

Article

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*

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 (T_s), 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 ($12.4 \pm 0.8 \text{ cm}^2$) and height ($177 \pm 4 \text{ cm}$) than those of *Q. ilex* ($9.7 \pm 0.8 \text{ cm}^2$ and $144 \pm 4 \text{ cm}$) [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 ($15 \text{ m} \times 20 \text{ m}$) 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 $14.3 \pm 0.8 \text{ cm}^2$ and $180 \pm 4 \text{ cm}$, respectively, and in the unthinned plots, those same characteristics were $7.7 \pm 0.8 \text{ cm}^2$ and $146 \pm 4 \text{ cm}$, 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 T_s 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 $1 \text{ L} \cdot \text{min}^{-1}$, 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 CO₂ concentration analysis. Soil moisture (cm³/cm³) 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, T_s , and soil moisture. The daily or seasonal averages were used in these analyses. The relationship between SR and T_s 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 ($\mu\text{mol C m}^{-2}\cdot\text{s}^{-1}$), 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 T_s by soil moisture regime. As models based on partitioning can only handle linear models, the equation above was transformed by linearizing with logarithms:

$$\ln R = \ln R_0 + KT \quad (3)$$

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 T_s 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 \pm standard error (SE).

3. Results

3.1. Temporal Variation in T_s 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 T_s 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 T_s ; the peak of T_s 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 (T_s) and soil respiration (SR) of *Q. ilex* and *Q. cerrioides*.

Variable	Treatment	<i>Q. ilex</i>	<i>Q. cerrioides</i>	Average
T_s (°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 ($\mu\text{mol C m}^{-2}\cdot\text{s}^{-1}$)	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 ($p < 0.05$).

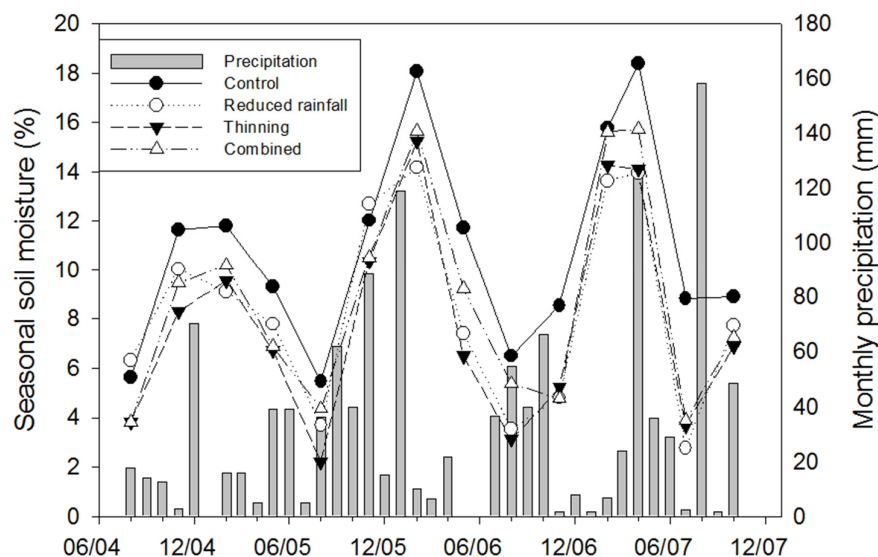


Figure 1. Seasonal variation in soil moisture (lines) and monthly variation in precipitation (bars) for each treatment during the study period. Different symbols represent different treatments. Labels on the x-axis represent time in month/year format.

3.2. Treatment Effect on SR

Within the four treatments, SR was between 0.00 and $1.82 \mu\text{mol C m}^{-2}\cdot\text{s}^{-1}$, with an overall mean ($\pm\text{SD}$) of $0.43 \pm 0.28 \mu\text{mol C m}^{-2}\cdot\text{s}^{-1}$. Reduced rainfall treatment significantly depressed SR, with around 26% lower in comparison to natural rainfall (Table 1). Selective thinning showed no effect on overall SR (Table 1). SR under *Q. ilex* ($0.44 \pm 0.28 \mu\text{mol C m}^{-2}\cdot\text{s}^{-1}$) was significantly higher than SR under *Q. cerrioides* ($0.41 \pm 0.28 \mu\text{mol C m}^{-2}\cdot\text{s}^{-1}$, $P < 0.001$). 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.

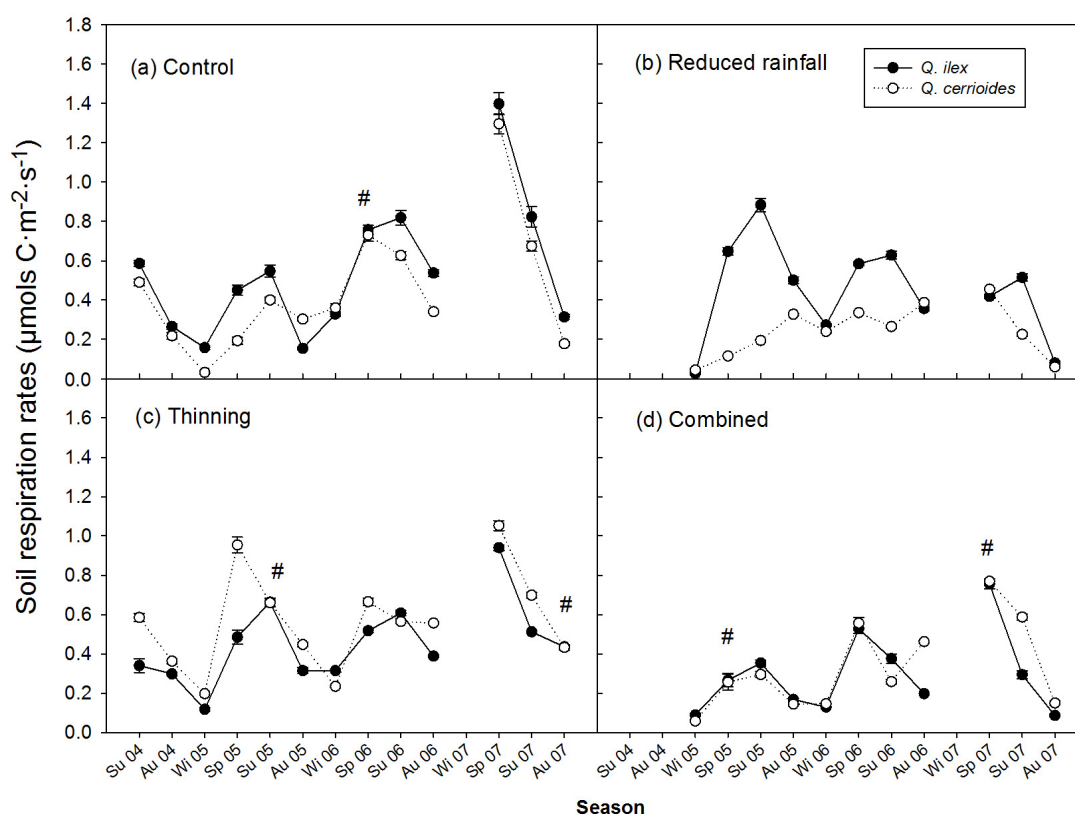


Figure 2. Seasonal variation in soil respiration of *Q. ilex* and *Q. cerrioides* for each treatment: (a) control; (b) reduced rainfall; (c) thinning; (d) combined treatment. Reduced rainfall treatment was installed at the end of 2004, therefore, the data for reduced rainfall and the combined treatments 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.

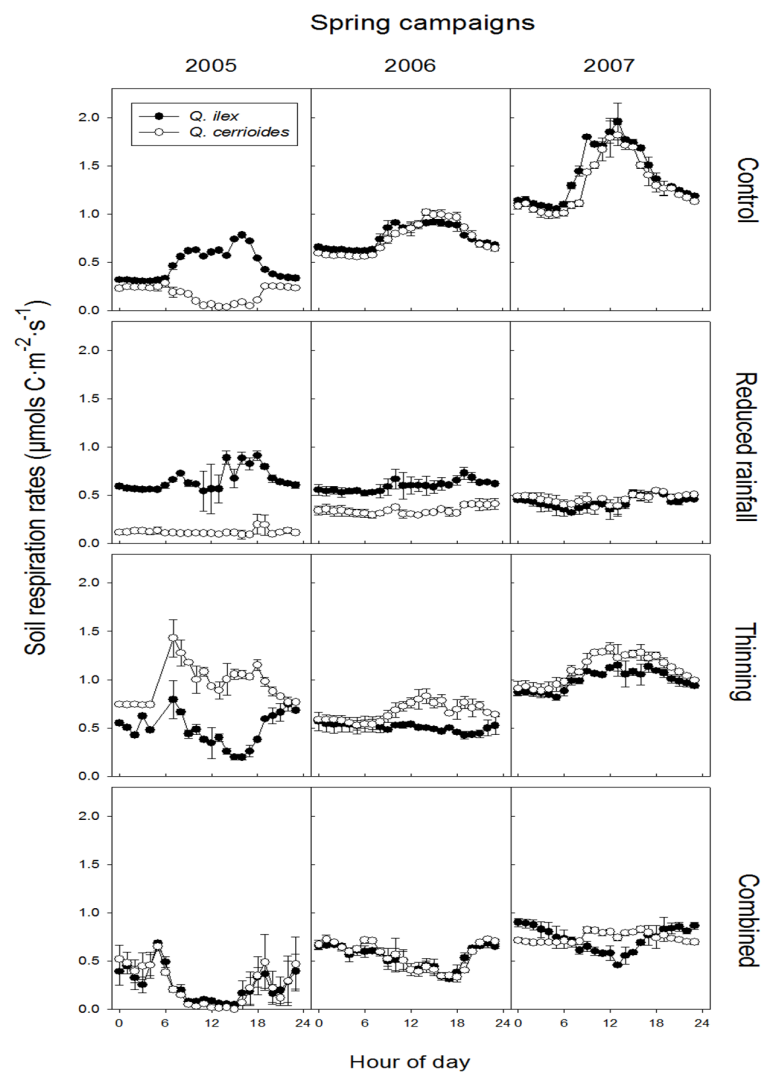


Figure 3. Diurnal variation of soil respiration rates (SR) with standard errors under *Q. ilex* and *Q. cerrioides* during spring in 2005, 2006, and 2007 (from left to right) and for each treatment: control, reduced rainfall, thinning, and combined treatment (from up to down). Shown are hourly rates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

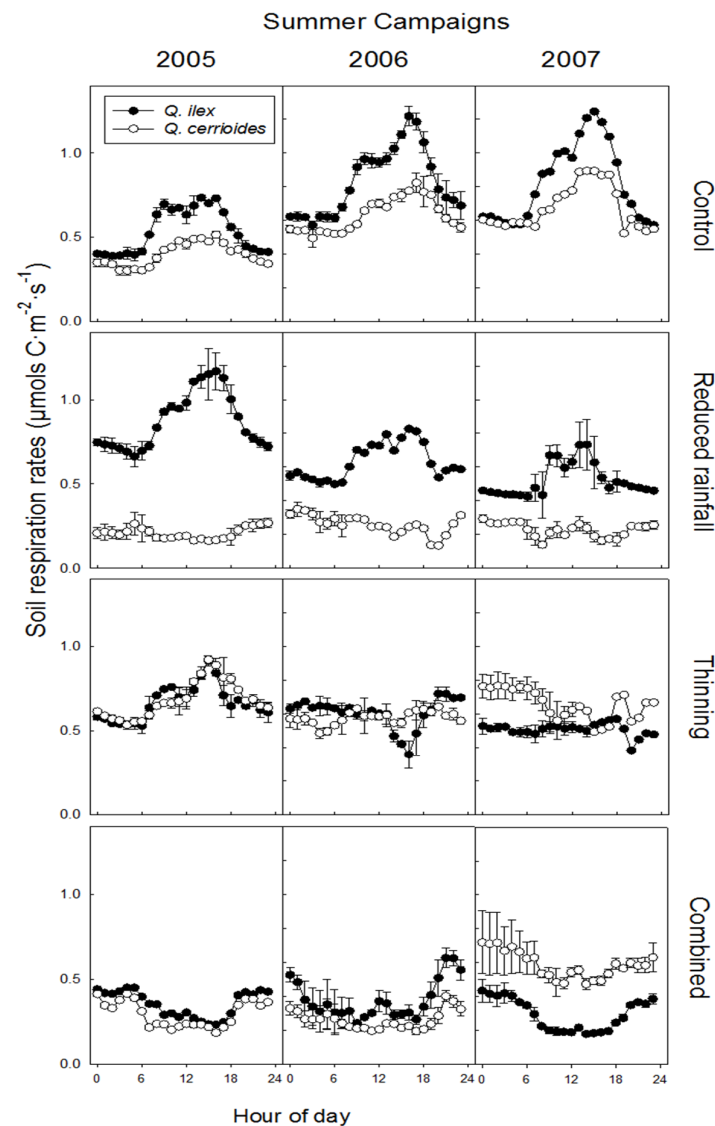


Figure 4. Diurnal variation of soil respiration rates (SR) with standard errors under *Q. ilex* and *Q. cerrrioides* during summer in 2005, 2006, and 2007 (from left to right) and for each treatment: control, reduced rainfall, thinning, and combined treatment (from up to down). Shown are hourly rates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

3.3. Relationship Between SR and T_s

By using recursive partitioning, we identified a soil moisture threshold around 8%–9%; when soil moisture was higher than 8%, SR and T_s were highly correlated, with apparent Q_{10} values from 2.99 to 3.83, and T_s 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 T_s 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 T_s , similar relationships between SR and T_s were found in all treatments except in the reduced rainfall treatment

(inset in Figure 5b and Figures 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 .

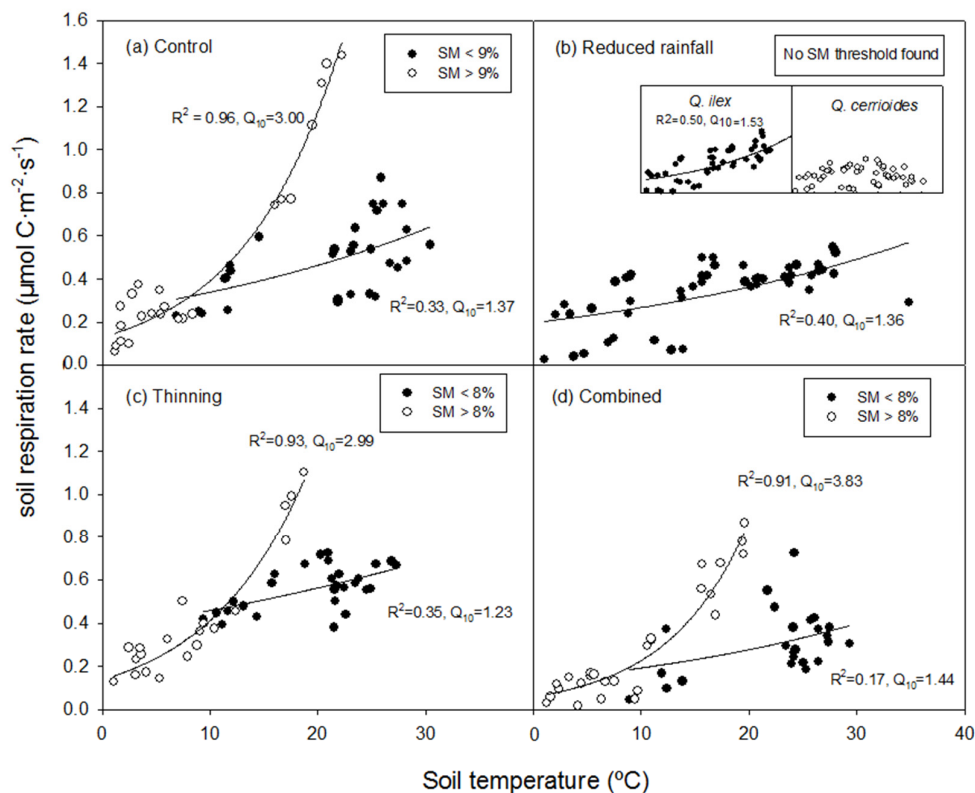


Figure 5. Relationship between daily SR and T_s (5cm) separated by soil moisture regime in each treatment: (a) control; (b) reduced rainfall; (c) thinning; (d) combined treatment. Closed circles indicate the lower soil moisture regime, and open circles indicate the higher soil moisture regime. Lines 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.

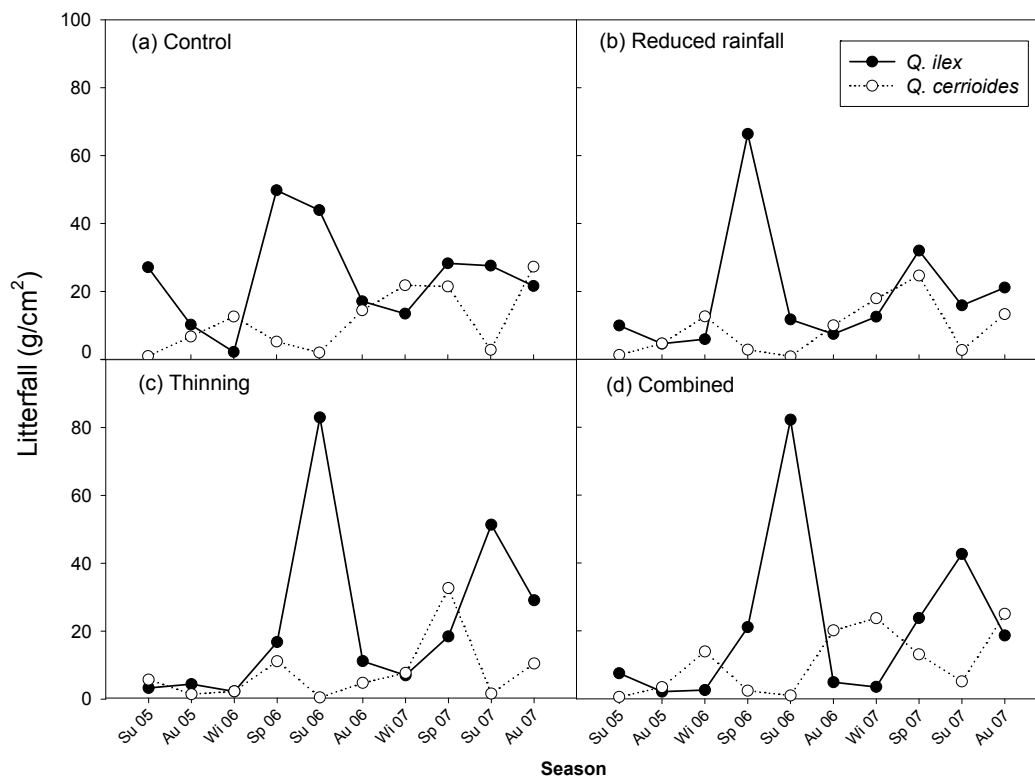


Figure 6. Seasonal variations in litter fall of *Q. ilex* and *Q. cerrioides* for each treatment: (a) control; (b) reduced rainfall; (c) thinning; (d) combined treatment. Reduced rainfall treatment was installed at the end of 2004, therefore, the data for reduced rainfall and combined treatments started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

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/7/11/263/s1>, Figure S1: Relationship between daily SR and Ts under *Q. ilex* and *Q. cerrioides* separated by soil moisture regime in the control treatment, Figure S2: Relationship between daily SR and Ts under *Q. ilex* and *Q. cerrioides* separated by soil moisture regime in the selective thinning treatment, Figure S3: Relationship between daily SR and Ts under *Q. ilex* and *Q. cerrioides* separated by soil moisture regime in the combined treatment.

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References

- Pan, Y.; Birdsey, R.A.; Fang, J.; Houghton, R.; Kauppi, P.E.; Kurz, W.A.; Phillips, O.L.; Shvidenko, A.; Lewis, S.L.; Canadell, J.G.; et al. A large and persistent carbon sink in the world's forests. *Science* **2011**, *333*, 988–993. [[CrossRef](#)] [[PubMed](#)]
- Schlesinger, W.H.; Andrews, J.A. Soil respiration and the global carbon cycle. *Biogeochemistry* **2000**, *48*, 7–20. [[CrossRef](#)]
- Melillo, J.M.; Steudler, P.A.; Aber, J.D.; Newkirk, K.; Lux, H.; Bowles, F.P.; Catricala, C.; Magill, A.; Ahrens, T.; Morrisseau, S.; et al. Soil warming and carbon-cycle feedbacks to the climate system. *Science* **2002**, *298*, 2173–2176. [[CrossRef](#)] [[PubMed](#)]
- Giorgi, F. Climate change hot-spots. *Geophys. Res. Lett.* **2006**, *33*, L08707. [[CrossRef](#)]
- Rowell, D.P.; Jones, R.G. Causes and uncertainty of future summer drying over Europe. *Clim. Dyn.* **2006**, *27*, 281–299. [[CrossRef](#)]
- Le Quéré, C.; Peters, G.P.; Andres, R.J.; Andrew, R.M.; Boden, T.; Ciais, P.; Friedlingstein, P.; Houghton, R.A.; Marland, G.; Moriarty, R.; et al. Global carbon budget 2013. *Earth Syst. Sci. Data Discuss.* **2013**, *6*, 689–760. [[CrossRef](#)]
- Raich, J.W.; Schlesinger, W.H. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B* **1992**, *44*, 81–99. [[CrossRef](#)]
- Raich, J.W.; Potter, C.S. Global patterns of carbon dioxide emissions from soils. *Global Biogeochem. Cycles* **1995**, *9*, 23–36. [[CrossRef](#)]
- Gårdenäs, A.I. Soil respiration fluxes measured along a hydrological gradient in a Norway spruce stand in south Sweden (Skogaby). *Plant Soil* **2000**, *221*, 273–280. [[CrossRef](#)]
- Fang, C.; Moncrieff, J.B. The dependence of soil CO₂ efflux on temperature. *Soil Biol. Biochem.* **2001**, *33*, 155–165. [[CrossRef](#)]
- Sullivan, B.W.; Kolb, T.E.; Hart, S.C.; Kaye, J.P.; Dore, S.; Montes-Helu, M. Thinning reduces soil carbon dioxide but not methane flux from southwestern USA ponderosa pine forests. *For. Ecol. Manag.* **2008**, *255*, 4047–4055. [[CrossRef](#)]
- Cheng, X.; Han, H.; Kang, F.; Liu, K.; Song, Y.; Zhou, B.; Li, Y. Short-term effects of thinning on soil respiration in a pine (*Pinus tabulaeformis*) plantation. *Biol. Fertil. Soils* **2013**, *50*, 357–367. [[CrossRef](#)]
- Sullivan, P.F.; Arens, S.J.T.; Chimner, R.A.; Welker, J.M. Temperature and Microtopography Interact to Control Carbon Cycling in a High Arctic Fen. *Ecosystems* **2008**, *11*, 61–76. [[CrossRef](#)]
- Wang, H.; Liu, W.; Wang, W.; Zu, Y. Influence of long-term thinning on the biomass carbon and soil respiration in a larch (*Larix gmelinii*) forest in Northeastern China. *Sci. World J.* **2013**, *2013*. [[CrossRef](#)] [[PubMed](#)]
- Ginn, S.E.; Seiler, J.R.; Cazell, B.H.; Kreh, R.E. Physiological and growth responses of eight-year-old loblolly pine stands to thinning. *For. Sci.* **1991**, *37*, 1030–1040.
- Peterson, J.A.; Seiler, J.R.; Nowak, J.; Ginn, S.E.; Kreh, R.E. Growth and physiological responses of young loblolly pine stands to thinning. *For. Sci.* **1997**, *43*, 529–534.
- Tang, Z.; Chambers, J.L.; Guddanti, S.; Barmett, J.P. Thinning, fertilization, and crown position interact to control physiological responses of loblolly pine. *Tree Physiol.* **1999**, *19*, 87–94. [[CrossRef](#)] [[PubMed](#)]
- Tang, J.; Qi, Y.; Xu, M.; Misson, L.; Goldstein, A.H. Forest thinning and soil respiration in a ponderosa pine plantation in the Sierra Nevada. *Tree Physiol.* **2005**, *25*, 57–66. [[CrossRef](#)] [[PubMed](#)]
- Selig, M.F.; Seiler, J.R.; Tyree, M.C. Soil carbon and CO₂ efflux as influenced by the thinning of loblolly pine (*Pinus taeda* L.) plantations on the Piedmont of Virginia. *For. Sci.* **2008**, *54*, 58–66.
- Tang, J.; Baldocchi, D.D. Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components. *Biogeochemistry* **2005**, *73*, 183–207. [[CrossRef](#)]
- Tian, D.-L.; Yan, W.-D.; Fang, X.; Kang, W.-X.; Deng, X.-W.; Wang, G.-J. Influence of Thinning on Soil CO₂ Efflux in Chinemse Fir Plantations. *Pedosphere* **2009**, *19*, 273–280. [[CrossRef](#)]
- Johnson, D.W.; Curtis, P.S. Effects of forest management on soil C and N storage: Meta analysis. *For. Ecol. Manag.* **2001**, *140*, 227–238. [[CrossRef](#)]
- Mooney, H.A. Carbon-gaining capacity and allocation patterns of mediterranean-climate plants. In *Mediterranean-Type Ecosystems*; Springer: Berlin, Germany, 1983; pp. 103–119.

24. Davidson, E.; Belk, E.; Boone, R.D. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Glob. Chang. Biol.* **1998**, *4*, 217–227. [[CrossRef](#)]
25. Kaye, J.P.; Hart, S.C. Restoration and canopy-type effects on soil respiration in a ponderosa pine-bunchgrass ecosystem. *Soil Sci. Soc. Am. J.* **1998**, *62*, 1062–1072. [[CrossRef](#)]
26. Borken, W.; Savage, K.; Davidson, E.A.; Trumbore, S.E. Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. *Glob. Chang. Biol.* **2006**, *12*, 177–193. [[CrossRef](#)]
27. Savage, K.E.; Davidson, E.A. Interannual variation of soil respiration in two New England forests. *Glob. Biogeochem. Cycles* **2001**, *15*, 337–350. [[CrossRef](#)]
28. Borken, W.; Davidson, E.A.; Savage, K.; Gaudinski, J.; Trumbore, S.E. Drying and Wetting Effects on Carbon Dioxide Release from Organic Horizons. *Soil Sci. Soc. Am. J.* **2003**, *67*, 1888. [[CrossRef](#)]
29. Liu, H.; Li, F.; Jia, Y. Effects of shoot removal and soil water content on root respiration of spring wheat and soybean. *Environ. Exp. Bot.* **2006**, *56*, 28–35. [[CrossRef](#)]
30. Asensio, D.; Penuelas, J.; Ogaya, R.; Llusà, J. Seasonal soil and leaf CO₂ exchange rates in a Mediterranean holm oak forest and their responses to drought conditions. *Atmos. Environ.* **2007**, *41*, 2447–2455. [[CrossRef](#)]
31. Leuschner, C.; Hertel, D.; Coners, H.; Büttner, V. Root competition between beech and oak: A hypothesis. *Oecologia* **2001**, *126*, 276–284. [[CrossRef](#)]
32. Puhe, J. Growth and development of the root system of Norway spruce *Picea abies* in forest stands—A review. *For. Ecol. Manag.* **2003**, *175*, 253–273. [[CrossRef](#)]
33. Stocker, T.F.; Qin, D.; Plattner, G.-K.; Tignor, M.; Allen, S.K.; Boschung, J.; Nauels, A.; Xia, Y.; Bex, V.; Midgley, P.M. Climate change 2013: The physical science basis. In *The Working Group I contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*; Cambridge University Press: New York, NY, USA, 2013.
34. Rey, A.N.A.; Pegoraro, E.; Tedeschi, V.; Parri, I.D.E.; Jarvis, G.; Valentini, R. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. *Glob. Chang. Biol.* **2002**, *8*, 851–866. [[CrossRef](#)]
35. Reichstein, M.; Rey, A.; Freibauer, A.; Tenhunen, J.; Valentini, R.; Banza, J.; Casals, P.; Cheng, Y.F.; Grünzweig, M.J.; Irvine, J.; Joffre, R.; et al. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Glob. Biogeochem. Cycles* **2003**, *17*, 1104. [[CrossRef](#)]
36. Valentini, R. EUROFLUX: An integrated network for studying the long-term responses of biospheric exchanges of carbon, water, and energy of European forests. In *Fluxes of Carbon, Water and Energy of European Forests*; Springer: Berlin/Heidelberg, Germany, 2003; pp. 1–8.
37. Ninyerola, M.; Pons, X.; Roure, J.M. A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. *Int. J. Climatol.* **2000**, *20*, 1823–1841. [[CrossRef](#)]
38. Cotillas, M.; Sabaté, S.; Gracia, C.; Espelta, J.M. Growth response of mixed mediterranean oak coppices to rainfall reduction: Could selective thinning have any influence on it? *For. Ecol. Manag.* **2009**, *258*, 1677–1683. [[CrossRef](#)]
39. Retana, J.; Espelta, J.M.; Gracia, M.; Riba, M. *Ecology of Mediterranean Evergreen Oak Forests*; Rodà, F., Retana, J., Gracia, C.A., Bellot, J., Eds.; Ecological Studies; Springer: Berlin/Heidelberg, Germany, 1999; Volume 137.
40. Espelta, J.M.; Rodrigo, A.; Habrouk, A.; Meghelli, N.; Ordóñez, J.L.; Retana, J. Land use changes, natural regeneration patterns, and restoration practices after a large wildfire in NE Spa. In *Challenges for Fire Ecology, Landscape, Restoration*; Trabaud, L., Prodon, R., Eds.; Fire and Biological Processes; Backhuys Publications: Leiden, The Netherlands, 2002; pp. 315–324.
41. Espelta, J.M.; Retana, J.; Habrouk, A. Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with contrasting leaf habits on two different sites. *For. Ecol. Manag.* **2003**, *179*, 401–414. [[CrossRef](#)]
42. Van't Hoff, J.H. *Lectures on Theoretical and Physical Chemistry*; Edward Arnold: London, UK, 1898.
43. Zeileis, A.; Hothorn, T.; Hornik, K. Model-Based Recursive Partitioning. *J. Comput. Graph. Stat.* **2008**, *17*, 492–514. [[CrossRef](#)]
44. Masyagina, O.V.; Prokushkin, S.G.; Koike, T. The influence of thinning on the ecological conditions and soil respiration in a larch forest on Hokkaido Island. *Eurasian Soil Sci.* **2010**, *43*, 693–700. [[CrossRef](#)]

45. Köster, K.; Püttsepp, Ü.; Pumpanen, J. Comparison of soil CO₂ flux between uncleared and cleared windthrow areas in Estonia and Latvia. *For. Ecol. Manag.* **2011**, *262*, 65–70. [[CrossRef](#)]
46. Bréda, N.; Granier, A.; Aussenac, G. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiol.* **1995**, *15*, 295–306. [[CrossRef](#)] [[PubMed](#)]
47. Olivar, J.; Bogino, S.; Rathgeber, C.; Bonnesoeur, V.; Bravo, F. Thinning has a positive effect on growth dynamics and growth-climate relationships in Aleppo pine (*Pinus halepensis*) trees of different crown classes. *Ann. For. Sci.* **2014**, *71*, 395–404. [[CrossRef](#)]
48. Skopp, J.; Jawson, M.D.; Doran, J.W. Steady-State Aerobic Microbial Activity as a Function of Soil Water Content. *Soil Sci. Soc. Am. J.* **1990**, *54*, 1619–1625. [[CrossRef](#)]
49. Schimel, J.; Balser, T.C.; Wallenstein, M. Microbial stress, response physiology and its implications for ecosystem function. *Ecology* **2007**, *88*, 1386–1394. [[CrossRef](#)] [[PubMed](#)]
50. Ruehr, N.K.; Offermann, C.A.; Gessler, A.; Winkler, J.B.; Ferrio, J.P.; Buchmann, N.; Barnard, R.L. Drought effects on allocation of recent carbon: From beech leaves to soil CO₂ efflux. *New Phytol.* **2009**, *184*, 950–961. [[CrossRef](#)] [[PubMed](#)]
51. Hasibeder, R.; Fuchslueger, L.; Richter, A.; Bahn, M. Summer drought alters carbon allocation to roots and root respiration in mountain grassland. *New Phytol.* **2015**, *205*, 1117–1127. [[CrossRef](#)] [[PubMed](#)]
52. Burton, A.J.; Pregitzer, K.S.; Zogg, G.P.; Zak, D.R. Drought reduces root respiration in sugar maple forests. *Ecol. Appl.* **1998**, *8*, 771–778. [[CrossRef](#)]
53. Yan, L.; Chen, S.; Huang, J.; Lin, G. Water regulated effects of photosynthetic substrate supply on soil respiration in a semiarid steppe. *Glob. Chang. Biol.* **2011**, *17*, 1990–2001. [[CrossRef](#)]
54. Brando, P.M.; Nepstad, D.C.; Davidson, E.A.; Trumbore, S.E.; Ray, D.; Camargo, P. Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: Results of a throughfall reduction experiment. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **2008**, *363*, 1839–1848. [[CrossRef](#)] [[PubMed](#)]
55. Lu, C.; Zhang, J. Effects of water stress on photosynthesis, chlorophyll fluorescence and photoinhibition in wheat plants. *Funct. Plant Biol.* **1998**, *25*, 883–892. [[CrossRef](#)]
56. Miguel, P.C. Respuestas Ecofisiológicas Y Estructurales a la Recurrencia, Duración E Intensidad de la Sequía en Plantaciones Y Bosques Mixtos de *Quercus ilex*, *Quercus pubescens* Y *Quercus cerrioides*. Doctoral Dissertation, Institut de Recerca i Tecnologia Agroalimentaries IRTA, Universitat Autònoma de Barcelona UAB, Catalonia, Spain, 2010. (In English)
57. Hinko-Najera, N.; Fest, B.; Livesley, S.J.; Arndt, S.K. Reduced throughfall decreases autotrophic respiration, but not heterotrophic respiration in a dry temperate broadleaved evergreen forest. *Agric. For. Meteorol.* **2015**, *200*, 66–77. [[CrossRef](#)]
58. Londo, A.J.; Messina, M.G.; Schoenholtz, S.H. Forest Harvesting Effects on Soil Temperature, Moisture, and Respiration in a Bottomland Hardwood Forest. *Soil Sci. Soc. Am. J.* **1999**, *63*, 637. [[CrossRef](#)]
59. Ma, S.; Chen, J.; North, M.; Erickson, H.E.; Bresee, M.; Le Moine, J. Short-term effects of experimental burning and thinning on soil respiration in an old-growth, mixed-conifer forest. *Environ. Manag.* **2004**, *33*, S148–S159. [[CrossRef](#)]
60. Jonsson, J.A.; Sigurdsson, B.D. Effects of early thinning and fertilization on soil temperature and soil respiration in a poplar plantation. *Icel. Agric. Sci.* **2010**, *23*, 97–109.
61. Olajuyigbe, S.; Tobin, B.; Saunders, M.; Nieuwenhuis, M. Forest thinning and soil respiration in a Sitka spruce forest in Ireland. *Agric. For. Meteorol.* **2012**, *157*, 86–95. [[CrossRef](#)]
62. Pang, X.; Bao, W.; Zhu, B.; Cheng, W. Responses of soil respiration and its temperature sensitivity to thinning in a pine plantation. *Agric. For. Meteorol.* **2013**, *171–172*, 57–64. [[CrossRef](#)]
63. Dai, Z.; Birdsey, R.A.; Johnson, K.D.; Dupuy, J.M.; Hernandez-Stefanoni, J.L.; Richardson, K. Modeling Carbon Stocks in a Secondary Tropical Dry Forest in the Yucatan Peninsula, Mexico. *Water Air Soil Pollut.* **2014**, *225*, 1925. [[CrossRef](#)]
64. Rustad, L.E.; Huntington, T.G.; Boone, R.D. Controls on soil respiration: Implications for climate change. *Biogeochemistry* **2000**, *48*, 1–6. [[CrossRef](#)]
65. Sohlenius, B. Short-Term Influence of Clear-Cutting on Abundance of Soil-Microfauna (Nematoda, Rotatoria and Tardigrada) in a Swedish Pine Forest Soil. *J. Appl. Ecol.* **1982**, *19*, 349. [[CrossRef](#)]
66. Janssens, I.A.; Lankreijer, H.; Matteucci, G.; Kowalski, A.S.; Buchmann, N.; Epron, D.; Pilegaard, K.; Kutsch, W.; Longdoz, B.; Grünwald, T.; et al. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Glob. Chang. Biol.* **2001**, *7*, 269–278. [[CrossRef](#)]

67. Kuzyakov, Y.; Cheng, W. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. *Soil Biol. Biochem.* **2001**, *33*, 1915–1925. [[CrossRef](#)]
68. Höglberg, P.; Nordgren, A.; Buchmann, N.; Taylor, A.F.S.; Ekblad, A.; Höglberg, M.N.; Nyberg, G.; Ottosson-Löfvenius, M.; Read, D.J. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* **2001**, *411*, 789–792. [[CrossRef](#)] [[PubMed](#)]
69. López, B.C.; Sabate, S.; Gracia, C.A. Thinning effects on carbon allocation to fine roots in a *Quercus ilex* forest. *Tree Physiol.* **2003**, *23*, 1217–1224. [[CrossRef](#)] [[PubMed](#)]
70. Aussenac, G.; Granier, A. Effects of thinning on water stress and growth in Douglas-fir. *Can. J. For. Res.* **1988**, *18*, 100–105. [[CrossRef](#)]
71. Jassal, R.S.; Black, T.A.; Novak, M.D.; Gaumont-Guay, D.; Nesic, Z. Effect of soil water stress on soil respiration and its temperature sensitivity in an 18-year-old temperate Douglas-fir stand. *Glob. Chang. Biol.* **2008**, *14*, 1305–1318. [[CrossRef](#)]
72. Suseela, V.; Conant, R.T.; Wallenstein, M.D.; Dukes, J.S. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Glob. Chang. Biol.* **2012**, *18*, 336–348. [[CrossRef](#)]
73. Suseela, V.; Dukes, J.S. The responses of soil and rhizosphere respiration to simulated climatic changes vary by season. *Ecology* **2013**, *94*, 403–413. [[CrossRef](#)] [[PubMed](#)]
74. Wang, B.; Zha, T.S.; Jia, X.; Wu, B.; Zhang, Y.Q.; Qin, S.G. Soil moisture modifies the response of soil respiration to temperature in a desert shrub ecosystem. *Biogeosciences* **2014**, *11*, 259–268. [[CrossRef](#)]
75. Aerts, R.; der Peijl, M.J. A simple model to explain the dominance of low-productive perennials in nutrient-poor habitats. *Oikos* **1993**, *66*, 144–147. [[CrossRef](#)]
76. Berendse, F. Competition between plant populations at low and high nutrient supplies. *Oikos* **1994**, *71*, 253–260. [[CrossRef](#)]
77. Thomas, D.S.; Eamus, D. Seasonal patterns of xylem sap pH, xylem abscisic acid concentration, leaf water potential and stomatal conductance of six evergreen and deciduous Australian savanna tree species. *Aust. J. Bot.* **2002**, *50*, 229–236. [[CrossRef](#)]
78. Eamus, D.; Myers, B.; Duff, G.; Williams, D. Seasonal changes in photosynthesis of eight savanna tree species. *Tree Physiol.* **1999**, *19*, 665–671. [[CrossRef](#)] [[PubMed](#)]



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