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Seasonality of net carbon exchanges of Mediterranean ecosystems across an altitudinal gradient

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ABSTRACT

In the present climate change context it is important to understand the carbon balance seasonality of Mediterranean areas, that will suffer important changes in precipitation according to the last climate change predictions. This work analyzed the seasonality of carbon exchanges of three Mediterranean ecosystems according to a variety of water and temperature regimes due to differences in altitude (alpine, subalpine and lowland). Results show that the timing and duration of the growing season depended on temperature at the alpine site, while the dependence on water availability increased as altitude decreased. Thus, maximum values of net carbon uptake occurred in late spring for the alpine and subalpine sites (up to 60 and 30 gC m^{-2} $month^{-1}$ respectively) whereas the lowland site absorbed carbon throughout winter (up to 30 gC m^{-2} $month^{-1}$). Similarly increases in aridity conditions resulted in monthly increases in carbon emissions during dry periods. Thus from May to October, the lowland emitted up to 60°gC°m^{-2}°$month^{-1}$, the subalpine emitted half that with a delay of two months, whereas the alpine site continued with slight uptake sequestration. Finally, the EVI could be used to provide reasonably accurate estimates of photosynthesis (R^2 around 0.6) but this relation varies depending on the site.

1. Introduction

The Mediterranean climate is distinctly characterized by mild temperatures (*T*) and asynchronous patterns of precipitation, versus light and *T*. The dry summer characteristic of this climate makes Mediterranean ecosystems very sensitive to climate change via land degradation, which can decrease the potential for plant carbon (C) assimilation (Mouat and Lancaster, 2006). In addition, the C and water balances are tightly linked as precipitation pulses (Inglima et al., 2009), soil water content (Rey et al., 2005), and the timing of precipitation (Xu and Baldocchi, 2004) have been shown to exert strong controls on the C balance. As predictions for climate change in this region indicate a decrease in water availability (via decreases in rain events and total precipitation (IPCC, 2007)), the link between the C and water cycles is expected to be tighter as the growing period is shortened due to drought (Janssens et al., 2005; Baldocchi, 2008). Therefore, monitoring and understanding the seasonality of net C exchanges in Mediterranean ecosystems and how they are linked to the water balance is essential to be able to understand the effects that future climate change will exert on the behavior of these ecosystems as sources or sinks of CO_2.

Grasslands and shrublands, representing the first stages of colonization in Mediterranean ecosystems, are the main vegetation types due to years of human intervention, deforestation and desertification (Dato et al., 2010). Moreover, in recent decades, 18.3 million ha of European agricultural areas (globally, 235 million ha) were abandoned (Rounsevell et al., 2003, 2006; FAO, 2004). This

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phenomenon is particularly relevant in the Mediterranean area (Correia, 1993), leading to shrubland encroachment (Maestre et al., 2009), changing former agricultural and grasslands to shrublands. However, most research on C and water balances in Mediterranean ecosystems has been focused on forest or semiarid grassland ecosystems (Janssens et al., 2005), paying less attention to shrublands with different water and *T* regimes.

The eddy covariance technique provides direct and continuous measurements of C and water exchanges between terrestrial ecosystems and the atmosphere, and has been applied to examine the potential of different ecosystems as C sinks (Dabberdt et al., 1993; Baldocchi, 2003). Such studies define net CO_2 fluxes (NEE) as the sum of photosynthetic, gross primary production (GPP) and ecosystem respiration (R_{eco}; Falge et al., 2002; Reichstein et al., 2005), neglecting non biological processes. However, recent studies reveal a contribution of abiotic fluxes to net C exchange (Kowalski et al., 2008; Stone, 2008; Xie et al., 2008; Ferlan et al., 2011). Such abiotic processes – mainly subsoil ventilation (Serrano-Ortiz et al., 2010) – provoke CO_2 releases during dry periods (Serrano-Ortiz et al., 2009; Rey et al., 2012) that are strongly related to wind speed (Pérez-Priego et al., 2013) and have relevant magnitudes at least on short time scales (Kowalski et al., 2008). In this context, such ventilation processes can be particularly important in Mediterranean ecosystems characterized by dry and warm summers.

To estimate CO_2 exchange over wide areas, the measured NEE from distributed points must be scaled up to spatially continuous estimates. Satellite vegetation indices, such as the Enhanced (EVI) or Normalized Difference (NDVI) Vegetation Index, were developed to optimize the area-averaged canopy photosynthetic capacity and are highly correlated with processes that depend on absorbed light, such as GPP (Potter et al., 2007). Several studies have shown that both vegetation indices have a linear relationship with GPP in various vegetation types (Xiao et al., 2004; Rahman et al., 2005; Huete et al., 2006; Sims et al., 2006; Nagai et al., 2010). Since the EVI and NDVI are structural indices, for evergreen Mediterranean ecosystems they may not provide good estimates of GPP because they should be largely insensitive to short-term leaf physiological changes that are independent of structure, such us reductions in GPP caused by water stress (Zarco-Tejada et al., 2013); however, a recent study reveals good agreement between annual values of EVI and annual stem diametric increment for Mediterranean forest (Garlbusky et al., 2012). Thus, further modeling efforts should be concentrated on sites with summer drought (Sims et al., 2006).

The main objective of this work is to characterize the seasonality of carbon fluxes in non-forested Mediterranean ecosystems, characterized by hot and dry summers, over a gradient of altitude, precipitation and temperature. Monitoring and understanding this seasonality will enable assessment of the effect that future climate change conditions will have on Mediterranean ecosystems in a more specific way. For this purpose, we have compared the net ecosystem carbon exchange measured by eddy covariance systems in three grassland and shrubland ecosystems at different altitudes, analyzing the seasonality and main variables controlling these fluxes as well as the main processes responsible for them in the three ecosystems studied. Finally, EVI and NDVI values are compared with GPP to test the use of this product for estimation of GPP in Mediterranean ecosystems.

2. Material and methods

2.1. Sites description

Measurements of CO_2 and water fluxes along with environmental variables were made during 2007 and 2008 at three Mediterranean sites located in the Southeast of Spain: an alpine meadow, Laguna Seca in the Sierra Nevada range (ALP); a subalpine plateau (SUB), el Llano de los Juanes in the Sierra de Gádor range; and a lowland alpha-grass steppe, Balsa Blanca in Cabo de Gata-Níjar natural park (LOW). Table 1 summarizes the main environmental values characterizing the three sites, separated by less than 90 km along an East–West transect.

2.2. Micrometeorological and eddy covariance measurements

During 2007, 2008 measurements of air temperature (*T*) and relative humidity (RH), incident and reflected photosynthetic photon flux densities (PPFD), net radiation (R_n), rainfall, volumetric soil water content (SWC), and soil heat flux (*G*) were carried out at the three study sites, and stored and averaged every 30 min in data loggers. Table 2 indicates the instruments used at each site and their deployment.

Densities of CO_2 and water vapor, the three components of the wind velocity vector and the sonic *T* were measured at 10 Hz, and means, variances and covariances were stored in data-loggers and converted to 30 min means following Reynolds rules. To obtain NEE and evapotranspiration (ET) a 2-D coordinate rotation (McMillen, 1988; Kowalski et al., 1997) and density corrections (Webb et al., 1980) were applied in post-processing.

Several filtering procedures were applied to the flux data to obtain reliable 30 min NEE and ET values following Reverter et al. (2010) and Serrano-Ortiz et al. (2009) such as half hourly values excluded when <75% of 18,000 possible data sets during each averaging period are available or data rejected due to rain or

Table 1
Characteristic climatic, vegetative and soil features of each site.

Features	Alpine (ALP)	Subalpine (SUB)	Lowland (LOW)
Location in Spain	Sierra Nevada (Granada)	Sierra de Gádor (Almería)	Cabo de Gata-Níjar (Almería)
Site code[a]	ES-LgS (Laguna Seca)	ES-LJu (Llano de los Juanes)	ES-Agu (Balsa Blanca)
Elevation [m a.s.l.]	2300	1600	195
Climate type	Med.-alpine	Med.-subhumid	Med.- semiarid
Mean annual *T* [°C]	5.5	12	18.1
Annual rainfall [mm]	800	538	271
P/ET_P[b]	1.3	0.8	0.3
Mean annual SWC_n[c]	0.21	0.39	0.44
Ecosystem type	Alpine shrubland	Shrubland plateau	Shrubland steppe
Dominant species[d]	*F. indigesta*, *Cytisus purgans*	*F. scariosa*, *G. pumila pumila*, *H. spinosa*	*S. tenacissima*
Mean vegetation height [m]	0.2	0.5	0.8
Maximum LAI [m^2∘m^{-2}]	2.9	2.1	1
Soil type	Alluvial silicates	Clay over carbonate bedrock	Alluvial with carbonate deposition
References	Reverter et al. (2010)	Serrano-Ortiz et al. (2007)	Rey et al. (2011)

[a] According to European Fluxes Database Cluster (http://www.europe-fluxdata.eu/home/sites-list).
[b] *P* – mean annual precipitation; ET_P – averaged potential annual evapotranspiration (measured during the studied period and calculating following Hargreaves and Samani (1982)).
[c] Species representing more than 10% of the vegetation cover of the site.
[d] SWC_n – mean annual normalized soil water content calculated following Equation (3).

Table 2
List of variables measured at ALP, SUB and LOW sites.

Measurement	Instrument	Model	Height	Data-logger & measurement/ average frequency
Air humidity and temperature	Thermohygrometer	ALP: STH-5031, Geonica, Madrid, Spain; SUB & LOW: HMP45-C, CSI*	ALP & SUB: 1.5 m LOW: 4 m	ALP: Meteodata 300 c, Geonica, 1 Hz/10 min; SUB & LOW: CR10X & CR23X, CSI[a], 10s/15min
PPFD (incident and reflected)	2 Quantum sensors	Li-190, LI-COR, Lincoln, NE, USA	ALP &SUB: 1.5 m LOW: 2 m	
Net radiation	Net radiometer	ALP: CN1-R, Middleton Solar, Brunswick, Australia; SUB & LOW: NR Lite, Kipp and Zonen, Delfi, The Netherlands	ALP &SUB: 1.5 m LOW: 2 m	
Rainfall	Tipping-bucket rain gauge	ALP: PLUVIOM 52203, RM Young, Traverse city, MI, USA; SUB & LOW: model 785 M, Davis Instruments Corp., Hayward, CA, USA	ALP, SUB & LOW: 1 m	
Soil heat flux	ALP, SUB & LOW: 4, 2 & 4 soil heat flux plates	HFP01, Hukseflux, Delft, Netherlands	ALP, SUB & LOW: −0.8 m	ALP: Meteodata 300 c, Geonica, 1 Hz/10 min; SUB & LOW: CR10X, CSI[a], 10s/30min
Soil temperature	ALP: 3 Temperature & soil water content sensors; SUB & LOW: 2 Thermocouples	ALP: EC-20, ECH2O, Decagon Devices, Pullman, WA, USA; SUB & LOW: TCAV, CSI.	ALP & LOW: −0.2 m, −0.6 m; SUB: −0.1, −0.3, −0.5, −0.7 m	
Soil water content (volumetric)	ALP: 3 Temperature & soil water content sensors; SUB & LOW: 1 & 2 ½ Time domain reflectometry (TDR)	ALP: EC-20, ECH2O, Decagon Devices, Pullman, WA, USA; SUB & LOW: CS616, CSI	ALP: −0.4 m; SUB: −0.15 m; LOW: −0.4 m.	
CO_2 and H_2O densities	Open-path gas analyser IRGA	LI-7500, LI-COR, Lincoln, NE, USA	ALP: 2.3 m; SUB: 2.5 m; LOW: 3.5 m	ALP: METEK, Elmshorn, Germany, 1 Hz/5s; SUB & LOW: CR23X, CSI[a], 10 Hz/15min
Wind speed (three component), and virtual temperature	Three axis sonic anemometer	ALP: USA-1, METEK, Elmshorn, Germany; SUB & LOW: CSAT-3,CSI		

[a] CSI – Campbell Scientific, Inc., Logan, UT, USA.

condensation marked by changes in the diagnostic parameter for window purity (AGC) of the IRGA. In addition, a friction velocity (u_*) threshold for each site, using the available "on-line" tool http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php, determined the filtered out night-time periods of low turbulence. After applying these filters, the percentages of missing NEE data for 2007/2008 were 38%/45% for ALP, 51%/49% for SUB and 26%/27% for LOW. For ET data, these percentages were 41%/35% for ALP, 41%/46% for SUB, and 23%/26% for LOW. Missing data were most frequent in autumn and winter, when rain and snow were most frequent. Thus, at the SUB site the NEE and ET data were missing for January, and February 2007 and December 2008. In addition, at the ALP site the ET data for August 2007 were missing, as well as the main micrometeorological variables in April 2008, due to instrument problems. To assess the monthly behavior of NEE and ET, short-term data gaps were filled following Reichstein et al. (2005) available online (http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php).

Other criteria used to determine the validity of the flux data were the degree of energy balance closure and analysis of the footprint of the EC tower. The energy balance closure – defined as the slope of the line relating the sum of the half-hourly latent and sensible heat fluxes (LE + H) to available energy (R_n-G) – was 72% for the SUB site (Serrano-Ortiz et al., 2009), 95% for the LOW site (Rey et al., 2012) and 72% for the ALP site ($R^2 = 0.9$, $n = 16{,}784$). All are well within the range reported from FLUXNET sites (Wilson et al., 2002; Stoy et al., 2013). Reverter et al. (2010), Serrano-Ortiz et al. (2009), and Rey et al. (2012) have shown that the footprints are well within the fetches of the ALP, SUB and LOW sites, respectively. Errors in monthly NEE and ET introduced by the gap-filling process were calculated using the variance of the gap-filled data. The standard deviation of each gap-filled value is provided by the on-line tool and was calculated by introducing artificial gaps and repeating the standard gap-filling procedure. The variance of each half hour filled data was calculated by squaring the standard deviation. Twice the standard deviation of sums of each half hour variance was taken as our monthly error.

2.3. Partitioning of CO_2 fluxes

Partitioning of NEE into GPP and R_{eco} was done via the hyperbolic light response algorithm proposed by Lasslop et al. (2010) according to the following equation:

$$NEE = \frac{\alpha\beta R_g}{\alpha R_g + \beta} + R_{15}\exp\left(E_0\left|\frac{1}{15-46.02} - \frac{1}{T+46.02}\right|\right) \quad (1)$$

where α (μmol C J^{-1}) is the canopy light utilization efficiency, β (μmol C °m^{-2} s^{-1}) is the maximum CO_2 uptake rate of the canopy at light saturation, R_g (W m^{-2}) is the global radiation (estimated from PPFD$_i$ (Ceulemans et al., 2003)), R_{15} (μmol C m^{-2} s^{-1}) is the base respiration at 15 °C and E_0 (°C) is the temperature sensitivity. Parameters α, β, E_0 and R_{15} were derived from day-time *NEE* data for each site.

This model has several advantages over other methods that make it suitable for use here. Firstly, compared to partitioning models that fit R_{eco} to night-time EC data, and then derive GPP from R_{eco} and day-time data (Reichstein et al., 2005; Desai et al., 2008), this model has the advantage of obtaining quasi-independent estimates of GPP and R_{eco}, avoiding cross correlation problems (Lasslop et al., 2010). This allowed estimation of modeled NEE (NEE$_m$) from the partitioning, as NEE$_m$ = −GPP + R_{eco}, that can be compared with measured NEE to assess the accuracy of the partitioning model. Moreover, this model has another important advantage, especially for the Mediterranean sites studied here, as it accounts for the effect of the vapor pressure deficit (D) limiting GPP in dry periods by replacing β with an exponentially decreasing function, as follows:

$$\beta = \left\{ \begin{array}{c} \beta_0 \exp(-k(D-D_0)), \quad D > D_0 \\ \beta = \beta_0 \quad D < D_0 \end{array} \right\} \quad (2)$$

The k parameter was estimated for each 4-day data window to quantify the response of the maximum carbon uptake to D, and D_0 is set to 10 hPa. Finally, E_0 was estimated from night-time data ($R_g < 4$ W m^{-2}), and once this variable was fixed, the parameters r_b,

α, β_0 and k were estimated from day-time data. Notice that the proposed model does not include any information about soil moisture, a crucial environmental variable in such water-limited ecosystems. This condition could limit the accuracy of the proposed model (see Appendix of Lasslop et al., 2010 for more details).

Positive values of NEE denote net CO_2 release to the atmosphere while negative values denote net CO_2 uptake. By contrast, GPP and R_{eco} will be represented as positive values.

2.4. Other variables

Vegetation indices (EVI and NDVI) were obtained from the MODIS-Terra sensor at 250 m and 16-day spatial and temporal resolutions (MOD13Q1), available from NASA and USGS (United States Geological Service), for 2007 and 2008. To examine a representative area of each site, we considered a 3 × 3 pixel area centered on the tower. We then averaged the EVI and NDVI values over each area, and obtained averaged values of both vegetation indices.

To be able to compare the volumetric soil water content (SWC) of the three sites, considering the heterogeneity of the soil and the different instrumentation used (Table 1), we have calculated the normalized soil water content (SWC_n) for each site, as:

$$SWC_n = (SWC - SWC_{min})/(SWC_{max} - SWC_{min}) \quad (3)$$

where SWC_{min} and SWC_{max} are the minimum and maximum values of SWC measured for the whole period studied (2007 and 2008), approximating the wilting point and field capacity, respectively.

2.5. Statistical analysis

The relation between abiotic factors and C fluxes were determined using the OriginPro software (version 8) providing information about the y-intercept, the slope and their respective standard errors together with the Pearson product–moment correlation coefficient (r), the coefficient of determination of a linear regression (R^2) and the critical probability of the analyses (p value).

3. Results

3.1. Seasonality of the main meteorological variables

As expected, meteorological differences between sites were determined by the altitudinal gradient. Compared to the coastal climate of the LOW site, the SUB and ALP sites were consistently several degrees cooler, particularly outside of the summer season (July, August, September; Fig. 1).

In winter (December, January and February), the mild climate of LOW contrasted strongly with the higher elevation sites where temperatures were low enough to limit biological activity. This is especially true for ALP, where daily mean temperatures were often near or below freezing. Generally, since precipitation also increased with elevation, SWC_n reached unity quite often at the ALP site during winter and spring. Most importantly, all sites experienced dry summers with less than 8 mm in July and August combined, excepting the ALP site where 39 mm were registered in August 2008 (Fig. 1).

3.2. Seasonality of the carbon and water fluxes and their relations with abiotic factors

Plant activity was strongly limited by such water restrictions, and also by winter temperatures at the high-elevation sites (Fig. 2). For every site, maximum values of GPP and ET occurred just prior to the onset of water limitations. For the LOW site, maximum absorption of up to 30 g C m^{-2} month^{-1} occurred in winter, as this site achieved values of SWC_n near 0 by June. By contrast, the higher elevation sites were frozen in winter, net CO_2 uptake started in late spring, and then showed maximum values of GPP and ET in May–June (SUB; up to 30 g C m^{-2} month^{-1}) or June–July (ALP; up to 60 g C m^{-2} month^{-1}). Only the highest elevation site continued with slight photosynthetic activity in August. During the water stressed period, the LOW and SUB sites presented net carbon release to the atmosphere (positive monthly NEE up to 60 g C m^{-2} and 30 g C m^{-2} respectively) due to low values of monthly GPP and ET, lower than 10 g C m^{-2} and 25 mm respectively (Fig. 2). However, this net carbon release period started in May for LOW while there was a delay of two months for SUB, and it ended in October for both sites, with the beginning of the rainy season (Fig. 1). By contrast, the ALP site usually continued slightly absorbing carbon (negative NEE) during the water-stressed period, presenting higher functional limitations in winter due to low temperatures (Fig. 1).

Significant relations were observed between abiotic factors and ET and C fluxes (Fig. 1). Thus, for the LOW site, monthly ET and net C emissions increased with increasing T and VPD and decreasing SWC_n (Table 3) due to a decrease in GPP. By contrast, the opposite relation was observed for the ALP site, where ET and C uptake increased with decreasing T and increasing SWC_n (Table 3) due to an increase in GPP. By contrast, no significant relations between ET

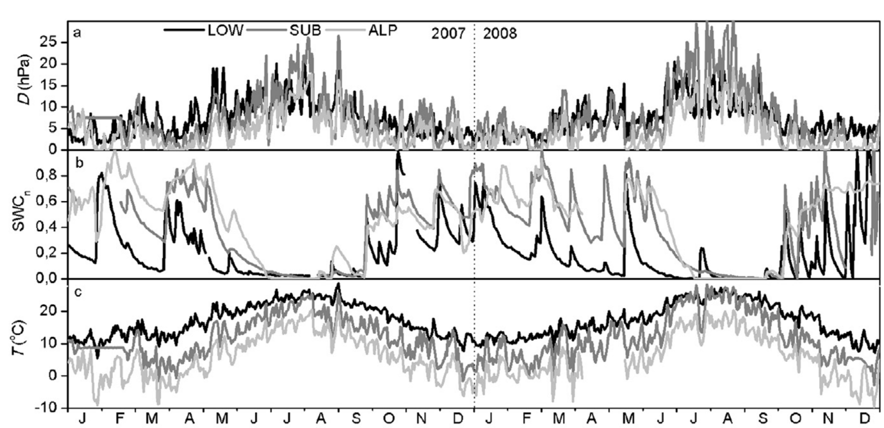

Fig. 1. Daily averages of air temperature (T), vapor pressure deficit (D), and normalized soil water content (SWC_n) for the three sites studied. ALP values for April 2008 were missing, and gap filled only in the case of T.

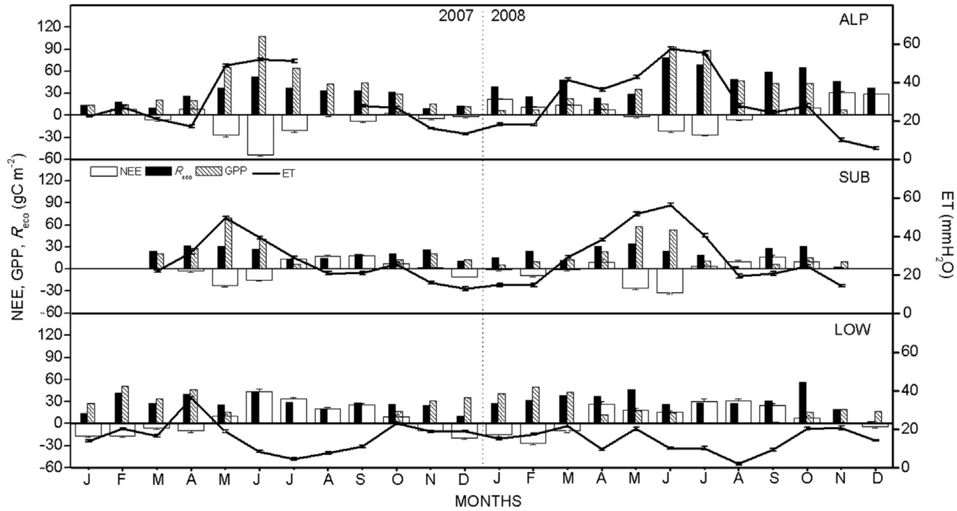

Fig. 2. Monthly values of ET, NEE, GPP and R_{eco}, for the two years studied, and the three sites considered in this work.

and C fluxes and abiotic factors were observed for the SUB site.

The seasonality of GPP is described by the Enhanced Vegetation Index (EVI; Fig. 3a). However, this relation varies depending on site. Thus, the LOW site, with the highest correlation ($R^2 = 0.65$; intercept $= -26 \pm 4$ gC m^{-2}), showed the lowest dependence of GPP on EVI (slope $= 209 \pm 23$ gC m^{-2}), whereas the ALP site presented the highest slope (Fig. 3a). The higher elevation sites presented similar patterns of EVI and GPP reaching maximum values in late spring and minima in winter (Fig. 4a). However, whereas similar values of EVI were measured during the most productive months for the ALP (June–July) and SUB (May–June) sites, monthly values of GPP were double for the ALP site. By contrast, the LOW site presented higher values of EVI and thus GPP during winter and early spring. Notice that for similar values of GPP during the most productive months (winter), the LOW site presented double values of EVI compared to the SUB site.

Regarding NDVI, this index also describes the seasonality of GPP, with an exception for the ALP site (Fig. 3b) presenting the lowest correlation ($R^2 = 0.29$). Finally, notice that NDVI values are double those obtained for EVI, and the slope of the relationship between GPP and NDVI decreases by around half.

3.3. Measured vs. modeled carbon fluxes

After modeling carbon fluxes the mean values and (range) of the ecophysiological parameters α, β and R_{15} were 0.03 (0.03) µmol C J^{-1}, 4 (2) µmol C m^{-2} s^{-1} and 1 (1) µmol C m^{-2} s^{-1} respectively. Excepting the ALP site, the proposed biological model for carbon flux partitioning did not accurately reflect the seasonality of the measured carbon fluxes (Fig. 5 and Table 4). For the ALP site the diurnal trends usually match between the measured and modeled carbon fluxes for all representative months of each season with some exceptions during night-time (Fig. 5). By contrast, the SUB and LOW sites presented better agreement in spring and late autumn/winter respectively, but the biological model reflected neither the CO_2 release measured during summer at the SUB and LOW sites, nor the midday emission peaks measured during winter and autumn at the SUB site (Fig. 5). Considering the whole measured dataset, the R^2 remained higher than 0.6 from May to October for the ALP site, during late spring for the SUB site and in winter for the LOW site (Table 4). During these matching periods, modeled fluxes underestimated the measured fluxes with a slope of around 0.8.

4. Discussion

These results show important seasonality in the carbon and water fluxes of the three sites, although both the beginning and duration of the growing season (monthly NEE°>°0) differ with altitude due to differences in the limiting factor for biological activities. The ALP site can be considered less water-limited and more temperature-limited due to the altitude (Huxman et al., 2003), with monthly net CO_2 assimilation throughout the whole year and only December showing net release of CO_2 (mean daily T lower than 0 °C). Here, contrary to the lower sites, maximum values of GPP and R_{eco} occur in summer (June and July) with mean daily T higher than 10 °C. By contrast, the duration of the growing season for the LOW and SUB sites is around two or three months starting in winter and late spring respectively. The mean daily T at the LOW site never drops below 10 °C and biological activities are clearly limited by water availability. The intermediate SUB site experiences both restrictions (temperature and water), showing an additional short period of net assimilation that occurred during mild winters with water availability. Finally, although the proposed biological model (Lasslop et al., 2010) does not include soil moisture as an input variable, it explained the fluxes measured during growing seasons quite well for the three study sites, indicating that R_{eco} and GPP are the main processes at work during these periods.

During dry periods, carbon exchange is characterized by a net monthly CO_2 release. The duration of this period of net emission decreases with altitude. Since the proposed biological model does not explain the fluxes measured during dry seasons we can infer that the processes involved in this high summer CO_2 release are not entirely physiological, but rather related to ventilation processes in the carbonaceous soils, during warmer and drier summer months, provoked by winds and low soil water contents (Kowalski et al., 2008; Serrano-Ortiz et al., 2009; Were et al., 2010; Rey et al., 2012). R_{eco} was not the process directly responsible for this high summer CO_2 release, as during the dry periods with extremely low soil moisture levels, soil microbial activity should be practically non-existent (Rey et al., 2002). Despite being nearer to ALP in terms of altitude, SUB behaved more like semiarid LOW during the summer; this is likely since percolation through the karstic substrate reduces soil water available for evaporation at this ecosystem (Contreras et al., 2008).

Finally regarding upscaling strategies, our results show that the use of EVI for modeling GPP over wide Mediterranean non-forested

Table 3
Coefficients of determination (r) and critical probability of the analyses (p) for simple linear regressions between averaged monthly abiotic factors (Vapour Pressure Deficit, air Temperature, normalized Soil Water Content) and monthly EvapoTranspiration and carbon fluxes (Net carbon Ecosystem Exchange, Gross Primary Production, ecosystem Respiration) for the three study sites.

		ET (mm)		NEE (gC m^{-2})		GPP (gC m^{-2})		R_{eco} (gC m^{-2})	
		r	p	r	p	r	p	r	p
ALP	VPD (hPa)	0.57	0.005[a]	−0.55	0.007	0.61	0.002	0.36	0.09
	T (°C)	0.70	0.0003[a]	−0.64	0.001[a]	0.79	<0.0001[a]	0.54	0.007
	SWC_n	−0.48	0.02	0.56	0.005[a]	−0.65	0.0007[a]	−0.43	0.02
SUB	VPD (hPa)	0.28	0.2	0.20	0.3	−0.14	0.5	−0.24	0.2
	T (°C)	0.39	0.06	0.26	0.2	−0.08	0.7	−0.02	0.9
	SWC_n	−0.21	0.3	−0.37	0.07	0.23	0.3	0.15	0.5
LOW	VPD (hPa)	−0.60	0.0002[a]	0.86	<0.0001[a]	−075	<0.0001[a]	0.14	0.5
	T (°C)	−0.59	0.0002[a]	0.87	<0.0001[a]	−0.81	<0.0001[a]	0.23	0.3
	SWC_n	0.52	0.009	−0.69	0.0002[a]	0.56	0.005[a]	−0.42	0.04

[a] p value $\leq$ 0.005.

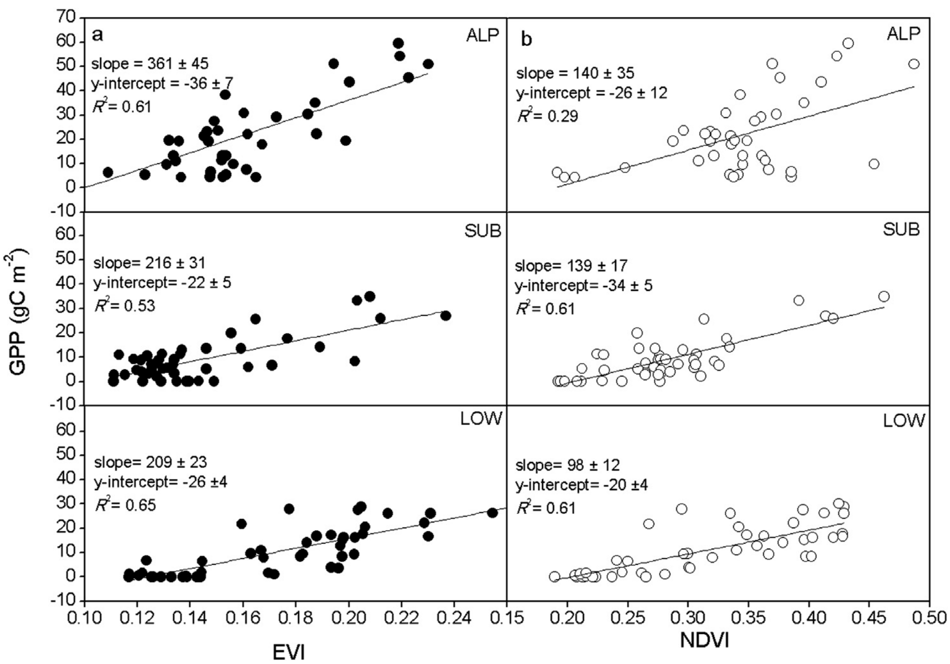

Fig. 3. Scatter plots of (a) GPP *vs.* EVI and (b) GPP *vs.* NDVI each 15 days.

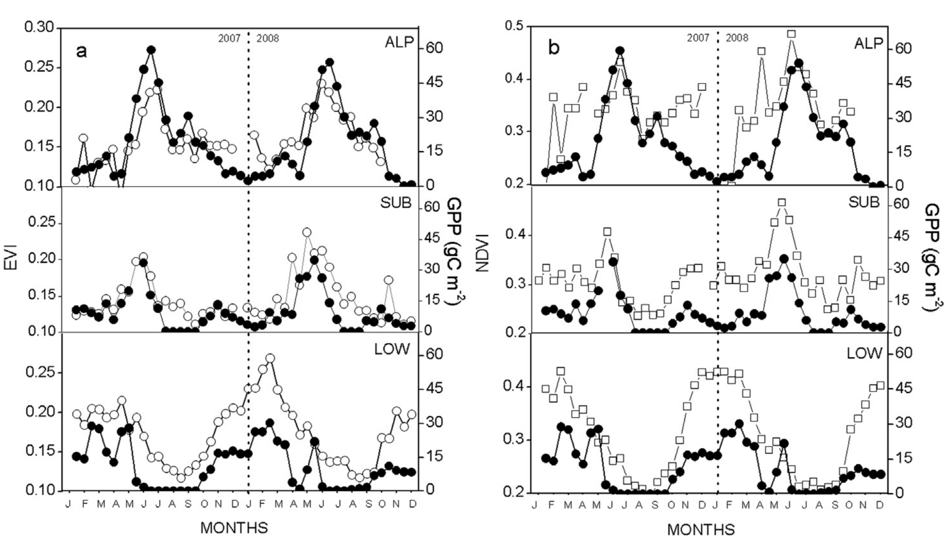

Fig. 4. Seasonal patterns of (a) EVI and GPP (b) NDVI and GPP for each site.

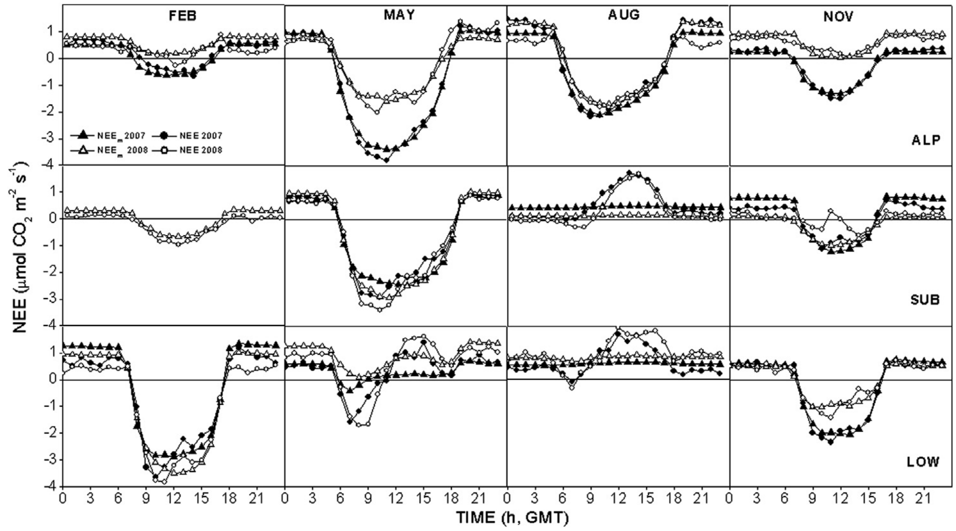

Fig. 5. Average measured NEE and modeled NEE_m for each hour of day and site, for 4 months representative of each season. Data for 2007 and 2008 are shown.

ecosystems could be possible. Similar to other studies with different vegetation types, seasonal dynamics of EVI followed those of GPP better than NDVI with a stronger linear relationship with GPP than NDVI (Xiao et al., 2004; Sims et al., 2006; Garlbuski et al., 2013). The EVI *vs.* GPP relationship is site-specific and, contrary to expectations (Sims et al., 2006; Zarco-Tejada et al., 2013), the highest correlation was observed for the most water-limited ecosystem (LOW site). The main reason could be the increase of cloudiness with altitude limiting the quality of EVI values (Nagai et al., 2010). In addition, whereas the ALP and SUB sites present several species that could increase the scatter via varying phenology, the LOW site is mostly covered by *Stipa tenacissima*. In this context, further research is needed for determining the appropriate use of the EVI for modeling carbon exchange in ecosystems with summer drought.

5. Conclusions

- In Mediterranean non-forested ecosystems, CO_2 and water fluxes are highly dependent on the spatial and temporal variability in water availability and temperature, characteristic of the Mediterranean climate. However, this dependency is variable according to the characteristics of the site.
- A gradient of altitude and average temperature showed that the growing season, where photosynthesis and respiration are the main processes, depends on temperature for the higher altitude and, therefore, colder ecosystems, and on water availability as altitude descends and, therefore, temperature and aridity increase.
- The subalpine site, being intermediate both in average temperature and in altitude, presents the limitations for carbon and

Table 4
Statistical comparison between measured and modeled CO_2 fluxes. "Slope" refers to the linear regression between observed CO_2 exchange and estimated CO_2 exchange, "*y*-int" is the *y*-intercept and RMSE is root mean square error. Shaded values are regressions with $R^2 > 0.60$.

Month	Year	ALP				SUB				LOW			
		Slope	*y*-int	RMSE	*n*	Slope	*y*-int	RMSE	*n*	Slope	*y*-int	RMSE	*n*
Jan	2007	0.52	−0.01	0.73	994	–	–	–	–	0.58	−0.53	0.91	515
	2008	0.45	0.05	0.31	817	0.27	−0.22	0.64	395	0.71	−0.32	1.14	739
Feb	2007	0.31	0.18	1.25	932	–	–	–	–	0.71	−0.44	1.08	626
	2008	0.43	0	0.54	784	0.30	−0.21	0.59	347	0.74	−0.13	1.16	946
Mar	2007	0.44	−0.13	0.96	982	0.33	−0.07	0.88	637	0.52	−0.33	1.15	828
	2008	0.57	−0.10	0.72	873	0.30	−0.10	0.85	639	0.42	−0.24	1.49	855
Apr	2007	0.62	0.01	1.01	632	0.48	−0.16	0.93	649	0.63	−0.18	1.17	857
	2008	0.51	−0.39	0.89	815	0.51	0.13	0.73	777	0.29	0.55	1.96	1069
May	2007	0.74	−0.43	1.18	1180	0.71	−0.36	1.07	867	0.31	0.15	1.42	831
	2008	0.77	0.46	1.00	685	0.59	−0.61	0.97	709	0.22	0.45	1.55	1019
Jun	2007	0.91	−0.11	1.07	1177	0.73	−0.27	0.86	737	0.20	1.25	2.13	856
	2008	0.87	−0.18	1.08	1155	0.94	−0.19	0.26	832	0.00	1.20	2.56	868
Jul	2007	0.76	−0.35	0.89	1254	0.20	0.13	0.99	864	0.08	0.97	1.64	854
	2008	0.82	−0.33	0.87	1162	0.17	0.11	1.21	982	0.06	0.96	1.58	986
Aug	2007	0.64	−0.17	1.24	1254	0.08	0.60	1.09	736	0.04	0.60	1.67	975
	2008	0.83	−0.16	0.62	1216	0.04	0.30	1.15	904	0.07	0.85	1.44	953
Sep	2007	0.86	0.21	1.24	1152	0.10	0.66	1.08	668	0.12	0.84	1.36	947
	2008	0.79	−0.16	0.70	792	0.14	0.57	1.17	686	0.10	1.02	1.36	891
Oct	2007	0.5	0.16	1.36	1109	0.36	−0.21	0.64	449	0.36	0.01	0.94	793
	2008	0.79	0.06	0.95	572	0.34	0.03	0.62	544	0.18	0.35	1.09	847
Nov	2007	0.79	0.09	0.76	891	0.60	−0.26	0.63	433	0.73	−0.24	0.93	616
	2008	0.10	0.44	0.80	648	0.41	−0.20	0.69	286	0.26	−0.11	1.48	837
Dec	2007	0.2	0.23	0.90	997	0.59	−0.20	0.46	375	0.69	−0.60	1.19	660
	2008	0.05	0.24	0.54	832	–	–	–	–	0.70	0.02	0.73	832

water fluxes characteristic of the other two more extreme sites: snow and low temperatures in the colder and more humid seasons, and drought in the warmer and more arid seasons.
- Finally, our results show that the EVI could be used to provide reasonably accurate estimates of GPP over a broad range of Mediterranean non forested ecosystems types. However, the EVI/GPP relationships vary between sites limiting their use at regional scales.

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