UNIVERSITAT DE BARCELONA

Soil water availability regulates soil respiration temperature dependence in Mediterranean forests

Chao-Ting Chang

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The variations of ecosystem and soil respiration are mainly driven by temperature and precipitation, but the importance of temperature and precipitation could vary across temporal and spatial. At diurnal to annual temporal scales, ecosystem and soil respiration generally increase with average annual temperature, but very low or very high soil moisture has been shown to diminish the temperature response of respiration. Therefore, in water-limited ecosystem, such as the Mediterranean region where the seasonal pattern is characterized with significant summer drought, precipitation patterns are likely to play a particularly important role in regulating ecosystem and soil respiration inter annual whereas temperature may be much less factor. In this dissertation, I try to reduce the uncertainties of terrestrial net ecosystem exchange in Mediterranean region by measuring the interaction between environmental factors and soil respiration at short (i.e., diurnal) and medium (i.e., seasonal-years) temporal scales. Three *in situ* experiments were employed to investigate how soil respiration responds to environmental variations and management. Together, these three studies gave a consistent picture on how soil moisture strongly affects the dynamic and magnitude of soil respiration in Mediterranean forests. Results elucidated a clear soil moisture threshold; when soil moisture is above this threshold, soil temperature is the main driver of soil respiration, meanwhile, when soil moisture is below this threshold, soil respiration decoupled from soil temperature and is controlled by soil moisture. This suggests that soil moisture modified, at least in Mediterranean ecosystems, the temperature sensitivity of respiration through threshold-like response.

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Programa de Doctorat en Ecologia Fonamental i Aplicada
Memòria presentada per Chao-Ting Chang
per optar el Grau de Doctor per la Universitat de Barcelona

Chao-Ting Chang

Barcelona, 2017

"Even the Broken Letters of the Heart Spell Earth "

Daniel Thompson

Tesi doctoral

Universitat de Barcelona

Facultat de Biologia – Departament d'Ecologia

Programa de doctorat en Ecologia Fonamental i Aplicada

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Report by thesis supervisor

In the following a short review is given by the thesis supervisors, Santi Sabaté on the impact factor of the published articles and the contribution in each article of the PhD student, Chao-Ting Chang.

Article 1. Published in *Biogeosciences*. Impact factor: 3.7

Chang, C. T., Sabaté, S., Sperlich, D., Poblador, S., Sabater, F., and Gracia, C.: Does soil moisture overrule temperature dependence of soil respiration in Mediterranean riparian forests? Biogeosciences, 11, 6173-6185, doi:10.5194/bg-11-6173-2014, 2014.

CTC carried out the main research tasks: design, field measurements data analyses and writing of the article. DS and PS contributed in the field campaigns and data analyses. SS participated in the work design and writing. All authors helped in the interpretation of the results, in the discussion and in the correction of the final version of the manuscript.

Article 2. Published in *Forests*. Impact factor: 1.6

Chang, C. T., Sperlich, D., Sabaté, S., Sánchez-Costa, E., Cotillas, M., Espelta J.M., and Gracia, C.: Mitigating the Stress of Drought on Soil Respiration by Selective Thinning: Contrasting Effects of Drought on Soil Respiration of Two Oak Species in a Mediterranean Forest. Forests, 7, 263, doi: 10.3390/f7110263, 2016

CTC carried out the main research tasks: design, field measurements data analyses and writing of the article. DS, SE, CM and EJM contributed in the field campaigns and data analyses. SS and GC participated in the work design. All authors helped in the interpretation of the results, in the discussion and in the correction of the final version of the manuscript.

Article 3. Submitted to *Forests*. Impact factor: 1.6

Chang, C. T., Sperlich, D., Sabaté, S., Sánchez-Costa, E., Cotillas, M., Espelta J.M., and Gracia, C.: From soil and stem respiration to leaf photosynthesis: influence of selective thinning on short and mid-term temporal drought responses of two coexisting Mediterranean oaks with contrasting leaf life span.

This study was conducted in parallel to the work presented in Article 2 and the contributions were the same.

Article 4. A manuscript based on chapter 5 & 8 is in preparation and will be submitted to *European Journal of Forest Research*. Impact factor: 2.0

Chang, C. T., Sperlich, D., Sabaté, S., Sánchez-Costa, E.: Responses of soil autotrophic and heterotrophic respiration to moisture availability and the influence of tree species.

CTC carried out the main research tasks: design, field measurements data analyses and writing of the article. DS, SS and SE contributed in the field campaigns and data analyses. All authors helped in the interpretation of the results, in the discussion and in the correction of the final version of the manuscript.

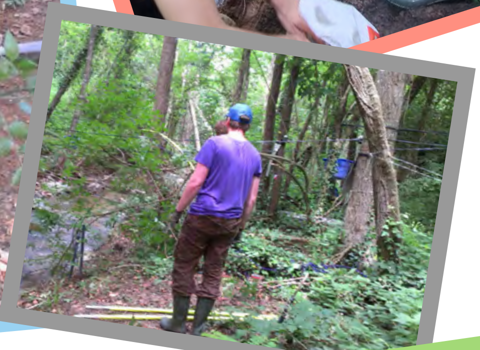
Signature

Santi Sabaté

Photo:D. Sperlich

謝謝我身邊所有的人

Thank you

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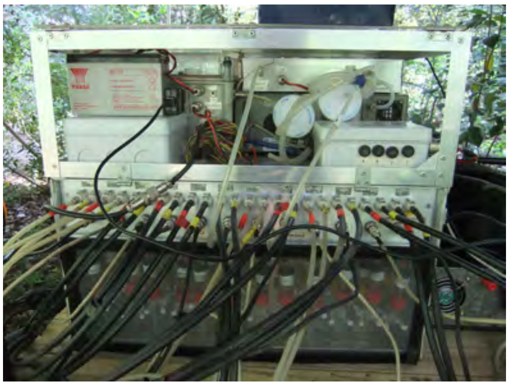


ABSTRACT OF THE DISSERTATION

Soil respiration, defined as the efflux of CO_2 from the soil to atmosphere, represents a major flux in the global carbon cycle. However, due to the complex and multiple controlling mechanisms that interact over different temporal and spatial scales, our ability to predict this flux remains limited. Temperature and soil moisture are the most important factors controlling soil respiration, but these two variables often covary together in most ecosystems and make it difficult to distinguish the relative importance of temperature and soil moisture on regulating soil respiration. Hence, Mediterranean ecosystems provide a unique opportunity to study the separately effects of soil temperature and soil water limitation on soil respiration as they experience cool, wet winters with hot dry summer and are typically subject to drought.

This study focus on the interaction between environmental factors and soil respiration at short (i.e., diurnal) and medium (i.e., seasonal-years) temporal scales. Three *in situ* experiments were employed to investigate how soil respiration responds to environmental variations and management. Together, these three studies gave a consistent picture on how soil moisture strongly affects the dynamic and magnitude of soil respiration in Mediterranean forests. Results elucidated a clear soil moisture threshold; when soil moisture is above this threshold, soil temperature is the main driver of soil respiration, meanwhile, when soil moisture is below this threshold, soil respiration decoupled from soil temperature and is controlled by soil moisture. This suggests that soil moisture modified, at least in Mediterranean ecosystems, the temperature sensitivity of

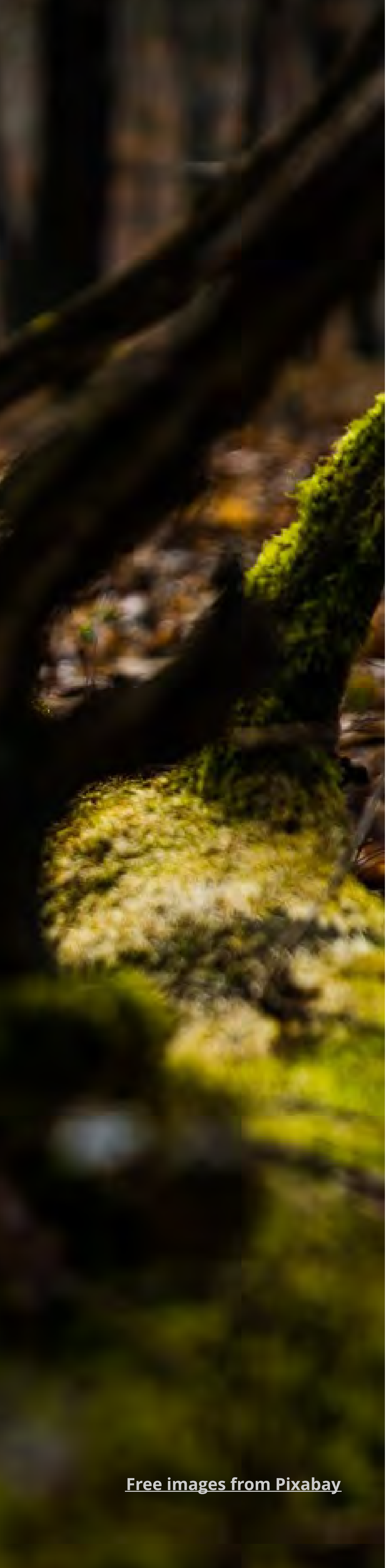
respiration through threshold-like response.

Collectively, this research demonstrated the important role of soil moisture on regulating soil respiration in semi-arid ecosystems and provided information for further model parameterization.

Keywords: soil respiration, carbon dioxide, Q_{10}, soil moisture, forest management

Chapter 1

Introduction and outline of the thesis



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Introduction

Carbon dioxide (CO_2) is one of the most important greenhouse gases and is also the primary greenhouse gas emitted through human activities. The exchanges of CO_2 among the land biosphere, the atmosphere, oceans and the earth's crust are called global carbon cycle. Currently, atmosphere contains around 750 Pg (1015 g) of CO_2 and the surface ocean contains around 1000 Pg C. Meanwhile, 3800 Pg of carbon is stored in the terrestrial ecosystems, with 3150 Pg C in the soil and 650 Pg C in the plants (Sabine et al., 2004). In the top soils to the depth of 1 meter, which are the most vulnerable to human activities such as land use change and agricultures, contains as high as 1500 Pg C (Jobbágy and Jackson, 2000). Each year, the amount of carbon uptake by plants through photosynthesis is approximately 120 Pg C, which is actually similar to the amount that is released back to atmosphere through ecosystem respiration. In the meantime, the anthropogenic emission, including human activities such as burning of fossil fuels, deforestation and fire, of CO_2 to the atmosphere is estimated to be 7.2 Pg Cyr-1. Although this amount of CO_2 emission caused by human activities seems to be small in comparison with the amount through other natural processes, it may, and might have already, upset the balance and dynamic of global carbon cycle. To understand how human perturbation and climate change affect the global carbon cycle, the knowledge of different aspects of carbon processes is indispensable. In terrestrial ecosystem, the two main pathways of CO_2 in the natural carbon processes are respiration and photosynthesis (Figure 1.1). Respiration, a term describing the process of gas exchange between organism and environment, is a set of metabolic processes in which substrate molecules are oxidized to yield energy needed for the maintenance, growth, ion uptake and reproduction of organisms. At the biochemical level, CO_2 produced by the living tissues, which is actually a by-product of metabolism mentioned above, shares common processes that are primarily through the tricarboxylic acid cycle (TCA cycle). Together with photosynthesis, respiration is the main carbon flux path of terrestrial ecosystem. But unlike photosynthesis, respiration never suspends nor halts, and it occurs continuously in every cell of every plant organ. Respiration consumes 25-75% of all carbohydrates assimilated by photosynthesis in the same period (Lambers et al., 1998). Thus, respiration is a critical piece of the puzzle in the earth's system and plays a crucial role in regulating atmospheric CO_2 concentration. To understand how respiration responds to the environmental change and account for their spatial and temporal variability will improve our ability to predict and mitigate the impacts of climate change.

As above-mentioned, soil carbon pool contains the majority of carbon in the terrestrial ecosystems and soil respiration comprised the second largest terrestrial carbon flux (Raich and Potter, 1995). In some ecosystem such as forests, soil respiration may in excess of 70% of total ecosystem respiratory efflux (Barron-Gafford et al., 2011; Law et al., 2001). Soil respiration is the sum of root respiration (autotrophic respiration) and microbial respiration (heterotrophic respiration). Due to their different origin, the responses of root respiration and microbial respiration to environmental and climate change may vary along different timescales (Kirschbaum, 2006). Though the flux of soil respiration can be measured, it is more difficult to separate it into autotrophic and heterotrophic respirations unequivocally (Hanson et al., 2000). Therefore, most current models still use simple and/or polynomial empirical relationship between total soil respiration and temperature. While such oversimplified relationships can explain much

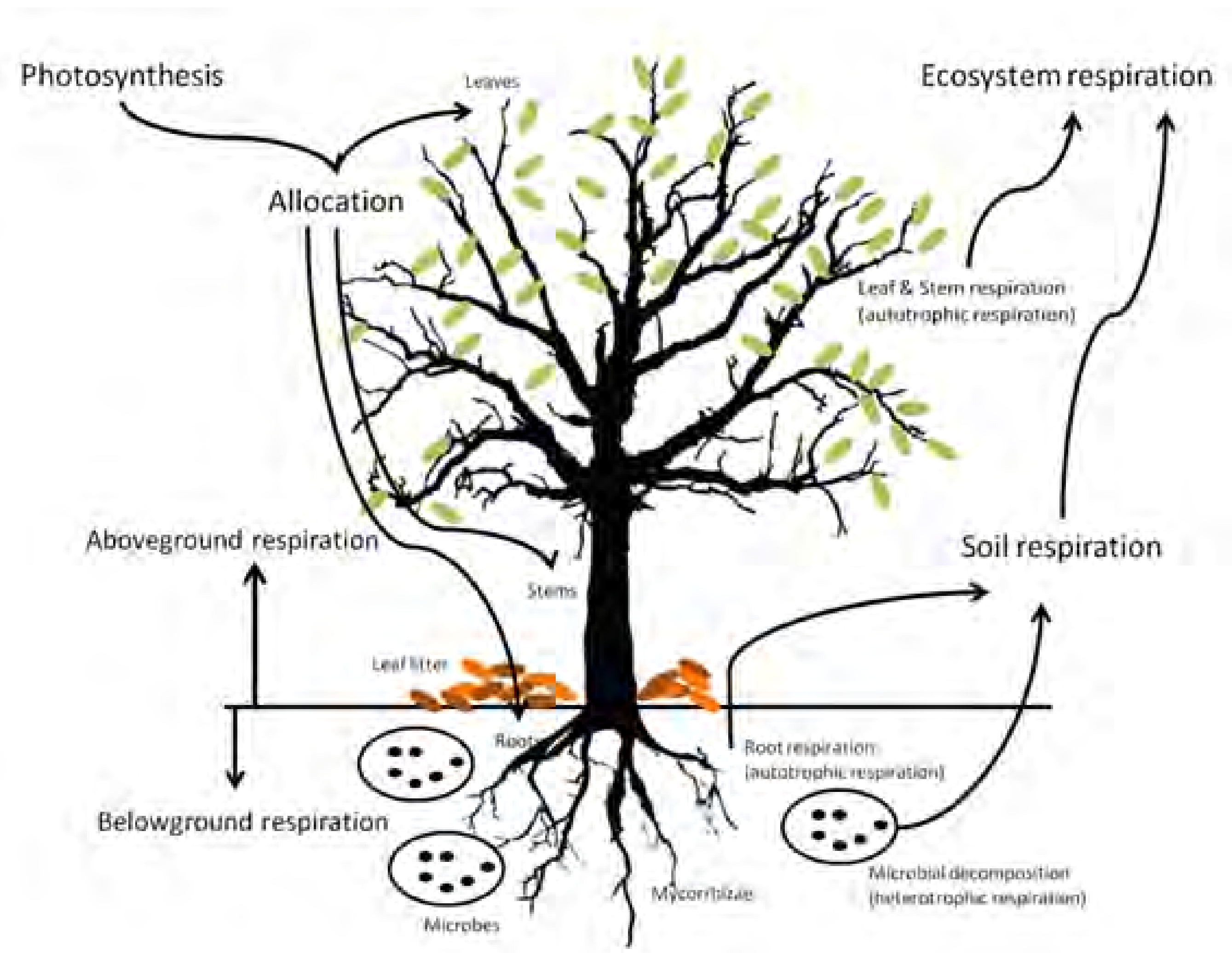

Figure 1.1. Schematic diagram of ecosystem carbon cycle.

of the variation at sites where there are no environmental or biological constraints, they generally do not well predict respiration variation across other space and timescales such as in semi-arid regions (Davidson et al., 2006; Trumbore, 2006). The inability to identify how each soil respiration component responds to environmental changes raises the uncertainty in predicting the terrestrial carbon, and also highlights the need of the reliable input parameters for a process-based model.

Plant growth can be limited by several factors, among which water stress is considered of major importance. Water is essential for maintaining physiological function of organs in the soil-plant-atmosphere continuum; water deficit can cause hydraulic failure in the plant or induce dormancy in soil organisms. But excessive amounts of water can also create anoxic conditions which is unfavourable neither to plant roots nor to aerobic soil organisms. At the plant physiological level, the balance between soil water availability and atmospheric water availability (vapour pressure deficit) maintains the stomata opening necessary for CO_2 uptake (Taiz and Zeiger, 2006). Water availability is thus a precursor for nutrient uptake. In soils, by contrast, water is the medium for nutrient availability, transporting dissolved nutrients to soil organisms or fine roots. Therefore, in semi-arid to arid climate region, soil water availability plays a crucial role in regulating ecosystem carbon cycle (Bell et al., 2008; Kurc and Small, 2007; Scott et al., 2009; Thomas et al., 2009). However, one of the difficulties in studying the effects of soil water content on soil respiration is that temperature, precipitation, soil moisture and evapotranspiration often covary, thus making it complex to separate the effects of soil moisture and temperature on soil respiration (Woods et al., 1998). Therefore, the water-limitation inherent to the Mediterranean region provides an opportunity to explore the mechanisms of different soil moisture conditions on ecosystem activity. It has been projected that under the climate change regime, Mediterranean regions will face a 15-20% decrease of precipitation (IPCC, 2013). In other words, the summer drought in the Mediterranean region will only intensify and be more severe. As the potential role of carbon sink or source under climate change, Mediterranean regions are important to the global carbon balance. Since we cannot control the foreseeable future, to be able to predict thereby attains primary importance. Quantifying the landscape-level carbon balance and understanding the drivers of carbon flux will improve our ability to assess potential changes and the possible feedback in Mediterranean regions.

Another increasingly important area of research that requires more detailed quantitative and qualitative knowledge is the influence of forest management on soil respiration and its potential of being plausible solution to mitigate climate change. As climate change is already a fact, how forest management can provide resilience to future climate-related stress would require more research. Forest management may alter carbon dynamic through improving plant growth, reducing competition, and increasing nutrient and water availability, etc. However, little is known about the implications of management on ecological processes and forest carbon cycle. How forest management practices affect soil carbon pools and dynamic and the possibility of using forest thinning as an adaptation strategy to reduce the forest vulnerability after climate change will need to be evaluated based on scientific experiments (North and Keeton, 2008).

Research objectives and organization

Motivated by the reasons detailed, the main objectives of this research focused on quantifying soil (both autotrophic and heterotrophic) and stem respirations in the Mediterranean region, with particular emphasis on the roles of soil water availability and also forest management. Specific objectives included:

- The characterization of the diurnal and seasonal patterns in soil respiration rates (both autotrophic and heterotrophic) of common Mediterranean tree species under different soil water availability regimes;
- The characterization of the observed respiration rates as functions of other plant and environmental variables;
- To separate the effects of temperature and water content on soil respiration by conducting experiment with reduced rainfall.
- To evaluate the effect of selective thinning on soil and stem respiration under the assumption of plausible mitigation strategy.

This dissertation is organized into nine chapters. Following this introduction, Chapter 2 (Literature review) provides a quick overview of the current state of knowledge on the broad subject of soil respiration. Chapter 3 (Materials and methods) is a general description of our study sites, instrumental and experimental setup, which is the common methodology used through all the chapters. Chapter 4 through 7 presented the experimental results and can be divided into two parts; the first part addresses how soil water availability regulates the relationship between soil temperature and soil moisture in two forests with contrasting soil water regimes. The second part aims to quantify drought effect on soil and stem respirations within the context of forest management and tree species. Part 1 is represented as Chapter 4 and 5. In chapter 4 I investigated the relationship between soil temperature and soil respirations, both total soil and heterotrophic respiration, at a semi-arid mix-oak forest. The primary objective of this study was to gain a better experimental understanding of the plant and microbial contribution to soil respiration, and how they respond to annual and seasonal changes in moisture.

Chapter 5 is a paper published in Biogeoscience (Chang et al., 2014); this chapter carries on the idea of chapter 4, but the temperature and moisture response of total soil and heterotrophic respirations were determined in a riparian forest. The experiment here is designed not only to examine the relationship between temperature and respiration, it also include soil water table as the other environmental factor. The following questions were addressed: does soil moisture play a role in the relationship between soil temperature and soil respiration even in a non-water-stress environment? If so, what is the soil moisture threshold that soil respiration is rather controlled by soil moisture than by temperature? Do other factors, such as tree species, nutrient availability or soil water table, also affect soil respiration and how?

Part 2 presents the experiment results from a four-year measurement in a study site where a factorial design of drought and selective thinning treatments was implemented. The primary objective of Part 2 is to provide an estimation of how drought affects soil (Chapter 6, published in Forests, Chang et al., 2016) and stem (Chapter 7) respirations and the implication of selective thinning as a mitigation practice in a Mediterranean oak forest. In this work, I intended to understand how drought affects respiration from different temporal scales and its mechanisms lay behind. I also wanted to know if selective thinning modify or mitigate the negative impact on respiration driven by drought?

Chapter 8 summarized the main results of this dissertation and analyzed the grouped data from our three sites. This chapter also contains a short literature review about soil moisture thresholds.

Lastly, Chapter 9 concluded the key findings of this dissertation and provided suggestions for future direction in related research.

Chapter 2

Literature review

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Controlling factors of respiration

Respiration, as early noted, is a complex process which involves different sets of chemical, physical and biological processes; as a result, the rate of respiration is regulated by several biotic and abiotic factors from different aspects and scales. At biochemical scale, the energy demand, substrate availability, temperature, moisture and oxygen supply are the main factors that drive respiration. For example, when substrate supply is low, the respiratory pathways become substrate-limited and thereafter slow down the respiration rate (Burton et al., 2000; Nadelhoffer, 2000). At the individual plant level, respiration rate of different components may be affected by plant species, age, aboveground photosynthesis, temperature, soil water and nutrients availability, and etc. On the ecosystem scale, respiration is influenced by climate, vegetation, ecosystem productivity, and plant phenology (Metcalfe et al., 2011).

It is worth noting that temperature affects directly or indirectly almost all aspects of respiratory processes from different scales. At biochemical level, low temperature limits respiration through its effects on enzyme activity, including capacity of both soluble and membrane-bound enzymes, the affinity of the enzyme for the substrate, and concentration gradients across cell membranes (Atkin and Tjoelker, 2003; Davidson et al., 2006). In high temperature, the forms of carbon that are available for use by microbial communities may change (Waldrop and Firestone, 2004). The enzymes may degrade in extreme high temperature and consequently depress the respiratory process. Temperature may also affect respiration via its effects on photosynthesis activity, substrate and O_2 transport at the individual plant level. For example, photosynthesis activity supplies carbohydrates from leaves to roots and rhizosphere and thus modulates soil respiration (Bahn et al., 2009; Högberg et al., 2001; Hölttä et al., 2009). On the ecosystem scale, temperature influences the seasonality of substrate supply and its effects on the phenology of plant growth (Dunne et al., 2003; Rustad et al., 2001). In a meta-analysis, Wu et al. (2011) indicated that global warming significantly stimulated total net primary production, increased ecosystem photosynthesis and ecosystem respiration. Elevated temperature also enhances soil nutrient mineralization (Grogan and Chapin III, 2000; Hartley et al., 1999; Melillo et al., 2002) and hence increases aboveground biomass (P. F. Sullivan et al., 2008).

Soil water availability or soil moisture is another important factor in regulating respiration process (Scott et al., 2009; Thomas et al., 2009). Water is essential for maintaining physiological function for organisms; insufficient water can cause hydraulic failure in plants (Tyree et al., 2002) or induce dormancy in soil organisms (Sylvia et al., 2005) while excessive amounts of water can create anoxic conditions favourable neither to plant roots nor to aerobic soil organisms. In general, respiration rate is low under dry conditions, reaches the maximal rate in intermediate soil moisture levels and starts to decrease when soil moisture is high. In biochemical level, soil moisture controls respiration via its effect on diffusion of substrates and O_2. For instant,


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when soil becomes drier, water-filled porosity reduces and water films around soil particles become thinner, thus inhibiting diffusion of extracellular enzyme and soluble organic carbon substrates (Davidson and Janssens, 2006; Moldrup et al., 2001; Skopp et al., 1990). At individual and ecosystem scales, soil moisture influences respiration through photosynthesis, plant growth and productivity, and substrate supply (Högberg et al., 2001; Yan et al., 2011). At global scale, soil respiration is found to linearly increase with precipitation (Raich and Schlesinger, 1992). In addition, studies also found that precipitation, which is usually the driving factor of the dynamic of soil moisture, plays a significant role regulating respiration particularly in semi-arid and arid regions. In some cases, individual large CO_2 pulse caused by rainfall event has accounted for substantial portions of seasonal and annual soil respiration (Tang et al., 2005a; Vargas and Allen, 2008; Xu et al., 2004).

Temperature dependence of respiration and the confounding factors

As the temperature is often the most important environmental factor controlling soil biological activity, global models use the temperature sensitivity of soil respiration as a core parameter in projecting carbon dynamic under climate change scenarios. There have been numerous empirical models developed to describe the relationship between temperature and soil respiration, from linear, exponential, Gaussian, the Van't Hoff, the Arrhenius to Lloyd-Taylor function (Fang and Moncrieff, 2001; Kätterer et al., 1998; Portner et al., 2010; Tuomi et al., 2008). The most common and simplest measure of sensitivity is temperature coefficient Q_{10}, which is defined as a factor by which soil respiration increases with a 10°C temperature increases and generally expresses as an exponential relationship. Many studies suggested that Q_{10} is a constant value of 2.0-2.3. However, studies also showed that this commonly used of Q_{10} value in the range 2.0-2.3 maybe only appropriate when the measurements conducted over short time periods or within certain temperature range (ca. 15-25 °C) (Atkin et al., 2005). Besides, given that temperature sensitivity of respiration is the intrinsic response, it doesn't include effects from other factors. Nevertheless, under field measurements or even in laboratory controlled experiments, it is almost impossible to exclude the influence from other factors and hence introduce the variability of measured Q_{10} values. For example, there are plenty evidence showed that the Q_{10} declines with increasing temperature and decreasing soil moisture (Curiel Yuste et al., 2003; Janssens and Pilegaard, 2003; Kirschbaum, 1995; Reichstein et al., 2002a; Reichstein et al., 2002b; Wood et al., 2013; Xu and Baldocchi, 2004; Xu and Qi, 2001). Even though when models take soil moisture into account, the chosen of soil water parameter is also a debate: some studies suggested that soil water potential is a more appropriate predictor (Miller and Johnson, 1964; Woods et al., 1998) while other studies presented plausible arguments of using soil water content (Fang and Moncrieff, 1999; Orchard and Cook, 1983) or a proportion of water-holding capacity (Joffre et al., 2003; Reichstein and Beer, 2008) as a predictor. Undoubtedly, soil moisture has a fundamental influence on plant and soil biological activity and may mask the relationship between temperature and respiration. However, there is still no consensus of whether the effects of moisture, as an additional controlling factor, on respiration-temperature function are simply additive, multiplicative, or may alter the function through interaction between soil moisture and temperature.

Except soil moisture, there are still many other factors that may confound the temperature dependence of soil respiration. For example, a number of studies have shown that the temperature sensitivity of litter decomposition can vary depending on substrates supply and substrate quality (Conant et al., 2008; Davidson et al., 2006; Fierer et al., 2006). According to enzyme kinetics principles, the temperature sensitivity of decomposition should be reciprocally related to litter carbon quality. Gu et al. (2004) showed that fast turnover pools of soil organic carbon can fluctuate widely at smaller timescales and the different seasonal distributions in plant litter inputs will distort the temperature sensitivity of soil respiration. They also suggested that care has to be taken when interpreting the temperature sensitivity of soil respiration without considering the seasonal dynamics of carbon pool size and autotrophic respiration contribution. Meanwhile, Curiel Yuste et al. (2004) also demonstrated that annual Q_{10} of soil respiration is affected by plant phonological patterns and suggested that the temperature sensitivity of soil respiration should characterize the different response of the autotrophic and the heterotrophic respirations. Except these inherent factors, Graf et al. (2008) and Subke and Bahn (2010) showed that the choice of the soil depth used for inferring the temperature sensitivity of soil respiration will significantly affect Q_{10} values. Sierra (2012) analyzed the different methods and theoretical measures and showed that even the choice of methods will yield different results. He also revealed that the observed behaviour of decline Q_{10} with increasing temperature may simply due to the mathematic artefact that Q_{10} is a function that depends on temperature. And last, Mahecha et al. (2010) developed a method to circumvent confounding effects on temperature sensitivity of ecosystem respiration. They separated the observed ecosystem respiration sequence into different bands by their time frequency and found that high frequency Q_{10}, which is sought to be the closed to the intrinsic Q_{10}, is independent of mean annual temperature and the Q_{10} value actually convergent to around 1.4 ± 0.1.

Forest management and carbon cycle

Forest management practices such as thinning, harvesting, fertilization, and prescribed fire may affect ecosystem carbon balance through changing ground surface energy balance, soil water content nutrition availability, and aboveground vegetation production (Campbell et al., 2009; Johnson and Curtis, 2001; Kowalski et al., 2004). Studies showed that forest thinning would increase soil temperature and its diurnal fluctuations, decrease the nutrient competition, enhance light and water availabilities or even prolong the growing period (Londo et al., 1999). Increased soil temperature and soil moisture may accelerate decomposition of litter layer and consequently increase soil respiration. The addition of fresh organic matter to the soil may also alter soil temperature and soil moisture (Roberts et al., 2005)

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and influence microbial respiration. Changes in root density, above and below-ground productivity caused by thinning also affect soil respiration and microbial quantity and activity (Bergeron et al., 2008; Concilio et al., 2006; Kowalski et al., 2003; Ma et al., 2004; Wic Baena et al., 2013). Jandl et al. (2007) reviewed how forest management influences soil carbon sequestration and summarized the effects of specific forest management actions, such as afforestation, tree species, stand management, disturbance and site improvement, on ecosystem carbon stock.

Recently, López-Serrano et al. (2016) studied how forest management practice affects soil respiration after fire disturbance in Mediterranean. They compared the soil respiration between the unburnt, burnt and burnt × thinning sites and found that soil respiration was lower in the burnt and burnt × thinning sites. Thinning significantly increased soil respiration, but the effect only can be seen in the first year after thinning practices. In the other earlier study, Concilio et al. (2006) examined the prescribed burning and thinning effects on soil respirations using a factorial design consisting of two levels of burning and three levels of thinning. Their results showed that thinning alone impacted the mean soil respiration the most and thinning effect lasted 3 years after treatments. Besides, they also found that the most important explanatory variable of soil respiration shifted from temperature in the pre-treatment to litter depth in the post treatment. They suggested that the existence of litter due to thinning practice allows longer retention of soil moisture and, consequently, increases the rate of soil respiration and decomposition.

Chapter 3

Common methodology

Soil chamber with root exclusion PVC. Photo: C.-T. Char

"Very common" way to trench

Photo: D. Sperlich

Common machine failure. Photo: C.-T. Chang

Definitions and terminology

Table 3.1 lists the abbreviations for the specific terms and symbols which will be used throughout the present work.

Table 3.1. Abbreviation and unit used in this study

Abbreviation	Unit	Explanation
SR	μmol C $m^{-2}s^{-1}$	Soil respiration
SR_{tot}	μmol C $m^{-2}s^{-1}$	Total soil respiration
SR_A	μmol C $m^{-2}s^{-1}$	Soil autotrophic respiration
SR_H	μmol C $m^{-2}s^{-1}$	Soil heterotrophic respiration
SOC	%	Soil organic carbon
SOM	%	Soil organic matter
Ts	°C	Soil temperature
SM	%	Soil moisture
SM_5	%	5 cm integral soil moisture
SM_{30}	%	30 cm integral soil moisture
SWC	%	Soil water content
VPD	kPa	Vapour pressure deficit
PAR	W/m^2	Photosynthetically active radiation
SPEI		Standardized Precipitation-Evapotranspiration Index
DBH	cm	Diameter at breast height
RGR	%	Relative growth rate
Q_{10}		Coefficient of temperature sensitivity of respiration
R_0	μmol C $m^{-2}s^{-1}$	Basal respiration rate at 0°C

The definitions of some important terms used in this thesis are as followed:

Soil respiration (SR) – soil respiration is the CO_2 produced by organism and plant parts in the soil. Due to the difference origins, soil respiration can be divided into soil heterotrophic respiration (SR_H), CO_2 by organisms such as soil microbes and fauna, and soil autotrophic respiration (SR_A) produced by roots and rhizomes.

Soil respiration rate – soil respiration rate is the total amount of CO_2 production in the soil during a specific period per unit area. It can be expressed as different unit such as μmol C $m^{-2}s^{-1}$, kg C $ha^{-1}d^{-1}$, mg C $m^{-2}h^{-1}$, etc.

Soil moisture (SM) – soil moisture generally refers to either the soil water content or the soil water potential. When soil moisture is mentioned in this present dissertation, it refers to soil water content.

Soil water content (SWC) – soil water content can be expressed as mass or volume of water in the soil. When soil water content is measured as mass unit, it is called gravimetric soil moisture content and is defined as:

$$\theta_g = M_{water}/M_{soil}$$

where M_{water} is the mass of the water in the soil sample and M_{soil} is the mass of dry soil that is contained in the sample. Meanwhile, the volumetric soil moisture content of a soil sample, θv, is defined as:

$$\theta_v = V_{water}/V_{sample}$$

where V_{water} is the volume of water in the soil sample and V_{sample} is the total volume of dry soil plus air and water in the sample. Both θ_g and θ_v are expressed in per cent, but now the volumetric soil moisture content also expresses as m^3/m^3.

Soil water availability – soil water availability is the available water storage, which is the difference between field capacity and wilting point, in the soil which can be used by plant. The actual water contents at which a soil reaches wilting point or field capacity depend on the soil textures and soil structure.

Coefficient of temperature sensitivity of soil respiration (Q_{10}) and basal respiration (R_0) –the relative increase in respiration rate with 10°C increase in temperature. Data were first fitted into the exponential Q_{10} model as followed:

$$R=R_0(eKT)$$

where R is the measured soil respiration rate (μmol C $m^{-2}\cdot s^{-1}$), R0 is the basal respiration at temperature of 0°C, T is the measured soil temperature (°C) at the depth of 5 cm and K is the fitted parameter. Thereafter the coefficient of temperature sensitivity of soil respiration can be derived as:

$$Q^{10}=e^{10k}$$

Study sites

The experiments of this study were conducted at three sites (Figure 3.1). Climate of these three sites are typically Mediterranean climate, with warm, dry summers and cold wet winters, but differed in the soil water availability due to the difference in topography, stand history and treatments.

Collserola (Barcelona)

The first study site is a well-developed mixed oak and pine forest located in Collserola Natural Park, Barcelona, NE Spain at 41°25 N, 2°04 E, at an altitude of 270 m. Annual precipitation and temperature averages 723mm and 15.1°C (1951-2000), respectively, with the majority of precipitation falling between October and May (Ninyerola et al., 2007a and 2007b). Soils are predominantly developed above lithological strata of shale and granite (Espelta et al., 2008). The vegetation is dominated by evergreen Holm Oak (*Quercus ilex* L.) and deciduous Pubescent Oak (*Quercus pubescens* Willd.), accompanied scattered Aleppo Pine (*Pinus halepensis* Mill.) and Strawberry tree (*A. unedo* L.). In spring 2011 tree density was 1429 trees per hectare, mean tree diameter at breast height (DBH) was 12.6 cm, and mean tree height was 10.8 m. The biggest DBH is the *P. halepensis*, with mean DBH of 33.7 cm, followed by *Q. pubescens* (12.0 cm), *Q. ilex* (11.9cm) and *A. unedo* (9.6 cm). The ecological and meteorological features of this study site have been characterized in Sánchez-Costa et al. (2015) and Sperlich et al. (2014).

Font de Regàs (Montseny)

The second site is in a riparian forest growing along Font de Regàs stream, a headwater tributary of La Tordera river, in the Montseny Natural Park (North of Barcelona; 41°50'N, 2°30'E, altitudinal range

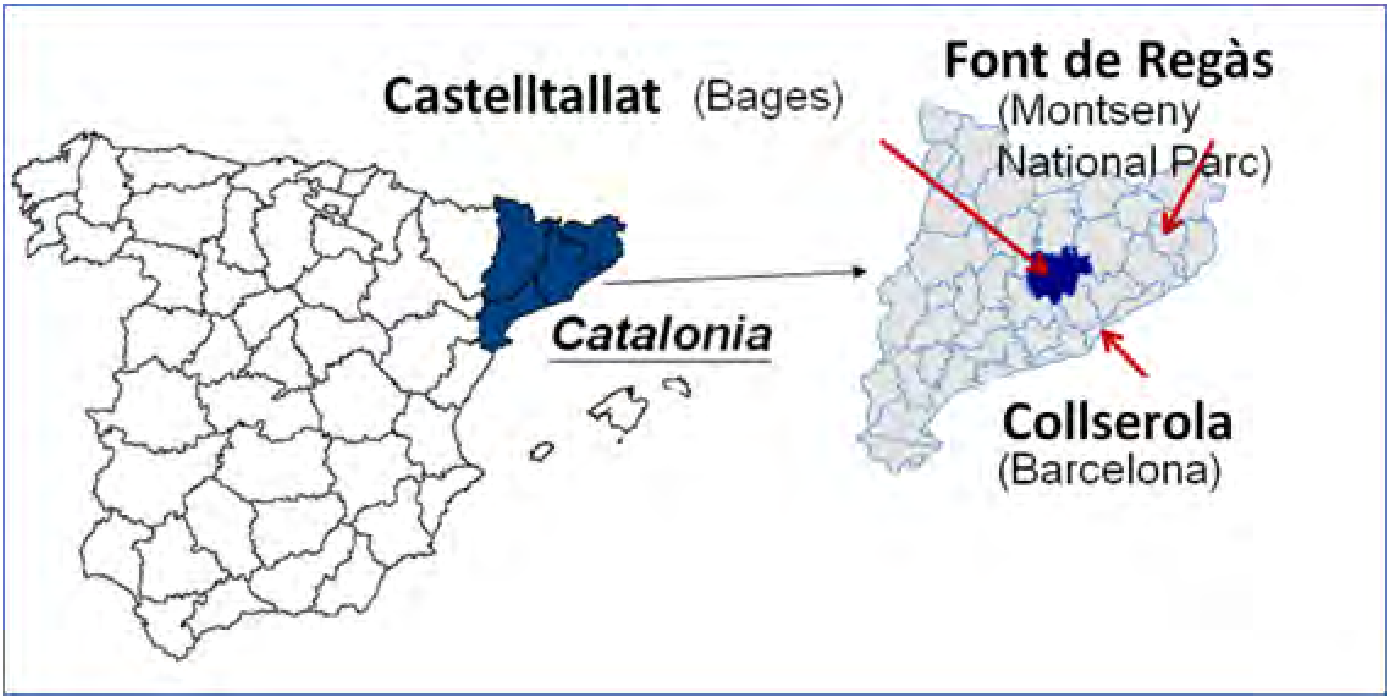


Figure 3.1. Location of our three study sites.

300-1200 m a.s.l.). Mean annual temperature is 12ºC with maximum and minimum average temperatures of 10 and 14ºC, respectively. The mean annual precipitation is 872 mm (1951-2010). The riparian soil is sandy-loam with low rock content (<13%), weakly acidic (pH of 6.7), and has an average bulk density of 1.09 g/cm3. The forest community of our study site consists of black alder (*Alnus glutinosa* L.), black locust (*Robinia pseudoacacia* L.), common ash (*Fraxinus excelsior* L.), and black poplar (*Populus nigra* L.). As result of water and nutrient availability, *A. glutinosa* and *P. nigra* are mostly distributed nearby the river whereas *F. excelsior* are located further away on the upper site, near to the hill and *R. pseudoacacia* trees scattered over the study area. In spring 2012 tree density was 1267 trees per hectare, mean tree diameter at breast height (DBH) was 15.5 cm, and mean tree height was 19.3 m. The biggest DBH is the *P. nigra*, with mean DBH of 31.9 cm, followed by *R. pseudoacacia* (17.7 cm), *A. glutinosa* (11.7cm) and *F. excelsior* (7.1 cm).

Castelltallat (Bages)

The third study site is in the region of Bages, Catalonia, NE Spain (41º 44 N, 1º39 E, 800 m a.s.l.). Mean annual temperature and precipitation are 12ºC and 600±135mm, respectively (1980-2000) (Ninyerola et al., 2000). According to the Thornwaite index (Thornthwaite, 1948), climate in this area is dry-subhumid Mediterranean. Soils are developed above calcareous substrate, surface rockiness is high, and the soil is moderately well drained with a mean depth ca. 25-50 cm.

This study site is a mixed oak coppice forest regenerated by resprouting after a large wildfire in 1998. *Q. ilex* (Holm oak) is the dominant tree species accompanied by winter *Q. cerrioides* Wilk & Costa and scattered *Pinus halepensis* Mill (Aleppo pine). *Q. ilex* is a sclerophyllous evergreen tree species that is distributed widely over the Iberian Peninsula. *Q. cerrioides* is a winter semi-deciduous (marcescent) species. Both tree species have the ability to resprout from stumps and roots after disturbances (Rodà et al., 1999).

This study site was set to understand the individual and interactive effects of drought and management on the Mediterranean forest ecosystem. To achieve this object, two levels of rainfall manipulation (natural rainfall and reduced rainfall) and selective thinning (no thinning and thinning) were factorially combined into four treatments, with three replicate plots of each treatment. The 12 plots (15*20 m) were distributed randomly in this study area with at least 10 m buffer surrounding every plot.

Figure 3.2. Reduced rainfall treatment implied in the Castelltallat study site. (Photo: S. Sabaé)

Figure 3.3. The automatic changeover open system. The upper left is IRGA, upper right is the cataloguer. The lower part is the rotameters, pumps and flowmeters. (Photo: S. Sabaté)

To simulate reduced rainfall, parallel drainage channels were installed at ca. 50 cm height above the soil and covered 15% of the ground surface at autumn 2004. Besides, to intercept runoff water, a ditch of ca. 50 cm depth was excavated along the entire top edge of the rainfall exclusion plots and covered with PVC strips.

Selective thinning was done in spring 2004. Traditional criteria of selective low-thinning for young oak coppices were applied (Espelta et al., 2003): the weakest stems were eliminated and one to three dominant stems per stump were left, which resulted in a reduction of 20-30% of stump basal area per plot. After selective thinning, mean stem basal area and height in thinning and combined treatments were 14.3±0.8 cm3 and 180±4 cm, respectively, and in the unthinned plots, those same characteristics were 7.7±0.8 cm3 and 146±4cm, respectively (Cotillas et al., 2009a).

Gas efflux measurements

When referring to respiration in this thesis, it is the observed value obtained from measurements of carbon dioxide efflux rates. We used an automatic changeover open system to measure soil and stem respirations (Figure 3.3). The system consisted of an infrared gas analyser (IRGA, LiCor 6262, LiCor, Inc., Lincoln, NE, USA), a data logger (CR10 Data logger, Campbell Scientific Inc., Logan, UT, USA), 12 pairs of channels, 12 chambers, 12 pairs of rotameters, 6 pumps, and 2 flowmeters. In the first two study sites (Collserola and Montseny Natural parks), all chambers were used to measure soil respiration. In the Castelltallat site, four pairs of channels were connected with the soil chambers while the other eight were connected to stem and leave chambers and measured in parallel.

Figure 3.4 is the schematic diagram of a soil chamber. The stainless steel soil chambers were closed cylindrical chambers 28 cm in diameter and 15 cm high. Each pair of channels and chamber were connected with two polyethylene tubes, one attached to the top of the chamber (reference CO_2 concentration) and another attached to the base for calculating the increment in CO_2 concentration (sample CO_2 concentration).

Both the reference air and the sample air coming from the 12 soil chambers were first dried in decantation tubes to prevent water and insects (Figure 3.5). The suction tubes coming from the 12 soil chambers led to a rotating valve, moving one position every 1 minute. The rotating valve connected one outlet to a diaphragm pump and the remaining 11 to open outlets, which means only one chamber at a time was directed to the gas analyzer. The flow rate from both pumps to the IRGA was kept around 1l min-1 by 2 rotameters. The rates of the reference and sample flow were adjusted to be roughly equal to minimize the pressure difference. When air was directed to the gas analyzer, only the last 40 seconds of recordings from the gas analyzer were averaged and recorded by the data logger. An additional zero calibration was carried out after each four rounds of full measurement cycle.

Soil chambers were shaded by placing a 50*50 cm green fine mesh on top to avoid possible heating by direct sunlight during the measurements. Ts in the upper 5 cm of soil were measured continuously with Pt100 temperature sensors (n=4) and recorded in parallel with the CO_2 concentration analysis.

In the Castelltallat site, soil moisture (cm^3/cm^3) in the upper 20 cm of soil was recorded manually once per day during the 3-day measurement of each plot using 10 Time Domain Reflectometry Probes (Tektronix, 1520C Beaverton, USA), which were installed randomly within each plot. In Collserola and Font del Regàs sites, 5 cm soil moisture was measured with impedance probes (Delta-T Theta Probe Soil Moisture Sensor, MI2x, Delta-T Devices, Cambridge, England). Additionally, 30 cm integral soil moisture (cm^3/cm^3, SM_{30}) in each level were determined and recorded half-hourly with moisture reflectometer (CS616, Campbell Scientific) in Font de Regàs site.

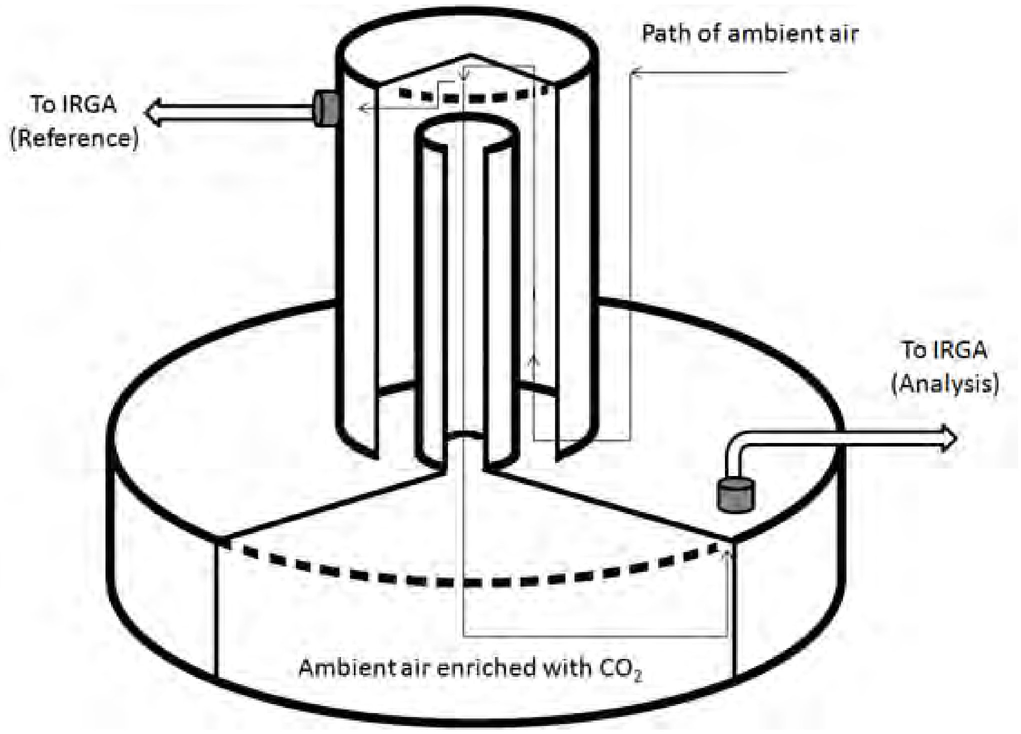


Figure 3.4. Schematic diagram of soil chamber.

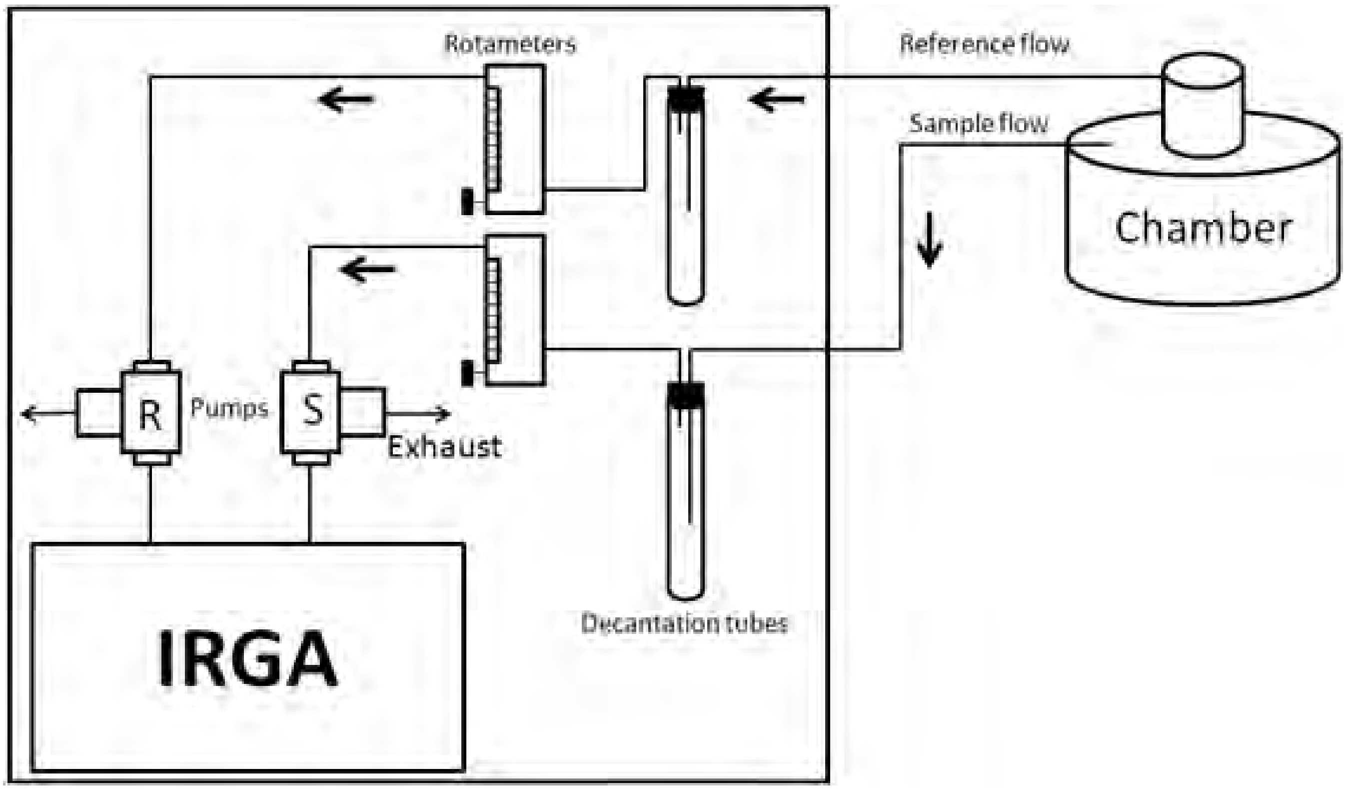
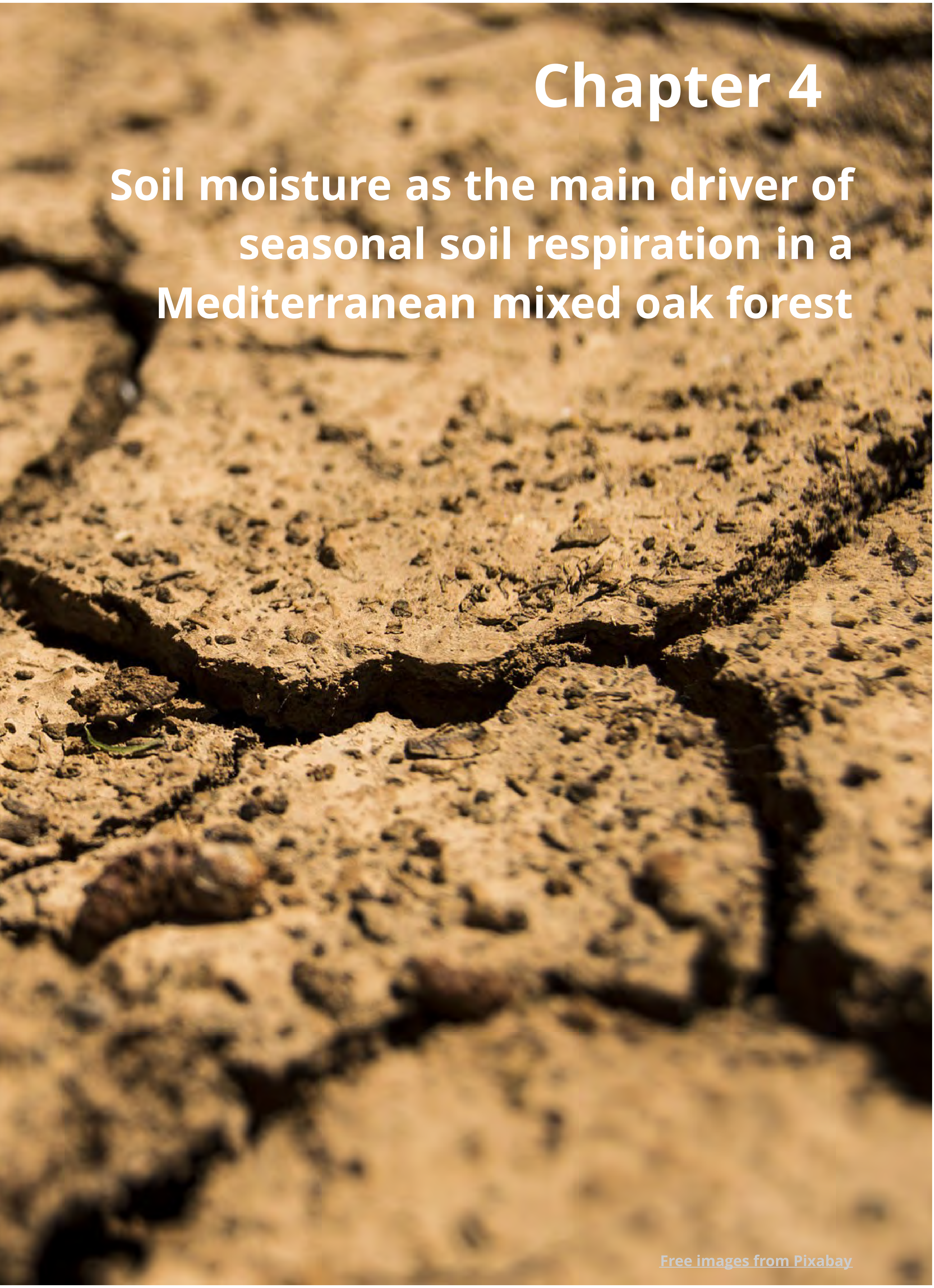


Figure 3.5. Schematic diagram of the gas automatic changeover system.

Chapter 4

Soil moisture as the main driver of seasonal soil respiration in a Mediterranean mixed oak forest



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Introduction

Studies have shown that soil respiration is controlled by many factors such as temperature (Fang and Moncrieff, 2001; Lloyd and Taylor, 1994), moisture (Gärdenäs, 2000; Taylor et al., 2011), vegetation phenology (Curiel Yuste et al., 2004; Sampson et al., 2007), human disturbance or other factors. Among those factors, temperature is recognized as the main abiotic driver of soil respiration due to its direct effect on metabolism driven by enzymatic kinetic whereas soil moisture as the second important one. Unlike the well documented and abundant literatures dealing the relationship between temperature and soil respiration, the link between soil moisture and respiration is less clear and yet well described. The functions that combine the effects of both temperature and moisture remain diverse in literature. Moreover, a growing number of studies have suggested that the temperature dependence of soil respiration in water limited ecosystem may be altered by the soil water regime (Janssens and Pilegaard, 2003; Markus Reichstein et al., 2002). Understanding how these two factors govern soil respiration and the interaction between temperature and soil moisture is important for predicting soil CO_2 fluxes under changing meteorological conditions in the Mediterranean region.

As soil respiration integrates several biological and physical processes, temperature and soil moisture may also affect these processes from different time scale (Gaumont-Guay et al., 2008; Schindlbacher et al., 2009). For example, diurnal variations of soil respiration are usually highly correlated with soil surface temperature fluctuations (Drewitt et al., 2002; Jassal et al., 2005). However, studies have also shown hysteresis-type relation or no relation between temperature and soil respiration under drought conditions (Parkin and Kaspar, 2003; Subke et al., 2003; Xu and Qi, 2001). At seasonal scale, temperature still strongly regulates soil respiration, meanwhile, the role of soil moisture is more pronounced at seasonal scale than at daily scale. At low soil moisture condition, soil respiration may decrease due to the reduction in decomposition rate and lower autotrophic activities (Savage and Davidson, 2001). Soil moisture conditions exerted a strong influence over the annual variation of soil respiration. For example, studies have shown that soil respiration may decline 40% during the severe dry year (Lavigne et al., 2004a) although the annual temperature was similar. However, it is difficult to examine the effect of moisture on the relationship between temperature and respiration because the variations in soil temperature and soil moisture are often correlated ad the independent effect of each variable is hard to detect or interpret (Woods et al., 1998). Moreover, considering soil respiration is the sum of autotrophic respiration from root and heterotrophic respiration from microbes, their responses to temperature and soil moisture may vary at different temporal scale and thus add more uncertainties when quantifying the ecosystem – biome level carbon cycle changes.

To date, global models usually use the temperature sensitivity of respiration as a parameter to simulate CO_2 fluxes change under global warming scenario. One of the most common sensitivity parameter is the temperature coefficient Q_{10}, which is the relative increase in respiration rate with 10^{o}C increase in temperature. At present, many ecosystem models assume that the effects of soil moisture are additive, and thus using a fix Q_{10} (Davidson et al., 2006; Zhou et al., 2009) multiplying a reducing function for moisture (Bauer et al., 2008; Parton et al., 1993; Potter et al., 1993; Raich et al., 1991). However, there is still no consensus if the effect of soil moisture on the relationship between temperature and respiration is simply additive, nonlinearly or may alter the function. Besides, within an ecosystem, we do not know if these interaction effects are consistent through time, or whether they vary in different temporal scale. Apart from the environmental factors, the spatial distribution of vegetation is also an important factor to bear in mind, because plants affect soil respiration through several pathways. First, plant influence microbial respiration through the timing, quantity and quality of litter input. Second, different rooting systems may influence soil microclimate and structure (Tufekcioglu et al., 1999). Third, the root biomass and tree phenology can affect root or rhizosphere respiration as a considerable fraction of daily assimilation from photosynthesis is consumed by roots (Högberg et al., 2001). Last, the tree physiology and phenology, and water use efficiency of different species may alter the soil moisture regime through the interception of precipitation and extraction of soil water via transpiration (Rutter and Morton, 1977).

Three objectives were addressed in this study. The first was to quantify soil respiration rate as a function of temperature and moisture. The second objective was to examine the difference in heterotrophic and total soil respiration, and their responses to environmental changes. The third objective was to investigate if tree species affect soil respiration through autotrophic activity and carbon input. We expected that: (i) soil moisture, rather than soil temperature, is the major factor controlling soil respiration rate in this Mediterranean forest. (ii) Tree species would provide the inter-spatial differences in soil respiration from both biological activity and carbon input.

Materials and Methods

Site description

To avoid the repetition, please refer to Chapter 3.

Field measurements

Soil respiration was measured seasonally from spring 2011 to summer 2012 using an automatic changeover open system. In each season, at least three consecutive days measurement were carried out. We chose the three main tree species in this study site: *Quercus ilex, Quercus pubescens* and *Pinus halepensis.* Four individual trees of each species are used to measure the soil respiration. To separate root respiration, we inserted a PVC tube (diameter: 65cm, height: 40cm) into the soil five months before starting the measurements. Soil chambers were placed 1.5 m from the stem of the target tree species. Stainless-steel rings were inserted permanently into the soil, down to 3 cm depth, as the base of the soil chambers, and kept free from seedlings throughout the experiment duration.

Figure 4.1. One pair of soil chambers, the right one is to measure heterotrophic respiration, with PVC tube as trench, while the left one is to measure the total soil respiration. (Photo: C.-T. Chang)

Sensitivity to temperature and soil moisture of soil CO_2 efflux

We used multiple linear and non-linear regressions to fit four soil respiration models for each species; three with and one without soil moisture term. We used the simple exponential Q_{10} model, which is the relative increase in respiration rate with 10°C increase in temperature, to assess the relative increase in soil respiration with temperature. Data were fitted into the exponential Q_{10} model for each season, species and trench treatment (control and trenched):

$$R=R_0(e^{KT}) \qquad (1)$$

where R is the measured soil respiration rate (μmol C $m^{-2}\cdot s^{-1}$), R0 is the basal respiration at temperature of 0°C, T is the measured soil temperature (°C) at the depth of 5 cm and K is the fitted parameter. Thereafter the temperature sensitivity of soil respiration can be derived as:

$$Q_{10}=e^{10k} \qquad (2)$$

The linear model (Eq. (3)) was used to describe the relationship between daily average soil respiration and soil moisture.

$$R=a+bM \qquad (3)$$

As the common used Q_{10} model doesn't account for the effect of soil moisture, we used a natural log-linear quadratic model (Eq. (4)) adapted from Martin & Bolstad (2005) and Gaussian model (Eq. (5)) to express the dependence of soil respiration on temperature and moisture:

Table 4.1. Environmental conditions of experiment period.

	Seasonal precipitation (mm)	Seasonal Air Temperature (°C) (Min – Max)	Seasonal VPD (kPa)	Mean air temperature (°C) during each campaign	Mean VPD (kPa) during each campaign	Seasonal SPEI
2011 Spring	197	16.6 (7.8-30.7)	0.6	25.8	0.7	0.17
2011 Summer	81	22.4 (11.8-34.4)	0.9	26.8	0.7	0.33
2011 Autumn	272	13.4 (1.2-31.03)	0.4	19.1	0.2	1.04
2012 Winter	25	7.3 (-4.0-25.2)	0.4	8.4	0.3	0.63
2012 Spring	141	16.3 (3.4-36.02)	0.8	25.5	1.2	0.35
2012 Summer	50	23.4 (10.4-36.88)	1.2	30.8	1.4	0.54

$$Ln(R)=a+b0*T+b1*T2+b2*M+b3*M2+b4*T*M \quad (4)$$

$$R = a *\exp(-0.5* (((T -b0)/b1)^2 +((M -b2)/b3)^2)) \quad (5)$$

where R is daily measured soil respiration, T is soil temperature (at 5 cm), M is soil moisture (at 5 cm), a and b0–b5 are fitting parameters.

Statistics

The software packages PASW 18.0 (SPSS Inc., Chicago, USA) and SigmaPlot 11.0 (Systat Software Inc., Chicago, USA) were used for statistical data analysis.

Results

Seasonal variation of environmental variables

During the studied period, the precipitation was mainly concentrated during spring and autumn, whereas the precipitation of winter 2012 was relatively lower (50mm) (Table 4.1). In comparison to climate average precipitation, annual precipitation in 2011 (804mm) was 30% higher and in 2012 (479mm) was 20% lower. As a result, the VPD of summer 2012 was 30% higher than of summer 2011. Seasonal VPD and mean VPD during the experiment campaign showed a similar trend, though the variability of VPD during the experiment campaign was higher.

Soil moisture was highest during spring and autumn 2011 and lowest during summer 2012 (Figure 4.2). Similar to the inter-annual precipitation pattern, soil moisture during growing season of 2011 was statistically higher than of 2012. Seasonal variation of soil moisture was smaller for *Q. pubescens.* Trenched treatment significantly affected soil moisture. Generally, soil moisture in control collar was lower than in trenched collar, except during autumn 2011, but the difference in soil moisture between control and trenched varied between seasons. During spring 2011, the difference in soil moisture between control and trenched collars was highest, with an almost 10% difference in soil moisture.

Seasonal evolution of soil respiration

The seasonal patterns of soil respiration were qualitatively similar between species. The seasonal evolution of soil respiration followed the variation of soil moisture rather than soil temperature, with higher during spring and autumn 2011 (Figure 4.3). Due to the effect of soil moisture, heterotrophic soil respirations were found to be higher than total soil respiration in some campaigns, especially for soil respiration of *Q. pubescens.* Moreover, the seasonal variability of heterotrophic soil respiration was lower than the total soil respiration, except for soil respiration of *Q pubescens.*

Sensitivity of respiration to soil temperature and moisture

Diurnal variation of soil respiration followed the change of soil temperature in most of the campaigns. Table 4.2 presents the basal respiration rate at 10°C and Q_{10} values for each species and treatments calculated with hourly means data in each season. In most of the cases, seasonal soil respiration (both heterotrophic and total respiration) showed no relation or weak relation with soil temperature (Figure 4.4-4.6), except during spring and autumn 2011 when precipitation and soil moisture were higher. In the meantime, seasonal soil respiration showed a significantly correlation with soil moisture, except soil respiration of *Q. pubescens* during winter 2012. The mean Q_{10} was always significantly greater for the seasons with higher soil moisture (spring, autumn 2011 and winter 2012). Meanwhile, we also found greater Q_{10} of heterotrophic soil respiration than of total respiration in these seasons. In contrast, when soil moisture was lower than 10%, Q_{10} of total respiration were greater than of heterotrophic respiration. Mean Q_{10} of 2012 were lower than of 2011. We also found that most of the mean Q_{10} values of 2012 were even lower than 1, indicating that soil respiration does not synchronize with soil temperature.

Discussion

In our study, we only found significant differences of soil respiration between treatments for the soil respiration of *Q. ilex* during the first campaign. The insignificant reduction of soil respiration in the trenched plot during the first campaign may due to the higher soil moisture and higher decomposition rate after trenching. The higher soil moisture found in the trenched plot due to the absence of the root and plant water uptake has been reported in several studies (Högberg, 2005; Ross et al., 2001; Staples et al., 2001). Comstedt et al. (2011) estimated the root decomposition and soil moisture effects in a trenching treatment and found 45% of respiration in the trenched plot was an artefact of treatment over the first 5 months after trenching. However, the effect of differences in soil moisture on soil respiration is often neglected in most of the studies that partitioning and estimate the contribution of different soil components. Nevertheless, in a semi - arid climate such as Mediterranean region, soil respiration is highly sensitive to soil moisture, even a

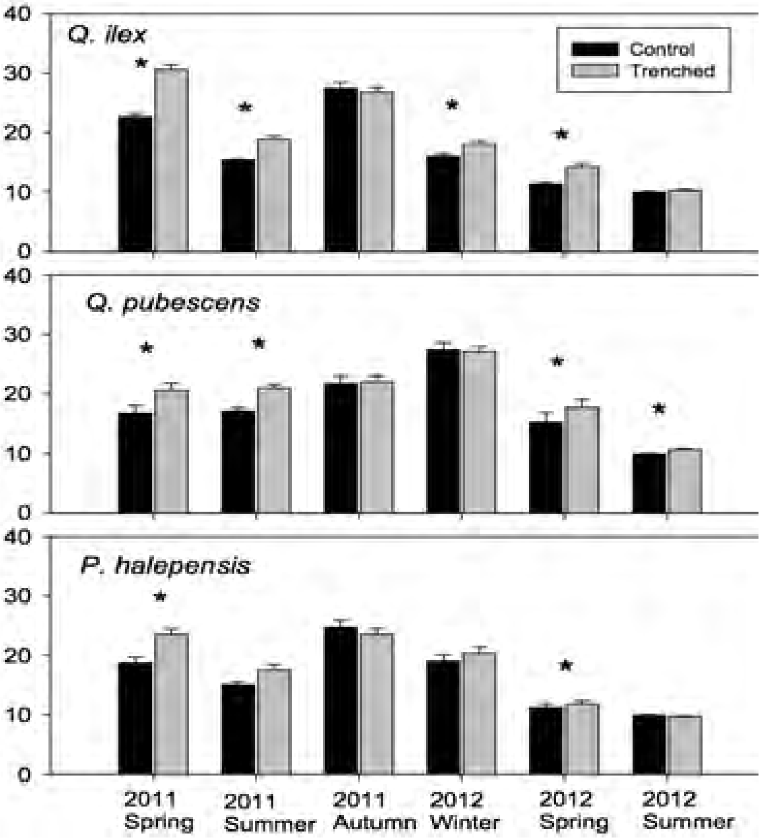


Figure 4.2. Mean soil, water content (5cm) of measured points (control and trenched) of the three study species for each campaign. Data with star mark means significant difference was found between treatments.

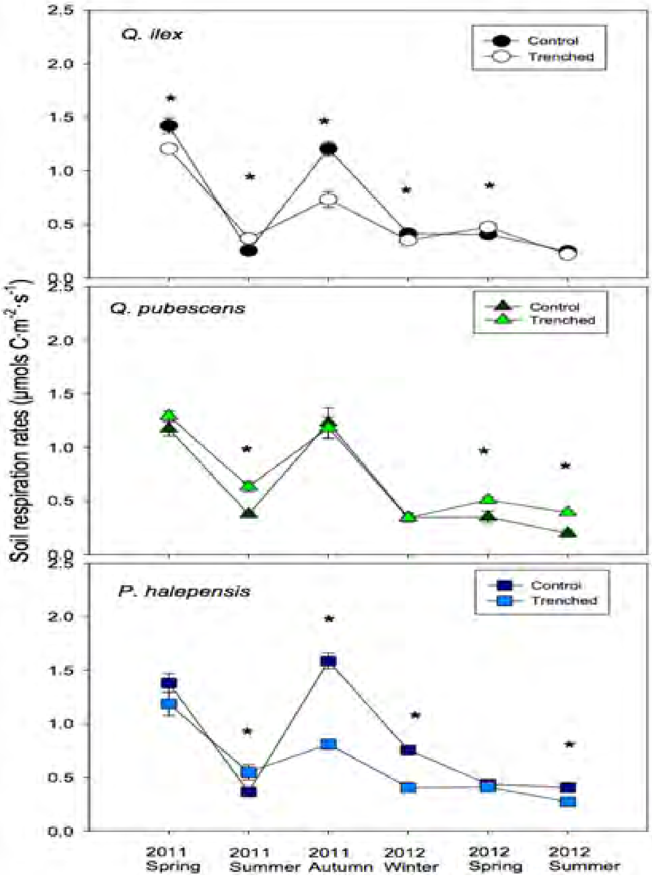


Figure 4.3. Seasonal variations of soil respiration (control and trenched) for each tree species. Error bars represent the standard error of the mean. Data with star mark means significant difference was found between treatments.

Table 4.2. Basal respiration rate at 10ºC (R_b) and Q_{10} of soil respiration (control and trenched) for each study species. Data were calculated with hourly means in each season.

	Q. ilex				*Q. pubescens*				*P. halepensis*			
	Control		Trenched		Control		Trenched		Control		Trenched	
	R_b	Q_{10}	R_b	Q_{10}	R_b	Q_{10}	R_b	Q_{10}	R_b	Q_{10}	R_b	Q_{10}
2011 Spring	1.08	1.11	0.68	1.52	1.02	1.18	1.05	1.53	0.78	1.40	0.93	1.44
2011 Summer	0.21	1.21	0.26	1.15	0.48	1.08	0.97	1.05	0.50	1.30	0.24	1.08
2011 Autumn	1.16	1.30	0.49	1.49	1.21	1.21	1.00	1.83	0.66	1.08	2.68	1.31
2012 Winter	0.50	1.05	0.34	1.18	1.08	2.16	–	–	0.46	1.06	0.57	1.27
2012 Spring	1.94	0.89	0.46	0.89	0.28	1.26	0.28	1.21	0.38	1.22	0.51	0.97
2012 Summer	0.24	0.75	0.93	0.71	–	–	1.12	0.84	0.30	1.29	0.27	0.92

–: no significant regression results.

slight difference may result in significant change. Without taking the difference in soil moisture caused by trenching into account, the relative contribution from heterotrophic respiration to total soil respiration may be overestimated.

Besides the difference in soil moisture caused by trenching, studies also indicated that trenching increases a considerable amount dead root biomass, which may last in soil from weeks to years (Epron, Daniel et al., 1999; Kuzyakov, 2006) and the fine root decomposition can be delayed for several months after trenching (Díaz-Pinés et al., 2010). Again, this decomposition of dead roots caused by trenching may inflate the heterotrophic respiration rate and result in an overestimation of heterotrophic respiration fraction. In our study, the trenching treatment was implied during winter and 3 months before the measurement, thus the dead roots may not yet be decomposed due to the low temperature and contribute to higher heterotrophic respiration rate during spring when the temperature and soil

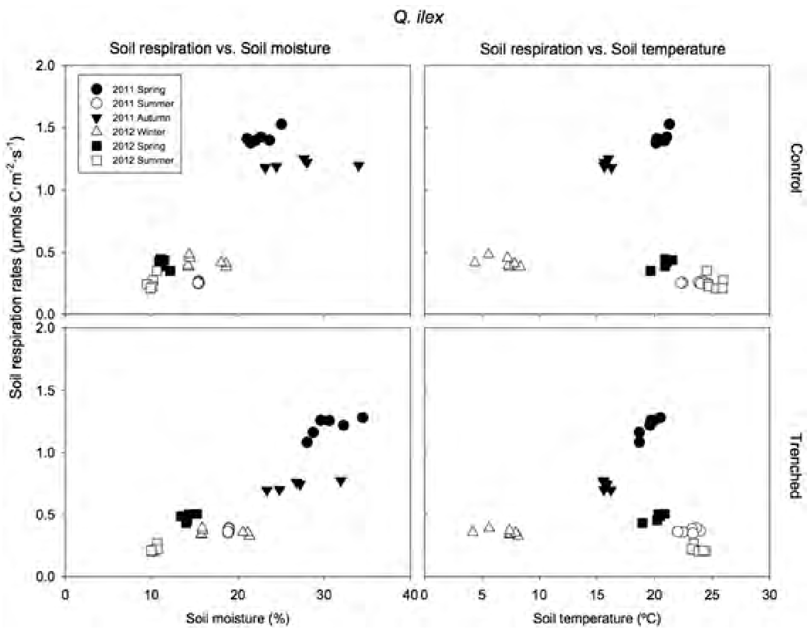


Figure 4.4. Mean daily soil respiration of *Q. ilex* (upper: control, lower: trenched) as a function of soil water content (left panels) and soil temperature (right panels).

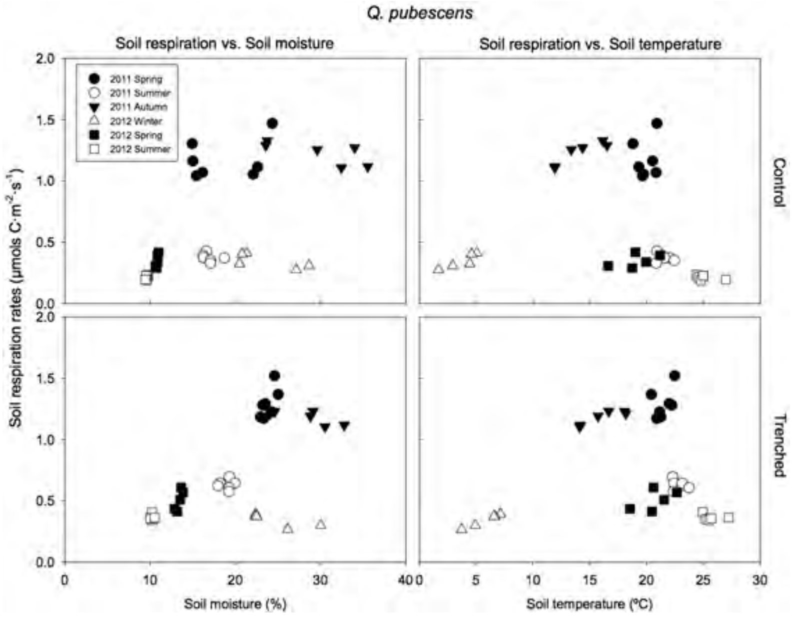


Figure 4.5. Mean daily soil respiration of *Q. pubescens* (upper: control, lower: trenched) as a function of soil water content (left panels) and soil temperature (right panels).

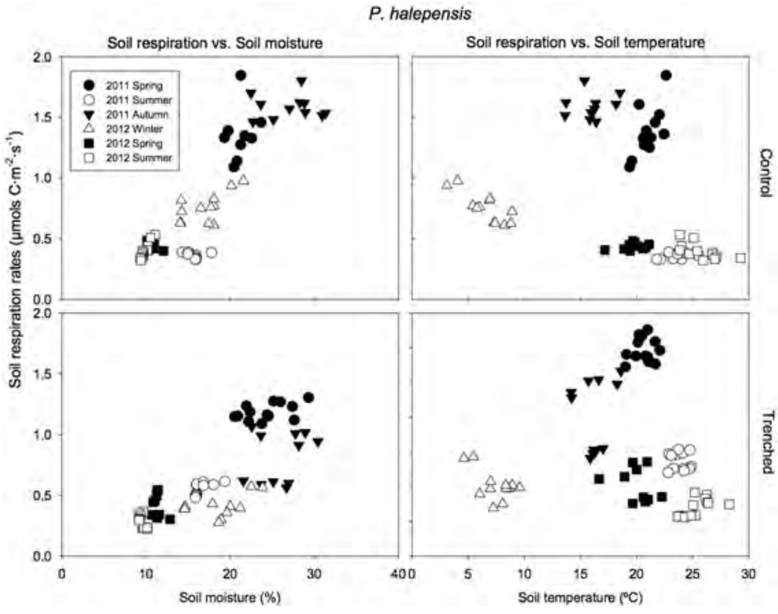
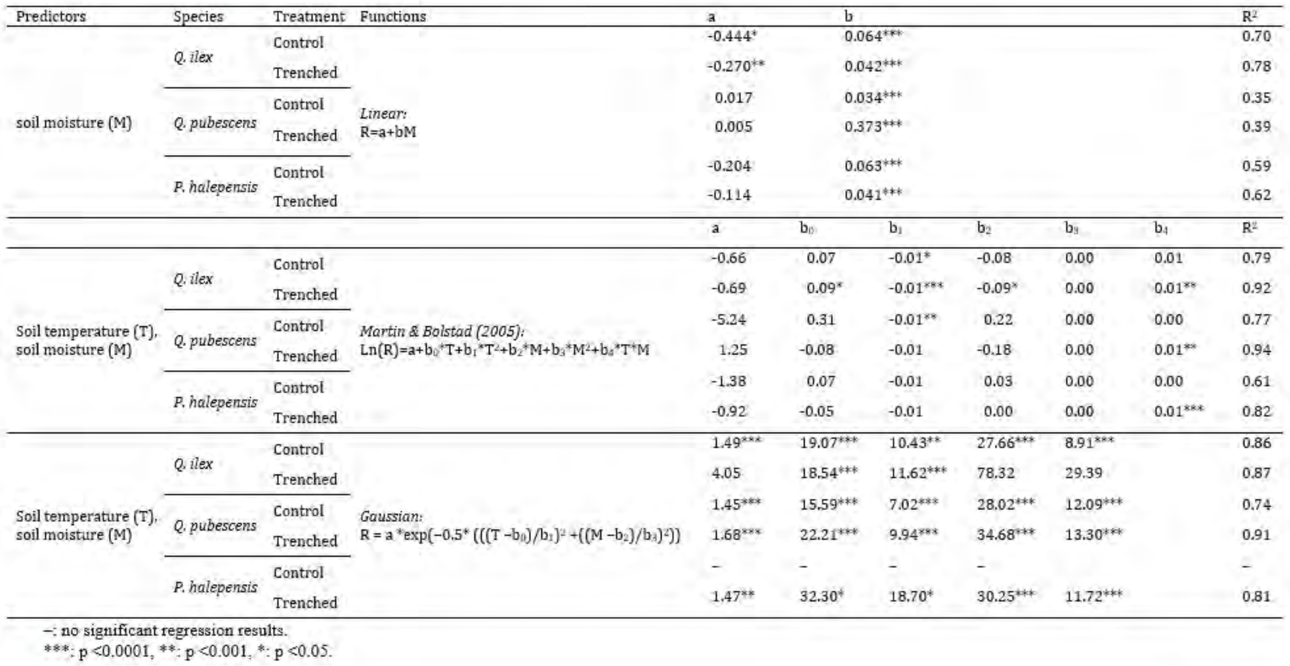


Figure 4.6. Mean daily soil respiration of *P. halepensis* (upper: control, lower: trenched) as a function of soil water content (left panels) and soil temperature (right panels).

Table 4.3. Temperature and moisture control on soil respiration



Predictors	Species	Treatment	Functions	a	b					R^2
soil moisture (M)	*Q. ilex*	Control	*Linear:* R=a+bM	-0.444*	0.064***					0.70
		Trenched		-0.270**	0.042***					0.78
	Q. pubescens	Control		0.017	0.034***					0.35
		Trenched		0.005	0.373***					0.39
	P. halepensis	Control		-0.204	0.063***					0.59
		Trenched		-0.114	0.041***					0.62
				a	b_0	b_1	b_2	b_3	b_4	R^2
Soil temperature (T), soil moisture (M)	*Q. ilex*	Control	*Martin & Bolstad (2005):* $Ln(R)=a+b_0*T+b_1*T^2+b_2*M+b_3*M^2+b_4*T*M$	-0.66	0.07	-0.01*	-0.08	0.00	0.01	0.79
		Trenched		-0.69	0.09*	-0.01***	-0.09*	0.00	0.01**	0.92
	Q. pubescens	Control		-5.24	0.31	-0.01**	0.22	0.00	0.00	0.77
		Trenched		1.25	-0.08	-0.01	-0.18	0.00	0.01**	0.94
	P. halepensis	Control		-1.38	0.07	-0.01	0.03	0.00	0.00	0.61
		Trenched		-0.92	-0.05	-0.01	0.00	0.00	0.01***	0.82
Soil temperature (T), soil moisture (M)	*Q. ilex*	Control	*Gaussian:* $R = a*\exp(-0.5*(((T-b_0)/b_1)^2+((M-b_2)/b_3)^2))$	1.49***	19.07***	10.43**	27.66***	8.91***		0.86
		Trenched		4.05	18.54***	11.62***	78.32	29.39		0.87
	Q. pubescens	Control		1.45***	15.59***	7.02***	28.02***	12.09***		0.74
		Trenched		1.68***	22.21***	9.94***	34.68***	13.30***		0.91
	P. halepensis	Control		–	–	–	–			–
		Trenched		1.47**	32.30*	18.70*	30.25***	11.72***		0.81

–: no significant regression results.
***: $p < 0.0001$, **: $p < 0.001$, *: $p < 0.05$.

moisture were in an optimum situation.

Autotrophic respiration contributed to total soil respiration varied with season and environmental conditions. In a review from Hanson et al. (2000), they summarized 37 studies and obtained an average percentage of 49% of autotrophic respiration to total soil respiration with a range from 10 - 90% among studies. Other studies carried out in Mediterranean regions indicated that the contribution of heterotrophic respiration to total soil respiration varied from 53% to 77% (Rey et al., 2002; Tang and Baldocchi, 2005; Xu et al., 2001). In our study, we observed a major contribution from heterotrophic respiration in most of the seasons. However, the rapid increased of autotrophic respiration contribution during autumn 2011, when environmental condition is not limited, implied that the low relative contribution from autotrophic respiration in our study site may only due to the water stress. Therefore, care has to be taken when this contribution ratio is used in a model to project the likely change in soil respiration under climate change scenarios.

Hanpattanakit et al. (2015) found that heterotrophic respiration is the main contributor to overall magnitude and temporal variation of total soil respiration in a tropical dry forest. Holding partially true with their finding, our result showed that although heterotrophic respiration is the main contributor of total soil respiration in our study site, but the seasonal variation is mainly caused by the autotrophic respiration, suggesting that autotrophic respiration had a major impact on temporal variation in soil respiration rate. This is in line with other studies showed that aboveground phenology affects the magnitude and timing of autotrophic respiration and also its relative contribution to total soil respiration (Comstedt et al., 2011; Savage et al., 2013). The low autotrophic respiration rate during spring and summer of 2012 may be the result of low plant activity caused by water stress (Sperlich et al., 2015). Meanwhile, the steep increase in total soil respiration and autotrophic respiration of *Q. ilex* and *P. halepensis* in autumn of 2011 may due to the increase in fine root production. López et al. (2001) investigated the seasonal root dynamic of *Q. ilex* and found that the fine root production of *Q. ilex* was highest during autumn and winter. Unlike *Q. ilex* and *P. halepensis*, the heterotrophic respiration of *Q. pubescens* showed no difference with total soil respiration. We conjecture two plausible explanations. First, the deep rooting system of *Q. pubescens* implied the relative few fine root amount in the upper soil layer (Herzog et al., 2003), thus the main CO2 fluxes we measured were from deep roots and heterotrophic respiration. Second, given that *Q. pubescens* is deciduous species, it provided more carbon resource for microbial during autumn litterfall, hence increased the heterotrophic respiration rate.

At diurnal scale, the main driver for soil respiration was the temperature. However, we also found that when soil moisture is low, soil respiration became decoupled with soil temperature (with Q_{10} values lower than 1). Meanwhile, during the wet season (spring and autumn 2011), the Q_{10} of heterotrophic respiration was found to be higher than Q_{10} of total soil respiration; this is in agreement with some studies (Rey et al., 2002) but also in contrary to the

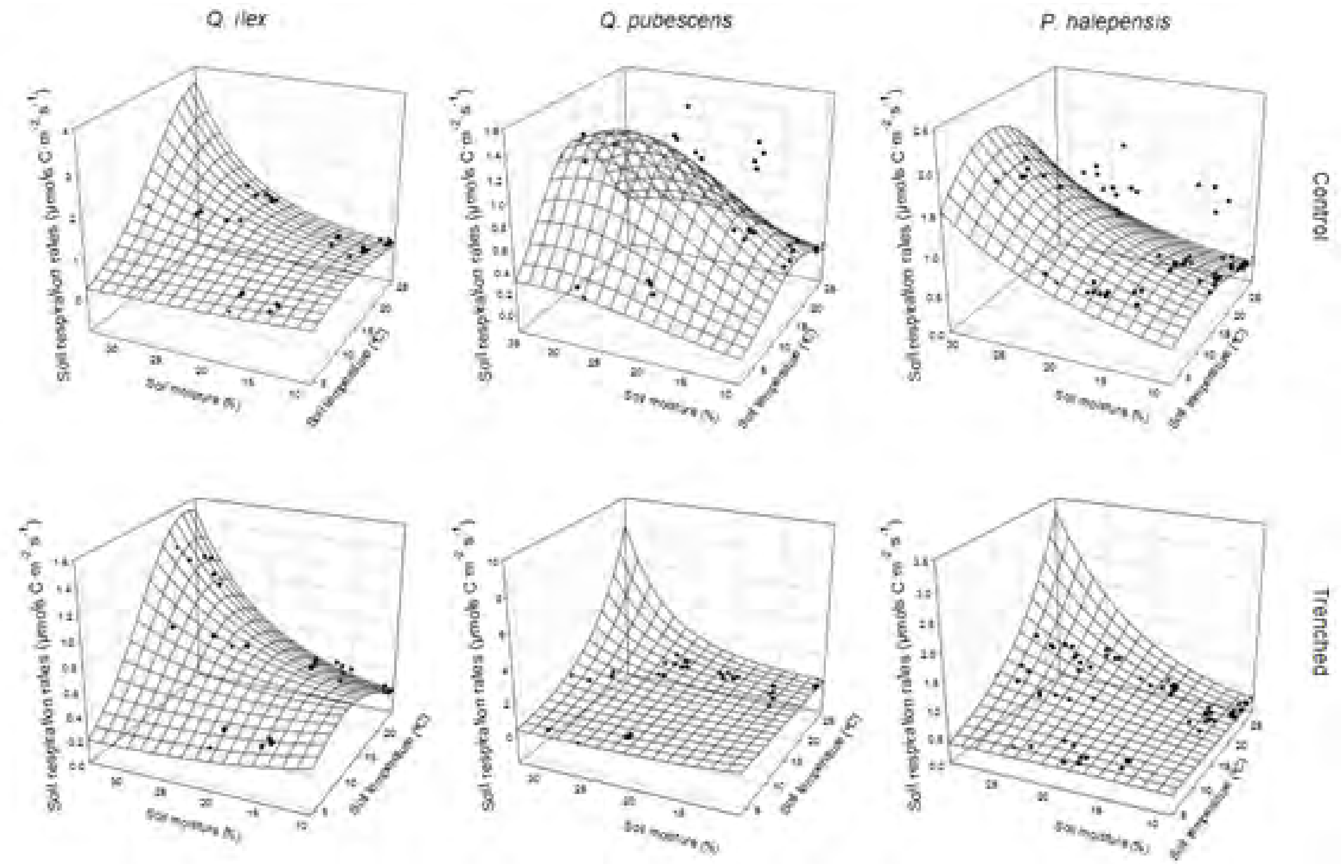


Figure 4.7. The general soil respiration fit of Eq. 4 for soil respiration of *Q. ilex, Q. pubescens* and *P. halepensis* (upper: control, lower: trenched.) The z-axis (soil respiration) in the figures of left panel has been transformed to the units of measured soil respiration to provided clarity and uniformity.

others (Boone et al., 1998; Epron, Daniel et al., 1999). However, for those studies which found higher Q_{10} for autotrophic respiration were carried out in forests where moisture was not limiting. At the seasonal scale, both total soil respiration and heterotrophic respiration were highly correlated with soil moisture and only partially correlated with soil temperature. In other words, the soil respiration in our study site is mainly driven by soil moisture at seasonal scale. On the other hand, studies have found that at the global scale, autotrophic respiration is found to be relatively insensitive to temperature when compared with heterotrophic respiration (Hartley et al., 2007; Heinemeyer et al., 2006; Jiang et al., 2005). Considering the water availability is the main limiting factor of tree growth, it is reasonable that autotrophic respiration, which has found to be positively correlated with photosynthesis, is more sensitive to soil moisture in large scale. This is also consistent with our observation during autumn 2011, when a greater increase in autotrophic respiration than heterotrophic respiration in response to the higher soil moisture.

The observed Q_{10} values for both total soil and heterotrophic respiration in our study were lower than other studies carried out in the Mediterranean region (Raich and Schlesinger, 1992; Rey et al., 2002; Woods et al., 1998). The main reason of difference in Q_{10} values is the different time scale used in calculating Q_{10}. For example, the Q_{10} values obtained in our study were calculated with hourly mean in each season, but the others may calculate with seasonal data. Sampson et al. (2007) reported that basal respiration exhibited significant seasonal variation and suggested that metabolic activity and plant growth phenology are the underlying mechanism. As a result, they indicated that the Q_{10} value may be overestimated if these seasonal variations in basal respiration are not properly account for.

Conclusion

The results from this study indicate that both seasonal total soil and heterotrophic respiration rates were highly correlated with soil moisture. Autotrophic respiration responded to water availability strongly and is the main component that caused the seasonality of soil respiration. The fraction of heterotrophic respiration with total soil respiration varied seasonally, but heterotrophic respiration is the main contributor of total soil respiration in our study site. In our study site, soil temperature alone was the main driver of diurnal variation, while the combination of soil moisture and soil temperature determined the seasonal variations.

Left: Vegetation of study site Collserola. Photo: D. Sperlich

Bottom: Measurement of soil respiration in Collserola. Photo: C.-T. Chang

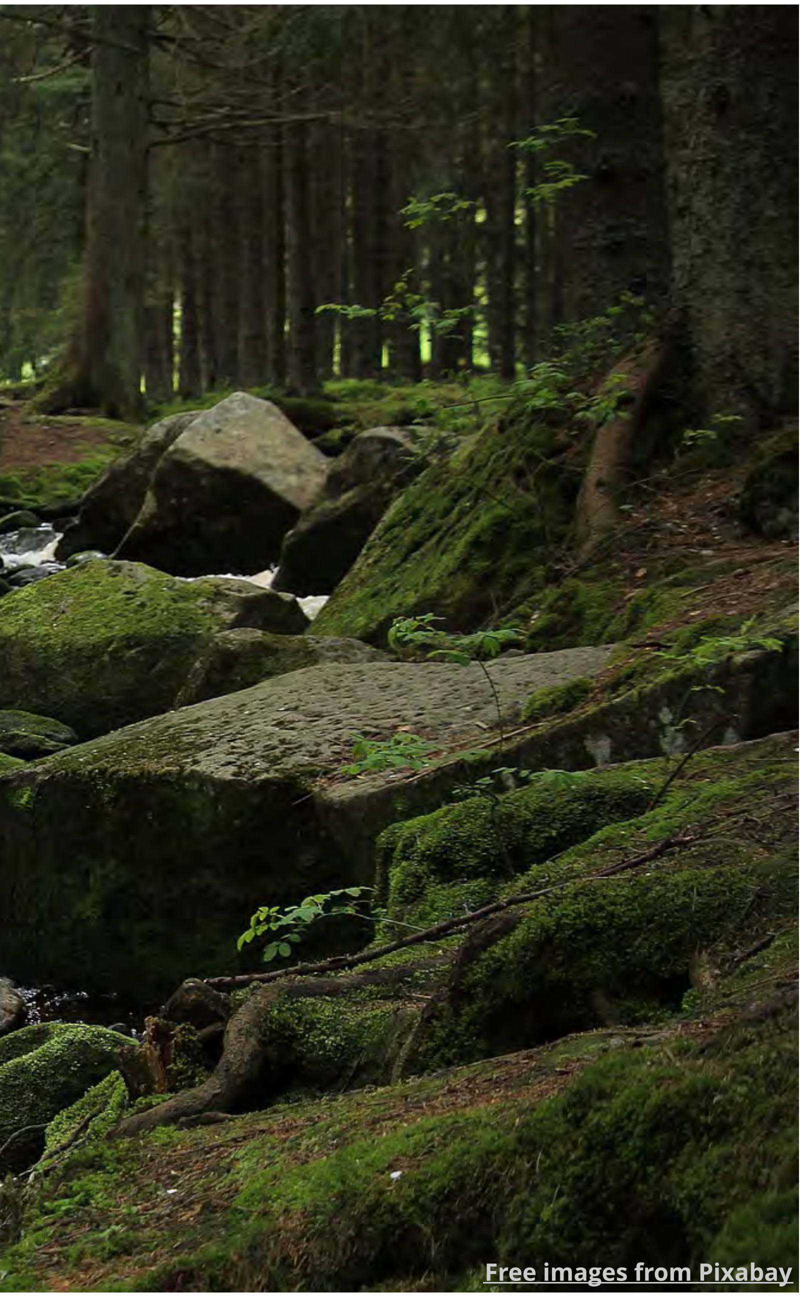
Chapter 5

Does soil moisture overrule temperature dependency of soil respiration in Mediterranean riparian forests?

Introduction

Soil is the largest pool of terrestrial organic carbon in the biosphere, storing around 2344 Pg C in the top 3 m (Jobbágy and Jackson, 2000). Soil respiration (SR) is the main carbon efflux from ecosystems to the atmosphere, accounting for 60-90% of the total ecosystem respiration (Raich et al., 2002; Schimel et al., 2001). Thus, SR plays an important role in the global carbon balance (Raich et al., 2002; Schimel et al., 2001), and even small changes of SR may induce positive feedbacks to climate change (Schlesinger and Andrews, 2000). Therefore, information of how SR interacts with environmental conditions, such as the response of specific components of soil respiration to temperature and moisture changes, will be a key prospect for the improvement of process-based models.

At the large scale, such as ecosystem and biome, net primary production (NPP) may be the most important factor controlling SR (Wardle et al., 2004). NPP provides the inputs to the soil from aboveground litter and also belowground organic detritus (Raich and Potter, 1995). Moreover, root respiration is strongly depended on the translocation of photosynthates from the aboveground part of the plant (Curiel-Yuste et al., 2004). At the smaller scale, SR has been found to be is very sensitive to soil temperature and soil moisture (Fang & Moncrieff, 2001). Soil temperature has been recognized as the most important environmental factor controlling SR because it affects the respiratory enzymes of both roots and soil microbial biomass (Schipper et al., 2014). In general, SR increases exponentially with increases of soil temperature (Epron, Daniel et al., 1999; Lloyd and Taylor, 1994; Mielnick and Dugas, 2000). In contrast to the positive relationship between SR and soil temperature, both very high and very low soil moisture has been shown to diminish the temperature response of SR (Londo et al., 1999;



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Welsch and Hornberger, 2004) due to the potential oxygen limitations under high soil moisture (Skopp et al., 1990) and due to metabolic drought stress under very low soil moisture (Orchard and Cook, 1983). Soil moisture also affects the plant composition and productivity (Häring et al., 2013) and thus, controls the quantity and quality of both soil organic matter (SOM) and root exudates supply (Rustad et al., 2000). Plenty studies have reported the effect of temperature or moisture on SR. However, studies about the combined effects of both factors are relatively few and the information of how soil moisture affects the relationship between soil temperature and SR is scarce (Bowden et al., 1998; Davidson et al., 2006; Curiel Yuste et al., 2007). In Mediterranean and semiarid ecosystems, SR is highly sensitive to soil moisture and the temperature-driven increases in SR are likely dampened by low soil moisture (Conant et al., 2004; Raich and Potter, 1995; Rey et al., 2002). It is still unclear that under which circumstance or environmental condition, the primary control factor of SR would switch from temperature to soil moisture. SR can be divided into autotrophic and heterotrophic respiration by different biological sources (Hanson et al., 2000). Autotrophic respiration, also known as root respiration, is mainly dependent on NPP, tree physiology such as photosynthesis substrate supply (Heinemeyer et al., 2007; Hogberg et al., 2001). Heterotrophic respiration is the sum of microbial decomposition of SOM (Fang et al., 2005; Knorr et al., 2005). In theory, due to the different origins of autotrophic and heterotrophic respiration, they may have different sensitivities toward environmental factors and respond differently to seasonality (Epron et al., 2001; Kuzyakov and Larionova, 2006; Yan et al., 2010).

Riparian areas represent higher soil moisture and more sustained water tables (McGlynn and Seibert, 2003). In these ecosystems, tree species composition and tree growth is strongly influenced by the topographic position concomitant with the changes in the soil water content. Thus, this may indirectly affect SR through litter input and nutrient availability. Because of the retardation of microbial decomposition with the frequent saturation of soil water, riparian areas tend to accumulate more SOM than hillslope areas do (Sjögersten et al., 2006). The main objectives of this study were: (1) to investigate the seasonal variations and relationships between SR and both soil temperature and moisture in a Mediterranean riparian forest along a groundwater level gradient; (2) To determine soil moisture thresholds at which SR is rather controlled by soil moisture than by temperature, even in such non-water stressed environments; (3) To compare SR responses under different tree species present in a Mediterranean riparian forest (*Alnus glutinosa, Populus nigra* and *Fraxinus excelsior*). With these aims, we carried out measurements of SR under different tree species along a groundwater level gradient in a riparian forest in NE Spain. The results of our study may help to better understand the interactions between different components of SR with soil temperature and moisture, as well as the role of different tree species. It also provides relevant information for SR model's parameterization.

Material and methods

Site description

Please refer to Chapter 3.

Experimental design

We divided the groundwater gradient (riparian-hillslope transect) into 4 levels according to

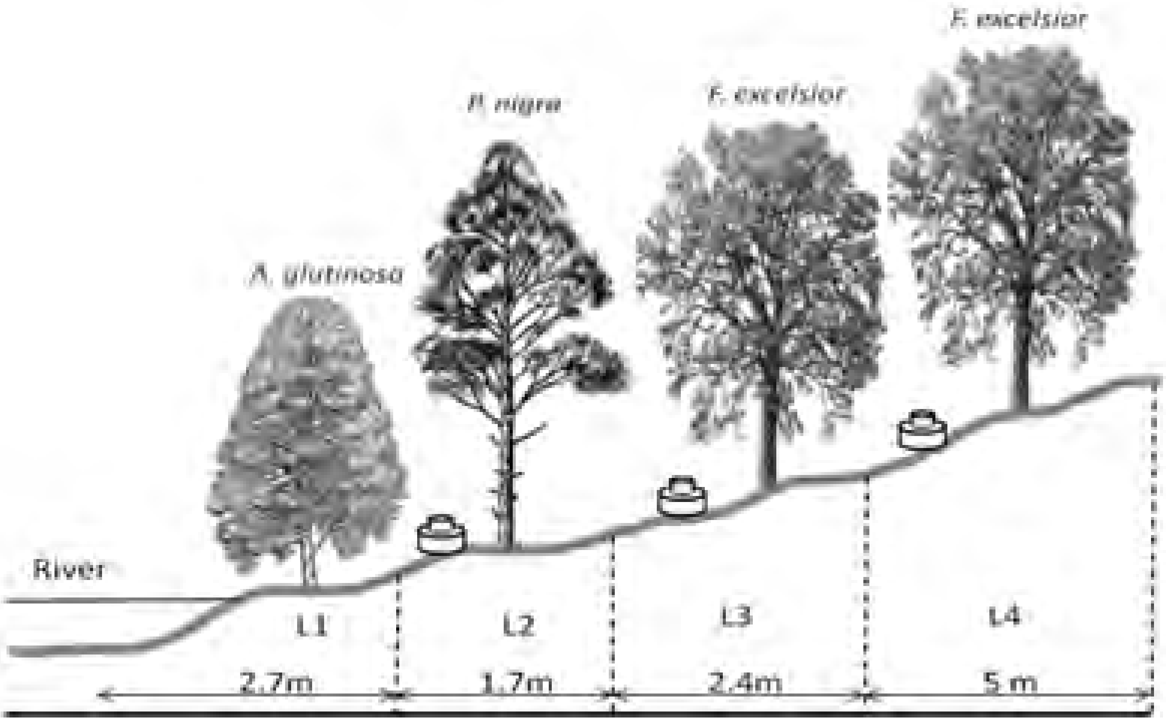


Figure 5.1. Sketch of levels in a gradient of soil water availability with tree species distribution and SRH chamber positions.

the distance from the riverside and tree species composition (Figure 5.1). The distances of level 1 to level 4 (L1 to L4) from the river centre were 2.7, 4.4, 6.8 and 11.8 m, respectively. The three target tree species, *A. glutinosa, P. nigra* and *F. excelsior* were located at level L1, L2 and L3, respectively. To examine the interaction effects on SR of tree species, soil moisture and temperature, we set three transects crossing the riparian-hill to measure the variation of total SR (sum of soil autotrophic and heterotrophic respiration, hereafter referred to collectively as total SR, SRtot) from different tree species. Soil chambers were placed 1.5 m from the stem of the target tree species. Moreover, we also set two transects to measure the topographic effects on soil heterotrophic respiration (SRH). Due to the difficulty of trenching next to the riverbank, chambers for SRH were set only at level L2, L3 and L4. To separate root respiration from SRH, we inserted a PVC tube (diameter: 65cm, height: 40cm) into the soil five months before starting the measurements. To avoid constraints on groundwater table level fluctuations by the PVC tube, we cut two opposite windows on the PVC tube and covered by 65 µm mesh to prevent root growth through the windows.

Stainless-steel rings were inserted permanently into the soil, down to 3 cm depth, as the base of the soil chambers, and kept free from seedlings throughout the experiment duration. The distances of each soil chamber from the riverside varied slightly due to the tree distribution.

Field measurement

SR and soil temperatures were measured seasonally from summer 2011 to autumn 2012. These measurements were conducted continuously for one week within each season. A heavy rainfall event took place in winter 2012, resulting in elevated water levels of the river that washed away most of the litter layers within three meters distance from the river bank.

Soil chambers were protected by placing a 50*50 cm green fine mesh on top to avoid possible heating by direct sun light during the measurements. Soil temperature of 5 cm depth was continuously measured with Pt100 temperature sensors and recorded in parallel with the CO_2 concentration analysis. Thirty cm integral soil moisture (cm3/cm3, SM30) in each level were determined and recorded half-hourly with moisture reflectometer (CS616, Campbell Scientific). Additionally, we also measured 5 cm integral soil moisture (SM5) next to each soil chamber once per day during each measuring field campaign, with impedance probes (Delta-T Theta Probe Soil Moisture Sensor, MI2x, Delta-T Devices, Cambridge, England). A grid of 28 wells (PVC tubes of 35mm in diameter) was installed to monitor groundwater table oscillation. Wells were distributed along the study site and at different distances from the stream: 2.7, 4.4, 6.8, 11.8 m (n=7). Groundwater levels were monitored manually every two weeks using a sounding device with acoustic and light signal (Eijelkamp, Agrisearch Euipment). In autumn of 2012, after concluding the measurements, litter layer and soil samples (15 cm depth) inside each chamber were collected. Litter layer samples were weighted after oven-drying at 65-70°C for 24h. Soil samples were first oven-drying at 105°C and then analyzed to determine their organic carbon and nitrogen content by using Walkley-Black method and Kjeldahl method, respectively.

Statistical analysis

Statistical analyses were performed with PASW statistics 18 (SPSS Inc., 2009, Chicago, IL). The missing data of soil temperatures were estimated from air temperature values based on a regression analyses between air and soil temperatures. SR, soil temperature and soil moisture data were analyzed using ANOVA to examine whether seasonal SR rates were different among levels and tree species. Data used to test the significance in ANOVA were based on daily means. Least significant difference (LSD) was used to detect differences among levels and tree species for each season. We used regression analysis to examine the relationship between SR and soil temperature. A univariate exponential equation was fitted van't Hoff (1898)

$$SR = R_0(e^{KT})$$

where SR is soil respiration rate (μmol C $m^{-2}\cdot s^{-1}$), T is soil temperature (°C), R_0 is basal respiration and K is the temperature sensitivity of SR. A Q_{10} value for the whole measurement period was computed for each topographic position and tree species on the basis of daily average SR rate and soil temperature. In addition, we estimated specific Q_{10} values for summer of 2011 and 2012. Data collected were fitted to the exponential equation. The apparent Q_{10} was calculated as:

$$Q_{10} = e^{10K}$$

In order to understand the interaction between soil temperature and soil moisture and the effect of soil moisture on regulating SR, we applied recursive partitioning analysis to search for the threshold of soil moisture. As models based on partitioning can only handle linear models, the equation above was transformed by linearizing with logarithms:

$$\mathbf{Ln\ SR = ln\ R_0 + KT}$$

Logarithmic transformed SR values were used as the dependent variable. Once the soil moisture thresholds were obtained, linear and nonlinear regression analyses were used to determine the relationship between SR, soil temperature and soil moisture in each soil moisture interval. The recursive partitioning analysis was conducted in the R statistical environmental using the *party* package (Zeileis et al., 2008).

Results

Seasonal variation of groundwater level, soil moisture and soil temperature

Seasonal variation of air temperature and precipitation was remarkable. The precipitation in 2011 was significantly higher than in 2012, especially in summer. Summer precipitation in 2011 was four

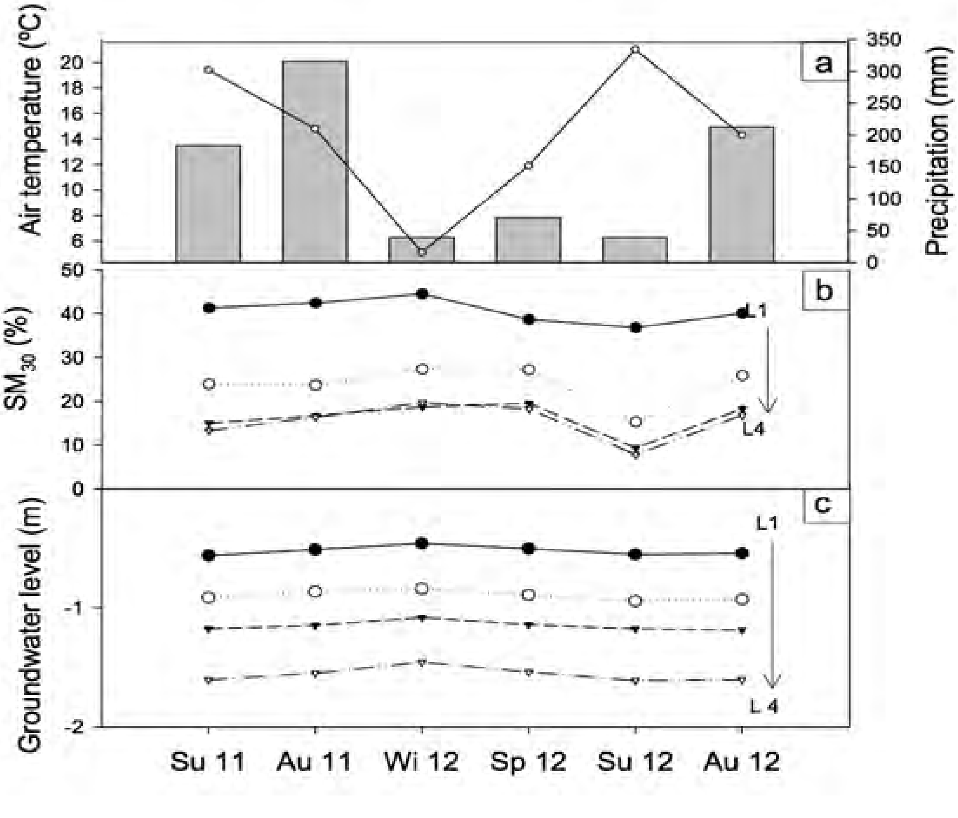
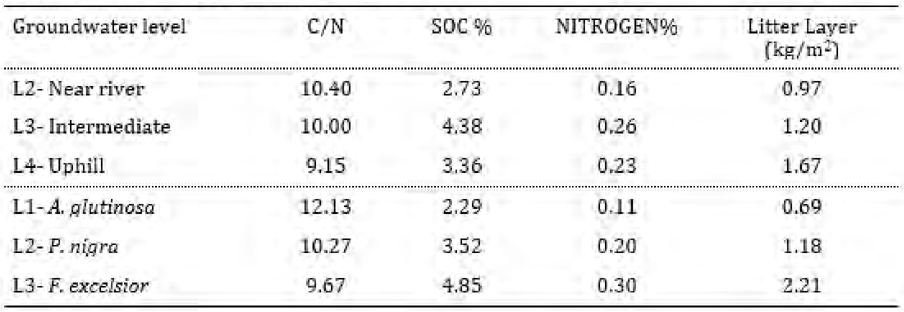


Figure 5.2. Seasonal changes of summer 2011 (Su11), autumn 2011 (Au11), winter 2012 (Wi 12), spring 2012 (Sp12) and autumn 2012 (Au12) in **a.** mean seasonal air temperature and precipitation; **b.** 30 cm integral soil moisture (SM_{30}); **c.** groundwater level, value represents the depth of groundwater level from soil surface (L1, L2, L3 and L4).

Table 5.1. Soil carbon and nitrogen content and litter L and F organic horizons on soil floor dry weight from soil respiration chambers.



Groundwater level	C/N	SOC %	NITROGEN%	Litter Layer (kg/m^2)
L2- Near river	10.40	2.73	0.16	0.97
L3- Intermediate	10.00	4.38	0.26	1.20
L4- Uphill	9.15	3.36	0.23	1.67
L1- *A. glutinosa*	12.13	2.29	0.11	0.69
L2- *P. nigra*	10.27	3.52	0.20	1.18
L3- *F. excelsior*	9.67	4.85	0.30	2.21

times higher (183 mm) than in 2012 (39 mm). SM_{30} was significantly higher at L1 (Figure 5.2). In summer 2012, due to a remarkable drought, SM_{30} at L1 only showed a small decrease with respect to summer 2011; while at the other levels (L2, L3 and L4) SM_{30} was markedly decreased. Groundwater levels showed no seasonal variation, but were significantly different among them. Soil nearby the river contained less organic carbon and nitrogen, but a higher C:N ratio, with a C:N ratio of 12.13 (Table 5.1). Soil C:N ratio decreased from the riverside to uphill whereas the dry weight of litter layer increased from the riverside to uphill. The largest amount of dry weight of litter layer was found under *F. excelsior*, and coincided with the highest soil organic carbon (SOC) and soil nitrogen concentration among levels.

Seasonal variation of SR_H along hillslope transect

SR_H rates ranged from 0.17μmol C m-2s-1 (in winter, L4) to 1.69μmol C m-2s-1 (in summer, L2, Figure 5.3). SR_H decreased significantly from riparian zone (L2) to hill zone (L4), especially in summer. SR_H measured from different levels were significantly different in all seasons ($P<0.05$). SR_H at L2 had a higher variability during the whole experiment. Minimum soil temperature coincided with maximum SM_5 in winter while maximum soil temperature was recorded in summer when SM_5 was lowest. SR_H varied markedly during the year following the change of soil temperature from summer 2011 to spring 2012, and the changes of SM_5 for summer and autumn 2012. As expected, SR_H was lower during winter when soil temperatures were the lowest of the year, and SR_H was higher during the growing season. SM_{30} at L2 was significantly lower than SM_{30} at L1, but higher than SM_{30} at L3 and L4.

Tree species effects on SR_{tot}

The observed variation of SR_{tot} of the three tree species followed the change of soil temperature over the year (Figure 5.3). SR_{tot} of *P. nigra* was the highest one, especially during summer, and SR_{tot} of *A. glutinosa* was the lowest one throughout the year. There were no significant differences of soil temperatures among tree species locations. SM_5 did not differ among tree species location but there was a tendency towards a higher SM_5 under *F. excelsior*. SM_{30} was significantly different between levels for all seasons. The variation of SM_{30} at L1 was lower and showed less seasonal variability, maintaining most of the SM_{30} values around 40%. During both summers 2011 and 2012, SM_{30} at L3 dropped to around 10%, which is even lower than the SM_5 at L4 where *F. excelsior* is found.

Drought and rain pulse effects on SR

The precipitation of 39 mm of summer 2012 was 21% lower than the precipitation of summer 2011. This lower precipitation caused a significant reduction of around 50% of SM_5, 14-35% of SM_{30} and at the same time a reduction of SR between 21 and 49%. The Q_{10} values ranged from 0.97 to 1.40 in summer 2011 and 0.63 to 1.14 in summer 2012 (Table 5.2). A rainfall event (13 mm) during the measurement period of summer 2012 caused a significant increase of soil moisture and SR rates at all levels (L1 to L4). The SM_5 increased around 21-74% after the rainfall event even though it only caused a 0-20% increase of the SM_{30} (Table 5.3). This rainfall event caused a sharp increase of SR from 0.41-0.99 μmol C $m^{-2}s^{-1}$ to 0.59-1.66 μmol C $m^{-2}s^{-1}$, which corresponds to an increase of SR around 34 to 68%.

The switch of primary control factor of SR

We identified three SM_5 intervals for each SR_H and SR_{tot} (Table 5.4), which suggest the existence of thresholds in soil moisture effect. SR was positively related ($P<0.001$) to soil temperature when soil moisture was higher than 23% for SR_H, or higher than 27% for SR_{tot}. The lower threshold for SR_H and SR_{tot} were 20% and 17% of SM_5 respectively. Under the low bound value, SR_H showed a significantly positive relation with SM_5 (Figure 5.4, linear

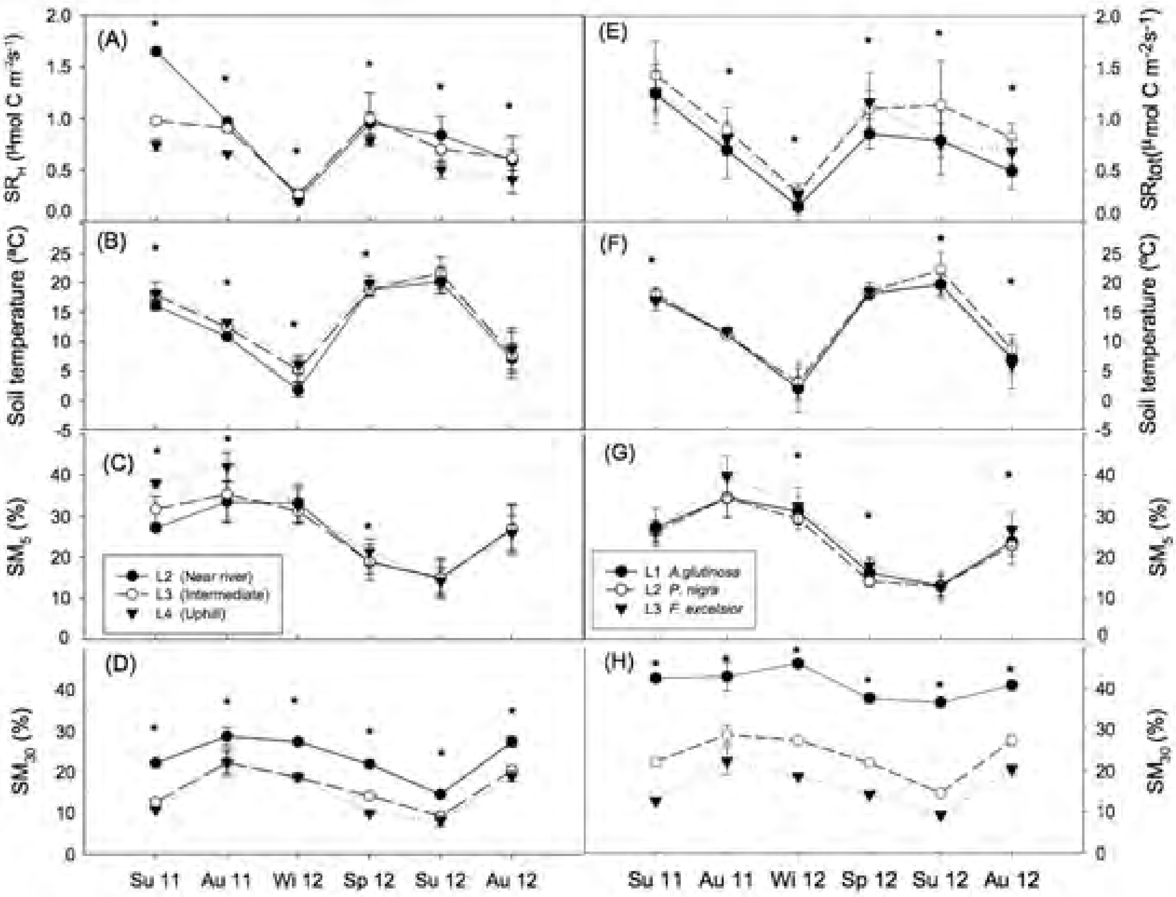
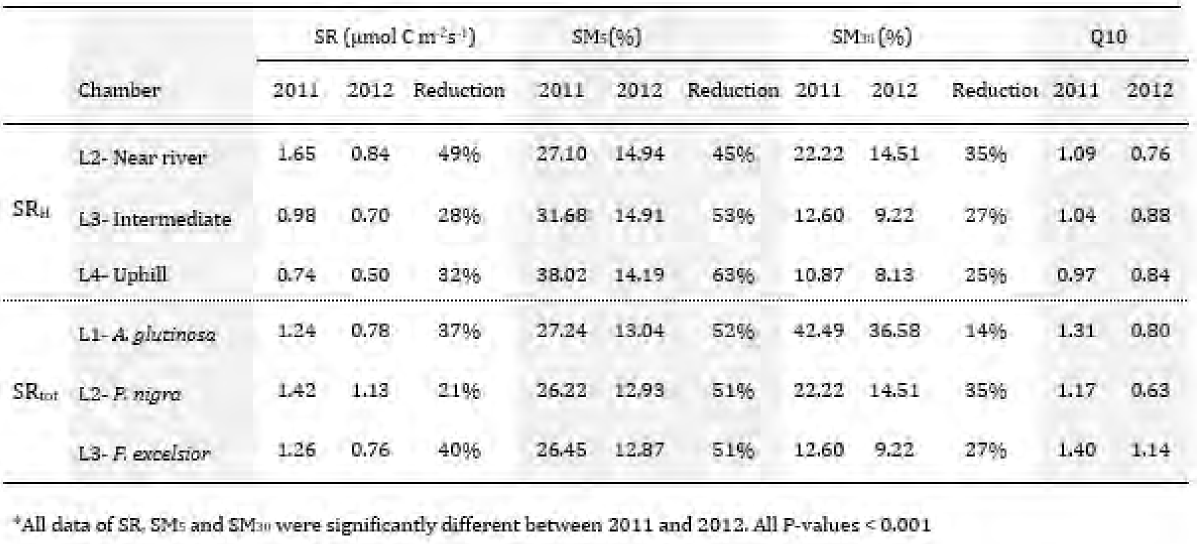


Figure 5.3. Seasonal changes of summer 2011 (Su11), autumn 2011 (Au11), winter 2012 (Wi 12), spring 2012 (Sp12) and autumn 2012 (Au12) in **A-D**. Data of soil heterotrophic respiration rates (SRH). **A**. SR$_H$ along groundwater level gradient. **B**. 5 cm soil temperature. **C**. 5 cm integral soil moisture (SM$_5$). **D**. 30 cm integral soil moisture (SM$_{30}$). **E-H**. Data of total soil respiration rates (SR$_{tot}$) of three tree species. **E**. SR$_{tot}$ under different tree species. **F**. 5 cm soil temperature. **G**. 5 cm integral soil moisture (SM$_5$). **H**. 30 cm integral soil moisture (SM$_{30}$). All values are mean ±SD. Data points marked with * indicate significant differences among species at *P*≤0.05 (Detail please refer to Annex A & B).

Table 5.2. Comparison of soil respiration rates (SR), soil moistures (SM) and Q$_{10}$ values in 2011 and 2012 summer campaigns. Heterotrophic SR (SR$_H$). Total SR (SR$_{tot}$). Five cm integral soil moisture (SM$_5$). Thirty cm integral soil moisture (SM$_{30}$).

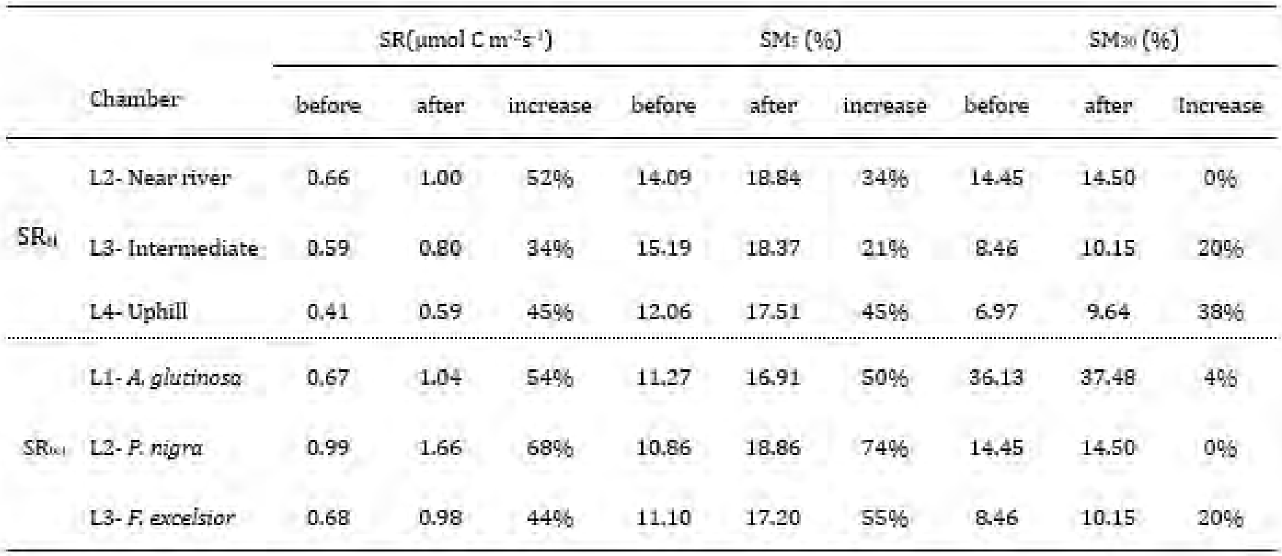


		SR (µmol C m^{-2}s^{-1})			SM$_5$(%)			SM$_{30}$ (%)			Q10	
	Chamber	2011	2012	Reduction	2011	2012	Reduction	2011	2012	Reductioı	2011	2012
SR$_H$	L2- Near river	1.65	0.84	49%	27.10	14.94	45%	22.22	14.51	35%	1.09	0.76
	L3- Intermediate	0.98	0.70	28%	31.68	14.91	53%	12.60	9.22	27%	1.04	0.88
	L4- Uphill	0.74	0.50	32%	38.02	14.19	63%	10.87	8.13	25%	0.97	0.84
SR$_{tot}$	L1- *A. glutinosa*	1.24	0.78	37%	27.24	13.04	52%	42.49	36.58	14%	1.31	0.80
	L2- *P. nigra*	1.42	1.13	21%	26.22	12.93	51%	22.22	14.51	35%	1.17	0.63
	L3- *F. excelsior*	1.26	0.76	40%	26.45	12.87	51%	12.60	9.22	27%	1.40	1.14

*All data of SR, SM$_5$ and SM$_{30}$ were significantly different between 2011 and 2012. All P-values < 0.001

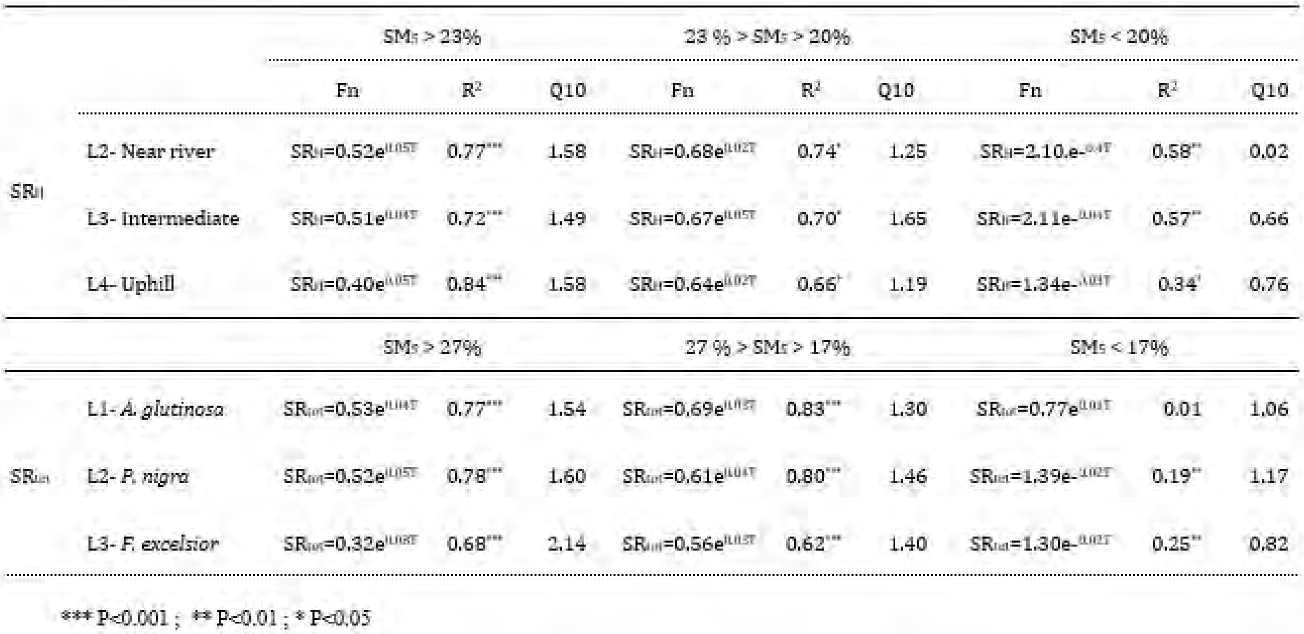
regression with r2 of 0.89, 0.92 and 0.91 for L2, L3 and L4) while SR$_{tot}$ showed a weak positive relation with SM$_5$ (Figure 5.5, linear regression with r2 of 0.56, 0.11 and 0.10 for L1, L2 and L3). The exponential model based on soil temperature accounts for 68% to 84% of the variation in both SR$_H$ and SR$_{tot}$ rates at the higher SM$_5$ interval values. The fitted Q$_{10}$ values in high SM$_5$ interval ranged from 1.49 to 2.14. Generally the Q$_{10}$ values of SR$_H$ were lower than the Q$_{10}$ of SR$_{tot}$.

Table 5.3. Comparison of soil respiration rates (SR), and soil moistures (SM) after a rainfall event of 13.5 mm in summer 2012. Heterotrophic SR (SR_H). Total SR (SR_{tot}). Five cm integral soil moisture (SM_5). Thirty cm integral soil moisture (SM_{30}). Data were averaged for two days before and two days after the rainfall event



		SR(µmol C $m^{-2}s^{-1}$)			SM_5 (%)			SM_{30} (%)		
	Chamber	before	after	increase	before	after	increase	before	after	Increase
SR_H	L2- Near river	0.66	1.00	52%	14.09	18.84	34%	14.45	14.50	0%
	L3- Intermediate	0.59	0.80	34%	15.19	18.37	21%	8.46	10.15	20%
	L4- Uphill	0.41	0.59	45%	12.06	17.51	45%	6.97	9.64	38%
SR_{tot}	L1- *A. glutinosa*	0.67	1.04	54%	11.27	16.91	50%	36.13	37.48	4%
	L2- *P. nigra*	0.99	1.66	68%	10.86	18.86	74%	14.45	14.50	0%
	L3- *F. excelsior*	0.68	0.98	44%	11.10	17.20	55%	8.46	10.15	20%

Table 5.4. Exponential relationships between soil respiration (SR) and soil temperature (T), and Q_{10} for different SM_5 intervals. Heterotrophic SR (SR_H). Total SR (SR_{tot}). (SM_5) is 5cm integral soil moisture.



		$SM_5 > 23\%$			$23\% > SM_5 > 20\%$			$SM_5 < 20\%$		
		Fn	R^2	Q10	Fn	R^2	Q10	Fn	R^2	Q10
SR_H	L2- Near river	$SR_H=0.52e^{0.05T}$	0.77^{***}	1.58	$SR_H=0.68e^{0.02T}$	0.74^{*}	1.25	$SR_H=2.10.e^{-0.4T}$	0.58^{**}	0.02
	L3- Intermediate	$SR_H=0.51e^{0.04T}$	0.72^{***}	1.49	$SR_H=0.67e^{0.05T}$	0.70^{*}	1.65	$SR_H=2.11e^{-0.04T}$	0.57^{**}	0.66
	L4- Uphill	$SR_H=0.40e^{0.05T}$	0.84^{***}	1.58	$SR_H=0.64e^{0.02T}$	0.66^{*}	1.19	$SR_H=1.34e^{-0.03T}$	0.34^{*}	0.76
		$SM_5 > 27\%$			$27\% > SM_5 > 17\%$			$SM_5 < 17\%$		
SR_{tot}	L1- *A. glutinosa*	$SR_{tot}=0.53e^{0.04T}$	0.77^{***}	1.54	$SR_{tot}=0.69e^{0.03T}$	0.83^{***}	1.30	$SR_{tot}=0.77e^{0.01T}$	0.01	1.06
	L2- *P. nigra*	$SR_{tot}=0.52e^{0.05T}$	0.78^{***}	1.60	$SR_{tot}=0.61e^{0.04T}$	0.80^{***}	1.46	$SR_{tot}=1.39e^{-0.02T}$	0.19^{**}	1.17
	L3- *F. excelsior*	$SR_{tot}=0.32e^{0.08T}$	0.68^{***}	2.14	$SR_{tot}=0.56e^{0.03T}$	0.62^{***}	1.40	$SR_{tot}=1.30e^{-0.02T}$	0.25^{**}	0.82

*** $P<0.001$; ** $P<0.01$; * $P<0.05$

Discussion

Effect of groundwater level and soil moisture on SR

In studies of Martin and Bolstad (2005) and Pacific et al. (2008), it was indicated that the amount and availability of soil water varies depending on landscape position and topography. Both studies also show that small differences in micro-topography appear to be important in driving soil moisture conditions. This is in accordance with our results; the overall seasonal trends of soil moisture were similar, but differences in the relative magnitude of soil moisture still can be found between levels.

In our study site, the SR_H was significantly higher at L2 and decreased with the distance from the river. At the same time, SRtot of *A. glutinosa* at L1 was significantly lower than the other two species found at L2 and L3. This result could be explained by limitations to SR imposed by the groundwater level in two different ways. First, when groundwater level is low, drought stresses soil microbial and root respiration activity, and secondly when groundwater level is high and close to topsoil surface, it limits soil aeration and likely reduces the effective respiring soil volume. Pacific et al. (2008) showed that the soil CO_2 concentrations were significantly higher in the riparian zone as a result of higher soil moisture. In contrast, Zanchi et al. (2011) found lower SR in plots after drainage, and suggested that the low C and N content in the topsoil near to the river, where most of the soil CO_2 respiration is produced, could partially explain that low SR. The discrepancy of these two studies could be associated to the different drainage regimes, as the poorly drained plots imply an anaerobic inhibition of SR. In our study, however, SR_H was measured at L2, L3 and L4 under well-drained conditions and SR_H decreased concomitantly with the decrease in the availability of soil water. Nonetheless, SR_{tot} of *A. glutinosa* was measured at L1, where the soils sometimes experienced flooding or not well-drained conditions, and the root respiration may be inhibited by the high groundwater level. Additionally, landscape position and topography not only altered the availability of soil water but also affected the annual range of soil moisture. This is shown by Zanchi et al. (2011) studying riparian SR in Amazonia. They indicate that riparian soil is very sensitive to the changes of water flooding regime. The high groundwater table in riparian zones implies intermittent anaerobic conditions and the inhibition of diffusion during water saturation. These differences in soil moisture caused by site topography may result in differences in SR even though the soil temperatures were similar between sites. The different behaviours of SR_H and SR_{tot} from L1 to L4 from our results indicate a different contribution of SR_H to SR_{tot}. As the root system of *A. glutinosa* may constantly experience a saturated water regime, the relative contribution from root respiration may be much lower than the one of the other two species.

Rain pulse and drought effects on SR

The Mediterranean climate is characterized by summer droughts that affect particularly the top soil layers, therefore rainfall events during these dry periods can trigger abrupt increases in SR for days (Bowling et al., 2011; Cisneros-Dozal et al., 2007; Lee et al., 2004; Unger et al., 2010). Lee et al. (2004) simulated precipitation and found that hardwood forest floors were very sensitive to changes in moisture in the upper soil layers. Moreover, Wang et al. (2012) noted that the response of litterfall respiration is very sensitive to rainfall, and the increase in soil moisture by rainfall primarily enhanced the litterfall respiration but depressed mineral SR. Similar results were published by Casals et al. (2011) reporting that SR after a precipitation pulse was mostly derived from SR_H with a contribution up to 70% of SR_{tot}. Hence, our findings seem to be consistent with these previous studies.

Confounded of temperature and moisture effects on SR

This study aimed at assessing the importance of soil moisture on soil respiration and determining the threshold of soil moisture at which soil moisture overrules temperature in controlling SR. The response of SR to soil moisture has been widely studied and described by various types of functions, such as linear or logarithmic functions depending on the soil type, climate or vegetation type (Comstedt et al., 2010; Epron, Daniel et al., 1999; Orchard and Cook, 1983). In our study, the seasonal courses of SRH and SRtot generally followed the seasonal cycle of temperature, but moderated by soil moisture. Such a relationship is in agreement with other previous studies (Davidson et al., 1998; Martin and Bolstad, 2005; Wang et al., 2013).

The positive linear relationship between SR and soil moisture in low soil moisture conditions found in our work agrees with many previous studies where low soil moisture constrains SR (Almagro et al., 2009; Keith et al., 1997; Qi and Xu, 2001; Rey et al., 2002; Y. Wang et al., 2013; Woods et al., 1998). In our study, lower soil moisture and warmer temperatures actually reduced SR rates, resulting in lower Q_{10} values at the lower soil moisture. A similar decline of Q_{10} with decreasing soil moisture has been reported by Conant et al. (2004), Curiel Yuste et al. (2003) and Wen et al. (2006). Low soil water content not only reduces the contact between substrate and

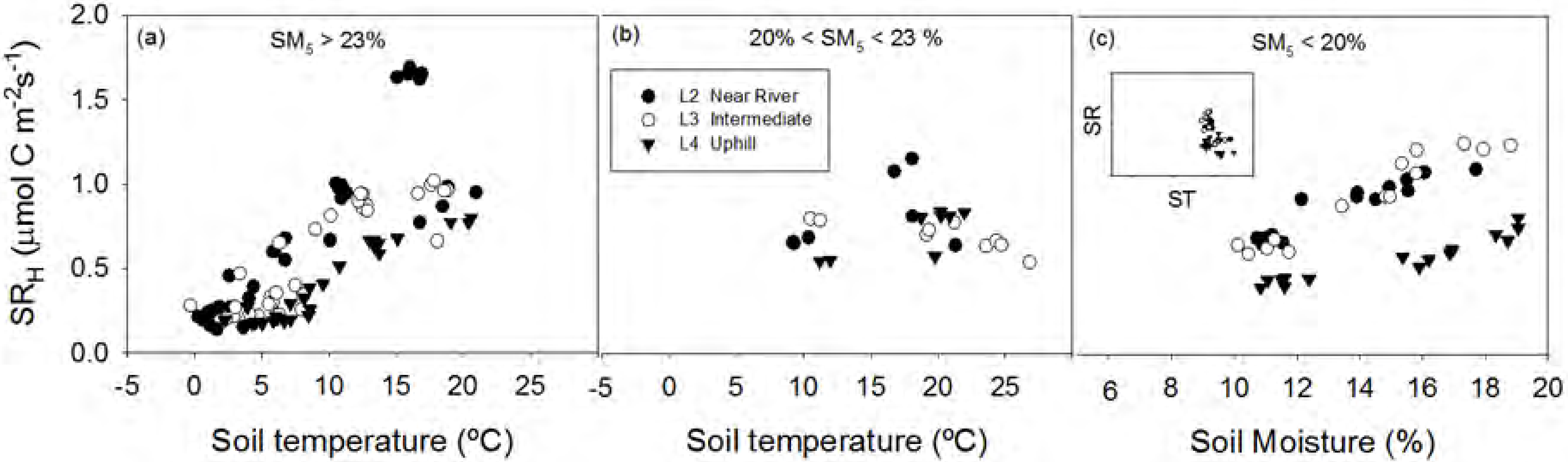


Figure 5.4. Differentiation of soil temperature (ST) and soil moisture (SM) as primary controlling factor for SR$_H$. (A) At SM$_5$ ≥ 23%, positive correlations of SR$_H$ with soil temperature in all levels. (B) At 20 % ≤ SM$_5$ < 23%, transition with no clear relationship of neither SM nor ST with SR$_H$. (C) At SM$_5$ < 20%, no relationship between SR and ST as the inset figure shows, it switches from ST to SM$_5$ as controlling factor with positive correlations between SR$_H$ and SM$_5$ for all levels. Campaigns with SM$_5$ < 20% were all from spring and summer 2012. SM$_5$ (5 cm integral soil moisture)

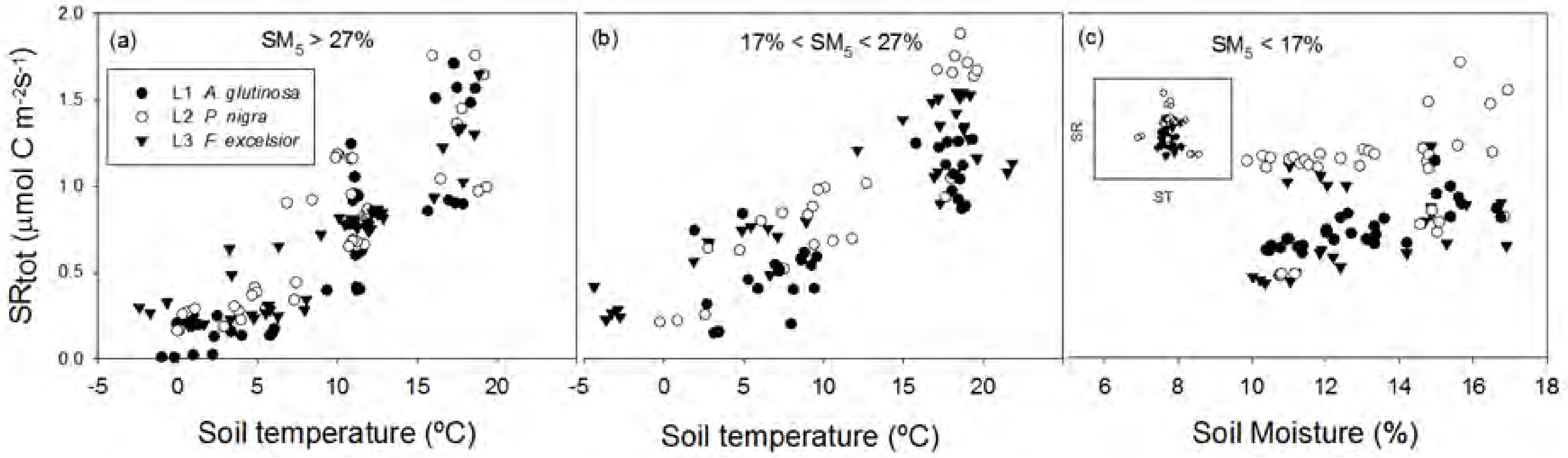


Figure 5.5. Differentiation of soil temperature (ST) and soil moisture (SM) as primary controlling factor for SR$_{tot}$. (A) At SM$_5$ ≥ 27%, positive correlations of SR$_{tot}$ with soil temperature under all tree species. (B) At 17 % ≤ SM5 < 27%, positive but slightly weaker correlations of SR$_{tot}$ with soil temperature under all tree species. (C) SM$_5$ < 17%, no relationship between SR and ST as the inset figure shows, it switches from ST to SM$_5$ as controlling factor with positive correlations between SR$_{tot}$ and SM$_5$ for all tree species. Campaigns with SM$_5$ < 17% were all from spring and summer 2012. SM$_5$ (5 cm integral soil moisture)

enzymes and microbes, it also decreases the substrate supply due to the increased drying-out of litter and topsoil layer (Davidson et al., 2006). Another possible reason for the observed lower Q_{10} is that the reduction of photosynthesis decreases the translocation of photosynthates to the rhizophere (Högberg et al., 2001; Nordgren et al., 2003).

In a Norway spruce stand, Gärdenäs (2000) found that litter moisture explained most of the variation of SR whereas mineral soil moisture, air or litter temperatures were not significantly affected. Our results showed that the seasonal variations of SR_H and SR_{tot} were mainly controlled by soil temperature, with secondary influence by soil moisture (SM_5). Using the recursive partitioning method, we have identified clear thresholds for SM_5 effects on the temperature sensitivity of SR. Soil moisture thresholds at which SR temperature sensitivity is reduced have been found in several studies, from different ecosystems (Fang and Moncrieff, 2001; Gaumont-Guay et al., 2006; Jassal et al., 2008; Lellei-Kovács et al., 2011; Palmroth et al., 2005; Y. Wang et al., 2013). However, the threshold values in soil moisture seem to be site specific, as the factors limiting water uptake by plants and microbes may differ among ecosystems. Even in the same climate region, different soil moisture thresholds have been found from previous studies. For example, Almagro et al. (2009) investigated how soil moisture modulated the sensitivity of soil respiration in different ecosystems in the Mediterranean region and found that the threshold value of soil moisture was 10%. Above this soil moisture values, Q_{10} ranged from 1.86 to 2.20 and decreased to 0.44 to 0.63 when soil moisture was lower than 10%. Furthermore, Rey et al. (2002) found in a Mediterranean oak forest that soil temperature accounted for 85% of the variation of SR when soil moisture was above 20% with a Q_{10} value of 2.34. Nonetheless, Xu and Qi (2001) found that with soil moisture higher than 14%, the Q_{10} value was 1.8 and decreased to 1.4 when soil moisture was lower than 14%.

Other factors affecting SR

In addition to soil moisture threshold values, we also found variations of SR_H and SR_{tot} among position and tree species in each soil moisture interval. For example, when SM_5 was lower than 20%, SR_H measured at L4 was always lower than SR_H measured at L2 and L3. When SM_5 was lower than 17%, SRtot of *P. nigra* was significantly higher than for the other two species, suggesting that there are still other factors affecting SR_H and SR_{tot} variations. Several explanations for this result are plausible. First, spatial variability in vegetation can affect SR due to differences in root respiration and the quantity and quality of detritus (Raich and Tufekcioglu, 2000). These biophysical gradients across landscape positions can lead to strong spatial heterogeneity in SR. Tree species in our study site exhibit different litterfall temporal patterns and may also contribute to the seasonal variation of the availability of SOC and nutrients to the microbial community and roots. Second, the vitality of tree species in responses to soil water regime could generate different root respiration rates. Additional data of daily sapflow of the studied trees from our study site (data not shown) confirmed the difference in tree transpiration and growth activity. For example, the water use efficiency of *P. nigra* was highest, followed by *F. excelsior* and *A. glutinosa*. Besides, the mean diameter at breast height (DBH) of *P. nigra* is larger than mean DBH of the other tree species. *P. nigra* may be more efficient in uptaking water and nutrients compared to the other two tree species.

Conclusions

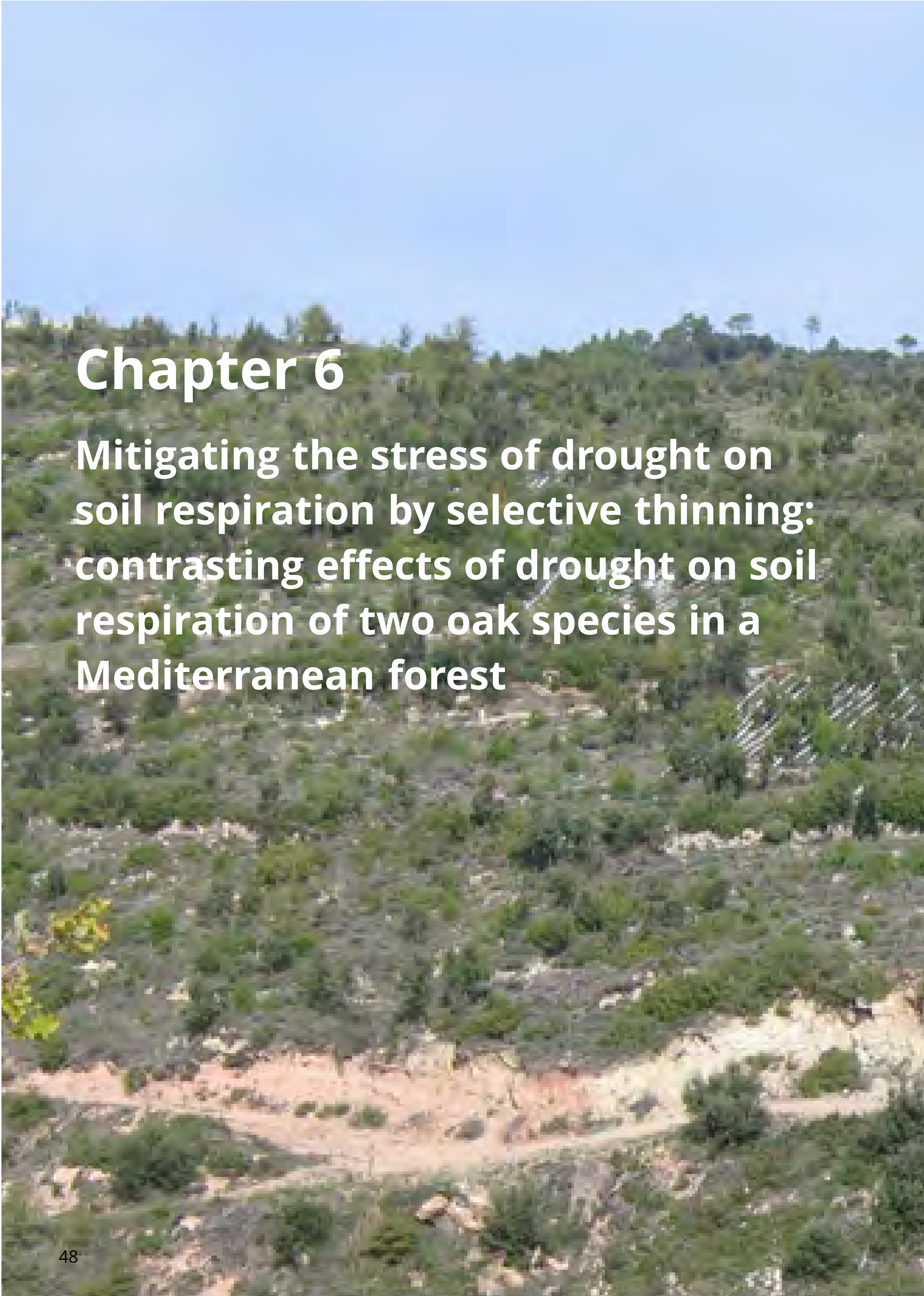
This research demonstrates how soil moisture constrains the relationship between SR and soil temperature. We present critical threshold values of soil moisture where SR dependency on soil moisture overrules soil temperature dependency. Our results also reveal the importance of soil moisture as a predictor of SR even in a non-water-stressed environment such as riparian forests. Our findings provide support for modelling approaches that include soil temperature and soil moisture, by making available parameters to predict SR rates. This study has also implications for a better understanding of global change impacts on the carbon cycle, since soil water availability will likely become an increasingly crucial factor for some regions that are expected to suffer more frequent and severe droughts under climate change.

Annex A. Analysis of variance (ANOVA) statistics for soil temperature (ST), soil moisture (SM):SM_5, SM_{30}, and heterotrophic soil respiration (SR_H) of different levels of the same season (Mean±SD). LSD was used to test post hoc. Means with the same letter are not significantly different ($P < 0.05$).

Champaign	ST			SM_5			SM_{30}			SR_H		
	L2	L3	L4	L2	L3	L4	L2	L3	L4	L2	L3	L4
2011 Summer	16.11±0.73(A)	17.88±0.88(AB)	18.12±2.02(B)	27.11±0.74(A)	31.68±3.20(B)	38.02±0.87(C)	22.22±0.23(A)	12.60±0.36(B)	10.87±0.1(C)0	1.65±0.03(A)	0.98±0.03(B)	0.52±0.32(C)
2011 Autumn	10.87±0.30(A)	12.48±0.24(B)	13.33±0.25(C)	33.51±4.75(A)	35.33±7.00(A)	42.05±3.40(B)	28.69±2.20(A)	22.31±3.32(B)	22.37±2.51(B)	0.97±0.04(A)	0.90±0.04(B)	0.66±0.01(C)
2012 Winter	1.75±1.22(A)	5.13±1.92(B)	6.11±1.50(B)	33.14±4.50(A)	31.21±3.00(A)	32.52±4.30(A)	27.35±0.22(A)	18.61±0.18(B)	18.90±0.24(C)	0.22±0.66(AB)	0.26±0.05(A)	0.20±0.03(B)
2012 Spring	18.82±1.13(A)	18.81±1.04(A)	20.03±1.25(B)	18.73±4.31(A)	18.87±2.89(A)	21.26±3.18(A)	21.91±0.41(A)	14.17±0.51(B)	9.96±0.25(C)	0.95±0.11(A)	1.00±0.25(A)	0.78±0.05(B)
2012 Summer	20.18±2.05(A)	21.70±2.74(A)	20.80±2.40(A)	14.94±4.99(A)	14.91±4.35(A)	14.19±3.04(A)	14.51±0.07(A)	9.22±0.78(B)	8.14±1.25(C)	0.84±0.18(A)	0.70±0.14(B)	0.50±0.08(C)
2012 Autumn	7.11±2.58(A)	7.66±3.98(A)	3.73±3.38(A)	26.87±6.08(A)	26.77±5.80(A)	25.84±4.21(A)	27.27±1.12(A)	20.38±1.03(B)	19.01±1.14(C)	0.59±0.10(A)	0.61±0.21(A)	0.41±0.14(B)

Top: automatic changeover open system and batteries. System power was supplied by six batteries. Photo:C.-T. Chang

Right: Canopy of study site Font de Regàs. Photo:C.-T. Chang



Chapter 6

Mitigating the stress of drought on soil respiration by selective thinning: contrasting effects of drought on soil respiration of two oak species in a Mediterranean forest

Photo: Pedro Vilar

Introduction

Forest ecosystems contain one of the largest stocks of carbon and they represent one of the most important potential carbon sinks (Pan et al., 2011). Globally, forest ecosystems are estimated to contain 681 ± 66 Pg of carbon, with ca. 383 ± 28 Pg C (44%) of that total contained in the soil (Pan et al., 2011). Therefore, forest soil respiration (SR) plays a crucial role in regulating soil carbon pools and carbon dynamics of terrestrial ecosystems under global warming (Melillo et al., 2002; Schlesinger and Andrews, 2000). Climate change scenarios project increases in mean annual temperature, increases in evapotranspiration, and decreases in precipitation (Giorgi, 2006; Le Quéré et al., 2013; Rowell and Jones, 2006). Hence, future climate change is expected to have a great impact on SR by altering its main environmental drivers: temperature and moisture (Raich and Schlesinger, 1992; Raich and Potter, 1995; Gärdenäs, 2000; Fang and Moncrieff, 2001). Because forest ecosystems may mitigate climate change through carbon sequestration (Sullivan et al., 2008), the effects of forest management practices on ecosystem carbon sinks need to be assessed. However, there is still no consensus on how forest management affects the soil's carbon balance; in addition, information on how forest management alters the response of SR to global warming is still limited (Cheng et al., 2013; Sullivan et al., 2008; H. Wang et al., 2013). Selective thinning is a common practice to improve forest health and productivity. Generally, after selective thinning, the remaining trees receive more solar radiation, soil water, soil organic matter, and nutrients, thus enhancing their photosynthetic capacity (Ginn et al., 1991; Peterson et al., 1997; Selig et al., 2008; Tang et al., 2005b, 1999). As a result, SR is expected to increase after forest thinning due to the increase in both soil organic matter and autotrophic respiration caused by the improvement of tree vitality. However, many studies have investigated the effect of forest management on SR with conflicting conclusions. Tang et al. (2005) observed a decrease of 13% in total SR after thinning and suggested the decrease may be associated with the decrease in root density. On the contrary, Tian et al. (2009) found an increase in SR up to 30% after thinning that slightly declined to 20-27% in the following 4-6 years in a Chinese Fir (*Cunninghamia lanceolata* (Lamb.) Hook) plantation. Johnson and Curtis (2001) concluded in their review that forest harvesting had little or no effect on soil carbon and nitrogen storage. Overall, the effect of thinning on SR is determined by many interactive factors, such as changes in soil temperature (Ts), soil moisture, microbial and root respiration, and decomposition of litter and woody debris. The responses of SR to thinning are the result of the combined effects of a "tug of war" between these factors.

In the Mediterranean region, summer drought has been identified as the main factor that limits plant species distribution and growth (Mooney, 1983). However, studies examining the extent to which drought affects SR have yielded inconsistent results. Some studies have shown that drought conditions will reduce SR due to low root and microbial activities (Borken et al., 2006, 2003; Kaye and Hart, 1998; Savage and Davidson, 2001; Woods et al., 1998). Others report that drought may increase SR through enhancement of root growth (Asensio et al., 2007; Liu et al., 2006). Contrasting responses of fine root growth to drought were also found; fine root growth was enhanced in beech (Leuschner et al., 2001), but inhibited in spruce (Puhe, 2003). Given its arid and semi-arid climate, the Mediterranean region is a suitable area to study the effects of drought on forest productivity. While being exposed to re-occurring summer droughts, Mediterranean forests are particularly vulnerable to further reductions in water supply under climate change scenarios. According to IPCC (2013)for instance, it calls for a 15-20% reduction of soil water availability over the next three decades in Mediterranean- type ecosystems. However, soil processes in Mediterranean ecosystems have received relatively little attention (Raich and Schlesinger, 1992; Raich and Potter, 1995; Rey et al., 2002), and are currently under-represented as priorities for research networks (Reichstein, 2003; Valentini, 2003). This study may provide a better understanding of responses of soil respiration to soil water deficits and the interaction with selective thinning. Selective thinning is a general practice to recover the structure of oak forests after wildfires, but it is also a potential drought mitigation practice.

The specific objectives of this study were (i) to examine the time-course of the effects of selective thinning on the pattern of SR under two dominant tree species, *Q. ilex* L. and *Q. cerrioides* Willk & Costa in a Mediterranean forest, (ii) to evaluate the possible responses of SR under these two species subjected to experimental drought, and finally, (iii) to investigate whether selective thinning reduces the negative effect of drought on SR. We expected that: (1) thinning would increase SR due to the deposition of the thinning material on the ground and the increase in nutrient availability; (2) reduced rainfall would decrease SR, especially during the growing season, as a result of decreased soil moisture; (3) due to the combined effect of thinning and reduced rainfall, thinning would compensate for the decrease in SR under drought conditions.

Material and methods

Site description and stand history

Please refer to Chapter 3.

Experimental design

Our experiment was designed to test the effects of thinning and experimental drought in a Mediterranean oak forest. A total of 12 plots were installed with three replicates each for (1) control, (2) 15 % rainfall exclusion, (3) selective thinning, and (4) combined (thinning with 15 % rainfall exclusion). The plots (15 m x 20 m) were distributed randomly in the sampling area with a minimum buffer of 10 m surrounding every plot. To intercept runoff water, a ditch of ca. 50 cm depth was excavated along the entire top edge of the rainfall exclusion plots and covered with PVC strips. Due to instrumental limitations, SR rates were measured only in one replicate of each treatment. Tree height, basal area, and density were measured before starting the experiment and no significant differences were found in structural characteristics among plots (Cotillas et al., 2009). Selective thinning was done in spring 2004. Traditional criteria of selective low-thinning for young oak coppices were applied (Espelta et al., 2002; Espelta et al., 2003): 20-30% of total stump basal area per plot was reduced, the weakest stems were eliminated, and from one to three dominant stems per stump were left. After selective thinning, mean stem basal area and height in thinning and combined treatments were 14.3±0.8 cm3 and 180±4 cm, respectively, and in the unthinned plots, those same characteristics were 7.7±0.8 cm3 and 146±4cm, respectively. In the reduced rainfall and combined treatment plots, parallel drainage channels were installed at ca. 50 cm height above the soil and covered 15% of the ground surface. The channels were installed after the measurement of autumn 2004. Further details of the experimental design are described in Cotillas et al. (2009).

Field measurements

Soil carbon fluxes and Ts under *Q. ilex* and *Q. cerrioides* individuals were measured seasonally from 2004 - to 2007 during 3-day periods for each plot. Details of the measurement system please refer to Chapter 3.

Data analysis

We used analysis of variance (ANOVA) with treatment (thinning, reduced rainfall, both thinning and reduced rainfall combined, and control), season (winter, spring, summer, autumn) and year (2004, 2005, 2006, and 2007) as main factors to examine their effects on SR, Ts, and soil moisture. The daily or seasonal averages were used in these analyses. The relationship between SR and Ts in different treatments was based on daily average data using regression analysis, where a univariate exponential model was fitted (van't Hoff 1898):

$$SR=R_0(e^{KT}) \qquad (1)$$

Where SR is the measured soil respiration rate (μmol C $m^{-2}\cdot s^{-1}$), R0 is the basal respiration at temperature of 0°C, T is the measured soil temperature (°C), and K is the fitted parameter. Thereafter, the temperature sensitivity of soil respiration can be derived as:

$$Q_{10} = e^{10K} \qquad (2)$$

where Q_{10} is the apparent field-observed proportional increase in SR related to a 10°C increase in temperature. We also used recursive partitioning analysis to separate the relationship between SR and Ts by soil moisture regime. As models based on partitioning can only handle linear models, the equation above was transformed by linearizing with logarithms:

$$\mathrm{Ln}\, SR = \ln R_0 + KT \qquad (3)$$

Logarithmic transformed SR values were used as the dependent variable. Once the soil moisture thresholds were obtained, nonlinear regression analyses (model 1) were used to determine the relationship between SR and *T*s in each soil moisture interval. All statistical analyses were performed with PASW statistics 18 (SPSS Inc., 2009, Chicago, IL), except the recursive partitioning analysis, which was conducted with R statistical software version 2.15.3 (R Development Core Team, 2013) using the *party* package (Zeileis et al., 2008). For all statistical tests, significance was accepted at $P<0.05$. Values are given as mean ± standard error (SE).

Results

Temporal variation in Ts and soil moisture

The average temperature showed no significant difference between treatments (Table 6.1). The seasonal course of soil temperature was pronounced in our study site. The highest recorded Ts was 32.2°C in summer 2005 and the lowest was -0.3°C in winter 2005. Soil moisture varied largely over the study period, ranging from 2.3 to 18.4% (Figure 6.1). Mean annual precipitation was lowest in 2006 (400mm) and highest in 2007 (830mm). The highest soil moisture occurred in winter and spring, but then dropped sharply in summer. The lowest soil moisture (2.3%) was recorded during the thinning treatment in summer 2005. Soil moisture was negatively correlated with Ts; the peak of Ts in summer coincided with the lowest soil moisture values.

Table 6.1. Treatment effects on soil temperature (Ts) and soil respiration (SR) of *Q. ilex* and *Q. cerrioides.*

Variable	Treatment	*Q. ilex*	*Q. cerrioides*	Average
Ts (°C)	Natural rainfall	14.88^{a}	14.98^{a}	14.93^{a}
	Reduced rainfall	16.77^{a}	15.99^{a}	16.38^{a}
	No Thinning	16.31^{a}	15.67^{a}	15.99^{a}
	Thinning	15.30^{a}	15.28^{a}	15.29^{a}
SR (µmol C m^{-2}·s^{-1})	Natural rainfall	0.45^{a}	0.47^{a}	0.46^{a}
	Reduced rainfall	0.38^{a}	0.30^{b}	0.34^{b}
	No Thinning	0.47^{a}	0.33^{a}	0.40^{a}
	Thinning	0.36^{b}	0.44^{b}	0.40^{a}

The different letters indicate the significant differences between treatments ($p < 0.05$).

Throughout the four monitored years, the mean seasonal soil moisture in the control treatment was consistently higher than in the other treatments. Despite the reduced rainfall treatment, we didn't find lower soil moisture in the plots subjected to reduced rainfall during the most of the measurement campaigns.

Treatment effect on SR

Within the four treatments, SR was between 0.00 and 1.82 µmol C·m^{-2}·s^{-1}, with an overall mean (±SD) of 0.43 ± 0.28µmol C·m^{-2}·s^{-1}. Reduced rainfall treatment significanly depressed SR, with around 26% lower in comparison to natural rainfal (Table 6.1). Selective thinning showed no effect on overall SR (Table 6.1). SR under *Q. ilex* (0.44± 0.28µmol C·m^{-2}·s^{-1}) was significantly higher than SR under *Q. cerrioides* (0.41± 0.28µmol C·m^{-2}·s^{-1}, P<0.001). Meanwhile, SR under *Q. ilex* showed no significant difference in subjected to reduced rainfall while SR under *Q. cerrioides* showed a pronounced decrease. Selective thinning, however, had different effects on SR under *Q. ilex* and *Q. cerrioides*; thinning enhanced SR under *Q. cerrioides,* but it reduced SR under *Q. ilex*. Figure 6.2 shows the mean seasonal variations of SR under *Q. ilex* and *Q. cerrioides* in the four treatments. Generally, SR was higher during the growing season and lower in winter. Due to high precipitation in spring 2007, the SR in the control, thinning, and combined treatments showed the highest peak during this period. In the control treatment, SR under *Q. ilex* was significantly higher than under *Q. cerrioides,* except in autumn 2005 and spring 2006. In the reduced rainfall treatment, SR under *Q. ilex* showed a significantly higher rate compared to SR under *Q. cerrioides*, especially in spring and summer. Besides, there was almost no seasonality of SR under *Q. cerrioides*. SR under *Q. ilex* even showed higher values in comparison to the SR in the control treatment in the first year after treatment installation. In the thinning treatment, SR under *Q. cerrioides* was significantly higher than under *Q. ilex*, especially in spring. In the combined treatment, the seasonal patterns of SR under both tree species were very similar in the first 2 years. In the following years, SR under *Q. cerrioides* showed a higher value, which was very similar to the pattern of SR in the thinning treatment. We also compared the diurnal variation in SR under the two tree species during spring and summer campaigns (Figure 6.3 & 6.4). During the spring campaigns, SR under both tree species in the control plot showed a clear diurnal pattern, except for SR under *Q. cerrioides* in spring 2005. Meanwhile, in the reduced rainfall plot, the diurnal changes of SR almost diminished. In the thinning plot, SR under *Q. ilex* in 2005 showed a reversed diurnal pattern, but in the following two years the patterns turned back to be flat. The diurnal patterns of SR under *Q. cerrioides* in the thinning plot were similar to the patterns in the control plot, but with limited range and a clear depressed SR at noon. In the combined plot, SR under both *Q. ilex* and *Q. cerrioides* showed a significant reduction during the day in 2005, but the reduction decreased in the following years. The diurnal variation of SR during summer campaigns was slightly different compared to spring. In the control plot, although SR under the two tree species showed similar daily patterns, the variation of SR under *Q. ilex* was much higher than SR under *Q. cerrioides.* In the reduced rainfall plot, SR under *Q. ilex* still exhibited a clear diurnal change, while SR under *Q. cerrioides* was almost steady. In both thinning and combined plots, SR under two tree species showed a pronounced reduction during the day.

Relationship between SR and Ts

By using recursive partitioning, we identified a soil moisture threshold around 8-9%; when soil moisture was higher than 8%, SR and Ts were highly

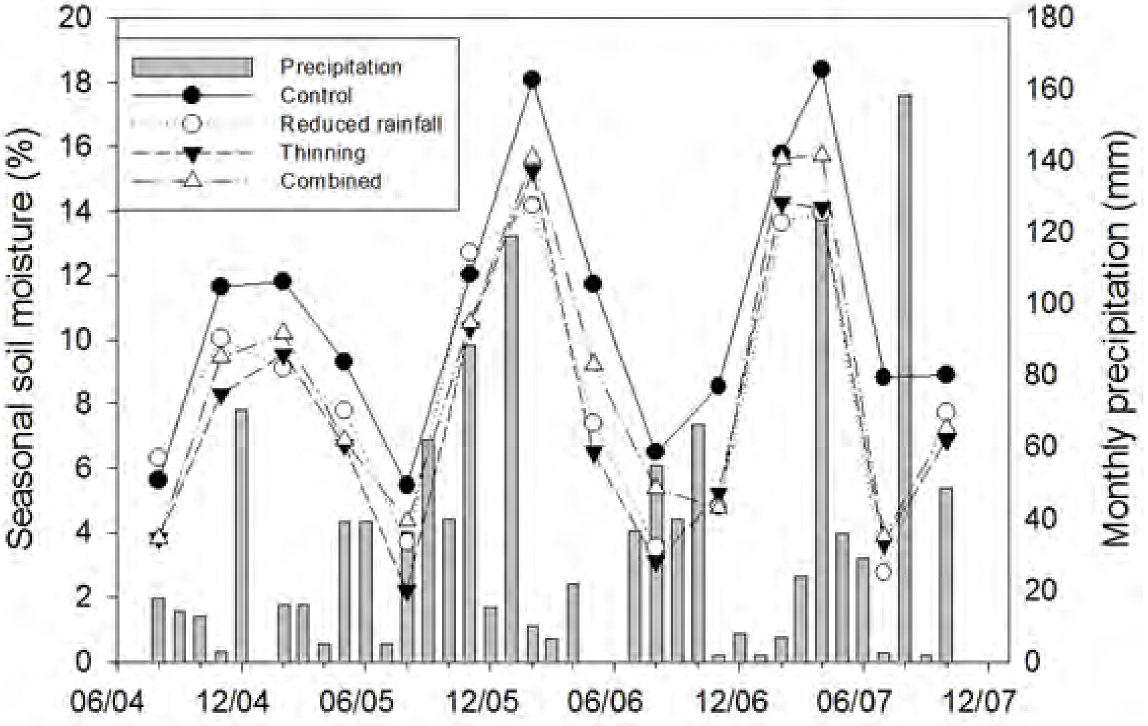


Figure 6.1. Seasonal variation in soil moisture (line plot) and monthly variation in precipitation (grey column) for each treatment plot during the study period. Different symbols represent different treatments. Labels on the x-axis represent time in month/year format.

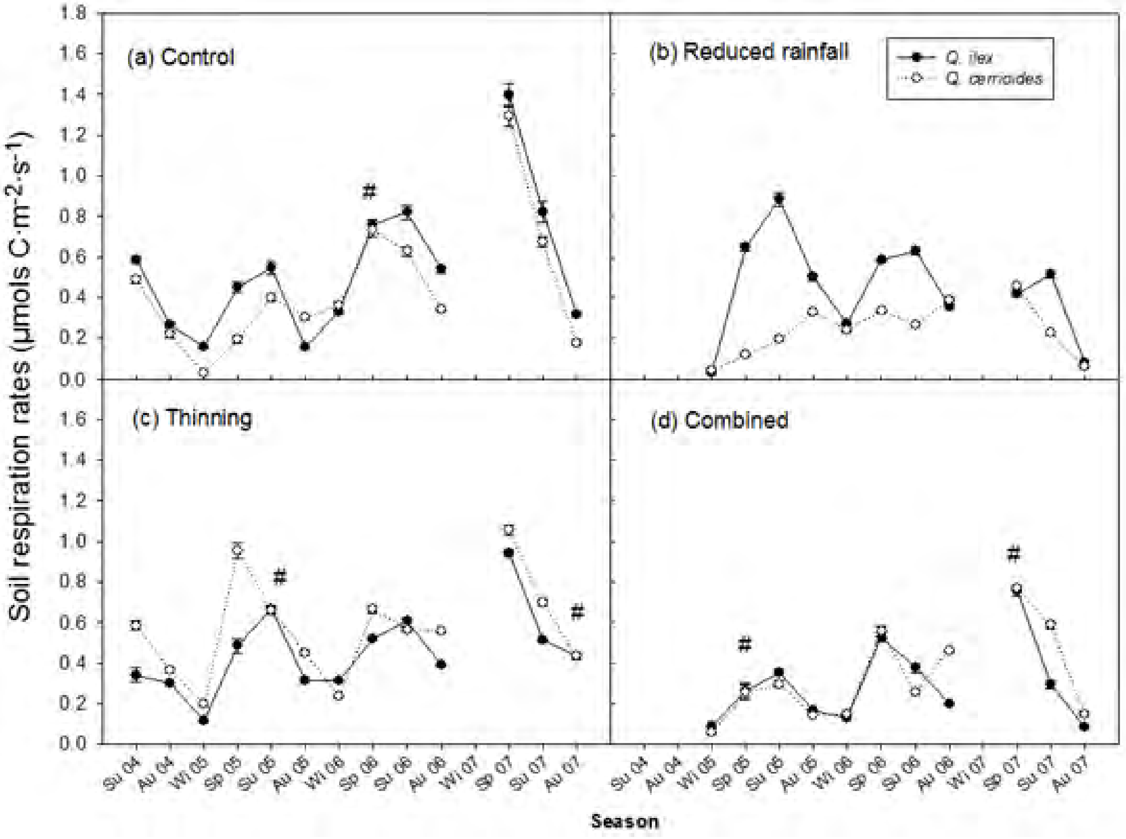


Figure 6.2. Seasonal variation in soil respiration of *Q.ilex* and *Q.cerrioides* for each plot: (a) control (b) reduced rainfall (c) thinning, and (d) combined treatment. Reduced rainfall treatment was installed at the end of 2004, therefore, the data for reduced rainfall and the combined treatments started in 2005. Data represent seasonal means with SE. Differences in SR between species were statistically significant except when marked with # ($P > 0.05$).

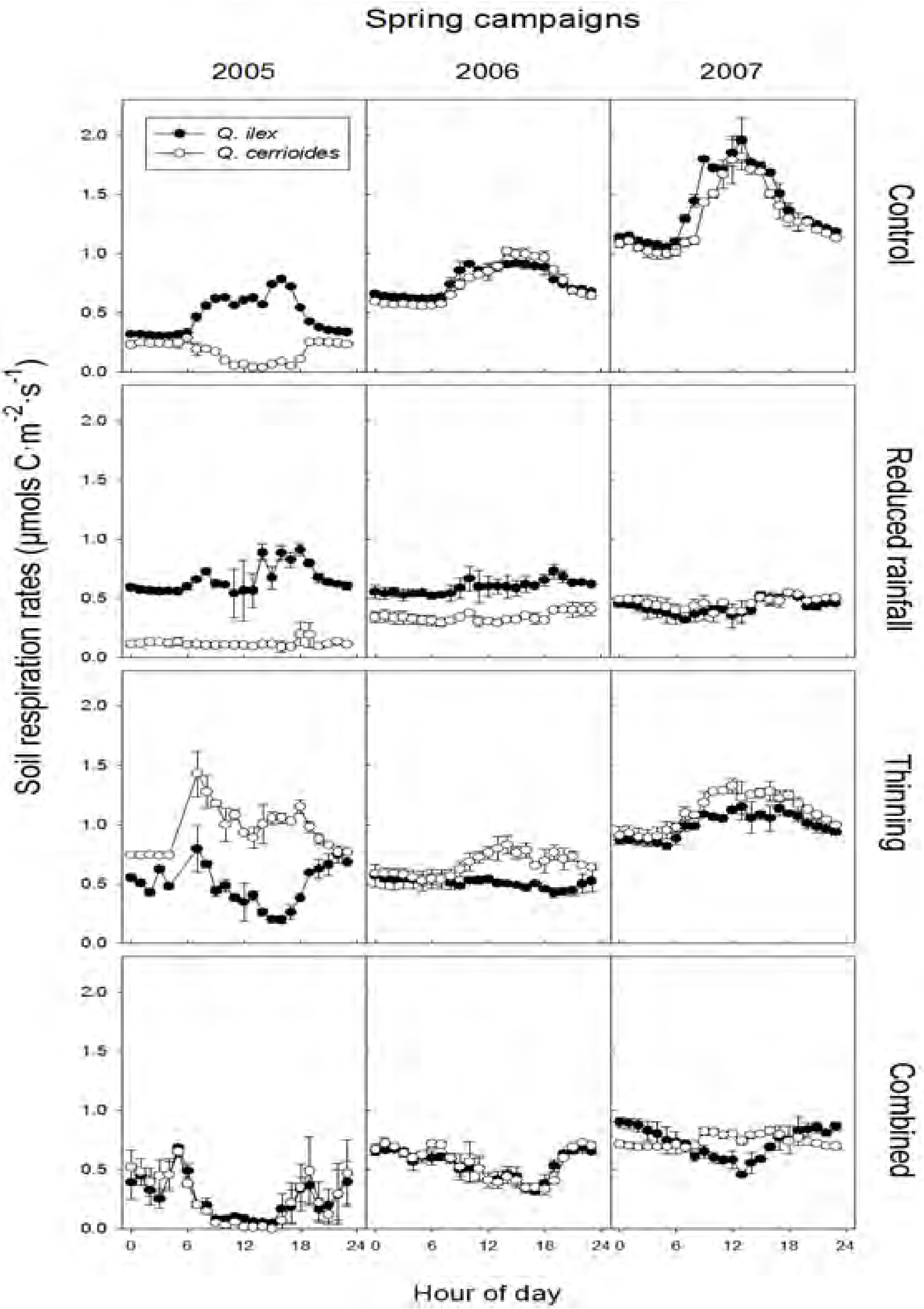


Figure 6.3. Diurnal variation of soil respiration rates (SR) with standard errors under *Q.ilex* and *Q.cerrioides* during spring in 2005, 2006, and 2007 (from left to right) and for each plot: control, reduced rainfall, thinning, and combined treatment (from up to down). Shown are hourly rates of SR averaged over each campaign.

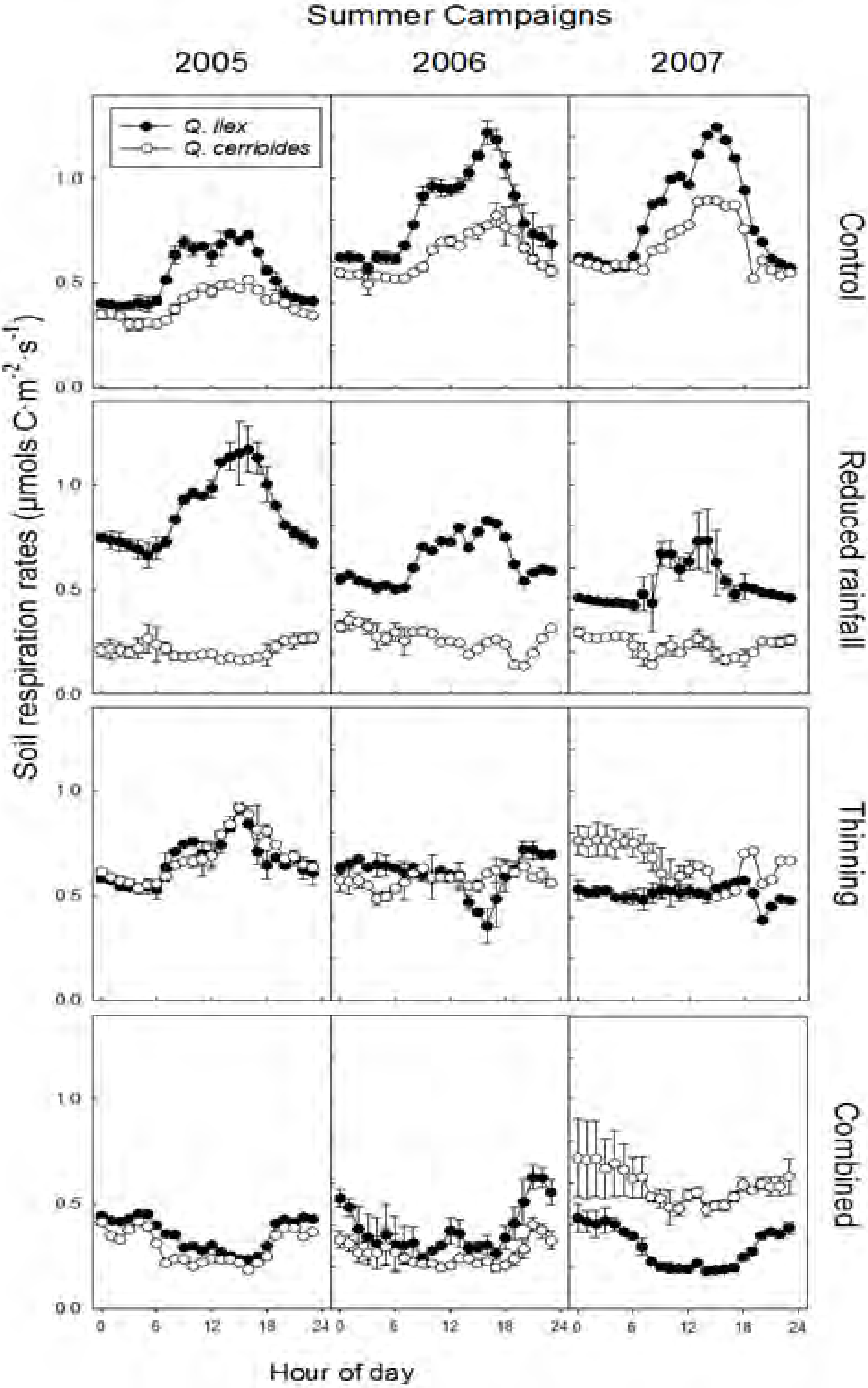


Figure 6.4. Diurnal variation of soil respiration rates (SR) with standard errors under *Q.ilex* and *Q.cerrioides* during summer in 2005, 2006, and 2007 (from left to right) and for each plot: control, reduced rainfall, thinning, and combined treatment (from up to down). Shown are hourly rates of SR averaged over each campaign.

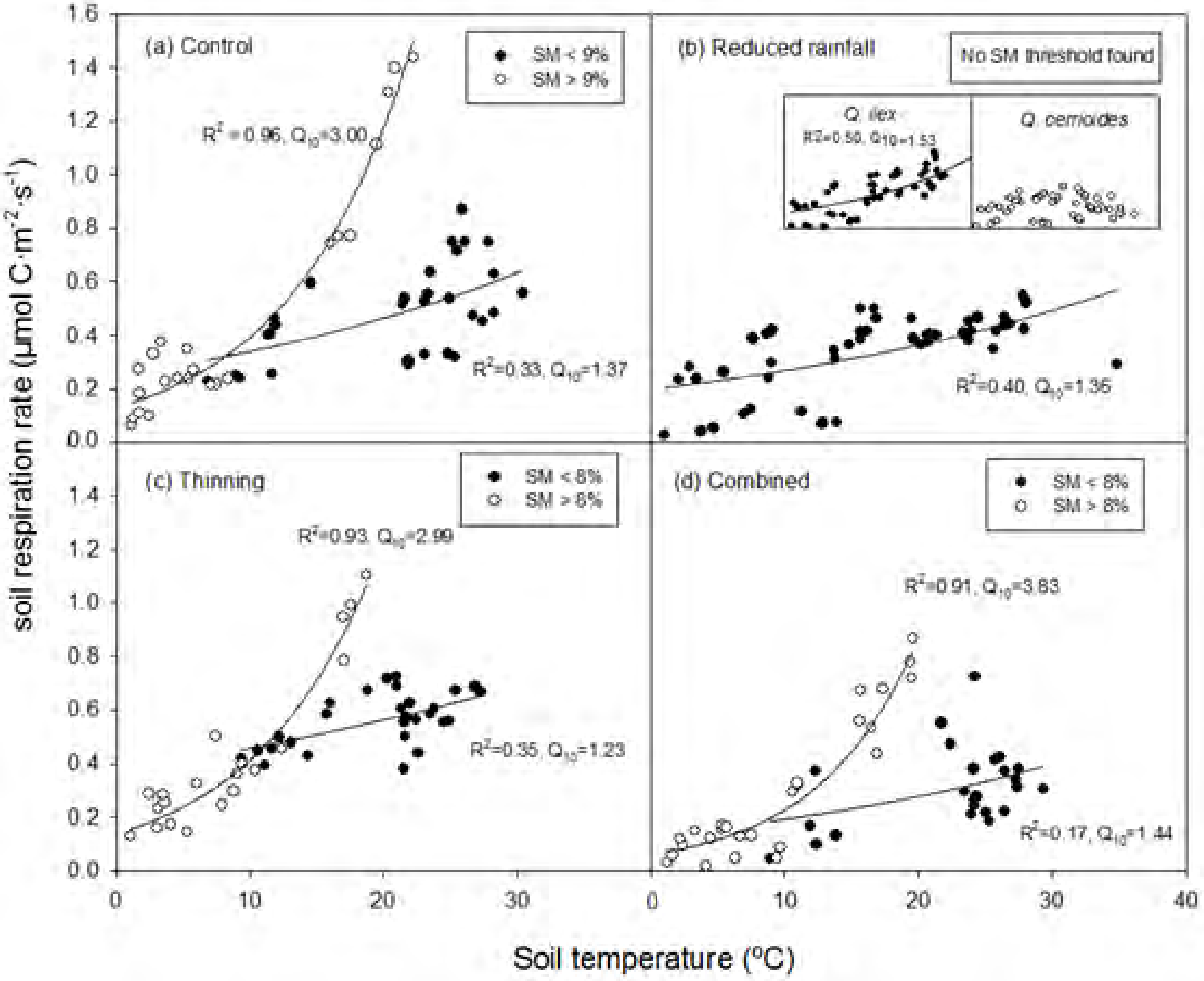


Figure 6.5. Relationship between daily soil respiration and soil temperature (5cm) separated by soil moisture regime in each treatment: (a) control (b) reduced rainfall (c) thinning, and (d) combined treatment. Closed circles indicate the lower soil moisture regime, and open circles indicate the higher soil moisture regime. Lines show fit to Equation 1 for SR and Ts within the same soil moisture regime. R^2 and Q_{10} values are given for each panel. In the reduced rainfall treatment, the relationship between SR and Ts cannot be separated by soil moisture regime by using recursive partitioning; therefore, the closed circles represent all soil moisture regimes. Inset in (b) shows the relationship between daily SR and Ts under two tree species (n=49-53).

correlated, with apparent Q_{10} values from 2.99 to 3.83, and TS explained 91-96% of the variation in SR. When soil moisture was lower than 8%, apparent Q_{10} values declined to 1.23 – 1.44. Figure 6.5 shows the daily average SR of each treatment as a function of Ts separated by soil moisture regimes. In the control treatment, apparent Q_{10} was 3.0 when soil moisture was higher than 9%, and declined to 1.37 when soil moisture was lower than 9%. Thinning and combined treatments showed a similar pattern, except that the soil moisture threshold was slightly lower than the threshold of the control. In the reduced rainfall treatment, we could not identify the soil moisture threshold by using recursive partitioning, although the recorded soil moisture ranged from 2.8 to 14.2%. The overall apparent Q_{10} in the reduced rainfall treatment was 1.36. When we separated the SR under different species and compared its relationship with Ts, similar relationships between SR and Ts were found in all treatments except in reduced rainfall treatment (inset in Figures 6.5b, supplementary figures); SR under *Q. ilex* showed a positive correlation with Ts with a Q_{10} of 1.53, whereas the SR under *Q. cerrioides* showed no relationship with Ts.

Temporal variation in litterfall

The peak of litterfall differed between the two tree species; in the control, *Q. ilex* mainly dropped leaves during spring and summer, while *Q. cerrioides* dropped leaves all year except during summer (Figure 6.6). In the reduced rainfall treatment, the peak of litterfall from *Q. ilex* was in spring, while *Q. cerrioides* remained the same throughout the year. In the thinning and combined treatments, the peak of litterfall from *Q. ilex* occurred in summer. Besides, the total litterfall amount from *Q. cerrioides* was less in the thinning treatment and showed a peak of litterfall in spring. Although *Q. ilex* is an evergreen species, the amount of litterfall from *Q. ilex* was larger than from *Q. cerrioides*, especially during the driest summer of 2006.

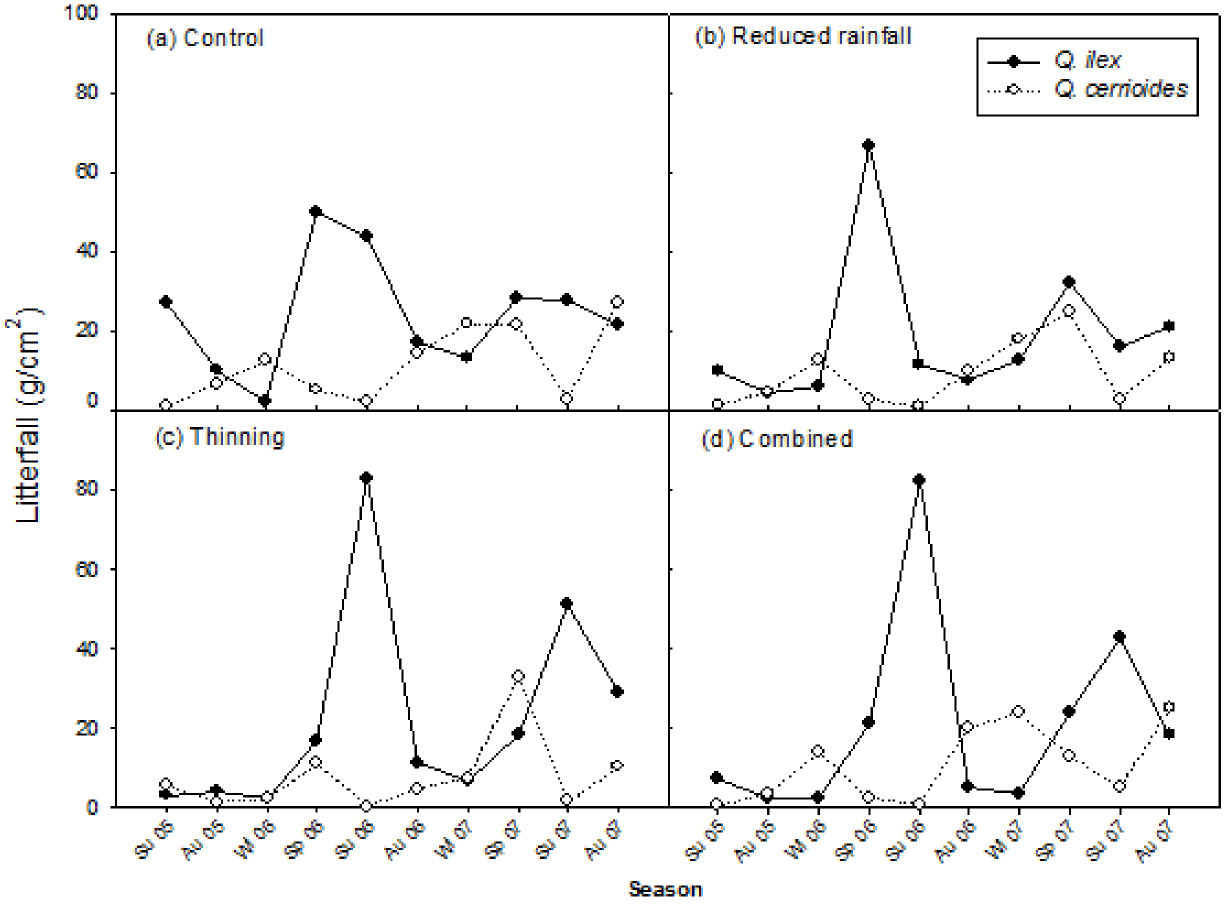


Figure 6.6. Seasonal variations in litter fall of *Q.ilex* and *Q.cerriodies* for each plot: (a) control (b) reduced rainfall (c) thinning, and (d) combined treatment. Reduced rainfall treatment was installed at the end of 2004, therefore, the data for reduced rainfall and combined treatments started in 2005.

Discussion

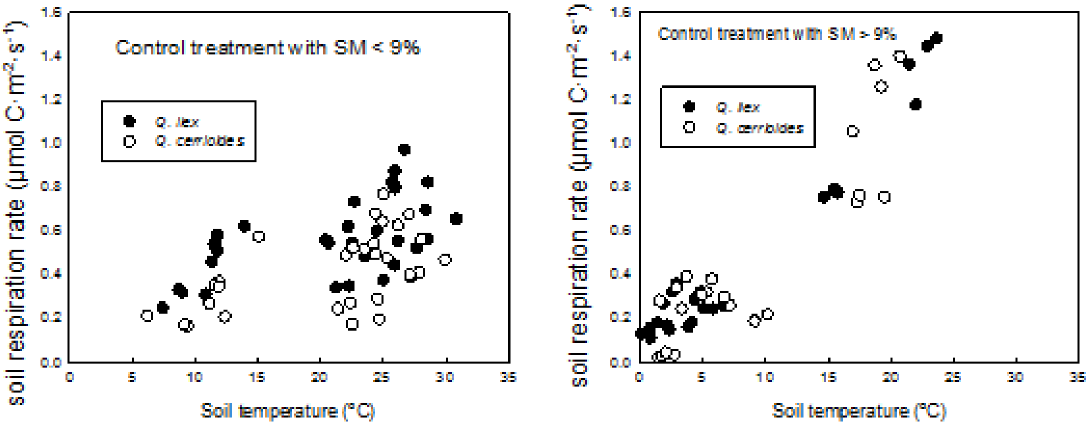
We expected to find the lowest soil moisture in the reduced rainfall treatment. However, the observed soil moisture data suggested that the channels installed in the reduced rainfall treatment only had partially or no effect. This may due to the low precipitation during our study period which probably diminished the treatment effect of reduced rainfall. We also suspect that the channels installed to reduce rainfall may have created some shadow and prevented somewhat the direct top-soil water evaporation. Despite the reduced rainfall treatment, we observed a tendency for soil moisture to be lower in the selective thinning treatments, especially during the summers of 2005 and 2006. Many studies have shown that thinning influences site-specific microclimatic conditions (Masyagina et al., 2010; H. Wang et al., 2013). The removal of aboveground vegetation is known to increase Ts (Köster et al., 2011) and soil moisture as a consequence of reduced root and canopy interception and, hence, reduced evapotranspiration (Bréda et al., 1995). The observed lower soil moisture in the selective thinning treatment may due to the way that selective thinning retained the roots, but increased the opening of the canopy. We also observed a marginal decrease on the diurnal variation of Ts by the selective thinning during summer. This may also explain the lower soil moisture because the higher evaporation rate caused by selective thinning may lead to a decrease in soil temperature and soil moisture (Cheng et al., 2014). Besides, the lower soil moisture in the selective thinning treatments may have been due to the higher transpiration rate of trees and a larger amount of sprouts (Bréda et al., 1995). The observed decrease in overall SR from our study is similar to other researches. Studies have shown how drought stress depressed SR from several aspects. First, the low water content of the soil created an environment that slowed the diffusion of solutes and, thus, suppressed microbial respiration by limiting the supply of substrate (Skopp et al., 1990). Additionally, microbes and plant roots have to invest more energy to produce protective molecules and this reduces their growth and respiration (Schimel et al., 2007). Drought has been shown to decrease the recently assimilated C allocation to roots ca. 33 – 50% (R. Hasibeder et al., 2014; Ruehr et al., 2009). The decrease in plant substrate and photosynthetic activity caused by drought may explain the reduction in SR (Burton et al., 1998; Yan et al., 2011). With the prolongation of reduced rainfall over time, annual SR, especially root respiration, would have decreased followed by the depression of forest productivity and growth. For example, Brando et al. (Brando et al., 2008) found a decline in net primary productivity of 13% in the first year and up to 62% in the following 4 years in a throughfall reduction experiment.

Interestingly, despite the effect of drought on SR, we observed an increase in SR under *Q. ilex* in the reduced rainfall treatment in the first year after the reduced rainfall treatment. A similar pattern was observed in South Catalonia, where Asensio et al. (Asensio et al., 2007) found significantly higher SR in the drought treatment compared to the control treatment during summer. First, they argued, that the prolonged low availability of soil water compelled roots to uptake deeper soil water; second, they also argued that moderate drought enhanced photosynthetic rates (Lu and Zhang, 1998) to support roots with the majority of the photosynthetic assimilates. In our study site, Peréz (Pérez, 2010) measured the treatment effects on mineral soil nutrients, root density and distribution during summers of 2007 and 2008, which is right after our measurement, and found an significant increase of fine roots of *Q. ilex* only in the reduced rainfall treatment. The high C/N ratio and low soil water content found in our study site (Pérez, 2010) also implied a very low microbial respiration. Hinko-Najera et al. (Hinko-Najera et al., 2015) also found that a reduction in throughfall mainly decreased autotrophic respiration, but not heterotrophic respiration, in a Mediterranean to cool temperate forest. As a result, we conjecture that the increase in SR under *Q. ilex* observed in our reduced rainfall treatment was caused by the increase of fine roots while the decrease in SR under *Q. cerrioides* may have been caused mainly by the decrease in root respiration. Peréz (Pérez, 2010) also found that the fine and small roots of *Q. cerrioides* were distributed mainly in the 0-30 cm depth layer, but the roots of *Q. ilex* were found to be deeper. In other words, the different responses of SR under *Q. ilex* and *Q. cerrioides* may have been due to different rooting systems. Previous studies have shown contradictory results of how thinning affects SR: SR has been found to increase, decrease, or even remain unchanged after thinning (Dai et al., 2014; Jonsson and Sigurdsson, 2010; Londo et al., 1999; Ma et al., 2004; Masyagina et al., 2010; Olajuyigbe et al., 2012; Pang et al., 2013; Tang et al., 2005b). The different responses likely are due to thinning intensity, timing, and duration of the measurement campaigns after thinning. In our study, we observed an increase in SR in the selective thinning treatment during the first two years after selective thinning. We also found a significant reduction in SR during daytime in the first summer campaign. We explain the possible reasons how thinning affects SR from a different temporal scale. Over the hourly to daily scales, selective thinning increased water and nutrient availability and, therefore, increased both microbial and root respiration. In the meantime, the woody debris and dead roots produced during thinning stimulated heterotrophic respiration (Rustad et al., 2000; Tian et al., 2009b). Additionally, Sohlenius (Sohlenius, 1982) found that slash produced by logging promoted productivity of soil microflora due to the increase in moisture and microbial biomass, which increased SR. But selective thinning may also decrease SR because of the lower soil moisture caused by more solar radiation and higher transpiration in the initial phase after selective thinning. From daily to seasonal scales, the enhancement of tree growth and photosynthesis due to selective thinning may promote more root respiration (Högberg et al., 2001; Janssens et al., 2001; Kuzyakov and Cheng, 2001). Cotillas et al. (Cotillas et al., 2009b) investigated tree growth in the same study site and observed a remarkable improvement in residual stem growth (ca. 50%) and a reduction in stem mortality after selective thinning. However, they also found that the positive effects of thinning declined rapidly during the 3-year experiment. López et al. (López et al., 2003) found an increase of more than 100% in root biomass and 76% in root production in a *Q. ilex* forest after thinning, especially during winter and autumn. We also found higher soil organic matter and soil phosphorous in the selective thinning treatments (Pérez, 2010), which may also enhance SR. From seasonal to annual scales, selective thinning increased annual SR as a result of a longer growing period due to the absence of drought (Aussenac and Granier, 1988). Supported by our litterfall data, the total amount of litterfall from *Q. cerrioides* was less in the thinning treatment; during the same time, we also observed a stronger effect of thinning on SR under *Q. cerrioides*. Overall, the effect of selective thinning on SR over time is likely to be reduced with the recovery of stands.

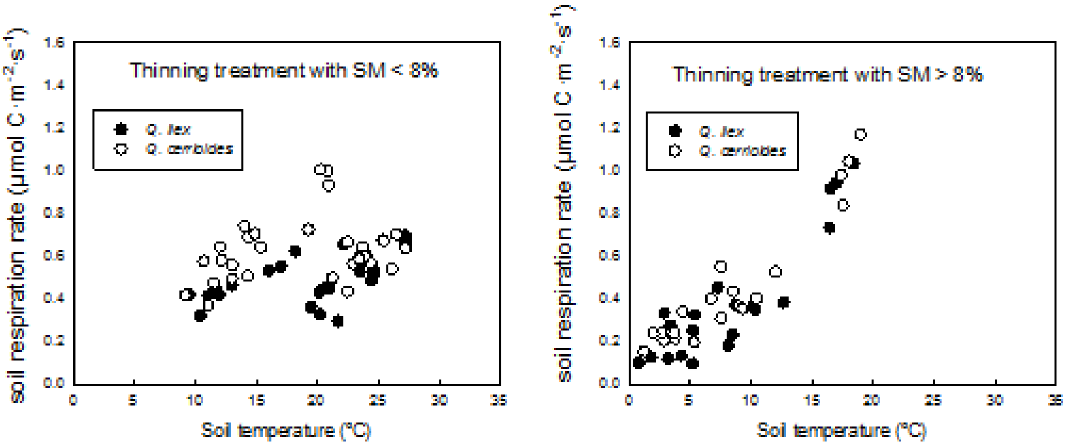
The apparent soil Q_{10} was affected significantly by soil moisture. However, this soil moisture threshold is not applicable to the relationship between SR and Ts in the reduced rainfall treatment. In the reduced rainfall treatment, we observed some campaigns with soil moisture higher than 8%, but SR of these campaigns were still lower than the SR in control treatment of the same campaigns. The reduction of Q_{10} due to drought has been found in many studies (Jassal et al., 2008; Suseela et al., 2012; Suseela and Dukes, 2013; Wang et al., 2014). As the apparent Q_{10} in this study was calculated as annual Q_{10}, the low Q_{10} in the reduced rainfall treatment could be attributed by the diminished seasonal amplitude of SR, especially SR under *Q. cerrioides*. We found relatively few studies on the response of Q_{10} to forest management. At our study site, we found Q_{10} did not vary in response to thinning, which is similar to the finding of Tang et al. (Tang and Baldocchi, 2005). Our result is also consistent with Pang et al. (Pang et al., 2013), who showed that thinning increased the seasonal Q_{10} significantly, but not the yearly Q_{10}. Overall, the different SR-Ts relationship between the reduced rainfall treatment and combined treatment indicated that selective thinning treatment had at least partially mitigated the drought stress by improving the SR in respond to environmental change.

Our study demonstrates that evergreen and deciduous trees growing in the same environmental conditions can emit different quantities of CO_2 from the soil. We found that thinning and reduced rainfall treatments have different effects on SR and litterfall of the two investigated tree species. This may be explained by the plant functional type, (i.e., evergreen and deciduous species). *Q. ilex* is an evergreen species, which is well adapted to poor environments, and has low resource-loss ratios (Aerts and der Peijl, 1993; Berendse, 1994). Therefore, the SR under *Q. ilex* was less affected by selective thinning. In contrast, deciduous species, such as *Q. cerrioides*, have a shorter period of active photosynthesis and a higher sensitivity to drought (Thomas and Eamus, 2002). Therefore, deciduous species may require higher levels of nutrient and water to support higher rates of foliar net CO_2 assimilation to compensate for the shorter active period (Eamus et al., 1999). In conclusion, we examined the effects of drought and thinning on SR in a Mediterranean oak forest and observed a significant change in SR due to thinning and reduced rainfall. Both treatments influenced SR over different time scales. The main conclusions drawn from this study are as follows:

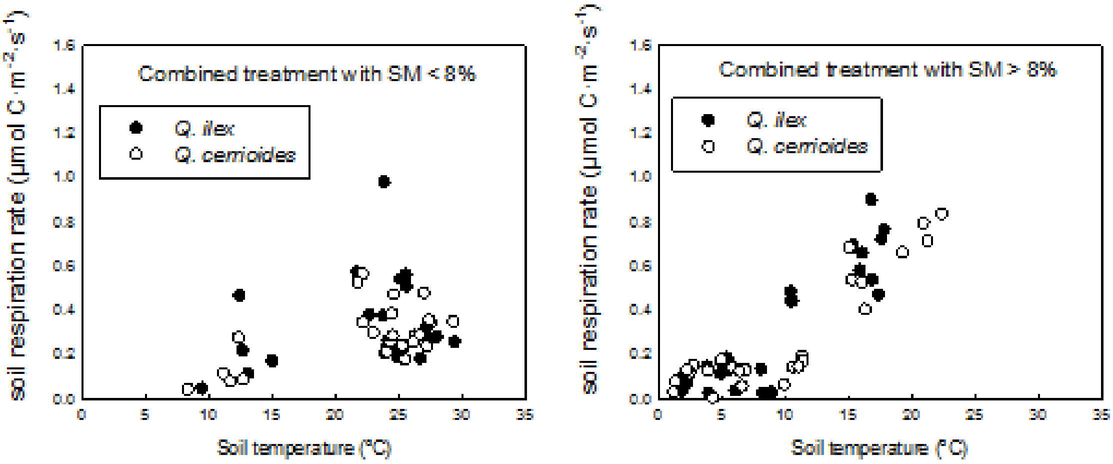
- Q_{10} of SR was clearly modulated by soil moisture, with a threshold value around 8-9%. Reduced rainfall decreased both SR and Q_{10}, unlike selective thinning;
- Selective thinning had less effect on SR under *Q. ilex,* but increased the SR rate under *Q. cerrioides* in the first two years;
- Reduced rainfall significantly depressed SR rate under *Q. cerrioides* by 50%, especially during the growing season, and the drought effect accumulated over years. Reduced rainfall increased SR rate under *Q. ilex* during the growing season by 50%;
- Selective thinning mitigated the negative effect of drought on SR rate under *Q. cerrioides*, although the mitigation was only significant during spring and during the last year of the experiment.



S1. Relationship between daily SR and Ts separated by soil moisture regime (left: soil moisture lower than the threshold, right: soil moisture higher than the threshold) in control treatment. The closed circles represent SR under *Q. ilex* and the open circles represent SR under *Q. cerrioides*.



S2. Relationship between daily SR and Ts separated by soil moisture regime (left: soil moisture lower than the threshold, right: soil moisture higher than the threshold) in thinning treatment. The closed circles represent SR under *Q. ilex* and the open circles represent SR under *Q. cerrioides*.



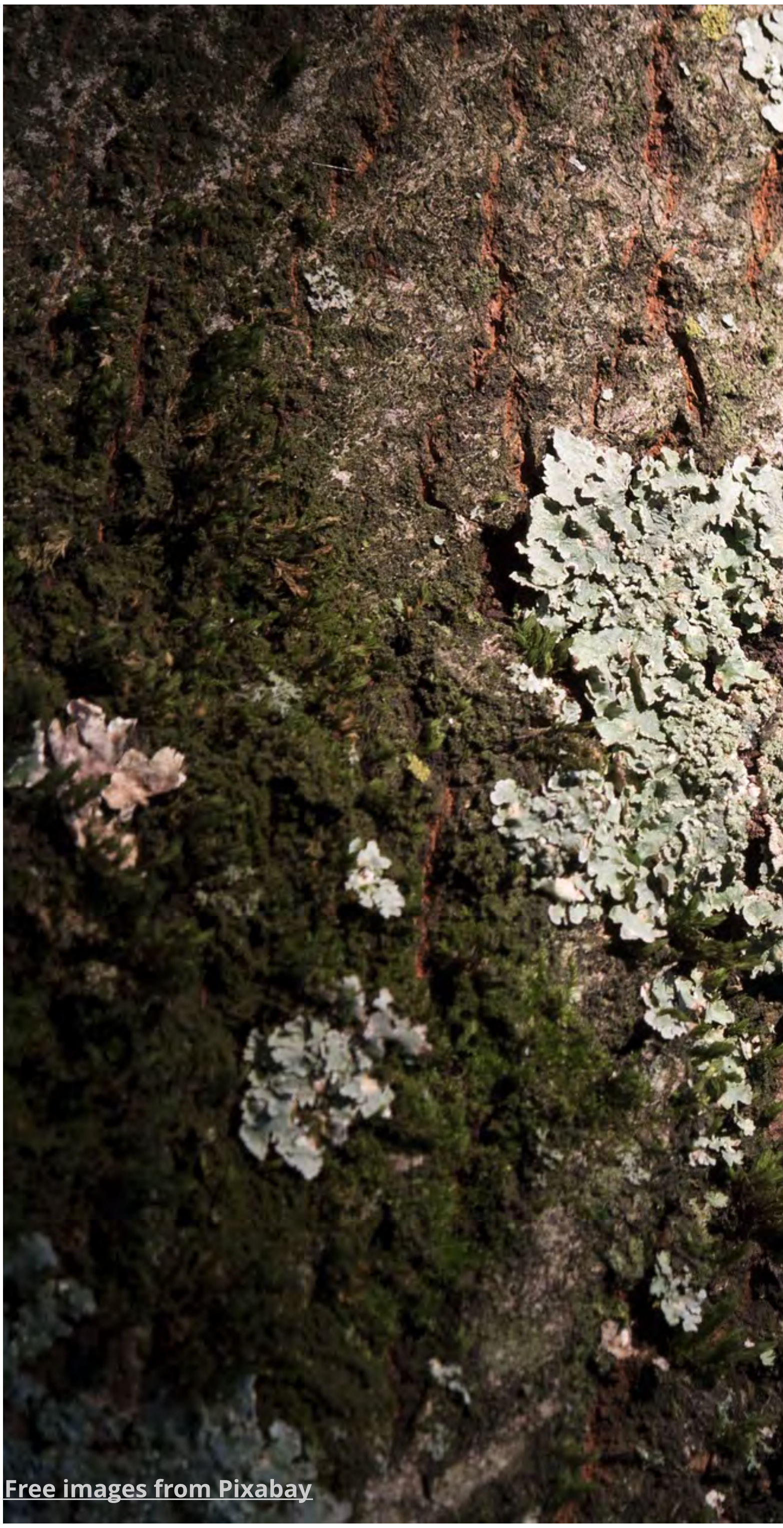
S3. Relationship between daily SR and Ts separated by soil moisture regime (left: soil moisture lower than the threshold, right: soil moisture higher than the threshold) in combined treatment. The closed circles represent SR under *Q. ilex* and the open circles represent SR under *Q. cerrioides*.

⇧Selective thinningtreatment. Photo: Santi Sabaté

Introduction

Respiration plays a key role in plant and ecosystem carbon budget and is crucial in predicting long-term trends in carbon sequestration. Ecosystem respiration can be divided into two main components-autotrophic and heterotrophic respirations. Autotrophic respiration includes leafs, stem and root respiration and heterotrophic respiration generally refer to microbial respiration. Total autotrophic respiration was estimated to consume between 30 and 70% of the carbon fixed by leaves (Ryan, 1991; Ryan et al., 1994), among which stem respiration accounts for 11-23% and 40-70% of the carbon assimilation in temperate and tropical forests, respectively (Chambers et al., 2004; Lim et al., 2012; Ryan, 1991; Ryan et al., 1994). Tree stems as the largest component of living biomass, it also releases large amounts of carbon. However, the relatively lower contribution of stem respiration to total carbon budget compared to soil respiration and photosynthesis makes the stem respiration receive little attention. Therefore, despite the likely importance of stem respiration, there is still little information on the responses of stem respiration to environmental stress and the evaluation of forest management as a mitigation practice is also limited.

Stem respiration can be partitioned into growth and maintenance respiration by their function. Growth respiration is, literally, respiration used to build dry matter, and is defined as the amount of carbohydrates respired in processes that result in a net gain of plant biomass. Maintenance respiration is used to maintain plant stay healthy and provide the energy for processes such as maintain ion gradients, replace the enzymes and repair membranes. Other factors such as species, age, or plant function type also affect growth and maintenance respiration from different aspects. For example, evergreen species grows a whole year around, while deciduous species may only exist growth respiration during growing season. As a result, the proportion of growth respiration to total respiration varies seasonally and differs between species and environmental conditions. There is broad consensus that temperature and water availability are the most important environmental factor that controlling respiration process. Respiration rate generally increases exponentially with an increase in temperature in most of the cases, but there are also studies shown that this relationship between respiration rate and temperature is less clear or absent. The sensitivity of respiration to temperature is usually expressed in terms of Q10, which is the change in rate with a 10°C change in temperature. Studies found that Q10 of stem respiration ranged from 1.7 to 2.6 in temperate forests (Acosta et al., 2008; Damesin et al., 2002; Yang et al., 2012), from 1.6 to 2.2 in tropical shrub (Levy and Jarvis, 1998) and around 1.9 in subtropical forests (Zhu et al., 2012). Moreover, studies of how soil water availability affects stem respiration yielded different results. For example, Levy and Jarvis (1998) and Stahl et al. (2011) found that stem respiration reduced by decreasing soil water availability, meanwhile others shown no changes (Zha et al., 2004).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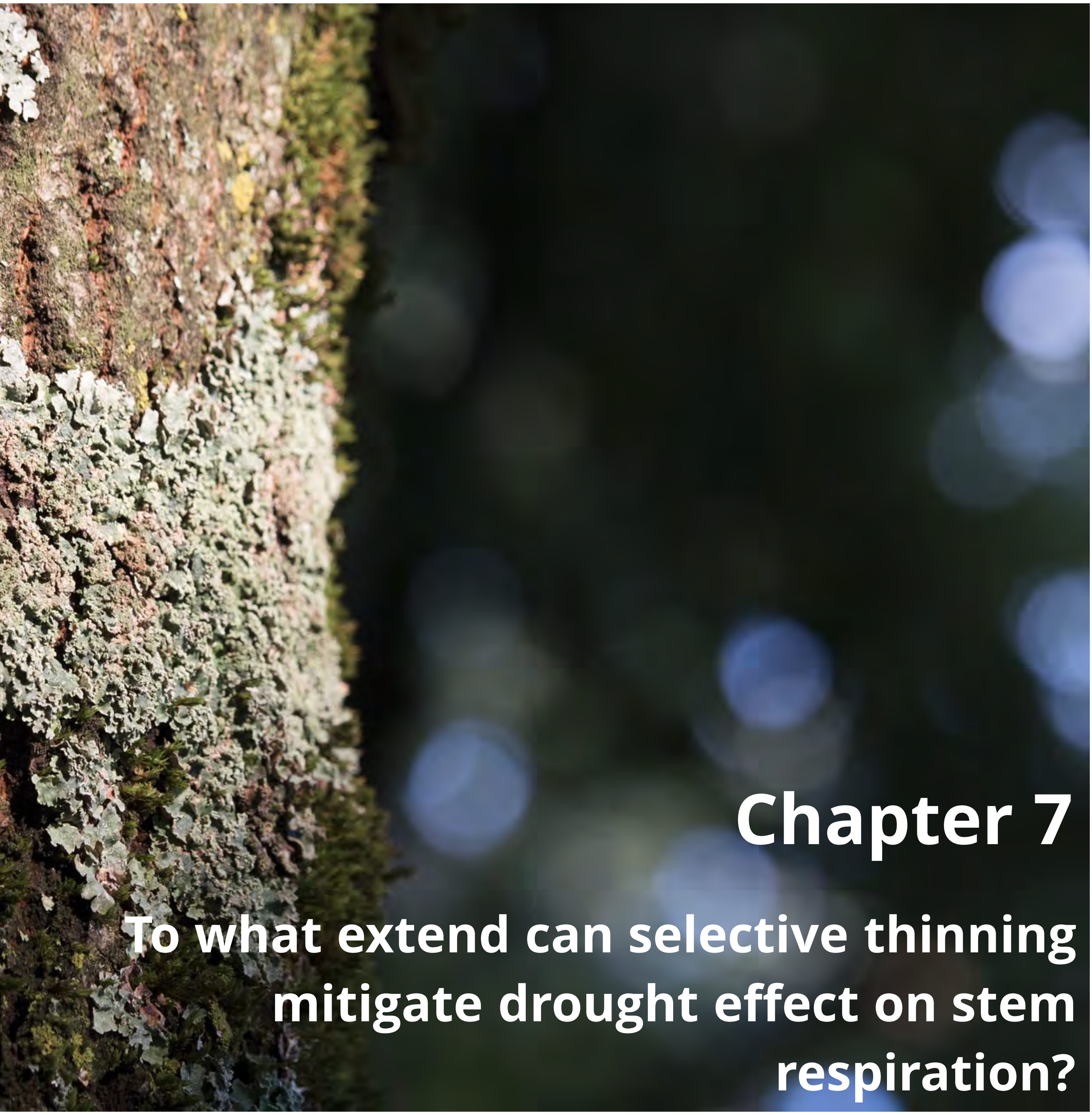
The total global area of Mediterranean-type climate is estimated to cover around 2.75 million km^2 (Hobbs et al., 1995). In the Mediterranean region, summer drought has been identified as the main factor which limits plant species distribution and growth (Mooney, 1983). Sabaté et al. (2002) used a process based model GOTILWA and projected a 15-20%



Chapter 7

To what extend can selective thinning mitigate drought effect on stem respiration?

reduction of soil water availability for the next three decades in Mediterranean ecosystems. The reduction of water supply and higher evaporative demand under climate change imply predictable suffering of the Mediterranean ecosystem. Coppicing is a traditional silviculture practice in Mediterranean region to obtaining charcoal and fuelwood. In Spain, coppices constitute 40% of the total area covered by spontaneous hardwood species, and the area covered by coppices of spontaneous hardwood species is about 20% of the total forest area of Spain. As a long term goal of "high forests", selective thinning has been suggested to improve the structure and the regeneration of these forests. Selective thinning, by cutting the weakest stems and leaving the other best stems, can improve forest health and productivity as thinning increases light and nutrient availability by reallocating growing space within stands (Ma et al., 2004; Tang et al., 2005).

To date, little research has been conducted into the drought and thinning effects on stem respiration. This would be important for a better estimation of ecosystem carbon budgets under future climate change. This study aims to address the drought effect on the diurnal and seasonal variations of stem respirations and the changes of stem respiration after an intervention of selective thinning. In this current study, we measured stem respirations of two dominant oak species in the Mediterranean region, *Quercus ilex* and *Q. cerrioides*, with factorial combined treatments of selective thinning and reduced rainfall. Measurements were taken seasonally over two years. We hope that this study can offer some idea on how stem respiration responds to summer drought from different time scale and if selective thinning can be used as a mitigation practice. With the reasons detailed, our objectives were: to determine the diurnal and seasonal variations of stem respirations; to examine the treatment effects on stem respirations over the different years and seasons; and to evaluate the effect of selective thinning as a potential mitigation practice on water stress.

Materials and methods

Site description and stand history

Please refer to Chapter 3.

Experimental design

The drought and selective thinning experiment was established in 2004. To test and simulate the effects of selective thinning and drought, two levels of rainfall (natural rainfall vs. reduced rainfall) and thinning (thinning vs. no thinning) were factorially combined in four treatments with three replicates. The four treatments hereafter are defined as follows:

- Control: no selective thinning nor reduced rainfall treatment.
- Reduced rainfall: 15% of reduced rainfall treatment (in autumn 2004).
- Selective thinning: 20-30% reduction of total stump basal area per plot (in Spring 2004).
- Combined: 15% of reduced rainfall (in autumn 2004) and 20-30% reduction of total stump basal area per plot (in Spring 2004).

In total, twelve rectangular plots (15m * 20m) were installed randomly within this oak forest at least a 10 m buffers surrounding every plot. Tree height, basal area, and density were measured before conducting of the experiment and no significant differences were found in structural characteristics among plots. In the selective thinning and combined treatment, selective thinning was done by hand and following the traditional criteria applied in these young oak coppices in spring of 2004: a reduction in 20-30% of total stump basal area per plot by leaving from one to three dominant stems per stump and eliminating the weakest ones. After the selective thinning, the mean stem basal area and height in thinning and combined treatment were 14.3±0.8 cm^3 and 180±4 cm whereas in the unthinned plots were 7.7±0.8 cm^3 and 146±4 cm, respectively. In the reduced rainfall and combined treatment plots, parallel drainage channels were installed at around 50cm height above the soil and covering 15% of the ground surface after the measurement of autumn 2004.

Field measurements

Stem carbon fluxes and stem temperature of *Q. ilex* and *Q. cerrioides* were measured seasonally from 2005 to 2006 in each treatment plot. The measurement was conducted in three days continuously in each season. As the instrumental limitations, stem respiration rates were only measured in one replicate of each treatment. Therefore the measurements were taken consecutively from one treatment plot to the other, which resulted an almost two weeks measured period per season. Measurements of CO_2 exchange were performed at 1.5 m above soil level on tree stem. The stems were enclosed in cylindrical PVC cuvettes (25 cm diameter). Air was continuously forced through all chambers by pumps. Only one chamber at a time was connected to the IRGA to analyze the CO_2 concentration of the respective chamber, while air from the others was exhausted to the atmosphere until their own turn. Signals from the IRGA were logged every 5 second for 1 min for each stem cuvettes and mean values were recorded by the data logger. The CO_2 efflux rates were expressed per unit of stem surface area (μmol C $m^{-2}s^{-1}$).

Soil moisture (cm3/cm3) was measured and recorded manually once per day during the 3-days measurement of each plot with TDR (Time Domain Reflectometry, Tektronix, 1520C, Beaverton, OR). Apart soil moisture, we also adapted the Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) as an indicator of drought index. SPEI is a multiscalar drought index which includes potential evapotranspiration as a parameter. It allows to compare drought severity through time and space, therefore is especially suitable to use in our study. A SPEI of 0 indicates a value corresponding to 50% of the cumulative probability of potential evapotranspiration. The lower the SPEI value, the more intense the drought. As it can be calculated in different temporal scale, we selected time scale of three months in accordance with our seasonal measurement. We also measured base stem increment annually in order to calculate the stem relative growth rate (RGR) in diameter.

Data analysis

Stem respiration was expressed on the basis of the surface area of stem. Mean hourly respiration values were used in the analysis of diurnal variation and covariance analysis, and mean daily values were used to test the annual and seasonal differences between treatments. Mean daily stem respirations were regressed against stem temperature as:

$$R = R_0 e^{KT}$$

Where R is the measured stem respiration rate (μmol C $m^{-2}s^{-1}$), R_0 is the basal respiration at temperature of 0°C, T is measured soil temperature (°C) and K is the temperature coefficient. The temperature sensitivity of stem respiration (Q_{10}) may be then calculated from K using the equation (Atkin et al., 2005):

$$Q_{10} = e^{10K}$$

GLM univariate ANOVA was used to examine the seasonal difference in respiration between treatments. Covariance analysis was used to analyze the effect of environmental factors, including air relative humidity, soil water content, photosynthetically active radiation (PAR) and stem temperature, on respiration. All statistical analyses were carried out using PASW 18 for Windows.

Results

Environmental conditions

Air and stem temperatures showed a clear seasonality with maximum values of 31.4°C (air) and 31.5 °C (stem) during summer, and 5.5°C (air) and -1.8°C (stem) during winter (Figure 7.1). Air temperatures were only slightly higher than stem temperature. There were no significant differences in stem temperature between treatments. Precipitation mainly concentrated during autumn and winter. The lowest seasonal precipitation was found in spring 2006, with only 28 mm from April to June. As the result of precipitation pattern, soil moisture was lowest during the summer and highest during winter. Between treatments, soil moisture was found to be highest in the control treatment, following by soil moisture in the combined treatment. Despite the rainfall exclusion treatment, we didn't find the lowest soil moisture in the reduced rainfall treatment, but in the thinning treatment.

Relative growth rate in stem diameter between treatments

The relative growth rate of stem and height varied between treatments and species (Figure 7.2). In general, we found highest RGR in the thinning treatment and lowest RGR in reduced rainfall treatment. Besides, RGR of *Q. ilex* in thinning treatment was significantly higher than RGR of *Q. cerrioides.*

Diurnal changes in stem respiration

The diurnal variations of stem respiration were

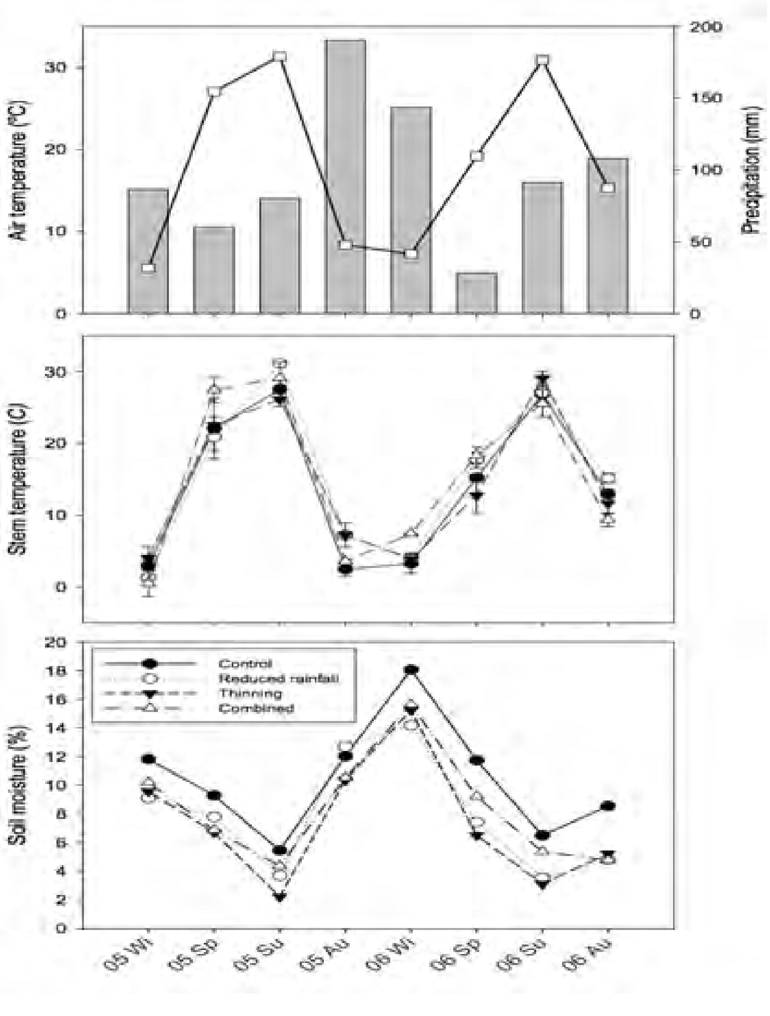


Figure 7.1. Seasonal variations in climatic variables over the study period. (a) Seasonally sum of precipitation and mean air temperature of measured days. (b) Mean soil moisture of each treatment. (c) Mean stem temperature of each treatment.

similar between treatments and years (Figure 7.3). For both tree species, stem respirations during winter were low and almost no diurnal changes were apparent. Stem respirations of both species showed clear diurnal variations during spring and summer, corresponding to the diurnal variation in stem respiration. Stem respiration of *Q. cerrioides* was significantly higher than stem respiration of *Q. ilex* during spring while the reversed result was found during the summer. There were clear daytime depression of stem respiration of *Q. cerrioides* in the control and combined treatments during spring. We also observed a significantly higher stem respirations in the thinning treatment during autumn, with around 2-fold higher than stem respirations of the other treatments in the meantime.

Treatment effects on variation of stem respiration and its relationship with SPEI

Stem respiration between treatment and species exhibited similar seasonal variation (Figure 7.4). Besides, the seasonal variation of stem respiration also showed the same trend as SPEI, especially stem respiration in the thinning treatment. For *Q. ilex*, thinning and combine treatments significantly increased its stem respiration rates during the growing season of first year (2005), but the effect seems to reduce in the second year. In the same time, thinning treatment also increased significantly the stem respiration of *Q. cerrioides* and the effect lasted at least two years after the treatment practice. Reduced rainfall treatment suppressed stem respiration of both *Q. ilex* and *Q. cerrioides* especially during spring. Reduced rainfall treatment also showed a more significant effect on *Q. cerrioides*, during the measured period, stem respiration of *Q. cerrioides* in reduced rainfall treatment was always lower than in the other treatments, except in summer 2006 (Appendix I).

Analysis of factors controlling stem respiration

The relationships between stem respiration and temperature were similar between species and treatments. Stem respiration was positive correlated with stem temperature in all treatments, with a good fit with eqn (1) ($r^2>0.62$; Figure 7.5). The annual Q_{10} was 1.86, 1.93, 1.97 and 2.14 for control, reduced rainfall, thinning and combined treatment, respectively, meanwhile annual stem basal respiration at 10 °C was 0.08, 0.06, 0.1 and 0.07 µmol m^{-2} s^{-1} (Table 7.1). When separated the growing season, Q_{10} values for winter and autumn were higher than for spring and summer, except in reduced rainfall treatment. As many other studies, we also found a time lag between stem respiration and stem temperature. The average time lag was 1 hour, but the lag time varied between seasons. However, the temperature coefficient did not improve even though the lag of temperature was applied. Except the significant effect of temperature on stem respiration, we found that other environmental factors that control stem respiration were different

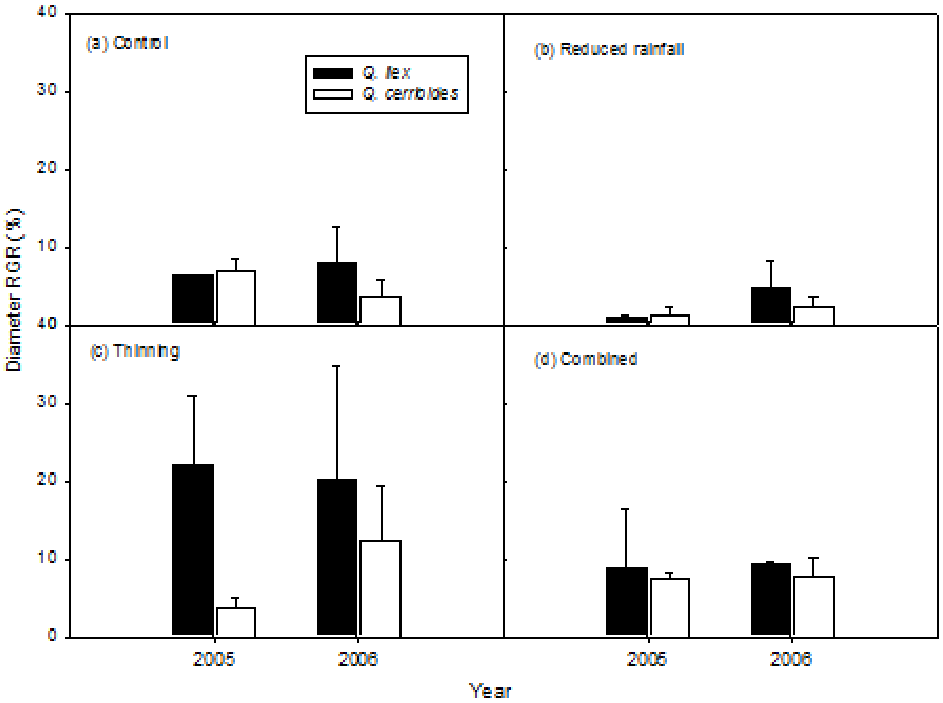


Figure 7.2. Relative growth rates of stem diameter of each treatment.

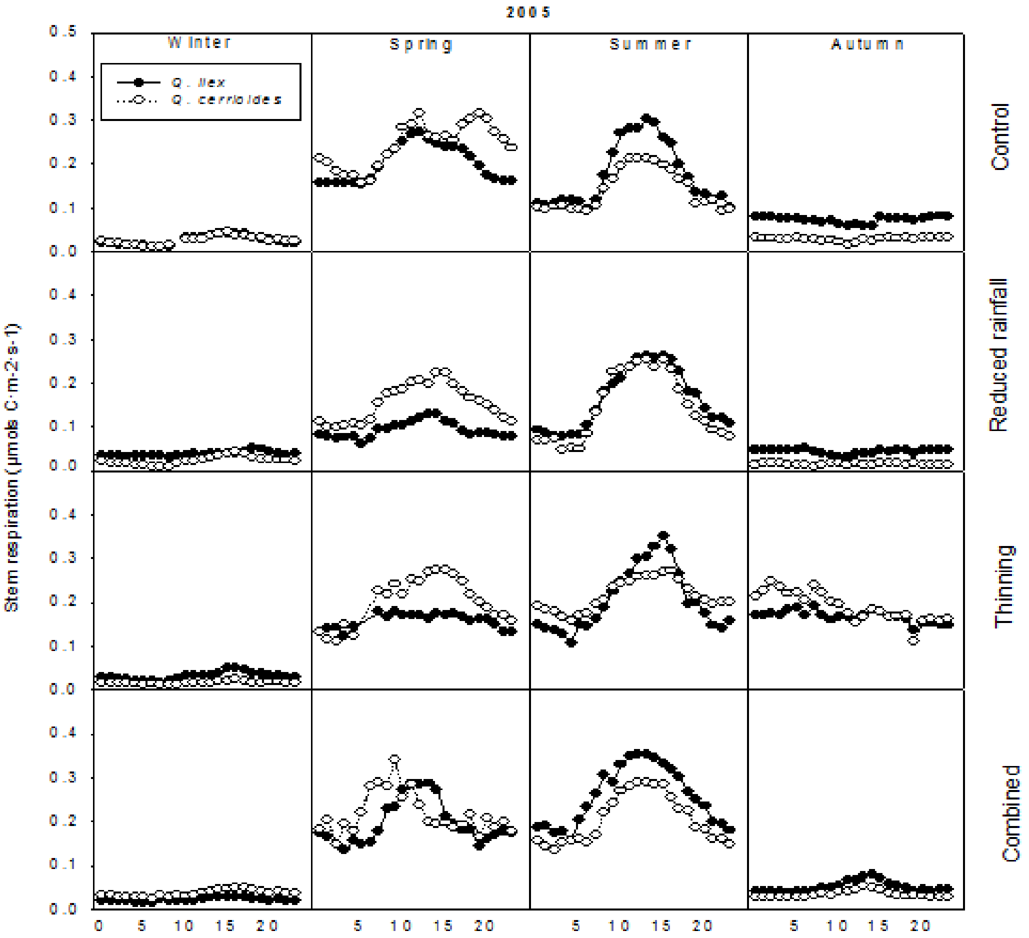


Figure 7.3. Diurnal variations of stem respiration between seasons and species in each treatment.

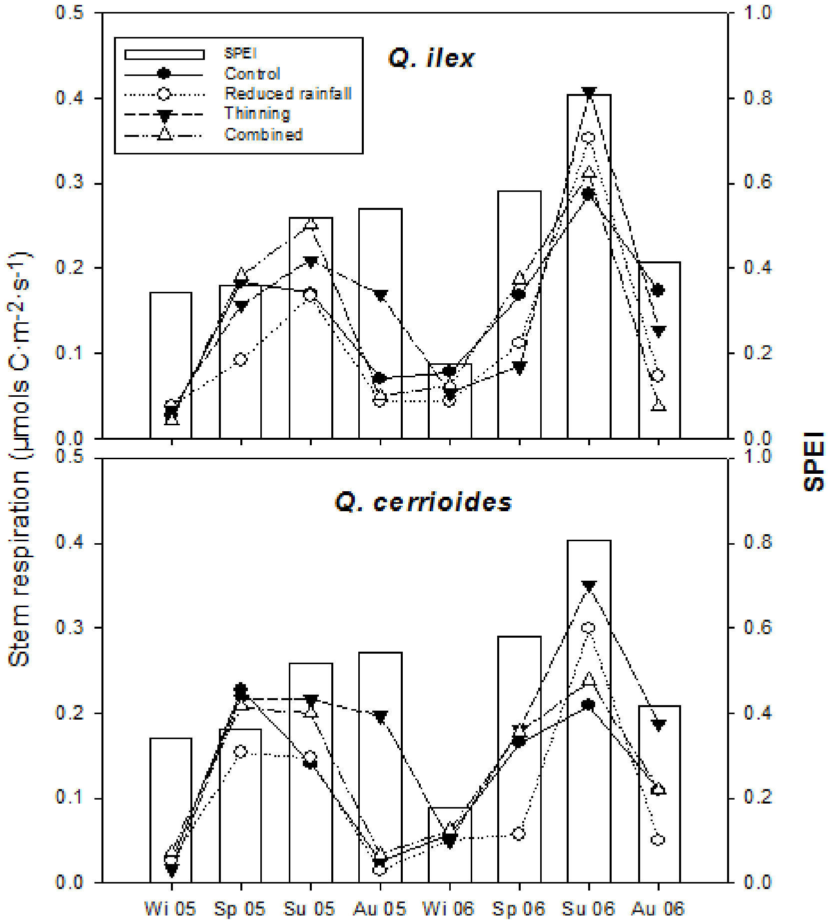


Figure 7.4. Seasonal variations of stem respiration and SPEI.

between treatments (Table 7.2). For example, only stem temperature had effects on stem respiration in reduced rainfall treatment while in thinning treatment, air relative humidity, stem temperature and PAR had significant effects on stem respiration. When we looked into details of how environmental factors affect stem respirations of *Q. ilex* and *Q. cerrioides*, we found that stem respiration of *Q. cerrioides* responded significantly to PAR. Besides, in thinning treatment, other factors such as air relative humidity and soil water content also played roles in regulating stem respiration of *Q. cerrioides*.

Discussion

Our results showed that variations of stem respiration rate in our study site were mainly influenced by diurnal and seasonal variations of stem temperature. During the study period, the maximum stem respiration rate occurred in the afternoon while the minimum occurred in the early morning. The mean seasonal Q_{10} values (1.86-2.14) in our study were comparable with other studies (Aanderud et al., 2010; Damesin et al., 2002; Guidolotti et al., 2013; Saveyn et al., 2007; Yang et al., 2012). Paembonan et al., (1992) and Stockfors and Linder (1998) found a clear seasonal variation of Q_{10} for *Chamaecyparis obtusa*. We also observed a higher Q_{10} values for stem respiration during autumn and winter, except the stem respiration in the reduced rainfall treatment. Lavigne (1987) hypothesized that at low temperature the capacity of stems to produce respiratory products may increase after thinning. This may be the reason that we found a significantly higher Q_{10} of autumn and winter stem respiration in the thinning treatment. In accordance to previous studies (Saveyn et al., 2007; Zach et al., 2010), we also found a decrease of stem respiration in the reduced rainfall treatment. Several authors have argued that reduction of cell turgor in the stem caused by drought could lead a transient reduction in the respiratory and metabolic activities of the living tissue, thus consequently suppress the stem respiration (Saveyn et al., 2007). The stem tissue obtained energy for growth and maintenance processes through respiration. When the water reserves in the living tissue are depleted, water

Table 7.1. Temperature sensitivity of stem respiration (Q_{10}), stem basal respiration at 10°C (R_{10}) for growing season (spring and summer) and non-growing season (winter and autumn) in each treatment.

	Control			Reduced rainfall			Thinning			Combined		
	R_{10}	Q_{10}	r^2	R_{10}	Q_{10}	r^2	R_{10}	Q_{10}	r^2	R_{10}	Q_{10}	r^2
All season	0.08	1.86	0.73	0.06	1.93	0.76	0.10	1.97	0.62	0.07	2.14	0.92
Spring & Summer	0.14	1.27	0.36	0.06	1.95	0.41	0.10	1.82	0.73	0.14	1.38	0.52
Winter & Autumn	0.09	2.41	0.46	0.03	1.34	0.23	0.12	3.06	0.38	0.07	2.29	0.85

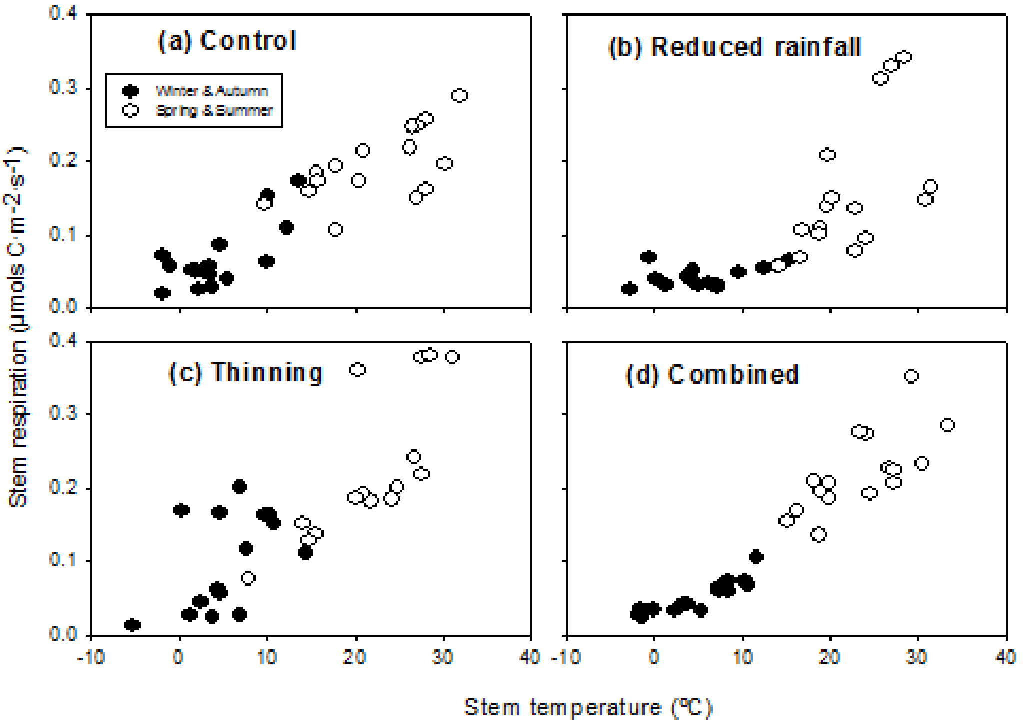
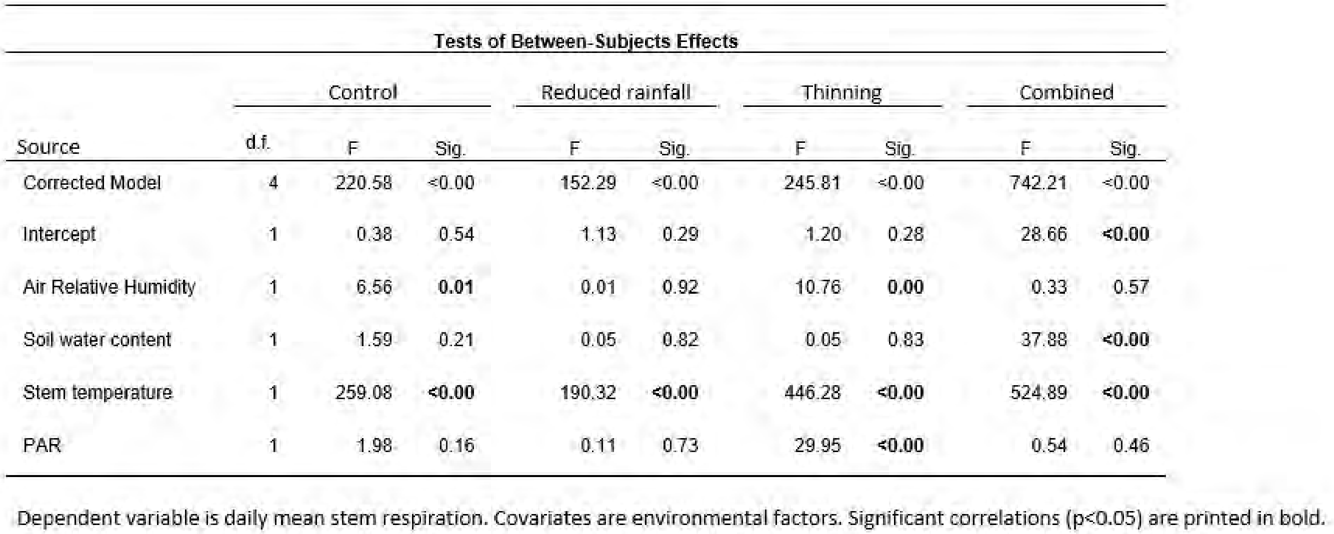


Figure 7.5. Relationship between mean daily stem temperature and stem respiration in each treatment.

Table 7.2. Results of covariance analysis based on two year mean daily respiration in each treatment ($m$mol CO_2 m^{-2} s^{-1}).



Tests of Between-Subjects Effects

		Control		Reduced rainfall		Thinning		Combined	
Source	d.f.	F	Sig.	F	Sig.	F	Sig.	F	Sig.
Corrected Model	4	220.58	<0.00	152.29	<0.00	245.81	<0.00	742.21	<0.00
Intercept	1	0.38	0.54	1.13	0.29	1.20	0.28	28.66	**<0.00**
Air Relative Humidity	1	6.56	**0.01**	0.01	0.92	10.76	**0.00**	0.33	0.57
Soil water content	1	1.59	0.21	0.05	0.82	0.05	0.83	37.88	**<0.00**
Stem temperature	1	259.08	**<0.00**	190.32	**<0.00**	446.28	**<0.00**	524.89	**<0.00**
PAR	1	1.98	0.16	0.11	0.73	29.95	**<0.00**	0.54	0.46

Dependent variable is daily mean stem respiration. Covariates are environmental factors. Significant correlations ($p<0.05$) are printed in bold.

deficits may temporarily reduce rates of growth and maintenance processes and the respiratory activity (Daudet et al., 2005; Kakubari, 1988; Lavigne, 1987; Wang et al., 2003). As the significantly higher RGR in the thinning treatment, we expected to observe a higher stem respiration rate. However, except the higher stem respiration rate during autumn, stem respirations were not significantly different from the other treatments during spring and summer. We hypothesized that it may due to the sampling frequency in our study was too low to record the growth respiration. In study of Stockfors and Linder (1998), it was noted that the lag between growth and respiration peaks varied between 10 and 20 days for *Picea abies*. Besides, due to the difference of stem basal area and height of *Q. ilex* and *Q. cerrioides* at the beginning of treatment, the thinning intensity applied to each species was different, and this might consequently affect the relative growth rate. Another possible explanation is that the measured position of stem respiration may introduce error. As the stem respiration also depends on the amount of living cells and their respiratory potential and activity, the distribution of living cells within the stem can affect the actual measured values (Ceschia et al., 2002). Other than that, the different component of plant may respond differently to the environmental drivers and may not reflect through stem respiration rate. For example, in the study of Way and Oren (2010), they found that some variables responded more strongly to daytime growth temperature (such as height), while other variables (such as stem diameter) were better explained by nocturnal temperatures. Another interesting finding was that stem respiration of *Q. cerrioides* in the thinning and combined treatments was highly correlated with air relative humidity, soil water content and PAR. It is general assumed that PAR affects stem respiration through its effect on photosynthesis, which also affects tree growth. Other plant activities like cambium activity and sap flow also play an important role in regulating stem respiration changes. Besides, we also found an significant increase in soil respiration of *Q. cerrioides* in the thinning treatment (see chapter 4). Therefore, it may be hypothesized that either (i) the better correlation of stem respiration with PAR and soil water content may simply due to the increase of transpiration rate caused by thinning or (ii) thinning was able to reduce the drought effect on *Q. cerrioides* therefore the stem respiration was synchronized with the other tree physiology. Thinning may or may not be able to reduce the drought effect on stem respiration, but it may help shorten the stress period or prolong the growing season (Lavigne et al., 2004). If so, thinning may have more effect on deciduous species, as the shorter growing period of deciduous species compared to evergreen species. In conclusion, our results showed that treatments had different effects on stem respirations of our target tree species. It seems that stem respiration of *Q. cerrioides* is more sensitive to drought also to thinning treatment. In the other hand, although stem respiration of *Q. ilex* showed less affected by treatment, the other components of tree such as litterfall or stem growth did respond to treatment.

Table 7.3. Results of covariance analysis based on two year mean daily respiration of *Q. ilex* and *Q. cerrioides* in each treatment (*m*mol CO_2 m^{-2} s^{-1}).

		Control				Reduced rainfall				Thinning				Combined			
		Q. ilex		*Q. cerrioides*		*Q. ilex*		*Q. cerrioides*		*Q. ilex*		*Q. cerrioides*		*Q. ilex*		*Q. cerrioides*	
Source	d.f	F	Sig.	F	Sig.	F	Sig.	F	Sig.	F	Sig.	F	Sig.	F	Sig.	F	Sig.
Corrected Model	4	304.24	**0.00**	282.77	**<0.00**	126.64	**<0.00**	153.77	**<0.00**	184.32	**<0.00**	275.22	**<0.00**	523.39	**<0.00**	566.85	**<0.00**
Intercept	1	1.72	0.19	5.02	**0.03**	6.71	**0.01**	0.35	0.56	1.35	0.25	1.60	0.21	3.11	0.08	67.96	**<0.00**
Air Relative Humidity	1	2.22	0.14	0.15	0.70	2.43	0.12	2.16	0.14	0.05	0.83	43.52	**<0.00**	1.90	0.17	8.21	**<0.00**
Soil water content	1	1.70	0.19	0.29	0.59	0.19	0.66	0.02	0.89	1.26	0.26	5.18	**0.02**	11.69	**<0.00**	58.77	**<0.00**
Stem temperature	1	305.03	**0.00**	357.87	**<0.00**	152.15	**<0.00**	193.88	**<0.00**	360.33	**<0.00**	446.58	**<0.00**	434.08	**<0.00**	326.99	**<0.00**
PAR	1	0.30	0.59	37.49	**<0.00**	1.73	0.19	4.72	**0.03**	32.97	**<0.00**	17.29	**<0.00**	0.13	0.72	2.39	0.12

Dependent variable is daily mean stem respiration. Covariates are environmental factors. Significant correlations (p<0.05) are printed in bold.

Appendix I. Description of stem respiration. Values are mean with SD.

	2005				2006			
	Control	Reduced R.	Thinning	Combined	Control	Reduced R.	Thinning	Combined
Winter	0.03 ± 0.00^{ab}	0.03 ± 0.01^{a}	0.02 ± 0.01^{b}	0.03 ± 0.00^{ab}	0.06 ± 0.02^{a}	0.05 ± 0.01^{a}	0.05 ± 0.01^{a}	0.05 ± 0.02^{a}
Spring	0.21 ± 0.04^{a}	0.13 ± 0.02^{b}	0.19 ± 0.01^{a}	0.20 ± 0.02^{a}	0.16 ± 0.02^{a}	0.08 ± 0.02^{b}	0.12 ± 0.03^{c}	0.18 ± 0.02^{a}
Summer	0.15 ± 0.04^{ab}	0.12 ± 0.04^{a}	0.21 ± 0.03^{b}	0.22 ± 0.06^{b}	0.25 ± 0.03^{a}	0.30 ± 0.06^{a}	0.37 ± 0.01^{b}	0.28 ± 0.06^{a}
Autumn	0.05 ± 0.01^{a}	0.03 ± 0.00^{b}	0.17 ± 0.02^{c}	0.04 ± 0.00^{ab}	0.12 ± 0.05^{a}	0.06 ± 0.01^{b}	0.14 ± 0.03^{a}	0.08 ± 0.02^{b}
All	0.11 ± 0.08^{ab}	0.08 ± 0.05^{a}	0.15 ± 0.08^{b}	0.12 ± 0.10^{ab}	0.15 ± 0.08^{a}	0.12 ± 0.11^{a}	0.18 ± 0.13^{a}	0.15 ± 0.10^{a}

Different letters separate significantly different means between treatments based on post-hoc Duncan tests at $P < 0.05$.

Appendix II. Description of stem respiration of *Q. ilex*. Values are mean with SD.

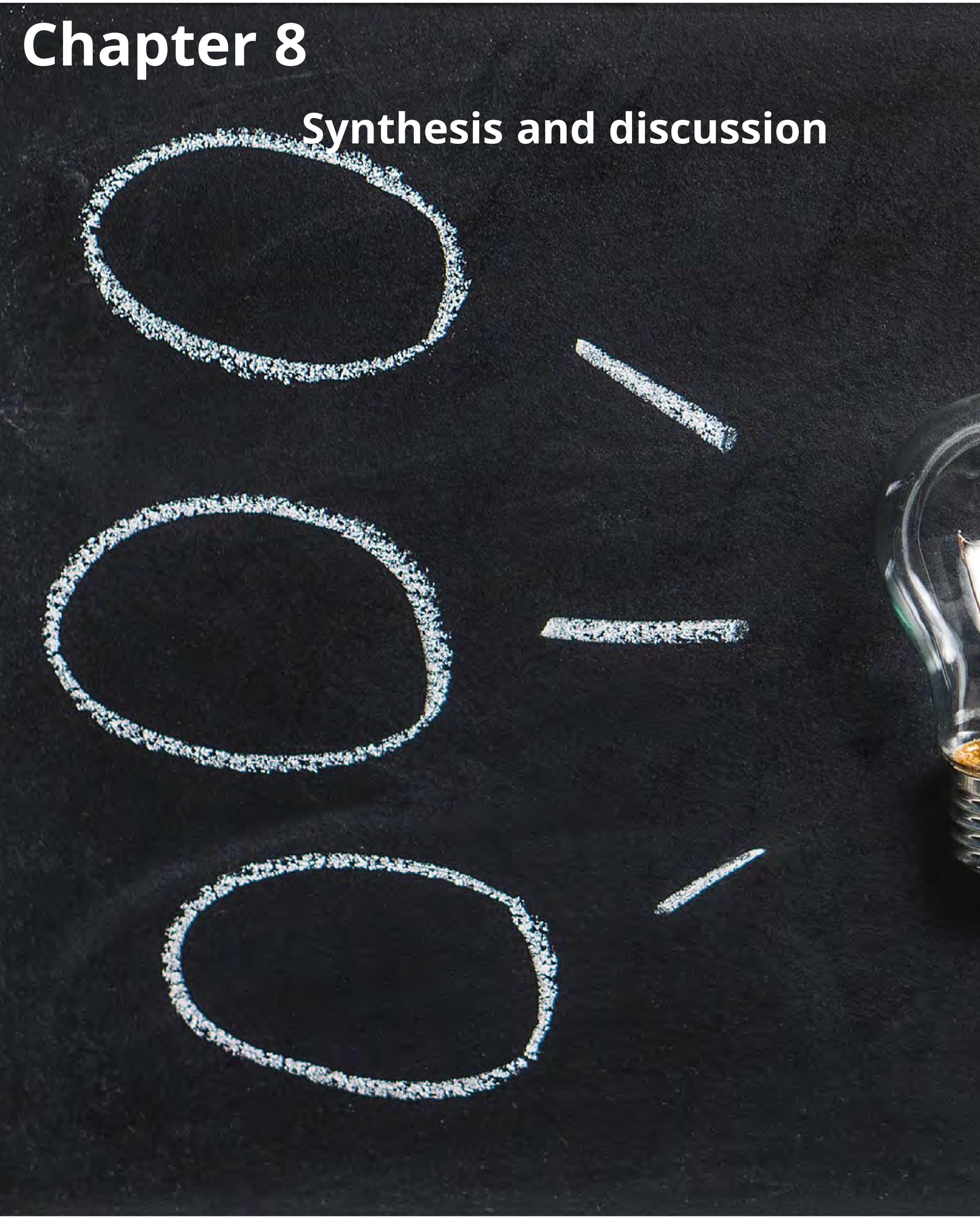
	2005				2006			
	Control	Reduced R.	Thinning	Combined	Control	Reduced R.	Thinning	Combined
Winter	0.03±0.00^{a}	0.04±0.01^{b}	0.03±0.01^{a}	0.02±0.00^{a}	0.07±0.03^{a}	0.05±0.01^{a}	0.06±0.01^{a}	0.05±0.01^{a}
Spring	0.19±0.03^{a}	0.09±0.01^{b}	0.16±0.01^{a}	0.19±0.04^{a}	0.17±0.02^{a}	0.11±0.03^{b}	0.08±0.02^{b}	0.19±0.02^{a}
Summer	0.17±0.05^{ab}	0.13±0.04^{a}	0.20±0.04^{ab}	0.24±0.07^{b}	0.29±0.05^{a}	0.32±0.06^{a}	0.40±0.01^{b}	0.32±0.05^{a}
Autumn	0.07±0.01^{a}	0.05±0.00^{b}	0.17±0.01^{c}	0.05±0.01^{b}	0.15±0.06^{a}	0.07±0.01^{bc}	0.11±0.02^{ab}	0.04±0.02^{c}
All	0.11±0.07^{ab}	0.08±0.01^{a}	0.14±0.07^{b}	0.12±0.10^{ab}	0.17±0.09^{a}	0.14±0.12^{a}	0.17±0.15^{a}	0.15±0.12^{a}

Appendix III. Description of stem respiration of *Q. cerrioides*. Values are mean with SD.

	2005				2006			
	Control	Reduced R.	Thinning	Combined	Control	Reduced R.	Thinning	Combined
Winter	0.03±0.01^{a}	0.02±0.01^{a}	0.02±0.00^{b}	0.04±0.00^{c}	0.05±0.02^{a}	0.06±0.01^{a}	0.05±0.01^{a}	0.06±0.02^{a}
Spring	0.23±0.05^{a}	0.18±0.03^{b}	0.22±0.01^{ab}	0.22±0.01^{ab}	0.16±0.02^{a}	0.06±0.02^{b}	0.17±0.05^{a}	0.18±0.03^{a}
Summer	0.14±0.03^{a}	0.11±0.04^{a}	0.22±0.02^{b}	0.20±0.05^{b}	0.21±0.01^{a}	0.27±0.06^{a}	0.34±0.01^{b}	0.24±0.07^{a}
Autumn	0.03±0.01^{a}	0.02±0.00^{a}	0.18±0.03^{b}	0.03±0.00^{a}	0.10±0.04^{a}	0.04±0.01^{a}	0.16±0.03^{b}	0.12±0.02^{a}
All	0.11±0.09^{ab}	0.08±0.07^{a}	0.16±0.09^{b}	0.12±0.09^{ab}	0.13±0.07^{ab}	0.11±0.10^{a}	0.19±0.11^{b}	0.15±0.08^{ab}

Chapter 8

Synthesis and discussion



This chapter is intended to make connections between some of the important findings of the previous chapters and to address the issues that go beyond the scope of those individual research topics. Most importantly, a brief synthesis of studies about the findings of the soil moisture thresholds is discussed in this chapter too.

This PhD dissertation focused on the investigation of biological and environmental controls on soil and stem respirations either in contrasting water regime forests and drought-management treatment in Mediterranean forests. The objectives of this study were to (i) determine the temporal variation of soil respiration, both autotrophic and heterotrophic respirations, under different water regimes and vegetation, (ii) estimate the possible drought effect on soil and stem respirations and the implication of thinning as a mitigation practice, and (iii) provide information of how soil moisture regulates the temperature sensitivity of respiration. These objectives were collectively motivated by the need to better understand terrestrial ecosystem plant and soil respiration dynamic in the Mediterranean region, and predict individually how soil water availability modulates the temperature and moisture responses of respiration.

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Synthesis of results

Temperature sensitivity of soil respiration vs. soil moisture

Table 8.1 lists the climate description and observed soil respiration from out three study sites. The highest mean soil respiration rate of our three study sites was found in Font de Regàs, followed by Collserola and Castelltallat. Mean annual precipitation and soil moisture also showed similar tendencies between sites. Although our three study sites are all classified as Mediterranean climate, the observed soil respirations from these three sites showed distinct seasonal variations. In Castelltallat and Font del Regàs, soil respiration followed the seasonal change of soil temperature, with interannual variation caused by different annual precipitation. In these two sites, soil temperature explained the majority of the seasonal variation of soil respiration (68-96%) when soil moisture is higher than certain threshold. In Collserola, soil moisture is the main driver of soil respiration. Using soil moisture alone could explain 35-78% of the annual variation of soil respiration.

The ratio of heterotrophic respiration to total soil respiration varied between seasons and sites, from 0.51-1.00. However, these values are biased due to the difference of soil moisture caused by trenching. For example, in Collserola the difference of 5 cm soil moisture between control and trench treatment may reach to 8%. The higher surface soil moisture significantly promoted heterotrophic respiration especially during drought period. We pooled soil respiration data (control treatment) from our three study sites and applied the recursive partitioning method, we identified two soil moisture thresholds, 10.6% and 16.3% (Figure 8.1).

However, considering that the measured soil moisture depths were different between our study sites (top 5 cm was measured in the Collserola and Font de Regàs and top 20cm was measured in the Castelltallat site), hereafter we only pooled the data from Collserola and Font de Regàs as both study sites share the same implication of experiment design. Unlike the previous analysis result, using recursive partitioning method on pooled data of Collserola and Font de Regàs, only one soil moisture threshold was identified: 17.8% of soil moisture for total soil respiration (Figure 8.2) and 20% of soil moisture for heterotrophic respiration (Figure 8.3)

When soil moisture was lower than the threshold, both total soil respiration and heterotrophic respiration showed positive correlations with soil moisture, excepted total soil respiration of Collserola measured in spring of 2011 (Figure 8.4 & 8.5). Besides, the observed heterotrophic respirations under soil moisture threshold at the Font del Regàs site are all from 2012 and can be separated clearly by season (spring and summer).

We also applied the same method to the data from the Castelltallat. However, we didn't find any clear relationship between soil moisture and soil respiration when soil moisture lower than the threshold.

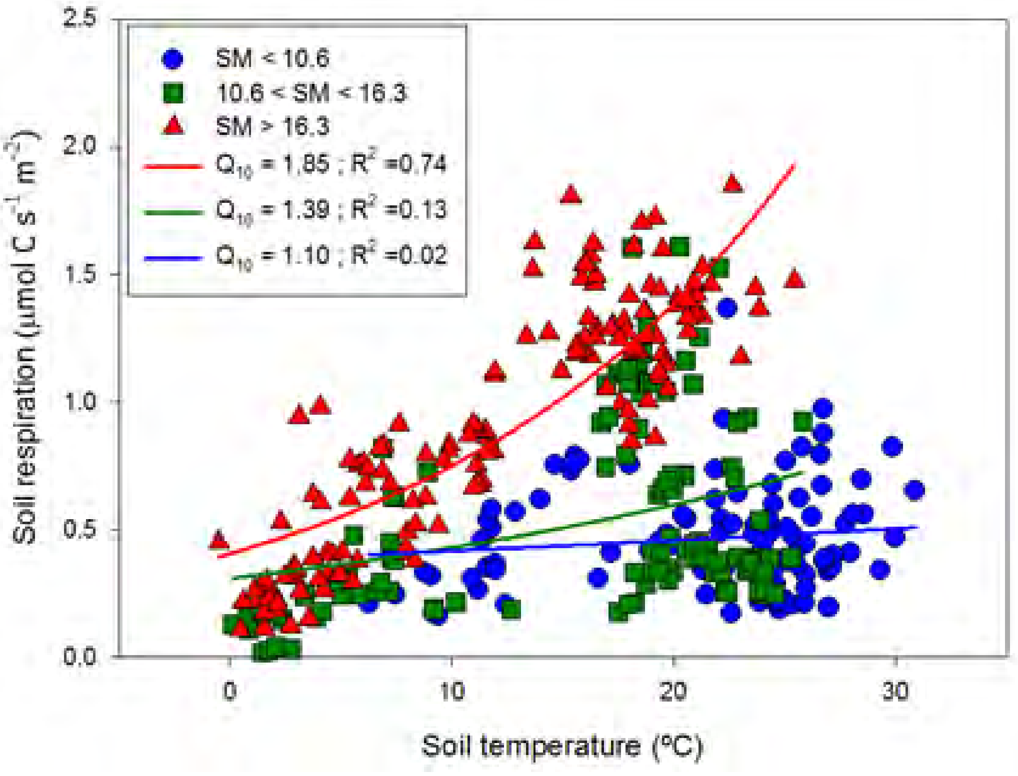


Figure 8.1. Relationship between soil temperature and soil respiration separated by different soil moisture regime. Data are from all three study sites.

Table 8.1. Climate description and soil respiration (SR) results of our three study site during measurements. Values are the means of each parameter during the experiment period.

Site (experiment year)	Mean air temperature (°C)	Mean annual precipitation (mm)	Mean SR rate (μmol C $s^{-1}m^{-2}$)	Mean soil moisture (cm^3/cm^3)	Mean VPD (kpa)	Q_{10} of control treatment
Castelltallat (2004-2007)	13.6 (6.6 - 21.6)	386 (361-434)	0.47(0.02-1.48)	10.1 (4.9-22.4)*	1.44(0.11-5.71)	3.00
Collserola (2011-2012)	15.2 (-4.0 - 36.9)	641 (479-804)	0.73(0.19-1.85)	17.0 (9.3-35.5)	0.76(0.03-2.82)	0.75-2.16
Font de Regàs (2011-2012)	15.0 (-1.6 – 29.2)	901 (515-1291)	0.80(0.11-1.72)	23.9(10.1-45.8)	0.60(0.07-1.84)	1.19-2.14

* The measured depth of soil moisture in Castelltallat is 20cm while in Collserola and Font de Regàs is 5cm.

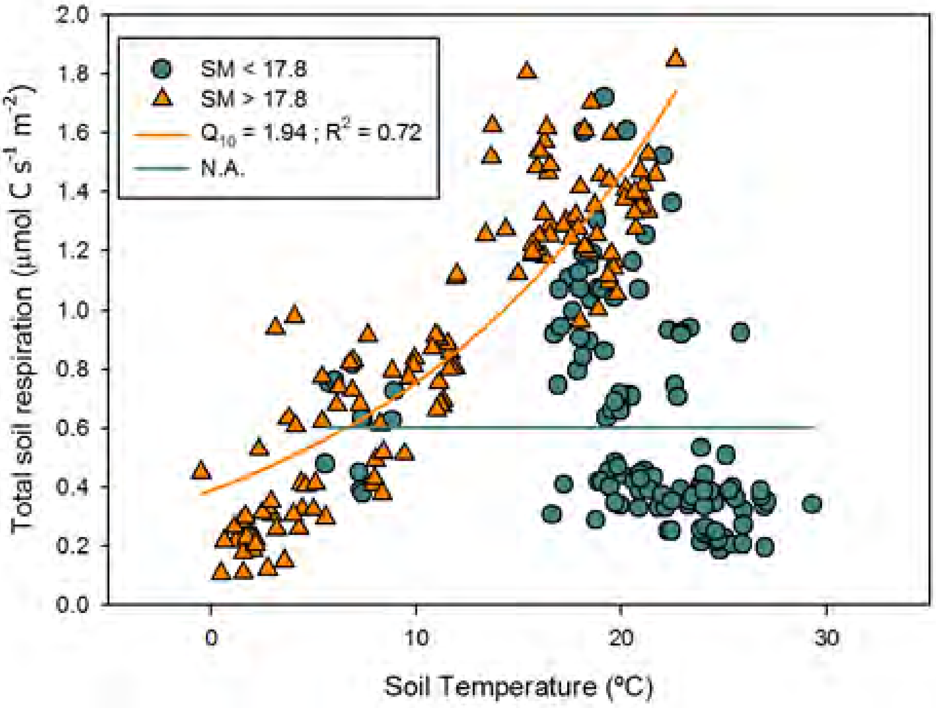


Figure 8.2. Total soil respiration data from Collserola and Font de Regàs against soil temperature divided by soil moisture classes. Data insides the circle correspond to soil respiration measured during summer.

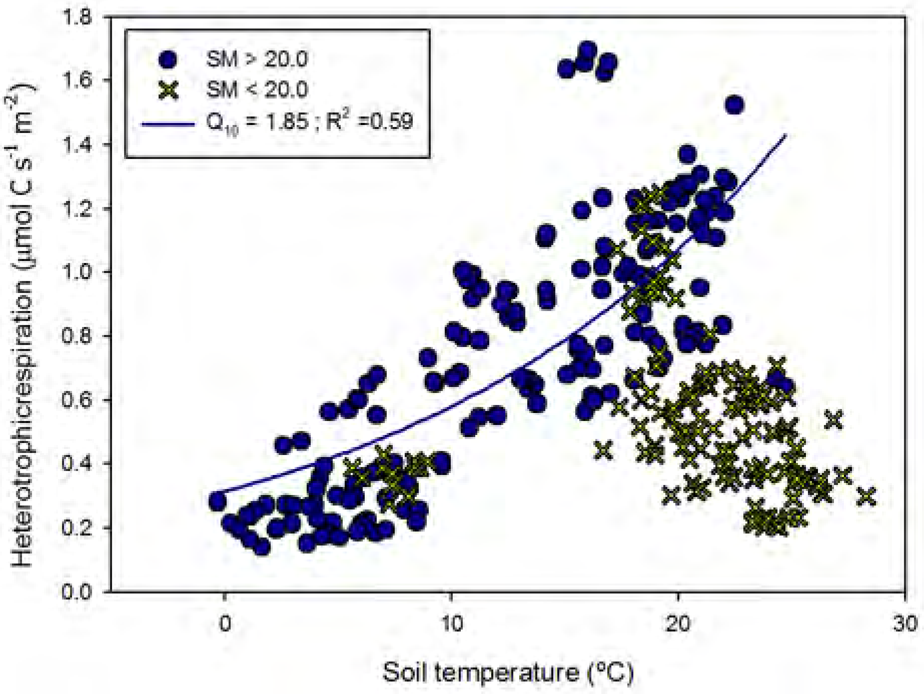


Figure 8.3. Pool data of soil heterotrophic respiration against soil temperature divided by soil moisture classes. Different colours represent different soil moisture regime.

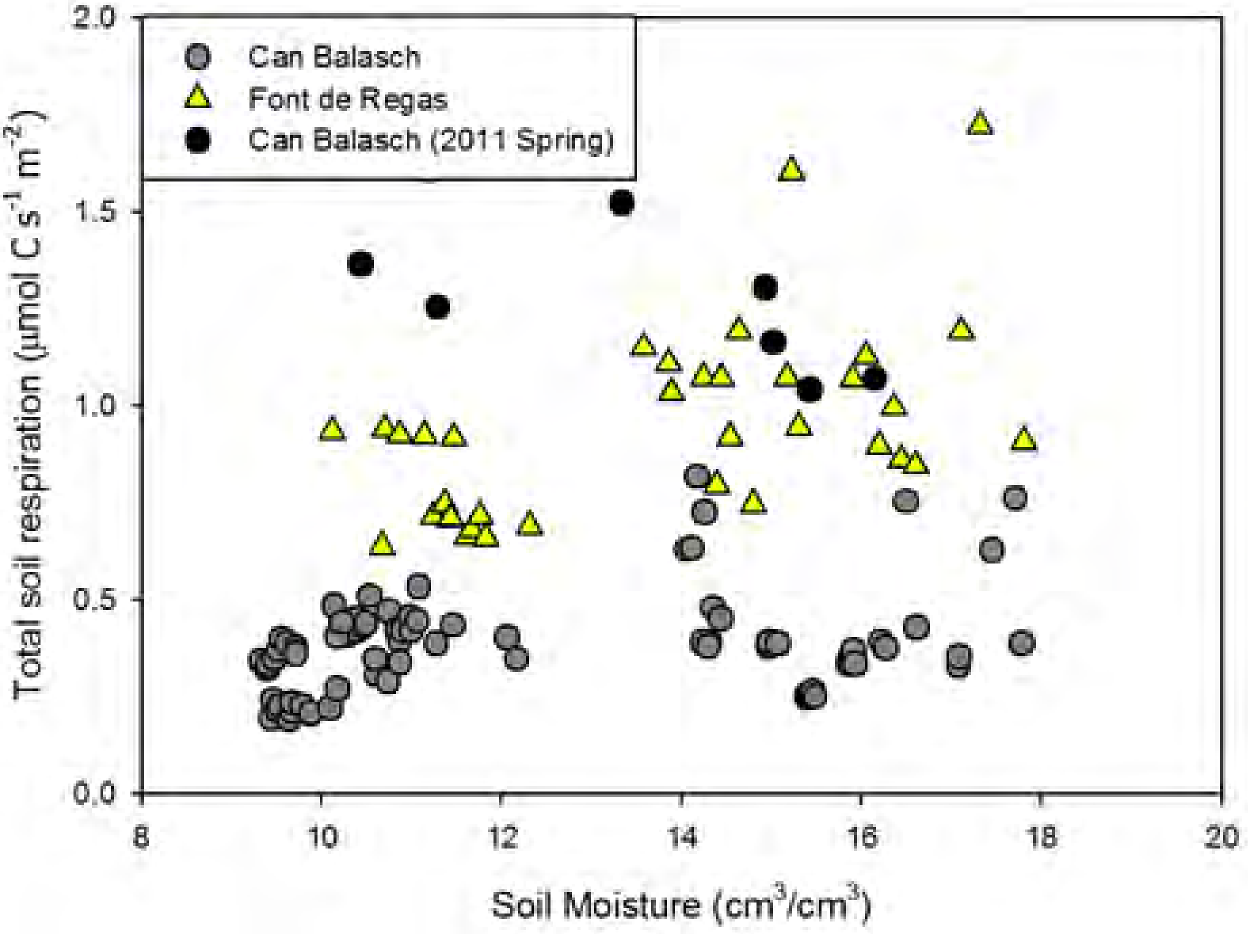


Figure 8.4. Pool data of total soil respiration when soil moisture lower than 17.8 % against soil moisture.

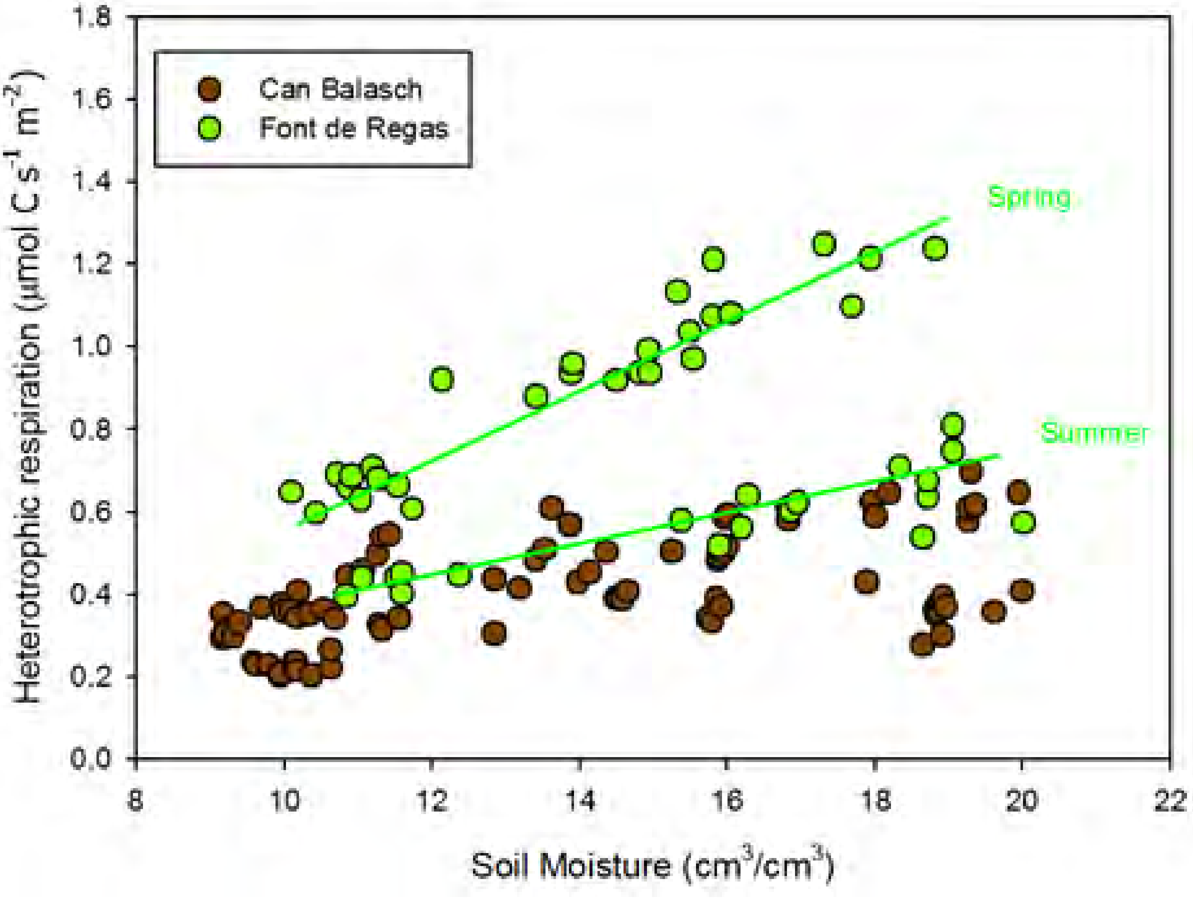


Figure 8.5. Pool data of soil heterotrophic respiration when soil moisture lower than 20.0 % against soil moisture. Different colours represent data from different sites.

Mitigation of drought stress by selective thinning? In chapter 6 and 7, I showed the experimental results of soil respiration and stem respiration subjected to reduced rainfall treatment and forest management. In this section, comparisons between soil respiration, stem respiration and photosynthesis from some of the experiment campaigns in the Castelltallat site are presented (Figure 8.6-8.8). Figures 8.6 and 8.7 show the diurnal variation of photosynthesis, soil and stem respiration from summer of 2005 and 2006. A clear midday depression of photosynthesis can be observed in almost all of the treatments and species. According to SPEI (see Figure 7.4), summer of 2006 was mild in comparison to summer of 2005. As a result, all three processes showed less affected by summer drought during 2006 (Figure 8.7). In some campaigns, for example, in the control plot of summer 2006, the influence of photosynthesis on soil respiration can be seen clearly. Figure 8.9 is the annual variation of photosynthesis, stem and soil respiration. Despite the treatment effect, we actually found higher assimilation rate, especially for *Q. ilex*, in the reduced rainfall treatment in some campaigns, coincide with our findings about soil respiration (Chapter 6).

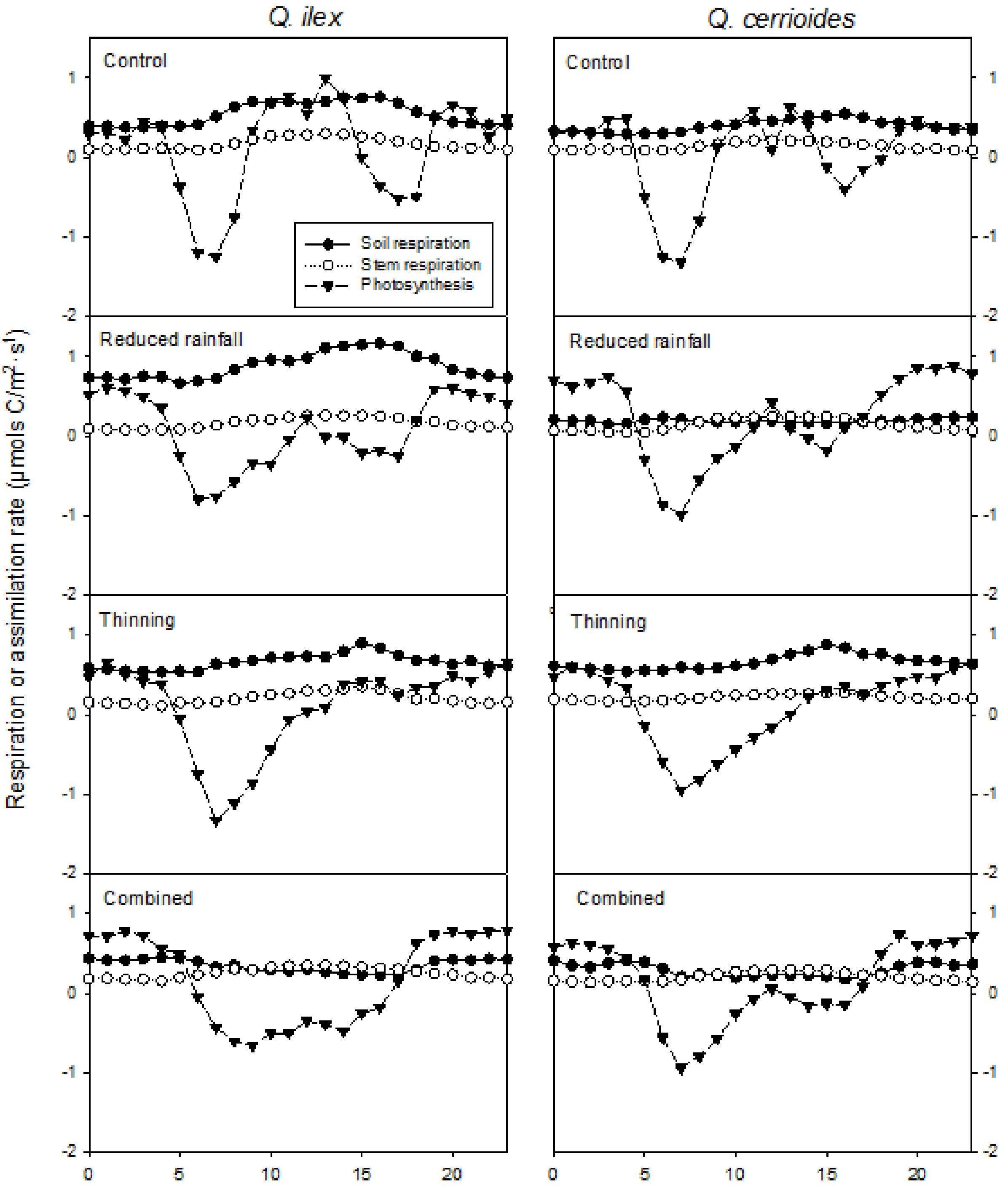


Figure 8.6. Diurnal variations of soil respiration, stem respiration and photosynthesis (assimilation) rate of *Q. ilex* (left panel) and *Q. cerrioides* (right panel) from four treatments (from top to down: control, reduced rainfall, thinning and combined) in summer of 2005.

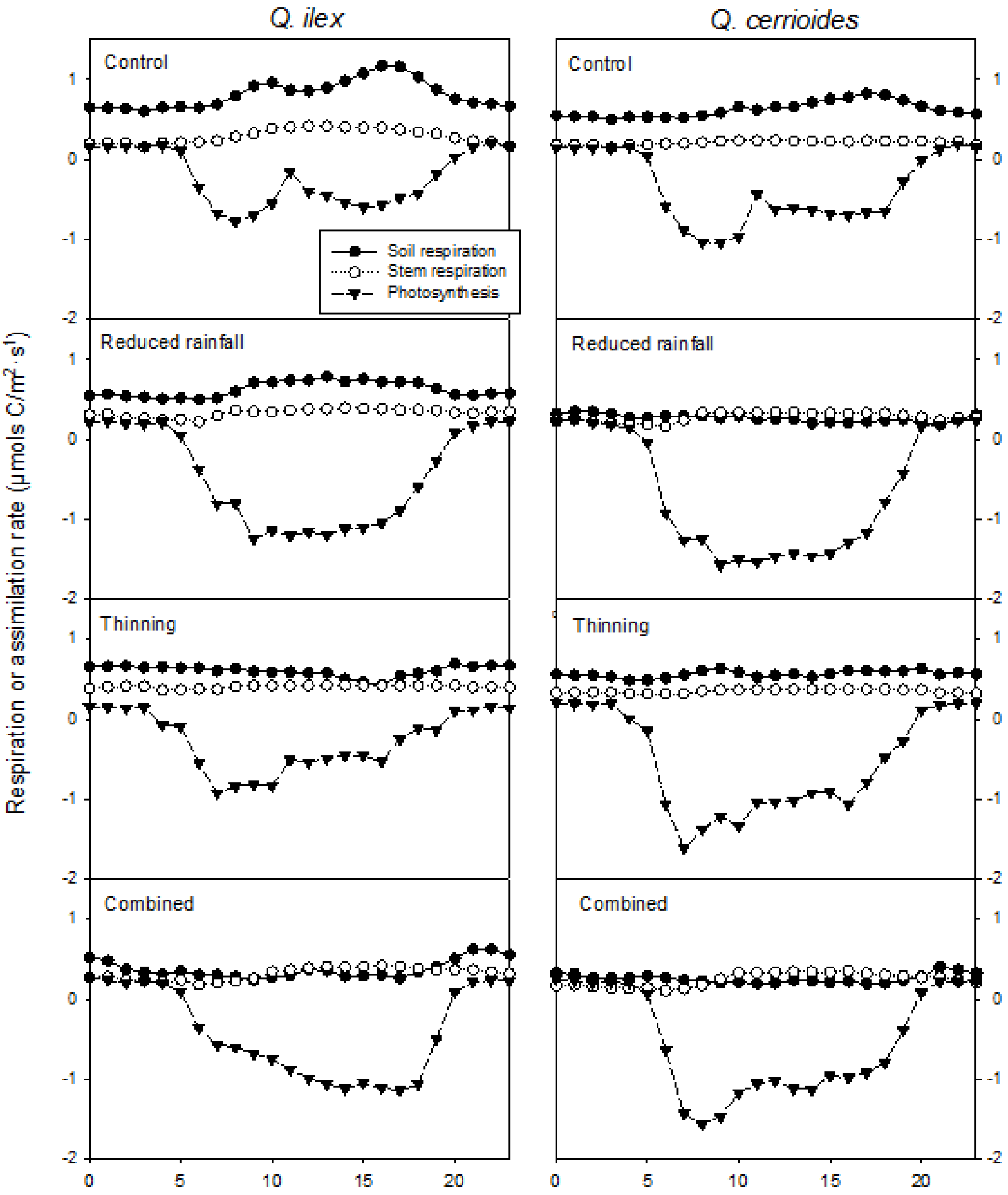


Figure 8.7. Diurnal variations of soil respiration, stem respiration and photosynthesis (assimilation) rate of *Q. ilex* (left panel) and *Q. cerrioides* (right panel) from four treatments (from top to down: control, reduced rainfall, thinning and combined) in summer of 2006.

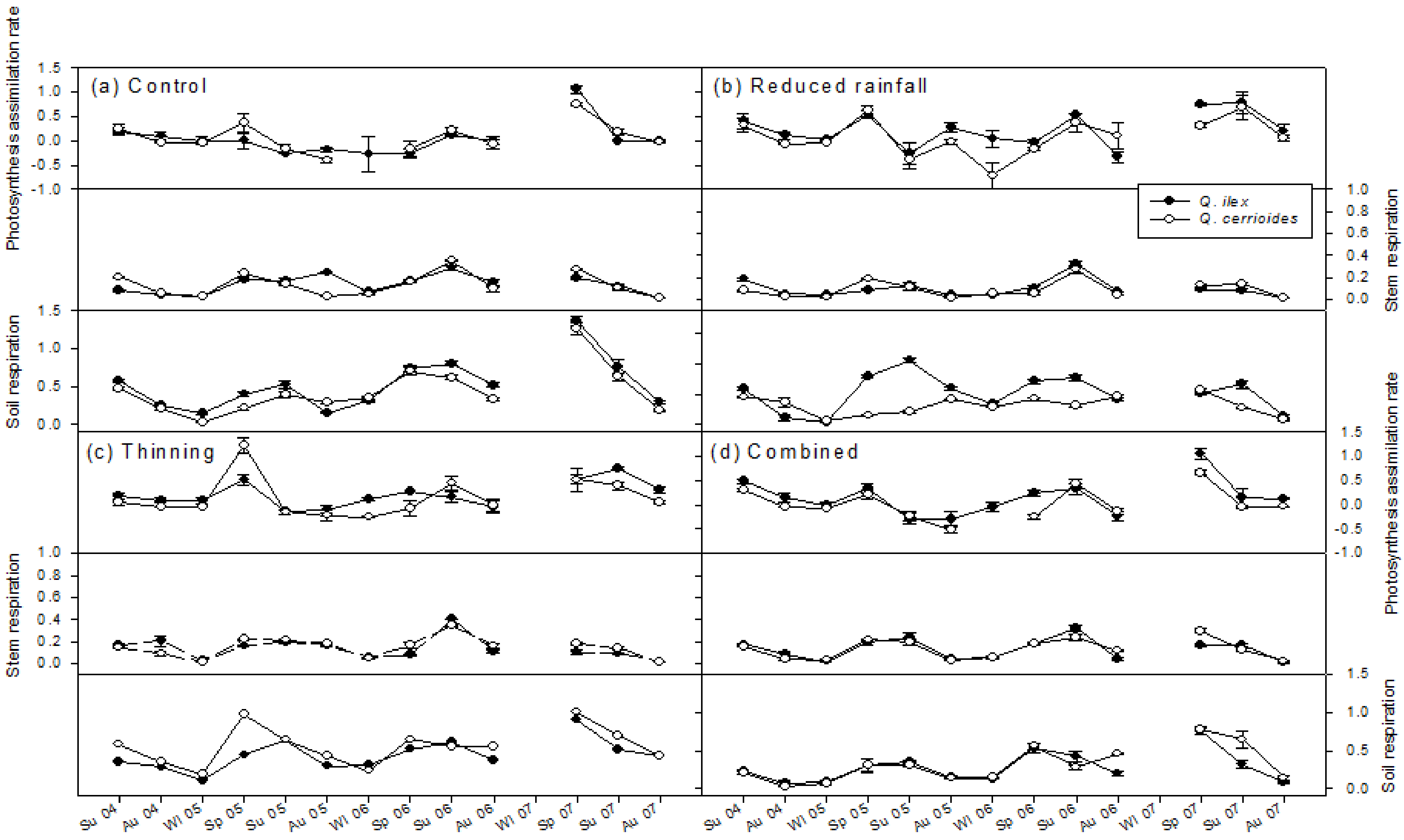


Figure 8.8. Annual variations of soil respiration, stem respiration and photosynthesis assimilation rate of *Q. ilex* and *Q. cerrioides* from four treatments.

General discussion

Knowledge about the temperature sensitivity of respiration is essential to predict the response of ecosystem carbon dynamics. In semi - arid regions such as the Mediterranean, the relationship between temperature and respiration is often masked or altered by soil moisture. All of our three experiments of soil respiration indicated the importance of soil moisture in the carbon dynamic of the Mediterranean forests. The results of our experiments either showed that soil moisture is the main driver of soil respiration, or exhibited a clear soil moisture threshold that would regulate the relationship between soil temperature and soil respiration. As mentioned in the introduction of this dissertation, there is still no consensus yet of how moisture interacts with soil temperature and soil respiration. Currently, it is often assumed in models of global change that the individual effects of soil temperature and soil moisture on soil respiration are multiplicative (Bauer et al., 2008; Bunnell et al., 1977; Fang and Moncrieff, 2001), with the expectation that Q_{10} is independent of soil water content while R_0 is a function of soil moisture. Nevertheless, how to incorporate soil functions into model is undoubtedly important as the choice of the soil functions used to model the respiration response to moisture alone may introduce an uncertainty of at least 4% in global carbon stocks (Falloon et al., 2011).

Our results showed that soil moisture modified, at least in our study sites, the temperature sensitivity of respiration through threshold-like response. Regarding the importance of soil moisture when modelling the global carbon cycle, how to determine this threshold value would be a critical task. Table 8.2 lists the literatures that indicating the existence of soil moisture threshold. Among these 22 studies (includes present study), there are 13 studies conducted in Mediterranean climate region, and two studies from arid-semiarid climate. However, almost none of them discussed this phenomenon in further detail. Therefore, one of the main objects in this general discussion section will be focused on the factors that affecting the soil moisture threshold, discussing how these factors explain phenomenon found in our study and also try to provide some practical suggestions for future study.

Factors affecting the soil moisture threshold

Soil water availability

The primary factor that affects the soil moisture threshold is the different soil water holding capacity due to the difference of soil texture, structure and the soil organic matter content. The soil available water, defined as the difference between moisture content at field capacity and permanent wilting point, is mainly determined by the soil texture. The different threshold values between sites may simply reflect the different wilting points or available water capacity of each ecosystem. Moreover, as soil organic matter can hold up to 20 times its own weight of water, the increase of organic matter content in soil will also increase the water holding capacity (Berman, 1994). This may explain the highest soil moisture threshold found in the first two literatures in Table 8.2, as both sites present thick litter layer.

Plant function types and species

Swift et al. (1979) found that fungi are generally better adapted to water stress than bacteria or soil fauna. As compared to microbes, which may easily be limited or inhibited by surface soil water stress, respiration of roots maybe less affected by surface soil water stress because many plants may compensate for soil water deficit by uptaking water from wetter and deeper soil depths. The different mechanisms of evergreen and deciduous species for surviving in a climate with a limited amount of soil water may lead to different soil moisture thresholds (Ogle and Reynolds, 2004). The evergreen species tends to have greater water use efficiency than deciduous species and the deciduous species may be more subject to water limitation than evergreen species (Hollinger, 1992). This is also supported by our results from the reduced rainfall treatment in Castelltallat; the drought tolerant species *Q. ilex* showed a weak relationship with temperature while the deciduous species *Q. cerrioides* showed no relation.

Plants uptake water through absorption and transport of water that driven by transpiration. The efficiency of soil water absorption depends on root system density and distribution. As a result, different plant function types and species imply different root system and water uptake efficiency. The difference in rooting system between species and ecosystems would cause the difference in soil moisture threshold values for autotrophic respiration. Grasses or other herbaceous plants are usual shallow-rooted while woody plants are more deep-rooted. Shallow soil water is relatively short-lived due to the high evaporative demand of arid ecosystem (Wythers et al., 1999), whereas deep soil water is more persistent and thus is available for uptake via root systems even during drought period (Caldwell and Richards, 1989; Williams and Albertson, 2004). For example, Padilla and Pugnaire (2007) found that the interaction between rooting depth and soil moisture determined the woody plant survival during drought. In comparison to a greater survival rate of deep-rooted species, shallow-rooted species, which in term relied on water from shallower soil layer, died as summer drought progressed. Similar evidence for this has been given by Neal (2012), he concluded that vertical soil water distribution and the timing of soil water availability at different depths is critical for ecosystem respiration in dryland.

Measured depth and timing

The distribution of soil water along a soil profile is not constant, and is determined by several factors such as the thickness of litter layer, soil texture, topography, vegetation cover, precipitation pattern, and rooting system, etc (Quesada et al., 2004; Ries et al., 2015; Wang et al., 2014). While soil water in deeper soil profile is more stable through time, shallow soil water is easily affected by precipitation or evaporation (Klein et al., 2014). As a result, the different measured depths of soil moisture between studies and the highly spatial (both vertical and lateral) heterogeneous of soil moisture simply caused the variety of soil moisture threshold values. Different timing and temporal scale of measurement also brought variability into the threshold values. For example, when applying the recursive partitioning method with Collserola data separated by year, the moisture threshold for 2011 (wet year) was 17.8% and for 2012 (dry year) was 10.1%. Besides, as the different plant function can avoid competition by exploring particularly interval of soil water availability that coincide with their phonologies (Reynolds et al., 2004), the different measured timing may detect different soil moisture thresholds of autotrophic respiration. Source of soil water for plant may differ between seasons; the main source of soil water was supply from shallow soil (0-10cm) during spring and shifted to deeper soil (20-40cm) during dry season (Klein et al., 2014). The time lag between precipitation and assimilation or respiration also has to be considered, especially for studies that are not measuring continuously. Ryan et al. (2015) showed that antecedent soil moisture and aboveground vegetation activity are critical to predicting ecosystem respiration at multiple timescales. For litter layer microbial respiration, it may be enhanced rapidly following a rain event, especially if the previous weeks were dry (Borken et al., 2003). But for root respiration, which is strongly correlated with the photosynthesis, the effect of precipitation may have a lag from hours to days (Kuzyakov and Gavrichkova, 2010; Tang et al., 2005a).

Mathematical artefact

Besides all these factors that affect the soil moisture threshold values, one other uncertainty comes from how one determines the threshold value. Among all these studies which presented soil moisture threshold, only one (Lellei-Kovács et al., 2011) used statistic method (recursive partitioning) to identify the threshold value. All other studies concluded the threshold values by data visually. In this study, if we determine the threshold values by visual data result, it actually comes out different values than using recursive partitioning. Even using recursive partitioning method itself may derive variety of results due to the different given minimum sample sizes.

Antecedent environmental condition

Antecedent environmental condition such as fire may alter the soil hydrologic condition and thus influence the water availability for microbe and plant growth (Kim et al., 2014). For example, fires may induce hydrophobic coating on the soil particles (DeBano, 1981) and form a strong hydrophobic layer that inhibits infiltration (Meeuwig, 1971; Scott and Van Wyk, 1990). Soil hydrophobicity is believed to be the primary cause of the erosion and loss of the protective litter layer (Sellström et al., 1996). Studies have shown that there are certain soil moisture threshold at which these soils cease to be hydrophobic and became easily wettable (Bodí et al., 2013; Doerr and Thomas, 2000; Huffman et al., 2001; MacDonald and Huffman, 2004; Poulenard et al., 2004; Regalado and Ritter, 2005). Generally, hydrophobic soil will recover over the next few years to pre-fire conditions (Dyrness, 1976; Reeder and Jurgensen, 1979). However, in Mediterranean soil, the recurrent fires may cause the recovery phase last a couple of decades (Malkinson and Wittenberg, 2011; Tessler et al., 2013). Other than the fire-caused change, intense or repeated drought condition has been shown to decrease soil moisture stable states in a recent experiment conducted by Robinson et al. (2016). These results, such as water repellency, hydrophobic and decrease of soil moisture stable states, are important especially for Mediterranean climate regions, as the future projections suggest a less frequent, more intense rainfall and prolonged drought period in this region (Viola et al., 2008).

One other thing has to bear in mind is that the behaviours of soil autotrophic and heterotrophic respirations are different (Shi et al., 2012; Wang et al., 2013). Heterotrophic respiration seems to have higher soil moisture threshold, in other words, it is less tolerant to drought in comparison to autotrophic respiration. As mentioned, heterotrophic respiration may easily be limited by surface soil water content as the majority of microbial activity is in the litter and very surface soil layers where are first to wet-up and dry-down with rainfall. As a result, heterotrophic respiration responds to soil water change more quickly than autotrophic respiration (Carbone et al., 2011). Besides, many studies have demonstrated that drying of soils can limit heterotrophic respiration when water potential falls below a certain threshold (Orchard & Cook, 1983; Skopp et al., 1990; Howard & Howard, 1993). But this threshold may vary from soil to soil and within the soil profile as soil organisms are differently adapted to water stress.

Table 8.1. Literature collection of soil moisture threshold information. (In order of litter layer presented and measured depth.)

Authors	Climate	Mean air temperature (ºC)	Mean annual precipitation (mm)	Q_{10} (when exceed SM threshold)	SM threshold (%)	SM measured depth (cm)	Note
Carbone et al. (2011)	Mediterranean	16.0	500	(N.A)	24	15	litter layer :3-15cm
Gaumont-Guay et al. (2006)	Boreal	0.3	456	3.8	30	15	litter layer :8-10cm
Jassal et al. (2008)	Seasonally dry temperate	9.6	1550	1.56-4.25	11	4	
Castillo-Monroy et al. (2011)	Mediterranean	13.8	388	1.51-4.11	$11^a/25^b$	5	^{a} plant and high biological soil crusts (BSC) cover. ^{b}Very low BSC
Escolar et al. (2015)	Mediterranean	15.0	349	1.5-2.2 1.6-3.3	$15^a/10^b/7^c$ $13^a/7^b/8^c$	5	^{a}Rainfall exclusion ^{b}Warming ^{c}Rainfallexgclusion+ Warming Data of low BSC
This study	Mediterranean	12.0	872	1.19-2.14	17	5	
Ruehr et al. (2010)	temperate	8.9-9.1	914-1032		15	6	
Tedeschi et al. (2006)	Mediterranean	14.0	755	2.25	20	7	Same study site with Rey et al. (2002)
Rey et al. (2002)	Mediterranean	14.0	755	2.32	20	10	
Correia et al. (2012)	Mediterranean	15.9	608	$2.01^a/1.31^b$	$10^a/15^b$	10	^{a}Forest;^{b}Grassland
Inclán et al. (2007)	Mediterranean	January:1.5-2.7; July:19.7-20.3	1400-1600	(N.A)	15	10	

Authors	Climate	Mean air temperature (ºC)	Mean annual precipitation (mm)	Q_{10} (when exceed SM threshold)	SM threshold (%)	SM measured depth (cm)	Note
Wang et al. (2013)	Arid-semiarid	8.1	292	1.50	8	10	
Suseela et al. (2012)	Temperate	10.3	1063	(N.A)	15	10	Only heterotrophic respiration
Fernandez et al. (2006)	Cold desert	Min:3.0; Max:20.0	207	(N.A)	9.5	10	
Lellei-Kovács et al (2011)	Atlantic temperate	16.4	505	(N.A)	7-9	11	
Curiel Yuste et al. (2007)	Mediterranean	Winter:0-9; Summer:14-27	1290	$1.77^a/2.11^b$	Around $25^a/20^b$	15	^{a}Heterotrophicrespiration;^{b}total soil respiration
Almagro et al. (2009)	Mediterranean	15.5	370	1.86-2.20	10	15	
Herbst et al. (2009)	(N.A)	(N.A)	(N.A)	(N.A)	16.5	15	Bare soil
This study	Mediterranean	12.0	600	3.00	9	20	
Curiel Yuste et al. (2003)	Temperate maritime	9.8	750	1.93-2.90	15	25-30	
Palmroth et al. (2005)	(N.A)	15.5	1140	2.77-3.35	20	30	
Xu & Qi (2001)	Mediterranean	January:0.6; July:28.3	1660	1.88	14	30	
Grünzweig et al. (2009)	Subhumid - Mediterranean	January:8.0-11.0; July:21.0-28.0	280	2.45	20	40	

Root respiration, on the other hand, is less affected due to their ability of uptaking water from deeper soil depths. Carbone et al. (2011) found that autotrophic and heterotrophic respirations have different temporal pattern: microbial respiration peaks first with surface soil moisture, whereas root respiration increases later through the growing season as temperatures warm and surface soil moisture steadily declines. To find out how biophysical factors control soil respiration, Vargas et al. (2010) analyzed the lags between soil CO_2 flux, temperature, soil moisture and GPP using regression tree analysis, which is also known as binary recursive partitioning. Their results showed that for deciduous and mixed forests, the seasonal pattern of soil CO_2 flux is first driven by a substantial increase in autotrophic respiration and then followed by an increase in heterotrophic respiration. Meanwhile, for evergreen coniferous forests, the seasonal soil CO_2 flux showed a contrast pattern, which first is driven by an increase in heterotrophic respiration followed by an increase in autotrophic respiration. The synthetic results from the previous section showed that heterotrophic respiration is closely correlated with soil moisture when soil moisture is lower than the threshold. Besides, in the Collserola site, data that lower than soil moisture threshold are from all seasons and showed similar trend against soil moisture. In comparison, data from Font del Regàs site are all from year 2012 (dry year) and can be divided into two parts, the higher correlated linear data are from spring while the lower ones are from summer. This different seasonal behaviour may due to the influence of soil water content deeper than 5 cm, as the 30 cm integral soil moisture in Font del Regàs showed a significant decrease from spring to summer (see Chapter 6). Similarly, total soil respiration under soil moisture threshold also showed a clear correlation, though more dispersed than heterotrophic respiration, with soil moisture except the observed data from spring 2011 at Collserola site (Figure 8.4). Since the total soil respiration is associated with root and microbial respiration, it is predictable that using 5 cm soil moisture is not enough to explain the variation. The spring campaign of soil respiration measurement started on the day 166 of 2011, and there were three rain events happened on day 158 (31.1mm), 159 (32.5mm) and 161 (21.2 mm). According to the 30 cm integral soil moisture record near the experiment plot, the effect of precipitation on soil moisture lasted until day 173 of 2011. As a result, the observed inconsistent behaviour from the data of spring 2011 should be the result of these rain events antecedent to the measurement as the effect of rainfall is longer on autotrophic respiration than heterotrophic respiration when precipitation exceeds a certain amount (Carbone et al. 2011). Although we identified soil moisture threshold for data from the Castelltallat, we found no clear relation between soil moisture and soil respiration under this threshold. We conjured that the largely wildfire occurred six years before the measurement may be the main cause of this decoupled interactions between soil respiration and soil moisture. Disturbances such as wildfire have been shown to change the soil structure, soil nutrient cycle and also plant phenology (Paritsis et al., 2006; Shakesby and Doerr, 2006). Results from Keesstra et al. (2016) showed that in post-fire Mediterranean forest, soil water repellence occurred when soil moisture is lower than 10%, and below the threshold, any change in soil moisture will not necessarily alter the strength of soil hydrophobicity (Doerr and Thomas, 2000). In addition, as the main source of soil water for plant may shift to deeper soil during dry season (Baldocchi and Xu, 2007; Klein et al., 2014), the 20 cm soil moisture data in our study are not able to represent the relationship between soil respiration and deeper soil water.

Tug of war between forest management and drought stress

Drought affects ecosystem carbon cycle from several aspect and temporal scale (Figure 8.9). First, the low water content of the soil created an environment that slowed the diffusion of solutes and, thus, suppressed microbial respiration by limiting the supply of substrate (Skopp et al., 1990). Additionally, microbes and plant roots have to invest more energy to produce protective molecules and this reduces their growth and respiration (Schimel et al., 2007). Under low soil water content, plants close their stomata to prevent water loss, but at the same time, the assimilation process stop (Gallé and Feller, 2007; Oren et al., 1999). From hourly to daily scales, drought has been shown to decrease the recently assimilated C allocation to roots ca. 33 – 50% (Hasibeder et al., 2014; Ruehr et al., 2009). The decrease in plant substrate and photosynthetic activity caused by drought would then reduce stem and soil respiration (Barthel et al., 2011; Burton et al., 1998; Yan et al., 2011). With the prolongation of reduced rainfall over time, tree may start to reduce their leaf area in order to maintain the transpiration rate (Mencuccini, 2003). Under severe drought, fine-root mortality also increased (Janssens et al., 2002; Meier and Leuschner, 2008). Consequently, followed by the decrease of leaf area and photosynthesis, forest productivity and growth depressed, and then reduced the stem and soil respiration. For example, Brando et al. (2008) found a decline in net primary productivity of 13% in the first year and up to 62% in the following 4 years in a throughfall reduction experiment. Although drought may induce root and plant mortality, studies have also shown that moderate drought can promote fine root production such as increase root surface or exploiter deeper soil profile in order to uptake soil water (Gaul et al., 2008; Zang et al., 2013).

In general, thinning management increases water and nutrient availability and, therefore, enhances tree vitality and growth through increased photosynthesis rate and root respiration (Högberg et al., 2001; Janssens et al., 2001; Kuzyakov and Cheng, 2001). In the meantime, the woody debris and dead roots produced during thinning stimulated heterotrophic respiration (Rustad et al., 2000; Tian et al., 2009). In our study site, Cotillas et al. (2009) observed a remarkable improvement in residual stem growth (ca. 50%) and a reduction in stem mortality after selective thinning while Pérez (2010) showed a higher soil organic matter and soil phosphorous after selective thinning. However, they also found that the positive effects of thinning declined rapidly during the 3-year experiment. López et al. (2003) found an increase of more than 100% in root biomass and 76% in root production in a *Q. ilex* forest after thinning, especially during winter and autumn. Additionally, Sohlenius (1982) found that slash produced by logging promoted productivity of soil microflora due to the increase in moisture and microbial biomass, which increased total soil respiration. However, contradictory results of how thinning affects soil respiration are also shown in many studies (Dai et al., 2014; Jonsson and Sigurdsson, 2010; Londo et al., 1999; Ma et al., 2004; Masyagina et al., 2010; Olajuyigbe et al., 2012; Pang et al., 2013; Tang et al., 2005b). The different responses likely are due to thinning intensity, timing, and duration of the measurement campaigns after thinning. In our study, we observed an increase in soil respiration in the selective thinning plot during the first two years after selective thinning. We also found a significant reduction in soil respiration during daytime in the first summer campaign. We conjured this is due to that, despite the enhancement of water availability, selective thinning may somehow decrease soil water availability in the shallow soil profile due to the more solar radiation and higher transpiration in the initial phase after selective thinning. Does thinning mitigate drought stress? From our study and previous researches, yes, thinning does mitigate drought stress under some circumstances - crucial is not only the tug of war between thinning and drought intensity, also the timing, species or even forest structure and individual size (Guillemot et al., 2014; Keenan, 2012; Kohler et al., 2010; Laurent et al., 2003; Magruder et al., 2013; Mérian and Lebourgeois, 2011; Pussinen et al., 2009; Rodríguez-Calcerrada et al., 2011; Sohn et al., 2012, 2013; Vayreda et al., 2012).

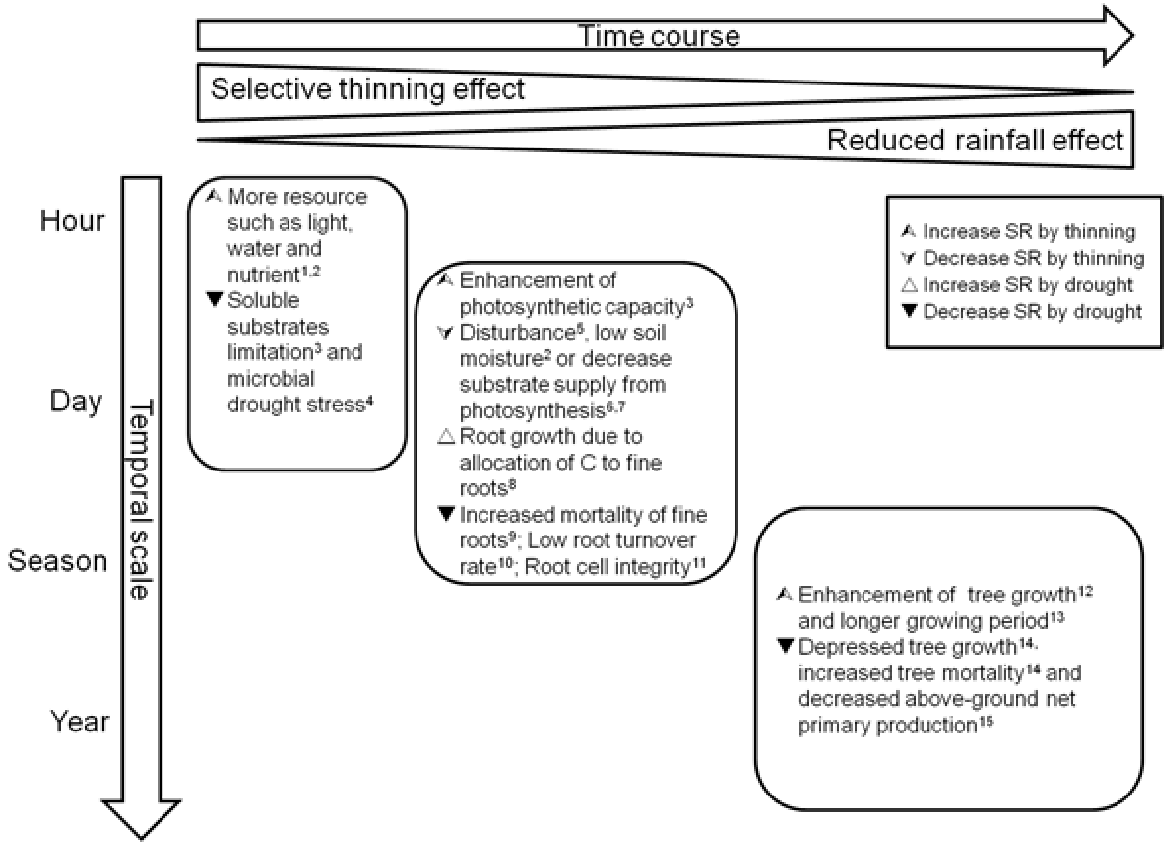
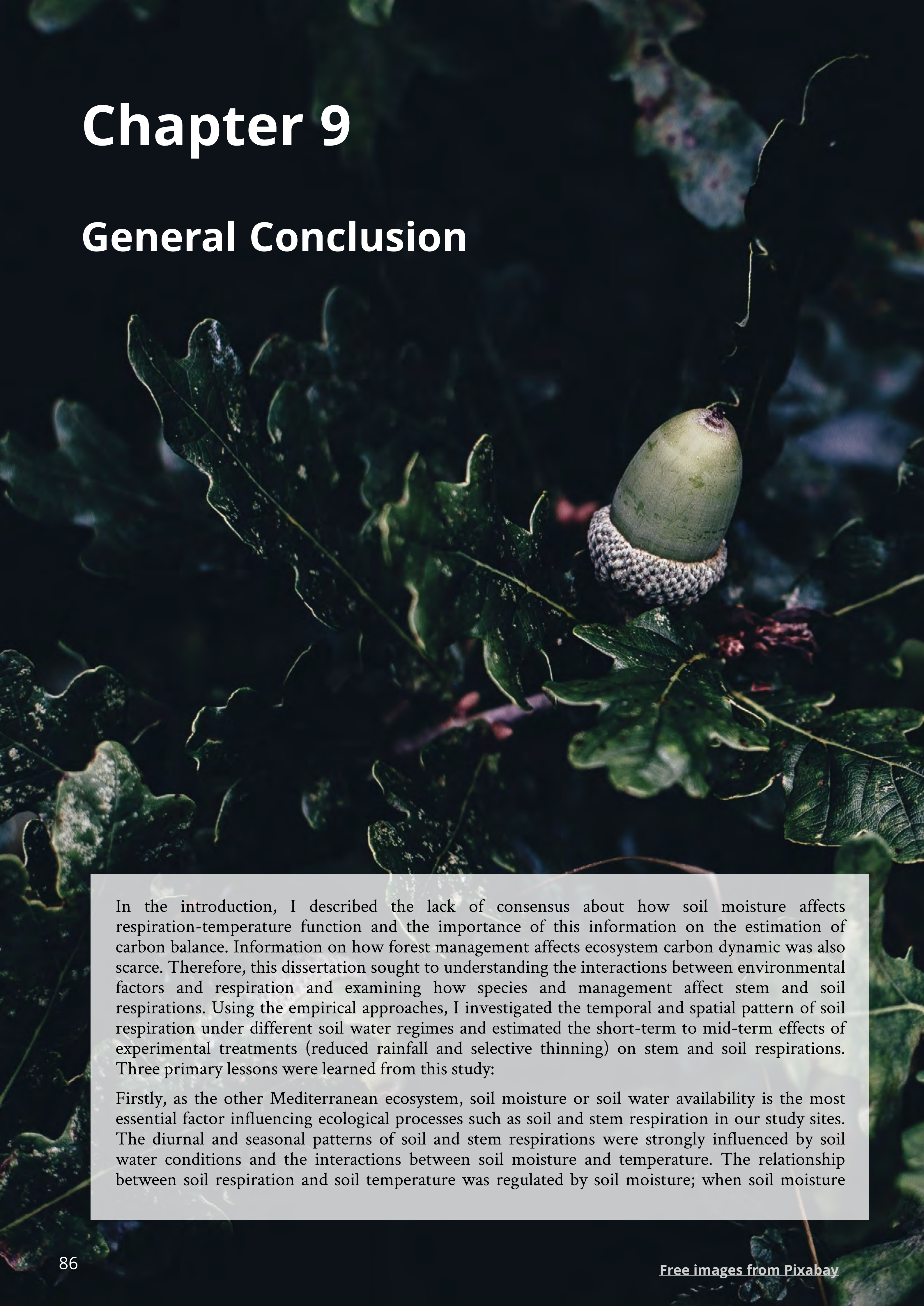


Figure 8.9. Schematic representation of selected temporal effects on SR over time. The left arrow indicates the dominant temporal scales of effects and processes influencing soil respiration. The arrow at the top of the figure indicates the time that each effect occurred and the magnitude of the drought and thinning effects. 1 McDowell et al., 2003; 2 Breda et al., 1995; 3 Medhurst and Beadle, 2005; 4 Manzoni et al., 2014; 5 Concilio et al. 2006; 6 Hogberg et al. 2001; 7 Atkin and Macherel, 2009; 8Asensio et al., 2007; 9 Gaul et al., 2008; 10 Hasibeder et al., 2014; 11 Huang et al., 2005; 12Sohn et al., 2012; 13 Eamus et al. 1999; 14 Barbeta et al., 2013; 15 Cotrufo et al., 2011

Chapter 9

General Conclusion



In the introduction, I described the lack of consensus about how soil moisture affects respiration-temperature function and the importance of this information on the estimation of carbon balance. Information on how forest management affects ecosystem carbon dynamic was also scarce. Therefore, this dissertation sought to understanding the interactions between environmental factors and respiration and examining how species and management affect stem and soil respirations. Using the empirical approaches, I investigated the temporal and spatial pattern of soil respiration under different soil water regimes and estimated the short-term to mid-term effects of experimental treatments (reduced rainfall and selective thinning) on stem and soil respirations. Three primary lessons were learned from this study:

Firstly, as the other Mediterranean ecosystem, soil moisture or soil water availability is the most essential factor influencing ecological processes such as soil and stem respiration in our study sites. The diurnal and seasonal patterns of soil and stem respirations were strongly influenced by soil water conditions and the interactions between soil moisture and temperature. The relationship between soil respiration and soil temperature was regulated by soil moisture; when soil moisture

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was higher than certain threshold value, the relationship between soil respiration and soil temperature was positive, and when soil moisture was lower than the threshold value, the controlling factor of soil respiration switched from temperature to moisture. Even in the riparian environment, a none water stress condition, this threshold-like phenology still can be observed. Thus, we concluded that soil moisture played a central role in determining the carbon dynamic in Mediterranean forests.

Secondly, in Castelltallat site, seasonal changes in soil respiration are driven more by changes in autotrophic than heterotrophic respiration. In the other two study site, Soil heterotrophic respiration was the main contributor of total soil respiration, but was easily affected by surface soil moisture. For our study sites, surface soil moisture (5cm) and temperature is a good indicator of soil respiration, explaining 82-94% variation of soil respiration.

Lastly, selective thinning affected soil and stem respiration from different aspects, but the effect and amplitude of selective thinning diminish with time. Selective thinning significantly increased soil respiration rates, especially during growing seasons. Meanwhile, selective thinning improved stem respiration rate only during summer, but it also prolonged the growing season. It is to say, using selective thinning as a drought mitigation practice does alleviate the drought impact on Mediterranean forests, but this practice effect is limited.

Overall, the results of this study provide valuable and fundamental soil and stem respirations information for assessing the effects of drought and selective thinning on ecosystem functions. This study also enhances our ability to model ecological processes, such as soil respiration, using basic environmental data and our understanding of the interaction between soil water availability, soil temperature and soil respiration in the Mediterranean region.

Future research opportunities

Our results highlight the importance of soil moisture/soil water availability when modelling ecosystem carbon dynamic in Mediterranean region. Without considering the threshold effect of soil moisture on soil respiration, it can lead to an overestimation of CO_2 efflux in the future climate change. A lot of questions came into focus over the course of this study and some ideas that could extend the frontier across spatial and temporal scales are proposed hereafter.

Our result indicated the different drought sensitivity of autotrophic and heterotrophic respiration owing to their different capacity for water resource. In chapter 4 it demonstrated that using surface soil moisture (5cm) and temperature are good predictors for soil respiration, explaining 82-94% variation of soil respiration in our study sites. However, in chapter 8 I also revealed that the correlation between surface soil moisture and autotrophic respiration is more dispersal, showing that deeper soil water measurement may be necessary to capturing better picture on autotrophic respiration during the critical growing season. But, to which soil depth should one measure and apply to model? Neal (2012) presented using shallow and deep soil profile to predict autotrophic and heterotrophic respiration, yet this idea hasn't yet well developed into model. As the present remote sensing technique can detect different soil properties and soil moisture up to top 1 m (Mohanty et al. 2017), it is possible now to integrate soil taxonomy map, soil moisture and temperature together to better predict soil respiration from global scale and also develop model with estimations of forest management effects on ecosystem functions.

Moreover, the results obtained from our experiments indicate one important fact - although temperature and water availability can be used to predict the respiration and carbon flux, it is still insufficient to project the whole carbon flux due to the lack of consideration of short-term adaptation and long-term acclimation of plant to drought, as both rely on the adjustment of physiological processes and morphological traits at the whole-tree level. To this reason, a mechanistic understanding of aboveground physiology, below-ground phenology, and allocation studies from whole tree level and even ecosystem aspect is needed in order to better quantify climate change controls on ecosystem carbon flux and sources.

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Does soil moisture overrule temperature dependence of soil respiration in Mediterranean riparian forests?

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Abstract. Soil respiration (SR) is a major component of ecosystems' carbon cycles and represents the second largest CO_2 flux in the terrestrial biosphere. Soil temperature is considered to be the primary abiotic control on SR, whereas soil moisture is the secondary control factor. However, soil moisture can become the dominant control on SR in very wet or dry conditions. Determining the trigger that makes soil moisture as the primary control factor of SR will provide a deeper understanding on how SR changes under the projected future increase in droughts. Specific objectives of this study were (1) to investigate the seasonal variations and the relationship between SR and both soil temperature and moisture in a Mediterranean riparian forest along a groundwater level gradient; (2) to determine soil moisture thresholds at which SR is controlled by soil moisture rather than by temperature; (3) to compare SR responses under different tree species present in a Mediterranean riparian forest (*Alnus glutinosa*, *Populus nigra* and *Fraxinus excelsior*). Results showed that the heterotrophic soil respiration rate, groundwater level and 30 cm integral soil moisture (SM_{30}) decreased significantly from the riverside moving uphill and showed a pronounced seasonality. SR rates showed significant differences between tree species, with higher SR for *P. nigra* and lower SR for *A. glutinosa*. The lower threshold of soil moisture was 20 and 17 % for heterotrophic and total SR, respectively. Daily mean SR rate was positively correlated with soil temperature when soil moisture exceeded the threshold, with Q_{10} values ranging from 1.19 to 2.14; nevertheless, SR became decoupled from soil temperature when soil moisture dropped below these thresholds.

1 Introduction

Soil is the largest pool of terrestrial organic carbon in the biosphere, storing around 2344 Pg C in the top 3 m (Jobbágy and Jackson, 2000). Soil respiration (SR) is the main source of carbon efflux from ecosystems to the atmosphere, accounting for 60–90 % of the total ecosystem respiration (Schimel et al., 2001; Raich et al., 2002). Thus, SR plays an important role in the global carbon balance (Schimel et al., 2001; Raich et al., 2002), and even small changes of SR may induce positive feedbacks to climate change (Schlesinger and Andrews, 2000). Therefore, information of how SR interacts with environmental conditions, such as the response of specific components of soil respiration to temperature and moisture changes, will be a key part of the improvement of process-based models.

On large scales, such as in ecosystems and biomes, net primary production (NPP) may be the most important factor controlling SR (Wardle, 2002). NPP provides the inputs to the soil from aboveground litter and also belowground organic detritus (Raich and Potter, 1995). Moreover, root respiration is strongly dependent on the translocation of photosynthates from the aboveground part of the plant (Curiel-Yuste et al., 2004). At the smaller scale, SR has been found to be very sensitive to soil temperature and soil moisture (Fang and Moncrieff, 2001). Soil temperature has been 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). In general, SR increases exponentially with increases of soil temperature (Epron et al., 1999; Lloyd and Taylor, 1994; Mielnick and Dugas, 2000). In contrast to the positive relationship

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between SR and soil temperature, both very high and very low soil moisture have been shown to diminish the temperature response of SR (Londo et al., 1999; Welsch and Hornberger, 2004) due to the potential oxygen limitations under high soil moisture (Skopp et al., 1990) and due to metabolic drought stress under very low soil moisture (Orchard and Cook, 1983). Soil moisture also affects plant composition and productivity (Häring et al., 2013) and thus controls the quantity and quality of both soil organic matter (SOM) and root exudate supply (Rustad et al., 2000).

Numerous studies have reported the effects of temperature and moisture on SR. However, studies about the combined effects of both factors are relatively few, and the information of how soil moisture affects the relationship between soil temperature and SR is scarce (Bowden et al., 1998; Davidson et al., 2006; Curiel-Yuste et al., 2007). In Mediterranean and semiarid ecosystems, SR is highly sensitive to soil moisture, and the temperature-driven increases in SR are likely dampened by low soil moisture (Conant et al., 2004; Raich and Potter, 1995; Rey et al., 2002). It is still unclear under which circumstances or environmental conditions would the primary control factor of SR switch from temperature to soil moisture.

SR can be divided into autotrophic and heterotrophic respiration by different biological sources (Hanson et al., 2000). Autotrophic respiration, also known as root respiration, is mainly dependent on NPP and tree physiology such as photosynthesis substrate supply (Heinemeyer et al., 2007; Hogberg et al., 2001). Heterotrophic respiration is the sum of microbial decomposition of SOM (Fang et al., 2005; Knorr et al., 2005). In theory, due to the different origins of autotrophic and heterotrophic respiration, they may have different sensitivities toward environmental factors and respond differently to seasonality (Epron et al., 2001; Kuzyakov and Larionova, 2006; Yan et al., 2010).

Riparian areas are characterized with high soil moisture and sustained water table. (McGlynn and Seibert, 2003). In these ecosystems, tree species composition and tree growth are strongly influenced by the topographic position concomitant with the changes in the soil water content. Thus, this may indirectly affect SR through litter input and nutrient availability. Because of the retardation of microbial decomposition with the frequent saturation of soil water, riparian areas tend to accumulate more SOM than hillslope areas do (Sjögersten et al., 2006).

The main objectives of this study were (1) to investigate the seasonal variations and relationships between SR and both soil temperature and moisture in a Mediterranean riparian forest along a groundwater level gradient; (2) to determine soil moisture thresholds at which SR is controlled by soil moisture rather than by temperature, even in such non-water-stressed environments; (3) to compare SR responses under different tree species present in a Mediterranean riparian forest (*Alnus glutinosa, Populus nigra* and *Fraxinus excelsior*). With these aims, we carried out measurements of SR under different tree species along a groundwater level gradient in a riparian forest in NE Spain. The results of our study may help to better the understanding of the interactions between different components of SR with soil temperature and moisture as well as the role of different tree species. It also provides relevant information for SR model parameterization.

2 Material and methods

2.1 Site description

The experiment was conducted in a riparian forest growing along the Font de Regàs stream, a headwater tributary of the Tordera River, in Montseny Natural Park (north of Barcelona; 41°50′ N, 2°30′ E, altitudinal range 300–1200 m a.s.l.). The forest community of our study site consists of black alder (*Alnus glutinosa* L.), black locust (*Robinia pseudoacacia* L.), common ash (*Fraxinus excelsior* L.) and black poplar (*Populus nigra* L.). As result of water and nutrient availability, *A. glutinosa* and *P. nigra* trees are mostly distributed near the river, whereas *F. excelsior* trees are located further away on the upper site, near the hill. *R. pseudoacacia* trees are scattered over the study area and were not monitored. Mean annual temperature is 12 °C with maximum and minimum average temperatures of 14 and 10 °C, respectively. The mean annual precipitation is 872 mm (1951–2010). The riparian soil is sandy loam with low rock content ($< 13\,\%$), weakly acidic (pH of 6.7) and has an average bulk density of $1.09\,\mathrm{g\,cm^{-3}}$.

2.2 Experimental design

We divided the groundwater gradient (riparian–hillslope transect) into four levels according to the distance from the riverside and by tree species composition (Fig. 1). The distances of level 1 to level 4 (L1 to L4) from the river centre were 2.7, 4.4, 6.8 and 11.8 m, respectively. The three target tree species, *A. glutinosa, P. nigra* and *F. excelsior* were located at levels L1, L2 and L3, respectively. To examine the interaction effects on SR of tree species, soil moisture and temperature, we set three riparian–hillslope transects to measure the variation of total SR (sum of soil autotrophic and heterotrophic respiration, hereafter referred to collectively as total SR, $\mathrm{SR_{tot}}$) from different tree species. Soil chambers were placed 1.5 m from the stem of the target tree species. Moreover, we also set two transects to measure the topographic effects on soil heterotrophic respiration ($\mathrm{SR_H}$). Due to the difficulty of trenching next to the riverbank, chambers for $\mathrm{SR_H}$ were set only at levels L2, L3 and L4. To separate root respiration from $\mathrm{SR_H}$, we inserted a PVC tube (diameter: 65 cm; height: 40 cm) into the soil 5 months before starting the measurements. To avoid constraints on groundwater table fluctuations by the PVC tube, we cut two opposite windows

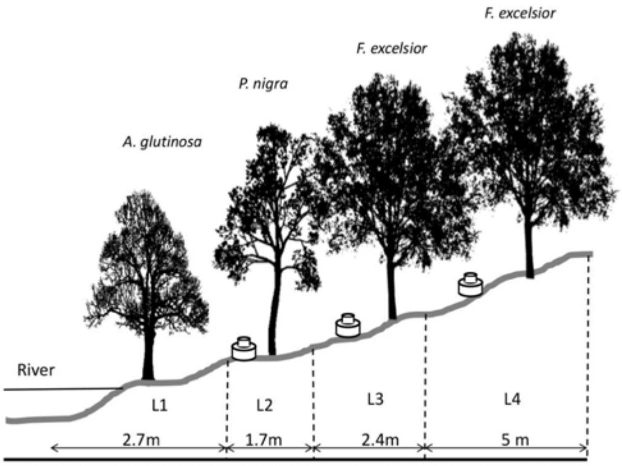

Figure 1. Sketch of levels along a gradient of soil water availability with tree species distribution and SR_H chamber positions.

into the PVC tube and covered by 65 µm mesh to prevent root growth through the windows.

Stainless steel rings were inserted permanently into the soil, down to 3 cm depth as the base of the soil chambers, and kept free from seedlings throughout the experiment duration. The distances of each soil chamber from the riverside varied slightly due to the tree distribution.

2.3 Field measurement

SR and soil temperatures were measured seasonally from summer 2011 to autumn 2012. These measurements were conducted continuously for 1 week within each season. A heavy rainfall event took place in winter 2012, resulting in elevated water levels of the river that washed away most of the litter layer within 3 m from the river bank.

CO_2 concentration was measured in situ with an automatic changeover open system. The system consists of an infrared gas analyser (IRGA, LiCor 6262, LiCor, Inc., Lincoln, NE, USA), a data logger (CR10, Campbell Scientific Inc., UT, USA), 12 pairs of channels, 12 soil chambers, 12 pairs of rotameters, 6 pumps and 2 flowmeters. Each pair of channels consists of two tubes connected to a soil chamber, one attached on the top of chamber (reference CO_2 concentration) and another attached at the base for calculating the increment of CO_2 concentration provided by SR. Soil chambers were placed at the beginning of each field campaign, and CO_2 concentrations were analysed and recorded sequentially over 1 min intervals at each chamber. Air was continuously forced through all chambers by pumps. Only one chamber was connected at a time to the IRGA to analyse the CO_2 concentration of the respective chamber, while air from the others was exhausted to the atmosphere until their own turn. The sequence was programmed every 4 cycles of differential IRGA measurements from 12 chambers, and an additional cycle of absolute IRGA measurement, which was then used to calculate the actual absolute ambient air concentration of CO_2 in ppm. The CO_2 concentration of the ambient air was determined as the difference between the scrubbed sample, which flows through soda lime and $Mg(ClO_4)_2$, and the ambient air sample.

Soil chambers were protected by placing a 50 cm × 50 cm green fine mesh on top to avoid possible heating by direct sunlight during the measurements. Soil temperature of 5 cm depth was continuously measured with Pt100 temperature sensors and recorded in parallel with the CO_2 concentration analysis. Thirty centimetre integral soil moisture ($cm^3\,cm^{-3}$, SM_{30}) in each level were determined and recorded half-hourly with a moisture reflectometer (CS616, Campbell Scientific). Additionally, we also measured 5 cm integral soil moisture (SM_5) next to each soil chamber once per day during each measuring field campaign with impedance probes (ThetaProbe soil moisture sensor, MI2x, Delta-T Devices, Cambridge, UK). A grid of 28 wells (PVC tubes of 35 mm in diameter) was installed to monitor groundwater table oscillation. Wells were distributed along the study site and at different distances from the stream: 2.7, 4.4, 6.8, 11.8 m ($n = 7$). Groundwater levels were monitored manually every 2 weeks using a sounding device with acoustic and light signal (Eijkelkamp Agrisearch Equipment). In autumn of 2012, after concluding the measurements, litter layer and soil samples (15 cm depth) inside each chamber were collected. Litter layer samples were weighted after oven drying at 65–70 °C for 24 h. Soil samples were first oven dried at 105 °C and then analysed to determine their organic carbon and nitrogen content by using the Walkley–Black and Kjeldahl methods, respectively.

2.4 Statistical analysis

Statistical analyses were performed with PASW statistics 18 (SPSS Inc., 2009, Chicago, IL, USA). The missing data of soil temperatures were estimated from air temperature values based on a regression analyses between air and soil temperatures. SR, soil temperature and soil moisture data were analysed using ANOVA to examine whether seasonal SR rates were different between levels and tree species. Data used to test the significance in ANOVA were based on daily means. Least significant difference (LSD) was used to detect differences between levels and tree species for each season. We used regression analysis to examine the relationship between SR and soil temperature. An univariate exponential equation was fitted (van 't Hoff, 1898):

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

where SR is soil respiration rate ($\mu mol\,C\,m^{-2}\,s^{-1}$), T is soil temperature (°C), a and b are fitted parameters.

The apparent Q_{10} was calculated as

$$Q_{10} = e^{10b} \tag{2}$$

Table 1. Soil carbon and nitrogen content and dry weight of litter L and F organic horizons from soil respiration chambers.

Groundwater level	C / N	SOC %	Nitrogen%	Litter Layer ($\mathrm{kg\,m^{-2}}$)
L2 – Near river	10.40	2.73	0.16	0.97
L3 – Intermediate	10.00	4.38	0.26	1.20
L4 – Uphill	9.15	3.36	0.23	1.67
L1 – *A. glutinosa*	12.13	2.29	0.11	0.69
L2 – *P. nigra*	10.27	3.52	0.20	1.18
L3 – *F. excelsior*	9.67	4.85	0.30	2.21

A Q_{10} value for the whole measurement period was computed for each topographic position and tree species on the basis of daily average SR rate and soil temperature. In addition, we estimated specific Q_{10} values for summer of 2011 and 2012. Data collected were fitted to the exponential equation. In order to understand the interaction between soil temperature and soil moisture and the effect of soil moisture on regulating SR, we applied recursive partitioning analysis to search for the threshold of soil moisture. As models based on partitioning can only handle linear models, the Eq (1) was transformed by linearizing with logarithms:

$$\ln \mathrm{SR} = \ln a + bT \tag{3}$$

Logarithmic transformed SR values were used as the dependent variable. Once the soil moisture thresholds were obtained, linear and nonlinear regression analyses were used to determine the relationship between SR, soil temperature and soil moisture at each soil moisture interval. The recursive partitioning analysis was conducted in the *R* statistical environmental using the *party* package (Zeileis et al., 2008).

3 Results

3.1 Seasonal variation of groundwater level, soil moisture, soil nitrogen and carbon content

Seasonal variation of air temperature and precipitation was remarkable. The precipitation in 2011 was significantly higher than in 2012, especially in summer. Summer precipitation in 2011 was 4 times higher (183 mm) than in 2012 (39 mm). SM_{30} was significantly higher at L1 (Fig. 2). In summer 2012, due to a remarkable drought, SM_{30} at L1 only showed a small decrease with respect to summer 2011; while at the other levels (L2, L3 and L4) SM_{30} was markedly decreased. Groundwater levels showed no seasonal variation but were significantly different between them.

Soil near the river contained less organic carbon and nitrogen, but a higher C : N ratio, with a C : N ratio of 12.13 (Table 1). Soil C : N ratio decreased from the riverside going uphill, whereas the dry weight of litter layer increased from the riverside going uphill. The largest amount of dry weight of litter layer was found under *F. excelsior*, and coincided with the highest soil organic carbon (SOC) and soil nitrogen concentrations between all levels.

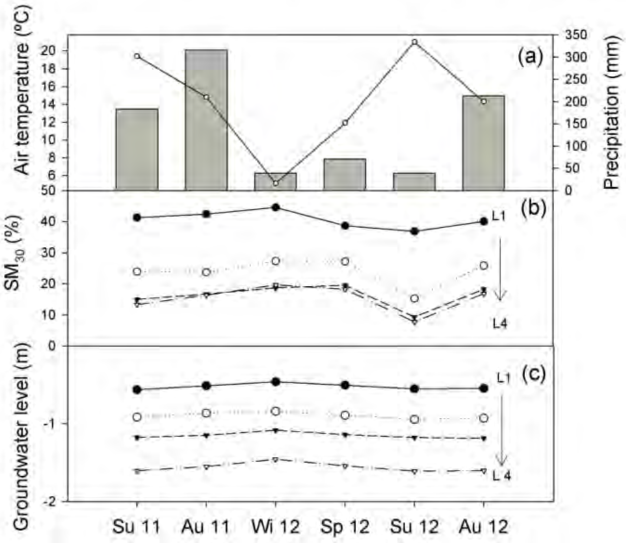

Figure 2. Seasonal changes of summer 2011 (Su 11), autumn 2011 (Au 11), winter 2012 (Wi 12), spring 2012 (Sp 12) summer 2012 (Su 12) and autumn 2012 (Au12) in **(a)** mean seasonal air temperature and precipitation; **(b)** 30 cm integral soil moisture (SM_{30}); **(c)** groundwater level, value represents the depth of groundwater level from soil surface (L1, L2, L3 and L4).

3.2 Seasonal variation of $\mathrm{SR_H}$ along hillslope transect

$\mathrm{SR_H}$ rates ranged from 0.17 $\mathrm{\mu mol\,C\,m^{-2}\,s^{-1}}$ (in winter, L4) to 1.69 $\mathrm{\mu mol\,C\,m^{-2}\,s^{-1}}$ (in summer, L2, Fig. 3a–d). $\mathrm{SR_H}$ decreased significantly from riparian zone (L2) to hill zone (L4), especially in summer. $\mathrm{SR_H}$ measured from different levels were significantly different in all seasons ($P < 0.05$). $\mathrm{SR_H}$ at L2 had a higher variability during the whole experiment. Minimum soil temperature coincided with maximum SM_5 in winter while maximum soil temperature was recorded in summer when SM_5 was lowest. $\mathrm{SR_H}$ varied markedly during the year following the change of soil temperature from summer 2011 to spring 2012, and the changes of SM_5 for summer and autumn 2012. As expected, $\mathrm{SR_H}$ was lower during winter when soil temperatures were the lowest of the year, and $\mathrm{SR_H}$ was higher during the growing season.

3.3 Tree species and topographic effects on $\mathrm{SR_{tot}}$ and SM_{30}

The observed variation of $\mathrm{SR_{tot}}$ for the three tree species followed the change of soil temperature over the year (Fig. 3e–h). $\mathrm{SR_{tot}}$ of *P. nigra* was the highest one, especially during summer, and $\mathrm{SR_{tot}}$ of *A. glutinosa* was the lowest one throughout the year. There were no significant differences of soil temperatures between tree species locations. SM_5 did not differ between tree species locations but there was a tendency

Table 2. Comparison of soil respiration rates (SR), soil moisture (SM) and Q_{10} values in 2011 and 2012 summer campaigns. Heterotrophic SR (SR_H). Total SR (SR_{tot}). Five centimetre integral soil moisture (SM_5). Thirty centimetre integral soil moisture (SM_{30}).

		SR (μmol C m^{-2} s^{-1})			SM_5 (%)			SM_{30} (%)			Q_{10}	
	Chamber	2011	2012	Reduction	2011	2012	Reduction	2011	2012	Reduction	2011	2012
SR_H	L2 – Near river	1.65	0.84	49 %	27.10	14.94	45 %	22.22	14.51	35 %	1.09	0.76
	L3 – Intermediate	0.98	0.70	28 %	31.68	14.91	53 %	12.60	9.22	27 %	1.04	0.88
	L4 – Uphill	0.74	0.50	32 %	38.02	14.19	63 %	10.87	8.13	25 %	0.97	0.84
SR_{tot}	L1 – *A. glutinosa*	1.24	0.78	37 %	27.24	13.04	52 %	42.49	36.58	14 %	1.31	0.80
	L2 – *P. nigra*	1.42	1.13	21 %	26.22	12.93	51 %	22.22	14.51	35 %	1.17	0.63
	L3 – *F. excelsior*	1.26	0.76	40 %	26.45	12.87	51 %	12.60	9.22	27 %	1.40	1.14

All data of SR, SM_5 and SM_{30} were significantly different between 2011 and 2012. All P values < 0.001.

Table 3. Comparison of soil respiration rates (SR) and soil moisture (SM) after a rainfall event of 13.5 mm in summer 2012. Heterotrophic SR (SR_H). Total SR (SR_{tot}). Five centimetre integral soil moisture (SM_5). Thirty centimetre integral soil moisture (SM_{30}). Data were averaged for the 2 days before and 2 days after the rainfall event.

		SR (μmol C m^{-2} s^{-1})			SM_5 (%)			SM_{30} (%)		
	Chamber	before	after	increase	before	after	increase	before	after	increase
SR_H	L2 – Near river	0.66	1.00	52 %	14.09	18.84	34 %	14.45	14.50	0 %
	L3 – Intermediate	0.59	0.80	34 %	15.19	18.37	21 %	8.46	10.15	20 %
	L4 – Uphill	0.41	0.59	45 %	12.06	17.51	45 %	6.97	9.64	38 %
SR_{tot}	L1 – *A. glutinosa*	0.67	1.04	54 %	11.27	16.91	50 %	36.13	37.48	4 %
	L2 – *P. nigra*	0.99	1.66	68 %	10.86	18.86	74 %	14.45	14.50	0 %
	L3 – *F. excelsior*	0.68	0.98	44 %	11.10	17.20	55 %	8.46	10.15	20 %

towards a higher SM_5 under *F. excelsior*. SM_{30} was significantly different between levels for all seasons. The variation of SM_{30} at L1 was lower and showed less seasonal variability, maintaining most of the SM_{30} values around 40 %. During both summers 2011 and 2012, SM_{30} at L3 dropped to around 10 %, which is even lower than the SM_5 at L4 where *F. excelsior* is found.

3.4 Drought and rain pulse effects on SR

The low precipitation of summer 2012 caused a significant reduction of around 50 % of SM5, 14–35 % of SM30 and at the same time a reduction of SR between 21 and 49 %. The Q_{10} values ranged from 0.97–1.40 in summer 2011 and 0.63–1.14 in summer 2012 (Table 2).

A rainfall event (13.5 mm) during the measurement period of summer 2012 caused a significant increase of soil moisture and SR rates at all levels (L1 to L4). The SM_5 increased around 21–74 % after the rainfall event even though it only caused a 0–38 % increase of the SM_{30} (Table 3). This rainfall event caused a sharp increase of SR from 0.41–0.99 μmol C m^{-2} s^{-1} to 0.59–1.66 μmol C m^{-2} s^{-1}, which corresponds to an increase of SR around 34 to 68 %.

3.5 The switch of primary control factor of SR

We identified three SM_5 intervals for each SR_H and SR_{tot} (Table 4), which suggests the existence of thresholds in soil moisture effects. SR was positively related ($P < 0.001$) to soil temperature when SM_5 was higher than 23 % for SR_H or higher than 27 % for SR_{tot}. The lower thresholds for SR_H and SR_{tot} were 20 and 17 % of SM_5 respectively. Under the lower bound value, SR_H showed a significantly positive relationship with SM_5 (Fig. 4, linear regression with r^2 of 0.89, 0.92 and 0.91 for L2, L3 and L4) while SR_{tot} showed a weak positive relationship with SM_5 (Fig. 5, linear regression with r^2 of 0.56, 0.11 and 0.10 for L1, L2 and L3). The exponential model based on soil temperature accounts for 68 to 84 % of the variation in both SR_H and SR_{tot} rates at the higher SM_5 interval values. The fitted Q_{10} values in high SM_5 intervals ranged from 1.49 to 2.14. Generally the Q_{10} values of SR_H were lower than the Q_{10} of SR_{tot}.

Table 4. Exponential relationships between soil respiration (SR) and soil temperature (T), and Q_{10} for different SM_5 intervals. Heterotrophic SR (SR_H). Total SR (SR_{tot}). (SM_5) is 5 cm integral soil moisture.

		$SM_5 > 23\,\%$			$23\,\% > SM_5 > 20\,\%$			$SM_5 < 20\,\%$		
		Fn	R^2	Q_{10}	Fn	R^2	Q_{10}	Fn	R^2	Q_{10}
SR_H	L2 – Near river	$SR_H = 0.52e^{0.05T}$	0.77***	1.58	$SR_H = 0.68e^{0.02T}$	0.74*	1.25	$SR_H = 2.10e^{0.4T}$	0.58**	0.02
	L3 – Intermediate	$SR_H = 0.51e^{0.04T}$	0.72***	1.49	$SR_H = 0.67e^{0.05T}$	0.70*	1.65	$SR_H = 2.11e^{-0.04T}$	0.57**	0.66
	L4 – Uphill	$SR_H = 0.40e^{0.05T}$	0.84***	1.58	$SR_H = 0.64e^{0.02T}$	0.66*	1.19	$SR_H = 1.34e^{-0.03T}$	0.34*	0.76
		$SM_5 > 27\,\%$			$27\,\% > SM_5 > 17\,\%$			$SM_5 < 17\,\%$		
SR_{tot}	L1 – *A. glutinosa*	$SR_{tot} = 0.53e^{0.04T}$	0.77***	1.54	$SR_{tot} = 0.69e^{0.03T}$	0.83***	1.30	$SR_{tot} = 0.77e^{0.01T}$	0.01	1.06
	L2 – *P. nigra*	$SR_{tot} = 0.52e^{0.05T}$	0.78***	1.60	$SR_{tot} = 0.61e^{0.04T}$	0.80***	1.46	$SR_{tot} = 1.39e^{-0.02T}$	0.19**	1.17
	L3 – *F. excelsior*	$SR_{tot} = 0.32e^{0.08T}$	0.68***	2.14	$SR_{tot} = 0.56e^{0.03T}$	0.62***	1.40	$SR_{tot} = 1.30e^{-0.02T}$	0.25**	0.82

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

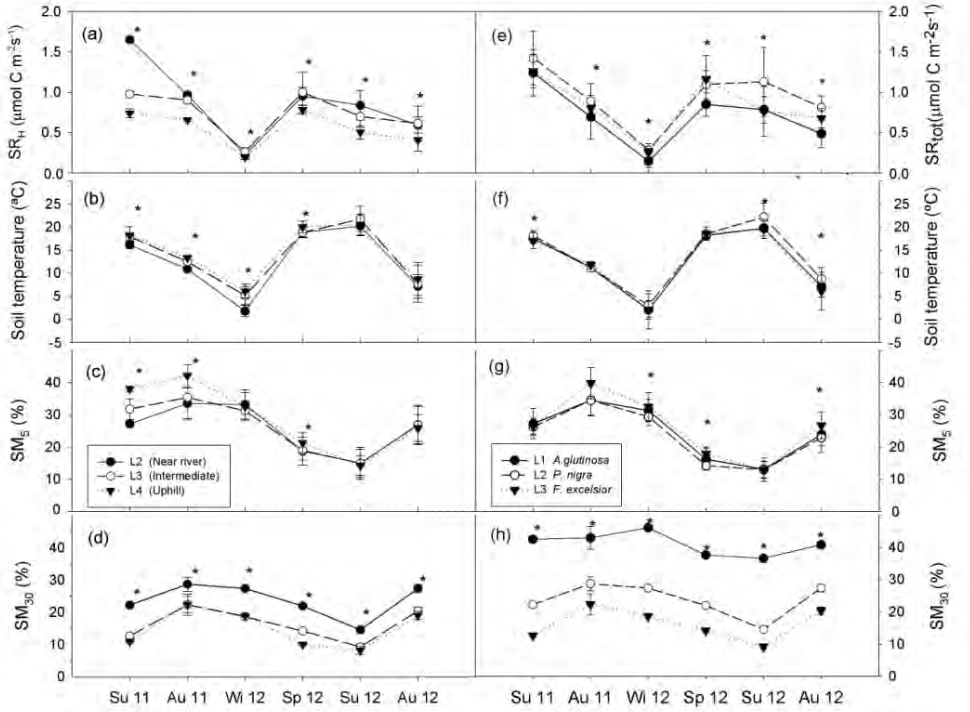

Figure 3. Seasonal variation of soil respiration, soil temperature and soil moisture. **(a–d)** Data of soil heterotrophic respiration: **(a)** SRH along groundwater level gradient. **(b)** 5 cm soil temperature. **(c)** 5 cm integral soil moisture (SM_5). **(d)** 30 cm integral soil moisture (SM_{30}). **(e–h)** Data of total soil respiration rates (SRtot) of three tree species. **(e)** SR_{tot} under different tree species. **(f)** 5 cm soil temperature. **(g)** 5 cm integral soil moisture (SM_5). **(h)** 30 cm integral soil moisture (SM_{30}) . All values are mean SD. Data points marked with indicate significant differences between species at $P < 0.05$ (For details, please see to Appendices A and B).

4 Discussion

4.1 Effect of groundwater level and soil moisture on SR

In the studies of Martin and Bolstad (2005) and Pacific et al. (2008), it was indicated that the amount and availability of soil water varies depending on landscape position and topography. Both studies also show that small differences in micro-topography appear to be important in driving soil moisture conditions. This is in accordance with our results; the overall seasonal trends of soil moisture were similar, but differences in the relative magnitude of soil moisture still can be found between different levels.

In our study site, the SR_H was significantly higher at L2 and decreased with the distance from the river. At the same time, SR_{tot} of *A. glutinosa* at L1 was significantly lower than the other two species found at L2 and L3. This result could be explained by limitations of SR imposed by groundwater

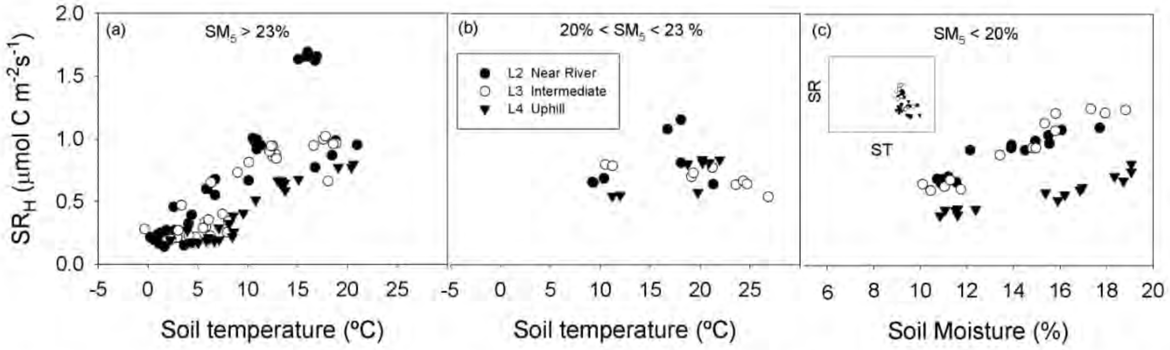

Figure 4. Differentiation of soil temperature (ST) and soil moisture (SM) as primary controlling factors for SR_H. At $SM_5 \geq 23\,\%$, there are positive correlations of SR_H with soil temperature in all levels **(a)**. At $20\,\% \leq SM_5 < 23\,\%$, there is a transition with no clear relationship of either SM or ST with SR_H **(b)**. At $SM_5 < 20\,\%$, there is no relationship between SR and ST as the inset figure shows **(c)**; it switches from ST to SM_5 as the controlling factor with positive correlations between SR_H and SM_5 for all levels. Campaigns with $SM_5 < 20\,\%$ were all from spring and summer 2012. SM_5 (5 cm integral soil moisture).

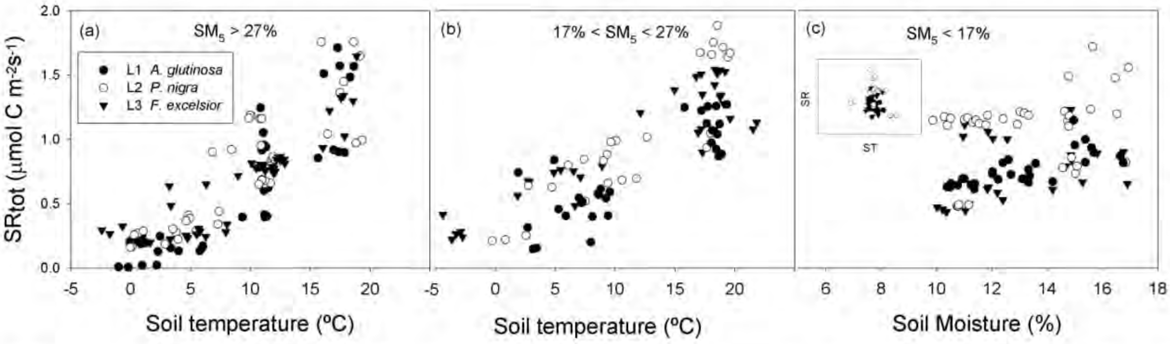

Figure 5. Differentiation of soil temperature (ST) and soil moisture (SM) as primary controlling factors for SR_{tot}. At $SM_5 \geq 27\,\%$, there are positive correlations of SR_{tot} with soil temperature under all tree species **(a)**. At $17\,\% \leq SM_5 < 27\,\%$, there are positive but slightly weaker correlations of SR_{tot} with soil temperature under all tree species **(b)**. At $SM_5 < 17\,\%$, there is no relationship between SR and ST as the inset figure shows **(c)**; it switches from ST to SM_5 as the controlling factor with positive correlations between SR_{tot} and SM_5 for all tree species. Campaigns with $SM_5 < 17\,\%$ were all from spring and summer 2012. SM_5 (5 cm integral soil moisture).

level in two different ways. First, when the groundwater level is low, the drought stresses soil microbial and root respiration activity; second, when groundwater level is high and close to topsoil surface, it limits soil aeration and likely reduces the effective respiring soil volume. Pacific et al. (2008) showed that the soil CO_2 concentrations were significantly higher in the riparian zone as a result of higher soil moisture. In contrast, Zanchi et al. (2011) found lower SR in plots after drainage, and suggested that the low C and N content in the topsoil near the river, where most of the soil CO_2 respiration is produced, could partially explain that low SR. The discrepancy of these two studies could be associated with the different drainage regimes as the poorly drained plots imply the anaerobic inhibition of SR. In our study, however, SR_H was measured at L2, L3 and L4 under well-drained conditions, and SR_H decreased concomitantly with the decrease in the availability of soil water. Nonetheless, SR_{tot} of *A. glutinosa* was measured at L1, where the soils sometimes experienced flooding or poor draining conditions, and the root respiration may be inhibited by the high groundwater level.

Additionally, landscape position and topography not only altered the availability of soil water but also affected the annual range of soil moisture. This was shown in Zanchi et al. (2011), studying riparian SR in Amazonia. They indicated that riparian soil is very sensitive to the changes of water-flooding regimes. The high groundwater table in riparian zones implies intermittent anaerobic conditions and the inhibition of diffusion during water saturation. These differences in soil moisture caused by site topography may result in differences in SR even though the soil temperatures were similar among all sites. The different behaviours of SR_H and SR_{tot} from L1 to L4 from our results indicate a different contribution of SR_H to SR_{tot}. As the root system of *A. glutinosa* may constantly experience a saturated water regime, the relative contribution from root respiration may be much lower than the one of the other two species.

4.2 Rain pulse and drought effects on SR

The Mediterranean climate is characterized by summer droughts that particularly affect the top soil layers; therefore, rainfall events during these dry periods can trigger abrupt increases in SR that last for days (Bowling et al., 2011; Cisneros-Dozal et al., 2007; Lee et al., 2004; Unger et al., 2010). Lee et al. (2004) simulated precipitation and found that hardwood forest floors were very sensitive to changes in moisture in the upper soil layers. Moreover, Wang et al. (2012) noted that the response of litterfall respiration is very sensitive to rainfall, and the increase in soil moisture by rainfall primarily enhanced the litterfall respiration but decreased mineral SR. Similar results were published by Casals et al. (2011), who reported that SR after a precipitation pulse was mostly derived from SR_H with a contribution up to 70 % of SR_{tot}. Hence, our findings seem to be consistent with these previous studies.

4.3 Confounding effects of temperature and moisture on SR

This study aimed at assessing the importance of soil moisture on soil respiration and determining the threshold of soil moisture at which soil moisture overrules temperature in controlling SR. The response of SR to soil moisture has been widely studied and described by various types of functions such as linear or logarithmic functions, depending on the soil type, climate or vegetation type (Comstedt et al., 2010; Epron et al., 1999; Orchard and Cook, 1983). In our study, the seasonal courses of SR_H and SR_{tot} generally followed the seasonal cycle of temperature, but were moderated by soil moisture. Such a relationship is in agreement with other previous studies (Davidson et al., 1998; Martin and Bolstad, 2005; Wang et al., 2013).

The positive linear relationship between SR and soil moisture in low soil moisture conditions found in our work agrees with many previous studies where low soil moisture constrains SR (Almagro et al., 2009; Davidson et al., 1998; Keith et al., 1997; Rey et al., 2002; Wang et al., 2013; Xu and Qi, 2001). In our study, the low soil moisture and warmer temperatures actually reduced SR rates, resulting in lower Q_{10} values at the lower soil moisture. A similar decline of Q_{10} with decreasing soil moisture was reported by Conant et al. (2004), Curiel-Yuste et al. (2003) and Wen et al. (2006). Low soil water content not only reduces the contact between the substrate, enzymes and microbes, it also decreases the substrate supply due to the increased drying-out of litter and topsoil layer (Davidson et al., 2006). Another possible reason for the observed lower Q_{10} is that the reduction of photosynthesis decreases the translocation of photosynthates to the rhizosphere (Hogberg et al., 2001; Nordgren et al., 2003).

In a Norway spruce stand, Gärdenäs (2000) found that litter moisture explained most of the variation of SR, whereas mineral soil moisture, air and litter temperature had no effects on SR. Our results showed that the seasonal variations of SR_H and SR_{tot} were mainly controlled by soil temperature, with a secondary influence of soil moisture (SM_5). Using the recursive partitioning method, we have identified clear thresholds for SM_5 effects on the temperature sensitivity of SR. Soil moisture thresholds at which SR temperature sensitivity is reduced have been found in several studies from different ecosystems (Fang and Moncrieff, 2001; Gaumont-Guay et al., 2006; Jassal et al., 2008; Lellei-Kovács et al., 2011; Palmroth et al., 2005; Wang et al., 2013). However, the threshold values in soil moisture seem to be site specific as the factors limiting water uptake by plants and microbes may differ by ecosystem. Even in the same climate region, different soil moisture thresholds have been found in previous studies. For example, Almagro et al. (2009) investigated how soil moisture modulated the sensitivity of soil respiration in different ecosystems in the Mediterranean region and found that the threshold value of soil moisture was 10 %. Above this soil moisture values, Q_{10} ranged from 1.86 to 2.20 and decreased to 0.44 to 0.63 when soil moisture was lower than 10 %. However, Rey et al. (2002) found in a Mediterranean oak forest that soil temperature accounted for 85 % of the variation of SR when soil moisture was above 20 % with a Q_{10} value of 2.34. Furthermore, Xu and Qi (2001) found that with soil moisture higher than 14 %, the Q_{10} value was 1.8 and decreased to 1.4 when soil moisture was lower than 14 %.

4.4 Other factors affecting SR

In addition to soil moisture threshold values, we also found variations of SR_H and SR_{tot} between location and tree species in each soil moisture interval. For example, when SM_5 was lower than 20 %, SR_H measured at L4 was always lower than SR_H measured at L2 and L3. When SM_5 was lower than 17 %, SR_{tot} of *P. nigra* was significantly higher than for the other two species, suggesting that there are still other factors affecting SR_H and SR_{tot} variations. Several explanations for this result are plausible. First, spatial variability in vegetation can affect SR due to differences in root respiration and the quantity and quality of detritus (Raich and Tufekcioglu, 2000). These biophysical gradients across landscape positions can lead to strong spatial heterogeneity in SR. Tree species in our study site exhibit different litterfall temporal patterns and may also contribute to the seasonal variation of the availability of SOC and nutrients to the microbial community and roots. Second, the vitality of tree species in responses to soil water regime could generate different root respiration rates. Additional data of daily sap flow of the studied trees from our study site (data not shown) confirmed the differences in tree transpiration and growth activity. For example, the water use efficiency of *P. nigra* was highest, followed by *F. excelsior* and *A. glutinosa*. Additionally, the mean diameter at breast height (DBH) of *P. nigra* is larger than mean DBH of the other tree species. *P. nigra* may be more efficient in taking up water and nutrients compared to the other two tree species.

5 Conclusions

This research demonstrates how soil moisture constrains the relationship between SR and soil temperature. We present critical threshold values of soil moisture where SR dependency on soil moisture overrules soil temperature dependency. Our results also reveal the importance of soil moisture as a predictor of SR even in a non-water-stressed environment such as riparian forests. Our findings provide support for modelling approaches that include soil temperature and soil moisture by making available parameters to predict SR rates. This study also has implications for a better understanding of global change impacts on the carbon cycle since soil water availability will likely become an increasingly crucial factor for some regions that are expected to suffer more frequent and severe droughts under climate change.

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Mitigating the Stress of Drought on Soil Respiration by Selective Thinning: Contrasting Effects of Drought on Soil Respiration of Two Oak Species in a Mediterranean Forest

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Abstract: Drought has been shown to reduce soil respiration (SR) in previous studies. Meanwhile, studies of the effect of forest management on SR yielded contrasting results. However, little is known about the combined effect of drought and forest management on SR. To investigate if the drought stress on SR can be mitigated by thinning, we implemented plots of selective thinning and 15% reduced rainfall in a mixed forest consisting of the evergreen *Quercus ilex* and deciduous *Quercus cerrioides;* we measured SR seasonally from 2004 to 2007. Our results showed a clear soil moisture threshold of 9%; above this value, SR was strongly dependent on soil temperature, with Q_{10} of 3.0–3.8. Below this threshold, the relationship between SR and soil temperature weakened. We observed contrasting responses of SR of target oak species to drought and thinning. Reduced rainfall had a strong negative impact on SR of *Q. cerrioides*, whereas the effect on SR for *Q. ilex* was marginal or even positive. Meanwhile, selective thinning increased SR of *Q. cerrioides*, but reduced that of *Q. ilex*. Overall, our results showed that the negative effect of drought on SR can be offset through selective thinning, but the effect is attenuated with time.

Keywords: reduced rainfall; selective thinning; soil respiration; *Quercus ilex*; *Quercus cerrioides*

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1. Introduction

Forest ecosystems contain one of the largest stocks of carbon and they represent one of the most important potential carbon sinks [1]. Globally, forest ecosystems are estimated to contain 681 ± 66 Pg (1 Pg = 10^{15} g) of carbon, with around 383 ± 28 Pg C (44%) of that total contained in the soil [1]. Therefore, forest soil respiration (SR) plays a crucial role in regulating soil carbon pools and carbon dynamics of terrestrial ecosystems under global warming [2,3]. Climate change scenarios project increases in mean annual temperature, increases in evapotranspiration, and decreases in precipitation [4–6]. Hence, future climate change is expected to have a great impact on SR by altering its main environmental drivers: temperature and moisture [7–10]. Because forest ecosystems may mitigate climate change through carbon sequestration [11], the effects of forest management practices on ecosystem carbon sinks need to be assessed. However, there is still no consensus on how forest management affects the soil's carbon balance; in addition, information on how forest management alters the response of SR to global warming is still limited [12–14].

Selective thinning is a common practice to improve forest health and productivity. Generally, after selective thinning, the remaining trees receive more solar radiation, soil water, soil organic matter, and nutrients, thus enhancing their photosynthetic capacity [15–19]. As a result, SR is expected to increase after forest thinning due to the increase in both soil organic matter and autotrophic respiration caused by the improvement of tree vitality. However, many studies have investigated the effect of forest management on SR with conflicting conclusions. Tang et al. [20] observed a decrease of 13% in total SR after thinning and suggested the decrease may be associated with the decrease in root density. On the contrary, Tian et al. [21] found an increase in SR up to 30% after thinning that slightly declined to 20%–27% in the following four to six years in a Chinese Fir (*Cunninghamia lanceolata* (Lamb.) Hook) plantation. Johnson and Curtis [22] concluded in their review that forest harvesting had little or no effect on soil carbon and nitrogen storage. Overall, the effect of thinning on SR is determined by many interactive factors, such as changes in soil temperature (Ts), soil moisture, microbial and root respiration, and decomposition of litter and woody debris. The responses of SR to thinning are the result of the combined effects of a "tug of war" among these factors.

In the Mediterranean region, summer drought has been identified as the main factor that limits plant species distribution and growth [23]. However, studies examining the extent to which drought affects SR have yielded inconsistent results. Some studies have shown that drought conditions will reduce SR due to low root and microbial activities [24–28]. Others report that drought may increase SR through enhancement of root growth [29,30]. Contrasting responses of fine root growth to drought were also found; fine root growth was enhanced in beech [31], but inhibited in spruce [32].

Given its arid and semi-arid climate, the Mediterranean region is a suitable area to study the effects of drought on forest productivity. While being exposed to re-occurring summer droughts, Mediterranean forests are particularly vulnerable to further reductions in water supply under climate change scenarios. Intergovernmental Panel on Climate Change [33], for instance, calls for a 15%–20% reduction of soil water availability over the next three decades in Mediterranean- type ecosystems. However, soil processes in Mediterranean ecosystems have received relatively little attention [7,8,34], and are currently under-represented as priorities for research networks [35,36]. This study may provide a better understanding of responses of SR to soil water deficits and the interaction with selective thinning. Selective thinning is a general practice to recover the structure of oak forests after wildfires, but it is also a potential drought mitigation practice.

The specific objectives of this study were: (i) to examine the time-course of the effects of selective thinning on the pattern of SR under two dominant tree species, *Quercus ilex* L. and *Quercus cerrioides* Willk & Costa in a Mediterranean forest; (ii) to evaluate the possible responses of SR under these two species subjected to experimental drought, and finally; (iii) to investigate whether selective thinning reduces the negative effect of drought on SR.

We expected that: (1) thinning would increase SR due to the deposition of the thinning material on the ground and the increase in nutrient availability; (2) reduced rainfall would decrease SR, especially during the growing season, as a result of decreased soil moisture; (3) due to the combined effect of thinning and reduced rainfall, thinning would compensate for the decrease in SR under drought conditions.

2. Materials and Methods

2.1. Site Description

The experiment was conducted in the region of Bages, Catalonia, NE Spain (41°44′ N, 1°39′ E, 800 m above sea level). Climate is dry, sub-humid Mediterranean, with a pronounced summer drought from July to September. Mean annual temperature and precipitation are 12 °C and 600 ± 135 mm, respectively (1980–2000) [37]. Soils are developed above calcareous substrate, surface rockiness is high, and the soil is moderately well drained with a mean depth ca. 25–50 cm. Additional information on the site is provided in Cotillas et al. [38].

2.2. Stand History and Tree Species Composition

Our study site is a mixed oak forest dominated by *Q. ilex* (Holm oak) and *Q. cerrioides* that regenerated by resprouting after a large wildfire in 1998. *Q. ilex* is a sclerophyllous evergreen tree species that is distributed widely over the Iberian Peninsula. *Q. cerrioides* is a winter semi-deciduous (marcescent) species. Both tree species have the ability to resprout from stumps and roots after disturbances [39]. When starting the experiment in 2004, the post-fire regeneration was six years old. The stem basal area and height of *Q. cerrioides* and *Q. ilex* from the study site were significantly different. *Q. cerrioides* individuals had a larger mean stem basal area (12.4 ± 0.8 cm^2) and height (177 ± 4 cm) than those of *Q. ilex* (9.7 ± 0.8 cm^2 and 144 ± 4 cm) [38].

2.3. Experimental Design

Our experiment was designed to test the effects of thinning and experimental drought in a Mediterranean oak forest. A total of 12 plots were installed with three replicates each for (1) control, (2) 15% rainfall exclusion, (3) selective thinning, and (4) combined (thinning with 15% rainfall exclusion). The plots (15 m × 20 m) were distributed randomly in the sampling area with a minimum buffer of 10 m surrounding every plot. To intercept runoff water, a ditch of ca. 50 cm depth was excavated along the entire top edge of the rainfall exclusion plots and covered with Poly Vinyl Chloride (PVC) strips. Due to instrumental limitations, SR rates were measured only in one replicate of each treatment. Tree height, basal area, and density were measured before starting the experiment and no significant differences were found in structural characteristics among plots [38]. Selective thinning was done in spring 2004. Traditional criteria of selective low-thinning for young oak coppices were applied [40,41]: 20%–30% of total stump basal area per plot was reduced, the weakest stems were eliminated, and from one to three dominant stems per stump were left. After selective thinning, mean stem basal area and height in thinning and combined treatments were 14.3 ± 0.8 cm^3 and 180 ± 4 cm, respectively, and in the unthinned plots, those same characteristics were 7.7 ± 0.8 cm^3 and 146 ± 4 cm, respectively. In the reduced rainfall and combined treatment plots, parallel drainage channels were installed at ca. 50 cm height above the soil and covered 15% of the ground surface. The channels were installed after the measurement of autumn 2004.

2.4. Field Measurements

SR and *Ts* under *Q. ilex* and *Q. cerrioides* individuals were measured seasonally from 2004 to 2007 during three-day periods for each treatment. In each plot, four stainless-steel rings were inserted permanently at a soil depth of 3 cm. The rings were weeded regularly. CO_2 concentration was measured in situ with an automatic changeover open system. The system consisted of an infrared gas analyzer (IRGA, LiCor 6262, LiCor, Inc., Lincoln, NE, USA), a data logger (CR10 Data logger, Campbell Scientific Inc., Logan, UT, USA), 12 pairs of channels, 12 chambers, 12 pairs of rotameters, six pumps, and two flowmeters. Four pairs of channels were connected with the soil chambers. Each pair of channels consisted of two tubes, one attached to the top of the chamber (reference CO_2 concentration) and another attached to the base for calculating the increment in CO_2 concentration (sample CO_2 concentration). The other eight pairs of channels were connected to leaf and stem chambers, which were measured in parallel, but are not presented in this work. The stainless steel soil chambers were closed cylindrical chambers 28 cm in diameter and 15 cm high. Air was pumped through all chambers continuously at 1 $L \cdot min^{-1}$, but only one chamber at a time was directed to the gas analyzer for 1 min. Meanwhile, air through the other chamber was exhausted to the atmosphere. When air was directed to the gas analyzer, only the last 40 seconds of recordings from the gas analyzer were averaged and recorded by the data logger. A complete measurement cycle took 60 min, including four rounds of measurements of absolute, ambient air, and CO_2 concentration (ppm) from all chambers and one additional zero calibration cycle.

Soil chambers were shaded by placing a 50 × 50 cm green fine mesh on top to avoid possible heating by direct sunlight during the measurements. Soil temperatures in the upper 5 cm of soil were measured continuously with Pt100 temperature sensors ($n = 4$) and recorded in parallel with the CO_2 concentration analysis. Soil moisture (cm^3/cm^3) in the upper 20 cm of soil was recorded manually once per day during the three-day measurement of each plot using 10 Time Domain Reflectometry Probes (Tektronix, 1520C Beaverton, OR, USA), which were installed randomly within each plot. Due to instrument failure, no SR data were recorded during winter 2007. Starting from summer 2005, seasonal litter fall per tree species was collected from each treatment. After collecting the litter, its fresh weight was determined. Samples were oven-dried at 65 °C for 48 h and then the dry weight was determined.

2.5. Data Analysis

We used analysis of variance (ANOVA) with treatment (thinning, reduced rainfall, both thinning and reduced rainfall combined, and control), season (winter, spring, summer, autumn) and year (2004, 2005, 2006, and 2007) as main factors to examine their effects on SR, *Ts*, and soil moisture. The daily or seasonal averages were used in these analyses. The relationship between SR and *Ts* in different treatments was based on daily average data using regression analysis, where a univariate exponential model was fitted [42]:

$$R = R_0 \left(e^{KT}\right) \quad (1)$$

where R is the measured soil respiration rate (μmol C $m^{-2} \cdot s^{-1}$), R_0 is the basal respiration at temperature of 0 °C, T is the measured soil temperature (°C), and K is the fitted parameter. Thereafter, the temperature sensitivity of soil respiration can be derived as:

$$Q_{10} = e^{10K} \quad (2)$$

where Q_{10} is the apparent field-observed proportional increase in SR related to a 10 °C increase in temperature. We also used recursive partitioning analysis to separate the relationship between SR and *Ts* by soil moisture regime. As models based on partitioning can only handle linear models, the equation above was transformed by linearizing with logarithms:

$$\text{Ln}\, R = \ln R_0 + KT \quad (3)$$

Logarithmic transformed SR values were used as the dependent variable. Once the soil moisture thresholds were obtained, nonlinear regression analyses (model 1) were used to determine the relationship between SR and *Ts* in each soil moisture interval. All statistical analyses were performed with PASW statistics 18 (SPSS Inc., 2009, Chicago, IL, USA), except the recursive partitioning analysis, which was conducted with R statistical software version 2.15.3 (*R* Development Core Team, 2013) using the *party* package [43]. For all statistical tests, significance was accepted at $P < 0.05$. Values are given as mean ± standard error (SE).

3. Results

3.1. Temporal Variation in Ts and Soil Moisture

The average temperature showed no significant difference between treatments (Table 1). The seasonal course of soil temperature was pronounced in our study site. The highest recorded *Ts* was 32.2 °C in summer 2005 and the lowest was −0.3 °C in winter 2005. Soil moisture varied largely over the study period, ranging from 2.3% to 18.4% (Figure 1). Mean annual precipitation was lowest in 2006 (400 mm) and highest in 2007 (830 mm). The highest soil moisture occurred in winter and spring, but then dropped sharply in summer. The lowest soil moisture (2.3%) was recorded during the thinning treatment in summer 2005. Soil moisture was correlated negatively with *Ts*; the peak of *Ts* in summer coincided with the lowest soil moisture values. Throughout the four monitored years, the mean seasonal soil moisture in the control treatment was consistently higher than in the other treatments. Despite the reduced rainfall treatment, we did not find lower soil moisture in the plots subjected to reduced rainfall during most of the measurement campaigns.

Table 1. Treatment effects on soil temperature (*Ts*) and soil respiration (SR) of *Q. ilex* and *Q. cerrioides*.

Variable	Treatment	*Q. ilex*	*Q. cerrioides*	Average
Ts (°C)	Natural rainfall	14.88 a	14.98 a	14.93 a
	Reduced rainfall	16.77 a	15.99 a	16.38 a
	No Thinning	16.31 a	15.67 a	15.99 a
	Thinning	15.30 a	15.28 a	15.29 a
SR (μmol C $m^{-2}{\cdot}s^{-1}$)	Natural rainfall	0.45 a	0.47 a	0.46 a
	Reduced rainfall	0.38 a	0.30 b	0.34 b
	No Thinning	0.47 a	0.33 a	0.40 a
	Thinning	0.36 b	0.44 b	0.40 a

The different letters indicate the significant differences between treatments ($p < 0.05$).

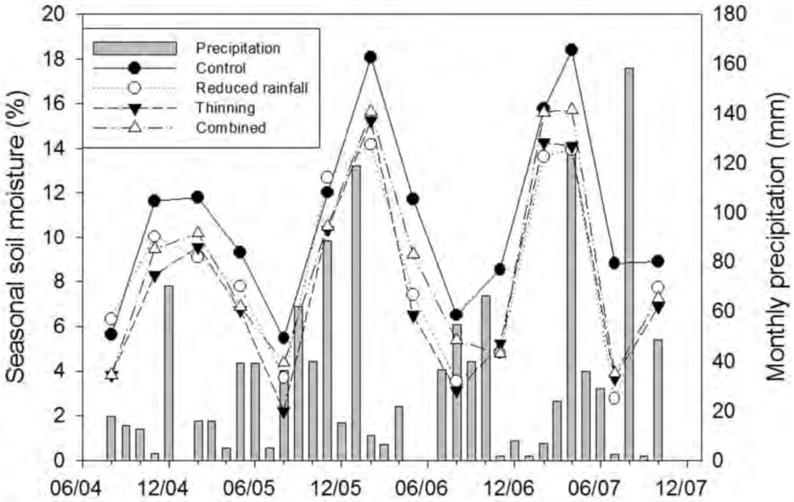

Figure 1. Seasonal variation in soil moisture (lines) and monthly variation in precipitation (bars) for each treatment during the study period. Different symbols represent different treatments. Labels on the *x*-axis represent time in month/year format.

3.2. *Treatment Effect on SR*

Within the four treatments, SR was between 0.00 and 1.82 μmol C $m^{-2}{\cdot}s^{-1}$, with an overall mean (±SD) of 0.43 ± 0.28 μmol C $m^{-2}{\cdot}s^{-1}$. Reduced rainfall treatment significanly depressed SR, with around 26% lower in comparison to natural rainfal (Table 1). Selective thinning showed no effect on overall SR (Table 1). SR under *Q. ilex* (0.44 ± 0.28 μmol C $m^{-2}{\cdot}s^{-1}$) was significantly higher than SR under *Q. cerrioides* (0.41 ± 0.28 μmol C $m^{-2}{\cdot}s^{-1}$, $P < 0.001$). Meanwhile, SR under *Q. ilex* showed no significant difference in subjected to reduced rainfall while SR under *Q. cerrioides* showed a pronounced decrease. Selective thinning, however, had different effects on SR under *Q. ilex* and *Q. cerrioides*; thinning enhanced SR under *Q. cerrioides*, but it reduced SR under *Q. ilex*.

Figure 2 shows the mean seasonal variations of SR under *Q. ilex* and *Q. cerrioides* in the four treatments. Generally, SR was higher during the growing season and lower in winter. Due to high precipitation in spring 2007, the SR in the control, thinning, and combined treatments showed the highest peak during this period. In the control treatment, SR under *Q. ilex* was significantly higher than under *Q. cerrioides*, except in autumn 2005 and spring 2006. In the reduced rainfall treatment, SR under *Q. ilex* showed a significantly higher rate compared to SR under *Q. cerrioides*, especially in spring and summer. Besides, there was almost no seasonality of SR under *Q. cerrioides*. SR under *Q. ilex* even showed higher values in comparison to the SR in the control treatment in the first year after treatment installation. In the thinning treatment, SR under *Q. cerrioides* was significantly higher than under *Q. ilex*, especially in spring. In the combined treatment, the seasonal patterns of SR under both tree species were very similar in the first 2 years. In the following years, SR under *Q. cerrioides* showed a higher value, which was very similar to the pattern of SR in the thinning treatment.

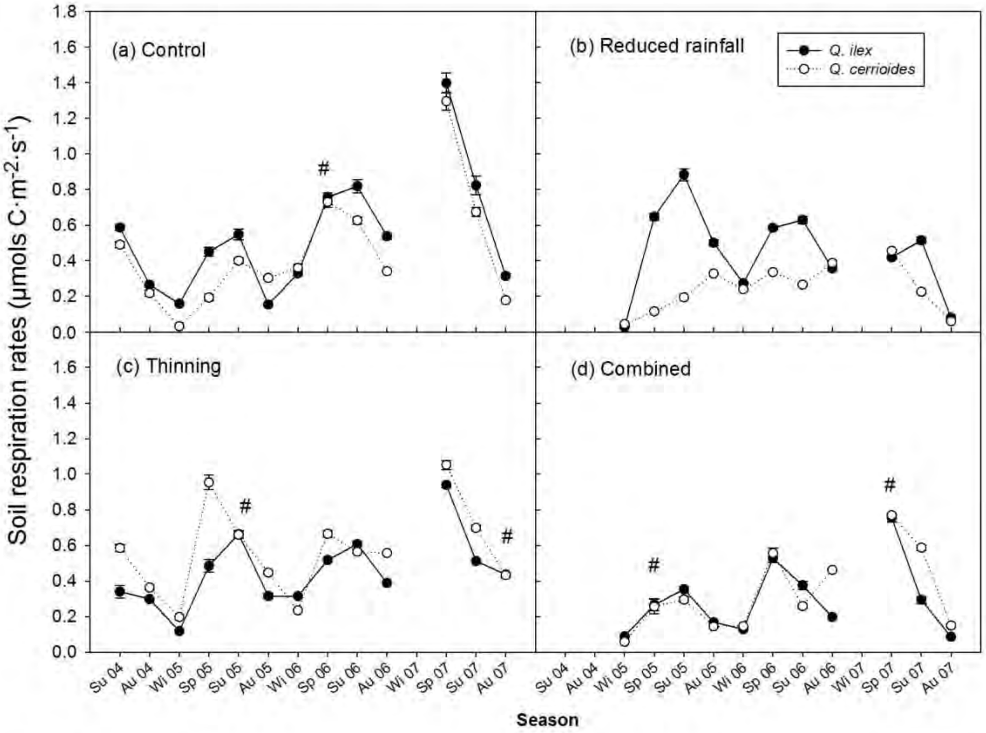

Figure 2. Seasonal variation in soil respiration of *Q. ilex* and *Q. cerrioides* for each treatment: (**a**) control; (**b**) reduced rainfall; (**c**) thinning; (**d**) combined treatment. Reduced rainfall treatment was installed at the end of 2004, therefore, the data for reduced rainfall and the combined treatments started in 2005. Data represent seasonal means with SE. Differences in SR between species were statistically significant except when marked with # ($p > 0.05$).

We also compared the diurnal variation in SR under the two tree species during spring and summer campaigns (Figures 3 and 4). During the spring campaigns, SR under both tree species in the control treatment showed a clear diurnal pattern, except for SR under *Q. cerrioides* in spring 2005. Meanwhile, in the reduced rainfall treatment, the diurnal changes of SR almost diminished. In the thinning treatment, SR under *Q. ilex* in 2005 showed a reversed diurnal pattern, but in the following two years the patterns turned back to be flat. The diurnal patterns of SR under *Q. cerrioides* in the thinning treatment were similar to the patterns in the control treatment, but with limited range and a clear depressed SR at noon. In the combined treatment, SR under both *Q. ilex* and *Q. cerrioides* showed a significant reduction during the day in 2005, but the reduction decreased in the following years. The diurnal variation of SR during summer campaigns was slightly different compared to spring. In the control treatment, although SR under the two tree species showed similar daily patterns, the variation of SR under *Q. ilex* was much higher than SR under *Q. cerrioides*. In the reduced rainfall treatment, SR under *Q. ilex* still exhibited a clear diurnal change, while SR under *Q. cerrioides* was almost steady.

In both thinning and combined treatments, SR under two tree species showed a pronounced reduction during the day.

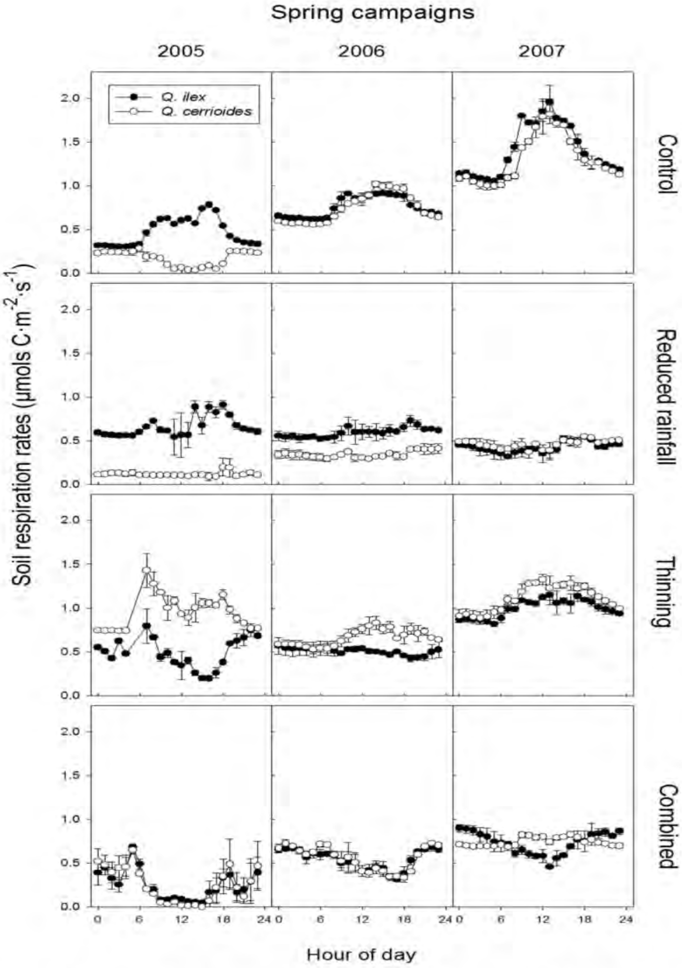

Figure 3. Diurnal variation of soil respiration rates (SR) with standard errors under *Q. ilex* and *Q. cerrioides* during spring in 2005, 2006, and 2007 (from left to right) and for each treatment: control, reduced rainfall, thinning, and combined treatment (from up to down). Shown are hourly rates of SR averaged over each campaign.

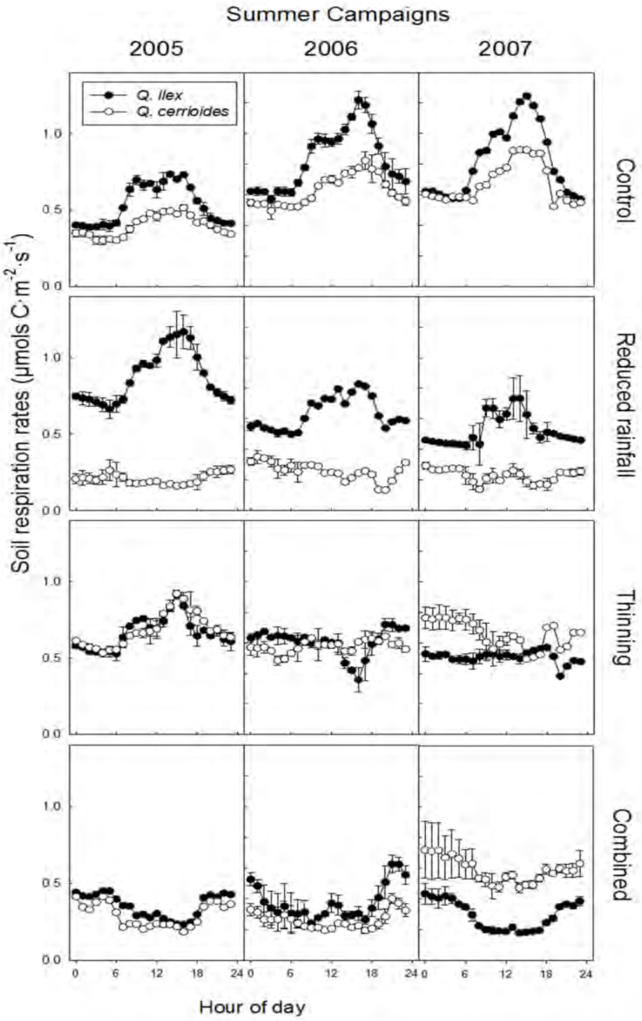

Figure 4. Diurnal variation of soil respiration rates (SR) with standard errors under *Q. ilex* and *Q. cerrioides* during summer in 2005, 2006, and 2007 (from left to right) and for each treatment: control, reduced rainfall, thinning, and combined treatment (from up to down). Shown are hourly rates of SR averaged over each campaign.

3.3. Relationship Between SR and Ts

By using recursive partitioning, we identified a soil moisture threshold around 8%–9%; when soil moisture was higher than 8%, SR and *Ts* were highly correlated, with apparent Q_{10} values from 2.99 to 3.83, and *Ts* explained 91%–96% of the variation in SR. When soil moisture was lower than 8%, apparent Q_{10} values declined to 1.23–1.44. Figure 5 shows the daily average SR of each treatment as a function of *Ts* separated by soil moisture regimes. In the control treatment, apparent Q_{10} was 3.0 when soil moisture was higher than 9%, and declined to 1.37 when soil moisture was lower than 9%. Thinning and combined treatments showed a similar pattern, except that the soil moisture threshold was slightly lower than the threshold of the control. In the reduced rainfall treatment, we could not identify the soil moisture threshold by using recursive partitioning, although the recorded soil moisture ranged from 2.8% to 14.2%. The overall apparent Q_{10} in the reduced rainfall treatment was 1.36. When we separated the SR under different species and compared its relationship with *Ts*, similar relationships between SR and *Ts* were found in all treatments except in the reduced rainfall treatment (inset in Figure 5b, S1–S3); SR under *Q. ilex* showed a positive correlation with *T*s with a Q_{10} of 1.53, whereas the SR under *Q. cerrioides* showed no relationship with *T*s.

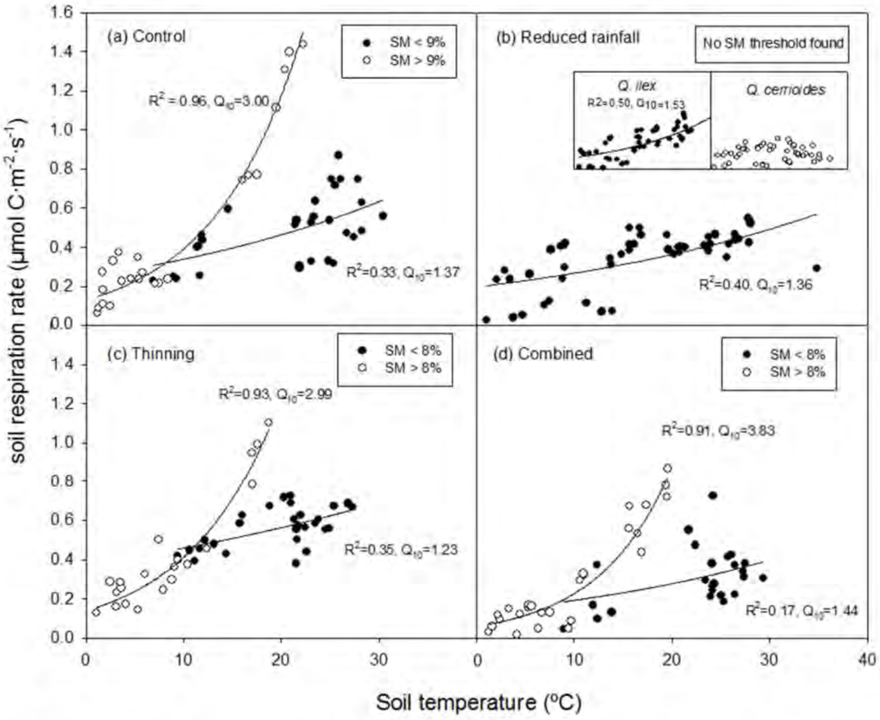

Figure 5. Relationship between daily SR and *T*s (5cm) separated by soil moisture regime in each treatment: (**a**) control; (**b**) reduced rainfall; (**c**) thinning; (**d**) combined treatment. Closed circles indicate the lower soil moisture regime, and open circles indicate the higher soil moisture regime. Lines show fit to Equation (1) for SR and *T*s within the same soil moisture regime. R^2 and Q_{10} values are given for each panel. In the reduced rainfall treatment, the relationship between SR and *T*s cannot be separated by soil moisture regime by using recursive partitioning; therefore, the closed circles represent all soil moisture regimes. Inset in (**b**) shows the relationship between daily SR and *T*s under two tree species (n = 49–53).

3.4. Temporal Variation in Litterfall

The peak of litterfall differed between the two tree species; in the control, *Q. ilex* mainly dropped leaves during spring and summer, while *Q. cerrioides* dropped leaves all year except during summer (Figure 6). In the reduced rainfall treatment, the peak of litterfall from *Q. ilex* was in spring, while *Q. cerrioides* remained the same throughout the year. In the thinning and combined treatments, the peak of litterfall from *Q. ilex* occurred in summer. Moreover, the total litterfall amount from *Q. cerrioides* was less in the thinning treatment and showed a peak of litterfall in spring. Although *Q. ilex* is an evergreen species, the amount of litterfall from *Q. ilex* was larger than from *Q. cerrioides*, especially during the driest summer of 2006.

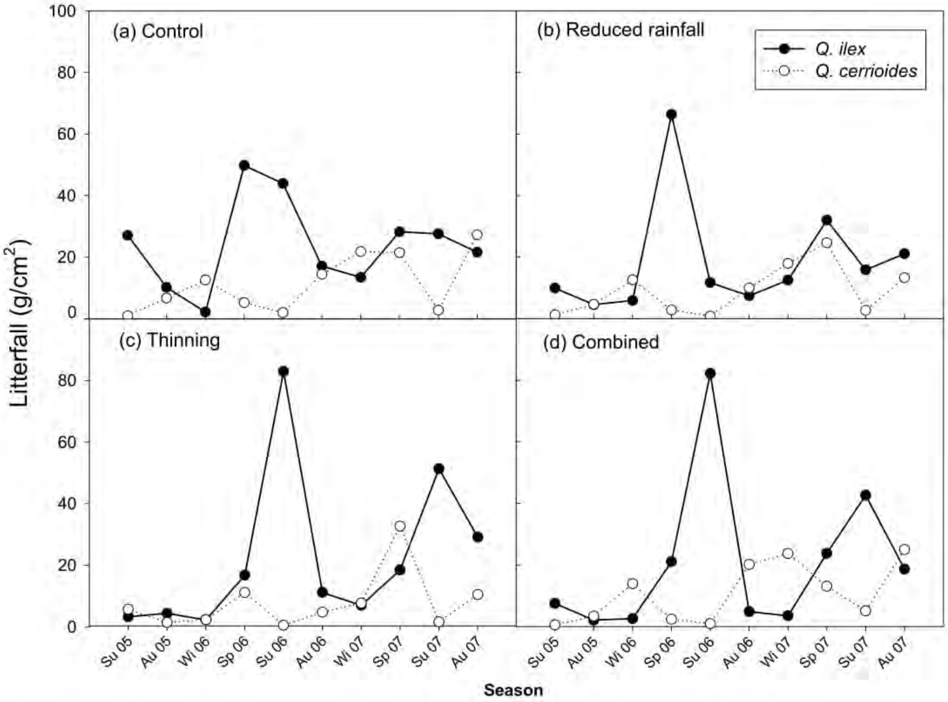

Figure 6. Seasonal variations in litter fall of *Q. ilex* and *Q. cerrioides* for each treatment: (**a**) control; (**b**) reduced rainfall; (**c**) thinning; (**d**) combined treatment. Reduced rainfall treatment was installed at the end of 2004, therefore, the data for reduced rainfall and combined treatments started in 2005.

4. Discussion

We expected to find the lowest soil moisture in the reduced rainfall treatment. However, the observed soil moisture data suggested that the channels installed in the reduced rainfall treatment only had partially or no effect. This may be due to the low precipitation during this period which probably diminished the treatment effect of reduced rainfall. We also suspect that the channels installed to reduce rainfall may have created some shadow and somewhat prevented the direct top-soil water evaporation. Despite the reduced rainfall treatment, we observed a tendency for soil moisture to be lower in the selective thinning treatments, especially during the summers of 2005 and 2006. Many studies have shown that thinning influences site-specific microclimatic conditions [14,44]. The removal of aboveground vegetation is known to increase *Ts* [45] and soil moisture as a consequence of reduced root and canopy interception and, hence, reduced evapotranspiration [46]. The observed lower soil moisture in the selective thinning treatment may be due to the way that selective thinning retained the roots, but increased the opening of the canopy. Moreover, thinning has been shown to increase transpiration rate through enhancement of tree growth, and this may consequently reduce soil moisture [46,47].

The observed decrease in overall SR from our study is similar to other research. Studies have shown how drought stress depressed SR from several aspects. First, the low water content of the soil created an environment that slowed the diffusion of solutes and, thus, suppressed microbial respiration by limiting the supply of substrate [48]. Additionally, microbes and plant roots have to invest more energy to produce protective molecules and this reduces their growth and respiration [49]. From hourly to daily scales, drought has been shown to decrease the recently assimilated C allocation to roots ca. 33%–50% [50,51]. The decrease in plant substrate and photosynthetic activity caused by drought may explain the reduction in SR [52,53]. With the prolongation of reduced rainfall over time, annual SR, especially root respiration, would have decreased followed by the depression of forest productivity and growth. For example, Brando et al. [54] found a decline in net primary productivity of 13% in the first year and up to 62% in the following four years in a throughfall reduction experiment.

Interestingly, despite the effect of drought on SR, we observed an increase in SR under *Q. ilex* in the reduced rainfall treatment in the first year after the reduced rainfall treatment. A similar pattern was observed in South Catalonia, where Asensio et al. [30] found significantly higher SR in the drought treatment compared to the control treatment during summer. First, they argued, that the prolonged low availability of soil water compelled roots to uptake deeper soil water; second, they also argued that moderate drought enhanced photosynthetic rates [55] to support roots with the majority of the photosynthetic assimilates. In our study site, Miguel [56] measured the treatment effects on mineral soil nutrients, and root density and distribution during the summers of 2007 and 2008, which is right after our measurement, and found a significant increase of fine roots of *Q. ilex* only in the reduced rainfall treatment. The high C/N ratio and low soil water content found in our study site [56] also implied a very low microbial respiration. Hinko-Najera et al. [57] also found that a reduction in throughfall mainly decreased autotrophic respiration, but not heterotrophic respiration, in a Mediterranean to cool temperate forest. As a result, we conjecture that the increase in SR under *Q. ilex* observed in our reduced rainfall treatment was caused by the increase of fine roots while the decrease in SR under *Q. cerrioides* may have been caused mainly by the decrease in root respiration. Miguel [56] also found that the fine and small roots of *Q. cerrioides* were distributed mainly in the 0–30 cm depth layer, but the roots of *Q. ilex* were found to be deeper. In other words, the different responses of SR under *Q. ilex* and *Q. cerrioides* may have been due to different rooting systems.

Previous studies have shown contradictory results of how thinning affects SR: SR has been found to increase, decrease, or even remain unchanged after thinning [18,44,58–63]. The different responses likely are due to thinning intensity, timing, and duration of the measurement campaigns after thinning. In our study, we observed an increase in SR in the selective thinning treatment during the first two years after selective thinning. We also found a significant reduction in SR during the daytime in the first summer campaign. We explain the possible reasons how thinning affects SR from a different temporal scale. Over the hourly to daily scales, selective thinning increased water and nutrient availability and, therefore, increased both microbial and root respiration. In the meantime, the woody debris and dead roots produced during thinning stimulated heterotrophic respiration [21,64]. Additionally, Sohlenius [65] found that slash produced by logging promoted productivity of soil microflora due to the increase in moisture and microbial biomass, which increased SR. However, selective thinning may also decrease SR because of the lower soil moisture caused by more solar radiation and higher transpiration in the initial phase after selective thinning [47]. From daily to seasonal scales, the enhancement of tree growth and photosynthesis due to selective thinning may promote more root respiration [66–68]. Cotillas et al. [38] investigated tree growth in the same study site and observed a remarkable improvement in residual stem growth (ca. 50%) and a reduction in stem mortality after selective thinning. However, they also found that the positive effects of thinning declined rapidly during the three-year experiment. López et al. [69] found an increase of more than 100% in root biomass and 76% in root production in a *Q. ilex* forest after thinning, especially during winter and autumn. We also found higher soil organic matter and soil phosphorous in the selective thinning treatments [56], which may also enhance SR. From seasonal to annual scales, selective thinning increased annual SR as a result of a longer growing period due to the absence of drought [70]. Supported by our litterfall data, the total amount of litterfall from *Q. cerrioides* was less in the thinning treatment; during the same time, we also observed a stronger effect of thinning on SR under *Q. cerrioides*. Overall, the effect of selective thinning on SR over time is likely to be reduced with the recovery of stands.

The apparent soil Q_{10} was affected significantly by soil moisture. However, this soil moisture threshold is not applicable to the relationship between SR and Ts in the reduced rainfall treatment. In the reduced rainfall treatment, we observed some campaigns with soil moisture higher than 8%, but SR of these campaigns were still lower than the SR in the control treatment of the same campaigns. The reduction of Q_{10} due to drought has been found in many studies [71–74]. As the apparent Q_{10}

in this study was calculated as annual Q_{10}, the low Q_{10} in the reduced rainfall treatment could be attributed by the diminished seasonal amplitude of SR, especially SR under *Q. cerrioides*. We found relatively few studies on the response of Q_{10} to forest management. At our study site, we found Q_{10} did not vary in response to thinning, which is similar to the finding of Tang et al. [20]. Our result is also consistent with Pang et al. [62], who showed that thinning increased the seasonal Q_{10} significantly, but not the yearly Q_{10}. Overall, the different SR-Ts relationship between the reduced rainfall treatment and combined treatment indicated that selective thinning treatment had at least partially mitigated the drought stress by improving the SR in response to environmental change.

Our study demonstrates that evergreen and deciduous trees growing in the same environmental conditions can emit different quantities of CO_2 from the soil. We found that thinning and reduced rainfall treatments have different effects on SR and litterfall of the two investigated tree species. This may be explained by the plant functional type (i.e., evergreen and deciduous species). *Q. ilex* is an evergreen species, which is well adapted to poor environments, and has low resource-loss ratios [75,76]. Therefore, the SR under *Q. ilex* was less affected by selective thinning. In contrast, deciduous species, such as *Q. cerrioides*, have a shorter period of active photosynthesis and a higher sensitivity to drought [77]. Therefore, deciduous species may require higher levels of nutrients and water to support higher rates of foliar net CO_2 assimilation to compensate for the shorter active period [78].

5. Conclusion

In conclusion, we examined the effects of drought and thinning on SR in a Mediterranean oak forest and observed a significant change in SR due to thinning and reduced rainfall. Both treatments influenced SR over different time scales. The main conclusions drawn from this study are as follows:

- Q_{10} of SR was clearly modulated by soil moisture, with a threshold value around 8%–9%. Reduced rainfall decreased both SR and Q_{10}, unlike selective thinning;
- Selective thinning had less effect on SR under *Q. ilex*, but increased the SR rate under *Q. cerrioides* in the first two years;
- Reduced rainfall significantly depressed SR rate under *Q. cerrioides* by 50%, especially during the growing season, and the drought effect accumulated over years. Reduced rainfall increased SR rate under *Q. ilex* during the growing season by 50%;
- Selective thinning mitigated the negative effect of drought on SR rate under *Q. cerrioides*, although the mitigation was only significant during spring and during the last year of the experiment.

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Author Contributions: Conceived and designed the experiments: Santiago Sabaté, Josep Maria Espelta, and Carlos Gracia; Performed the experiments: Elisenda Sánchez-Costa, Santiago Sabaté, and Miriam Cotillas; Analyzed the data: Chao-Ting Chang, Elisenda Sánchez-Costa, and Dominik Sperlich; Wrote the paper: Chao-Ting Chang.

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