

Article

Stem CO₂ Efflux as an Indicator of Forests' Productivity in Relict Juniper Woodlands (*Juniperus thurifera* L.) of Southern Spain

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Abstract: There are considerable uncertainties about the C cycle in semi-arid ecosystems. Hence, studies that have focused on *Juniperus* in Mediterranean woodlands are non-existent. This study provides a survey of the effect of the juniper woodland type (young and mature woodlands; joint effect of maturity and forest productivity) on stem respiration. We checked the seasonal variation of stem respiration, evaluating the effects of stem temperature on stem CO₂ efflux. For this, we measured the stem CO₂ efflux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) over the four seasons on 16 junipers using LI-6400 equipment. The results showed that in the more productive site (young woodland), the stem CO₂ efflux was higher. This variable followed a clear seasonal trend, being higher during the spring and progressively decreasing in cold periods. In both juniper woodlands, and especially in the older forests, the Q₁₀ coefficients were low (<2), typical of cold forests and slow-growing species. The exponential model also confirmed that the Q₁₀ was significantly higher in young juniper trees. Thus, stem CO₂ efflux was an indicator of the growth in this juniper woodland that is well adapted to a semi-arid climate.

Keywords: stem respiration; Spanish juniper; thermophilic woodlands; temperature coefficient; Q₁₀; slow-growing species; relict forests; semi-arid climate



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1. Introduction

Autotrophic respiration is an important component of ecosystem-scale carbon budgets. In forests, Net Primary Production (NPP) is defined as the difference between gross primary production and autotrophic respiration [1]. Soil autotrophic respiration is the CO₂ produced from plant root and microbials metabolism, whereas aboveground autotrophic respiration has two major components: total wood respiration, which comprises stem and branch respiration, and foliar respiration [2]. In this balance, stem respiration makes an important contribution to total ecosystem respiration. It was estimated that the annual CO₂ efflux from stem tissues consumed 26% of the annual gross primary production [3]. Therefore, stem respiration is regarded as an important factor in the regulation of forest productivity and C storage, and it is one of the main components of the CO₂ efflux that release C to the atmosphere in forest ecosystems [4]. Although it does not usually reach the importance (in magnitude) of soil respiration, it is a variable component of the C cycle that allows us to analyze forests from the point of view of their productivity [2].

Stem respiration of trees is a major, but still poorly studied, component of the C balance in forests [5]. Although knowledge of the respiratory process and its responses to environmental changes is broad, it is still not as great as that of photosynthesis, and even less than that which occurs at the stem level [6]. In tree stems, most of the respiration process occurs in the new phloem and xylem adjacent to the cambium [7]. This important process is responsible for generating chemical energy in the form of ATP (Adenosine triphosphate), as well as metabolites (or C skeletons of cellular components), necessary for the growth and production of biomass (growth respiration) and for the maintenance of existing living cells (maintenance respiration), absorption of H₂O, and translocation of C and nutrients [8]. In this process, CO₂ is also generated, which is released into the atmosphere, in addition to H₂O [9].

Chamber-based measurements are often used to estimate stem respiration, scaling-up point measurements to stand or whole-tree scales [10]. CO₂ efflux measured through bark is a reasonable and practical proxy to study stem respiration [5,11]; it comprises the sum of three principal terms: woody tissue respiration (+flux), re-fixation of respiratory CO₂ by bark photosynthesis and chlorenchyma (−flux), and flux from CO₂ dissolved in the xylem sap [4,10]. In general, diffusion of CO₂ is low and xylem sap can move CO₂ from wood toward foliage [11,12]. Resistance to radial CO₂ diffusion may introduce some additional bias in stem respiration estimation [4]. In addition, in illuminated young stems and branches, CO₂ efflux can be reduced (photorespiration, cuticular photosynthesis or inhibition of mitochondrial respiration), and in the dark, respiratory CO₂ is released to the atmosphere [13]. However, it can be assumed that the stem CO₂ efflux is an excellent indicator of the respiration rate of this component of the tree [14]. For example, in the study of Salomon et al. [11], stem respiration was mainly explained by stem CO₂ efflux (>90%).

It is known that the respiration in the stem per unit area varies as a function of the growth rate of the cambium [8]. Consequently, respiration can vary depending on different factors that control forest growth, such as age, available nutrients, light, climate, temperature [1,9], or the level of water stress [5]. As a consequence, previous studies have found a positive correlation between a forests' productivity and respiration [15]. Competition and abiotic stress also influence respiratory costs associated with stem wood biomass production and maintenance [16].

Stem activity is also an important process of the C cycle as stems store carbon for long periods compared with foliage and fine roots [3]. Despite this ecological importance, information on the C flux from stems in Mediterranean environments remains scarce. More specifically, studies carried out in ecosystems dominated by the *Juniperus* genus in Mediterranean climate are practically non-existent. The *Juniperus* genus comprises approximately 50 coniferous trees and shrubs species that are widely distributed throughout the temperate and subtropical regions of the Northern Hemisphere [17]. The *Juniperus* genus is a major component of arid and semi-arid tree/shrub ecosystems throughout the Northern Hemisphere [18]. The species has its origin in the remote times of the Tertiary, where it grew in colder climates. *Juniperus* probably originated in Eurasia and was a part of the south Eurasian Tethyan vegetation of the Eocene to Oligocene [19]. Therefore, it is a relic of Tertiary forests, well adapted to continental climates with very cold winters and hot, dry summers typical of semi-arid climates [20].

The Spanish juniper (*Juniperus thurifera* L., Cupressaceae) is an endemic dioecious species of the western Mediterranean that is protected by law in part of its habitat. In general, Spanish juniper is a slow-growing evergreen conifer, and *J. thurifera* var. *hispanica* Mill. is only found in Spain and the French Pyrenees [21], due to its rarity and slow growth, it has been included in several catalogs of endangered species in Spain and is protected by law. In addition, the phytoclimatic area of this species is correlated to severe continental climates [22], such as those predicted in climate change scenarios [23]. For this reason, this species can be utilized for forest restoration in poor sites with low potential productivity such as arid and semi-arid areas [18].

Thermophilic juniper woodlands occupy the driest areas of the distribution of this species in Spain [21], and they constitute relict forests with slow-growth [24] that can be classified into two levels of maturity and productivity [25]. The first are old or mature woodlands, and these generally contain trees that are over 150 years old and are characterized by stony soils with a low tree density. The second level is young woodlands, dominated by trees that are less than 100 years old. Young woodlands grow in abandoned farmlands (i.e., areas with better soils), and thus these forests have higher growth rates and tree density, presenting greater productivity [25,26].

The characteristics of the two thermophilic Spanish juniper woodlands that exist allowed us to study the stem CO₂ efflux in two forests with different degrees of maturity and productivity (due to age and soil quality) in a semi-arid Mediterranean climate and throughout the different seasons. We can hypothesize that variation in CO₂ efflux between stems is proportional to differences in the respiratory activity from these woody tissues. For this, seasonal estimations of stem respiration are required under naturally changing conditions of growth [7].

This main hypothesis of our research is applied on the fact that the type of juniper woodland, growing season (seasonality), and different climatic conditions (which are mainly reflected in the stem temperature) should significantly affect the CO₂ efflux of the juniper stems. Therefore, the CO₂ efflux measured from the stem and that which mainly comes from stem respiration should be an estimator of the productivity of the two juniper woodlands.

Thus, the specific objectives of the study were the following: (i) to analyze the effects of the juniper woodland type (young and mature woodlands; effect of soil quality and forests productivity) on the stem CO₂ efflux; (ii) to check the seasonal variation of the stem CO₂ efflux in the two juniper woodlands; (iii) to evaluate the effects of stem temperature on stem CO₂ efflux for both types of woodlands, which have different growth rates.

2. Materials and Methods

2.1. Study Area

The study was carried out in the Spanish juniper woodlands of El Campo de Montiel Mountains (southern Spain; Figure 1). These forests must be classified as thermophilic according to [21]. The climate of the area is semi-arid cold (BSk type, KÖPPEN [27]), continental, with extreme temperatures between 43 and −21 °C (data from “El Bonillo” station: 38°57′ N, 01°09′ W, 1068 m.a.s.l., period of 30 years; this station is located within 7 km of the research area, and owned by the State Meteorological Agency of Spain), with an average annual temperature of 12.8 °C. The precipitations correspond to a dry ombroclimate, with annual rainfall of 450 mm.

The juniper trees in which stem CO₂ efflux was measured were selected from the two types of thermophilic juniper woodlands (Figure 2 and Table 1): (i) a mature woodland with an average age of 170 years, growing in lithic leptosols (soil depth less than 15 cm) with stands of moderate slope (0–10%) and (ii) a young woodland, with a mean age of 66 years, which grows in abandoned farmlands and with deeper soils.

In each type of juniper woodland, a homogenous experimental area (approximately 1 hectare) was selected, representative of the forests studied. Both areas are less than 1 km apart, ensuring that both stands are growing under the same climatic conditions. Thus, both experimental areas were similar in elevation (1050 m.a.s.l.), slope (gentle slopes; average 5°), exposure (paramo formation with flat surfaces), and total rainfall (450 mm) due to their close proximity.

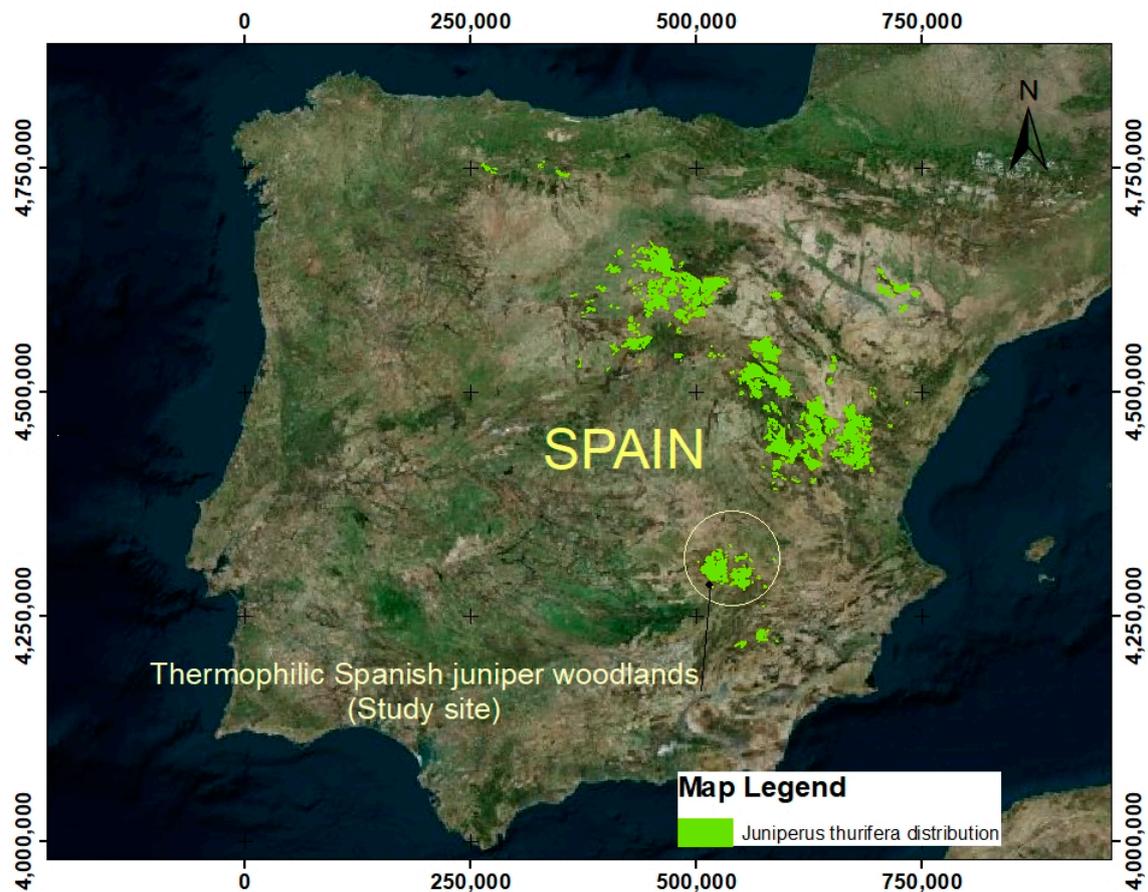


Figure 1. Location of El Campo de Montiel junipers woodlands within the rest of the Spanish juniper stands (Spain). Source: own elaboration with the Forest Map of Spain in its digital version, provided by the Biodiversity Data Bank of the Ministry of Agriculture and Environment of Spain, and the information published in [21]. UTM coordinates (ETRS89).



Figure 2. Study area: young, more productive juniper woodland (at the left), and mature woodland in Leptosols (at the right).

Table 1. Characteristics of the two juniper woodlands [24,26]. Errors: standard error.

Characteristics of Woodland	Young Woodland	Mature Woodland
Mean age (years)	66 ± 4	170 ± 5
Woodland density (trees ha ⁻¹)	308 ± 40	95 ± 12
Juniper cover (%)	65 ± 23	32 ± 14
Net primary productivity (t ha ⁻¹ year ⁻¹)	1.91 ± 0.14	0.44 ± 0.01
Total biomass (t ha ⁻¹)	30.8 ± 2.6	7.6 ± 0.6
Litter fall (t ha ⁻¹ year ⁻¹)	0.98 ± 0.13	0.24 ± 0.05
LAI (m ² m ⁻²)	1.03	0.32
Mean diameter at breast height (cm)	13.3 ± 0.7	16.7 ± 0.5
Stem diameter growth (mm year ⁻¹)	2.96 ± 1.32	1.50 ± 1.12
Sapwood (%) at breast height (1.30 m)	73.3 ± 8.2	55.9 ± 4.5
Soil taxonomy (FAO; [28])	Calcaric cambisol	Lithic leptosol
Mean soil depth	0.42 ± 0.04	0.10 ± 0.02
Soil texture (sand; %)	50 ± 5	58 ± 5
Soil texture (clay; %)	28 ± 1	12 ± 1
Soil pH	8.3 ± 0.1	8.6 ± 0.1
Soil organic C (%)	2.7 ± 0.8	3.7 ± 1.1
Apparent density of soil (g cm ⁻³)	1.37 ± 0.01	1.54 ± 0.02

The two juniper woodlands studied are located in lime-rich substrates (Jurassic dolomites), thus presenting a basic pH (Table 1). The soils in the young woodland have a greater clay content than those in mature woodlands. Conversely, the mature woodland soils contain more sand. Thus, bulk density was slightly greater in the mature woodland. The existence of a greater amount of organic C in the mature woodland is noteworthy, a consequence of the greater cumulative deposition of organic matter over the years. Biomass stocks and productivity were scarce in both woodlands, but the aboveground biomass in the young stand was similar to that of a more productive, paramo community [25]. We found that for mature woodlands, the few references that did exist for the *Juniperus* genus indicate a significantly larger biomass, and in the majority of studies carried out on other conifer species, biomass very often exceeded 50 Mg ha⁻¹ [25]. Juniper trees in young woodland have a slow growth, and trees in mature woodland represent very slow-growing species.

2.2. Measurement of Stem CO₂ Efflux and Stem Temperature in Juniper Trees, and Soil Water Content

We measured the stem CO₂ efflux per unit of stem surface area (in μmol CO₂ m⁻² s⁻¹), assuming that the stem CO₂ efflux is a practical proxy for stem respiration [5]. Measurements were carried out in situ for 18 days, spread over the four seasons (3 days in winter, summer, and autumn and 9 days in spring, the more important growing season). Within the experimental areas, metallic collars (10.5 cm in diameter, and 5 cm in height) were installed (see methodology in Xu et al. [29]) on the stem of 16 adult junipers (8 per juniper woodland; to eliminate the effect of age) at a standardized height (breast height, 1.30 m above soil). Loose bark was removed and 100% silicone sealant was used to attach and seal the collars to the south-facing side of stem surfaces (Figure 3). To check the variation of the respiratory flux along the stem, measurements were previously made at different heights of the trunk, although the height was not a factor that affected the CO₂ efflux (analysis not shown).



Figure 3. Metallic collar to measure stem CO₂ efflux in juniper trees in diameter at breast height.

The mean diameters at breast height of the junipers measured were 29.5 ± 12.4 cm, and 22.47 ± 9.8 cm for mature and young woodland, respectively (means \pm standard deviation). Stem respiration was measured using the LI-6400 portable CO₂ measurement equipment (LI-COR, Inc., Lincoln, NE, USA) to which the LI-6400-09 measurement chamber was attached. In each measurement, 3 repetitions of the CO₂ efflux were taken, the mean of the measurements being the values for the data analysis. Measurements were made by reducing CO₂ concentration inside the chamber and then letting it increase to an upper concentration limit (gas analyzer in closed system configuration). These limits changed depending on the respiration rate of the measured stem and the atmospheric CO₂ concentration. For this, before starting each measurement, ambient CO₂ concentration was measured and used as the target. This air CO₂ concentration ranged between 372–411 p.p.m. along the full experimental period. The air flow ($\mu\text{mol air s}^{-1}$) to pumping down was fixed depending on efflux level (200–700, for low and high efflux levels, respectively). The rate of change of CO₂ inside the chamber was calculated in the three consecutive measurement cycles. Measurements were made at different times of the day to obtain greater variability in the dataset. The total dataset in the analysis included 288 measures.

The stem temperature (T_s ; °C) was measured using temperature sensors installed next to the cylinders and with the sensor in contact with the sapwood. Stem temperature was recorded on a half-hourly basis close to each collar using a temperature probe (PB-5002-1M5, Gemini data loggers Ltd., Chichester, UK) inserted to a depth of 20 mm via a drilled ($\text{Ø} < 5$ mm) hole sealed with silicone; data were monitored with Tinytag Ultra 2 TGU-4020 data loggers (Gemini data loggers Ltd., Chichester, UK). Temperature data were automatically stored in the data loggers and associated with the time of efflux measurements.

Finally, soil water content (SWC, %) was measured with a moisture sensor (VH400-LV, Vegetronix, UT, USA), close to the sample tree. Measurements were recorded with HOBO data loggers (Onset Computers, Bourne, MA, USA). The moisture sensors were calibrated by the gravimetric method. Data loggers were downloaded while taking CO₂ efflux measurements.

2.3. Data Analysis

To detect the effects of the woodland type and seasonality on stem CO₂ efflux, GLM (multifactorial analysis of variance, MANOVA, $p < 0.05$) was performed including two fixed factors, juniper woodland type (W ; two levels: young and mature woodland) and season (S ; 4 levels: winter, spring, summer, and autumn) and their interaction (cross effect $W \times S$), with the response variable being stem CO₂ efflux (E_s ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$):

$$E_s = \mu + W + J(W) + S + (W \times S) + \varepsilon \quad (1)$$

In the model 1, “J” is the juniper sample (16 levels) and J(W) is the nested effect of this juniper sample (16 junipers or “plots”) within each woodland type (W). “Juniper” (J) was nested within “woodland” (W) as different juniper trees were measured in each woodland, and “J” we also considered a random factor as the sample trees were a random sample from the total junipers (randomized design, [30]). Thus, Model 1 represents a linear mixed-effects model with fixed and nested random effects [31]. In addition, μ is the overall mean of E_s ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and ε is the random residual. The rest of the interactions were excluded from the full model for their minimum significance and were included in the error term. The effect “between woodlands” on the response variable “within each season” was also analyzed ($p < 0.05$). Fisher’s LSD test (Least Significant Difference) was used to make comparisons between means if the main factor was significant. It is remarkable that “woodland type”(W) is a confounded effect of both maturity (age) and soil quality, i.e., it represents the site productivity of the juniper woodlands.

To evaluate the effect of stem temperature (T_s ; °C) and the juniper woodland type on stem CO_2 efflux (E_s ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) throughout the seasons, the following model with a qualitative or dummy variable (woodland type: $W = 0$ for young woodland, and $W = 1$ for mature woodland) was fitted through multiple regression (Model 2):

$$E_s = \exp^{(\beta + \beta'W) + (\alpha + \alpha'W) \times T_s + \varepsilon} \quad (2)$$

This model was fitted including all the variations in stem temperature measured in the field ($n = 288$). Model 2 shows an exponential trend that reflects the variation of the respiration of living plant cells and temperature, demonstrated in previous studies [5]. In our experiment, it was necessary to include the dummy variable (W ; woodland type) to provide the joint effect of age and productivity (both effects are confounded), thus representing the two juniper stands. The selection of significant parameters in Model 2 was carried out by means of logarithmic transformation (Model 3; linearization of the exponential function; [32]) and stepwise regression (“forward selection” procedure):

$$\log(E_s) = (\beta + \beta'W) + (\alpha + \alpha'W) \times T_s + \varepsilon \quad (3)$$

This corresponds with the comparison of two regression lines (Model 4 and 5):

For young woodland:

$$\log(E_s) = \beta + \alpha \times T_s + \varepsilon \quad (4)$$

For mature woodland:

$$\log(E_s) = (\beta + \beta') + (\alpha + \alpha') \times T_s + \varepsilon' \quad (5)$$

The coefficients with a value of $p < 0.05$ were considered significant [31]. The significance of the model and the goodness of fit were assessed according to the F ratio ($p < 0.05$), the adjusted R^2 , and the standard error of the estimate (SEE). The Conditional Sums of Squares analysis was additionally used to determine whether the intercepts and the slopes of the two equations (Models 4 and 5) were significantly different. Observations with $\text{DIF} > 2 \times \sqrt{\frac{n}{p}}$ were considered influential points (p is the number of coefficients, and n is the number of data [33]) and eliminated. Statistical analyses were performed using the Statgraphics Centurion XVIII[®] software (Statgraphics Technologies, Inc., Virginia, USA).

Finally, in the significant equations of Model 3 (Model 4 and 5), the temperature coefficient Q_{10} (rate of variation of E_s when the stem temperature (T_s) increased by 10 °C [34]) was calculated. Thus, the significant equations were formulated in their exponential form (Model 6) [35,36]:

$$E_s = R_r \times Q_{10}^{\frac{T_s - T_r}{10}} \quad (6)$$

Where E_s is stem CO_2 efflux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at stem temperature T_s (°C); R_r is the respiration at the reference temperature (T_r); and Q_{10} is the temperature coefficient of

respiration. In our study, the temperature of reference (Tr) was fixed at 0 °C, representing respiration in the non-growing or dormancy period [7,36].

3. Results

3.1. Effects of Juniper Woodland Type on Stem CO₂ Efflux

The “woodland type” factor (W) significantly affected ($F = 16.9$; $p < 0.00$) the stem CO₂ efflux (Es), with this dependent variable being higher in the young juniper woodland (Tables 2 and 3).

Table 2. MANOVA carried out (Model 1) to evaluate differences between the stem CO₂ efflux (Es, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in the two juniper woodlands and throughout the four seasons ($n = 288$). The F ratios and the p -values are represented for the two main effects (woodland, season) and their interaction, as well as the effect of the woodland type within each season. The effects are significant if $p < 0.05$ (95% probability). LSD: least significant difference. W: woodland type; J: juniper tree (sample tree); S: season.

Effects	Seasons									
	Total Annual		Winter		Spring		Summer		Autumn	
	F	p	LSD	p	LSD	p	LSD	p	LSD	p
W	16.9	<0.00	0.74	0.72	0.34	<0.00	0.61	<0.00	0.60	0.29
J (W)	1.18	0.29	-	-	-	-	-	-	-	-
S	28.6	<0.00	-	-	-	-	-	-	-	-
W × S	3.32	0.02	-	-	-	-	-	-	-	-

Table 3. Mean values (\pm standard error) of stem CO₂ efflux (Es) in function of woodland type (W) and seasons (S). Averages of the levels within each effect followed by different letters reflect significant differences in the MANOVA performed (Fisher’s LSD test, 95% probability, $p < 0.05$; $n = 288$).

Main Effects	Levels	Es ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
W (Woodland type)	Young woodland	1.95 ± 0.11^a
	Mature woodland	1.26 ± 0.11^b
S (Season)	Winter	0.84 ± 0.15^a
	Spring	2.33 ± 0.09^b
	Summer	1.92 ± 0.15^c
	Autumn	1.31 ± 0.15^d

In addition, stem CO₂ efflux depending on the juniper woodland was found to be significant in the spring and summer ($p < 0.00$; Table 2), which seems to determine the more important growth period. In the winter and autumn, this significance was not found.

3.2. Seasonal Variation of Stem CO₂ Efflux in the Juniper Woodlands

The “season” factor (S) showed a significant effect ($F = 28.6$; $p < 0.00$) on the response variable Es (Table 2). Overall, the measurements of stem CO₂ efflux were higher in spring (mean value of $2.33 \pm 0.09 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Table 3). On the contrary, the stem CO₂ efflux was significantly reduced in winter ($0.84 \pm 0.15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

The interaction between the treatment variables was also significant ($F = 3.32$; $p = 0.02$; Table 2). Thus, significant differences were observed in stem CO₂ efflux depending on the woodland type (W). The measured CO₂ of juniper trees was higher in spring and summer for the young woodland (Figure 4), whereas young woodland maintained similar stem CO₂ efflux in these two seasons, and the stem respiration decreased from spring to summer in the older juniper woodland. In the cold seasons, winter and autumn, there were no significant differences between woodland type.

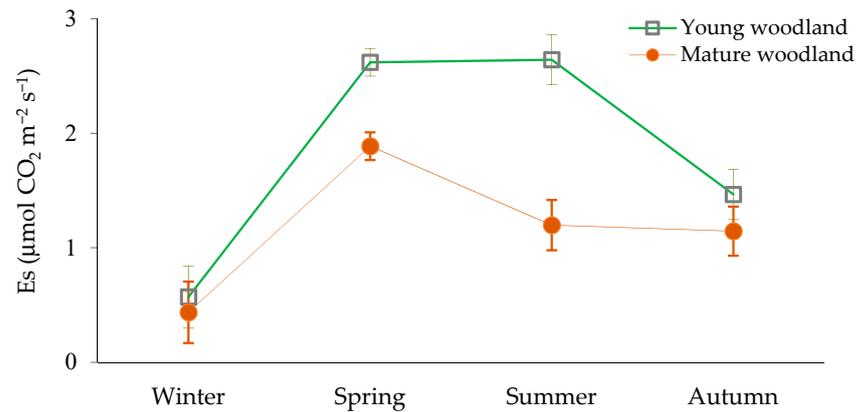


Figure 4. Seasonal variation of stem CO₂ efflux (E_s ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for the two juniper woodlands. Error bars: least significant difference (LSD; 95% probability).

3.3. Climatic Conditions: Stem Temperature (T_s ; °C) and Soil Water Content (SWC; %)

Stem temperatures ranged from -2.7 °C to 27.9 °C (total range of 30.6 °C), and the mean stem temperature was 14.02 ± 8.88 °C (mean \pm standard error). Seasonal stem temperatures (mean \pm standard error) were: winter (3.34 ± 0.79 °C), spring (16.05 ± 0.46 °C), summer (25.12 ± 0.79 °C), and autumn (7.81 ± 0.78 °C). This seasonal behavior of stem temperature indicated a positive correlation between this variable and the stem CO₂ efflux: the higher stem CO₂ efflux were obtained under the higher values of stem respiration, i.e., in spring and summer (Figure 5 and Table 3).

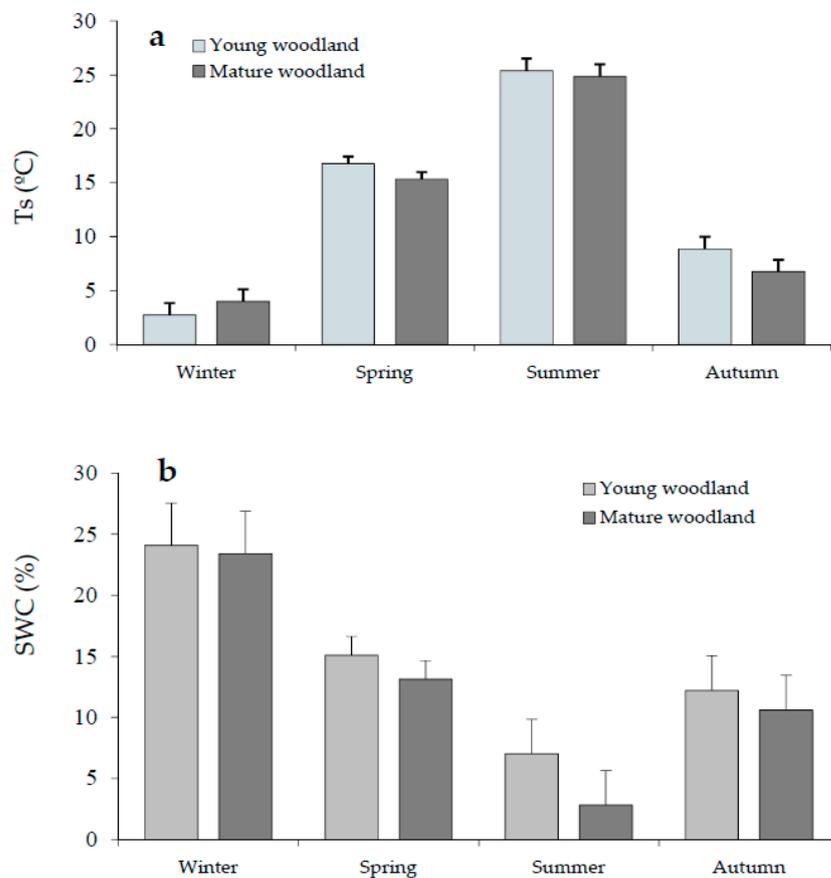


Figure 5. Stem temperature (T_s , in °C; **a**) and soil water content (SWC, in %; **b**) across the seasons and in the function of woodland type ($n = 288$). Error bars: standard error.

Soil water content (SWC; %) ranged from 24.1% (winter in young woodland) to 2.8% (summer in mature woodland; Figure 5). Seasonal soil moisture contents (mean \pm standard error) were: winter ($23.7 \pm 2.5\%$), spring ($14.1 \pm 1.1\%$), summer ($4.9 \pm 2.1\%$), and autumn ($11.4 \pm 2.0\%$). Contrary to what happened with the trunk temperature, the seasonal variation of soil moisture was not correlated to stem CO₂ efflux: when soil moisture was maximum, the efflux was minimal (winter), and the low value of soil moisture in summer did not correspond to the lower stem CO₂ efflux rates.

No differences were found in stem temperature (°C) or soil water content (%) between the juniper sites in the same season ($p < 0.05$; Figure 5). Thus, climatic conditions were similar in both juniper woodlands at the time of efflux measurements.

3.4. Effects of Stem Temperature on Stem CO₂ Efflux

When adjusting the regression model of stem CO₂ Efflux (Es) as a function of stem temperature (Ts; °C) and the juniper woodland type (Model 2), it was found that the dummy variable (W) was significant in the model, thus generating two independent equations for each juniper site (Table 4). This model was significant ($F = 192, p < 0.00$), and the goodness of fit statistics reflected that the variability of Es was explained by Ts in a percentage of 71.4% (adjusted R²), obtaining an SEE = 0.36 (relatively low).

Table 4. Adjusted coefficients, standard errors, and statistics of the coefficients (t and p values) in Table 2. efflux (Es) as a function of stem temperature (Ts) and woodland type (W). In Model 2, the dependent variable was log-transformed-log(Es)- to obtain the intercept and slopes in function of woodland type (W). The summary statistics for the fitted model were adjusted R-squared (R²) = 71.4%; standard error of estimation (SEE) = 0.36; mean absolute error = 0.30.

Parameters	Coefficients	Standard Error	t	p-Value
Intercept	−0.350	0.0623	−5.62	0.000
Ts/10	0.684	0.0375	18.18	0.000
W = Mature	−0.129	0.0875	−1.48	0.139
(Ts/10) \times (W = Mature)	−0.113	0.0543	−2.07	0.038

Table 5 shows the Conditional Sums of Squares analysis (ANOVA) to confirm whether the intercepts and the slopes of the two lines of Model 2 were significantly different. As the p-value was less than 0.05, the intercepts and slopes of the lines varied significantly amongst the two levels of the categorical factor “woodland type” (young and juniper woodland; 5% significance level).

Table 5. ANOVA for independent variables in the order fitted. The F-test for intercepts and slopes checks the “null hypothesis”: intercepts and slopes of the lines are all equal (alt. hypothesis: intercepts and slopes of the lines are not all equal; 5% significance level). Dependent variable: log(Es).

Source	Sum of Squares	df	Mean Square	F	p-Value
Ts/10	71.66	1	71.66	560.1	0.000
Intercepts	4.95	1	4.95	38.7	0.000
Slopes	0.55	1	0.55	4.3	0.038
Model	77.17	3			

This corresponds to two separate regressions, and Model 3 can be written separately for each juniper woodland as follows:

$$\text{Young woodland (Model 4): } \log(\text{Es}) = -0.350 + 0.0684 \times \text{Ts} + \varepsilon$$

$$\text{Mature woodland (Model 5): } \log(\text{Es}) = -0.480 + 0.057 \times \text{Ts} + \varepsilon'$$

The generation of two significant equations from Model 2 confirmed different rates of stem CO₂ efflux for both types of juniper woodland as a function of the temperature. Thus, the exponential equation form (Model 6) was used to establish the relationship between the stem CO₂ efflux and stem temperature:

$$\text{Young woodland: } E_s = 0.704 \times 1.98^{\frac{T_s}{10}}$$

$$\text{Mature woodland: } E_s = 0.619 \times 1.77^{\frac{T_s}{10}}$$

The exponential equations reflected that for a certain increase in stem temperature (T_s), the variation in stem CO_2 efflux (E_s) was significantly greater in the young juniper woodland, which was the most productive (Figure 6). Consequently, the temperature coefficient Q_{10} (rate of respiration increase when the temperature increases by 10°C) was significantly higher for the young woodland (1.98) than for the mature one (1.77). The respiration at 0°C was 0.70 and $0.62 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for young and mature woodland, respectively (significantly higher in the young woodland). We considered that at the temperature reference of 0°C (R_0), diameter growth was negligible, and thus the respiration in this non-growing instance should be an estimator of the maintenance component. Regardless of the temperature of reference, Q_{10} was invariant when the annual data were fitted by utilizing the exponential form.

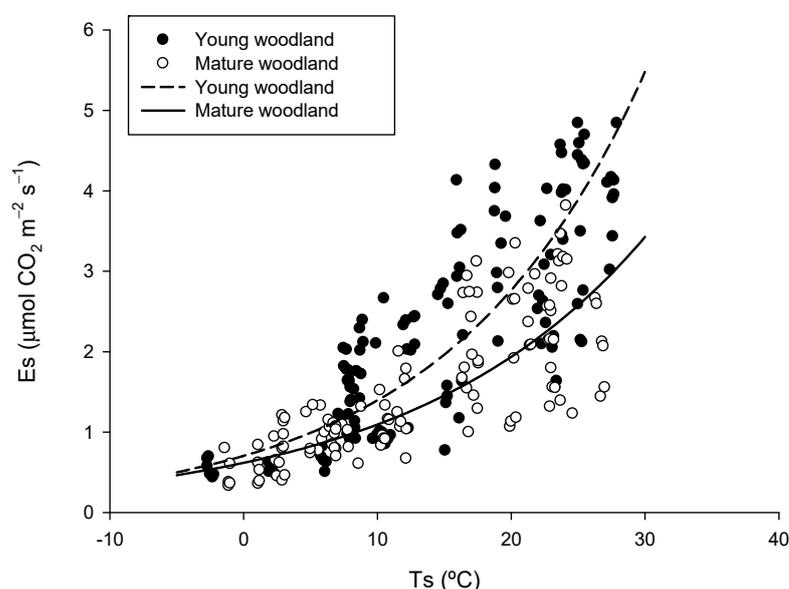


Figure 6. Exponential equations ($E_s = R_0 \times Q_{10}^{(T_s-0/10)}$) for stem CO_2 efflux (E_s : $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) as a function of stem temperature (T_s ; $^\circ\text{C}$), by juniper woodland type.

4. Discussion

4.1. Effects of Juniper Woodland Type on Stem CO_2 Efflux

In the more productive site (young woodland), the annual rate of stem CO_2 efflux was higher, and there would therefore be a greater respiratory activity. Parameters that define the productivity of the site, such as LAI, and % of sapwood in the stems, are correlated with greater stem respiration [1,14], a consequence of photosynthesis partially regulating stem growth and respiration [7]. The respiratory rate determines the amount of carbohydrates that can be invested in the maintenance (maintenance respiration) and development (growth respiration) of juniper trees, and therefore has an important relation on production of biomass [8]. Thus, measured CO_2 efflux in juniper trees is the result of growth and maintenance stem respiration. There are an important link between total respiration and growth, even though growth respiration is only a percentage of total respiration (50% for wood [37]); maintenance respiration are also linked with the metabolic processes that will promote growth [38].

Additional factors could affect the correlation between stem respiration and measurements of stem CO_2 efflux. Photosynthesis in bark or chlorenchyma can refix CO_2 and hence lower net respiration rates for stems [3,4]. As the periderm blocks light to the photosynthetic tissue, photosynthetic rates are greatest in young stems and branches, and the effect of bark photosynthesis on net CO_2 efflux from stems declines with stem size and

age [12]; thus bark photosynthesis would be negligible in juniper trees with more than 50 years old. By carefully peeling off layers of the dead outer bark of juniper stems, and analyzing a cross section of trunk, the total absence of a green color indicated the absence of chlorophyll-containing tissues [39].

Although the stem CO₂ efflux rates measured at both juniper woodlands fit the ranges previously reported (0.5–5 μmol CO₂ m⁻² s⁻¹) for forest species [6,40], the annual mean values of CO₂ efflux seem to be low (1.95 and 1.26 μmol CO₂ m⁻² s⁻¹, for young and mature junipers, respectively), if we compare them with other conifer species. For example, [6] offers mean values (μmol CO₂ m⁻² s⁻¹) of 0.5–3.7 for *Pinus canariensis*, [34] 4–7 for *Pinus ponderosa*, and [41] 0.8–9 for *Larix*. This is an indicator that Spanish juniper trees behaves as a slow-growing species. The semi-arid climate with a warm and dry season alternating with a very cold, wet season is decisive for this behavior.

4.2. Seasonal Variation of Stem CO₂ Efflux in the Two Juniper Woodlands

Our results also reflect the existence of great seasonality in stem CO₂ efflux in both juniper woodlands, and it was higher during the growing season (spring) and progressively decreased from the warm to cold periods. Climatic seasonality in Mediterranean ecosystems is decisive for soil and vegetation activity to also be seasonal [42] as growth respiration is mainly affected by temperature [8]. Thus, in spring, it is expected that the highest stem respiration will be obtained, as it is the season of greatest stem diameter increments [6] and growth activity [7]. On the contrary, our study reflected that in autumn, and especially in winter, the respiratory activity of junipers was slowed down. In general, respiration measurements taken in the middle of April and at the end of September can be considered to be in the growth period [3].

It is noteworthy that in summer, the levels of stem respiration were greatly reduced in mature woodland. These results are in accordance with Rodríguez-Calcerrada et al. [5], which indicated that stem CO₂ efflux decreases with drought in Mediterranean forests. Given the scarcity of water resources in this site with the worst soil, it is likely that older junipers adapt to episodes of water stress by reducing their respiration. In general, water stress consists of a decrease in growth, and therefore the growth component of respiration should decrease [5].

Nonetheless, our study has also shown that in summer, stem CO₂ efflux was important in the young woodland. In general, as occurred in our results, previous research on the effect of water stress on respiration frequently show contradictions: while studies have shown decreased respiration [5], others have shown unaffected rates or an increased rates [43]. For example, at more severe levels of water stress, maintenance respiration may increase as a consequence of osmoregulation [44]. However, species that show slow growth rates (such as older juniper trees) present minor variations in response to stress than faster-growing species [43], such as young junipers.

Another hypothesis to explain the maintenance of stem respiration in summer for the young woodland is related to the quality of the soil. We hypothesized that water availability seems to be essential to maintaining growth respiration. In the woodland with better soil, vegetal activity could be continued in summer due to a greater reserve of water and nutrients. Several authors have also shown that the growth respiration of stems continued for 4 or 6 weeks after diameter growth ceased [45]. In the study site, the soil bedrock is a fissured and karstified dolomite, which permits the formation of small water pockets, and juniper vegetation probably obtains water from the deeper soil profiles in the summer [26]. Results in similar Mediterranean environments confirmed that deep-rooted trees improve water availability in dry seasons [46]. In the dry season, high temperatures can accelerate the process of autotrophic respiration [2]. At the end of this season, the more-or-less constant decline in respiration begins and continues until winter [8].

4.3. Effects of Stem Temperature on Stem CO₂ Efflux

In the present study, the stem temperature accounted for 71% of the variations in stem respiration, in line with previous results found in semi-arid climate; for example in *Pinus canariensis* [6] and in *Pinus halepensis* [40]. Stem temperature is closely related to and is an efficient predictor of stem respiration, better than other environmental variables such as soil water content [7], in accordance with our results.

The two values of Q_{10} obtained for each juniper woodland were within the range of 1.0–4 reported for other conifer species [6,32,47]. For most species and organs, the Q_{10} factor varies between 1.9 and 2.8 when respiration is measured between 5 and 30 °C [9], similar to the range in our study. However, in both juniper woodlands, and especially for the older forests, the Q_{10} temperature coefficients are low (<2), which is the value usually taken as the reference mean [9,48]. This is in accordance with the low values of stem CO₂ efflux measured. The respiration rate obtained in our research was more typical of cold ecosystems, i.e., forests with low productivity [9,47]. *Juniperus* has its origin in the Tertiary where it grew under colder climates [19], and slow-growing species show slower respiration rates even with high water availability [49]. The environmental limitations resulting from climatic extremes, such as very cold winter and summer drought, typical of semi-arid climates, condition the respiration–temperature relationship [6]. The potential phytoclimatic of this species is related to severe continental climates [22], such as those predicted in the climate change scenario [23].

Q_{10} quotient may vary depending on the season, growth rate, or acclimatization situations [50]. Based on our results, the coefficient Q_{10} in juniper woodlands depends on the site. Thus, our results have concluded that respiration rates vary within the same species in function of contrasting ecological requirements (soil quality), as has been previously cited [16]. Finally, our data showed that respiration at 0 °C was significantly higher in the young woodland (0.70 vs. 0.62 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). In accordance with Zha et al. [7], we can assume that respiration in this non-growing period (stem temperature of 0 °C) can be correlated with the maintenance respiration. This reflected that trees with higher growth rates exhibit higher maintenance respiration than slower growing ones, suggesting a balance between C supply and demand mediated by growth [16]. The other fraction of measured stem CO₂ efflux reflects the growth respiration, the energetic cost of constructing the new tissues [38], which is higher in the young woodland.

5. Conclusions

Our results confirm the hypothesis that in the juniper stands there is a high correlation between stem respiration and forest productivity. Thus, stem CO₂ efflux measured at diameter at breast height is an estimator of forest productivity in Spanish juniper woodlands.

Therefore, our study represents an advance in knowledge about the variation in stem respiration in classic juniper forests (mature and young woodlands) growing at their distribution limit in a semi-arid climate. Stem temperature and seasonality are decisive factor to understand the variations in stem respiration of this juniper species.

The uniqueness of this juniper species has again become apparent in our study. Their low respiratory rates (especially in the older stands) and temperature coefficients are typical of species linked to cold climates, and scarcely productive forests. The slow-growing behavior of this species has been explained in terms of stem respiration. This is the result of its adaptability to a severe climate, such as the semi-arid climate of Southern Spain (hot, dry summers, and very cold winters with low rainfall). Thus, we think that this species could be utilized for forest restoration in sites with low potential productivity, such as in arid and semi-arid areas, and in the context of climate change.

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