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Analyzing the major drivers of NEE in an alpine Mediterranean shrubland

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Two years of continuous measurements of net ecosystem exchange (NEE) using the eddy covariance technique were made over a Mediterranean alpine shrubland. These ecosystems are little studied, since they have little CO₂ exchange potential. Nevertheless, their high susceptibility to environmental changes is far from being understood, introducing some uncertainty in terrestrial CO₂ and water vapour assessments. High altitude sites might be undergoing a transition from sink to source of CO₂, due to their high vulnerability to climate change. Indeed, this ecosystem was found to be a net source of CO₂ (+52 g C m⁻² and +48 g C m⁻² for 2007 and 2008) during the two-year study period. To understand the reasons underlying this net release of CO₂ into the atmosphere, we analysed the drivers of seasonal variability in NEE across these two years. We observed that the soil water availability – driven by the precipitation pattern – and the photosynthetic photon flux density (PPFD) are the key factors for understanding both the carbon sequestration potential and the duration of the photosynthetic period during the growing season. Finally, the effects of the Burba correction for both NEE and evapotranspiration (ET) are evaluated. This correction can sometimes be neglected on a daily basis, but becomes rather important in long-term assessments. For instance, the annual CO₂ budget in 2007 turned from sink (–136 g C m⁻²) to source (+52 g C m⁻²) when the Burba correction was taken into account.

1 Introduction

The concentration of carbon dioxide and other greenhouse gases in the atmosphere has been increasing since the industrial revolution, and is believed to be causing global surface temperatures to rise (Forster et al., 2007). Global warming is a serious concern as it seems to be driving global climate change (IPCC, 2007). The consequences of climate change are far from being completely quantified, and of particular concern is its impact on terrestrial ecosystems.

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In the recent decades, the eddy covariance technique (Baldocchi, 2003) has emerged as one of the most reliable techniques for tracking gases with infrared absorption bands such as CO₂ and H₂O, the main greenhouse gases. The eddy covariance technique is currently applied worldwide covering many different terrestrial ecosystem types with the aim of understanding the positive or negative feedbacks that climate change will have on Earth's surface. These sites have been grouped into different continental networks assessing net ecosystem exchange (NEE) such as EUROFLUX (Aubinet et al., 2000), AmeriFlux (Pryor and Barthelmie, 1999), and ChinaFLUX (Yu et al., 2006) forming the global FLUXNET (Baldocchi et al., 2001). Nonetheless, gaps in knowledge regarding some ecosystems still lead to uncertainties in global assessments.

In this regard little is known about high altitude sites (Schimel et al., 2002). The mountain and alpine regions of the world cover 10% of the Earth's terrestrial surface (Spehn and Körner, 2005). Understanding the patterns and drivers of NEE in these environments is very important for accurate determinations of the global carbon budget and for creating new perspectives in policymaking (Mountain Research Initiative; Becker and Bugmann, 2001). However, these ecosystems are usually excluded by modellers because their verticality distinguishes them from the surrounding ecosystems at lower altitude. In fact, there is not much data available to parameterize or validate models on alpine shrublands.

The effect of climate change on the carbon balance of high altitude ecosystems is a pressing subject of debate (Becker and Bugmann, 2001). As global temperatures rise, an earlier snow melt results in a longer growing seasons which may lead to increased carbon assimilation (Lafleur and Humphreys, 2007). However, this increase in the growing season may result in a smaller carbon sequestration, as a result of water limitations (Hu et al., 2009). On the other hand, permafrost melt in the tundra, which arises after temperatures increase, is enhancing soil microbial respiration to a larger degree than photosynthetic carbon assimilation (Oechel et al., 1993). Understanding the complexity of biosphere-atmosphere interactions and the drivers of seasonal

changes in NEE in cold-limited, high altitude ecosystems is far from resolved, particularly for high-altitude shrublands, where eddy covariance stations are still lacking.

Another factor adding uncertainty to NEE estimates of extreme cold ecosystems is related to the anomalous downward CO₂ fluxes observed during off-seasons (Amiro et al., 2006a, b; Grelle and Burba, 2007; Ono et al., 2008) or during snow covered periods when assessed by open-path eddy covariance (Skinner, 2007; Lafleur and Humphreys, 2007). Small photosynthesis rates ($<0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$) have been observed over snow-covered vegetation (Starr and Oberbauer, 2003), if the snowpack is not too thick. However, the contribution of soil respiration through the snow cracks (soil temperatures are still high enough below the snowpack) should overcome any small uptake by photosynthesis (Musselman et al., 2005; Monson et al., 2006a). The recently-published Burba correction (Burba et al., 2008) rectifies such apparent net CO₂ uptake. The relevance of the Burba correction for the accurate determination of the carbon balance in cold ecosystems remains controversial. It has been experimentally observed that its contribution may be negligible at some sites (Haslwanter et al., 2009), but not elsewhere where caution has been urged in its use (Blanken et al., 2009).

In this study we present two years (2007 and 2008) of CO₂ fluxes over an alpine shrubland. The general goals of this paper are: a) to identify the main variables driving the annual behaviour on NEE, b) to examine, focusing mainly in 2007, the reason of seasonal and daily changes in NEE and c) to assess the role of the Burba correction for accurate measurements of the carbon balance.

2 Experimental site description and methods

2.1 Site description

The area of study is situated within an endorheic basin (2300 m a.s.l.) belonging to the Sierra Nevada mountain range, in the southeast of Spain (37°05' N 2°57' W), 39 km

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from the Mediterranean coast. The basin is an ancient cirque stemmed by a moraine and subsequently remodeled in the glacial age (Sánchez et al., 1988). Mean annual precipitation is 800 mm and mean annual temperature is 5.5 °C (Aguilar et al., 1986).

The site is usually snow covered from December to March. The subsequent snow melt causes water to flow across the basin and accumulate at the bottom creating a small lagoon that usually remains for approximately one month during the onset of the growing season. The flux tower is situated on a gentle slope separated from the lagoon by a fetch exceeding 150 m.

Festuca indigesta and *Cytisus purgans* are the dominant plant species, reaching to 20 cm height and homogeneously covering 45% of the ground. A remaining part of 35% corresponds to litter and 20% is bare soil. The presence of other plant species is intermittent throughout the year, and very sparse. Measurements of leaf area index (LAI), assessed with destructive methods, provided an average value of 1.23 which is approximately constant across the seasons.

The soil is composed of sand (56%), silt (30%) and clay (14%) with a bulk density of 1110 kg m⁻³, determined in situ using soil cores. The permanent wilting point was estimated to occur as volumetric water content is below 2.6%. Organic matter ranged from 3.9% to 4.6% in the area around the flux tower. Soil analysis were conducted following recommendations from the American Society of Agronomy and Soil Science Society of America (Klute, 1986; Sparks, 1996).

2.2 EC and meteorological and soil measurements

Carbon dioxide and water vapor densities along with the 3 components of wind speed were measured at 20 Hz using an open-path infrared gas analyzer (IRGA, Li-7500, Lincoln, NE, USA) and a sonic anemometer (USA-1, METEK, Elmshorn, Germany), fixed to a tower at 2.25 m above ground. Data were collected as 5-s averages, variances and covariances by a logger (METEK, Elmshorn, Germany). We applied 2-D coordinate rotations (McMillen, 1988; Kowalski et al., 1997), density corrections (Webb et al., 1980) and the Burba correction (Burba et al., 2008) as well as a quality control checks

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with home-made MATLAB routines. The IRGA was calibrated bimonthly (except when weather limited access to the site) with gas standards of N₂ for zero and 479.5 ppm as a span CO₂ reference.

Air temperature and humidity were measured by a thermohygrometer (STH-5031, Geonica, Madrid, Spain) at 1.5 m above the ground. Incident and reflected photosynthetic photon flux densities (PPFD) were measured by two quantum sensors (Li-190, Li-cor, Lincoln, NE, USA), also at 1.5 m. Net radiation was measured with a net radiometer (CN1-R, Middleton Solar, Brunswick, Australia) at 1 m above the surface. Rainfall was measured by a tipping bucket (0.2 mm) rain gauge (PLUVIOM 52203, RM Young, Traverse city, MI, USA). Below ground, six heat flux plates were distributed both under bare soil and under plants, buried at 8 cm to assess the soil heat flux (HFP01, Hukseflux thermal sensors, Delft, Netherlands). Three temperature and soil water content (ECH2O, Decagon Devices, Pullman, WA, EEUU) sensors were also installed at 4 cm depth under both bare soil and plant cover having a sensitivity of 0.1 °C and 0.2%, respectively. These measurements were made at 1 Hz, but then 10-min-averaged and stored in data loggers (Meteodata 3000c, Geonica).

2.3 Data quality control, gap filling and statistical analysis

The 5-s data that did not satisfy a de-spiking routine were eliminated. Half-hours statistics were not computed when eliminated data exceeded 25% of the total. The subsequent processed half-hour statistics were also excluded from further analysis when rain or condensation (including frequent fog or dew) caused poor performance of the open-path IRGA. Nighttime data below the u_* threshold of 0.2 m s⁻¹ were also rejected for not fulfilling the turbulence measurement premise (Carrara et al., 2003; Wohlfahrt et al., 2005). There were 16% and 20% of gaps in the 2007 and 2008 datasets due to electronic malfunction, calibration, power outages and poor performance of the anemometer and Li-7500 during inclement meteorological conditions. Nights lacking turbulence resulted in 11% and 9% of data removed from 2007 and 2008 dataset. Finally, 6% and 3% were also rejected, respectively from the two years due to spikes on half-hour

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timescales. To obtain a continuous dataset for assessing the annual NEE, data were gap-filled following (Falge et al., 2001; Reichstein et al., 2005).

3 Results and discussion

3.1 Meteorological conditions in 2007 and 2008

5 Both years showed very similar patterns of air and soil temperature and PPFD (Fig. 1a–c). In fact, annual mean air temperature was 5.8°C in both years and PPFD averaged 37.6 mol m⁻² d⁻¹ in 2007 and 35.4 mol m⁻² d⁻¹ in 2008. Annual rainfall was 402 mm in 2007 and 390 mm in 2008. Our precipitation measures are likely underestimated during winter, since rain gauges are not designed to measure solid precipitation.
10 Furthermore, thirty-seven days of rain-gauge measurements were missing during 2008, due to instrument malfunction and bad weather. However, soil water content (SWC) at the end of this 37-day period (DOY 129) was comparable for both years (12.6% for 2007, and 13.6% for 2008), suggesting that precipitation, at least during the last days of this period, was comparable.

15 3.2 Winter/spring dynamics and the onset of the first growing season

Although no differences were apparent in annual temperature or precipitation, we did observe important differences on seasonal and weekly scales, which developed into large annual NEE differences. For instance, some snow fall events (Fig. 1d), assessed via the reflected/incident PPFD ratio, occurred at different times of the year, and nearly
20 three times as much rain fell during summer in 2007 (42 mm) than in 2008 (15 mm) (Fig. 2a and b).

Differences in the time courses of precipitation and temperature appear to have affected the onset of the growing season as reflected in the temporal trend in NEE between both years (Fig. 2c and d). The low values of NEE between the days 70 and

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77 seem to indicate an early onset of the growing season in 2007. However, a sudden rainfall (Fig. 2a) on day 78, enhancing soil respiration, and subsequent considerable snow cover that began day 85, prevented growth development. Indeed, favourable synoptic weather conditions in early spring (days 125 to 150) appear to be fundamental, marking the onset of the growing season and the transition from source to sink of CO₂.

During this time, air temperature and PPFD were much higher in 2007 than in 2008 (Fig. 1a and c), probably due to decreased cloudiness in the 2007 early spring. Although the transition from source to sink of CO₂ happens between days 125–150 in both years, the strength of the CO₂ sink is higher in 2007 than in 2008. This indicates that air temperature and PPFD are key variables driving the onset of the growing season. Water availability is seldom a limiting factor during the alpine Mediterranean spring (SWC was much higher than the permanent wilting point, around 15.4% in 2007 and 15.7% in 2008). In fact, there was more rainfall and therefore higher SWC in 2008, as compared to 2007 (Fig. 2a and b) in this period, which supports the notion that temperature and PPFD, and not precipitation, control the onset of the growing season. Maximum daily CO₂ uptake in 2007 was -2.2 g C m^{-2} , and took place around mid June (DOY 167), whereas maximum daily CO₂ uptake in 2008 was lower (-2 g C m^{-2}) and happened approximately one month later (Fig. 2c and d).

3.3 Summer dynamics and the end of the first growing season

Maximum ecosystem carbon assimilation occurred during mid June (DOY 167) and mid July (DOY 200) in 2007 and 2008, respectively. During this period, the ecosystem was characterized by mild air temperatures and high PPFD, which would favour the photosynthetic period to continue. However, after that time the lack of water resources (Fig. 2a and b), which arises from the typical summer drought in the Mediterranean, starts to limit photosynthetic activity, and strongly constrains NEE (Fig. 2c and d).

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3.4 Autumn dynamics and the onset of the second growing season

The lack of water resources limits biological activity by the mid and late summers (from DOY 163 and 200 on) of 2007 and 2008, respectively. Even so, some photosynthesis continues, as hydrological resources from the soil water stock are still available. This trend continues until the last days of summer when the first rains come after a long dry period. These autumn rains were accompanied by soil remoistening (Fig. 2a and b) that activated heterotrophic respiration, causing large, sudden releases of carbon (Huxman et al., 2004). These new water inputs ease plant stress and foster tissue repair and rehydration in the days following rainfall (Sala et al., 1982). Such plant recovery, which may last up to 7 days (Sala et al., 1982), provokes NEE to turn negative again, starting a second growing season (around day 250 of Fig. 2c). This phenomenon is characteristic of Mediterranean climates where the first rains after a long drought period usually arrive either in the last days of the summer or in the first days of autumn, and summer-like meteorological conditions continue afterwards for a while (the so-called *Veranillo de San Miguel*). The extended sunny period that favoured the 2007 growing season, right after the first summer/autumn rains, did not take place during 2008.

3.5 Diurnal and monthly differences between 2007 and 2008

Some diurnal differences are encountered between the two years. Figure 3a and b represents the daily evolution of NEE throughout the year 2007 and 2008, respectively. We found that CO₂ uptake follows PPFD throughout each year, except during precipitation or water stress, which alter the relationship between PPFD and NEE. The same figure also displays asymmetry in NEE around noon. A higher daily uptake, peaking around 10 h, is found in 2007 and between 9 h and 12 h in 2008. The means for months of higher photosynthetic activity are displayed in Fig. 4, which further shows such asymmetry: maximum uptake before noon and subsequent NEE reduction in the afternoon. This afternoon depletion may also be observed in the daily relationship between NEE and PPFD, such that NEE was more negative for a given level of PPFD

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in the morning that in the afternoon (Fig. 5), representing hysteresis. This could be due to a series of interacting factors, which may be viewed as either environmental or endogenous (that is, resulting from plant behaviour). Temperature is typically higher in the afternoon than in the morning for a given level of PPFD, which could stimulate soil respiration. Figure 6a displays different nocturnal respiration trends as a function of temperature for different classes of SWC. We found positive exponential trends for every SWC class ($R^2=0.56$ for $SWC<18\%$, $R^2=0.80$ for $12\%<SWC<18\%$ and $R^2=0.51$ for $8\%<SWC<12\%$) except for the lowest values ($SWC<8\%$), for which warming, such as that in the afternoon, does not increase soil respiration. When the light-response curve (Fig. 6b) is plotted for such a dataset ($SWC<8\%$) a clear hysteresis cycle is observed. Thus, afternoon NEE reduction appears not to be due exclusively to an enhancement of soil respiration in the afternoon.

There are several factors that can potentially interact to shape the observed hysteresis in NEE-PPFD relationship. First, as the Bowen ratio and VPD increase at midday, stomatal conductance drops to avoid runaway cavitation (Tyree and Sperry, 1988), at the expense of diminishing carbon uptake. Water stored within the stem xylem diminishes during the day such that, after midday stomatal closure, plants are not fully capable of recovering the level of stomatal conductance they had in the morning (Sperry et al., 2008; Hölttä et al., 2009). Second, the accumulation of sugars within a leaf may lead to a feedback inhibition of rubisco activity (Lambers et al., 1998). Third, daily patterns of carbon assimilation have been shown to undergo circadian regulation, such that plants are “programmed” to have a higher carbon uptake in the morning than in the afternoon, independent of environmental factors (Webb, 2003; Doughy et al., 2006; Resco et al., 2009).

3.6 Annual differences between 2007 and 2008

Differences in the length and strength of the growing season and in the timing of the rain and snow fall seem to be responsible for general NEE disparities between the two years. The study site is a net source of CO_2 during both years. Annual emissions of

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CO₂ were +52 g C m⁻² and +48 g C m⁻² for 2007 and 2008, respectively. These differences are due mainly to disparities in carbon uptake during the growing season. The growing season of 2007 was shorter and more skewed than that of 2008 (Fig. 2c and d). It lasted longer in 2008 and presented a less steep slope, but ultimately with less area and therefore less CO₂ uptake. Rain pulse events following long dry periods took place in both years bringing about large emissions, but in different amounts depending on their timing. Both years presented large releases during the first 125 days contributing for being large source of carbon. Each of three events of snowfall and thawing during these 125 first days of 2007 (Fig. 1d) may have contributed to net release (Monson et al., 2006a). Snow inhibits the photosynthetic activity covering the vegetation leaves, but not bacterial processes since the snow cover prevents soil temperature from lowering excessively (Monson et al., 2006b). During snow-covered periods respiration is expected to dominate NEE, and therefore the timing of snows-thaws may also account for annual differences between the two years.

3.7 The Burba correction

Although some have claimed the Burba correction to be negligible (Haslwanter et al., 2009) or even problematic (Wohlfahrt et al., 2008), we found it to be very important for our experimental site. Figure 7 shows daily NEE with and without the correction during the first weeks of 2007. The shaded areas indicate periods of snow cover. It is evident that the final Burba-corrected CO₂ flux is larger than the uncorrected CO₂ flux. During the first week-long snow period, an apparent net uptake of 0.38 g C m⁻² is corrected to yield an emission of 3.8 g C m⁻², which seems much more reasonable as the average air temperature during these 7 days was just 3.4 °C and the ecosystem was completely snow covered. A second snowfall took place on day 23, where non-corrected values estimated six days of implausible uptake, which disappears once the correction is applied.

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The Burba correction eliminates apparent uptake, and also introduces a nearly constant increment that strongly affects long-term integrations. In fact, it is so important as to reverse conclusions regarding the annual CO₂ source/sink behaviour. Figure 8a displays the cumulative NEE throughout the year 2007, yielding -135 g C m^{-2} without correction versus a source of 52 g C m^{-2} when applying the Burba considerations. For the year 2008 applying the Burba correction converted an annual CO₂ sink of -100 g C m^{-2} that turns to a source of 48 g C m^{-2} (data not shown).

Figure 8b shows cumulative evapotranspiration (ET) for the year 2007. In contrast to the cumulative NEE, the effect of applying the correction changes to a lesser extent. The corrected data yield an annual ET of 386 mm, versus a non-corrected value of 346 mm. These small differences in ET are similarly reflected at the daily timescale ($<1\%$). Differences in ET when the correction is applied are in fact bigger than differences in NEE, but not in relative terms. The annual balance is hardly affected, since the Burba correction has its greatest impact during extreme cold when ET and water vapor densities are minimal.

4 Conclusions

Seasonal variability in NEE at this high-altitude ecosystem seems to be mainly driven by the interaction between PPFD and precipitation/snow and to some extent to one or more environmental or endogenous factors on daily timescales. When snow covers the site, respiration dominates over photosynthetic processes. During spring when snow melts, moistening soil and roots, increases in temperature and PPFD drive the beginning of the growing season. At this point fair weather conditions are fundamental for development of the growing season, not only for high uptake rates but also for enduring uptake. The lack of water resources in the soil likely halts the growing season, thus reducing the uptake period. From that time on, water limitation is the major driver of carbon fluxes (Granier et al., 2007) until the first rains arrive after a dry summer. Once the soil is remoistened, large respiration rates occur followed by a second uptake season

during late summer or early fall if meteorological conditions permit. Hysteresis was found in the light response curves that we attributed to endogenous or environmental factors, or to both of them.

Although some have found a negligible effect when applying the Burba correction, it may have profound impacts on annual budgets. Such bias may not be evident for ecosystems with great CO₂ exchange potential, but large relative changes are observed here. The Burba correction strongly affects annual NEE of CO₂, converting the system from sink to source, but influencing the annual ET budget to a far lesser extent. Apparently, this correction is necessary for achieving credible carbon exchange measurements in very cold conditions, particularly for ecosystems with near-neutral capacity as carbon sources/sinks.

Our alpine site was a carbon source for both 2007 and 2008. It may be that high-altitude ecosystems are undergoing a CO₂ uptake depletion in the same manner as tundra sites (Oechel et al., 1993). The study site may have been a carbon sink in previous years, but the enhancement of the mean global temperature and the reallocation of the rain patterns as a consequence of the climate change might have caused a positive feedback, at least temporarily, turning our ecosystem into a net carbon source. There is therefore a pressing need to develop longer time series to address how alpine shrublands may respond to climate change.

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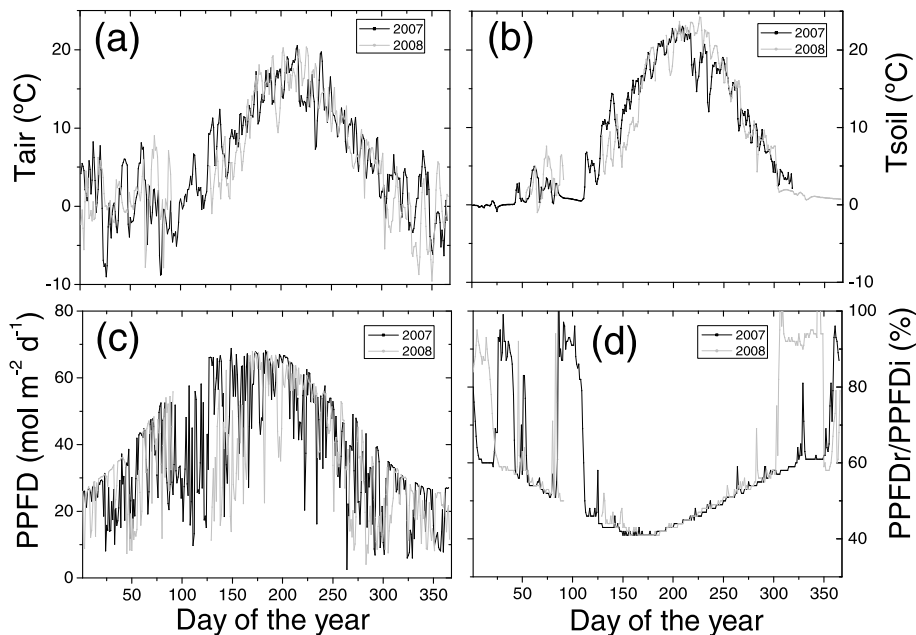


Fig. 1. Average daily environmental conditions in the alpine Mediterranean shrubland located in Sierra Nevada mountain range (southeast of Spain). **(a)** Air temperature, **(b)** soil temperature, **(c)** absorbed photosynthetic photon flux density, **(d)** reflected to incident photosynthetic photon flux density.

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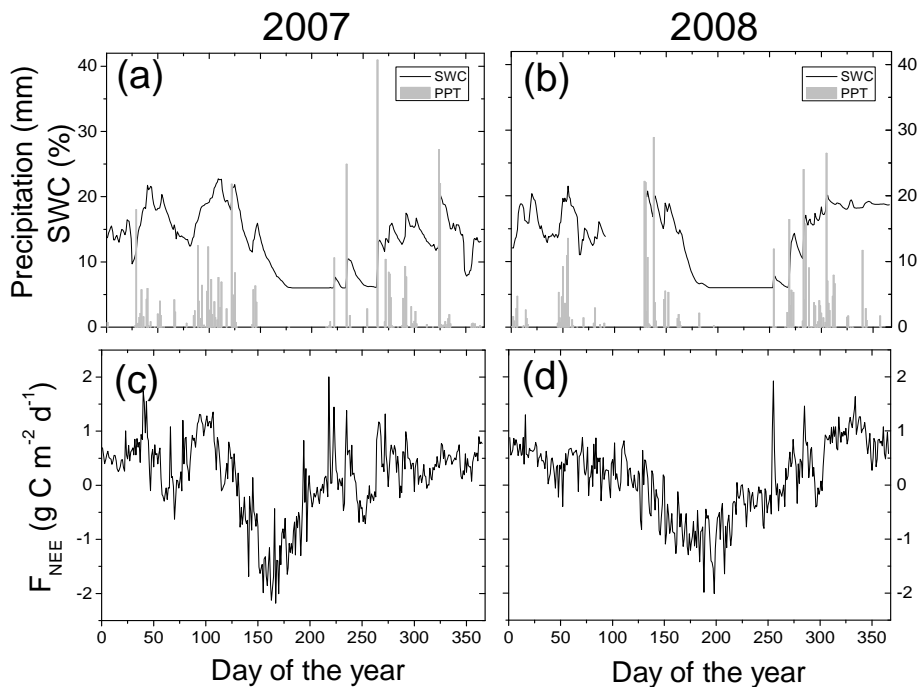


Fig. 2. Average daily environmental conditions in the alpine Mediterranean shrubland located in Sierra Nevada mountain range (southeast of Spain): **(a)** precipitation (grey bars) and soil water content throughout 2007, **(b)** precipitation (grey bars) and soil water content throughout 2008, **(c)** net ecosystem exchange in 2007, **(d)** net ecosystem exchange in 2008.

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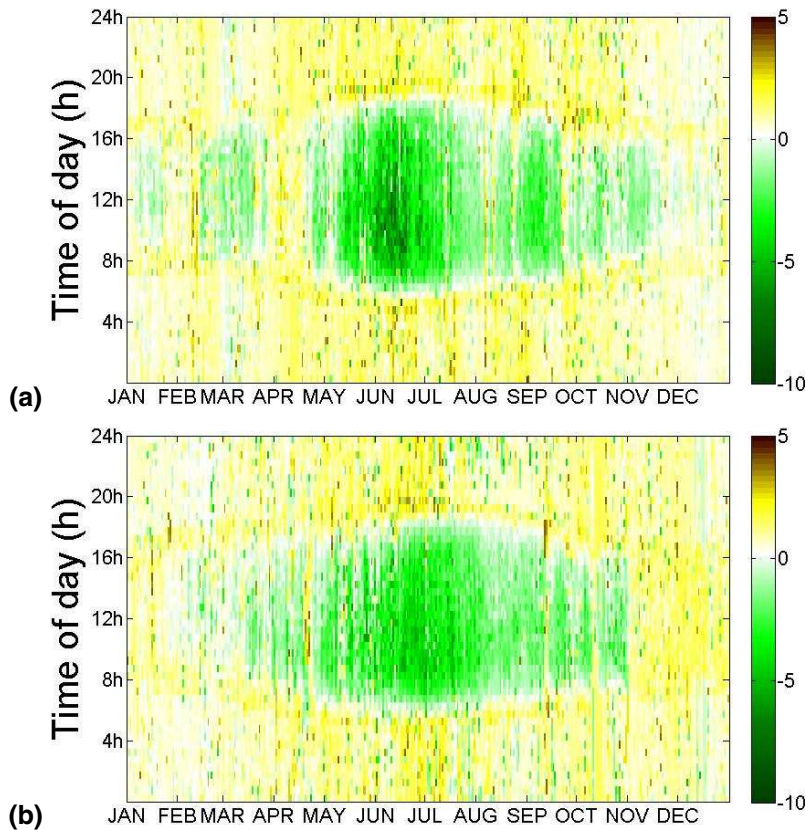


Fig. 3. (a) Annual and daily evolution of NEE flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in 2007 in the alpine Mediterranean shrubland located in Sierra Nevada mountain range. (b) Annual and daily evolution of NEE flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in 2008 in the alpine Mediterranean shrubland located in Sierra Nevada mountain range.

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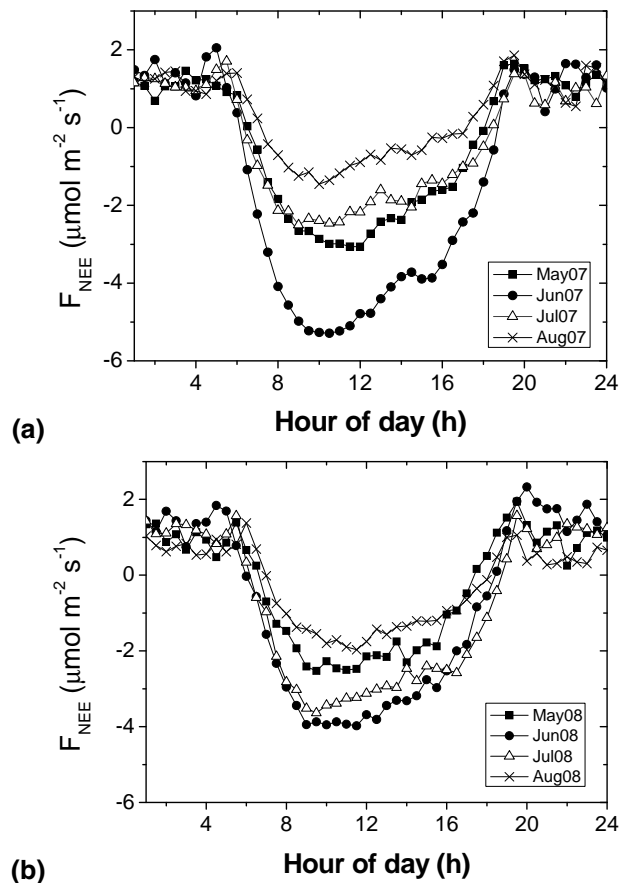


Fig. 4. (a) Mean diurnal NEE flux during May, June, July and August 2007 in the alpine Mediterranean shrubland located in Sierra Nevada mountain range. (b) Mean diurnal NEE flux during May, June, July and August 2008 in the alpine Mediterranean shrubland located in Sierra Nevada mountain range.

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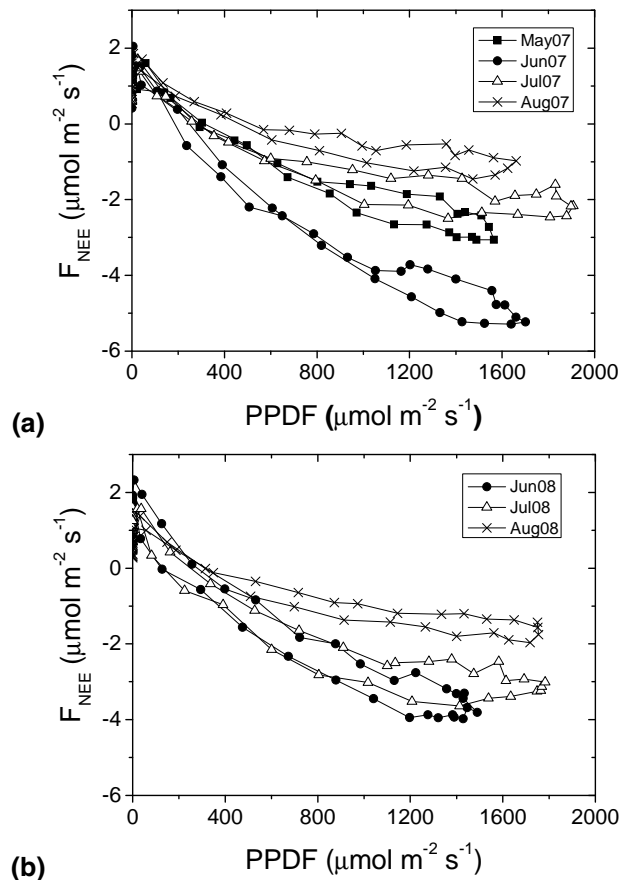


Fig. 5. (a) Mean hourly NEE flux vs. PPFD during May, June, July and August 2007. Hysteresis was found for every month, with the temporal trend proceeding counter-clockwise. **(b)** Mean hourly NEE flux vs. PPFD during June, July and August 2008. Hysteresis was found for every month, with the temporal trend proceeding counter-clockwise. May was removed for lack of data.

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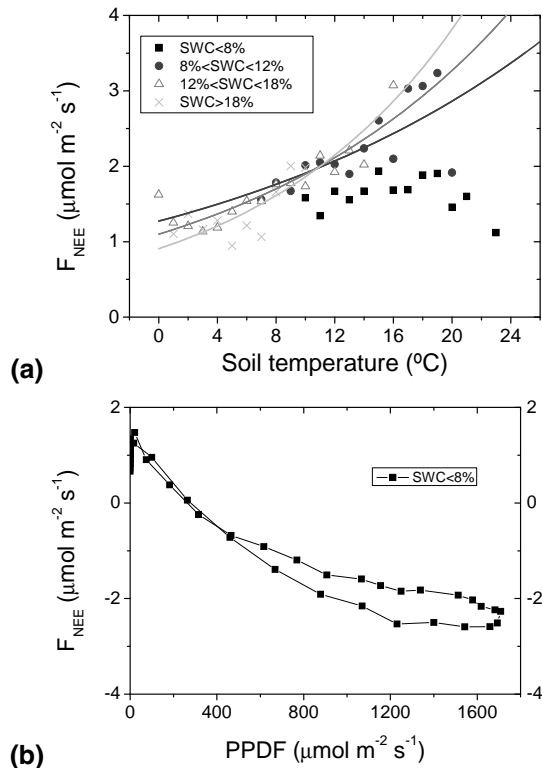


Fig. 6. (a) Mean nocturnal NEE in 2007 vs. soil temperature for different soil water content classes. Three classes of SWC (those for SWC > 8%) were fitted to exponential dependency with soil temperature (fine line: SWC > 18%; medium line: 12% < SWC < 18%; dark line: 8% < SWC < 12%). No good agreement was found for SWC < 8%. (b) Mean hourly NEE flux vs. PPDF for SWC < 8% in 2007. Clear hysteresis was found for lowest SWC values. NEE flux for the lowest values of SWC does not present any increasing relationship with temperature (a), however, it does present a clear hysteresis cycle indicating that afternoon soil temperature enhancement (and soil respiration with it) is not the explanation for hysteresis.

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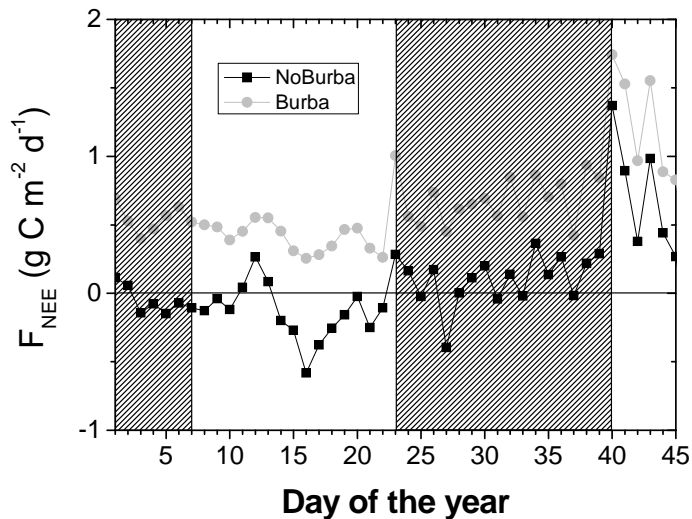


Fig. 7. The NEE flux during the first 45 days of 2007. Black line with squared points is the NEE flux with no correction. Grey line with round points is the same NEE but corrected. Shaded areas show periods when the ecosystem was snow-covered. Some snowed days have an apparent downward CO₂ flux when not correction was applied. The NEE flux corrected from Burba is always above the non-corrected one.

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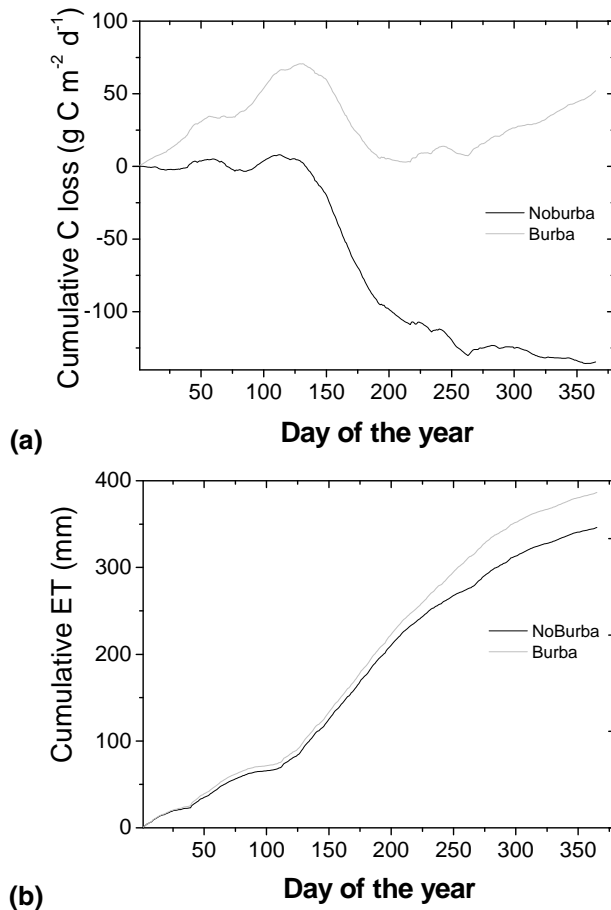


Fig. 8. (a) Cumulative net ecosystem exchange (g C m^{-2}) through the year 2007 (black line without and grey line with the Burba correction applied). (b) Cumulative evapotranspiration (mm) throughout the year 2007 (black line without and grey line with the Burba correction applied).

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