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Article

Warm and Fertile Sub-Humid Conditions Enhance Litterfall to Sustain High Soil Respiration Fluxes in a Mediterranean Cork Oak Forest

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Abstract: Soil respiration is a major component of the global carbon budget and Mediterranean ecosystems have usually been studied in locations with shallow soils, mild temperatures, and a prolonged dry season. This study investigates seasonal soil respiration rates and underlying mechanisms under wetter, warmer, and more fertile conditions in a Mediterranean cork oak forest of Northern Tunisia (Africa), acknowledged as one of the most productive forests in the Mediterranean basin. We applied a soil respiration model based on soil temperature and relative water content and investigated how ecosystem functioning under these favorable conditions affected soil carbon storage through carbon inputs to the soil litter. Annual soil respiration rates varied between 1774 gC m^{-2} $year^{-1}$ and 2227 gC m^{-2} $year^{-1}$, which is on the highest range of observations under Mediterranean climate conditions. We attributed this high soil carbon flux as a response to favorable temperatures and soil water content, but this could be sustained only by a small carbon allocation to roots (root/shoot ratio = 0.31–0.41) leading to a large allocation to leaves with a multiannual leaf production, enhanced annual twig elongation (11.5–28.5 cm) with a reduced leaf life span (<1 year) maintaining a low LAI (1.68–1.88) and generating a high litterfall (386–636 gC m^{-2} $year^{-1}$). Thus, the favorable climatic and edaphic conditions experienced by these Mediterranean cork oak forests drove high soil respiration fluxes which balanced the high carbon assimilation leading to a relatively small overall contribution (10.96–14.79 kgC m^{-2}) to soil carbon storage.

Keywords: modelling; soil respiration; cork oak forest; Mediterranean climate

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1. Introduction

Soil respiration (R_s) is the dominant flux of total ecosystem respiration [1–4] globally releasing 10 times as much CO_2 to the atmosphere as the combustion of fossil fuels [5]. Major efforts have then been devoted to quantify and identify underlying processes of soil respiration as a significant contributor to the atmospheric CO_2 budget [6].

Given the projected decrease in precipitation and increase in temperatures for the Mediterranean basin [7–9], soil respiration has a potential role either to amplify global warming due to its sensitivity to environmental conditions [10–12], or to mitigate climate change due to enhanced soil carbon sequestration and reduced CO_2 efflux [13,14]. One main assumption is the stimulation of organic matter decomposition increasing the loss of organic carbon stored in the soils towards the atmosphere under global warming [15–19] or changes in the precipitation pattern [1,4]. Other biotic and abiotic factors, ranging from soil chemistry and physics to stand structure, have been reported to influence soil respiration, as soil organic matter quantity and quality [20,21], soil acidity, and site fertility [1,22,23] which may modify the relationships between soil respiration and environmental parameters according to the ecosystem [24,25].

According to the hypothesis formulated by Raich and Nadelhoffer [26], soil respiration is not only driven by the direct climate control on decomposition rates, but is also indirectly controlled by climate through the amount of carbon assimilated (Net Primary Production NPP) and the subsequent litterfall (FA). Total belowground carbon allocation (TBCA) can also balance this relationship by affecting both root biomass and indirectly the carbon allocated to leaves, and must be considered as a significant process to account for [27]. Chen *et al.* [28] then recently argued that the main response of soil respiration to increasing temperature was due to an increased soil carbon (FA and/or TBCA) input and not to an acceleration of the soil organic matter decomposition rate. In Mediterranean ecosystems, summer drought is the main driver of carbon assimilation and partitioning [29], and induces strong ecophysiological adjustments such as reduced stem growth [30], reduced leaf area and the subsequent effects on litterfall [31], and an increased root/shoot ratio [32]. Several studies have dealt with soil respiration in Mediterranean ecosystems submitted to prolonged summer droughts [33–36] and growing on the most frequently observed shallow and rocky soils. Few, if any, forest soil respiration studies have been conducted on fertile warm and humid conditions within the Mediterranean, as these favorable environments are mostly used for agriculture, so the range of study cases hardly cover the full panel of climatic/edaphic conditions. These fertile sites, however, may provide some key understandings of ecosystem carbon cycle under optimal conditions hardly ever met, and may allow reassessing hypotheses formulated under more constrained environments [37]. Northern Tunisia, located on the southern bound of the Mediterranean basin in North Africa has long been called the “granary of Rome” during the Roman empire due to fertile soils and a mild and wet climate on the Mediterranean coast. Site index for cork oak stands [38] define northern Tunisia among the most favorable conditions for the productivity of this ecosystem. This creates a peculiar study case on carbon fluxes in Mediterranean forests growing in a favorable environment, as they could be observed before the intensive agricultural era when forest systems were covering most of the Mediterranean bioclimate area. The present study focuses on exploring forest soil CO_2 efflux in a humid cork oak forest characterized by a high soil fertility and biological activity [39–41], concomitantly with ecophysiological measurements regarding forest function potentially affecting soil carbon input available for decomposition. We hypothesized that under these favorable climatic and edaphic conditions (1) the biological drivers (FA and TBCA) are modified and provide more carbon input for soil respiration through an enhanced litterfall rather than an increased root fraction due to ecophysiological adjustments, so that (2) soil respiration is on the highest range of observations for similar ecosystems across the Mediterranean basin, resulting in (3) a mild carbon accumulation in soils as a result of either an enhanced basal respiration or a direct climate positive effect which was tested for by using a standard soil respiration model. The successive steps of this study were (1) to measure the seasonal pattern of soil respiration and its biological/climatic drivers, (2) to test for the consistency, under these unusual conditions, of the effects of soil temperature and soil water availability on soil respiration as implemented in standard models, and (3) to identify the relative contribution of candidate drivers leading to the annual carbon flux in this extremely favorable Mediterranean study site within the range of previously observed soil respiration rate registered in global databases.

2. Materials and Methods

2.1. Study Site

The study area is situated in the Bellif national forest, located in the North Western part of Tunisia (North Africa, Southern bound of the Mediterranean basin) in the Nefza forest subdivision (Figure 1), claimed to be the most productive cork oak forest in Tunisia [40,41], due to fertile soils, mild temperatures, and heavy rainfall on its coastal foothills [42]. The climate is Mediterranean sub-humid, characterized by hot and dry summers and mild and wet winters. Precipitation mainly occurs from September to March and a drought period extends from May to August (Figure 2). The annual precipitation is 1113 mm and the average annual temperature is 19.3 °C. Absolute maximum and minimum air temperatures were +47.2 °C and +0.1 °C, respectively for the year 2008 during which we performed our analysis.

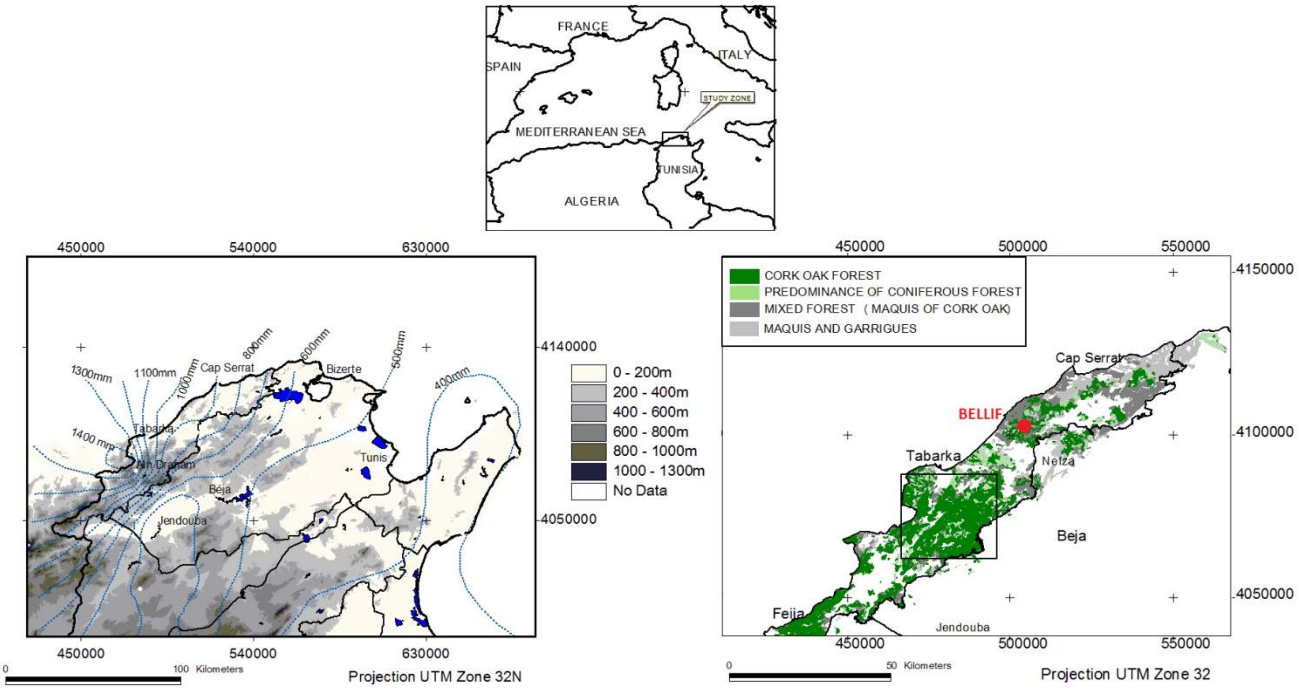

Figure 1. Location of the study area (Bellif national forest) in the Mediterranean basin. Altitude and precipitation isohyets (left) and forest cover types (right) are also shown.

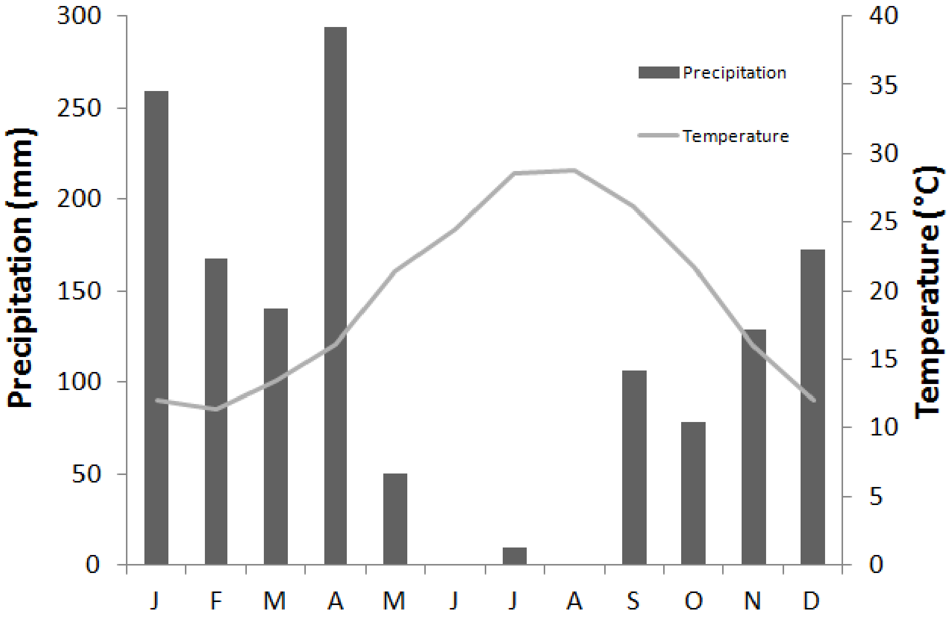

Figure 2. Climate diagram for the 2008–2009 period in the Bellif study site.

Two stands (25 m × 25 m each) of different age classes were chosen in a monospecific and self-regenerated forest of *Quercus suber* managed for cork production. *Quercus suber* naturally produces cork around its bark for fire protection, regularly removed (every 7 to 12 years according to cork extraction practices [43]) by the local population for industrial use in isolation material or wine bottle stoppers. This species covers 2.5 Mha across the western Mediterranean basin [44], and 90,423 ha on the northern coast of Tunisia [45]. In the first stand (young stand (YS)), cork oak trees are even-aged due to the windstorm of 1974. The second stand (mature stand (MS)) is dominated by uneven aged trees ranging from 71 to 102 years. The understory vegetation (1 m high) is composed of sparse shrubs (10% to 20%) in YS and (20% to 40%) in MS with *Pistacia lentiscus*, *Erica arborea*, and *Myrtus communis* being the most abundant shrub species in the two sites.

The two stands belong to the same soil type, which can be characterized as a deep Ferric luvisol [46]. The single parent material is an oligocene sandstone interspersed with clay layers, yielding brown soils with strong biological activity [39]. The location of the stands, their edaphic and ecological characteristics are given in Table 1.

Table 1. Main characteristics of the young stand (YS) and the mature stand (MS) at the Bellif forest study site.

Site Characteristics	YS	MS
Latitude	37°02′41.70″ N	37°02′12.44″ N
Longitude	09°06′08.04″ E	09°03′44.25″ E
Altitude (m)	125	121
Vegetation type	*Quercus suber* (even-aged)	*Quercus suber* (uneven-aged)
Shrub stratum	*Pistacia lentiscus, Erica arborea, Myrtus communis*	*Pistacia lentiscus, Erica arborea, Myrtus communis*
Tree cover	53%	69%
Field capacity (0–150cm)	340 mm	450 mm
Soil type	Ferric Luvisol	Ferric Luvisol

2.2. Soil and Vegetation Ecophysiological Measurements

For each stand, the number, height, and diameter at breast height (DBH) were recorded. The leaf area index (LAI) was measured every meter along two diagonal transects per stand in May 2009 using Licor-2000 (Licor Inc., Lincoln, NE, USA).

Measurements of soil respiration were performed on a monthly basis from spring to fall in 2008 (four measurements) and 2009 (three measurements), corresponding to the period out of which soil temperatures are too low for sustaining microbial activities. To avoid strong diurnal fluctuations, measurements were made between 9:00 a.m. and 1:00 p.m. at both stands on the same days. To get a more accurate estimation, eight replicates (permanent plots resampled for each date) of soil respiration (R_s) were measured in each stand during each sampling campaign. Plots to be measured were randomly selected at each date to avoid biased estimates due to the timing of the measurement. Soil respiration was measured using a closed dynamic system (IRGA: CIRAS-1, Hitching, UK) and an attached closed system chamber (SRC-1, PP-systems, Hitchin, UK). The chamber covered an area of 78 cm^2 and had a volume of 1170 cm^3.

Soil temperature (T) at 15 cm depth was measured with a digital thermometer simultaneously adjacent to each R_s measurement. Soil water content at 30 cm depth was determined gravimetrically. Soil samples were transported to the laboratory in sealed bags to avoid evaporation. These wet samples were weighed, oven-dried for 24 h at 105 °C, and re-weighed after drying. The soil water content was calculated as the percentage difference between wet and dry weights. Four measurements were performed in each plot and averaged.

Surface litter was collected at the same time from regularly distributed 25 cm × 25 cm permanent quadrats at 5-m intervals arranged in two series resulting in 10 samples per stand. Tree water constraint was assessed by their predawn water potentials (pressure chamber). Shoot elongations, leaf mass per area (LMA), and the number of leaves on each yearly apical twig module (as a proxy for leaf life span) were determined.

2.3. Soil Sampling and Analyses

At the end of the measurement period (in 2010), a trench was dug on each site down to 1.50 m depth. Soil samples were collected after the profile was described and horizon boundaries were identified. From each horizon, five pseudo-replicate volume-specific samples were collected using 100 cm^3 stainless steel rings. The physico-chemical analyses were carried out in the laboratory. The bulk density of each soil layer was determined on the basis of the mass difference between wet and dry sediments. The soil samples were dried, crushed, and passed through a sieve (2 mm). The field capacity and the permanent wilting point [47] were determined using pressure plates and particle-size distribution was determined by the International Pipette Method [48]. The organic carbon content was determined by using a dichromate oxidation procedure described by Anne [49]. Total nitrogen was measured by the Kjeldahl method [50]. In each stand, additional information on above- and belowground biomass was measured. After the experiment, trees were cut and weighed (stems, branches and leaves), while roots were sampled with an excavator down to 2.5 m depth and weighed for a full measurement of above- and belowground biomass production.

2.4. Data Analyses and Modelling

2.4.1. SOC Stocks Estimation

SOC stocks for a given depth were calculated by summing SOC stocks by layer determined as a product of D_b, SOC concentration, and layer thickness [51]. For an individual profile with *n* layers, we estimated the organic carbon stock by the following equation:

$$\mathrm{SOCs} = \Sigma \mathrm{D_{bi}} \times \mathrm{C}_i \times \mathrm{D}_i \times (1 - \mathrm{CE}) \quad (1)$$

where SOCs is the soil organic carbon concentration (%) in layer *i* and D_i is the thickness of this layer (cm), CE is the percentage of coarse elements (relative to the mass of the soil) [52,53].

2.4.2. Soil Respiration Modelling

Soil respiration on a daily time step was simulated from soil temperature (*T*) and topsoil relative water content (RWC). Soil respiration (R_s) was modelled using equation (2) designed for water-limited Mediterranean ecosystems where the effect of temperature is expressed as a linear function of soil moisture. The model is described in Joffre *et al.* [54].

$$R_s = R_{s,ref} \times \mathrm{RWC} \times e^{((\mathrm{b\ RWC} + \mathrm{c})(T - T_{ref})/10)} \quad (2)$$

With T = soil temperature at 15 cm depth, $T_{ref} = 0$ °C and $R_{s,ref}$ being the respiration under standard conditions, *b* and *c* being the two parameters fitting the strength of the soil respiration response to climate variables T and RWC. RWC was expressed as a percentage of soil water content at field capacity.

$$RWC = 100 \times SWC/SWC_{fc} \quad (3)$$

with SWC (mm) as the current soil water content and SWC_{fc} (mm) the soil water content at field capacity. We used this model to extrapolate measured soil respiration values to the entire period of our experiment and get the annual carbon flux. SWC was then simulated on a daily time step for the 0–30 cm top soil layer from meteorological variables and soil texture following Mouillot *et al.* [55] (and further used in the region [42]) and validated against soil moisture measurements. T was modelled from registered air temperature at the Nefza meteorological station and following the linear regression $T = \alpha \times T_{air} + \beta$. We estimated α and β to be respectively 0.91 and 2.58, $R^2 = 0.98$ (data source: minimum and maximum daily air temperature, daily precipitation for years 2008 and 2009 from the Nefza weather station, Institut National de la Météorologie, Nefza, Tunisia).

The fit of the R_s model (Equation (2)) was evaluated by calculating the coefficient of correlation R^2 and the root mean squared error (RMSE) for a set of parameters $R_{s,ref}$, b and c, and we selected the best two R^2 RMSE combinations [54] using R cran ©. The Statistica 7.1 software (StatSoft, Inc., Tulsa, OK, USA) was employed to perform all statistical analyses; the level of significance a = 0.05 was accepted in all cases. The normality of variables was checked using Lilliefors' and Shapiro–Wilk's tests on datasets. The effects of treatment (stand age) on ecophysiological variables were examined using a one-way ANOVA, and a repeated measures ANOVA was used to examine stand effects on seasonal variations of soil respiration rate, soil temperature, and soil moisture. Regression analyses were applied to explore the relationship between modelled and measured values. All the results further indicate mean values and their standard error (± SE).

3. Results

3.1. Site Characteristics and Ecosystem Functioning

Within similar climate conditions, the two sites slightly differed in stand structure (LAI, DBH and tree height). LAI was estimated to be 1.88 (±0.02) in YS and significantly lower in MS (1.68 ± 0.03) ($p < 0.05$) (Table 2). Stand density was 560 and 512 stems ha^{-1} with mean tree diameter at breast height (DBH) of 24.3 (±4.77) cm and 31.1 (±1.71) cm and mean tree height of 11.2 (±0.13) m and 12.8 (±0.38) m in YS and MS respectively, overall leading to respective aboveground biomass of 16.96 (±1.52) and 31.24 (±2.19) kg DM m^{-2} and belowground biomass of 7.09 (±0.40) and 9.88 (±0.49) kg DM m^{-2}, all being significantly higher in MS than YS ($p < 0.05$). Annual litterfall (leaves, twigs, and acorns/flowers) was significantly higher in MS (636.42 (±55.59) gC m^{-2} $year^{-1}$) than YS (386.30 (±30.21) gC m^{-2} $year^{-1}$) ($p < 0.05$) (Table 2) with a seasonal pattern showing 2/3 of the annual litterfall happening between March and June during the budburst of new leaves, and 1/3 in fall when a second generation of leaves has been observed (Figure 3).

Table 2. Stand characteristics for aboveground vegetation and soil chemical and physical properties of the topsoil layer (30 cm) in the young (YS) and the mature (MS) forests of *Quercus suber* in the Bellif study site.

Stand Characteristics	**Young Stand (YS) (Mean +/− SE)**	**Mature Stand (MS) (Mean +/− SE)**
LAI	1.88 (±0.02) [b]	1.68 (±0.03) [a]
LMA gC m^{-2}	146.19 (±7.99) [a]	121.28 (±16.27) [a]
Height (m)	11.2 (±0.13) [a]	12.8 (±0.38) [b]
DBH (cm)	24.3 (±4.77) [a]	31.1 (±1.71) [b]
Stem number (stems ha^{-1})	560	512
Aboveground biomass (kg DM m^{-2})	16.96 (±1.52) [a]	31.24 (±2.19) [b]
Belowground biomass (kg DM m^{-2})	7.09 (±0.40) [a]	9.88 (±0.49) [b]
Root/Shoot ratio	0.41	0.31
Annual litterfall (gC m^{-2})	386.30 (±30.21) [a]	636.42 (±55.59) [b]
Age (years)	35	71–102
Cork removal	2000–1988	2005–1992–1980–1968–1956
Soil C content (%)	3.26 (0.02) [a]	4.15 (0.05) [b]
Soil N content (%)	0.28 (0.002) [a]	0.31 (0.007) [b]
C/N	11.46 (0.10) [a]	13.42 (0.43) [b]
SOC (kgC m^{-2})	10.96 (1.64) [a]	14.79 (2.31) [b]
Soil bulk density (g cm^{-3})	1.23 (0.007) [a]	1.30 (0.004) [b]
Clay (%)	25.36 (0.49) [a]	24.11 (0.67) [a]
Silt (%)	46.54 (0.27) [a]	33.22 (0.37) [b]
Sand (%)	28.10 (0.33) [a]	42.66 (0.84) [b]
Soil texture	loam	loam
Bed rock	sandstone [39]	sandstone [39]

For each parameter, letters ([a] and [b]) indicate statistically significant differences ($p < 0.05$) between the two stands (one-way ANOVA).

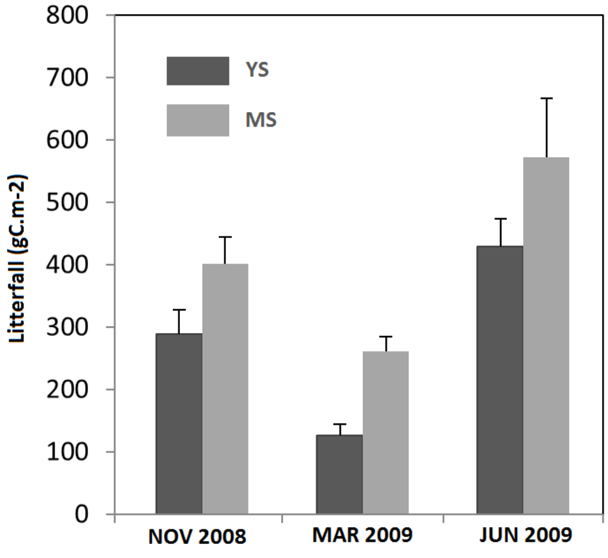

Figure 3. Seasonal litterfall (gC m^{-2}) measured on the young stand (YS) and the mature stand (MS) in 2008 and 2009. Error bars are standard errors of the mean.

Annual apical twig elongation varied between 11.5 cm and 28.5 cm for both stands, with 104 (±38) leaves per twig module, and an average 7 (±2) leaves of the previous year per module. The number of leaves on twig modules remaining from the previous year were small (<10%) so we estimated the leaf life span to be mostly lower than one year. LMA was estimated to be 146.19 (±7.99) gC m^{-2} (YS) and 121.28 (±16.27) gC m^{-2} (MS) without significant differences ($p > 0.05$) for mature leaves at the end of summer and before the secondary growth. Winter predawn water potentials were close to −1 MPa and similar for both sites (−1.11 (±0.07) MPa in YS and −1.06 (±0.06) MPa in MS; $p > 0.05$) and lower during the summer dry period to reach significantly drier conditions in YS (−5.75 (±0.42) MPa) than MS (−2.83 (±0.10) MPa) ($p < 0.05$).

Soil textures were similar in both sites (Table 2) but the total N and C contents in the top 30 cm of soil in MS (N = 0.31 (±0.007)%; C = 4.15 (±0.05)%) were significantly higher than in YS (N = 0.28 (±0.002)% ; C = 3.26 (±0.02)%) ($p < 0.05$). SOC was 14.79 (±2.31) kgC m^{-2} in MS and 10.96 (±1.64) kgC m^{-2} in YS ($p < 0.05$).

3.2. Seasonal Variation of Soil Temperature and Soil Moisture

The dry season in the study site lasted for approximately three months (from the beginning of June until the end of August) in 2008 until intensive autumn rainfalls in September recharged the whole topsoil profile to field capacity (Figure 4). Soil temperature increased rapidly between early April (20 °C) and late June (29 °C), remained relatively constant during July and early August, and declined slowly between September and November (Figure 5). Maximum soil temperatures in July and August were concomitant with minimum soil water contents during the summer (Figures 4 and 5). In both stands, seasonal trends of SWC and soil temperatures in the upper soil layer were well described by the models with $R^2 = 0.93$ and 0.97 (YS) and $R^2 = 0.95$ and 0.98 (MS) respectively between observed and simulated values (Figures 4 and 5). No significant differences in mean annual soil temperatures measured at 15 cm depth, were found among stands ($p > 0.05$). SWC also showed non-significant differences among the two stands and followed the same temporal pattern along the year ($p > 0.05$).

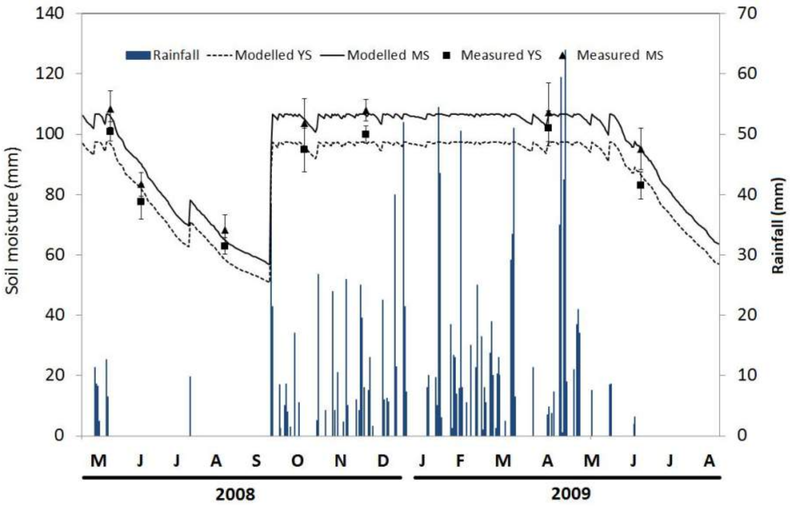

Figure 4. Seasonal variations of observed precipitations (black bars) as well as modelled (YS: dotted line, MS: solid line) and observed (YS: filled square, MS: filled triangle) soil SWC of the top soil layer (0–30 cm). Error bars are standard errors of the mean.

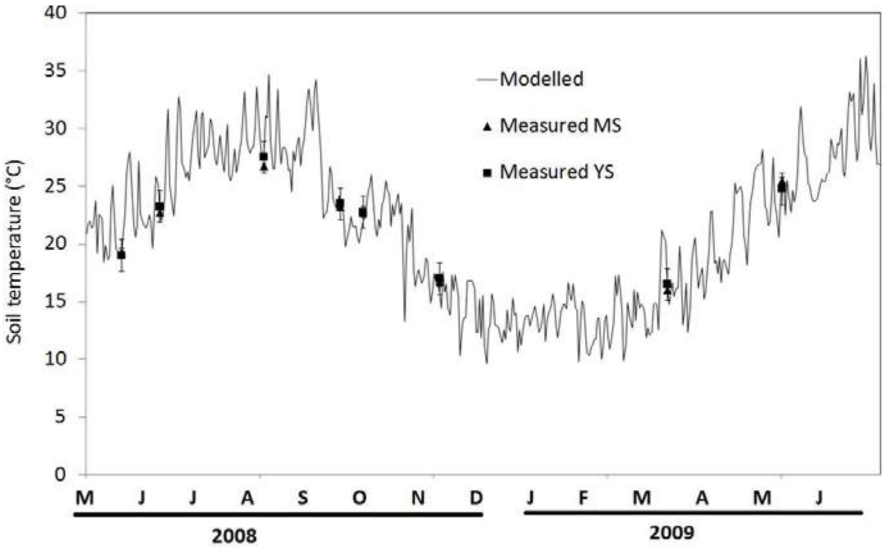

Figure 5. Seasonal variations of modelled (solid line) and observed (YS: filled square, MS: filled triangle) soil temperature of the top soil layer (0–30 cm). Error bars are standard errors of the mean.

3.3. Carbon Flux from Soil Respiration: Measurements and Modelling

Measured soil respiration R_s for the two sites varied between 2.70 (±0.33) µmol CO_2 m^{-2} s^{-1} in the dry season to a maximum rate of 12.42 (±1.17) µmol CO_2 m^{-2} s^{-1} in fall 2008. Measurements during the coldest period varied between 4.15 (±0.59) µmol CO_2 m^{-2} s^{-1} in YS and 5.44 (±4.46) µmol CO_2 m^{-2} s^{-1} in MS, so we could capture the seasonal pattern of soil respiration. To capture the full seasonal pattern and its daily variations, we fitted the "expo" model from Joffre *et al.* [54]. Minimum RMSE for model calibration reached 2.22 for YS and 2.62 for MS, leading to $R^2 = 0.91$ (YS) and $R^2 = 0.93$ (MS) for the model *vs.* measured regression (Figure 6). Adjusted parameters for $R_{s,ref}$, *b* and *c* for equation (2) of the "expo" model were 0.3, 1.45 and 0.08 for YS, and 0.67, 1.15 and 0.08 for MS. When applying this model to the daily values of simulated soil temperatures T and RWC, we observe a marked seasonality in the pattern of soil respiration with high day to day variations (Figure 6). Soil respiration increased in spring and peaked in May–June, in phase with the increasing soil temperature when soil water content was moderate. Soil respiration then decreased after June, mostly controlled by the decreasing SWC in summer and early autumn despite the still increasing soil temperature. The abrupt soil rewetting in autumn during high rainfall events lead to a sharp respiration pulse with up to five times more soil respiration fluxes than just before rewetting. In the early winter, although the autumnal rainfalls refilled SWC to field capacity, R_s was still low as a result of the low soil temperature. The lowest simulated soil respiration values were observed during winter with 1.31 µmol CO_2 m^{-2} s^{-1} and 2.19 µmol CO_2 m^{-2} s^{-1} for YS and MS respectively. By contrast, values of soil respiration peaked in May and September in the two stands with almost similar maximum rates of 16.3 µmol CO_2 m^{-2} s^{-1} and 16.6 µmol CO_2 m^{-2} s^{-1} observed in September at YS and MS, respectively. The total amounts of soil respiration over the year 2008 were respectively 1774 gC m^{-2} $year^{-1}$ and 2227 gC m^{-2} $year^{-1}$ for YS and MS.

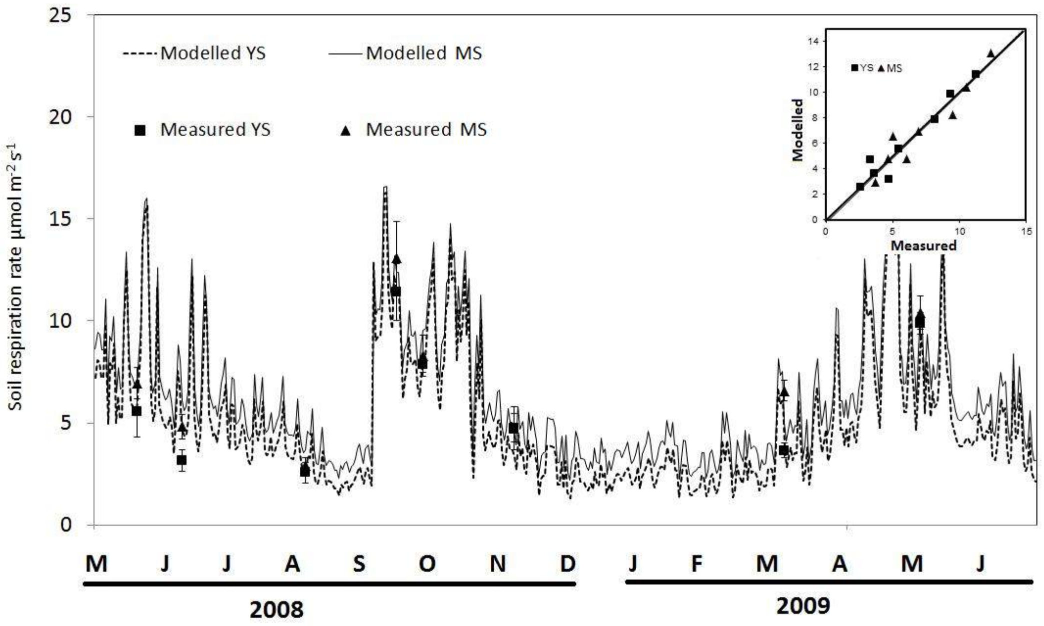

Figure 6. Seasonal variations of modelled (YS: dotted line, MS: solid line) and observed (YS: filled square, MS: filled triangle) soil respiration rate (R_S). Error bars are standard errors of the mean. Measured against modelled soil respiration in the young stand (YS: thin line) and the aged stand (MS: tick line), using Expo model are presented in the top right window. The dashed line represents the 1:1 line.

Finally, we tested for the temperature sensitivity of respiration to soil water status for both sites. The temperature sensitivity of respiration $g(\theta)$ (see Joffre *et al.* [54] for details) was identified as a linear function of RWC (Figure 7). At low RWC (0.56), an increase of 1 °C induced an increase of soil respiration of 15.4% in the YS and 15.7% in the MS. For non-limiting soil water conditions, at RWC = 1, the increases of respiration caused by a 1 °C temperature increase are +16.3% and +17% for YS and MS, respectively.

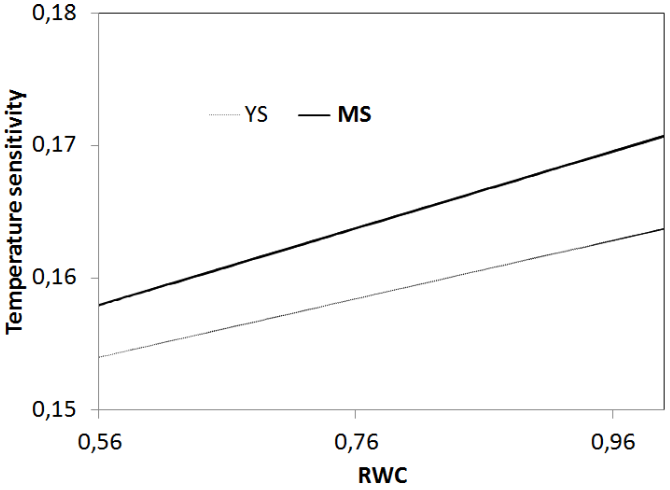

Figure 7. Dependency of temperature sensitivity of respiration on relative water content (RWC). The thin line corresponds to soil respiration in the young stand (YS) and the thick line corresponds to soil respiration in the mature stand (MS).

4. Discussion

4.1. Bellif Ecosystem Peculiar Fertile Conditions within the Mediterranean Context

We based our study on the peculiar climatic and edaphic conditions of the Bellif study site, on the most favorable range of the Mediterranean climate combining a high mean annual temperature (MAT) and a high mean annual precipitation (MAP) (as reviewed by [56] in the global database illustrated in Figure 8), associated with an exceptionally deep soil allowing for a high field capacity (more than 450 mm) in a region where forest systems mostly remain on shallow soils not used for agriculture. Within this context, we hypothesized a high forest productivity and soil activity potentially affecting soil carbon fluxes and storage.

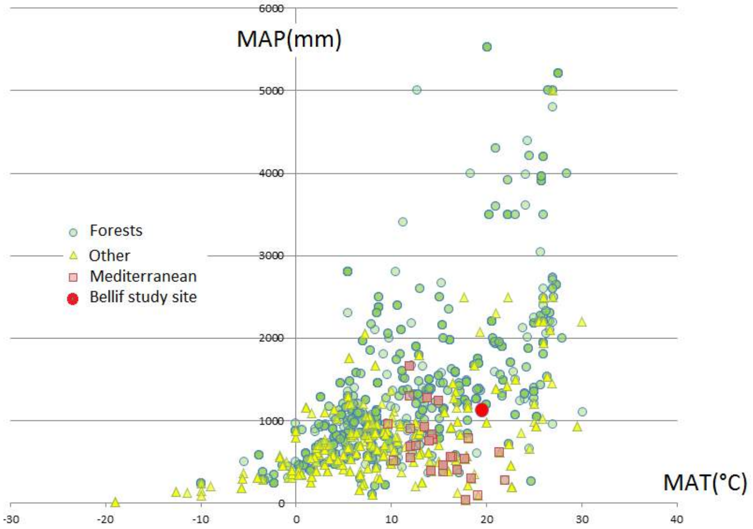

Figure 8. Bellif study site within the referenced study sites in the soil respiration global database [56] characterized by their Mean Annual Temperature (MAT, °C) and Mean Annual Precipitation (MAP, mm).

Indeed, our estimates of aboveground biomass (16.96 ± 1.52 kg DM m^{-2} in YS and 31.24 ± 2.19 kg DM m^{-2}) and root biomass (7.09 ± 0.40 kg DM m^{-2} in YS and 9.88 ± 0.49 kg DM m^{-2} in MS) lead to a low root/shoot ratio (0.41 for YS and 0.31 for MS) compared to other Mediterranean ecosystems (Puéchabon forest (*Quercus ilex*): 1.05 [57]; Hardwood tree species (Spain): 0.47 [58]). This result is in agreement with the hypothesis that the deep soil layer and wet climatic conditions usually induce low water scarcity, and in turn, low investment in root foraging [32]. We also observed a low LMA (121 to 146 gC m^{-2}) compared to other studies on the same species (167 to 189 gC m^{-2} for [59] or 155 gC m^{-2} for [60]). This supports our statement of a well-watered site based on the observed plasticity of this functional trait according to drought [61,62].

From this first observation, we then conclude that the carbon assimilated by trees is preferentially allocated to the aboveground biomass (leaf and stems), and the measured stem biomass is actually in the highest range of referenced forest sites in the Mediterranean basin [57,63,64], with impressive twig elongations (up to 28.5 cm) compared to [65] where apical twig elongations usually vary between 3.3 cm and 19.6 cm. However, this high aboveground biomass did not lead to a particularly high LAI

(1.68 for MS and 1.88 for YS) that we could expect according to the ecohydrological equilibrium theory where, in water limited environments, ecosystems adjust their leaf area to maximize biomass and minimize drought stress [66] and this is usually valid for Mediterranean forests [67]. As wetter and more fertile conditions tend to decrease leaf life span [68,69], we face here mild drought conditions (predawn water potentials hardly reaching −2.83 MPa and −5.75 MPa) leading to shorter leaf life span (less than 12 months) than usually reported for *Quercus suber* (15 months for [60], 12 to 20 months in [70], 14 to 16 months in [59] and 12 months in [71]). Our result of short leaf life span concomitant with low LMA is in accordance with [60] stating that a short leaf life span is usually observed in nutrient rich ecosystems [70]. The observed systematic second growth (and concomitant litterfall) in Autumn is actually very unusual for *Quercus suber*, despite already being observed for *Quercus* species [71–73] during exceptional years of low drought conditions and high fall temperatures. Our estimates of the annual rate of litterfall (YS: 804.8 g DM m^{-2} and MS: 1325.8 g DM m^{-2}) are indeed higher than other cork oak forests in surrounding areas in Tunisia (ranging between 226 g DM m^{-2} and 285 g DM m^{-2}, [64]) or the neighboring Sicily (Italy) (360 g DM m^{-2}, [74]), as well as functionally-close species as holm oak (325.4 g DM m^{-2} [75] or 428 g DM m^{-2} [76]) reviewed in [71]. Our site can then be defined as a highly productive site, with reduced water deficit during the dry season due to an important field capacity and allowing more carbon in aboveground biomass than other Mediterranean sites, but with a high turn-over rate of leaves in the canopy overall, leading to a high litterfall feeding the soil carbon pool.

The organic carbon stocks in the 0–30 cm depth profile (10.96 kgC m^{-2} cm in the YS and 14.79 kgC m^{-2} in the MS) were however in the range of those reported for soil organic carbon stocks in Tunisia (0.12–19.98) kgC m^{-2} as reviewed in [77], suggesting that the additional amount of carbon assimilated by this productive system at the canopy level is not converted into a higher soil carbon accumulation. This suggests that the assimilated carbon has been respired by high rates of heterotrophic respiration. The annual soil respiration (1774 gC m^{-2} and 2227 gC m^{-2} in YS and MS, respectively) actually falls on the highest range of those reported for Mediterranean ecosystems (Table 3) for this peculiar region within the Mediterranean basin, overall leading to a coherent fast carbon cycle across the ecosystem. We should still take into account that using a manual chamber method potentially overestimates soil carbon fluxes [78].

4.2. Relationships between Soil Temperature, Soil Moisture, and Soil Respiration

From the ecosystem's carbon fluxes described below, we tested for the climate controls on soil respiration. In spring, SWC was generally a non-limiting factor. During this season, higher air temperatures and radiation stimulate photosynthesis and the subsequent allocation of photosynthates to new root growth [79]. At this time, both root respiration and microbial decomposition are high, and lead to a peak value of total soil respiration. The autumn period experiences high rainfalls which also favor the development of fine roots, coupled with a high root [80] and microbial [81] activity.

Table 3. Review of annual respiration rates measured in the Mediterranean region, including forest type, mean annual air temperature (MAT), mean annual precipitation (MAP), annual litterfall, annual soil respiration (R_s), and soil type and depth.

Site	Vegetation	MAT (°C)	MAP (mm)	Rs (μmol m^{-2} s^{-1})	Annual Litterfall (gC m^{-2} $year^{-1}$)	Annual R_S (gC m^{-2} $year^{-1}$)	Soil Type and Depth (m)	Reference
Puechabon	*Quercus* forest (61 years)	13.5	883	0.7 min., 5.59 max.	205	762	rhodo-chromic luvisol (0.90)	[15]
California	Oak–grass savanna	16.3	556	0.5	-	488	Lithic haploxerepts (0.75)	[28]
Cabo de Gata/Spain	Degraded Steppe alpha grass	18	220	0.8	-	293.86	Lithic Leptosol/Calcaric (0.10)	[80]
Cabo de Gata/spain	Natural Steppe alpha grass	18	220	1.1	-	405.06	Mollic Lithic Leptosol (Calcaric) (0.20)	[80]
Roccarespampani Italy	Coppiced oak chronosequence (1 to 17 years)	14	755	1.7 min., 7.8 max.	36.48 min., 138.24 max.	-	Luvisoil (0.90)	[82]
Italy2	*Quercus ilex* forest (30 years)	14.5	770	-	-	1456	-	[3,83]
Bellif	*Quercus suber* (71–102 years)	19.29	1113	5.89	636	2227	Ferric luvisol (1.50)	This issue
Bellif	*Quercus suber* (35 years)	19.29	1113	4.69	386	1774	Ferric luvisol (1.50)	This issue

We then observed the well-documented drastic drop in soil respiration during the dry season [17,84], when temperature is high and the soil surface is dry, prohibiting the decomposition of the surface litter as a response of microbial activity to drought stress [84,85]. In winter, soil respiration reached the lowest values as a consequence of low temperatures [86]. Although Davidson *et al.* [17] and Rey *et al.* [84] reported that high soil water contents may limit soil respiration by limiting oxygen availability for both microbial decomposition and autotrophic activities, it should not be the main driver on our leachable soil type containing a significant amount of sand.

In most ecosystems, soil temperature alone is sufficient to explain seasonal variations of soil respiration [87–90], and temperature sensitivity of soil respiration (Q_{10}) has been widely discussed in modelling soil respiration [16,87,91]. In Mediterranean [54,80] and semi-arid [92] ecosystems, the temporal variation of soil respiration is controlled by both temperature and soil moisture, supporting our choice for the use of ‘expo’ model [54]. The temperature sensitivity of soil respiration in our study was more affected by the top soil water status than in a Mediterranean evergreen *Quercus ilex* forest ($g(\theta) = 5.7\%$, RWC = 0.4) [54], suggesting an eventual higher contribution of heterotrophic respiration in an ecosystem with high litterfall and a low root/shoot ratio.

4.3. Suitability of a Generic Drought/Temperature-Driven Soil Respiration Models

From the previously described storyline of the fast carbon cycle in our system, we explored the biological and climatic drivers of soil respiration by using the ‘exponential’ soil respiration model [54]. Our modelling approach could simulate the seasonal pattern of soil respiration and the large soil respiration pulses measured shortly after rainfall [93], with up to a five-time respiration increase after rewetting, a pulse intensity usually observed in Mediterranean environments [94]. Our model fitting revealed a higher basal reference respiration rate $R_{s,ref}$ for MS (0.67) than YS (0.3) consistent with a higher soil carbon content and root biomass as the labile pool of SOC provides important substrate for microbial respiration [95–97]. In turn, respiration rates were higher under the stand with the highest mean DBH (MS), in accordance with Søe and Buchmann [98], or [99,100]. In our fertile study site, we could expect more important carbon stocks, and in turn higher basal respiration rates. However the estimated basal reference respiration rate $R_{s,ref}$ (0.3 in YS, 0.67 in MS) was only slightly higher than other drier Mediterranean ecosystems (0.551, 0.771 in [54]), so that no functional difference could be identified from this parameter for our site. Other parameters b and c controlling soil respiration were also close to other studies [54], so the favorable climate alone could explain the high carbon respiration rate. This result partly balances the hypothesis stated by Chen *et al.* [28] where soil respiration responds to increased MAT by increasing belowground carbon input more than an acceleration of soil C decomposition. We show here that higher temperatures and lower soil dryness alone actually drive the increased soil respiration (without increasing basal respiration), but that these climate conditions would not lead to an increased respiration without higher additional carbon input in the soil layer by enhanced litterfall in this non-accumulating soil carbon region.

5. Conclusions

Current studies on *in situ* soil respiration on the African continent are scarce [101,102] and we presented here a peculiar site in the Mediterranean part of the continent at its Northern bound. The site offers a deep and fertile soil, a high soil water content, and a high mean annual precipitation associated with hot and dry summers, overall leading to extremely favorable conditions in the range of Mediterranean climates covered by the global dataset assemblage [56] (Figure 8). This allowed us to investigate how carbon fluxes adjust to favorable conditions for a usually water-limited ecosystem. We provided an estimation of the annual rate of soil respiration and determined some key climatic, edaphic, and biological processes tracing the fate of carbon across the ecosystem. Soil temperature and SWC explained most of the seasonal variations in soil respiration including important respiration pulses following soil rewetting, but more particularly, we showed here that the expected high carbon storage in this extremely productive Mediterranean forest was compensated by similarly high soil respiration fluxes. This high carbon flux was a consequence of ecosystem functional adjustments to favorable climatic and edaphic conditions, as an increased carbon allocation to aboveground biomass lead to an unusual pluri-annual growth period for twig elongation and leaf cohorts, a significantly reduced leaf life span, overall leading to an important litterfall feeding the soil litter submitted to decomposition and supporting our first hypothesis. Within this context, we also showed high rates of soil respiration as stated in our second hypothesis. We could conclude that highly productive forests under sub-humid Mediterranean conditions can act as potential larger carbon sinks than standard drier forests as a consequence of their enhanced aboveground carbon storage in the woody component. However an increased litterfall feeding the soil carbon pool, mild temperatures, and wet conditions induced a high respiration rate so that the soil pool could not benefit from this high carbon assimilation, a similar conclusion as stated for fertile temperate forests by Varik *et al.* [37]. The expected benefits to soil carbon storage under such favorable conditions for these Mediterranean forest ecosystems should therefore be tempered as they are considerably reduced, and the increased carbon sequestration under this productive environment is mostly related to the increased carbon stock in the long-lived woody component.

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Author Contributions

All authors contributed to the design, implementation, and analysis of this research. Lobna ZRIBI and Florent Mouillot jointly wrote the paper. Lobna Zribi lead the study and performed field measurements and data analyses. Florent Mouillot performed water and carbon modelling runs and analyses.

Conflicts of Interest

The authors declare no conflict of interest.

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