Soil respiration dynamics in fire affected semi-arid ecosystems: Effects of vegetation type and environmental factors

Miriam Muñoz-Rojas [a,b,c,*], Wolfgang Lewandrowski [a,b], Todd E. Erickson [a,b], Kingsley W. Dixon [a,b,c], David J. Merritt [a,b]

[a] The University of Western Australia, School of Plant Biology, Crawley 6009, WA, Australia
[b] Kings Park and Botanic Garden, Kings Park, Perth 6005, WA, Australia
[c] Curtin University, Department of Environment and Agriculture, Perth 6845, WA, Australia

HIGHLIGHTS

- We assess the impacts of a wildfire on soil respiration in a semi-arid ecosystem
- Larger rates of CO_2 efflux were found in the burnt areas compared to the unburnt
- Rs was higher under *Eucalyptus* trees and *Acacia* shrubs versus grasses or bare soil
- CO_2 fluxes were triggered with higher temperatures and water availability
- Q10 was significantly higher in the burnt site compared to the control.

GRAPHICAL ABSTRACT
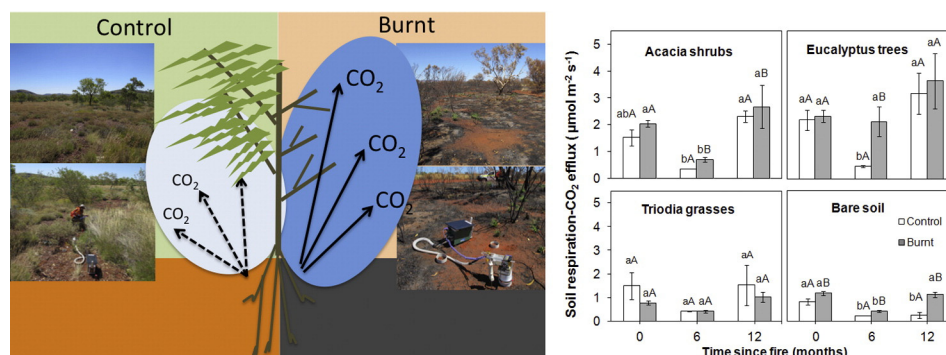
ARTICLE INFO

ABSTRACT

Soil respiration (Rs) is the second largest carbon flux in terrestrial ecosystems and therefore plays a crucial role in global carbon (C) cycling. This biogeochemical process is closely related to ecosystem productivity and soil fertility and is considered as a key indicator of soil health and quality reflecting the level of microbial activity. Wildfires can have a significant effect on Rs rates and the magnitude of the impacts will depend on environmental factors such as climate and vegetation, fire severity and meteorological conditions post-fire. In this research, we aimed to assess the impacts of a wildfire on the soil CO_2 fluxes and soil respiration in a semi-arid ecosystem of Western Australia, and to understand the main edaphic and environmental drivers controlling these fluxes for different vegetation types. Our results demonstrated increased rates of Rs in the burnt areas compared to the unburnt control sites, although these differences were highly dependent on the type of vegetation cover and time since fire. The sensitivity of Rs to temperature (Q10) was also larger in the burnt site compared to the control. Both Rs and soil organic C were consistently higher under *Eucalyptus* trees, followed by *Acacia* shrubs. *Triodia* grasses had the lowest Rs rates and C contents, which were similar to those found under bare soil patches. Regardless of the site condition (unburnt or burnt), Rs was triggered during periods of higher temperatures and water availability and environmental factors (temperature and moisture) could explain a large fraction of Rs variability, improving the relationship of moisture or temperature as single factors with Rs. This study demonstrates the importance of assessing CO_2 fluxes considering both abiotic factors and vegetation types after disturbances such as fire which

* Corresponding author at: The University of Western Australia, School of Plant Biology, Crawley, WA 6009, Australia.
E-mail addresses: miriammunozrojas@gmail.com, miriam.munoz-rojas@uwa.edu.au (M. Muñoz-Rojas).

Please cite this article as: Muñoz-Rojas, M., et al., Soil respiration dynamics in fire affected semi-arid ecosystems: Effects of vegetation type and environmental factors, Sci Total Environ (2016), http://dx.doi.org/10.1016/j.scitotenv.2016.02.086

is particularly important in heterogeneous semi-arid areas with patchy vegetation distribution where CO_2 fluxes can be largely underestimated.

1. Introduction

Soil respiration (Rs) is the second largest carbon flux in terrestrial ecosystems and globally accounts for 68–98 Pg C yr^{-1}, or ten times that produced by fossil fuel combustion (Bond-Lamberty and Thompson, 2010; Hashimoto, 2012). This biogeochemical process plays a crucial role in global carbon (C) cycling and is closely related to ecosystem productivity and soil fertility (Wu et al., 2014). In recent years, Rs has become a major research focus given the increase in atmospheric CO_2 emissions and the large contribution of CO_2 fluxes from soils (Feng et al., 2014; Van Groenigen et al., 2014). Total respiration from soils originates from the activity of root and rhizosphere organisms (autotrophic respiration), and the microbial decomposition of organic matter (heterotrophic respiration) (Luo and Zhou, 2006; Wei et al., 2010). Therefore, in addition to its importance in the global C cycle, Rs is a key indicator of soil health and quality reflecting the level of microbial activity and providing an indication of the ability of soils to support plant growth (Oyonarte et al., 2012; Rey et al., 2011).

Recent research has focused on analysing the effects of disturbances on soil C contents and CO_2 fluxes, such as wildfire or controlled burning (Granged et al., 2011; Marañón-Jiménez et al., 2011; Smith et al., 2010; Sun et al., 2014), litter thinning, harvesting, removal, or addition (Concilio et al., 2006; Jonasson et al., 2004; Wu et al., 2014), land use conversions (Muñoz-Rojas et al., 2015; Willaarts et al., 2015; Zhang et al., 2015), or land degradation (Rey et al., 2011). But despite the global importance of this process, there is still limited knowledge of the variability of Rs across ecosystem types, vegetation communities, and responses to natural or human disturbances (Harmon et al., 2011; Metcalfe et al., 2011).

Carbon pools can be severely disturbed by fire (González-Pérez et al., 2004; Santín et al., 2012), which can lead to an abrupt release of C to the atmosphere by vegetation and soil litter combustion (Bento-Gonçalves et al., 2012; Cerdà and Robichaud, 2009). For instance, wildfires can have a significant effect on Rs rates through reducing vegetation cover and decreasing the albedo effect on the soil surface, which increases soil temperatures and decomposition rates (Irvine et al., 2007; Smith et al., 2010). Additionally, changes in vegetation composition and litter quality can affect decomposition and root production (Bond-Lamberty et al., 2004), leading to an altered ecosystem that acts as a source of C for long periods of time, e.g. from a few months to several years (Marañón-Jiménez et al., 2011). The magnitude of these processes will depend on environmental factors such as climate and vegetation and generally, post-fire Rs will increase with warm temperatures, sufficient soil moisture, and C addition into the soil (Irvine et al., 2007; Knapp et al., 1998). Other factors such as fire severity and meteorological conditions post-fire can also have a significant influence on Rs (Bodi et al., 2014; Pereira et al., 2012, in press).

The sensitivity of Rs to temperature is often referred to as Q10 (Chen et al., 2010; Lloyd and Taylor, 1994) and in general it is assumed that Q10 is exponentially related to temperature (Jenkins and Adams, 2011; Lloyd and Taylor, 1994). Both Q10 and the temperature response of soil CO_2 efflux have been the focus of many studies as temperature is commonly an adequate predictor of Rs where soil moisture is not a limiting factor (Conant et al., 2004; Davidson and Janssens, 2006; Zhang et al., 2015). Although C substrate availability is crucial in the regulation of Rs (Saetre and Stark 2005; Berryman et al. 2013), the availability of water in soils in arid and semi-arid environments can be critical to determine the response of Rs to temperature by restricting access to C substrates and limiting microbial respiration (Moyano et al., 2012; Rey et al., 2011). In these water limited environments, both soil temperature and soil moisture may be decisive controlling factors of soil CO_2 efflux and can

potentially explain a large variation in Rs (Domingo et al., 2011; Feng et al., 2014; Lai et al., 2012; Moyano et al., 2013; Oyonarte et al., 2012).

Soil respiration largely varies among ecosystem types (Bahn et al., 2010). Several studies of Rs have focused on different biomes: temperate forests (Davidson et al., 1998; Reichstein et al., 2003), boreal forests (Allison et al., 2008), semi-arid or arid environments (Maestre and Cortina, 2003; Oyonarte et al., 2012; Zhang et al., 2015), alpine forest (Chen et al., 2010), tropical systems (Adachi et al., 2006), or croplands and plantations (Lai et al., 2012). Due to the low productivity of arid and semi-arid lands, and their low CO_2 fluxes, Rs processes in these environments have received considerably less attention than other ecosystems (Cable et al., 2011; Conant et al., 2004). However, arid lands cover a large portion of the Earth's land surface and store more than 25% of the global terrestrial carbon (Maestre et al., 2013). The predicted increases in temperature and changes in rainfall patterns in these drylands make these ecosystems particularly vulnerable to global change processes (Anaya-Romero et al., 2015; Cable et al., 2011), and C cycling in particular may be especially sensitive to global climate change (Muñoz-Rojas et al., 2013). Higher turnover of C pools in semi-arid ecosystems can be crucial to assess inter-annual variability in the global C cycle and recent studies suggest that these biomes may be more relevant drivers than tropical ecosystems in the near future (Poulter et al., 2014).

Most arid lands are characterized by large temporal (diurnal, seasonal, or inter-annual) and spatial variability in soil moisture and temperature (Rey et al., 2011; Zhang et al., 2015). This spatial variability is related to the patchy distribution of vegetation which may result in higher respiration rates beneath plants in relation to intercanopy spaces, or bare ground with low substrate and organic content (Cable et al., 2008; Maestre and Cortina, 2003). Moreover, differences in litter composition, litter quality, and root production across different vegetation types will affect Rs, with high variation not only between ecosystem types but even between adjacent vegetation communities (Lai et al., 2012).

In a context of global change, modifications of the vegetation composition due to disturbances such as fire are likely to occur more frequently in the near future (Knox and Clarke, 2012; Abella and Fornwalt, 2015). Vegetation type is a crucial determinant of Rs, and these potential changes in vegetation distribution can modify the responses of ecosystems to environmental factors (Han et al., 2014). In this research we aimed to assess the impacts of a wildfire on the soil CO_2 fluxes and soil respiration in a semi-arid ecosystem of Western Australia, and to understand the main drivers controlling these fluxes for different vegetation types. The specific objectives of this study were (a) to assess the effects of wildfire on Rs rates under different vegetation types, (b) to determine the influence of edaphic and environmental factors (soil moisture and temperature) as drivers of soil respiration for different vegetation covers in burnt and unburnt areas and (c) to analyse the sensitivity of Rs to temperature (Q10) for these vegetation types and burnt status.

2. Materials and methods

2.1. Site description

This study was conducted in the Pilbara biogeographical region of Western Australia (22°03′S, 118°07′E to S23°, 19′S, 119°43′E), which covers a total area of 179,000 km^2 (McKenzie et al., 2009). The Pilbara has a semi-arid climate with a sub-tropical influence and two main seasons: a wet, hot summer, from November to April, and a mild, dry winter, from May to October. Mean annual temperatures range between

19.4 and 33.2 °C (25–40 °C during the summer and 12–29 °C during the winter). Annual rainfall varies from 250 to 400 mm and is generally concentrated in the summer months (between December and February) but there is a high inter- and intra-annual variability as a result of thunderstorms and tropical cyclones (Bureau of Meteorology, Australian Government, 2015). Soils are red, shallow, stony soils on hills and ranges, and sands on the lower lying plains comprising Red Kandosols, Red Ferrosols and Leptic Rudosols (Isbell, 2002). These soils have developed over Phanerozoic, Proterozoic and Devonian limestone (Pepper et al., 2013). Vegetation is composed by hummock grasslands, tussock grasslands, sclerophyll shrublands, and woodlands with a tussock grass understorey (Van Vreeswyk et al., 2004).

The study site was selected following a wildfire that affected 25 ha in February 2014. To identify the precise location of the burnt area and determine the surface affected by wildfire, the FireWatch application was used (Thornton and Wright, 2013). This application is based on Moderate Resolution Imaging Spectroradiometer (MODIS) data and a cell-based approach with an underlying irregular grid. Fire severity in the study area was classified as moderate according to the classification proposed by Keeley (2009). Some of the tree canopy (*Eucalyptus* trees) was killed but leaves not consumed, and all understorey plants (*Acacia* shrubs and *Triodia* grasses) charred with the pre-fire soil organic layer largely consumed but root crowns intact.

2.2. Experimental design and field measurements

Immediately after the wildfire (1 week), 24 permanent plots (1 m²) were set up in the study area and maintained in the same location over time during one year. These plots comprised 12 plots in the burnt site (B) within a 400 m² area, and 12 plots in an adjacent unburnt control site, 100 m distant from the burnt area, and also within a 400 m² area. Both burnt and unburnt sites were located in flat areas and had the same soil type (Red Ferrosols) and similar conditions of aspect, slope and elevation. At each site, three plots were installed below the canopy of each of the most representative vegetation types of the areas: *Eucalyptus* trees, *Acacia* shrubs and *Triodia* grasses, and three on bare soil. A distance of at least 2 m was maintained between individual plants.

In each plot, soil respiration was measured with a 6400-09 portable soil CO_2 flux chamber attached to a LI-COR 6400 (LI-COR Inc. Lincoln, NEB, USA) using PVC soil collars (n = 3 per plot) inserted to a depth of 2 cm into the soil. Soil collars were installed at least 24 h before the measurement of Rs to minimize soil disturbance, and Rs measurements were taken between 9:00 and 17:00 h. Soil temperature was measured with a Thermocouple probe 6000-09TC, attached to the LI-COR 6400 and the volumetric soil water content (%) or soil moisture was determined with a portable Moisture Probe MP406 (ICT International, Armidale, NSW, Australia). Both temperature and soil moisture were measured adjacent to the collars and simultaneously with Rs at 5 cm depth. Field measurements and soil sampling were carried out one week after wildfire in the summer-wet season (February 2014) and measurements were repeated six months afterwards (in July 2014, during the winter-dry season) and twelve months after the wildfire (in February 2015, during the following summer-wet season).

2.3. Soil sampling and analysis

Soil samples were taken from the first 5 cm of the topsoil with a 7.5 cm diameter soil core. Three samples were collected from each of the selected vegetation cover types and bare soil near the soil collars in both burnt and control areas. Samples were air-dried and sieved (2 mm mesh) for physical and chemical analysis. Soil pH and electrical conductivity (EC) were measured in deionised water (1:2.5 and 1:5 w/v, respectively), using a AD8000 microprocessor-based pH, conductivity, and temperature bench meter (Adwa instruments). Organic C was estimated by dichromate oxidation (Walkley and Black, 1934) and total N with the Kjeldahl method (Bremner and Mulvaney, 1982).

Particle size was analysed by laser diffraction using a Mastersizer 2000 (Malvern Instruments, Malvern, England) after removal of organic matter with H2O2. Bulk density (BD) was determined based on pedotransfer functions from the analyses of soil texture and organic matter according to Rawls (1983).

2.4. Statistical analysis

All data were tested for normality and homogeneity of variances using the Shapiro-Wilk and Levene's tests. Differences in soil variables between burnt and control sites and across vegetation types and differing times since fire were tested using ANOVA and comparisons between means were performed with the *Least-significant differences* (LSD) test. Repeated-measures analysis of variance (RM ANOVA) was used to determine the direct and interactive effects of vegetation type, burn status, time since fire on soil respiration, soil temperature, and soil moisture content. The analysed variables were log transformed or rank-normalized if needed to meet the assumptions for ANOVA (presented data are non-transformed). Pearson's correlations were used to test relationships between pairs of measured edaphic and environmental variables and Rs. Differences for ANOVA test and correlation analyses were considered significant at the 0.05 level. All analyses were performed with R statistical software version 3.1.2 (R Core Team, 2014). Packages and functions used were: *Anova* function from the *car* package for RM ANOVA, *LSD.test* function from the *agricolae* package for the post-hoc analyses and *rcorr* function from the *Hmisc* package for the correlation analysis.

2.5. Soil respiration models

An exponential model and the standard temperature-based Q10 model (Lloyd and Taylor, 1994) were used to describe the relationship between Rs and soil temperature for each vegetation type in control and burnt areas according to the following equations:

$$Rs = ae^{bT}, \tag{1}$$

$$Q10 = e10^b, \tag{2}$$

where Q10 is the increase in the flux rate for a 10 °C increase in temperature, a and b are fitted constants, and T is the soil temperature (°C) at 5 cm depth.

To describe the relationship between Rs and soil moisture, linear, quadratic and exponential functions (Davidson et al., 1998; Lai et al., 2012) were tested:

$$\text{Linear}: Rs = a + bW, \tag{3}$$

$$\text{Quadratic}: Rs = a + bW + cW^2, \tag{4}$$

$$\text{Exponential}: Rs = ae^{bW}, \tag{5}$$

where a, b and c are fitted constants, and W is the soil moisture (%) at 5 cm depth.

An exponential-exponential function was used to describe the effects of soil temperature and soil moisture on Rs (Lai et al., 2012; Lavigne et al., 2004).

$$Rs = ae^{bW} e^{cT} \tag{6}$$

where a, b and c are fitted constants, T is the soil temperature (°C) and W is the soil moisture (%), both measured at 5 cm depth.

Linear functions were used to fit the predicted versus the measured Rs rates in both burnt and unburnt sites.

3. Results

Soil chemical variables (organic C, N, pH and EC) were higher in the burnt site compared to the control but differences were only significant ($P < 0.05$) for N and EC (Table 1). Although soil temperature and moisture were marginally higher in the burnt site, these differences were not significant ($P < 0.05$). Soil texture slightly differed between burnt and control sites but there was not a clear trend; however, bulk density was significantly higher ($P < 0.05$) in control areas. The largest contents of C and N were found under *Eucalyptus* trees in both sites followed by *Acacia* shrubs. *Triodia* grasses, the most abundant vegetation type in terms of area of occupancy, showed similar values of C and N to bare soil. EC was significantly ($P < 0.05$) higher in *Eucalyptus* trees compared to the other vegetation types in the burnt areas. Pearson's correlation analysis showed a significant ($P < 0.05$) positive correlation of Rs with soil moisture ($r = 0.39$), organic C ($r = 0.35$) and N ($r = 0.42$), and negative with BD ($r = -0.28$) (Table 2). Both organic C and N were positively correlated with soil moisture ($r = 0.27$) and negatively with soil temperature ($r = -0.49$ and -0.36, respectively). Neither pH nor EC were significantly correlated with Rs but significant ($P < 0.05$) relationships were found between EC and C ($r = 0.75$), N ($r = 0.61$) and T ($r = -0.45$).

Soil CO_2 efflux showed significant differences between vegetation types ($P < 0.001$) and burn status (burnt versus control, $P < 0.001$) (Fig. 1; Table 3). The interactive effects of vegetation type with both time since fire and burn status were also significant ($P < 0.05$ and $P < 0.01$, respectively). Soil temperature and moisture also varied with vegetation, time since fire and burn status ($P < 0.001$) with strong interactions found between combinations of factors, particularly for soil moisture (Table 3).

Rs was consistently higher under *Eucalyptus* trees compared to other vegetation covers in both burnt and control sites ranging between 2.14 ± 0.54 and 3.64 ± 1.01 µmol m^{-2} s^{-1} in the fire affected area, and from 0.50 ± 0.03 to 3.19 ± 0.75 µmol m^{-2} s^{-1} in the control sites (Fig. 1). Under *Acacia* shrubs, rates of Rs varied between 0.70 ± 0.08 and 2.67 ± 0.79 µmol m^{-2} s^{-1} in the burnt site and between 0.35 ± 0.01 and 2.32 ± 0.21 µmol m^{-2} s^{-1} in the unburnt control site. The lowest Rs rates were found under *Triodia* grasses, with averages of 0.91 ± 0.29 and 0.44 ± 0.19 µmol m^{-2} s^{-1} in the burnt and the unburnt control sites, respectively. These values were similar to those found under bare soil.

Significantly ($P < 0.05$) larger Rs rates were apparent in the burnt sites compared to the unburnt control areas six months after wildfire under *Acacia* shrubs, *Eucalyptus* trees and bare soil, and 12 months after wildfire under *Acacia* shrubs and bare soil. A different trend was found under *Triodia* grasses where the CO_2 efflux was higher in the unburnt areas; however these differences were not significant ($P < 0.05$). Immediately after the fire, differences in Rs were only significant ($P < 0.05$) in bare soil when compared against all other vegetation covers.

The exponential regressions with T as a single controlling factor of Rs were significant ($P < 0.01$) for *Acacia* shrubs in both burnt and control (unburnt) sites and explained 62.4% and 88.5% of the variation in Rs (Fig. 2, Table 4). Under *Eucalyptus* trees, the regression was effective only in the control sites ($r^2 = 0.786$), and in *Triodia* grasses and bare soil was effective only in the burnt areas ($r^2 = 0.60$ and $r^2 = 0.76$, respectively) (Fig. 2, Table 4). The exponential regressions with W as a single explanatory variable of Rs, were significant in the burnt site ($P < 0.05$) under *Eucalyptus* trees (exponential function) and BS (polynomial function) with W explaining 79.2% and 77.0%, respectively (Fig. 3, Table 5). In the control sites, these relationships were only significant under *Acacia* shrubs ($r^2 = 0.75$) and bare soil ($r^2 = 0.9$). Temperature and moisture together improved the correlation coefficients of the regression equations, e.g. 91% of Rs variability was explained under *Acacia* shrubs in the control site and 64% in the burnt areas (Table 5). Considering all vegetation covers together, predicted versus measured Rs

Table 1
Soil physicochemical characteristics of burnt and control areas under different vegetation types (Mean ± SE). AS: *Acacia* shrubs, ET: *Eucalyptus* trees, TG: *Triodia* grasses and BS: bare soil. T: temperature (°C); W: soil water content (%) C: soil organic carbon (%); N: total nitrogen; EC: electrical conductivity (dS m^{-1}); BD: bulk density (g cm^{-3}). Different lower case letters indicate significant differences among vegetation type within the same fire status and upper case letters indicate significant differences between burnt and control sites for each vegetation cover (LSD test, $P < 0.05$).

Fire status	Vegetation type	T	W	C	N	pH	EC	Clay	Silt	Sand	BD
Control	AS	39.8 ± 1.4[Aa]	0.88 ± 0.09[Aa]	0.36 ± 0.02[Bab]	0.017 ± 0.002[Ba]	7.31 ± 0.04[Aa]	2.91 ± 0.19[Ba]	2.2 ± 0.1[Bb]	15.8 ± 0.7[Aab]	82 ± 0.8[Aab]	1.6 ± 0.01[Ad]
	ET	39.9 ± 0.9[Aa]	0.83 ± 0.07[Aa]	0.45 ± 0.03[Ba]	0.032 ± 0.002[Ba]	7.24 ± 0.01[Aa]	2.52 ± 0.09[Ba]	3.4 ± 0.1[Aa]	20.1 ± 0.4[Bab]	76.5 ± 0.4[Bb]	1.61 ± 0.01[Ac]
	TG	43.3 ± 1.5[Aa]	0.70 ± 0.08[Aa]	0.16 ± 0.01[Bc]	0.003 ± 0.001[Bb]	7.05 ± 0.00[Ab]	2.71 ± 0.15[Ba]	2.6 ± 0.1[Ab]	16.3 ± 0.9[Aab]	81.1 ± 0.9[Aab]	1.64 ± 0.01[Ab]
	BS	41.5 ± 0.8[Aa]	1.23 ± 0.12[Aa]	0.20 ± 0.01[Bc]	0.009 ± 0.001[Bb]	7.26 ± 0.01[Aa]	2.47 ± 0.17[Ba]	2.6 ± 0.1[Bb]	12.0 ± 0.7[Ab]	85.4 ± 0.8[Aab]	1.65 ± 0.01[Aa]
Burnt	AS	41.2 ± 1.3[Aa]	0.82 ± 0.08[Aa]	0.74 ± 0.03[Ab]	0.031 ± 0.003[Ab]	7.54 ± 0.06[Aa]	5.33 ± 0.31[Aab]	3.5 ± 0.1[Aab]	26.9 ± 0.1[Ba]	69.6 ± 0.1[Bb]	1.58 ± 0.01[Ba]
	ET	42.0 ± 1.3[Aa]	1.21 ± 0.09[Aa]	1.6 ± 0.05[Aa]	0.053 ± 0.003[Aa]	7.41 ± 0.07[Aa]	9.73 ± 0.39[Aa]	3.5 ± 0.1[Aab]	12.6 ± 1.1[Ab]	83.8 ± 1.1[Aa]	1.57 ± 0.01[Bb]
	TG	40.2 ± 1.1[Aa]	1.68 ± 0.13[Aa]	0.8 ± 0.01[Ab]	0.011 ± 0.001[Aa]	7.21 ± 0.03[Aa]	6.87 ± 0.16[Ab]	4.5 ± 0.3[Aa]	14.9 ± 0.2[Ab]	80.7 ± 0.2[Aa]	1.52 ± 0.01[Bd]
	BS	45.3 ± 1.1[Aa]	1.21 ± 0.1[Aa]	0.8 ± 0.01[Ab]	0.011 ± 0.001[Ab]	7.12 ± 0.02[Aa]	5.88 ± 0.18[Ab]	2.5 ± 1.0[Ab]	16.8 ± 0.7[Ab]	80.7 ± 0.6[Aa]	1.55 ± 0.01[Bc]

Table 2

Correlation matrix with main relationships between measured soil variables (n = 24). Pearson's correlation coefficients (r) with bold-face are significant at $P < 0.05$. Rs: soil respiration, T: soil temperature (°C); W: soil moisture (%); C: soil organic C (%); N: total nitrogen (%); EC: electrical conductivity (dS m^{-1}); BD: bulk density (g cm^{-3}).

Variables	T	W	C	N	EC	pH	Clay	Silt	Sand	BD
Rs	0.18	**0.39**	**0.35**	**0.42**	0.21	0.06	0.05	0.14	−0.14	**−0.28**
T		**0.47**	**−0.49**	**−0.36**	**−0.45**	−0.17	−0.22	−0.05	0.08	**0.56**
W			**0.27**	**0.27**	0.18	−0.12	0.12	−0.1	0.07	−0.22
C				**0.86**	**0.75**	0.17	**0.38**	0.01	−0.08	**−0.81**
N					**0.61**	0.17	**0.36**	0.13	−0.19	**−0.7**
EC						**0.54**	**0.29**	−0.01	−0.04	**−0.73**
pH							0.1	0.15	−0.16	−0.16
Clay								0.1	**−0.28**	**−0.42**
Silt									**−0.98**	−0.22
Sand										**0.28**

showed similar fits ($P < 0.05$) in both burnt ($r^2 = 0.64$) and control ($r^2 = 0.67$ sites (Fig. 4). Q10 ranged from 0.62 ± 0.04 to 1.09 ± 0.01 in the control area and between 1.29 ± 0.01 and 2.58 ± 0.25 in the burnt site, and the highest Q10 was found under *Acacia* shrubs in burnt areas (Table 4).

A larger variability of Rs and soil moisture was generally found in the summer-wet season compared to the winter-dry season (Fig. S1). Soil temperature on the contrary showed a large variability in both seasons in both burnt and control areas.

4. Discussion

Our results showed larger rates of Rs in the burnt areas compared to the unburnt control sites, although these differences were highly dependent on the type of vegetation cover and time since fire. Some studies have reported an increase in heterotrophic respiration following fire, attributed in part to the decomposition of organic substances (Hicke et al., 2003; Irvine et al., 2007). Wildfire removes the vegetation cover and resets the vegetation succession (Pereira et al., 2013), and increased productivity of recruited plants at early growth stages with higher quality and quantity of detritus may promote higher decomposition rates by microbes (Irvine et al., 2007). Although fire may restrain autotrophic Rs in the short term due to root mortality, this effect can be shrouded by the increase in heterotrophic Rs as a result of the fire (Smith et al., 2010). The removal of vegetation, ashes and part of the soil organic layer can have a large effect on nutrient availability and the microbial composition (Bodi et al., 2014; Pereira et al., 2014). However, microbial biomass and activity can usually recover much faster than vegetation after fire (Goberna et al., 2012; Muñoz-Rojas et al., 2016).
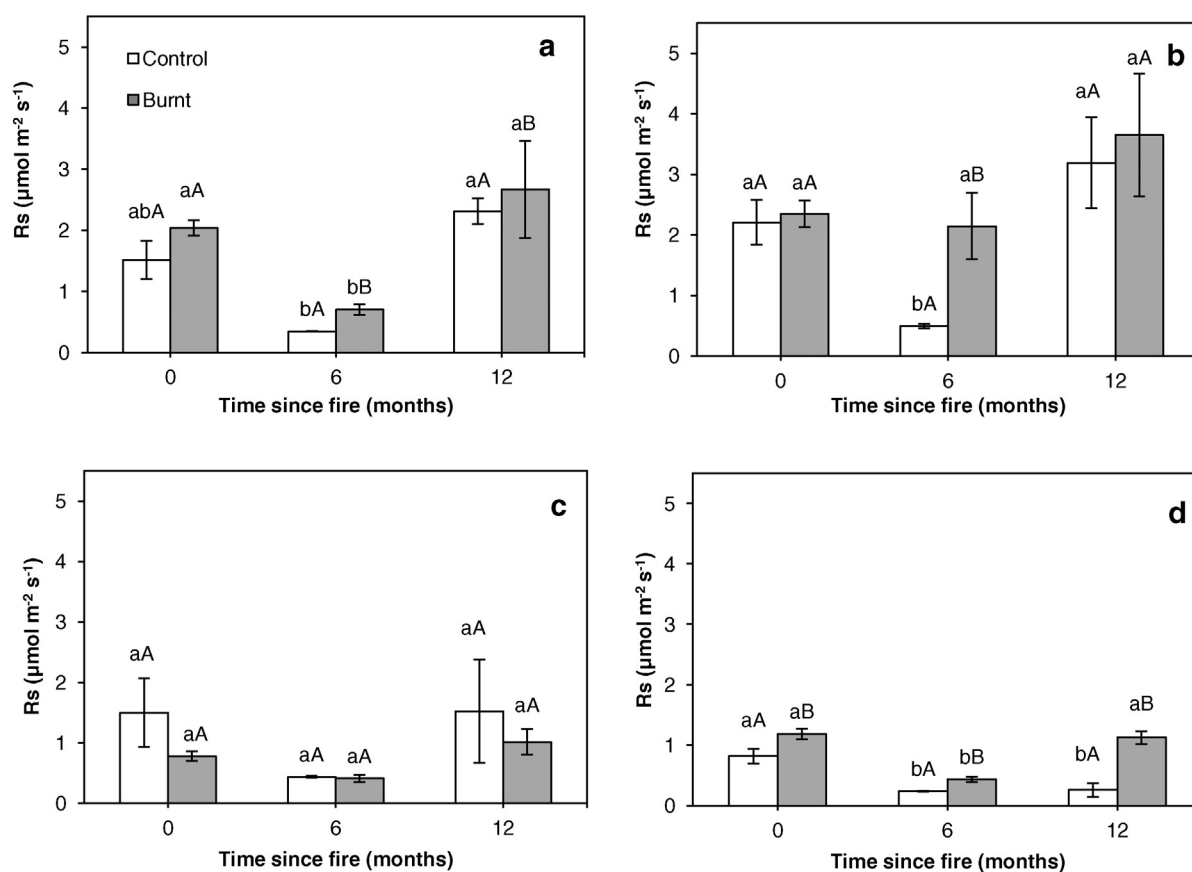

Fig. 1. Temporal evolution of soil respiration (Rs) in burnt and control areas (mean ± SE): (a) *Acacia* shrubs, (b) *Eucalyptus* trees, (c) *Triodia* grasses and (d) bare soil. Different lower case letters indicate significant differences over time in burnt and control soils and upper case letters indicate significant differences between control and burnt site at each time period (LSD post hoc test, $P < 0.05$).

Table 3

Effects of vegetation type (V), time since fire (TSF), and burn status (burnt (B) versus control/un-burnt), and interactive effects of these factors on soil respiration (Rs, μmol m^{-2} s^{-1}), soil temperature (T, °C) and soil moisture (W, %). Statistical significance levels: *NS*: not significant, ***$P < 0.001$, **$P < 0.01$, * $P < 0.05$.

Factors	Rs		T		W	
	F value	P value	F value	P value	F value	P value
V	31.889	***	28.576	***	10.213	***
TSF	0.017	NS	34.514	***	29.826	***
B	15.089	***	445.709	***	26.646	***
V × TSF	4.023	*	4.008	*	2.859	*
V × B	5.389	**	15.323	***	12.532	***
TSF × B	2.342	NS	0.192	NS	79.973	***

Rs rates differed significantly among vegetation types in both burnt and unburnt areas with efflux rates ranging from 0.44 to 3.65 μmol m^{-2} s^{-1} and from 0.24 to 3.19 μmol m^{-2} s^{-1} in the burnt and control sites, respectively. These values are broadly similar to those reported in other arid and semi-arid ecosystem studies (Maestre and Cortina, 2003; Oyonarte et al., 2012; Rey et al., 2011). However, the high Rs rates obtained in *Eucalyptus* trees during the summer-wet season were above these levels and more similar to values reported for *Quercus* and *Pinus* forests of temperate areas (Vargas and Allen, 2008). These larger rates under *Eucalyptus* might be partly explained by the amount of C attained by photosynthesis in the plants driving the belowground fluxes, as the assimilated C is likely to be higher in plant species that prioritize resource acquisition with larger leaf area (Metcalfe et al., 2011). The effects of vegetation on Rs can be associated to temperature and moisture levels at the soil surface or other microclimate aspects (Curiel-Yuste et al., 2004). Nonetheless, the strong correlations found between Rs rates and C and N, and the largest values of these soil elements found under *Acacia* shrubs and particularly under *Eucalyptus* trees, suggest that the response of Rs under different vegetation covers

can most likely be attributed to differences in C cycling as a result of ash and litter incorporation (Pereira et al., 2013) and microbial decomposition (Luo and Zhou, 2006). Both *Acacia* shrubs and *Eucalyptus* trees are resprouting plants and can regrow their biomass after fire (Pausas and Keeley, 2014), which can influence Rs rates when compared to seeder plants such as *Triodia* grasses. Resprouters and seeders differ in their patterns of allocation of photoassimilates and nutrient resources. Approximately 75% of new photoassimilates are allocated to roots in resprouters and 75% of this C directed belowground is respired CO_2. Seeders, on the other hand, allocate <50% of new photoassimilates to roots and invest more on developing a leafy canopy (Verdú, 2000).

Differences in Rs rates between vegetation types and bare soil patches have been observed in other arid and semi-arid regions (Cable et al., 2008; Maestre and Cortina, 2003). However, Rey et al. (2011) did not find significant differences between plant cover and bare soil, and have partly attributed this lack of variation to photodegradation processes. The recent evidence of photodegradation, where the breakdown of organic matter can occur via solar radiation in water limited conditions, therefore warrants further investigation as it may provide some insight into previously documented variation in Rs across many studies (Almagro et al., 2015; Austin, 2011; Austin and Vivanco, 2006; Barnes et al., 2015). For instance, if photodegradation plays a significant role in arid environments, data from our study might explain the similar C contents and Rs rates found in *Triodia* grasses and bare soil. Both covers had a similar exposure level of UV radiation given the short stature and more open canopy of many *Triodia* grasses, when compared to *Eucalyptus* trees and *Acacia* shrubs, which may permit similar degradation processes of bare soil.

Because of the well-known sensitivity of temperature to soil respiration (Lloyd and Taylor, 1994), Q10 has been widely studied (Chen et al., 2010; Vargas et al., 2012; Zhang et al., 2015) and soil temperature has been commonly used as a reliable predictor of Rs in areas without severe incidence of drought (Jenkins and Adams, 2011). In our study,
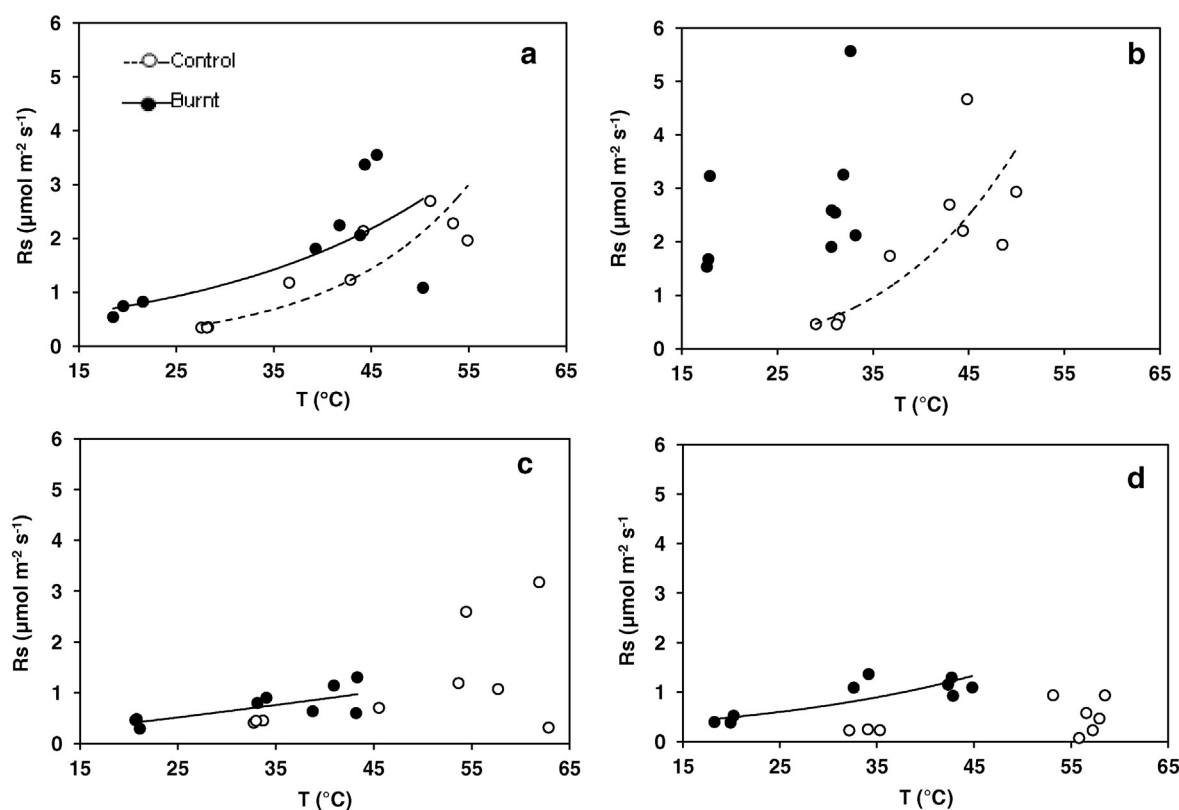

Fig. 2. Relationships between soil respiration (Rs) and soil temperature (T) under: (a) *Acacia* shrubs, (b) *Eucalyptus* trees, (c) *Triodia* grasses and (d) bare soil. Equations and statistical parameters are shown in Table 4. Fitted lines are shown for significant ($P < 0.05$) relationships.

Table 4
Fitted parameters of exponential equations for the relationship between soil respiration (Rs, μmol m^{-2} s^{-1}) and temperature (T, °C) and Q10 values for vegetation types. AS: *Acacia* shrubs, ET: *Eucalyptus* trees, TG: *Triodia* grasses and BS: bare soil. Statistical significance levels: *NS*: not significant, ***P < 0.001, **P < 0.01, * P < 0.05. Q_{10}: Mean ± SE. Different lower case letters within the same column indicate significant differences between vegetation types and upper case letters indicate significant differences between control and burnt site at each time period (LSD test, P < 0.05).

Vegetation type	Control				Burnt			
	Equation	r^2	P	Q_{10}	Equation	r^2	P	Q_{10}
AS	Rs = 0.0710e$^{0.0739T}$	0.885	***	0.99 ± 0.01Ba	Rs = 0.3178e$^{0.0428T}$	0.624	*	2.58 ± 0.25Aa
ET	Rs = 0.0305e$^{0.0972T}$	0.786	**	1.09 ± 0.01Aa	Rs = 1.2642e$^{0.0254T}$	0.198	NS	1.58 ± 0.16Ab
TG	Rs = 0.1448e$^{0.0362T}$	0.298	NS	1.07 ± 0.01Aa	Rs = 0.1937e$^{0.0377T}$	0.601	*	1.37 ± 0.07Ab
BS	Rs = 0.1129e$^{0.0223T}$	0.098	NS	0.62 ± 0.04Bb	Rs = 0.2202e$^{0.0400T}$	0.759	**	1.29 ± 0.01Ab

average Q10 values were 0.94 ± 0.11 in the control area and 1.71 ± 0.29 in the burnt site, and were within average values of similar arid or semi-arid areas (Cable et al., 2011; Lai et al., 2012; Rey et al., 2011). Cable et al. (2011) analysed Q10 in drylands of Northern America and reported average values ranging between 1.0 and 1.5 in areas like the Mojave and the Sonoran deserts. These values are similar to those obtained by Wang et al. (2014) in a desert shrub ecosystem, which varied between 1.3 and 1.6. In general, values in desert shrub systems tend to be lower than other types of ecosystems due to their lower amounts of soil carbon and microbial activity (Cable et al., 2011; Conant et al., 2004; Wang et al., 2014). Nevertheless, comparisons of Q10 can be difficult because of the different approaches used for its determination, and thus values of Q10 can largely vary depending on the location and ecosystem type (Lloyd and Taylor, 1994). Some authors have associated Q10 to the contribution of roots and the relevance of substrate availability of different vegetation types to Rs (Davidson et al., 1998; Davidson and Janssens, 2006). Our results showed that Q10 did not differ to a large extent among different vegetation types but it was significantly higher in the burnt site compared to the control. This difference can be attributed to the impact of fire on root material (senescence due to

plant death after fire), but also to the higher temperature sensitivity of labile carbon in burnt soils versus stable carbon (Thornley and Cannell, 2001). However, different studies on the relative temperature sensitivity of labile versus recalcitrant SOC have shown contradictory results and this subject is still unresolved (Conant et al., 2011; Plante et al., 2010).

From our results it is evident that higher Rs, regardless of the site condition (unburnt or burnt), is generally triggered during periods of higher temperatures and water availability, as observed during the summer rainfall season. Carbon and water cycles are strongly linked through biogeochemical processes such as photosynthesis and soil respiration (Domingo et al., 2011) and several studies have highlighted soil moisture as a decisive driver of Rs particularly in dry environments, considering it even more relevant than soil temperature (Almagro et al., 2009; Conant et al., 2004; Moyano et al., 2013; Rey et al., 2011). In our study, the relationships between Rs and the environmental variables (soil temperature and moisture) varied among vegetation types and although soil temperature seems to be a better predictor than soil moisture to explain variation in Rs, different trends were found. Moisture as a single factor could explain 77–89% of the variability in Rs in areas
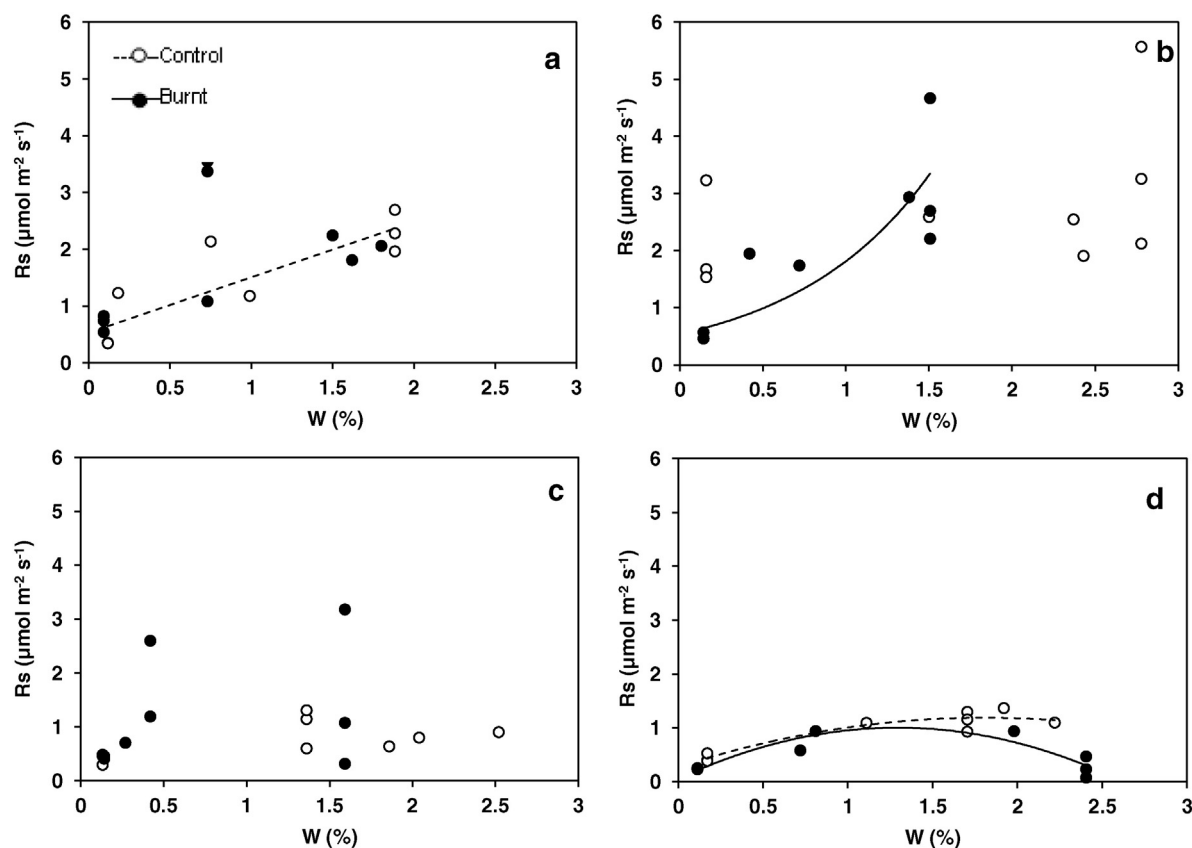

Fig. 3. Relationships between soil respiration (Rs) and soil moisture (W) under: (a) *Acacia* shrubs, (b) *Eucalyptus* trees, (c) *Triodia* grasses and (d) bare soil. Equations and statistical parameters are shown in Table 5. Fitted lines are shown for significant (P < 0.05) relationships.

Table 5
Fitted parameters of the equations for the relationships of soil respiration (Rs, μmol m^{-2} s^{-1}) with soil moisture (W, %) and temperature (T, °C) for vegetation types. AS: *Acacia* shrubs, ET: *Eucalyptus* trees, TG: *Triodia* grasses and BS: bare soil. Statistical significance levels: NS: not significant, ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

Vegetation type	Control			Burnt		
	Equation	r^2	P	Equation	r^2	P
Rs = f(W)						
AS	$Rs = 0.9748W + 0.5332$	0.749	*	$Rs = 0.891e^{0.6253}$	0.390	NS
ET	$Rs = 0.4629W^2 + 0.8958W + 2.3144$	0.226	NS	$Rs = 0.5390e^{1.2124W}$	0.792	*
TG	$Rs = -0.2225W2 + 0.7314W + 0.3357$	0.597	NS	$Rs = -3.6840W^2 + 7.1872W + 0.5746$	0.355	NS
BS	$Rs = -0.2802W^2 + 1.0122W + 0.2737$	0.891	**	$Rs = -0.5686W^2 + 1.4716W + 0.0499$	0.770	*
Rs = f(W,T)						
AS	$Rs = 0.0488e^{0.5970T}e^{0.7054W}$	0.908	***	$Rs = 1.80876^{0.0043T}e^{0.1576W}$	0.637	*
ET	$Rs = 0.0908e^{0.0552T}e^{39.1612W}$	0.815	**	$Rs = 0.3974e^{0.0477T}e^{0.1267W}$	0.207	NS
TG	$Rs = 0.0496e^{0.0687T}e^{-0.7129W}$	0.397	NS	$Rs = 0.2213e^{0.0285T}e^{0.1433W}$	0.638	*
BS	$Rs = 0.0125e^{0.0894T}e^{-0.8776W}$	0.496	NS	$Rs = 0.4065e^{0.0021T}e^{0.5323W}$	0.838	**

without vegetation cover (bare soil). However, under vegetation cover, the exponential-exponential interactions of soil temperature with soil moisture were the best fit to explain the Rs response, which suggest that the role of temperature in substrate decomposition is critical to explain the CO_2 fluxes. Similar approaches have been previously used in earlier studies to predict variations in Rs for different ecosystems or vegetation types (Lai et al., 2012; Wang et al., 2014).

There are several mechanisms connecting the water and C cycles that remain unexplained (Moyano et al., 2012) and more detailed analyses of the links between aboveground and belowground processes could contribute to a better knowledge of these cycles. For example, root respiration depends on a large extent on the amount of photosynthesis translocated from the plant aboveground and different vegetation types have specific strategies of C allocation (Curiel-Yuste et al., 2004). Regardless of the fire status, the varied response of the CO_2 fluxes and its relation to C contents of different vegetation types in our study suggests that Rs is a distinctive attribute of the type of vegetation or ecosystem, underpinning its potential use as an indicator of the biological soil status (which integrates abundance and activity of microbial communities) of particular ecosystem types (Oyonarte et al., 2012).

It is crucial to acknowledge the variability among vegetation types, not only to understand Rs variability but to obtain accurate estimates of CO_2 fluxes in these semi-arid ecosystems with large patchy distribution in the vegetation cover, distinct C contents and inputs, and diverse Rs rates (Irvine et al., 2007; Maestre and Cortina, 2003). Due to this large variability in Rs, future studies should also consider separating its source components (contributions of autotrophic and heterotrophic respiration to the CO_2 efflux) to thoroughly understand the mechanisms behind Rs following fire. This will provide more insight into ecosystem physiological processes after disturbances. Several studies with different approaches have focused on studying the partitioning between microbial and root respiration (Harmon et al., 2011; Kuzyakov, 2006; Tang and Baldocchi, 2005) but large uncertainties remain and most methods have proved to be challenging (Bond-Lamberty et al., 2004; Wei et al., 2010).

5. Conclusions

The major findings of our study are:

- Larger rates of Rs were found in the burnt areas compared to those unburnt which is likely due to an increase in heterotrophic respiration following fire from decomposition of organic substances by the microbial communities.
- Regardless of the burnt status, higher Rs rates were triggered during periods of higher temperatures and water availability.
- Rs showed a large variation among vegetation types in both burnt and burnt areas for each time period following fire and both Rs and C were consistently higher under *Eucalyptus* trees, followed by *Acacia* shrubs. *Triodia* grasses had the lowest Rs rates and C contents

which were similar to those found under bare soil patches.
- Q10 did not differ to a large extent among different vegetation types but it was significantly higher in the burnt site compared to the control.
- Environmental factors (temperature and moisture) could explain a large fraction of Rs variability, improving the relationship of moisture or temperature as single factors with Rs. Therefore, the roles of both water availability and temperature are critical to explain the CO_2 fluxes in these environments. However, these relations are variable and change across vegetation types; therefore specific models need to be used to accurately estimate Rs rates.
- Fire in these fire-prone semi-arid ecosystems contributes to atmospheric C both as a result of combustion and as shown here, through elevated Rs rates indicating that elevated levels of human-induced fire in these systems may increase atmospheric CO_2 levels.
- This study demonstrates the importance of assessing CO_2 fluxes considering both abiotic factors and vegetation types after disturbances such as fire. This is particularly important in heterogeneous semi-arid areas with patchy vegetation distribution where CO_2 fluxes can be largely underestimated. The high variability in Rs, differences of the efflux between vegetation types and relation to C and N contents suggest that Rs could be used as an indicator of the soil and ecosystem status. Further studies should consider partitioning between autotrophic and heterotrophic respiration to fully understand the processes and mechanisms behind soil respiration in arid and semi-arid environments.

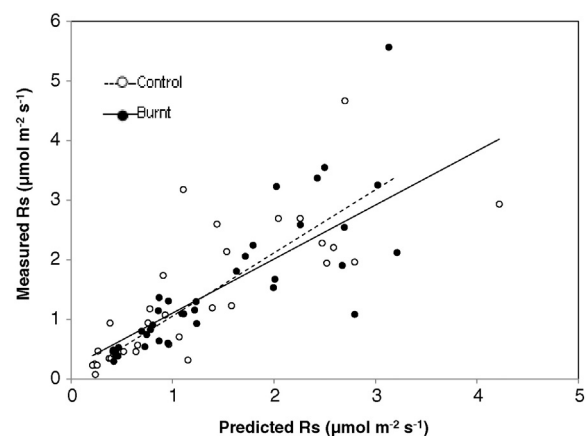Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.02.086.

Fig. 4. Predicted soil respiration (Rs, μmol m^{-2} s^{-1}) versus measured values for burnt and control areas. Control: Rs predicted $= 0.4303e^{0.702 \text{ Rs measured}}$ ($R^2 = 0.7394$; $P < 0.05$); Burnt: Rs predicted $=$ Rs measured $^{0.9999}$ ($R^2 = 0.7661$; $P < 0.05$).

Acknowledgements

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