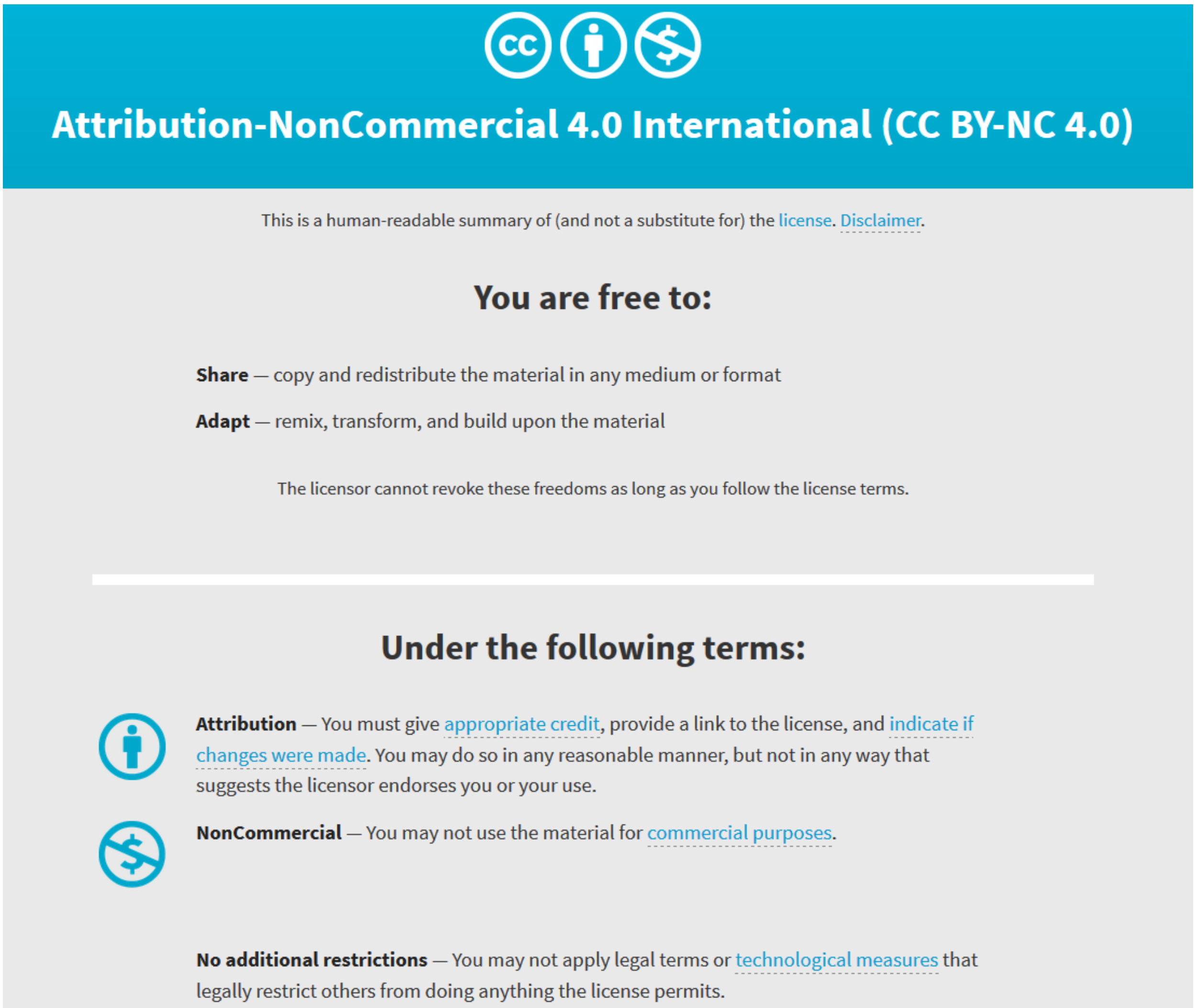
Qiaoqi Sun, Wayne S. Meyer, Georgia R. Koerber, Petra Marschner

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

Journal of Soil Science and Plant Nutrition, 2017; 17(1):62-73

Originally published at:
http://doi.org/10.4067/S0718-95162017005000005



Journal of Soil Science and Plant Nutrition, 2017, 17 (1), 62-73
RESEARCH ARTICLE

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

Qiaoqi Sun[1*], Wayne S. Meyer[1], Georgia R. Koerber[1], Petra Marschner[2]

[1]Department of Ecology and Environment Science, School of Biological Sciences, The University of Adelaide, SA 5005, Australia. [2]School of Agriculture, Food and Wine, The University of Adelaide, SA 5005, Australia.
**Corresponding author: qiaoqi.sun@adelaide.edu.au*

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 length 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 impact wildfire and drying-rewetting (DRW) events on nutrient cycling differ among vegetation patches of a native semiarid woodland which 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.

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 (ψm= -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 Sun *et al*., (2015) 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

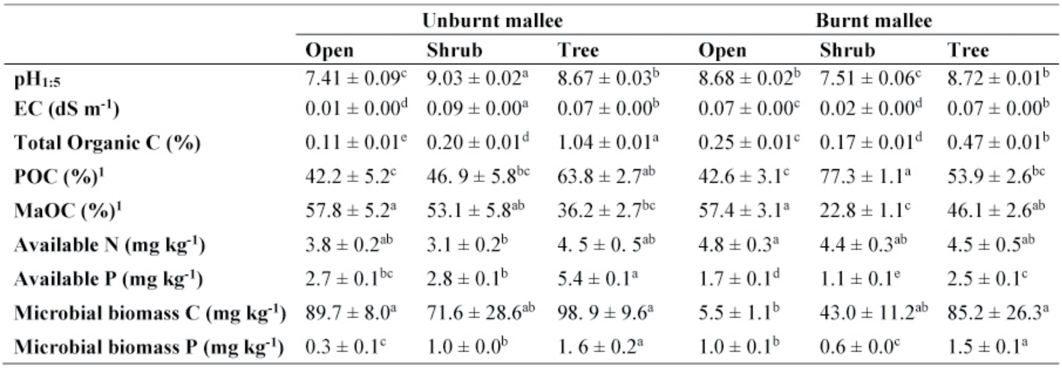
Two-way analysis of variance (ANOVA) with a post-hoc Tukey test was used to determine effects of burning (unburnt and burnt) and patch (open, shrub and tree) on soil properties at the start of the experiment and on the ratio of cumulative respiration (amended/non-amended) on day 24. Cumulative respiration 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 (www.r-project.org).
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.

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).

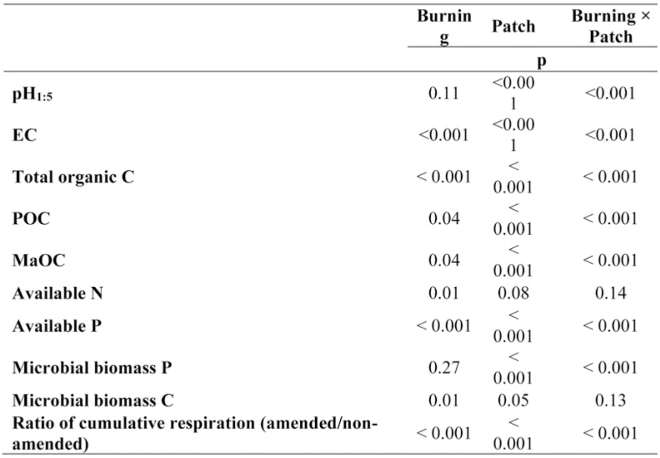


	Unburnt mallee			**Burnt mallee**		
	Open	**Shrub**	**Tree**	**Open**	**Shrub**	**Tree**
$pH_{1:5}$	7.41 ± 0.09^{c}	9.03 ± 0.02^{a}	8.67 ± 0.03^{b}	8.68 ± 0.02^{b}	7.51 ± 0.06^{c}	8.72 ± 0.01^{b}
EC (dS m^{-1})	0.01 ± 0.00^{d}	0.09 ± 0.00^{a}	0.07 ± 0.00^{b}	0.07 ± 0.00^{c}	0.02 ± 0.00^{d}	0.07 ± 0.00^{b}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

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 than 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.

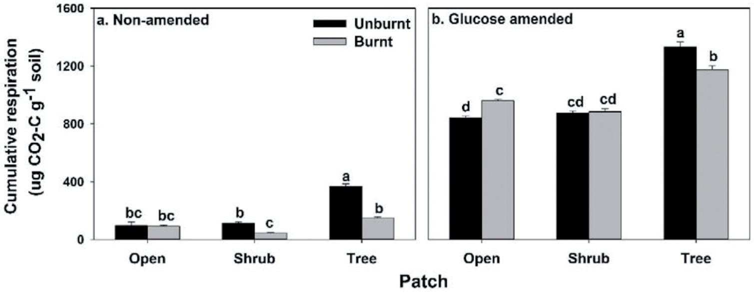


Figure 1. Cumulative respiration on day 24 in non-amended (a) and glucose amended soils (b) from unburnt and burnt semi-arid woodland in open areas or under shrubs and trees (mean ± standard error, n=4). Within each graph, columns with different letters are significantly different at $p<0.05$.

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.

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

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 ($F_{1, 22} = 4.40$, $r^2 = 0.17$, $p < 0.05$).

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}

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.

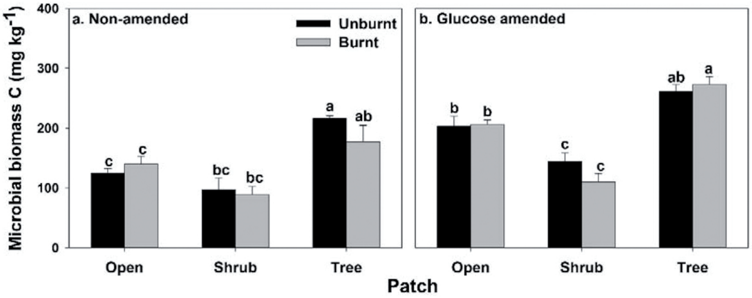


Figure 2. Microbial biomass carbon (MBC) (mean ± standard error, n=4) in non-amended (a) and glucose amended soils (b) from unburnt and burnt semi-arid woodland in open areas or under shrubs and trees on day 24 (mean ± standard error, n=4). Within each graph, columns with different letters are significant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

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 unamended 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. Conclusions

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.

Acknowledgements

This work was partly supported by grants from the Australian Government's Terrestrial Ecosystems Research Network (TERN) (www.tern.gov.au). TERN is a research infrastructure facility established under the National Collaborative Research Infrastructure Strategy and Education Infrastructure Fund, Super Science Initiative, through the Department of Industry, Innovation, Science, Research, and Tertiary Education. We greatly appreciate the support and assistance from the Australian Landscape Trust that facilitated access to the site on Calperum Station and particularly to Dr Grant Whiteman and Dr Peter Cale. Qiaoqi Sun's postgraduate research at the University of Adelaide was supported by a scholarship from the Chinese Scholarship Council.

References

Alamgir, M., Marschner, P. 2016. Changes in P pools over three months in two soils amended with legume residues. Journal of Soil Science and Plant Nutrition. 16, 76-87.

Anderson, J., Ingram, J. 1993. Tropical soil biology and fertility: A handbook of methods, CAB international Wallingford, UK.

Baldock, J.A. 2007. Composition and cycling of organic carbon in soil. In: Marschner P & Rengel Z (eds) Nutrient cycling in Terrestrial Ecosystems, pp 1-35. Springer, Verlag Berlin Heidelberg.

Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K. 2005. A temporal approach to linking aboveground and belowground ecology. Trends in ecology & evolution. 20, 634-641.

Bertin, C, Yang, X.H., Weston, L.A. 2003. The role of root exudates and allelochemicals in the rhizosphere. Plant and Soil. 256, 67-83.

Boerner, R.E.J., Giai, C, Huang, J, Miesel, J.R. 2008. Initial effects of fire and mechanical thinning on soil enzyme activity and nitrogen transformations in eight North American forest ecosystems. Soil Biology and Biochemistry. 40, 3076-3085.

Cambardella, C.A., Elliott, E.T. 1992. Particulate soil organic-matter changes across a grassland cultivation sequence. Soil Science Society of America Journal. 56, 777-783.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia. 143, 1-10.

Clarke, P.J., Lawes, M.J., Murphy, B.P., Russell-Smith, J., Nano, C.E.M., Bradstock, R., Enright, N.J., Fontaine, J.B., Gosper, C.R., Radford, I., Midgley J.J., Gunton, R.M. 2015. A synthesis of postfire recovery traits of woody plants in Australian ecosystems. The Science of the total environment. 534, 31-42.

Cortez, C.T, Nunes, L., Rodrigues, L.B, Eisenhauer, N., Araujo, A.S.F. 2014. Soil microbial properties in Eucalyptus grandis plantations of different ages. Journal of Soil Science and Plant Nutrition. 14, 734-742.

Elmajdoub, B., Marschner, P. 2015. Response of microbial activity and biomass to soil salinity when supplied with glucose and cellulose. Journal of Soil Science and Plant Nutrition. 15, 816-832.

Forster, J.C. 1995. Soil nitrogen. In: Alef K & Nannipieri P (eds) Methods in applied soil microbiology and biochemistry, pp 79-87. Academic Press, London.

Gallardo, A., Schlesinger, W.H. 1992. Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems. Biogeochemistry. 18, 1-17.

Goberna, M., Pascual, J.A., García, C., Sánchez, J. 2007. Do plant clumps constitute microbial hotspots in semiarid Mediterranean patchy landscapes? Soil Biology and Biochemistry. 39, 1047-1054.

Head, L., Adams, M., McGregor, H.V., Toole, S. 2014. Climate change and Australia. Wiley Interdisciplinary Reviews: Climate Change. 5, 175-197.

Hoyle, F.C., Murphy, D.V., Brookes, P.C. 2008. Microbial response to the addition of glucose in low-fertility soils. Biology and Fertility of Soils. 44, 571-579.

IPCC. 2014. Climate Change. 2014. Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In: The Core Writing Team, Pachauri RK & Meyer LA (eds), pp 1-151. IPCC, Geneva, Switzerland.

Jobbagy, E.G., Jackson, R.B. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Appl. 10, 423-436.

Kouno, K., Tuchiya, Y., Ando, T. 1995. Measurement of soil microbial biomass phosphorus by an anion exchange membrane method. Soil Biology and Biochemistry. 27, 1353-1357.

Kuzyakov, Y., Subbotina, I., Chen, H., Bogomolova, I., Xu, X. 2009. Black carbon decomposition and incorporation into soil microbial biomass estimated by 14C labeling. Soil Biology and Biochemistry. 41, 210-219.

Laird, D., Fleming, P., Wang, B., Horton, R., Karlen, D. 2010. Biochar impact on nutrient leaching from a Midwestern agricultural soil. Geoderma. 158, 436-442.

Miranda, K.M., Espey, M.G., Wink, D.A. 2001. A rapid, simple spectrophotometric method for simultaneous detection of nitrate and nitrite. Nitric Oxide-Biol Ch. 5, 62-71.

Orians, G.H., Milewski, A.V. 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. Biological Reviews. 82, 393-423.

Rayment, G.E., Higginson, F.R. 1992. Australian laboratory handbook of soil and water chemical methods, Inkata Press, Melbourne.

Sardans, J., Peñuelas, J. 2013. Plant-soil interactions in Mediterranean forest and shrublands: impacts of climatic change. Plant and Soil. 365, 1-33.

Shakesby, R.A. 2011. Post-wildfire soil erosion in the Mediterranean: Review and future research directions. Earth-Science Reviews. 105, 71-100.

Sun, Q., Meyer, W.S., Koerber, G.R., 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., 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.

Tongway, D.J., Ludwig, J.A. 1994. Small-scale resource heterogeneity in semi-arid landscapes. Pacific Conservation Biology. 1, 201-208.

Vance, E.D., Brookes, P.C., Jenkinson, D.S. 1987. An extraction method for measuring soil microbial biomass-C. Soil Biology & Biochemistry. 19, 703-707.

Walkley, A., Black, I.A. 1934. An examination of the degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Science. 37, 29-38.

Wan, S.Q., Hui, D.F., Luo, Y.Q. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: A meta-analysis. Ecol Appl. 11, 1349-1365.

White, D.A., Welty-Bernard, A., Rasmussen, C., Schwartz, E. 2009. Vegetation controls on soil organic carbon dynamics in an arid, hyperthermic ecosystem. Geoderma. 150, 214-223.

Wilke, B-M. 2005. Determination of chemical and physical soil properties. In: Margesin R & Schinner F (eds) Monitoring and Assessing Soil Bioremediation, pp 47-95. Springer Berlin Heidelberg, Berlin.

Wright, B.R., Clarke P.J. 2008. Relationships between soil temperatures and properties of fire in feathertop spinifex (Triodia schinzii (Henrard) Lazarides) sandridge desert in central Australia. Rangeland J. 30, 317-325.