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

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Abstract

Semi-arid woodlands, which are characterised by patchy vegetation interspersed with bare, open areas, are frequently exposed to wild fire. 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 wild fire. 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 wild fire 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 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. Wild fire 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 of the impact wild fire and DRW events on nutrient cycling differ among vegetation patches of a native semiarid woodland which is related to organic matter amount and availability.

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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, 2004; 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 wild fire 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 soil is a sandy loam (2 % clay, 4 % silt and 94 % sand) with a bulk density of 1.6 $g\,cm^{-3}$ in 0–30 cm depth, classified as Tenosol in the Australian Soil classification (Isbell, 2002), and as Aridisol in the US Soil Taxonomy (Soil Survey Staff, 1996). A recent wild fire (from 15th to 19th January 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 wild fire 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 (< 3 mm) 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. Three soil samples were taken from each patch and location. The three samples were combined, mixed and then subsampled to give the four replicates in the experiment, sieved to < 2 mm and air-dried at 30 °C. 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

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of four days, the water content gradually decreased but then remained stable. The experiment was stopped when the espiration 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 ($\psi_m = -10$ 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-

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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) × treatment (constantly moist or dry-rewet). All statistical analyses were carried out with R software (R development Core Team, 2013). 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

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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 (Fig. 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 Appendix 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 (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 3). The available N concentration did not differ among patches and was not affected by fire or moisture regime. (Fig. 3, Table A1).

The available P concentration was two to three-fold higher under trees than under shrubs and in open areas (Fig. 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 ar-

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eas or under shrubs than under trees. The recent wild fire 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 Fig. 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).

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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 (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 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

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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 (Fig. 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 (Fig. 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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Appendix A:

Outputs of Two-Way or Three-Way Analysis of Variance (ANOVA) analyses (Table A1).

Author contributions. Q. Sun, P. Marschner and W. S. Meyer designed the experiment and Q. Sun carried it out. Q. Sun, G. Koerber and W. S. Meyer preformed field soil sampling. Q. Sun and P. Marschner prepared the manuscript with contributions from all co-authors.

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Table 1. Properties of unburnt and burnt Mallee soils under shrubs, trees or in open areas (mean ± standard error, $n = 4$ for pH and TOC values, $n = 2$ for water capacity data). For pH and TOC, different letters indicate significant differences for the burning × 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]

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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 $p < 0.05$.

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}

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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

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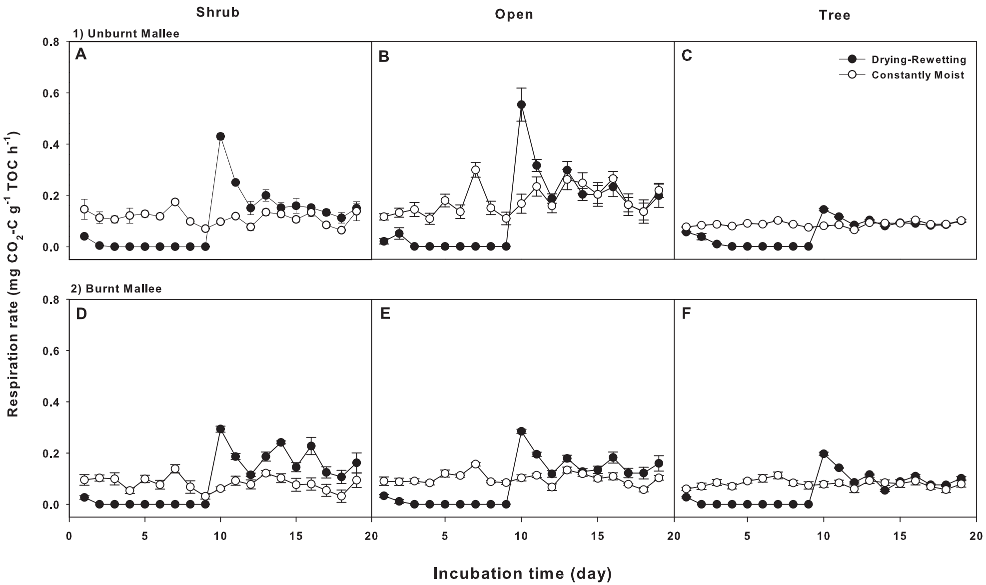

Figure 1. Soil respiration rate per g TOC in soil from under shrubs, trees and in open areas of unburnt (**a, b,** and **c**) and burnt (**d, e** and **f**) Mallee woodlands under constantly moist and dry-rewetting treatments (mean ± standard error, $n = 4$).

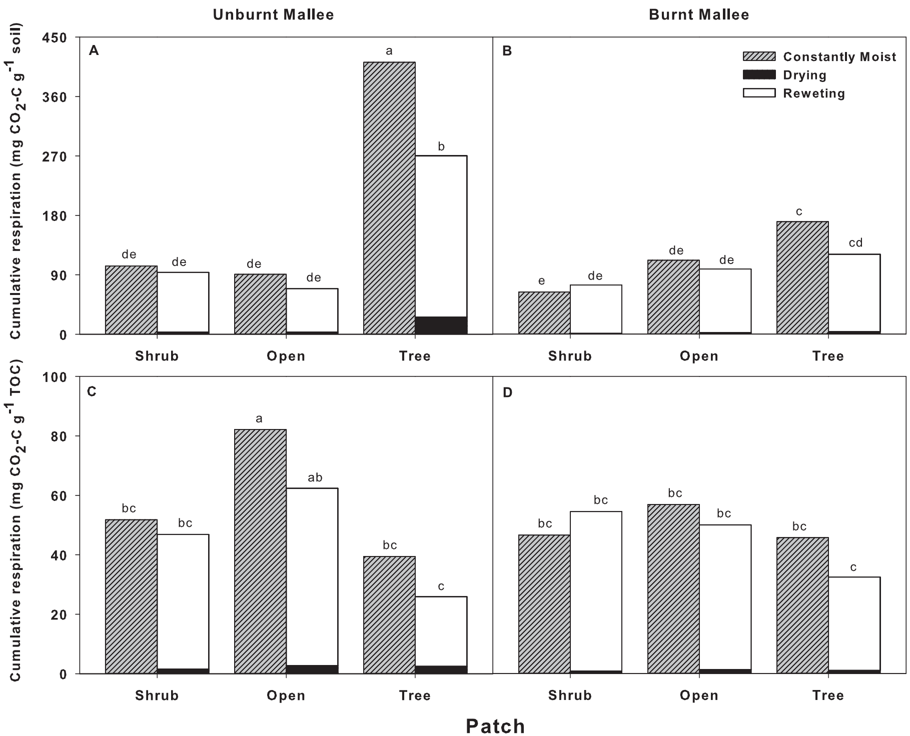

Figure 2. Cumulative respiration per g soil (**a** and **b**) and per g TOC (**c** and **d**) in constantly moist (CM) and dry-rewetting (DRW) (9-day dry and 10-day moist) soils from unburnt and burnt Mallee under shrubs, trees or in open areas (mean, $n = 4$).

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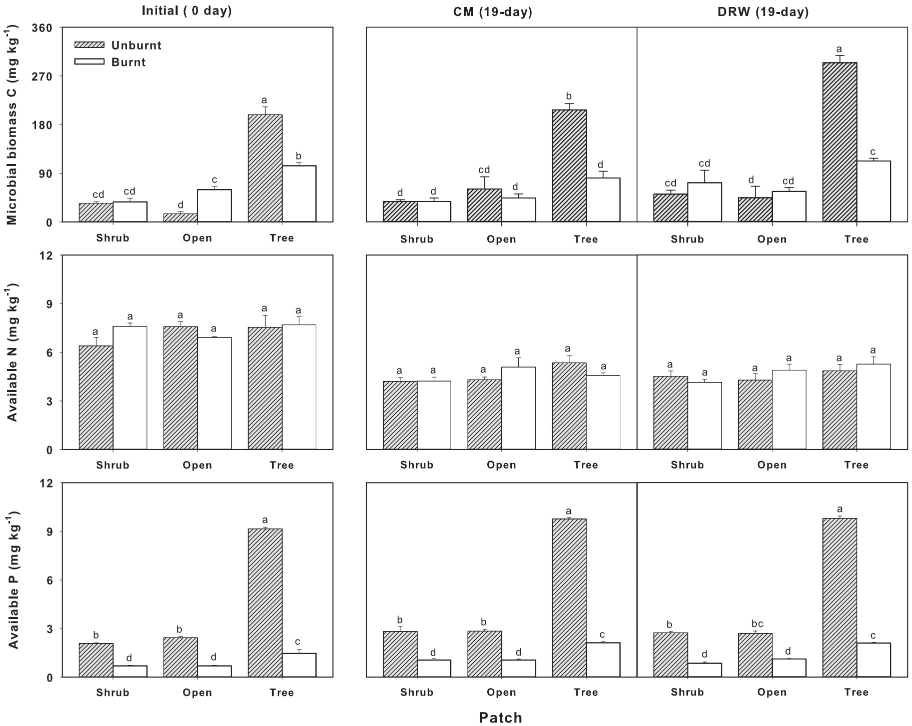

Figure 3. Soil microbial biomass C, available N and P in soil under shrubs, trees or in open areas of unburnt and burnt Mallee woodlands at the start (initial) and end (soils under both constantly moist – CM and dry-rewetting – DRW treatments) of the experiment (mean ± standard error, $n = 4$). Different letters indicate significant differences for the burning × patch × (either with or without) moisture treatment interaction at $p < 0.05$.

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