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RESEARCH PAPER

## Soil respiration across a disturbance gradient in sclerophyllous ecosystems in Central Chile

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### Abstract

**H.E. Bown, J.P. Fuentes, J.F. Perez-Quezada, and N. Franck. 2014. Soil respiration across a disturbance gradient in sclerophyllous ecosystems in Central Chile. Cien. Inv. Agr. 41(1): 89-106.** Sclerophyllous shrubs and forests are predominant in semiarid Central Chile and have a long history of degradation by fire, cultivation, firewood extraction and grazing. The aim of this study was to compare the amount and environmental drivers of soil respiration across a disturbance gradient in sclerophyllous ecosystems in the National Reserve Roblería del Cobre de Loncha in Central Chile. In a north-facing toe slope, four disturbance conditions were identified: slightly (D1) and moderately disturbed (D2) sclerophyllous forest, (D3) strongly disturbed thorn scrub and (D4) most disturbed *A. caven* savanna. Twelve 25×25-m plots (625 m<sup>2</sup>) were distributed equally across D1, D2, D3 and D4. Soil respiration ( $R_s$ ), soil temperature ( $T_s$ ), volumetric water content ( $\theta_v$ ) and exchangeable nitrogen ( $N_s$ ) were measured at six dates in each plot between August 2009 and May 2010. Additionally,  $T_s$  and  $\theta_v$  were continuously recorded from July 2010 to August 2012 (30-minute intervals) in one plot per disturbance condition (*i.e.*, 4 out of 12 plots). The values of  $R_s$  increased linearly with  $\theta_v$  with similar slopes but different intercepts, which increased as the disturbance receded. Once soil water content was taken into account,  $R_s$  increased with  $T_s$  with the same slope but with a disturbance-dependent intercept. Additionally, the response of  $R_s$  to  $T_s$  was more pronounced as  $\theta_v$  increased. The values of  $N_s$  were uncorrelated with  $R_s$ . The annual values of  $R_s$  were 4.4-fold greater in D1 (1,735 g C m<sup>-2</sup> yr<sup>-1</sup>) compared with D4 (392 g C m<sup>-2</sup> yr<sup>-1</sup>). Disturbance presumably decreased  $R_s$  by reducing the litter layer, soil organic matter, root biomass and soil water content, particularly in the hot-dry season. Under a predicted climate change scenario of a 40% decrease in rainfall and 4°C increase in air temperature by the year 2100, we found that annual  $R_s$  would be reduced on average by 28% compared with the current climate, with that reduction being more pronounced under more disturbed conditions, suggesting that less disturbed conditions would be more resistant to climate change, thus further justifying the restoration of these damaged ecosystems.

**Key words:** *Acacia caven* savanna, disturbance gradient, sclerophyllous forest, soil respiration, thorn scrub.

### Introduction

The total global emission of CO<sub>2</sub> from soils is the second largest flux (98±12 Pg C yr<sup>-1</sup>) in the

global carbon (C) cycle after photosynthesis (Raich and Potter, 1995; Raich and Schlesinger, 1992; Schlesinger and Andrews, 2000, Reichstein *et al.*, 2003; Li *et al.*, 2008; Bond-Lamberty and Thomson, 2010), accounting for approximately 25% of the global CO<sub>2</sub> exchange (IPCC, 2001). Soils also contain the largest C reservoir in the

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biosphere (~1,500 Pg C), approximately twice the atmospheric CO<sub>2</sub>-C pool (IPCC, 2001; Jia *et al.*, 2006), which implies that a more rapid oxidation of soil organic matter due to global warming may significantly increase the atmospheric CO<sub>2</sub> concentration (Raich and Potter, 1995; Davidson and Janssens, 2006). Hence, soil respiration ( $R_s$ ) is an important regulator of climate change as well as a determinant of the global carbon balance (Heinmann and Reichstein, 2008).

Predicting  $R_s$  and understanding the drivers that underlie the seasonal and spatial variation of soil respiration are fundamental to predict ecosystem responses to climate change (Li *et al.*, 2008, Raich and Schlesinger, 1992; Vargas *et al.*, 2011a).  $R_s$  has been reported to differ across temporal and spatial scales (*e.g.*, Jia *et al.*, 2006; Li *et al.*, 2008; Vargas *et al.*, 2010) as a result of changes in soil temperature (Lloyd and Taylor, 1994; Subke and Bahn, 2010), soil moisture (Gaumont-Guay *et al.*, 2006; Moyano *et al.*, 2012), vegetation (Buchmann, 2000; Bahn *et al.*, 2010), topography (Kang *et al.*, 2003), soil texture (Dilustro *et al.*, 2005; Pumpanen *et al.*, 2008) and primary productivity (Bahn *et al.*, 2008; Vargas *et al.*, 2011b). Thus, better estimates of  $R_s$  at longer times and larger spatial scales would require both better understanding of its biotic and abiotic controls and a better spatial representation of  $R_s$  across different biomes (Vargas *et al.*, 2011a).

Drylands cover approximately 40% of the world's land area as well as Chile's continental territory, and more than 2 billion and 11 million people, respectively, live in these areas (MEA, 2005; Benites *et al.*, 1994; INE, 2013). A substantial reduction in the provision of ecosystem services of drylands is occurring as a result of water scarcity, land degradation and climate change (MEA, 2005). Global warming will affect arid lands through temperature increases and rainfall decrease across the world, with only a few exceptions (Loik *et al.*, 2004; IPCC, 2007; Dai, 2010), leading to likely losses of ecosystem productivity and biodiversity (MEA, 2005).

Semiarid sclerophyllous (*i.e.*, woody plants with small leathery evergreen leaves) shrublands and forests extend between latitudes 32-36° S (~345,000 ha) in Central Chile (Armesto *et al.*, 2007, CONAF, 1999). Holmgreen (2002) argues that sclerophyllous forests and shrublands largely covered Central Chile in pre-Columbian times and were progressively replaced, primarily in the area between the Andes and the Coastal Ranges, by extensive savannas dominated by the invasive legume N-fixing tree *Acacia caven*, which was originally restricted to the Gran Chaco region in north-central Argentina. Currently, sclerophyllous ecosystems are usually restricted to dry slopes as isolated forest or shrub clumps (Holmgreen, 2002). Because most of the population lives in Central Chile, sclerophyllous ecosystems have suffered a long history of degradation by fire, cultivation, firewood extraction, and grazing.

The aim of this study was to examine environmental drivers controlling  $R_s$  across a land degradation gradient and to integrate  $R_s$  on an annual scale under current climate and climate change scenarios. Because  $R_s$  represents the second largest flux after photosynthesis in the global carbon cycle, this study is an important step towards estimating primary productivity as determined by land degradation for this understudied biome.

## Materials and methods

### Study site

The study was performed in the National Reserve 'Roblería del Cobre de Loncha' (34° 08' S, 71° 03' W), located in the Coastal Range, approximately 80 km southwest of the city of Santiago in the Metropolitan region in Chile. The physiography of the National Reserve watershed (5,870 ha) is formed by non-continuous peaks cut by deep ravines and valleys, which largely determine the location of human settlements (UNDP, 2011). Par-

ent materials are typically granitic, granodioritic and volcanic rocks (ODEPA, 1968; SERNAGEOMIN, 1982). The climate is Mediterranean, dry and semi-arid, with a mean annual precipitation of 503 mm, water deficit of 956 mm and mean annual temperature of 14.9 °C. Summer droughts extend for 6–8 months typically from October to April (CONAF, 2008).

The studied site was located in a toe slope in a north-aspect position. Soils developed from colluvial materials that belong to the coarse-loamy, mixed, thermic Typic Xerochrepts family (Soil Survey Staff, 1999) and locally associated with the Quilamuta Series (CIREN, 1996). Soil textures varied from loamy clay in the more disturbed sites to loamy sand in the less disturbed sites.

The natural flora of the site is dominated by the tree sclerophyllous species *Cryptocarya alba* (Mol.) Looser. (Lauraceae), *Quillaja saponaria* Mol. (Quillajaceae), *Lithraea caustica* (Mol.) Hook. et Arn. (Anacardiaceae) and *Peumus boldus* Mol. (Monimiaceae), the invasive small N-fixing tree legume *A. caven* (Mol.) Mol. (*Fabaceae*) and the shrub species *Colliguaja odorifera* Mol. (Euphorbiaceae) and *Retanilla trinervia* (Gillies et Hook.) Hook. et Arn. (*Rhamnaceae*). These tree and shrub species are typical of the sclerophyllous forest, thorn scrub and *A. caven* savanna in Central Chile (Gajardo, 1994; Luebert and Plischoff, 2006; Armesto *et al.*, 2007).

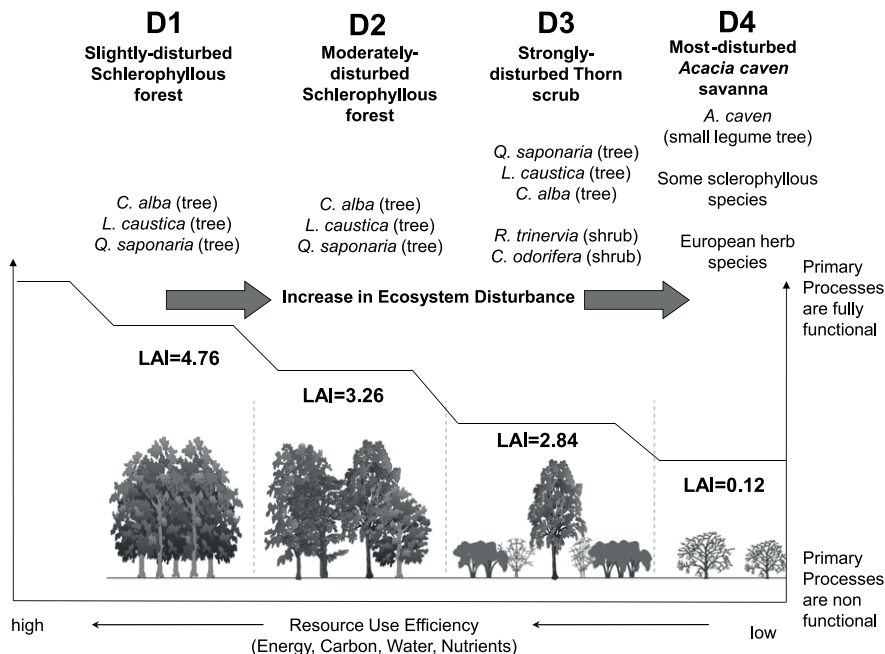
#### *Disturbance gradient*

Twelve 25×25 m plots (625 m<sup>2</sup>) were distributed equally across four clearly different disturbance conditions (Figure 1), henceforth identified as D1, D2, D3 and D4, where D1 was the least-disturbed and D4 the most-disturbed condition (“D” stands for disturbance). Plots ranged in altitude between 300 and 800 m. The slightly disturbed sclerophyllous forest (D1) and the moderately disturbed sclerophyllous forest (D2)

are dominated by the tree species *C. alba*, *Q. saponaria* and *L. caustica*, with a tree cover >75% (leaf area index, *LAI*~4.76 m<sup>2</sup>×m<sup>-2</sup>) and 50–75% (*LAI*~3.26 m<sup>2</sup>×m<sup>-2</sup>), respectively (Figure 1). In condition D1, approximately half of the trees are seed-regenerated, while the remaining are second growth-coppices perpetuated presumably by low intensity fire and firewood extraction prior to the creation of the National Reserve in 1996. Condition D2 is a second growth-coppice. The strongly disturbed thorn scrub (D3) has a sparse tree cover of sclerophyllous species (<15%), notably *Q. saponaria* (up to 16 m in height) but also *C. alba*, *L. caustica* and *A. caven*, with medium shrub cover (~ 50%) of primarily *C. odorifera* and the thorny *R. trinervia* of less than 4 m in height (*LAI*~2.86 m<sup>2</sup>×m<sup>-2</sup>, both shrub and tree cover) (Figure 1). The most-disturbed *A. caven* savanna (D4) is a xerophytic open woodland dominated by the invasive leguminous tree *A. caven* and emerging infrequent sclerophyllous trees of *Q. saponaria*, *C. alba* and *L. caustica*, with a dense herbaceous cover composed primarily of European annual herbs and grasses (e.g., slender wild oat, *Avena barbata* Pott ex Link) that are typically associated with grazing pastures (Armesto *et al.*, 2007) (Figure 1).

#### *Plot measurements*

Diameter at breast height (dbh) was measured for all shoots with a dbh >5 cm within each plot. Shoots were attributed to stools to determine the number of shoots per stool. Tree heights were measured for a random sample of 10 trees per plot. The leaf area index (LAI) of the woody plants, which is the total one-sided area of leaf tissue per unit of ground surface area (Bréda, 2003), was estimated using a ceptometer (AccuPAR LP-80, Decagon Devices, Pullman, WA, USA). Litter biomass was determined using three composite random samples of 30×30 cm per plot that were oven dried at 70 °C followed by recording of the dry mass. These measurements were taken during the summer of 2010.



**Figure 1.** Hypothetical model of the soil and vegetation disturbance of shrubland and sclerophyllous forests in Central Chile (based on Whisenant, 1999). The average leaf area index, LAI, ( $m^2 m^{-2}$ ) measured using a ceptometer is shown for each category.

*Soil respiration measurements*

Ten soil collars per plot made of polyvinyl chloride (100 mm inner diameter and 50 mm length) were randomly inserted into the soil in June 2009. Soil respiration ( $R_s$ ) was measured in all collars within each plot using a closed chamber (100 mm inner diameter, Model SRC-1, PP Systems, Amesbury, MA, USA) connected to an infrared gas analyzer (Model EGM-4, PP Systems, Amesbury, MA, USA). Measurements were performed on rainless days between 10 am and 4 pm on the following dates: August 29, 2009 (winter), September 28, 2009 (spring), November 3, 2009 (spring), January 12, 2010 (summer), March 16, 2010 (summer) and May 10, 2010 (autumn). Soil temperature ( $T_s$ ) was measured simultaneously to  $R_s$  to a depth of 10 cm using a digital thermometer (CheckTemp1, Hanna, USA). At each sampling date, four soil samples were randomly cored to a depth of 30 cm from each plot to determine the soil gravimetric water content ( $\theta_g$ ) and available nitrogen

( $N_s$ ) (Bremner, 1965). The bulk density ( $r_b$ ) was determined using the paraffin-sealed clod method (Blake, 1965). The volumetric water content ( $\theta_v$ ) was calculated as  $\theta_v = r_b \times \theta_g$ .

*Soil sampling*

Composite soil samples (three per plot) were extracted using a hammer-driven soil core (5.4-cm diam.) sampler (Soilmoisture Equipment Corp.) at a 0-10-cm soil depth in August 2010. Total C and N contents were measured via dry combustion (Dumas method) using a total CNS analyzer (LECO Corp, USA). Particle size distribution was determined using the Hydrometer Method (Gee and Or, 2002).

*Auto- and heterotrophic respiration*

The values of  $R_s$  were partitioned for each disturbance condition into autotrophic ( $R_a$ ; mostly roots

and micorrhizae) and heterotrophic respiration ( $R_h$ ; soil microbes, micro- and meso-fauna) using the  $y$ -intercept method (Kucera and Kirkham, 1971; Baggs, 2006; Kuzyakov, 2006). Briefly, this method fits a linear model of  $R_s$  versus root biomass, taking the  $y$ -intercept to be heterotrophic respiration (*i.e.*, soil respiration in the absence of roots). Measurements were performed over a period of 12 days ending on July 27, 2011 (winter) when water was not limiting. Five points were randomly selected within each plot, measuring  $R_s$  prior to progressively coring and removing the soil to a 30-cm depth in the exact same positions in which the  $R_s$  values were measured using a 100-mm inner diameter and 40-cm length soil auger. Soil samples were sieved and washed to recover roots through flotation. Root samples were oven-dried at 70 °C, and the constant mass was recorded. The  $y$ -intercept of the linear relationship between  $R_s$  and root biomass ( $W_R$ ) for each disturbance condition were considered  $R_h$ , while  $R_a$  was calculated as  $R_s - R_h$ .

#### *Soil respiration on an annual basis*

Soil moisture and temperature sensors (5-TM, Decagon Devices, USA) were installed at three soil depths (5, 15, 25 cm) in one plot per disturbance condition (*i.e.*, 4 out of 12 plots) recording continuously at 30 min intervals (data logger EM-50, Decagon Devices, USA) for approximately two years starting in July 2010. Models of  $R_s$  to  $T_s$  and  $\theta_v$  developed specifically in this study from discrete sampling were applied over the two-year series to determine the annual values of  $R_s$  under a current climate scenario. CONAMA (2006) predicted a temperature increase of 2–4 °C and rainfall decrease of up to 40% for Central Chile by the year 2100. We simulated  $R_s$  under a climate change scenario (CONAMA (2006)) by increasing  $T_s$  by 4 °C (a surrogate for an air temperature increase of 4 °C) and decreasing  $\theta_v$  by 40% (a surrogate for a rainfall decrease of 40%) over the recorded two-year climatic series.

#### *Data analysis*

All analyses were performed using R (R Development Core Team, 2010). Variables were tested for normality and homogeneity of variance, and transformations were made as necessary to meet the underlying statistical assumptions of the models used. A one-way analysis of variance (ANOVA) was used to test the primary effects of disturbance conditions on those vegetation and soil variables measured once at the plot level. A one-way ANOVA was also used to test the primary effects of disturbance conditions on  $R_s$ ,  $T_s$ ,  $\theta_v$  and  $N_s$  separately for each sampling date. A two-way ANOVA was used to test the primary effects of disturbance conditions and sampling date on the  $R_s$ ,  $T_s$ ,  $\theta_v$  and available N. The responses of  $R_s$  to  $T_s$ ,  $\theta_v$  and  $N_s$  were fitted using linear and nonlinear models and by considering all sampling dates. An analysis of covariance was performed to test whether the slopes and intercepts of the linear relationship between  $R_s$  and  $W_R$  significantly differed between disturbance conditions.

## **Results**

#### *Vegetation and soil description*

Most biometrical and soil variables exhibited significant differences regarding disturbance conditions (Table 1). The basal area was 12.4-fold greater in D1 (31.1 m<sup>2</sup> ha<sup>-1</sup>) compared with D4 (2.5 m<sup>2</sup> ha<sup>-1</sup>), while D2 (23.8 m<sup>2</sup> ha<sup>-1</sup>) and D3 (7.9 m<sup>2</sup> ha<sup>-1</sup>) showed intermediate values between these two extremes. The average tree height was smallest in D4 (2.6 m), with increasing values observed for D3 (7.6 m), D2 (8.4 m) and D1 (9.9 m). The leaf area index was 0.12, 2.84, 3.26 and 4.76 m<sup>2</sup> m<sup>-2</sup> for the four conditions in decreasing order of disturbance (*i.e.*, D4, D3, D2, D1). Stools (*i.e.*, roots and stumps, which give rise to several shoots from dormant and adventitious buds) per hectare varied approximately six-fold when comparing D1 with D4 (1,611 vs. 240) (Table 1).

**Table 1.** Soil and vegetation variables across a disturbance gradient in the National Reserve Roblería del Cobre de Loncha in Central Chile.

Variable	Unit	Disturbance condition				Sampling date (S)	ANOVA Disturbance condition (D)	S×D
		Most disturbed <i>Acacia caven</i> Savanna (D4)	Strongly disturbed Thorn Scrub (D3)	Moderately disturbed Sclerophyll. Forest (D2)	Slightly disturbed Sclerophyll. Forest (D1)			
<b>Vegetation</b>								
Basal Area	(m <sup>2</sup> ha <sup>-1</sup> )	2.5 ± 0.7 a	7.9 ± 2.7 ab	23.8 ± 3.4 b	31.1 ± 7.9 b	-	**	-
Tree height	(m)	2.6 ± 0.6 a	7.6 ± 1.3 b	8.4 ± 0.5 b	9.9 ± 0.6 b	-	**	-
Live crown height	(m)	0.9 ± 0.2 a	1.7 ± 0.3 a	4.2 ± 1.1 ab	5 ± 0.2 b	-	**	-
Leaf Area Index	(m <sup>2</sup> m <sup>-2</sup> )	0.12 ± 0.01 a	2.84 ± 0.59 ab	3.26 ± 0.75 ab	4.76 ± 1.42 b	-	*	-
Stools per hectare	-	240 ± 88 a	277 ± 140 a	1728 ± 384 b	1611 ± 91 b	-	**	-
Shoots per hectare	-	363 ± 77 a	619 ± 311 a	2736 ± 226 b	2811 ± 607 b	-	**	-
Shoots per stool	-	1.7 ± 0.3 a	2.5 ± 0.3 a	1.8 ± 0.5 a	1.7 ± 0.3 a	-	ns	-
Diam. at breast height	(cm)	8.7 ± 1.9 a	15.9 ± 4.9 a	9.5 ± 0.3 a	10.9 ± 1.1 a	-	ns	-
Litter biomass	(g m <sup>-2</sup> )	13.1 ± 2.6 a	52.1 ± 8.8 ab	71.3 ± 16.8 ab	109.8 ± 16.6 b	-	*	-
Root biomass	(kg m <sup>-2</sup> )	2.36 ± 0.59 a	2.52 ± 0.34 a	4.69 ± 0.40 b	5.60 ± 0.66 b	-	*	-
<b>Soil</b>								
Textural Class		Loamy clay	Loam	Loamy sand	Loamy sand			
Sand		24.62 ± 5.57 a	44.76 ± 3.66 ab	54.66 ± 3.01 ab	62.49 ± 2.36 b	-	***	-
Loam		37.57 ± 3.59 a	38.37 ± 3.90 a	31.98 ± 2.85 a	24.67 ± 1.65 a	-	ns	-
Clay		37.81 ± 7.38 b	16.87 ± 1.59 a	13.36 ± 1.08 a	12.84 ± 1.25 a	-	*	-
Bulk density	(g cm <sup>-3</sup> )	1.70 ± 0.03 a	1.58 ± 0.05 a	1.61 ± 0.03 a	1.50 ± 0.05 a	-	ns	-
Soil C	(%)	2.03 ± 0.42 a	2.92 ± 0.58 ab	5.49 ± 0.89 b	6.31 ± 0.50 b	-	**	-
Soil N	(%)	0.21 ± 0.07 a	0.25 ± 0.08 a	0.41 ± 0.08 a	0.48 ± 0.05 a	-	ns	-
Soil C/N	-	10.9 ± 1.6 a	12.4 ± 1.4 a	13.5 ± 0.6 a	13.2 ± 0.3 a	-	ns	-
Soil temperature at 10 cm	(°C)	26.2 ± 2.8 a	17.3 ± 1.8 b	15.8 ± 1.7 bc	12.8 ± 1.1 c	***	***	ns
Volumetric water content	(v/v)	0.16 ± 0.03 a	0.19 ± 0.03 ab	0.22 ± 0.02 ab	0.23 ± 0.02 b	***	***	***
Soil Exchangeable NO <sub>3</sub> <sup>-</sup> - N	(mg N kg <sup>-1</sup> dry soil)	3.2 ± 0.7 a	3.1 ± 1.0 ab	2.3 ± 0.6 ab	1.5 ± 0.4 b	***	*	ns
Soil Exchangeable NH <sub>4</sub> <sup>+</sup> - N	(mg N kg <sup>-1</sup> dry soil)	5.7 ± 2.1 a	3.2 ± 0.5 a	2.8 ± 0.6 a	3.0 ± 0.5 a	***	ns	ns
Soil Exchangeable N	(mg N kg <sup>-1</sup> dry soil)	8.9 ± 2.7 a	6.3 ± 1.2 a	5.1 ± 0.8 a	4.5 ± 0.7 a	***	ns	ns
Soil respiration	(μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	2.13 ± 0.47 a	1.79 ± 0.25 a	3.47 ± 0.36 b	4.46 ± 0.53 b	***	***	***

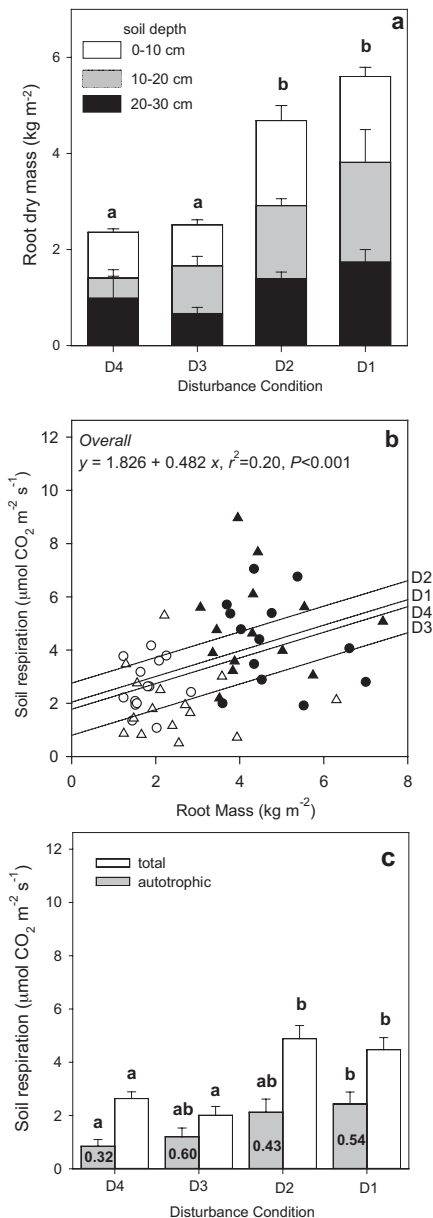
Soil and vegetation variables are presented as the means (± 1 SE, n=3) for each disturbance condition. Soil respiration, soil water content, soil temperature and exchangeable nitrogen are presented as the means (± 1 SE, n=18) for each disturbance condition. The significance of the main effects of the sampling date (S) and disturbance condition (D) or the interaction between the sampling date and disturbance condition (S × D) are shown as the P range; ns: not significant; \*: significant at P≤0.05; \*\*: significant at P≤0.01; \*\*\*: significant at P≤0.001. Separation of the means was determined using a Tukey test when applicable. Different letters indicate significant differences at P≤0.05. The soil texture, bulk density, carbon and nitrogen contents were measured for the 0-10 cm soil depth, while exchangeable N and volumetric water content were measured for the 0-30 cm soil depth.

The physical and chemical properties of soils (0-10 cm depth) differed drastically between disturbance conditions. The most-disturbed D4 condition had a greater proportion of clay (38%) and smaller proportion of sand (25%) than the other disturbance conditions, while all conditions exhibited similar proportions of loam. Although not significantly, the bulk density tended to be greater in D4 ( $1.70 \text{ g cm}^{-3}$ ) compared with D1 ( $1.50 \text{ g cm}^{-3}$ ), while D2 ( $1.58 \text{ g cm}^{-3}$ ) and D3 ( $1.61 \text{ g cm}^{-3}$ ) showed intermediate values between these two extremes. Soil C measured 6.31, 5.49, 2.92 and 2.03% for conditions D1, D2, D3 and D4, respectively. Although not significantly, soil N appeared to be greater in D1 and D2 (0.45%) compared with D3 and D4 (0.23%). The soil C/N ratio did not differ significantly between conditions. Litter biomass also changed drastically across the disturbance gradient and was 8.4-fold greater in D1 ( $110 \text{ g dry matter m}^{-2}$ ) compared with D4 ( $13 \text{ g m}^{-2}$ ). Root biomass to a soil depth of 30 cm was approximately two-fold greater in D1 ( $5.6 \text{ kg dry matter m}^{-2}$ ) compared with D4 ( $2.4 \text{ kg m}^{-2}$ ) (Table 1, Figure 2a).

#### Soil respiration and potential drivers

The values of  $R_s$ ,  $T_s$  and  $\theta_v$  were strongly controlled by the effects of the season ( $F_{5,48} > 25.9$ ,  $P \leq 0.001$ ) and disturbance condition ( $F_{3,48} > 21.5$ ,  $P \leq 0.001$ ), while their interaction was relatively weak ( $F_{15,48} < 4.0$ ,  $P \leq 0.001$ ) to not significant ( $F_{15,48} = 1.3$ ,  $P = 0.25$ ). Disturbance drastically reduced  $R_s$  by half, from  $3.98 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the two least-disturbed conditions (D1, D2) compared with  $1.96 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the two most-disturbed conditions (D3, D4) (Table 1). The values of  $\theta_v$  slightly decreased with disturbance being, on average, 0.23, 0.22, 0.19 and 0.16  $\text{m}^3 \text{ m}^{-3}$  for D1, D2, D3 and D4, respectively (Table 1). The opposite occurred with  $T_s$ , with an average of 12.8, 15.8, 17.3 and 26.2 °C for conditions D1, D2, D3 and D4, respectively.

On a seasonal basis,  $R_s$  changed drastically being generally greater in winter ( $3.41 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and spring ( $3.98 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) than



**Figure 2.** (a) Fine root biomass across disturbance conditions (July 2011), (b) the relationship between soil respiration and root biomass and their ratio (numbers inside grey bars) across disturbance conditions. In (a) and (c), the values are presented as the means ( $\pm 1$  SE) for each disturbance condition. The separation of means was determined using a Tukey test, when applicable. Different letters indicate significant differences at  $P \leq 0.05$ . In (b), the disturbance conditions are: D1; slightly disturbed sclerophyllous forest (closed circles); D2, moderately disturbed sclerophyllous forest (closed triangles); D3, strongly disturbed thorn scrub (open triangles); and D4, most disturbed Acacia caven savanna (open circles). The intercepts of the linear relationship between soil respiration and root biomass (heterotrophic respiration) in (b) were 1.778 (indicated as D4), 0.796 (indicated as D3), 2.758 (indicated as D2), and 2.044 (indicated as D1).

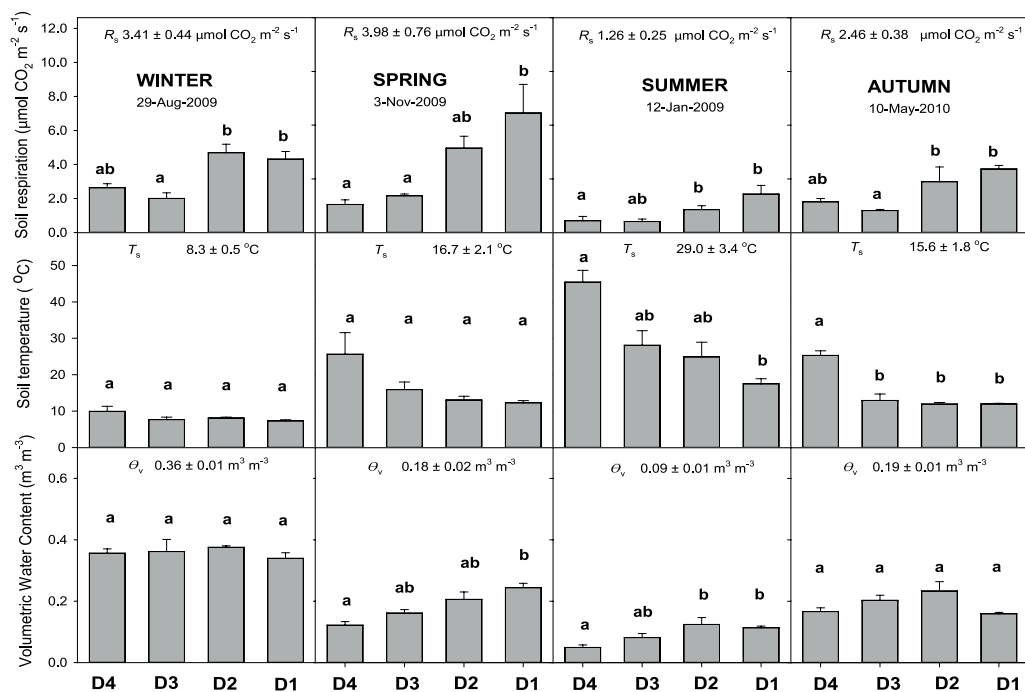
summer ( $1.26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and autumn ( $2.46 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) (Figure 3). The values of  $\theta_v$  also changed drastically with the season mimicking the values of  $R_s$ , being greater in winter ( $0.36 \text{ m}^3 \text{ m}^{-3}$ ) and falling in spring ( $0.18 \text{ m}^3 \text{ m}^{-3}$ ) and summer ( $0.09 \text{ m}^3 \text{ m}^{-3}$ ) to increase again in autumn ( $0.19 \text{ m}^3 \text{ m}^{-3}$ ) (Figure 3). The values of  $T_s$  followed the opposite trend with  $\theta_v$  being lowest in winter ( $8.3 \text{ }^\circ\text{C}$ ), increasing in spring ( $16.7 \text{ }^\circ\text{C}$ ), rising abruptly in summer ( $29.0 \text{ }^\circ\text{C}$ ) and decreasing in autumn ( $15.6 \text{ }^\circ\text{C}$ ) (Figure 3).

The values of soil exchangeable  $\text{NO}_3^- \text{-N}$ ,  $\text{NH}_4^+ \text{-N}$  and their sum were strongly influenced by the season ( $F_{4,40} > 3.9$ ,  $P \leq 0.01$ ) and disturbance condition [but only for  $\text{NO}_3^- \text{-N}$  ( $F_{3,40} = 3.1$ ,  $P = 0.04$ )], while the season  $\times$  disturbance interaction was insignificant ( $F_{12,40} < 0.8$ ,  $P > 0.13$ ). Soil exchangeable N ( $\text{NO}_3^- \text{-N} + \text{NH}_4^+ \text{-N}$ ) was greater in autumn ( $12.7 \text{ mg N kg}^{-1}$  dry soil) and winter ( $10.8 \text{ mg N kg}^{-1}$  dry soil) than

summer ( $6.5 \text{ mg N kg}^{-1}$  dry soil) and spring ( $2.4 \text{ mg N kg}^{-1}$  dry soil). The same seasonal trend was observed for either ammonium or nitrate alone. Soil exchangeable  $\text{NO}_3^- \text{-N}$  was significantly greater under the disturbance condition D4 [dominated by the N-fixing leguminous tree *A. caven* ( $3.21 \text{ mg N kg}^{-1}$  dry soil)] compared with conditions D3 ( $3.07 \text{ mg N kg}^{-1}$  dry soil), D2 ( $2.26 \text{ mg N kg}^{-1}$  dry soil) and D1 ( $1.53 \text{ mg N kg}^{-1}$  dry soil) (Table 1).

### Soil respiration model

Soil respiration increased linearly and significantly with  $\theta_v$  consistently for all disturbance conditions (Overall Model,  $R_s = 1.0462 + 9.5342\theta_v$ ,  $r^2 = 0.25$ ,  $P < 0.001$ ). A covariance analysis showed that adding disturbance conditions to the linear model contributed an additional 21% to explaining the total variance (Overall,  $r^2 = 0.46$ ,  $P \leq 0.001$ ). The



**Figure 3.** Soil respiration, soil temperature and volumetric water content across disturbance conditions for representative sampling dates (4 out of 6). Values are presented as the means ( $\pm 1$  SE,  $n=3$ ) for each disturbance condition and season. The separation of means was determined using a Tukey test when applicable. The disturbance conditions are D1; slightly disturbed sclerophyllous forest; D2, moderately disturbed sclerophyllous forest; D3, strongly disturbed thorn scrub; and D4, most disturbed *Acacia caven* savanna. Different letters indicate significant differences at  $P \leq 0.05$ . The overall values of  $R_s$ ,  $T_s$  and  $\theta_v$  across disturbance conditions are presented as the means ( $\pm 1$  SE,  $n=12$ ) centered in the upper part of each bar graph.



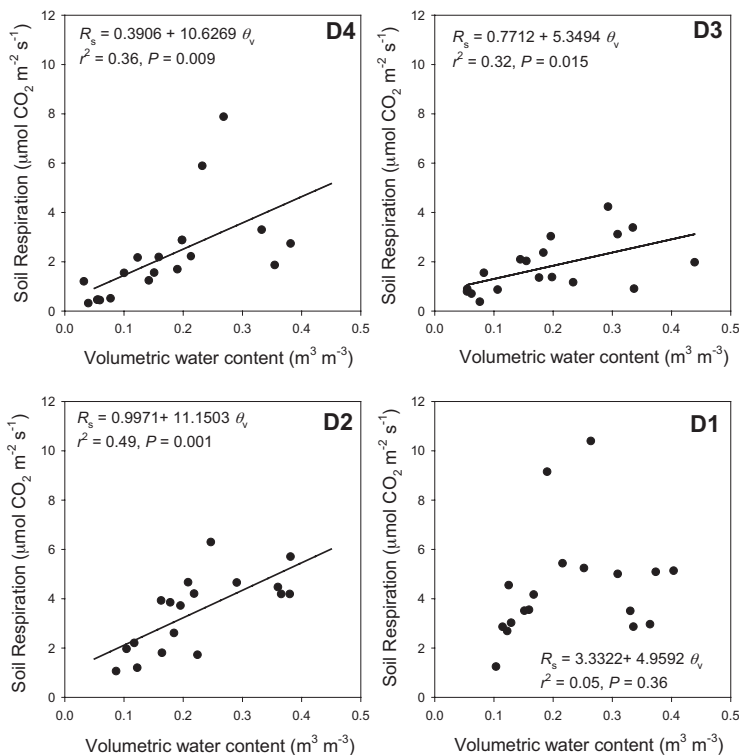
intercepts ( $F_{3,64} = 7.61, P < 0.001$ ) but not the slopes ( $F_{3,64} = 0.84, P = 0.48$ ) of these linear relationships were significantly different between disturbance conditions (Figure 4). It is worth noting that intercepts increased as disturbance receded, *i.e.*, the D4 condition exhibited the smallest intercept (0.391) compared with D3 (0.771), D2 (0.997), and D1 (3.332).

The relationship between  $R_s$  and  $T_s$  depended strongly on  $\theta_v$ . In fact,  $T_s$  and  $\theta_v$  were strongly autocorrelated (Pearson  $r = -0.74, P < 0.001$ ). However, the linear relationship between  $R_s$  and  $\theta_v$  ( $r^2 = 0.46, P < 0.001$ ) was significantly enhanced when  $R_s$  was correlated with the product of  $T_s \times \theta_v$  ( $r^2 = 0.59, P < 0.001$ ). The intercepts ( $F_{3,64} = 14.7, P < 0.001$ ) but not the slopes ( $F_{3,64} = 1.8, P = 0.15$ ) of these linear relationships were significantly influenced by disturbance conditions. Hence, the

same slope (0.914) but different intercepts were used to represent the  $R_s$  versus  $T \times \theta_v$  relationship, *i.e.*,  $R_s = -0.828 + 0.914 T \times \theta_v$  (D4);  $R_s = -0.608 + 0.914 T \times \theta_v$  (D3);  $R_s = 0.739 + 0.914 T \times \theta_v$  (D2);  $R_s = 2.108 + 0.914 T \times \theta_v$  (D1). The value of the intercepts for these linear relationships can be related to disturbance, *i.e.*, the smallest intercept was found for D4 (-0.828), compared with D3 (-0.608), D2 (0.739), and D1 (2.108).

An important implication of this model is that the responsiveness of  $R_s$  to  $T_s$  decreases as the soil  $\theta_v$  diminishes, independent of the disturbance condition. This model is used below to scale  $R_s$  to an annual basis under current climate and climate change scenarios.

Available  $\text{NO}_3^-$ -N (Pearson  $r = -0.15, P = 0.16$ ),  $\text{NH}_4^+$ -N (Pearson  $r = -0.02, P = 0.84$ ) and their



**Figure 4.** Relationship between soil respiration and soil volumetric water content across disturbance conditions. Each point is the average of 10 soil respiration measurements for each plot at each sampling date (3 plots per condition  $\times$  6 sampling dates = 18 points per condition). Disturbance conditions are: D1; slightly disturbed sclerophyllous forest; D2, moderately disturbed sclerophyllous forest; D3, strongly disturbed thorn scrub; and D4, completely disturbed *Acacia caven* savanna.

sum (Pearson  $r = -0.08$ ,  $P = 0.46$ ) were not significantly correlated with  $R_s$  and were therefore not considered in the model, which was exclusively explained by  $\theta_v$ ,  $T_s$  and disturbance conditions.

### *Separating autotrophic and heterotrophic respiration*

The values of  $R_s$  increased with root biomass ( $W_r$ ,  $\text{kg m}^{-2}$ ) to 30 cm of soil depth ( $R_s = 1.826 + 0.482 W_r$ ,  $r^2 = 0.20$ ,  $P < 0.001$ ), and this relationship was significantly enhanced when we accounted for disturbance conditions ( $r^2 = 0.42$ ,  $P < 0.001$ ) (Figure 2b). The intercepts ( $F_{3,48} = 6.8$ ,  $P < 0.001$ ) but not the slopes ( $F_{3,52} = 0.3$ ,  $P = 0.85$ ) of the linear relationship between  $R_s$  and  $W_r$  were significantly influenced by disturbance conditions, *i.e.*, 2.044, 2.758, 0.796 and 1.778  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for conditions D1, D2, D3 and D4, respectively (Figure 2b). The fitted intercepts (assumed to be heterotrophic respiration) enabled us to determine the autotrophic respiration based on the total respiration.

Autotrophic (root) respiration was found to be three-fold greater in D1 ( $2.46 \pm 0.44 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) compared with D4 ( $0.82 \pm 0.25 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), while D2 ( $2.15 \pm 0.51 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and D3 ( $1.20 \pm 0.32 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) exhibited intermediate values between these two extremes (Figure 2c). The ratio of the autotrophic to total soil respiration was smaller in condition D4 (0.32) compared with D3 (0.60), D2 (0.43), and D1 (0.54), with an overall average ( $\pm 1 \text{ SD}$ ) for the last three values of  $0.48 \pm 0.12$ .

### *Annual values of soil respiration*

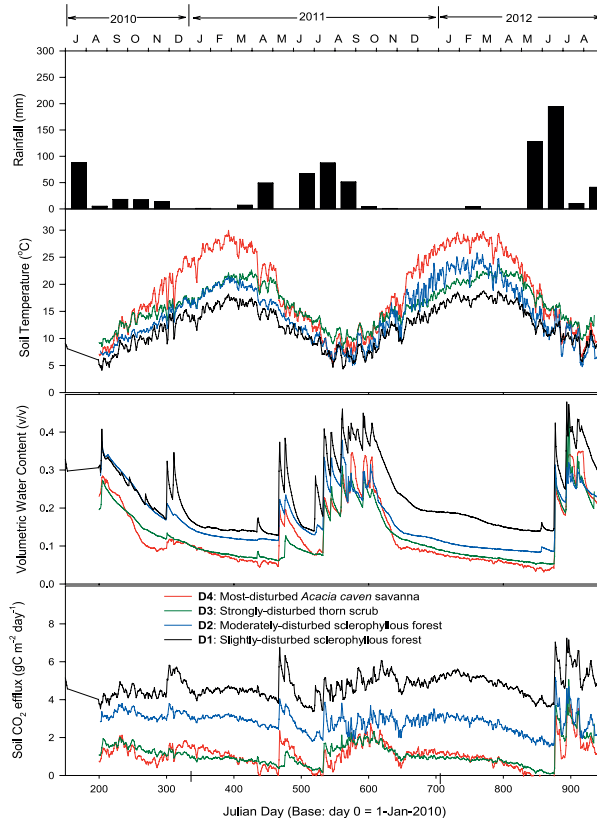
The modeled daily values of  $R_s$  closely followed the values of  $\theta_v$  but also the  $T_s$  series (Figure 5). On an annual basis, the values of  $R_s$  were 4.4-fold greater in condition D1 ( $1,735 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) compared with D4 ( $392 \text{ g C m}^{-2} \text{ yr}^{-1}$ ), while D3 ( $420 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) and D2 ( $1,073 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) showed intermediate values between these two extremes (Table 2).

Under a climate change scenario predicting a 40% decrease in rainfall and a 4 °C increase in air temperature by the year 2100 (Table 2), we found that the annual  $R_s$  would be reduced by 28% on average compared with the current climate and that the reduction would be greater under more disturbed conditions (*i.e.*, 11% in D1 compared with 45% in D4). Therefore, the slightly disturbed condition proved to be more resistant to the climate change scenario.

## **Discussion**

The modeled annual values of  $R_s$  ranged from 371 to 1,803  $\text{g C m}^{-2} \text{ yr}^{-1}$  (Table 2). On average ( $\pm 1 \text{ SD}$ ), the values for this study ( $905 \pm 591 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) were 27% higher than those reported for Mediterranean woodlands and shrubs ( $713 \pm 317 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) by Luo and Zhou (2006) but had confidence intervals that were largely overlapping. The annual values of  $R_s$  were 4.4-fold greater in the least-disturbed D1 condition compared with the most-disturbed D4 condition. Comparing the least- versus the most-disturbed conditions, disturbance induced a reduction in  $R_s$  arguably as a result of (1) diminished organic substrates in the litter layer and in the soil, which in turn reduced microbial, micro- and meso-fauna activity (heterotrophic respiration); (2) reduced root biomass and activity and C exudates below ground (autotrophic respiration); and (3) reduced soil water content in the most disturbed conditions, particularly in the dry-hot season.

In temperate forests, approximately 50% of  $R_s$  is heterotrophic respiration ( $R_h$ ) generated by the activity of microbial populations that decompose plant debris and soil organic matter (Hanson *et al.* 2000; Rey *et al.*, 2011; Saiz *et al.*, 2007; Fuentes *et al.*, 2013). Several studies have demonstrated that the absence of litter-humus layers can decrease  $R_s$  in the order of 25 to 30% (*e.g.*, Luo and Zhou, 2006; Saiz *et al.*, 2007). We found a nine-fold difference in litter biomass, 110  $\text{g m}^{-2}$  vs. 13  $\text{g m}^{-2}$ , which likely contributed to the two-fold differ-



**Figure 5.** Soil temperature, soil volumetric water content and modeled soil respiration across disturbance conditions for the period of July 2010-July 2012. Disturbance conditions are: D1: slightly disturbed sclerophyllous forest (black line), D2: moderately disturbed sclerophyllous forest (blue line), D3: strongly disturbed thorn scrub (green line), and D4: most disturbed *Acacia caven* savanna (red line).

**Table 2.** Modeled soil respiration for the periods from July 1, 2010-June 31, 2011 (year 1) and July 1, 2011-June 31, 2012 (year 2) across disturbance conditions in the National Reserve Roblería del Cobre de Loncha in Central Chile.

Climate Scenarios	Year	Modeled soil respiration per year (g C m <sup>-2</sup> yr <sup>-1</sup> )			
		Most disturbed <i>A. caven</i> savanna (D1)	Strongly disturbed thorn scrub (D2)	Moderately disturbed sclerophyllous forest (D3)	Slightly disturbed sclerophyllous forest (D4)
Current Climate	1	371	384	1,111	1,667
	2	414	455	1,034	1,803
(a)	Mean	392	420	1,073	1,735
Climate Change (year 2100)	1	199	232	924	1,494
	2	236	286	855	1,606
(b)	Mean	218	259	889	1,550
(b)/(a) × 100		55%	62%	83%	89%

A climate change scenario for year 2100 predicting a 40% decrease in rainfall (simulated as a 40% decrease in volumetric water content) and a 4 °C increase in air temperature (simulated as a 4 °C increase in soil temperature) is also presented. Averages of soil respiration for a current (a) and a climate change scenario (b) and their ratio (b/a) are presented.

ence in  $R_s$  (4.46 vs. 2.13  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) when comparing the least – and the most-disturbed conditions (Table 1). Furthermore, a three-fold C concentration difference in the upper 10 cm (6.3% vs. 2.0%) between extremes in disturbance may as well have substantially contributed to differences in  $R_s$ . Soil microorganisms consume a range of substrates, from simple sugars contained in fresh residues and root exudates to complex humic acids in SOM, and because respiratory  $\text{CO}_2$  release is linearly related to substrate availability (Luo and Zhou, 2006), it could be expected that soils richer in C may also exhibit greater microbial activity and hence soil respiration as occurred in our study.

The other ~50% of  $R_s$  is usually derived from the metabolic activity of the rhizosphere; this is termed autotrophic respiration ( $R_a$ ) (Ryan and Law, 2005). Soil respiration increased as disturbance receded, and this can be partly attributed to heterotrophic respiration driven by soil and litter C substrates. However, we also found that  $R_s$  was strongly correlated with root biomass; root biomass increased as disturbance receded and therefore soil respiration was partly driven by root activity. It is now well accepted that the substrate supply from canopy photosynthesis exerts a strong effect on root and microbial respiration (Franck *et al.*, 2011; Högberg *et al.*, 2001; Luo and Zhou, 2006). Large differences in the leaf area index across disturbance conditions suggest that photosynthesis (and its integral, gross primary productivity) decreased in the series D1, D2, D3 and D4, which may have driven root activity and soil respiration in our study.

Temporal variations are known to be greater than spatial variations in  $R_s$  in natural ecosystems (Rey *et al.*, 2011; Zhang *et al.*, 2010), and this appears to be mostly explained by the temporal heterogeneity in soil water content in Mediterranean climate ecosystems (Reichstein *et al.*, 2002). A correlation analysis confirmed that  $R_s$  was primarily driven by soil water content in our study, which appears to be a frequent pattern in arid and semiarid environments (Jia *et al.*, 2006; Rey *et al.*, 2011; Perez-Quezada *et al.*, 2012).

Land degradation appears to commonly decrease soil water content in dry periods in semiarid environments (Rey *et al.*, 2011); this appears to be partly explained by a lower canopy cover in more disturbed conditions that favor topsoil water loss, particularly during the dry- hot seasons (Breshears *et al.*, 1998; Raz-Yaseef *et al.*, 2012). The less disturbed forest ecosystems in our study also exhibited a protective litter layer that may decrease evaporative water loss, increase infiltration and decrease runoff, which more effectively conserves water in the soil.

Soil respiration was weakly but significantly correlated with soil temperature, and this appears to be common in semiarid environments (Rey *et al.*, 2011; Perez-Quezada *et al.*, 2012). Given that soil water is usually the limiting resource in semiarid environments, several authors argue that the response of soil respiration to soil temperature must depend on soil water availability (Jia *et al.*, 2006; Rey *et al.*, 2011). Recently, Zhang *et al.* (2010) found that soil water content enhances the response of soil respiration to temperature, as has also been observed in irrigated agro-ecosystems in arid zones (Franck *et al.*, 2011). Our results confirm these findings. Using our fitted model of  $R_s$  to  $\theta_v$  and  $T_s$ , we can deduce that for given  $\theta_v$  values of 0.3, 0.2 and 0.1  $\text{m}^3 \text{ m}^{-3}$ , the slopes of the  $R_s$  to  $T_s$  relationship would be 0.274, 0.183 and 0.091, respectively.

More N was available at the most disturbed condition under the N-fixing legume tree *A. caven*, which likely prevented us from observing a significant relationship between soil respiration and available N. Odum (1969) proposed that, in more disturbed conditions, the inorganic nutrients tend to be extrabiotic as opposed to intrabiotic in the less disturbed conditions; this corroborates the results of our study. N availability can play a key role in organic matter decomposition, microbial activity and potentially in a greater abundance of invasive species, which we observed in the most-disturbed condition. Plant litter decomposition is influenced by several factors, including its C/N ratio, the presence of

recalcitrant compounds, and soil physical (*e.g.*, particle size distribution) and chemical properties. However, soil respiration was unaffected by N availability, which was likely due to water rather than N driving most biological processes in these ecosystems.

One of the key questions regarding climate change is whether global warming will promote positive feedback between the global carbon cycle and the climate system that would, in turn, enhance global warming (Luo and Zhou, 2006). Current global estimates of soil respiration are in the range of  $98 \pm 12 \text{ Pg yr}^{-1}$  and are predicted to increase annually by  $\sim 0.1 \text{ Pg}$ ; this increase is likely associated with air temperature increases (Bond–Lamberty and Thomson, 2010). CONAMA (2006) predicts temperature increases of up to  $4 \text{ }^\circ\text{C}$  and rainfall decrease of up to 40% in Central Chile by the year 2100. Under this scenario, we predict that soil respiration will be reduced, not enhanced, in the studied ecosystems, although the net change will depend on the effect of temperature increase and rainfall decrease on other components of the carbon balance. This surprising result is primarily explained by soil water content controlling soil respiration to a greater extent than soil temperature. Annual soil respiration was reduced under a climate change scenario, and it was more pronounced in the most disturbed ecosystems, *i.e.*, 11% in the least-disturbed D1 compared with 45% in the most-disturbed D4 conditions. Soil water content was markedly higher in the least-disturbed compared with the most-disturbed conditions under the current climate scenario; this would also likely occur under a potential climate change scenario. Therefore, less-disturbed ecosystems would be less affected by climate change than more-disturbed ecosystems due to their superior water conservation. Because better-conserved sclerophyllous ecosystems may better resist climate change, the restoration of disturbed sclerophyllous ecosystems may contribute to ameliorating the negative effects of climate change. We are

aware that the estimation of  $R_s$  under a climate change scenario was performed using models of soil respiration that were developed using a current climate scenario. This scenario neglected the process of acclimation and is thus speculative, although we believe the direction of the change to be correct.

In conclusion, in the studied shrub and sclerophyllous ecosystems in Central Chile, disturbances reduced heterotrophic respiration by decreasing litter C and soil C and also decreased autotrophic respiration by reducing root activity. Disturbances decreased soil water content, particularly in the dry-hot season. Under a climate change scenario, annual soil respiration is expected to decrease, an effect that would be further enhanced by an anthropogenic disturbance. This effect further justifies the restoration of these damaged ecosystems.

### Acknowledgements

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### Resumen

**H.E. Bown, J.P. Fuentes, J.F. Perez-Quezada y N. Franck. 2014. Respiración de suelos en un gradiente de perturbaciones en ecosistemas esclerófilos en Chile Central. Cien. Inv. Agr. 41(1): 89-106.** Los matorrales y bosques esclerófilos son la formación vegetacional dominante en Chile Central, existiendo una larga data de degradación producto del fuego, cultivos, extracción de leña y pastoreo. El objetivo del estudio fue comparar la respiración de suelos y los factores que la controlan a lo largo de un gradiente de perturbaciones en ecosistemas esclerófilos en la Reserva Nacional Roblería del Cobre de Loncha en Chile Central. En bajos de ladera en una exposición norte se identificaron cuatro grados de perturbación: bosques esclerófilos que fueron levemente- (D1) y moderadamente perturbados (D2), matorral espinoso fuertemente perturbado (D3) y sabana de *A. caven* completamente perturbada (D4). Se establecieron doce parcelas de 25×25 m (625 m<sup>2</sup>) distribuidas equitativamente en D1, D2, D3 and D4. La respiración de suelos ( $R_s$ ), temperatura de suelos ( $T_s$ ), contenido volumétrico de agua en el suelo ( $\theta_v$ ) y nitrógeno intercambiable ( $N_s$ ) fueron medidos en todas las parcelas en seis fechas entre Agosto de 2009 y Mayo de 2010. Adicionalmente,  $T_s$  y  $\theta_v$  fueron registrados de forma continua, desde Julio de 2010 hasta Agosto de 2012 (cada 30 minutos), en una parcela por nivel de perturbación (*i.e.* 4 de 12 parcelas). Los valores de  $R_s$  aumentaron linealmente con  $\theta_v$  con similares pendientes pero diferentes interceptos que aumentaron en la medida que las perturbaciones disminuyeron. Una vez contabilizado el contenido de agua en el suelo,  $R_s$  aumentó con  $T_s$  con la misma pendiente pero con un intercepto que depende del nivel de perturbación. Adicionalmente la respuesta de  $R_s$  a  $T_s$  fue más pronunciada en la medida que  $\theta_v$  aumentó. Los valores de  $N_s$  no se correlacionaron con  $R_s$ . Los valores acumulados de  $R_s$  fueron 4.4 mayores en D1 (1735 g C m<sup>-2</sup> yr<sup>-1</sup>) comparado con D4 (392 g C m<sup>-2</sup> yr<sup>-1</sup>). Las perturbaciones presumiblemente disminuyeron  $R_s$  mediado por reducciones en la capa de hojarasca, materia orgánica del suelo, biomasa de raíces y contenido de agua particularmente en la temporada seca y cálida. Bajo un escenario de cambio climático que implica una disminución de 40% de las precipitaciones y un aumento de 4°C en la temperatura del aire para el año 2100, encontramos que el  $R_s$  anual se reduciría en promedio en 28% comparado con el clima actual, con esta reducción siendo más pronunciada en las condiciones más perturbadas sugiriendo que las condiciones menos perturbadas serían más resistentes al cambio climático justificando aún más la restauración de estos ecosistemas.

**Palabras clave:** Bosques esclerófilos, gradiente de perturbaciones, matorrales espinosos, respiración de suelos, sabana de *Acacia caven*.

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