem carbon fluxes to a large rainfall event in a semi-arid woodland. We hypothesised that: (i) irrespective the background of rainfall history, gross primary productivity and ecosystem respiration rates will be enhanced by large rainfall events, which lead to a change in net ecosystem carbon exchange. This is based on the assumption that soil microbes and plant (root and shoot) growth and development are strongly limited by availability of water. Thus once the ecosystem is recharged by large rainfall event, the gross primary productivity and ecosystem respiration rates will be increased. And (ii) the increase in gross primary productivity and ecosystem respiration rates after a rainfall event will be short-lived, lasting only for 1-7 days. This is because in semi-arid ecosystems (e.g. grass- and/or shrub-based), responses of gross primary productivity and ecosystem respiration rates to incident available water commonly denoted as a carbon dioxide flush. This flush varies among ecosystems but is generally reported to be short-lived.

2. Methods and Materials

2.1 Site description

The field site was at Calperum Station (34.04° S, 140.71° E), adjacent to the Chowilla floodplain of the River Murray in South Australia. The area is classified as semi-arid with annual median rainfall of 242 mm and an annual average of 41 rain days. The mean maximum and minimum air temperatures are 24.9 and 9.6 °C (data recorded from 1996 to 2014, from http://www.bom.gov.au/). The site is part of the Terrestrial Ecosystem Research Network's (TERN) OzFlux and Australian Supersite Network (ASN) programs (Karan et al., 2013) and the global FLUXNET (http://fluxnet.ornl.gov/). It is equipped with an eddy covariance monitoring system mounted on a 20 m high tower and described below. Onsite rainfall was measured with the tipping bucket gauge (CS7000, Hydrologic services, Warwick, NSW, Australia) (0.2 mm resolution) mounted on a stand at 0.65 m in a tree-free area. In the 1249 days from tower establishment to the end of 2013, 264 days had rainfall greater than 0.2 mm. The average daily rainfall (considering only rain days with > 1 mm) was 8.0 mm. Daily rainfall > 35 mm was considered a large event.

The mallee woodland is a eucalypt-shrub association. The area around Calperum and surrounding properties contain over one million hectares of mallee habitat, that is the largest continuous remnant of this vegetation association in Australia (Nulsen et al., 1986). The tree vegetation is dominated by four multi-stemmed eucalypt species (*Eucalyptus dumosa*, *E. incrassata*, *E. oleosa* and *E. socialis*) with sparse leaf canopies between 3 to 5 metres aboveground. The understory, often in the space between trees, is mainly spinifex (*Triodia basedowii*) that grows in spreading clumps to a height of ca. 0.7 metres. The rest of the ground surface is largely bare, with occasional and limited coverage by ephemeral grasses.

The alkaline sandy soil (94% sand, 4% silt and 2% clay) at the study site is classified as a Tenosol in the Australian Soil Classification (Isbell, 2002), and as an Aridisol in the US Soil Taxonomy (Soil Survey Staff, 1996). At 0-30 cm depth the soil had a bulk density of 1.6 g cm^{-3} (Sun et al., 2015), was non-saline ($EC_{1:5} < 0.4$ dS m^{-1}) and a $pH_{1:5}$ of 8.3. Soil carbonate content was 0.2-0.3%, soil total organic C and total nitrogen varied from 0.35% to 1.02% and from 0.03% to 0.07% respectively (Sun et al., 2016).

2.2 Eddy covariance measurement and data processing

The 20 m high eddy covariance (EC) tower was erected in June 2010 to measure fluxes of CO_2, H_2O and energy. The footprint of the EC tower covers ca. 34 hectares. A detailed description of the instrumentation can be found in Meyer et al. (2015). Briefly, measurements of three-dimensional wind speed (CSAT3 sonic anemometer, Campbell Scientific Inc., Logan, UT, USA), virtual temperature (CSAT3), as well as air water vapour density and CO_2 density using an open-path infra-red gas analyser (IRGA, *LI-COR* LI7500, *LI-COR* Biosciences, Lincoln, NE, USA), were recorded at a frequency of 10 Hz.

Auxiliary observations of solar irradiance, air temperature, vapour pressure deficit and rainfall, soil temperature and soil water content were also collected concurrently. Incident solar irradiance was recorded by a four component radiometer that was positioned at a height of 20 m (CNR4, Kipp and Zonen, Delft, the Netherlands). Vapour pressure deficit was determined as the difference between atmospheric vapour pressure (kPa) and saturation vapour pressure at air temperature (HMP45C, Vaisala, Helsinki, Finland) at a height of 2 m. Soil water content sensors (CS650, Campbell Scientific, Townsville, Australia) were placed 10 metres away from the tower base in bare soil and beneath eucalypt and shrub canopies with multiple depths in March 2012, ranging from 0.1 m to 1.8 m. Soil water content sensors (CS650, Campbell Scientific, Townsville, Australia) were placed 10 metres away from the tower base in bare soil and beneath eucalypt and shrub canopies with multiple depths in March 2012, ranging from 0.1 m to 1.8 m.

Covariances were computed every 30 min to generate fluxes following standard OzFlux QA/QC correction procedures (Calperum Tech, 2013; Cleverly et al., 2013; Eamus et al., 2013) and cross-checked with methods described in Thomas et al. (2011). Removal of latent energy flux and sensible heat flux spikes, gap filling, night-time flux filtering (where solar radiation < 20 W m^{-2}) and friction coefficient threshold determination were carried out as described in Reichstein et al. (2005) and Thomas et al. (2011), using the add-on package 'REddyProc' (Reichstein and Moffat, 2015) in R program (R development Core Team, 2014). A friction coefficient threshold was calculated and set to 0.33, 0.18, 0.29 and 0.29 m s^{-1} for the years 2010, 2011, 2012 and 2013 respectively.

The tower measures of CO_2 flux give net ecosystem exchange (NEE) that is partitioned into ecosystem respiration (Reco) using night time exchange to estimate full day respiration and gross primary productivity (GPP). Net ecosystem productivity (NEP) was calculated by subtracting partitioned Reco from GPP. Thus positive NEP values indicate net C uptake (sequestration) by the vegetation; while negative NEP values indicate a net C loss from the ecosystem. Daily average measurements of NEP, GPP and Reco were calculated.

Three large rainfall events with contrasting previous rainfall patterns between 2010 and 2013 were chosen for this study. Each of these events was followed by at least 35 days with little or no rain. The central rainfall events were 38.2 mm on 03-Sep-2010 (40.6 mm rainfall in the 60 days prior to this central event), 55.2 mm on 20-Mar-2011 (118.8 mm rainfall in the prior 60 days); and 35.6 mm on 27-Feb-2013 (with no rainfall in the prior 60 days).

NEP, partitioned Reco and GPP flux rates 28 days prior to and 35 days after the three central rainfall events were studied. Average weekly NEP, Reco and GPP were also calculated. Flux data recorded on rainy days was excluded from the analyses because it is often highly variable due to interference of water films on the open path IRGA.

Ratios of NEP, GPP and Reco to normalised difference vegetation index (NDVI) were calculated to adjust for differences in leaf mass among research periods. NDVI data was extracted from MODIS imagery at 250 m spatial resolution. The ratio of NEP to air temperature was also calculated to take into account differences in temperature. Partitioning NEP into GPP and Reco is based on a temperature dependent algorithm, therefore ratios of GPP and Reco to air temperature were not calculated.

2.3 Soil water addition experiment

To measure the response of soil respiration to a large rainfall event after a long dry period, a water addition experiment was conducted in-situ. Five PVC collars (20 cm diameter and 20 cm height) were inserted to a depth of about 15 cm into the ground under tree canopies for each treatment (control and water treatments) in late October 2014, 30 days before measurements commenced. Ten soil collars were randomly placed, 2-5 metres apart from each other and remained undisturbed throughout the experiment. Any seedlings that germinated inside the collars were carefully removed to minimise surface disturbance.

A volume of water equivalent to 30 mm rainfall was sprinkled on five soil collars and the immediate surrounding areas (together ca. 0.5 m^2) on November 16 2014. In the 45 days prior to this rainfall simulation, the site had only received 4.8 mm of rain. Soil CO_2 release was measured immediately after water addition (0 hour), 24 hours and 48 hours post-event on both water treated and control collars with a manual chamber connected to an IRGA (LI-8100, *LI-COR* Inc., Lincoln, Nebraska, USA). The chamber was placed over the PVC soil collars and each measurement took approximately three minutes.

2.4 Statistical analysis

One-way Analysis of Variance (ANOVA) was used to compare differences in air temperature and normalised difference vegetation index (NDVI) among three experimental periods.

A general linear mixed model was used for NEP, Reco and GPP to analyse the effects of previous rainfall patterns (three treatment levels associated with the three large rain events), time (28 days prior to and 35 days after the rain events, at 7-day intervals) and their interactions as fixed effects. The analysis was performed with the 'lmer()' function, fitted into 'lme4' package (Bates et al., 2015) and p values were obtained by using the 'lmerTest' package (Kuznetsova et al., 2016) in R (R development Core Team, 2014). Significance was set at $p < 0.05$. A pairwise post hoc Tukey test was also conducted to test differences in combinations of previous rainfall patterns and time, by using the 'multcompView' package (Graves et al., 2015) in R. A Student's t test was used to compare soil water content 6-week average prior to rainfall event (27-Feb-2013) with the average weekly data collected 6 weeks post rain. For the pre-event soil water content, 7 observations were randomly chosen out of the 42 (6×7) data points.

The effect of water addition (water and control treatments), time [immediately after water addition (0 hour), 24 hours and 48 hours post-event] and their interaction on in situ soil respiration were also tested by using a linear mixed model in R.

3. Results

3.1 Microclimate and NDVI prior to and after central rainfall event

Air temperature during the study periods was highest in January-March 2013 and lowest in August-October 2010 ($F_{2, 6} = 12.2$, $p < 0.01$) (Table 1). The different rainfall patterns prior to the selected large rainfall event are illustrated in Fig. 1 and detailed in Table 2. In the 60 days prior to the central rainfall event, 40.6 mm fell in 13 rain days to 03-Sep-2010, 118.8 mm in 10 rain days to 20-Mar-2011and 0.0 mm to 27-Feb-2013 period. In the 35 days after the central rainfall event, rainfall amounts for 03-Sep-2010, 20-Mar-2011 and 27-Feb-2013 were

8.8, 7.6 and 2 mm in 2, 3 and 1 rain days, respectively. In 6 weeks prior to the 27-Feb-2013 event, soil water contents at 10 cm and 25 cm depths were relatively stable, with average values of 0.022 and 0.048 v/v (Fig. A.1 and Table A.1). In the first week after the event, soil water content was 252% and 114% higher than pre-event in 10 and 25 cm depth. From the third to the sixth week, water content was 69-33% and 24-12% higher than pre-event for 6 weeks. The normalised difference vegetation index (NDVI) was greater in February-April 2011 than the other two periods ($F_{2, 6} = 11.5$, $p < 0.01$) (Table 1).

3.2 Ecosystem carbon fluxes

NEP, Reco and GPP responded differently to the central rainfall event in the three study periods (Fig. 2 and Table 3). There was also a significant interaction between time and the previous rainfall pattern on ecosystem C fluxes.

Weekly averaged NEP in the 28 days prior to the central rainfall event did not differ among the study periods despite differences in rainfall patterns (Fig. 2a and Table A.2). However in the 14 days after the central rainfall event, NEP rates were more negative in the 27-Feb-2013 period than before the event while they remained stable in the two other study periods. Between 15 and 21 days after the central event, NEP rates in the 27-Feb-2013 period increased and were similar to those in the other two study periods after day 21. Net ecosystem productivity normalised to NDVI or air temperature (NEP/NDVI and NEP/Tair) showed similar patterns (Fig. A.2 and Fig. A.3).

Weekly averaged Reco in the 28 days prior to the central rainfall event was highest in the 20-Mar-2011 period and lowest in the 03-Sep-2010 period (Fig. 2b and Table A.2). The central rainfall event induced a pulse of Reco in the first week in the 27-Feb-2013 period, but had no effect on Reco in the other two study periods. In the second week Reco in the 27-Feb-2013 period remained higher than prior to the central rainfall event, but then decreased gradually to reach similar rates as prior to the central rainfall event after 28 days.

GPP rates were highest in the 20-Mar-2011period and fluctuated over time, but these fluctuations were not related to rainfall events (Fig. 2c and Table A.2). GPP rates were similar in the 27-Feb-2013 and the 03-Sep-2010 periods although in the month prior to the central rainfall event less rainfall was recorded in February 2013 (0 mm) compared to September 2010 (16 mm). In both study periods, fluctuations in GPP rates over time were not related to rainfall events.

3.3 Flush of soil respiration after water addition

The simulated rainfall after 45 days with only 4.8 mm rainfall induced a flush of soil respiration within the first 30 minutes and rates remained two-fold higher than the unwatered control for the next 48 hours (Fig. 3 and Table 4). Soil respiration rates for both the control and simulated rainfall treatments did not change over the 48 hours of the experiment.

4. Discussion

This study showed that response of ecosystem carbon fluxes to a natural, large rainfall event (35-55 mm) in a semi-arid woodland depended on the preceding rainfall pattern. After a period with several medium to large rainfall events, the central rainfall event had little effect on Reco and NEP (03-Sep-2010 and 20-Mar-2011). In contrast, a central rainfall event on 27-Feb-2013 after a period with very little rainfall induced an increase in Reco for about 3 weeks and thus a decrease in NEP. Thus both the first hypothesis (irrespective the background of rainfall history, gross primary productivity and ecosystem respiration rates will be enhanced by large rainfall events inducing net carbon uptake) and the second hypothesis (the increase in gross primary productivity and ecosystem respiration rates after a rainfall event will be short-lived, lasting only for 1-7 days) have to be declined.

The long dry period prior to the central rainfall event in the 27-Feb-2013 study period was associated with lower NEP and GPP compared to the other periods, particularly the 20-Mar-2011 period which had the greatest rainfall amount (Fig. 1 & 2). This was not due to a smaller leaf biomass in the 27-Feb-2013 period because GPP and NEP normalised to NDVI was also lower in this study period compared to the 20-Mar-2011 period (Fig. A.2). This suggests that the ecosystem was particularly water-limited in the long dry period prior to the central rainfall event on 27-Feb-2013. Other studies have also showed that GPP is lower than normal in dry periods (Haverd et al., 2016; Poulter et al., 2014; Cleverly et al., 2013; Pereira et al., 2007).

The simultaneous but opposite effect of the rainfall event in the 27-Feb-2013 study period on NEP and Reco suggests that the decline in NEP can be explained by the increase in Reco while GPP rates remained stable. The ecosystem changed from carbon neutral prior to the event to an apparent carbon source. This was most pronounced in the first week after the central rainfall event. Two weeks after the rainfall event, Reco had declined and at three weeks it was at pre rainfall values. GPP tended to increase after the rainfall event but was only significantly greater than pre rainfall event values 21 days after the event (Table A.1). The large increase in Reco after the central rainfall event can, at least partly, be explained by an increase in soil respiration upon rewetting. Large increases in Reco with little change in GPP after a single large rainfall event have been reported in other semi-arid to arid ecosystems (e.g., Hamerlynck et al., 2012; Liu et al., 2013; Huang et al., 2015), resulting in net carbon release rather than carbon sequestration. Our watering experiment which was carried out after a long dry period showed that a simulated rainfall event of similar magnitude can induce a doubling of the soil respiration rate which is of similar magnitude as the increase in Reco observed after the central rainfall event of 27-Feb-2013 (Fig. 3). A flush of respiration upon rewetting of dry soil has been observed in many studies (e.g., Kim et al., 2012) and has been explained by the release of readily available carbon and nutrients when dry soil is suddenly rewet (Borken and Matzner, 2009; Nielsen and Ball, 2015). Higher respiration rates than before the watering event were maintained for at least 48 h which agrees with previous studies (e.g., Vargas et al., 2012; Hamerlynck et al., 2012). However, in incubation experiments in the absence of roots the flush upon rewetting usually lasts only for 1-3 days (e.g., Sun et al., 2015; Wang et al., 2016). The higher Reco for 2-3 weeks after the central rainfall event in February 2013 suggests that not only heterotrophic respiration, but also root respiration was stimulated by the central rainfall event (Shim et al., 2011b). In a separate study in the same ecosystem (Sun et al., 2016), we found that soil water content in 0-5 cm depth is very low 4 weeks after large rainfall events. But this study showed that water contents at both 10 cm and 25 cm depths were higher than before the rainfall event for 6 weeks even if the top few centimetres dried quickly. Therefore, root respiration could be increased for longer than heterotrophic respiration because of the greater supply of carbohydrates and the higher soil water content in deeper soil layers compared to the top soil where heterotrophic respiration predominantly occurs.

Reco was in general lower in the September period than the other two periods (Fig. 2), most likely because of the lower temperature (Fig. 1). Therefore, the lack of response of Reco to the central event in September was possibly due to more rainfall prior to the event and lower air temperature compared to the February. However, in the March period, when temperatures were similar to those in the February period, the effect of the central rainfall event on Reco was also limited. This can be explained by previous rainfall pattern. Prior to central rainfall event, rainfall was twice as high as evaporation in March 2011 whereas it was ten-fold lower in February 2013 (Table 1). Thus, the soil was moister in March which lead to greater Reco prior to the central event (Fig. 2). This indicates that soil microbes and roots were less water-limited in March and therefore were less predisposed to respond to the central rainfall event.

5. Conclusion

This study suggests that the response of C fluxes in dryland ecosystems to a single large rainfall event depends on the rainfall amounts and pattern prior to the event. Soil respiration and NEP may only change following a large rainfall event after a long dry period, but not if several moderate amounts of rainfall occur in the previous four weeks. The prolonged increase in soil respiration may be specific to this woodland on sandy soil dominated by deep-rooted eucalypt species that are well adapted to low and often erratic rainfall and use incident available water conservatively. Therefore, previous rainfall history should be considered when interpreting the response of ecosystem C fluxes to rainfall events in dryland ecosystems.

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Table 1 Monthly mean air temperature (°C), total rainfall (mm), evaporation (mm) and normalised difference vegetation index (NDVI) at Calperum Station (34.00°S, 140.59°E) in three months around the central rainfall event.

	Period around 03-Sep-2010			Period around 20-Mar-2011			Period around 27-Feb-2013		
	Aug.	Sep.	Oct.	Feb.	Mar.	Apr.	Jan.	Feb.	Mar.
Air temperature (°C)	11.0	13.0	17.1	23.5	20.4	17.2	25.1	25.2	22.8
Rainfall (mm)	24.2	47.6	66.6	109.0	63.4	4.4	1.0	36.8	2.2
Evaporation (mm)	18.9	15.8	22.1	47.2	32.9	25.0	10.7	7.4	19.2
NDVI	0.33	0.31	0.29	0.39	0.43	0.42	0.31	0.36	0.38

Table 2 Summary of distribution of rain 60 days, 35 days, 28 days and 14 days prior to and post the central rainfall events

	Total amount of rainfall (number of rainfall days, mm)							
	- prior to				- post			
Central rainfall event	60 days	35 days	28 days	14 days	14 days	28 days	35 days	60 days
03-Sep-2010	40.6 (13)	24.2 (8)	16.2 (5)	3 (1)	8.8 (2)	8.8 (2)	8.8 (2)	74.8 (9)
20-Mar-2011	118.8 (10)	20.6 (5)	3 (2)	3 (2)	3.6 (1)	7.6 (3)	7.6 (3)	7.6 (3)
27-Feb-2013	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (1)	2 (1)	11.6 (2)

Table 3 ANOVA outputs of general linear mixed model analyses of effects of rainfall patterns prior to the central rainfall event (03-Sep-2010, 20-Mar-2011 and 27-Feb-2013), time (between 28 days prior to and 35 days after rainfall events, at 7-day intervals) and their interactions on net ecosystem productivity (NEP), ecosystem respiration (Reco) and gross primary productivity (GPP).

Explanatory variables	**ndf**	**ddf**	**F value**	**p**
NEP				
Events	2.00	174.00	72.05	< 0.001
Time	8.00	174.00	6.69	< 0.001
Events × Time	16.00	174.00	4.57	< 0.001
Reco				
Events	2.00	174.00	586.07	< 0.001
Time	8.00	174.00	27.10	< 0.001
Events × Time	16.00	174.00	31.76	< 0.001
GPP				
Events	2.00	167.34	452.75	< 0.001
Time	8.00	168.06	5.14	< 0.001
Events × Time	16.00	167.85	6.73	< 0.001

ndf, numerator degrees of freedom; ddf, denominator degrees of freedom.

Table 4 Outputs of general linear mixed model analyses of effects of water (control and water added), time (0 hour – immediately after water addition, 24 hours and 48 hours after watering and their interactions on soil respiration.

Explanatory variables	**ndf**	**ddf**	**F value**	**p**
Water addition	1	26.49	59.06	< 0.001
time	2	20.00	1.05	0.37
Water addition × time	2	27.49	1.45	0.25

ndf, numerator degrees of freedom; ddf, denominator degrees of freedom.

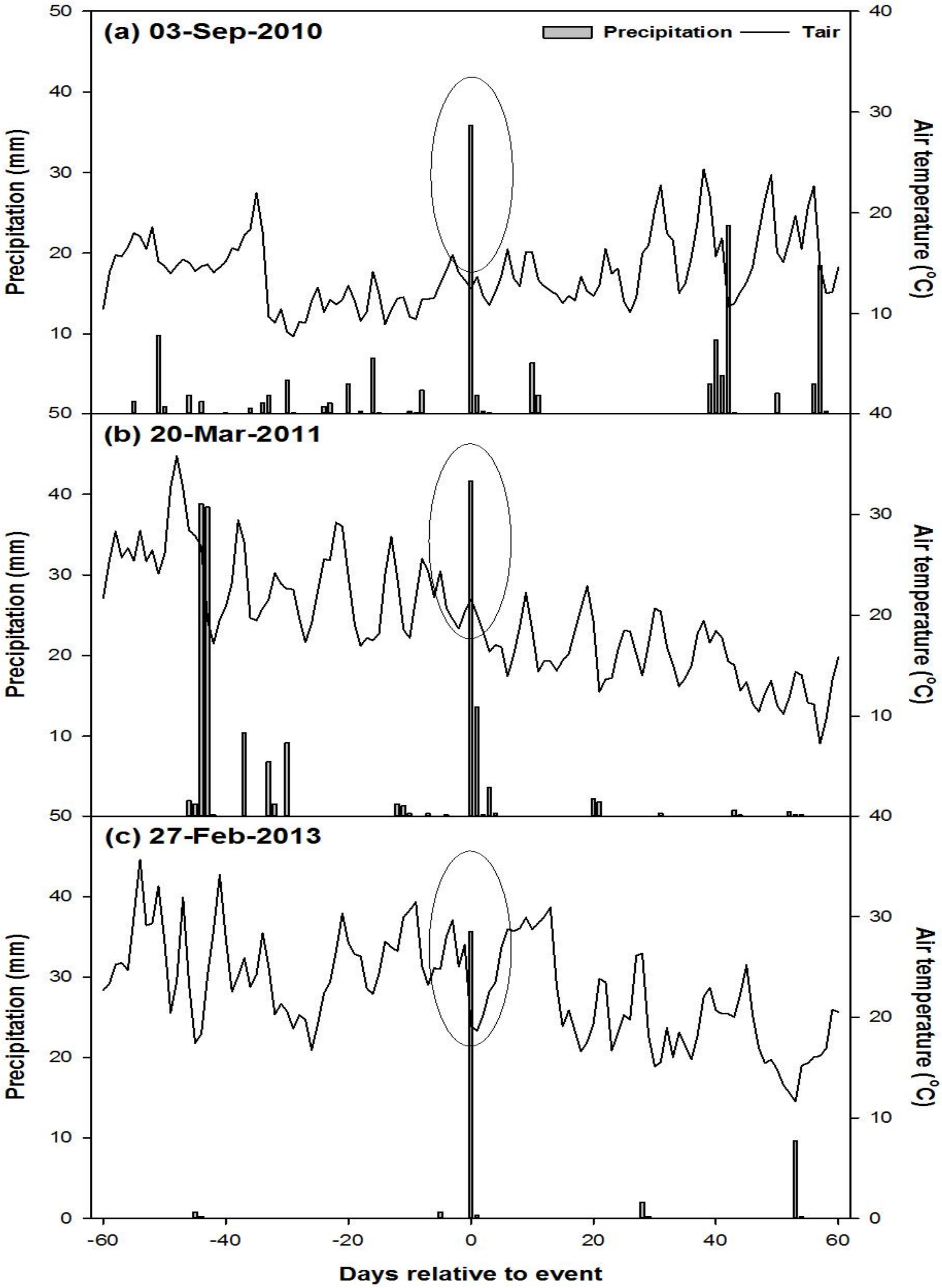

Fig. 1. Daily rainfall and air temperature prior to (-60 days) and after (60 days) three central rainfall events (circled) of comparable magnitude: (a) 03-Sep-2010, (b) 20-Mar-2011 and (c) 27-Feb-2013.

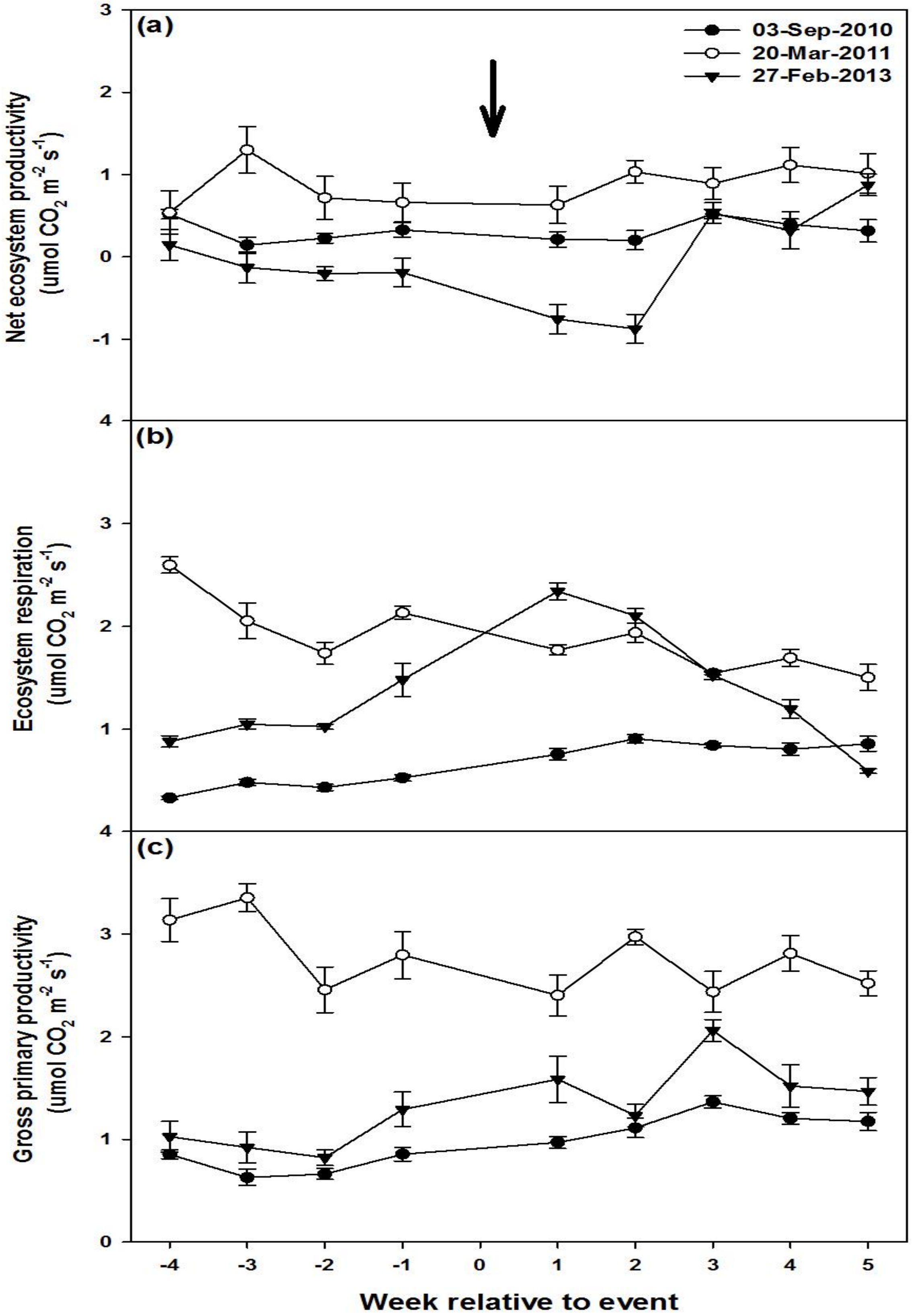

Fig. 2. Weekly average of (a) net ecosystem productivity, (b) ecosystem respiration, and (c) gross primary productivity between 28 days prior to and 35 days after the central rainfall event (mean ± standard error, n=5-7). Arrow indicates central rainfall event.

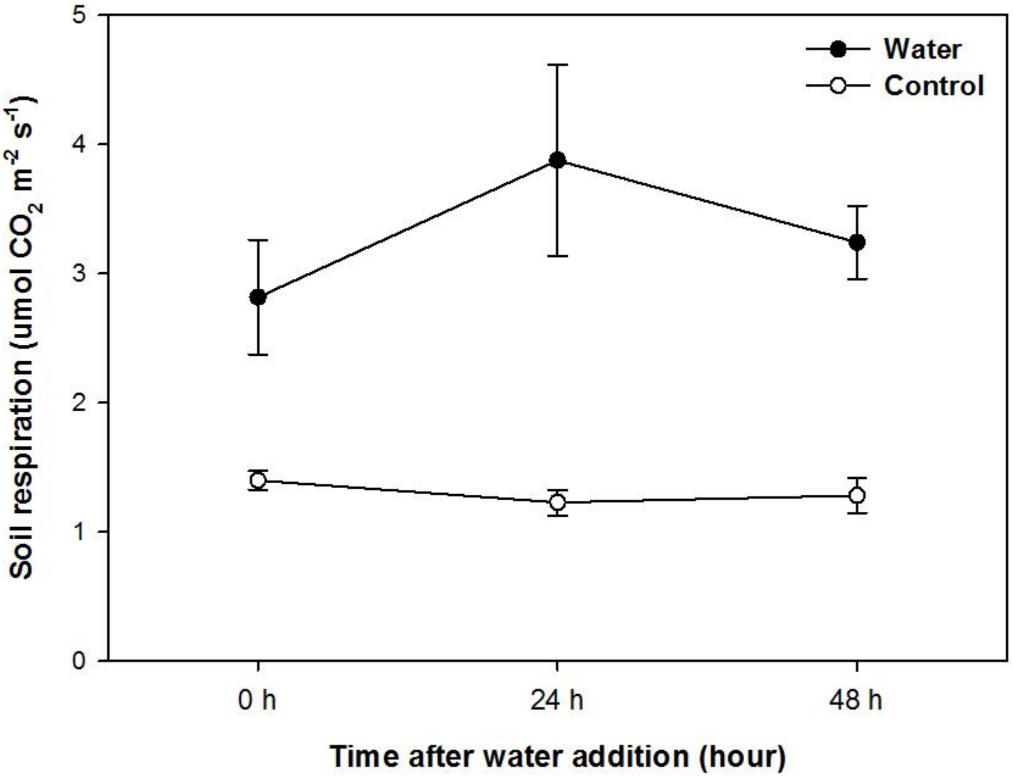

Fig. 3. Soil respiration rates (µmol CO_2 m^{-2} s^{-1}) over 48 hours in unwatered control and after addition of 30 mm water (mean ± standard error, n=5).

Supplementary Material

Table A.1 Soil water content (SWC) at 10 cm and 25 cm depths of given periods and relative increase of soil water content data post rainfall compared to 6-week average prior to the rainfall event on 27-Feb-2013.

	Period	SWC at 10 cm (v/v)		SWC at 20 cm (v/v)	
		The average of the given period	Increase (%)	The average of the given period	Increase (%)
Prior to	16th Jan - 26th Feb	0.022		0.048	
Post	28th Feb - 6th Mar	0.076	252%*	0.102	114%-
	7th - 13th Mar	0.047	115%*	-	-
	14th -20th Mar	0.037	69%*	0.059	24%-
	21st - 27th Mar	0.033	50%*	0.058	22%*
	28th Mar – 3rd Apr	0.030	38%*	0.054	14%*
	4th - 10th Apr	0.029	33%*	0.053	12%*

The '*' indicates significant difference ($p < 0.001$) when comparing the average of the 6 weeks prior to the event with the average weekly data collected 6 weeks post rain; the '-' indicates that information is unavailable due to data missing.

Table A.2 Pairwise post hoc Tukey testing for all previous rainfall patterns and time combinations. Different letters indicate significant differences for the period × week interaction.

	Days to rainfall event								
	Prior to				Post				
	-28	-21	-14	-7	7	14	21	28	35
NEP									
03-Sep-2010	cdef	bcde	cde	cde	cde	bcde	cdef	cde	cde
20-Mar-2011	cdef	f	cdef	cdef	cdef	def	def	ef	def
27-Feb-2013	cd	abc	abc	abc	ab	a	cdef	cde	def
Reco									
03-Sep-2010	a	abc	ab	abc	abcd	cd	bcd	bcd	bcd
20-Mar-2011	k	hij	fghi	ij	fghi	ghij	efg	fgh	ef
27-Feb-2013	cd	d	d	ef	jk	ij	ef	de	abc
GPP									
03-Sep-2010	abc	a	a	ab	abc	abc	abcd	abc	abc
20-Mar-2011	fg	g	ef	fg	ef	fg	ef	fg	ef
27-Feb-2013	abc	abc	ab	abc	cd	abc	de	bcd	bcd

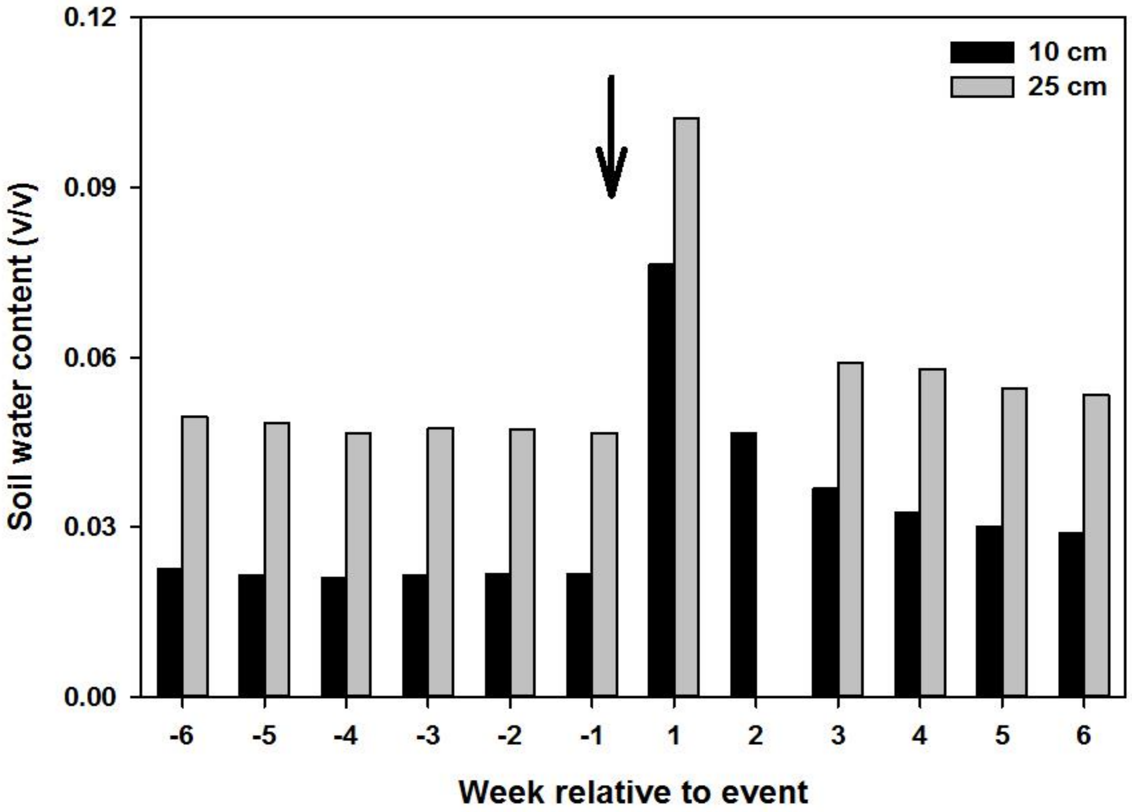

Fig. A.1 Weekly average of soil water content (SWC) at 10 cm and 25 cm depths prior to (-42 days) and after (42 days) the central rainfall event on 27-Feb-2013. Arrow indicates central rainfall event. SWC at 25 cm depth data is not available for the 2nd week post rain.

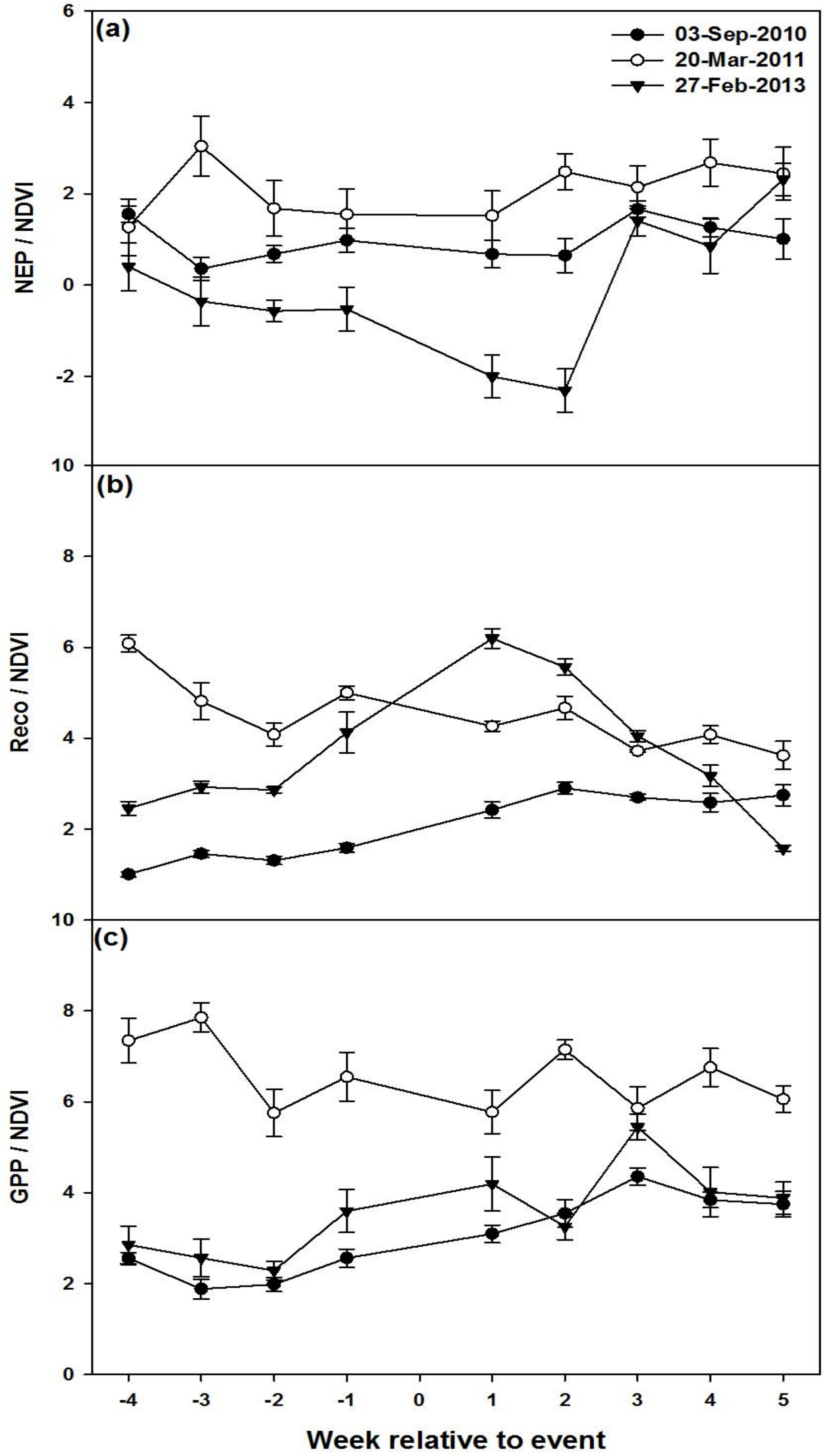

Fig. A.2 Net ecosystem productivity (NEP), ecosystem respiration (Reco) and gross primary productivity (GPP) normalised to vegetation index (NDVI) in periods between 28 days prior to and 35 days post three central rainfall events.

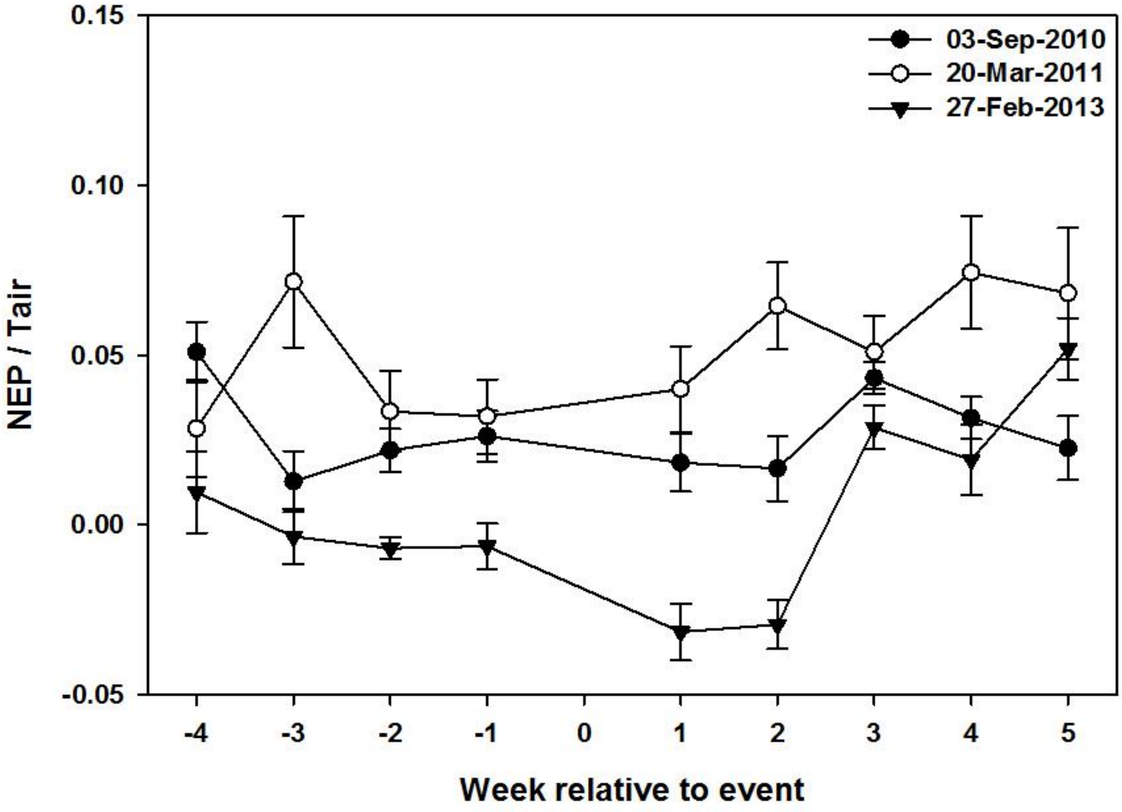

Fig. A.3 Net ecosystem productivity (NEP) normalised to air temperature (Tair) in periods between 28 days prior to and 35 days post three central rainfall events.

Chapter 6

A short heavy rainfall in summer enhances soil respiration in a semi-arid floodplain woodland for two months without rain

Statement of Authorship

Title of Paper	A short heavy rainfall in summer enhances soil respiration in a semi-arid floodplain woodland for two months without rain	
Publication Status	☐ Published ☑ Submitted for Publication	☐ Accepted for Publication ☐ Unpublished and Unsubmitted work written in manuscript style
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Principal Author

Name of Principal Author (Candidate)	Qiaoqi Sun		
Contribution to the Paper	Experimental development, data collection, analysis and manuscript writing.		
Overall percentage (%)	80		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature	[redacted]	Date	02/02/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above); ii. permission is granted for the candidate in include the publication in the thesis; and iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Wayne S. Meyer		
Contribution to the Paper	Supervised experimental design and completion of the work, data interpretation and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature	[redacted]	Date	02/02/2017

Name of Co-Author	Petra Marschner		
Contribution to the Paper	Supervised experimental design and completion of the work, data interpretation and manuscript evaluation. I hereby certify that the statement of the contribution is accurate.		
Signature	[redacted]	Date	06/02/2017

Name of Co-Author			
Contribution to the Paper			
Signature		Date	

Abstract

Rainfall amounts and timing as well as air temperature influence soil respiration (R_{soil}) especially in semi-arid to arid ecosystems. However, information about R_{soil} in semi-arid floodplains and its response to rainfall events is particularly limited. This study measured R_{soil} monthly in-situ from July 2014 to August 2015 under eucalyptus canopies and inter-canopy of a semi-arid floodplain woodland, adjacent to the River Murray, Australia. R_{soil} and soil organic C content were greater under canopy than inter-canopy. Five days of rainfall (total of 62 mm) in summer (air temperature ca. 23 °C) increased R_{soil} by 70-85% four days after the last rainfall event compared to that before the rainfall. R_{soil} remained high over the following two months with no rain, although soil water content in the top soil (0-5 cm) was very low. This suggests that in the months following the short rain period, roots in the moist subsoil were the major contributors to R_{soil}. On the other hand, a single rainfall event (51 mm) in autumn (air temperature ca. 17 °C) did not increase R_{soil} although top soil water content was three times higher than in the previous dry period. Therefore R_{soil} in this ecosystem is influenced by a complex interaction between rainfall amount, soil temperature as well as, possibly, distribution of the rainfall. This study emphasized the importance of quantifying Rsoil in similar dry floodplains to better predict their role in the global carbon cycle, particularly in light of the predicted changes in rainfall patterns in many semi-arid regions.

Keywords: floodplain; rainfall event; semi-arid woodland; soil respiration; water content

1. Introduction

Soil respiration is the second largest carbon flux in the global carbon cycle and is generally considered to have two components, microbial (heterotrophic) and root (autotrophic) respiration (Davidson and Janssens, 2006; Raich and Schlesinger, 1992; Kuzyakov, 2006). Both microbial and root respiration are strongly influenced by available soil water content and therefore highly dependent on rainfall regimes, especially in semi-arid to arid ecosystems (Austin et al., 2004; Nielsen and Ball, 2015). The magnitude and duration of increased soil respiration ("a pulse") following rainfall is influenced by the interaction between rainfall amount and timing and air temperature (e.g., Huxman et al., 2004; Yan et al., 2014; Unger et al., 2010; Thomey et al., 2011). While a respiration pulse following rainfall is regularly observed, the magnitude and duration is highly variable. This variability is likely caused by different ecosystems and differences in soil water content prior to rainfall (e.g., Norton et al., 2012; Shi and Marschner, 2014; Shim et al., 2009). The flush in microbial soil respiration after rewetting of dry soil has been attributed to increased availability of substrates from death of part of the microbial biomass, release of osmolytes accumulated during the dry period and by aggregate breakdown increasing accessibility of previously protected organic matter (Borken and Matzner, 2009). Enhanced soil respiration after rewetting of dry soil in the field may also be due to increased root respiration. Carbone et al. (2011) suggested that soil respiration after rewetting of dry soil is initially dominated by microbial respiration increasing within hours, whereas root respiration responds more slowly over days.

In situ soil respiration has been studied extensively but mainly in ecosystems with large amounts of annual rainfall (> 300 mm) (Bond-Lamberty and Thomson, 2014). Less attention has been given to regions with lower annual rainfall (< 300 mm). However these systems are also more likely to experience long periods of drying and hence have relatively large responses of soil respiration to rainfall events. The large global extent of semi-arid to arid ecosystems means that these areas are collectively important in the global carbon cycle. Ahlstrom et al (2015) suggested that inter-annual variability of the global carbon cycle is strongly influenced by rainfall in these dry regions. Semi-arid and arid ecosystems are further important for global carbon cycling because of the large amount of carbon stored in them (Lal, 2004). Improved quantification of soil respiration in these dry systems is therefore important. Information from dry floodplain ecosystems is particularly limited.

Floodplains are the interface between terrestrial and aquatic ecosystems and are hot spots of biogeochemical cycling compared to adjacent regions because occasional flooding saturates the soil profile and redistributes sediment and nutrients (McClain et al., 2003; Capon et al., 2013; Bayley, 1995). Due to extensive worldwide river regulation for agricultural, domestic and industrial water use (Rood et al., 2005), nearly 90% of floodplains in Europe and North America have been modified (Tockner and Stanford, 2002). Many floodplain wetlands in Australia (Kingsford, 2000) and globally (e.g., Sankey et al., 2015; Perry et al., 2012) either no longer experience inundation or are flooded very infrequently. Without temporal inundation, carbon cycling in semi-arid to arid climates depends more on rainfall input (Belnap et al., 2005) and CO_2 emission is mainly due to aerobic respiration (Kayranli et al., 2010; Sun et al., 2013). Reduced floodplain inundation also influences groundwater recharge and extent. The lowering of the groundwater table is likely to extend periods of aerobic soil conditions and therefore increased carbon dioxide emission from soil from both aerobic decomposition and root respiration (Kuzyakov, 2006). A better understanding of soil respiration in these ecosystems is important for estimation of the contribution of floodplains to the global C cycle.

This study addressed the knowledge gap. In very dry climates such as those in southern Australia, floodplains are often covered by woodlands that are characterised by patchy vegetation surrounded by large areas with little or no plant cover (Tongway and Ludwig, 1994). As a result of the greater C input into the soil by trees, C cycling in such ecosystems is characterised by hot spots under trees compared to the adjacent bare soil. The first aim of this study was to quantify soil respiration under tree canopies and from adjacent bare soil in a semi-arid floodplain woodland. The second aim was to determine the response of soil respiration rates to natural rainfall events. Previous studies showed that rapid rewetting of air-dry soil causes a short pulse of soil respiration which typically lasts only for a few days, the so-called ‘Birch effect’ (Birch, 1958). Therefore the hypothesis was that soil respiration will be positively correlated with soil water content and therefore increase after rainfall events and then decrease as the top soil dries. And further, that these changes in soil respiration will be greater under canopy than in bare soil.

2. Materials and methods

2.1 Site description

The study site was in native floodplain woodland (34°2'41.11" S, 140°45'43.17" E) adjacent to the River Murray near Renmark in South Australia. The study site contains sensitive wetlands recognised under the Ramsar Convention and three other international treaties (http://www.daff.gov.au/natural-resources/). Previously, the floodplains were flooded near annually, but due to drought and flood regulation, this area was flooded only twice in the last two decades, in 1997 (Siebentritt et al., 2004) and in 2010. The area is semi-arid and has a Mediterranean climate with wet, cool winters, and hot, dry summers with occasional heavy rainfall events. The median annual rainfall is 242 mm, but single heavy rainfall events with 60-70 mm can occur (data recorded from 1996 to 2014, from http://www.bom.gov.au/). In order to get more precise information, rainfall data was obtained for the study period from a nearby flux tower (ca. 10 km from this study area) (Meyer et al., 2015). Rainfall was measured with a tipping bucket gauge (CS7000, Hydrologic services, Warwick, NSW, Australia) (0.2 mm resolution) mounted on a stand at 0.65 m height in a tree-free area.

Vegetation in the floodplain is dominated by patches of river red gum (*Eucalyptus camaldulensis*), black box (*E. largiflorens*) and of the shrub lignum (*Mueblenbeckia florulenta).* The rest of the soil surface is mostly bare with very sparse cover by ephemeral grasses. The floodplain soil in the 0-30 cm depth zone is a silty clay loam (8% clay, 56% silt and 36% sand), with a bulk density of 1.3 g cm^{-3}. The soils are Tenosol in the Australian Soil Classification (Isbell, 2002) and Aridisols in US Soil Taxonomy (Soil Survey Staff, 1996).

2.2 Soil sampling and property analysis

Soil from two distinct patches in the floodplain woodland was collected in May 2014, under eucalyptus canopies (hereafter referred to as “under canopy”), and in open areas in between vegetation patches (referred to as “inter-canopy”).

Three transects (100 m long, > 50 m apart from each other) were randomly selected for soil sampling. All transects started from the edge of river and ran perpendicular inland. Three soil samples (at 0-30 cm depth, after removing the litter layer) per transect were taken from each under canopy and inter-canopy. The nine samples from a given patch were then combined, mixed, sieved to < 2 mm and air-dried at 30 °C for soil property measurement. Soil pH and electrical conductivity (EC), soil water holding capacity, total organic C content, and soil calcium carbonate were measured as described in Sun et al. (2015).

2.3 In-situ soil respiration measurement

Polyvinyl chloride (PVC) collars (20 cm in diameter and 15 cm in height) were inserted the ground leaving about 5 cm aboveground, five each, under canopy and inter-canopy, in late May 2014, two months prior to the start of measurements. The placement of the five soil collars under and inter canopy was selected randomly, 2-4 metres apart from each other. The collars remained undisturbed until the end of experiment. Any visible seedlings that germinated inside the collars were removed.

Soil respiration was measured monthly from July 2014 to August 2015. In total, 12 sampling campaigns were conducted; two months (August 2014 and June 2015) were missed due to poor weather conditions. The measurements were carried out as described by Sun et al. (2016). Briefly, soil respiration was quantified using an infra-red gas chamber (LI-8100, LI-COR Inc., Lincoln, Nebraska, USA). Each measurement took approximately three minutes and all measurements were carried out between 14.00 pm and 16.00 pm (local time). Soil temperature (LI-8100-203 Soil Temperature Thermistor) and soil water content (LI-8100-204 Soil Moisture Probe) were concurrently recorded at 0-5 cm depth next to soil collars.

Diurnal measurements of soil respiration, temperature and water content (24 h) under canopy were conducted twice, in November 2014 and April 2015. An automated sampling chamber (LI-8100-104) was used to take measurements at 30-min intervals, yielding 48 measurements over 24 hours.

2.4 Statistical analysis

One-way analysis of variance (ANOVA) with a post hoc Tukey test was used to determine the effect of patch (under canopy and inter-canopy) on soil $pH_{1:5}$ and $EC_{1:5}$, maximum water holding capacity, total organic C content and calcium carbonate content.

A general linear mixed model was used to analyse the effects of patch (under canopy and inter-canopy), time (month) and their interactions as fixed effects, collars and collar × month as random effects on in-situ soil respiration, soil water content (0-5 cm) and soil temperature (0-5 cm). The analysis was performed with the 'lmer()' function, fitted into 'lme4' package (Bates et al., 2015) and p values were obtained by using the 'lmerTest' package (Kuznetsova et al., 2016) in R (R development Core Team, 2014). Significance was set at $p < 0.05$. A pairwise post hoc Tukey test was also conducted to test differences in months, by using the 'multcompView' package (Graves et al., 2015) in R.

A general linear model in R was used to detect relationships between soil respiration, soil temperature and soil water content at 0-5 cm depth. Since soil respiration differed significantly between under canopy and inter-canopy, soil respiration rates from the two patches were modelled separately.

3. Results

3.1 Soil properties

Soil $pH_{1:5}$ and Total organic C content were higher under canopy than inter-canopy (Table 1). There were no differences between under canopy and inter-canopy in salinity ($EC_{1:5} < 0.4$ dS m^{-1}) and calcium carbonate content.

3.2 Rainfall distribution and air temperature prior to soil respiration measurement

During the study period (18th June 2014 – 31st August 2015), the area received a total of 252 mm rainfall and the mean air temperature was 16.9 °C, with a minimum of 7.0 °C in July 2014 and a maximum of 34.9 °C in January 2015 (Fig. 1). In the 457 days of the observation period, 40 days had rainfall greater than 1 mm. On rainy days the average amount of rainfall was 6.3 mm. Rainfall events in January and April 2015 prior to soil respiration measurements together amounted to 113.6 mm, which was nearly 50% of the annual rainfall amount (Table 2). The 62.8 mm rainfall in January was comprised of 5 events between 8th and 13th January, ranging from 4.6 mm to 23.8 mm per day. In the following 82 days until 5th April 2015, no rainfall was recorded. On the other hand, there was only one single large rainfall event (50.8 mm) on 17th April 2015. Soil respiration sampling was commonly conducted within two weeks from the last rainfall event, with rainfall events varying from 1.2 mm to 18.4 mm per day. Mean air temperature for soil respiration measurements was relatively similar from November 2014 to March 2015 (22.0 – 24.6 °C) and higher compared to other sampling months (Table 2).

Soil temperature at 0-5 cm depth ranged between 11.0 °C and 47.5 °C (Fig. S1). It was significantly higher inter-canopy than under canopy, and followed the same pattern over time as air temperature (Fig. 1; Table 3). Volumetric soil water content at 0-5 cm depth, generally matched rainfall distribution and significantly varied over time, but there were no consistent differences between patches (Fig. 1; Table 3). Soil water content was higher in January 2015 and during most of winter (April – Jun 2015) compared to the rest of the sampling period, with a maximum value of 0.17 v/v. The soil water content was lower during the two dry periods with no or less than 1 mm rainfall (October – November 2014 and February – March 2015), with a minimum value < 0.01 v/v. For both patches, the average volumetric water content across the year was 0.08 v/v.

3.3 Soil respiration

Soil respiration rates were 0.6 to 2.8 times greater under canopy than inter-canopy (Table 2), and differed among months (Fig. 1; Table 3). They were significantly influenced by the interaction between patch and month. Soil respiration varied from a minimum of 2.53 (in July 2014) to a maximum of 8.53 µmol CO_2 m^{-2} s^{-1} (in January 2015) under canopy, and from 0.97 (in August 2015) to 4.29 µmol CO_2 m^{-2} s^{-1} (in February 2015) inter-canopy. Soil respiration was affected by the interaction between soil temperature and soil water content at 5 cm depth under canopy ($F = 11.37$, $p < 0.001$, $R^2 = 0.38$) and in inter-canopy areas ($F = 27.07$, $p < 0.001$, $R^2 = 0.59$). After the 62.8 mm rainfall in January 2015, soil respiration rates from January to March sampling in both patches remained significantly higher than the other months although the measurements were conducted 4, 19 and 68 days after the last rainfall event(s) and soil water content in 0-5 cm was lower in February and March than in January (Table 2). Soil respiration in January was 1.9 and 1.7 times higher under canopy and inter-canopy areas than in December 2014 when air temperature was similar.

Soil respiration over 24 hours showed a diurnal pattern with increasing respiration rates during the morning and low rates at night (Fig. S2). Soil water content was lower in November 2014 than in April 2015, and correspondingly, respiration rates were higher in April.

4. Discussion

This study confirmed that a short period of heavy rainfall in summer increases soil respiration. However, soil respiration rates remained high over the following two months with no rain, although soil water content in the top soil was very low. This suggests that, at least in this ecosystem, top soil water content is not a suitable parameter for estimating soil respiration. Therefore, we can only partly confirm the hypothesis that soil respiration will be positively correlated with soil water content and therefore increase after rainfall events and then decrease as the top soil dries. The relative increase and decrease was similar under canopy and in bare soil. Therefore, we have to decline the second part of the hypothesis (these changes in soil respiration will be greater under canopy than in bare soil). Moreover, the effect of high rainfall followed by a dry period differed. The increase in soil respiration induced by the January rainfall lasted for three months. However, the single high rainfall event in April did not increase soil respiration and respiration rates were lower in the following months although the soil water content was higher than in February and March. This suggests that the response of soil respiration in this ecosystem is influenced by a complex interaction between rainfall amount, soil temperature as well as, possibly, distribution of the rainfall.

The increase in soil respiration induced by the January rainfall events is in agreement with other studies (e.g., López-Ballesteros et al., 2016; Thomey et al., 2011; Carbone et al., 2011). It is also in agreement with the simulated rainfall experiment result in this study (Fig. S1), which was conducted by using soil without plants from the same study area. Similarly, both soil water content and temperature at the top surface influenced soil respiration, which has also been shown in previous studies in a wide range of ecosystems (e.g., Jha and Mohapatra, 2011; Rey et al., 2011; Correia et al., 2012). However, the linear models for both patches performed poorly. This is most likely because soil respiration rates in February and March remained high as in January 2015 despite the much lower soil water content compared to January (Fig. 1).

The January rainfall of 63 mm fell over 5 days with moderate rainfall amounts (5 to 24 mm per day) (Fig. 1 and Table 2). The repeated rainfall events are likely to have allowed the water to penetrate the soil deeply whereas a proportion of the single rainfall event in April may have runoff or evaporated. Therefore, the soil profile will remain moist although the top soil dried quickly due to the high temperature in the following long dry period. This will have allowed roots in the deeper soil layers to remain active and continuously release CO_2. We propose that soil respiration measured in January (4 days after the last rainfall) was primarily heterotrophic respiration but that the proportion of autotrophic respiration increased with time after the last rainfall. Root respiration in drier upper horizons may have been maintained through hydraulic lift from deeper roots during the night as suggested by Cleverly et al. (2016) for Mulga woodlands in interior Australia. Under the canopy, root respiration is likely to be mainly from tree roots. In the inter canopy area, where soil respiration rates were lower but also remained high for three months, roots of grasses and shrubs as well as tree roots contributed to autotrophic soil respiration. The roots of eucalyptus species have been shown to extend well beyond the canopy area and possibly as far as 30 metres from the centre of the trunk (Colloff, 2014; Abernethy and Rutherfurd, 2001).

The rainfall event in April was of similar magnitude (51 mm), but occurred in a single event and may not have soaked into the soil as much as did the January rainfall. Moreover, temperatures were lower; 17 °C compared to about 23 °C in January to March. The lower temperature may explain why soil respiration rates did not increase as much as might be expected following the January rainfall. Further, lower evaporation resulted in higher water content in the top soil than after the January rainfall.

In agreement with previous studies, soil respiration was higher under canopy than inter-canopy areas (e.g., Tang and Baldocchi, 2005; Sun et al., 2016; Potts et al., 2008) which can be explained by at least two factors. Firstly, the higher soil organic matter content and greater amount of plant litter under canopy (De Deyn et al., 2008; Epron et al., 2004; Raich and Schlesinger, 1992; Robertson et al., 1999) which stimulates heterotrophic soil respiration. Secondly, root density and thus autotrophic respiration is likely to be higher under canopy (Janssens et al., 2001). Average soil respiration rates during the measurement period under canopy and inter-canopy were 5.20 and 2.39 g C m^{-2} d^{-1} respectively. In the study area approximately 45% is under tree canopy, therefore averaged total soil respiration of the area is 3.65 g C m^{-2} d^{-1}. Compared to other floodplain studies in forests, woodlands, grass or shrub lands over a range of annual rainfall values (from < 300 mm to > 2600 mm), soil respiration in this floodplain soil in a semi-arid environment is at the upper end of the reported values (Table S1). In previous studies, there is little or no relationship between soil respiration and mean annual temperature or mean annual rainfall (Table S1). In the floodplain studied here the water table was within 2 m of the soil surface. The soil profile below 30 cm will generally remain moist from capillary upflow from the water table. In this generally warm climate, organic carbon turnover will be high, while total carbon in the soil will be low, as measured (Table 1). These observations indicate that riparian areas (floodplains) adjacent to river systems may have high annual soil respiration rates, especially in warmer environments and therefore influence regional and global carbon cycles to a greater extent than would be expected based on area alone.

5. Conclusion

In this semi-arid woodland, repeated rainfall over several days during summer increased soil respiration for three months although the water content in the top soil was low. However, a single event with similar rainfall in April (autumn) did not induce a strong increase in soil respiration. A field study such as this that relies on natural rainfall events cannot untangle the effect of soil water status and temperature on soil respiration. This would require simulated rainfall corresponding to a single heavy event or several moderate rainfall events carried out at the same time of the year. These should be combined with measurement of soil water content at different soil depths. Such studies are needed to better predict the contribution of semi-arid woodlands to global CO_2 flux particularly in light of the predicted changes in rainfall patterns in many semi-arid regions.

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Table 1 Soil properties of a semiarid floodplain woodland under canopy and inter-canopy (mean ± standard error, n=3).

	Patch relative to canopy		
	Inter-canopy	**Under canopy**	**p value**
$pH_{1:5}$	5.6 ± 0.0	6.0 ± 0.0	**<0.001**
$EC_{1:5}$ (dS m^{-1})	0.3 ± 0.0	0.3 ± 0.0	0.877
Maximum water holding capacity (g water g^{-1} soil)	0.3 ± 0.0	0.3 ± 0.0	0.132
Total Organic C (%)	1.0 ± 0.0	1.7 ± 0.0	**<0.001**
Calcium Carbonate (%)	0.2 ± 0.0	0.3 ± 0.0	0.468

Table 2 Detailed information of rainfall and air temperature prior to each soil respiration measurement in a semi-arid floodplain woodland

		Sampling since last rainfall event[1]		**Total rainfall[1] (mm)**	**Mean air temperature (°C)**	**Soil respiration (μmol CO_2 m^{-2} s^{-1}, mean ± standard error, n=5)**	
Month	**Sampling date**	**Days between sampling and last rainfall**	**Amount of last rainfall before measurement (mm)**	**between measurements**		**Under canopy**	**Inter-canopy**
July 2014	18-Jul-14	8	1.6	7.4	11.2	2.5 ± 0.2	1.3 ± 0.1
Aug[2]	-	-	-	-	-	-	-
Sep	18-Sep-14	13	1.2	23.8	14.0	4.1 ± 0.6	1.5 ± 0.1
Oct	14-Oct-14	19	18.4	18.4	18.2	5.2 ± 0.9	2.4 ± 0.3
Nov	17-Nov-14	1	4.2	4.2	22.0	3.8 ± 0.3	2.3 ± 0.1
Dec	16-Dec-14	5	9.0	15.6	24.2	4.6 ± 0.4	2.4 ± 0.1
Jan 2015	18-Jan-15	4	62.8	70.0	24.1	8.5 ± 0.9	4.0 ± 0.1
Feb	2-Feb-15	19	62.8	0.0	22.2	8.0 ± 1.1	4.3 ± 0.4
March	23-Mar-15	68	62.8	0.0	24.6	7.7 ± 1.8	3.9 ± 0.2
April	26-Apr-15	8	50.8	64.6	16.7	4.9 ± 0.4	1.8 ± 0.1
May	25-May-15	5	8.6	8.6	14.0	4.4 ± 0.3	1.8 ± 0.1
June[2]	-	-	-	-	-	-	-
July	27-Jul-15	11	1.4	3.8	10.4	2.9 ± 0.2	1.1 ± 0.1
Aug	24-Aug-15	6	1.4	18.8	12.0	3.7 ± 0.4	1.0 ± 0.0

[1] Only rainfall events greater than 1 mm.

[2] No measurements in August 2014 and June 2015 due to poor weather conditions.

Table 3 ANOVA output of general linear mixed model analyses of effects of patch (under or inter-canopy), month and their interaction on soil respiration, soil temperature (0-5 cm) and volumetric soil water content (0-5 cm).

Explanatory variables	**ndf**	**ddf**	**Soil respiration**		**Soil temperature**		**Soil water content**	
			F	**p-value**	**F**	**p-value**	**F**	**p-value**
patch	1	10	41.3	<0.001	876.1	<0.001	0.2	0.648
month	11	110	27.2	<0.001	557.6	<0.001	49.1	<0.001
patch × month	11	110	2.7	0.005	60.8	<0.001	2.1	0.029

ndf, numerator degrees of freedom; ddf, denominator degrees of freedom.

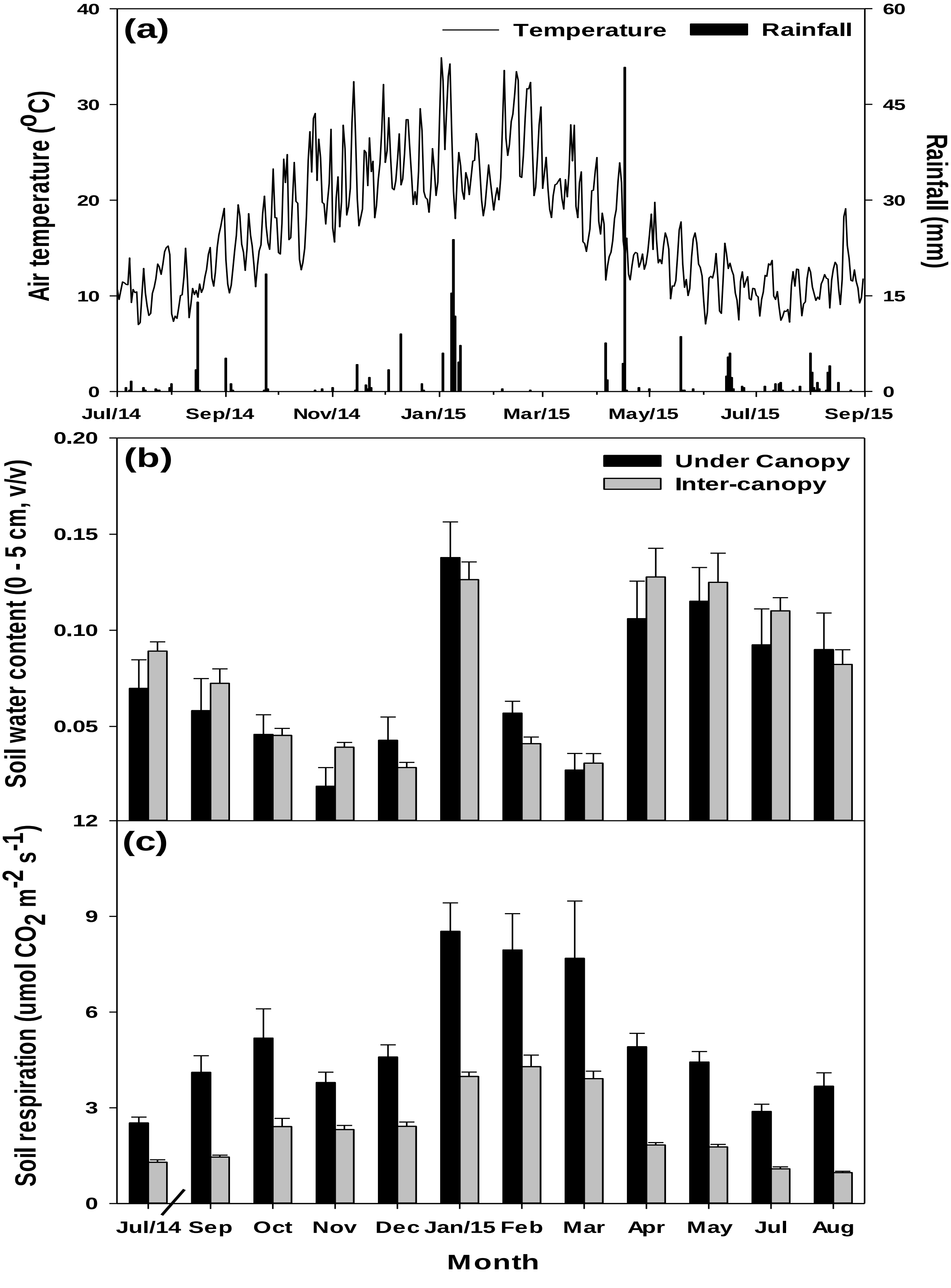

Fig. 1. (a) Air temperature (°C) and rainfall (mm), (b) volumetric soil water content at 0-5 cm depth and (c) in-situ soil respiration rates (µmol CO_2 m^{-2} s^{-1}) under canopy and inter-canopy of semiarid floodplain woodland from July 2014 to August 2015 (mean ± standard error, n=5). No measurements in August 2014 and June 2015 due to poor weather conditions.

Supplementary material

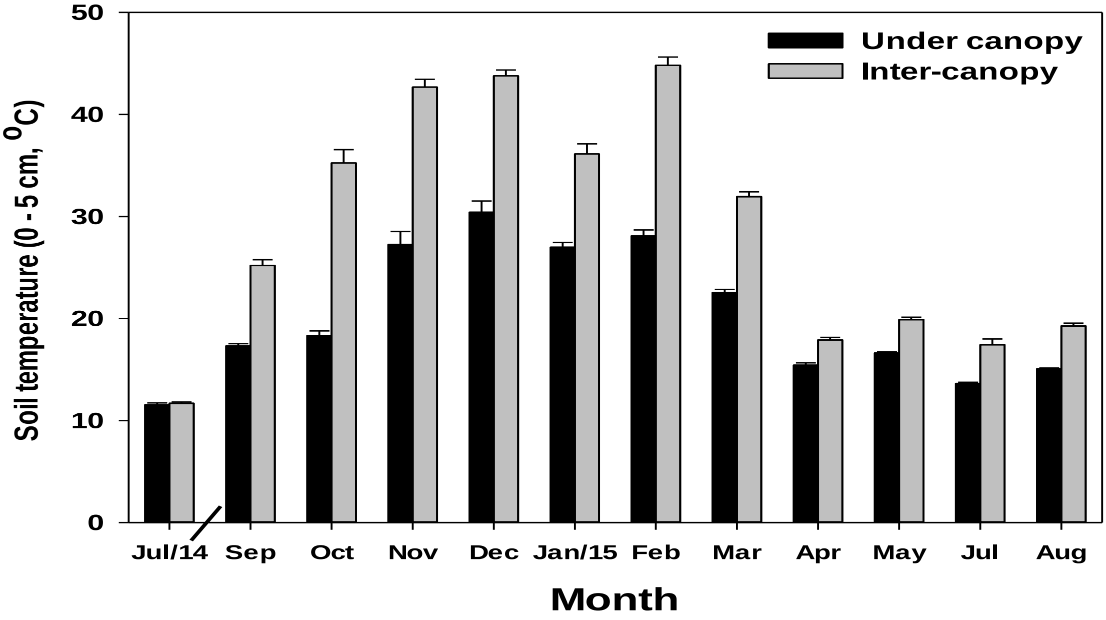

Fig. S1. Soil temperature at 0-5 cm depth at time of sampling of soil respiration under canopy and inter-canopy of semiarid floodplain woodland from July 2014 to August 2015 (mean ± standard error, n=5). Measurements were not carried out in August 2014 and June 2015 due to poor weather condition.

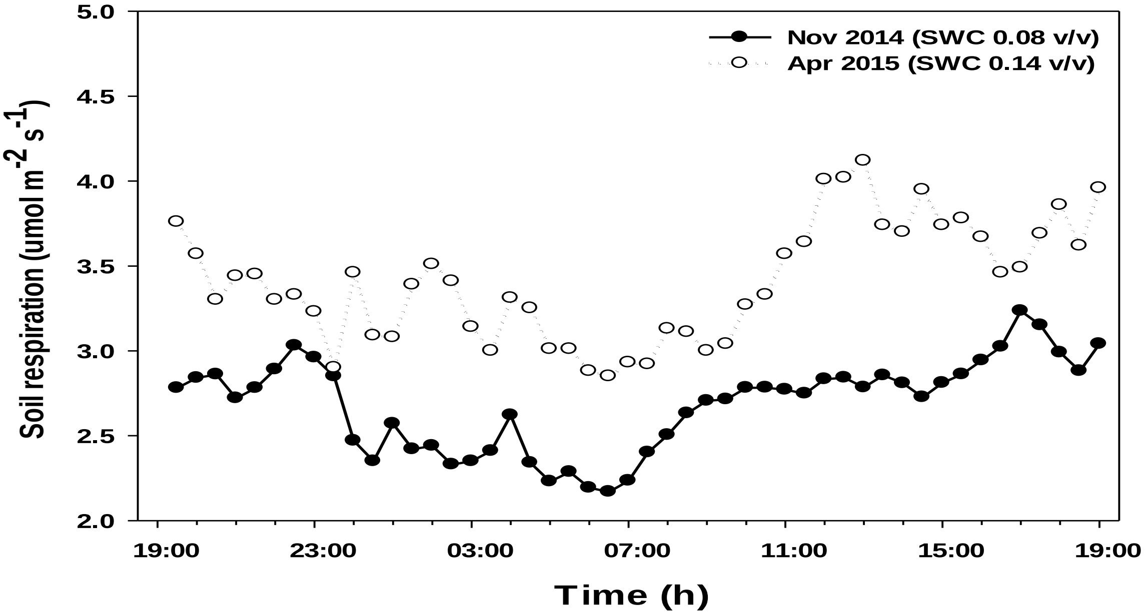

Fig. S2. Diurnal soil respiration rates (µmol m^{-2} s^{-1}) under canopy of semiarid floodplain woodland at two dates with different soil temperature 0-5 cm and water content 0-5 cm (mean values of 21°C and 0.08 v/v in November 2014 and 16 °C and 0.14 v/v in April 2015).

Table S1 Review of in-situ soil respiration studies in floodplain/riparian ecosystems across the globe (MAP – Mean annual precipitation; MAT – Mean annual temperature; actual research period only considered real time in-situ measurement).

Biome	**Ecosystem type**	**Location**	**Actual research period (month)**	**MAP (mm)**	**MAT (°C)**	**Soil respiration (g C m^{-2} d^{-1})**	**Reference**
Mediterranean	semiarid woodland (inter-canopy)	South Australia, Australia	12	242	18.7	2.39	**This study**
Mediterranean	semiarid woodland (under canopy)	South Australia, Australia	12	242	18.7	5.2	**This study**
Mediterranean	forest	Italy	4	1400	11	2.76	(Doering et al., 2011)
Mediterranean	forest	Barcelona, Spain	4	872	12	1.29-1.47	(Chang et al., 2014)
Mediterranean	semiarid (herbaceous vegetation)	Toledo, Spain	5	355	19.1	0.91-2.13	(Sanchez-Andres et al., 2010)
Mediterranean	shrub dominated	California, USA	7	110-136	16.5	2.27-3.08	(Hart and Disalvo, 2005)
Temperate	forest	Switzerland	4	908	9.3	1.88	(Samaritani et al., 2011)
Temperate	forest	Texas, USA	17	1320	19.4	4.38	(Messina et al., 1997)
Temperate	forest	Montana, USA	3	880	0	3.33	(Pacific et al., 2011)
Temperate	forest	Rhode Island, USA	12	2604	10.8	1.81	(Ricker et al., 2014)
Temperate	forest	Ontario, Canada	6	912	7.2	1.27	(Oelbermann and Raimbault, 2015)
Temperate	forest (rehabilitated)	Iowa, USA	24	836	8.7	3.34	(Tufekcioglu et al., 2001)
Temperate	forest (rehabilitated)	Indiana, USA	27	1050	11	2.13	(Jacinthe, 2015)
Temperate	grassland	Switzerland	4	908	9.3	3.34	(Samaritani et al., 2011)
Temperate	grassland	Ontario, Canada	6	912	7.2	2.03-2.33	(Oelbermann and Raimbault, 2015)
Temperate	grassland (rehabilitated)	Iowa, USA	24	836	8.7	2.99	(Tufekcioglu et al., 2001)
Temperate	semiarid shrubland	Arizona, USA	5	350	26	1.84-2.65	(Cable et al., 2012)
Temperate	urbanised	Virginia, USA	24	1050	12.7	3.21	(Batson et al., 2015)
Tropical	rainforest	Manaus, Brazil	2	2442	26.7	3.84- 4.67	(Zanchi et al., 2014)
Subtropical	forest	India	17	725	17 - 32	1.82-2.35	(Jha and Mohapatra, 2011)
Subtropical	rainforest	Queensland, Australia	4	1709	18.8	1.87-2.7	(Rowlings et al., 2012)
Arctic	shrub dominated	Mongolia	9	290-300	-4.5	6.12	(Sharkhuu et al., 2013)

Reference

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Chapter 7

Conclusions and future research

Conclusions

Ecosystem carbon flux and soil respiration are influenced by abiotic factors such as air temperature and rainfall regimes (e.g., Weltzin et al., 2003a; Noy-Meir, 1973; Beer et al., 2010) and biotic factors such as vegetation composition and soil characteristics (e.g., McCulley et al., 2007). The cycling of carbon is also linked to landscape modifications such as wildfire disturbance (e.g., Tongway and Hodgkinson, 1992). In this thesis, the effect of rainfall size and distribution, as well as wildfire on ecosystem C fluxes and soil respiration in semi-arid woodlands was investigated.

Previous studies had shown that drying and rewetting (DRW) events induced a strong pulse of soil respiration and influenced nutrient availability (Borken and Matzner, 2009). The laboratory incubation DRW experiment with Mallee soil clearly showed a respiration pulse but there was little effect on nutrient availability (Chapter 2). Similarly, wildfire only had a limited effect on nutrient availability and soil respiration, which was in agreement with results from monthly in-situ soil respiration measurements (Chapter 4). It is highly likely that the low nutrient availability in the sandy Mallee soil limited any significant response of nutrient availability to either drying and wetting or fire.

It is well-known that microbial density and activity are greater in the rhizosphere than bulk soil due to release of low molecular weight substrates from roots. These exudates are more rapidly degradable than soil organic matter. Another laboratory incubation experiment focussed on response of soil respiration to labile carbon addition (Chapter 3). The response of respiration and microbial biomass in soils from different patches to addition of available C was related to TOC content, being greater in soils with low TOC content and also greater in soils under burnt areas which suggests lower availability of charred organic matter. It also showed that in the Mallee woodland, only the presence of trees increased TOC content, available P, MBP and MBC concentrations compared to inter-canopy areas, whereas the presence of shrubs had little effect. This may be due to the inherent low fertility of the soils in this area and wind and water erosion. The effect of wildfire on the measured parameters differed among patches, but was generally small, likely because the amount of surface dry matter (shrubs, spinifex and tree litter) was small and hence fire intensity was low.

Chapter 4 confirmed that rainfall and therefore soil water content is a major driver of soil respiration and ecosystem C flux in semi-arid mallee woodland. This chapter also showed that wildfire induced a period of net carbon loss. It took about a year for the woodland to return to net carbon uptake. In situ soil respiration in this woodland was not influenced by wildfire and instead was correlated with soil water content and temperature. Thus the wildfire influenced aboveground (canopy) more than belowground processes. This was the first study on net ecosystem productivity, gross primary productivity and ecosystem respiration shortly after a wildfire in a semi-arid ecosystem. By also including soil respiration measurements in different patches, this study provided a comprehensive picture of the response of semi-arid woodlands to rainfall and fire. It showed that ecosystem C fluxes were related to rainfall pattern, but the relationship was not very strong. This lead to a further study in unburnt mallee which examined the effect of large rainfall events in relatively dry periods on C fluxes (Chapter 5).

The study described in Chapter 5 suggested that in the mallee woodland, the previous rainfall pattern determines response of net ecosystem carbon exchange to a single large rainfall event. Only a large rainfall event following four weeks with very little rainfall induced an increase in ecosystem respiration for about three weeks and thus a decrease in net ecosystem productivity, but not if a large rainfall event followed four weeks with several moderate rainfalls. The strong increase in ecosystem respiration after the large rainfall event can, at least partly, be explained by an increase in soil respiration upon rewetting. Initially, this was likely heterotrophic respiration. But when the top soil dried, the dominant source of soil respiration was most likely associated with roots in deeper soil horizons that remained moist for longer. The prolonged increase in soil respiration may be specific to this woodland on sandy soil dominated by deep-rooted eucalypt species that are well adapted to low and often erratic rainfall and use incident available water conservatively. Therefore, previous rainfall history should be considered when interpreting the response of ecosystem C fluxes to rainfall events in dryland ecosystems. The question arose if a prolonged effect of summer rainfall on soil respiration could also be found in the floodplain woodland adjacent to the Mallee woodland where the soil is finer textured and nutrient-richer than in the Mallee.

In a semi-arid floodplain woodland, repeated rainfall over several days during summer increased soil respiration for three months although the water content in the top soil was low (Chapter 6). This suggests that in the months following the rain period, similar to what was observed in ecosystem respiration in the Mallee, roots in the moist subsoil were the major contributors to soil respiration. On the other hand, a single event with similar rainfall in autumn did not induce a strong increase in soil respiration. Therefore soil respiration in this ecosystem is influenced by a complex interaction between rainfall amount, soil temperature as well as, possibly, distribution of the rainfall. Both Chapters 5 and 6 confirmed that top soil water content is not sufficient to explain soil respiration after rainfall in summer because of the contribution of roots to soil respiration.

Future research

The studies in this thesis provided new insights into the drivers of ecosystem C fluxes, but could also be used as a basis for future research.

In the Mallee woodland, the response of net ecosystem carbon fluxes to a large rainfall event, depended on the previous rainfall pattern. The net carbon release post rain was mainly due to increased ecosystem respiration because gross primary productivity responded little to large rainfall events. Climate models show that the frequency of prolonged drought interrupted with extreme rainfall events is likely to increase in dry ecosystems (Hughes, 2003; IPCC, 2014). Therefore it is important to assess long term effects (over months and years) of rainfall variability on plant productivity and ecosystem carbon fluxes in a range of deep-rooted ecosystems of dry regions. As indicated above, water content in the topsoil layer (0 – 10 cm), especially in coarse textured soils is a limited descriptor of soil respiration response to rainfall. It would be more informative to have data on soil water content throughout the root zone which would likely give a clearer understanding of the relationship between soil respiration and soil profile water content in field studies. Such studies over multiple sites could be accompanied by measurement of ecosystem water use efficiency.

The effect of wildfire on ecosystem carbon fluxes and soil respiration is determined by fire intensity as well as fire frequency. This project showed that a single wildfire event strongly affected ecosystem C fluxes but also revealed rapid recovery after the fire. The frequency of fires is predicted to increase as the climate becomes drier in ecosystems such as Mallee woodland (Noble et al., 1996). Future studies could investigate the effect of fire frequency on the capacity of the ecosystem to recover after fire.

Both semi-arid Mallee woodland and floodplain woodland had higher soil respiration rates under tree canopies than the inter-canopy areas (bare soil). Quantifying spatial variation in soil respiration underneath tree canopies is also important to understand the extent of the patch effect. In future studies, soil respiration at different distances from trees could be investigated. Moreover, spinifex (*Triodia basedowii*), commonly grows in the space between mallee trees in this ecosystem. Further studies in quantifying the role of spinifex in soil respiration and nutrient cycling could be carried out. Such studies of soil respiration could be accompanied by quantification of soil water content and roots at different depths to estimate the contribution of lower soil horizons to soil respiration and how this is influenced by water content.

A better understanding of C sequestration and contribution of semi-arid woodlands to atmospheric CO_2 concentrations, particularly in relation to precipitation and wildfire, soil respiration could be simulated by modelling. In the first step, it could be tested how well current process-based soil C models (e.g., RothC) correspond to the measured data. If the correlation between measured and modelled data is poor, the model parameters would have to be adjusted in the second step. Once the model can reliably estimate soil respiration, the impact of future climate scenarios or wildfire frequency could be tested. Soil respiration data from this project could be incorporated.

This project has provided information on net ecosystem carbon exchange, as well as soil respiration (or termed as soil CO_2 flux) in different patches in the mallee woodland. There is only one previous study where trace gases were measured in this mallee community which was conducted more than 25 years ago (Galbally et al., 2010). Longer term measurements of trace gases such as methane and nitrous oxide over a range of semi-arid woodlands are necessary to improve the understanding of contribution of semi-arid woodlands in greenhouse gas fluxes.

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