

SOIL RESPIRATION BEHAVIOUR IN A MEDITERRANEAN ALEPPO PINE FOREST IN NORTH TUNISIA

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Abstract. Little is known about the relationship between soil respiration and biophysical factors in the Tunisian Aleppo pine forest. We conducted our studies in two adjacent forests in Djebel Mansour region with the same micrometeorological conditions, but they differed in soil properties. The main goal of this research was to quantify soil respiration and its seasonal variations under two different soil characteristics. Soil respiration measurements were performed between May 2008 and July 2009. The magnitude of the soil respiration varied from 0.80 to 6.65 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in Sidi Ouedet forest (deep soil) and from 0.60 to 5.90 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in Oued El kbir forest (shallow soil). Results showed that soil respiration exhibited a same seasonal pattern in both sites, and it was controlled mainly by the soil moisture. The highest rates of soil respiration were observed in autumn and in spring and the lowest in summer, coinciding with the drought period. In autumn, high rates of soil respiration were observed immediately after rainfall events. Hence, annual soil respiration was higher in the deep soil than in the shallow soil (870.4 g C $\text{m}^{-2} \text{y}^{-1}$ vs 492 g C $\text{m}^{-2} \text{y}^{-1}$). As such, soil properties (depth, texture and structure) may indirectly drive soil respiration by controlling the soil moisture and site productivity through litter input.

Keywords: *soil respiration, soil moisture, Mediterranean Aleppo pine, soil properties*

Introduction

Soil CO₂ flux is a major component of the global carbon cycle (Houghton, 1995) and represents the second largest carbon flux in forest ecosystems (Raich et Schlesinger, 1992). It is known to be highly sensitive to different environmental factors, especially soil temperature and moisture (Joffre et al., 2003; Reichstein et al., 2003), and sensitive to future climate change (Cox et al., 2000; Raich et al., 2002). Thus, it is important to understand which environmental factors control soil respiration, and how these factors affect CO₂ emissions from soils, especially in semiarid and dry ecosystems, where water availability and primary production are drought-limited for a considerable period of time (Almagro et al., 2009).

At the smaller scale, soil respiration (SR) was very sensitive to soil temperature and soil moisture (Fang and Moncrieff, 2001). Soil temperature was recognized as

the most important environmental factor controlling SR because it affects the respiratory enzymes of both roots and soil microbial biomass (Xu et al., 2011). However, it has been shown that in Mediterranean-climate ecosystems, which are subjected to prolonged summer droughts, soil moisture is the critical environmental determinant limiting the response to temperature (Reichstein et al., 2002; Rey et al., 2002, 2005; Jarvis et al., 2007). Very low soil moisture has been shown to diminish the temperature response of SR (Welsch and Hornberger, 2004) due to metabolic drought stress (Orchard and Cook, 1983). In these ecosystems, rainfall causes pulses of soil respiration and ecosystem respiration, which may affect the annual carbon budget (Xu et al., 2004; Curiel Yuste et al., 2003).

Annual carbon soil efflux correlates directly with gross primary productivity (GPP) (Raich and Tufekciogul, 2000; Janssens et al., 2001). As such, underground root and microbial respiration are greatly promoted by aboveground photosynthesis (Kuzakov and Gavrichkova, 2010). Many researchers (Li et al., 2004; Atarashi-Andoh et al., 2012) estimated the contribution of aboveground litter to total soil CO₂ efflux. Zak et al. (1994) reported that plants control heterotrophic activity via their carbon supply.

Nevertheless, others researchers highlighted the role of soil properties on soil CO₂ efflux. It has been reported that topsoil organic carbon (SOC) has a strong influence on soil carbon dynamics (Ryan and Law, 2005; Moyano et al., 2012). Bahn et al. (2008) and Chen et al. (2010) reported that respiration rates among major biomes were significantly related to SOC. Likewise, soil properties, which influence dynamics of soil moisture and site productivity, may play an important role in explaining spatial respiration (Sotta et al., 2006), especially in arid and semi-arid regions.

Aleppo pine (*Pinus halepensis* Mill.) is the most important forest tree species in North Africa especially in Algeria and Tunisia (Ben Touati and Bariteau, 2005). There is a general interest in this species in the Mediterranean basin due to the importance of its ecological and protective characteristics, such as their wide distribution in addition to soil protection in areas where other species could not survive or carbon sink properties even in areas with low site quality (Montero et al., 2001). Indeed, the Aleppo pine habitat is broadly characterized by warm and cold winters, in addition to dry summers with periods of prolonged drought (Ayari and Khouja, 2014). This species is very important for both the economic role, such as timber and seed production promoting local employment, and for the ecological value, such as the high resilience and resistance (FAO, 2001, Sghaier and Ammari, 2012).

In Tunisia, the Aleppo pine forests cover 361,221 ha, representing more than 53.19% of Tunisian woodlands (DGF, 2010). In contrast with the abundant literature on reproductive characteristics of Aleppo pine in Tunisia (Ayari et al., 2011a; Ayari et al., 2011b; Ayari et al., 2012; Ayari and Khouja, 2014), soil respiration, carbon dynamics and soil properties under this ecosystem have been relatively neglected. The goals of this study were (1) to study seasonal pattern of SR, (2) to quantify annual SR in a shallow soil (site 1) and a deep soil (site 2) in the Djebel Mansour forest, and (3) to identify the main source of its spatial variability.

Materials and methods

Study area

The study was conducted in the Djebel Mansour forest of the semi-arid region of North-East Tunisia (El Fahs, Zhaghouan, 36.23N, 9.8'E). The total area of the Djebel Mansour forest is 5,800 ha, covered mostly by Aleppo pine (*P. halepensis*). The forest is divided in two parts. The first is the Djebel Mansour 1 forest (EW) extended on a rocky massif and the second is the Djebel Mansour 2 forest (NE- SW) extended on a moderately stony massif.

In these areas, two sites were selected to perform this study: one (site 1: Oued El kbir), in Djebel Mansour 1, was developed on a shallow soil and the other (site 2: Sidi Ouedet), in Djebel Mansour 2, on a deep soil. In the Djebel Mansour 1 forest, the overstorey was dominated by *Pinus halepensis* L. and the major understorey shrubs were the rosemary (*Rosmarinus officinalis* L.), the phillyrea (*Phillyrea latifolia* L.) and the mastic tree (*Pistacia lentiscus* L.). The vegetation of Djebel Mansour 2 is largely dominated by *Pinus halepensis* L. and by a sparse shrubby < 2 m layer with prickly juniper (*Juniperus oxycedrus*). The two sites were located approximately 15 km apart. Despite these differences, the climatic conditions did not vary between the sampled sites.

The study region, in the upper semiarid zone, has a typical Mediterranean climate with two distinct wet and dry seasons. Average annual precipitation and air temperature for the region were 403 mm and 18.8 °C, respectively (40 years average, Zaghouan Meteorological Service). The soil types, in general, were represented by carbonate soils (calcic-magnesian), regularly cover calcareous parent materials (Mtimet, 1999).

Experimental design

In spring 2007, we selected a permanent stand (25 m × 25 m) in each forest site. The vegetation distribution was mainly patchy, with different proportions of plant cover at each stand. Density, mean diameter at breast height (DBH) and height (H) were performed for each stand using data collected during the tree survey. A summary of the site characteristics is given in *Table 1*.

Soil and vegetation ecophysiological measurements

Soil respiration was measured in situ with a portable closed dynamic chamber (SRC model, PP-Systems Ltd, Hitchin, UK) connected to an infrared gas analyzer (CIRAS 1, PPSystems Ltd). To get a more accurate estimation, eight replicates (2 measurements × 4 permanent plots) of soil respiration were measured in each stand during each sampling campaign. Soil respiration measurements were taken between 9:00 and 12:00 AM to avoid diurnal fluctuation from May 2008 to July 2009. Simultaneously with soil respiration, soil temperature (T) and soil water content (SWC) were measured at 0–10 cm depth at each sampling point. Soil temperature was measured with a soil digital thermometer and soil water content was determined gravimetrically by oven-drying the soil at 105°C for 24h.

Ten permanent quadrats of 25 cm × 25 cm were sampled at each site in 2008 to estimate the annual litterfall. The litter was, then, oven-dried at 70°C to a constant mass. Leaf area index (LAI) was measured every meter along two diagonal transects per stand with a Li-Cor LAI-2000 (Licor Inc., Lincoln, NE, USA) in Mai 2008.

Table 1. Characteristics of study sites in Djebel Mansour Aleppo pine forest.

	Oued Kebir (site 1)	Sidi Ouedet (site 2)
Main characteristics		
Main Species	<i>Pinus halepensis</i>	<i>Pinus halepensis</i>
Longitude	E 009.81358033°	E 009.78231250°
Latitude	N 36.23529550	N 36.224968633
Elevation (m)	515,38	615,24
Annual temperature (°C)	18.8	18.8
Annual precipitation (mm)	403	403
Stand characteristics		
Leaf area index	1.04	1.59
Tree density (tree ha ⁻¹)	2448	720
Tree height (m)	4.4	10.3
Diameters at breast height (cm)	7.7	21.47
Soil characteristics		
Soil depth (cm)	40	70
Soil texture	Silt loam	Clay loam
Soil holding capacity (mm)	41.04	77.55

Modelling soil respiration

Soil respiration was estimated using the Expo model proposed by Joffre et al. (2003) driven by year-round daily-interval data of soil temperature and relative water content. Relative soil water content (RWC) is expressed as soil water content relative to the soil water content at field capacity (RWC):

$$RWC = SWC / SWC_{FC} \quad (\text{Eq.1})$$

where SWC (mm) is the actual soil water content, SWC_{FC} is the soil water content at field capacity.

Soil respiration data were analyzed using a nonlinear regression model as follows:

$$SR = SR_{ref} \times RWC \times e^{((b \text{ RWC}) + c) (T - T_{ref})/10} \quad (\text{Eq.2})$$

with T = soil temperature at 10-cm depth, SR_{ref} being the respiration under standard conditions (at T_{ref} and no limiting soil moisture), T_{ref} was fixed at 0°C. b and c fitted parameters.

Soil water content and soil temperature models were used to study the seasonal pattern and to quantify the annual soil respiration in each site. Soil water content was estimated following to Mouillot et al. (2001). Soil temperature was simulated using simple regression:

$$T = \alpha T_{air} + \beta \quad (\text{Eq.3})$$

We estimated α and β to be 0.91 and 2.58, respectively. These models have been validated in the same period by Zribi et al. (2015) in a cork oak forest in Tunisia. The Daily meteorological data were provided from the weather station at the Oued Elkbir (Elfahs, Zaghuan).

Soil sampling and analysis

Pits were dug at each site to collect samples for physical and chemical analyses. The particle-size distribution was carried out by the International Pipette Method (Burt, 2004), and the percentage of coarse fragments was performed by sieving. Organic carbon was determined according to Anne (1945). A correction factor of 1.32 was used to account for incomplete oxidation of organic C (Nelson and Sommers, 1996). Total organic nitrogen was measured by the Kjeldhal method according to Bremner and Mulvaney (1982). To determine soil bulk density, five pseudo replicates of soil samples were collected using 100 cm³ stainless steel rings at each soil profile and each soil layer. The soil water holding capacity was measured using a pressure plate (Walker and Skogerboe, 1987). The amount of SOC (kg m⁻²) stored in each layer was estimated using the following equation (Broos and Baldock, 2008):

$$\text{SOC} = (\text{D}) \times (\text{BD}) \times (\text{OC}) \times (100 - \text{CF}) \times 0.001 \quad (\text{Eq.4})$$

where D is depth (cm), BD is bulk density (g/cm³), O is organic carbon content (%), CF is coarse fragment content (%) and 0.001 is a unit conversion factor.

Statistical analyses

The SIGMASTAT 3.0 software (Systat Software Inc., San Jose, CA, USA) was used to perform statistical analyses. For each variable measured, the data were analyzed by one-way ANOVA using Student-Neuman-Keuls test ($p < 0.05$) to make a comparison between sites. Repeated measures ANOVA was used to evaluate site effects on seasonal variations of relative water content, soil temperature, and respiration rate. All the results further indicate mean values and their standard error (\pm SE).

Results

Site characteristics and soil properties

Given the proximity of the study sites, total annual rainfall and temperature were roughly the same. Tree density, diameter at breast height (DBH), tree height (H) and annual litterfall (*Tables 1 and 2*) were significantly higher in the deep soil (Sidi Ouedet forest, site 2) compared to the shallow soil (Oued El kbir forest, site 1). The tree densities were 2448 tree ha⁻¹ in the site 1 and 720 tree ha⁻¹ in the site 2. Mean tree heights were 7.4 m and 10.3 m and mean diameters at breast height were 7.4 cm and 21.47 cm in the site 1 and site 2, respectively. Interestingly, the highest organic matter, water holding capacity and C/N were registered in the site 2 with deep soil (*Table 2*).

Table 2. Main physical and chemical properties of soil (0-10 cm) and annual litterfall in Djebel Mansour forest.

	Oued Kebir (site 1)	Sidi Ouedet (site 2)	
<i>Sand (%)</i>	52.15	45.95	***
<i>Clay (%)</i>	10.84	16.68	***
<i>Silt (%)</i>	37.01	37.37	***
<i>Coarse (%)</i>	64.94 ± 2.41	35.19 ± 2.09	***
<i>WHC (mm)</i>	9.9±1.07	11.4±2.15	***
<i>Organic matter (%)</i>	3.6 ± 0.11	11.17 ± 0.07	***
<i>C/N</i>	5.20 ± 0.15	9.13 ± 0.17	***
<i>SOC(kg m⁻²)</i>	1.04 ± 0.10	4.53 ± 0.40	***
Annual Litterfall (g m⁻²)	416.93 ± 34.47	854.82 ± 76.13	***

Means and standard errors for n = 5. Values were significantly different (p<0.05)

Seasonal variation in relative water content and soil temperature

Soil moisture content differed significantly between the two sites and sampling dates (p<0.05) (Fig. 1). Overall, site 2 had a significantly higher RWC than site 1. From winter to mid spring (April), the soil was completely recharged because of continuous rainfall. In May 2008, the RWC was 0.37 in the shallower site (site1) and 0.45 in the deeper site (site 2). From June, the water was depleted and values of RWC fell to 0.19 in the site 1 and 0.32 in the site 2. A similar depletion was seen in 2009 in the same period. During the drought period, which lasted from June to August, there was no rainfall until October when it started again intensively; thus leading to a complete recharge of the soil (Fig. 1).

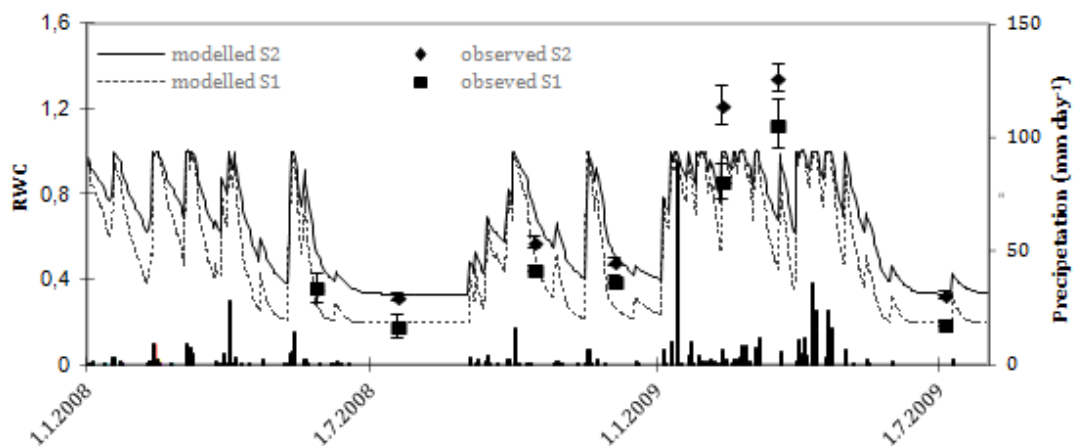


Figure 1. Daily rainfall, modelled (dashed line corresponds to S1 and solid line to S2) and observed (square represents S1 and circle S2) relative soil water content (RWC) in the upper soil layer (0–10 cm depth) during the 2008–2009 period (Vertical bars indicate ± SD).

Soil temperature differed significantly between sampling dates (p<0.05) but showed a similar trend for both sites without significant differences between sites (Fig. 2). It

increased steadily until midsummer to a maximum mean of 26.5°C and 27 °C in July 2008 and 2009, respectively. Then, it gradually fell through autumn and winter to reach the lowest values of ≈ 11 in February 2008 in the two sites.

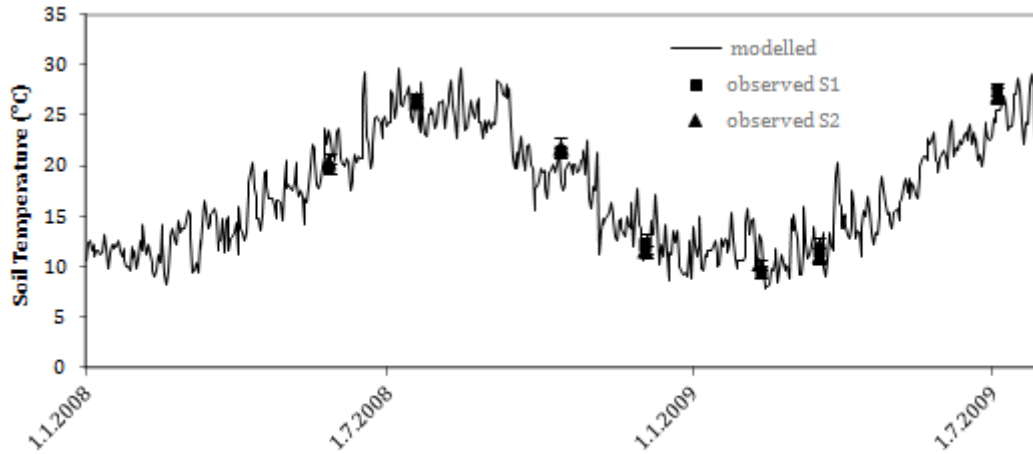


Figure 2. Time course of modelled (full line) and observed (square corresponds to S1 and circle to S2) daily soil temperature at 10 cm depth during the 2008–2009 period (Vertical bars indicate \pm SD).

Annual soil respiration and its seasonal pattern

The total annual soil respiration rates over the study period were 492g C m⁻² y⁻¹ in the shallower site and 870.4 g C m⁻² y⁻¹ in the deeper site. The seasonal pattern of soil respiration was similar in both sites. It increased quite steadily from a winter minimum to reach an initial peak in spring (April). After a fall in summer, soil respiration increased to a second seasonal peak in autumn (October) when soil moisture was recovered and soil temperature was still favorable (Fig. 2). Soil respiration varied significantly between both sites ($p < 0.05$). Rates ranged from 0.60 to 5.90 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the site 1 and from 0.80 to 6.65 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the site 2 (Fig. 3).

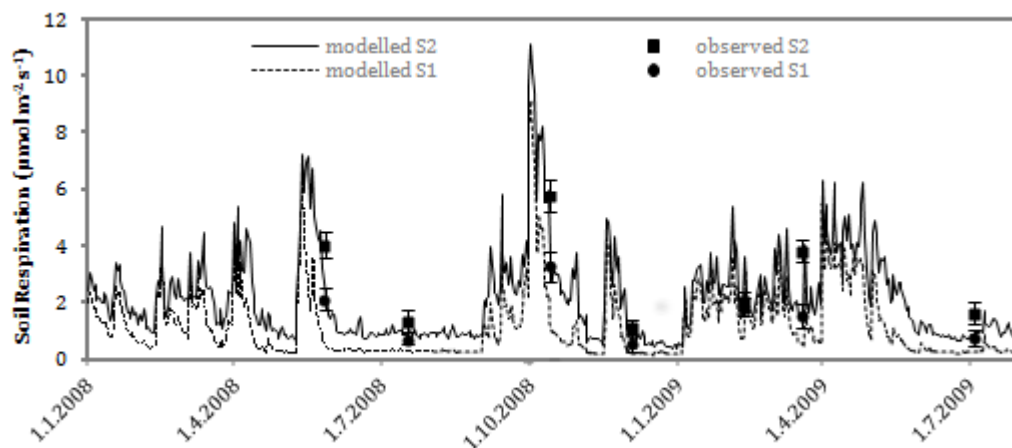


Figure 3. Time course of modelled (dashed line corresponds to S1 and solid line to S2) and observed (square represents S1 and circle S2) soil respiration in the site 1 and site 2 during the 2008–2009 period (Vertical bars indicate \pm SD).

Discussion

Annual soil respiration rate

The Djebel Mansour Aleppo pine forest has a typical Mediterranean climate characterized by extended periods of summer drought with scattered precipitation events. The total annual carbon losses through soil respiration were $492 \text{ C m}^{-2} \text{ y}^{-1}$ in the shallow soil (site 1) and $870.4 \text{ g C m}^{-2} \text{ y}^{-1}$ in the deep soil (site 2). These rates were similar to the range cited by Raich and Schlesinger (1992) for Mediterranean forests. Furthermore, the annual respiration rates were similar to those of a young pine forest in Oregon (Irvine and Law, 2002; $427\text{--}519 \text{ C m}^{-2} \text{ y}^{-1}$), in mixed conifer forest in California (Ma et al., 2005; $660 \text{ C m}^{-2} \text{ y}^{-1}$), in a ponderosa pine forest in the Sierra Nevada (Tang et al., 2005; $915 \text{ C m}^{-2} \text{ y}^{-1}$) and in Aleppo pine forests in Spain (Almagro et al., 2009; $766 \text{ C m}^{-2} \text{ y}^{-1}$).

Seasonal variation of soil respiration

In spring, when both soil temperature and soil water content were moderate, soil respiration reached its seasonal peak. Peaks in late spring (*Fig. 2*) are probably of both autotrophic and heterotrophic origin. During the growing season, Aleppo pine allocates a great proportion of the photosynthetic assimilate to growth (Sanz-Pérez et al., 2009). Root respiration and microbial decomposition had a high value (Tang et al., 2005), corresponding to a peak of total soil respiration.

In summer, the decrease in SR is in accordance with the onset of the dry period of Mediterranean climate when the Aleppo pine exhibits slow growth (Monnier et al., 2012; Sanz-Pérez et al., 2009). Water stress would limit photosynthesis and reduce current carbon assimilation (Sanz-Pérez et al., 2009; Law et al., 1999) resulting in a decrease in root respiration (Höberg et al., 2001). Earlier published reports (Joffre et al., 2003; Asensio et al., 2007; Almagro et al., 2009; Matías et al., 2012) showed that SR covaried mainly with water availability during dry months of the year.

In autumn, high rainfalls, which favor the development of fine roots, are coupled with a high root (Rey et al., 2011) and microbial (Xu et al., 2004) activity. Early autumn peak can be attributed to the mineralization of eagerly degradable compounds of microbial or plant litter origin accumulated on the soil surface during the dry months (Rey et al., 2002; Huxman et al., 2004). In the same context, Carbone et al. (2011) in a central California pine forest and Matteucci et al. (2015) in the San Rossore conifer forest reported that autotrophic soil respiration peaks after the precipitation events.

In winter, soil respiration reached the lowest rates as a consequence of low temperatures (Saiz et al., 2006). Excessive soil moisture can lead to decreases in soil respiration by reducing the oxygen supply for both microbial decomposition and autotrophic activities (Xu and Qi, 2001).

Soil type effects on soil respiration

Although the two ecosystems were only several kilometers apart and had similar temperature and precipitation patterns, the annual soil respiration differed largely. The soil respiration was consistent with rates in arid regions in the Oued El kbir forest (site 1); whereas with those in humid and sub-humid regions in Sidi Ouedet forest (site 2).

These findings proved that, in the Djebel Mansour forest, the amount of carbon lost by soil respiration depended on soil moisture which is correlated, as were the precipitation events, to the pedological conditions, especially soil properties. Soil texture can be an important predictor of soil respiration via the dynamic of soil moisture that is different for sandy and clayey soils (Sotta et al., 2006). In the top soil (10 cm depth), we noticed a variation in clay-sized particles with 16.68% in the deep soil (site 2) resulting in a high soil water holding capacity 11.4 mm and only 9.9 mm in the shallow soil (site 1). Accordingly, Balogh (2011) and Moyano et al. (2012) reported a correlation between the amount of clay and optimum water content for soil respiration.

Presumably, the high organic matter content (11%) in the site 2 improved texture and water holding capacity by increasing pore space (*Table 2*). However, the site 1 has less silt, clay and organic matter than the site 2, and therefore the lowest water holding capacity (*Table 2*). Thus, we can explain this behavior with the high accumulation of coarse fragments (64.94%, *Table 2*). Aside from clay content, other studies revealed that water holding capacity depended on the level of organic carbon (Ramesh et al., 2008) and on coarse fragment content (Baetens et al., 2009; Cousin et al., 2003). In the deep soil (site 2), the higher accumulation of SOC and higher C/N (*Table 2*) could reflect the low decomposability of plant detritus and indicate the lowest contribution of heterotrophic respiration to total soil respiration. Similar results were reported for the arid Mediterranean ecosystem (Moro and Domingo, 2000; Zhang et al., 2008).

In light of the above, the higher soil respiration rate in the site 2 compared to site 1 could be explained by the favorable water status in the upper soil layer at 10 cm depth. Soil depth is another soil parameter can be considered to explain the soil respiration. Indeed, soil depth could control root zone water availability (Cable et al., 2008) and, consequently, affecting plant activity (McAuliffe, 2003). The site 2 is characterized by a deep soil (70 cm) and so, a higher WHC (77.55 mm).

Consistent with available related literature (Reichstein et al., 2003; Hibbard et al., 2005; Baldocchi et al., 2006), annual litterfall can affect soil respiration by substrate availability and input. The annual litterfall were significantly higher in the deep soil with 854.82 g m⁻² than the shallow soil with 416.93 g m⁻². These results are in the range of other Mediterranean Aleppo pine forests in France (410 g m⁻²; Rapp, 1976), in Greece (530 g m⁻²; Marmari, 1991) and other conifers: *Pinus Pinaster* in southern France (446g m⁻²; Kurz et al., 2000), *Pinus Sylvestris* in central Spain (411. 6 g m⁻²; Martnez-Alonso, 2007), *Pinus Pinea* in France (790 g m⁻²; 319; Rapp, 1984).

Conclusion

Soil respiration is a key ecosystem process that releases carbon as CO₂ from soil. In our case of study, SR showed a pronounced seasonal fluctuation, and it was predominantly controlled by soil moisture. Soil properties played an important role in determining spatial variation of SR by affecting soil moisture. In Sidi Ouedet forest, a deep soil, substrate availability and soil carbon input (litterfall) through plant productivity may have stimulated root and microorganism activity. In this calcareous Mediterranean soil, further study of heterotrophic and autotrophic respiration is needed for a better understanding of soil respiration mechanism in the context of a climate-change scenario of increasing aridity.

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