Variations in daytime net carbon and water exchange in a montane shrubland ecosystem in southeast Spain

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Abstract

Carbon and water fluxes in a semiarid shrubland ecosystem located in the southeast of Spain (province of Almería) were measured continuously over one year using the eddy covariance technique. We examined the influence of environmental variables on daytime (photosynthetically active photons, F_P >10 μmol m^{-2} s^{-1}) ecosystem gas exchange and tested the ability of an empirical eco-physiological model based on F_P to estimate carbon fluxes over the whole year. The daytime ecosystem fluxes showed strong seasonality. During two solstitial periods, summer with warm temperatures (>15 ºC) and sufficient soil moisture (>10 % vol.) and winter with mild temperatures (>5 ºC) and high soil moisture contents (>15 % vol.), the photosynthetic rate was higher than the daytime respiration rate and mean daytime CO_2 fluxes were *ca.* –1.75 and –0.60 μmol m^{-2} s^{-1}, respectively. Daytime evapotranspiration fluxes averaged *ca.* 2.20 and 0.24 mmol m^{-2} s^{-1}, respectively. By contrast, in summer and early autumn with warm daytime temperatures (>10 ºC) and dry soil (<10 % vol.), and also in mid-winter with near-freezing daytime temperatures the shrubland behaved as a net carbon source (mean daytime CO_2 release of *ca.* 0.60 and 0.20 μmol m^{-2} s^{-1}, respectively). Furthermore, the comparison of water and carbon fluxes over a week in June 2004 and June 2005 suggests that the timing—rather than amount—of spring rainfall may be crucial in determining growing season water and carbon exchange. Due to strongly limiting environmental variables other than F_P, the model applied here failed to describe daytime carbon exchange only as a function of F_P and could not be used over most of the year to fill gaps in the data.

Additional key words: carbon dioxide flux; eddy covariance; phenology; photon flux density; shrubland; water vapour flux.

Introduction

Arid and semiarid ecosystems exist on every continent and comprise nearly a third of the total land surface (Schlesinger *et al.* 1990, Okin 2001). Semiarid lands are the dominant ecosystems in Mediterranean climates, and are characterised by patches of vegetation and bare soil (Domingo *et al.* 1999). Such ecosystems are very sensitive to perturbations such as climate change, fire, drought, and land use (Smith *et al.* 2000, Asner *et al.* 2003). However, little is known about their functional behaviour, including processes of CO_2 and water vapour exchange with the atmosphere. This information is essential in order to achieve reliable regional (and ultimately global) estimates of carbon and water cycling, as well as to predict the response of semiarid ecosystems to climate change.

In addition to the absorbed flux of photosynthetically active photons (F_P), any number of environmental variables—air temperature (T_a), soil water content (SWC), and vapour pressure deficit (VPD)—and the phenological state of vegetation may strongly influence carbon uptake in semiarid ecosystems. Furthermore, biological resources such as water and nutrients, and consequently plant biomass, typically undergo periods of high and low availability in these ecosystems

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(Schwinning and Sala 2004). Short periods of high resource availability can be triggered by rainfall events (Schwinning and Sala 2004), as modelled by the "pulse-reserve" paradigm (Noy-Meir 1973). In the last decades many measurements and modelling studies have been carried out in temperate forest ecosystems and have yielded reliable estimates of their carbon and water balance. However, despite their complexity, arid and semiarid ecosystems have received little attention and great uncertainty remains on their contribution to the global carbon balance. Thus, the interest in obtaining a better understanding of relationships between environmental variables, precipitation, and ecosystem processes in arid and semiarid lands has increased in recent years.

Here we present data on seasonal variations in the daytime (F_P >10 μmol m^{-2} s^{-1}), CO_2 flux (F_C), and evapotranspiration (E) by a semiarid montane shrubland ecosystem as adaptations to relatively extreme environmental conditions. We examined the influence of several environmental variables on ecosystem daytime gas exchange and the importance of precipitation timing in determining the phenological cycle and productivity of this ecosystem. We also explored the relationship between daytime ecosystem gas exchange and F_P as a first step towards modelling the functional behaviour of this ecosystem that is distinct from the behaviour of well-known temperate forest ecosystems.

Materials and methods

Field site: The study was carried out at "El Llano de los Juanes", a shrub-land plateau at 1 600 m altitude in the Sierra de Gádor (Almería, Southeast Spain; 36º55'41.7''N; 2º45'1.7''W). The site is characterized by a semiarid montane Mediterranean climate, with a mean annual temperature of 12 ºC and mean annual precipitation of *ca.* 475 mm, falling mostly during autumn and winter, and by a very dry season in summer.

The parent soil material of the ecosystem is a dark dolomite with a layered distribution and 30–40 % rock fragment content. Soils are classified as *Lithic Haploxeroll* (Soil Survey Staff 1999) with two horizons: surface "A" (0–10 cm) with silt loam texture and subsurface "B" (10–35 cm) with clay loam. These characteristics explain the high water retention (14.3 and 22.8 mm in horizons A and B, respectively) (Solé-Benet, personal communication).

The vegetation is bio-diverse and somewhat sparse with predominance of two perennial species, *Festuca scariosa* (Lag.) Hackel (19.0 %) and *Genista pumila* (Vierh) ssp. *pumila* (11.5 %). These two show the highest abundance (Moro, personal communication), but many species such as *Hormathophylla spinosa* (L.) P. Küpfer, *Thymus serpylloides* Bory, *Phlomis lychnitis* L., *Lavandula lanata* Boiss, *Salvia lavandulifolia* Vahl., and *Eryngium campestre* L. are also present. The average height of the vegetation is *ca.* 0.5 m, although some species can reach up to 1.2 m, such as *Festuca scariosa* when it is in flower.

Field measurements: Fluxes of CO_2 and H_2O were estimated from 10 Hz eddy covariance measurements mounted at the top of a 2.5 m tower. Densities of CO_2 and H_2O were measured by an open-path infrared gas analyser (*Li-Cor 7500*, Lincoln, NE, USA), calibrated monthly using an N_2 standard for zero and a 508.3 μmol(CO_2) mol^{-1} gas standard [and 479 μmol(CO_2) mol^{-1} since December, 2004] as a span. Wind speed and sonic temperature were measured by a three-axis sonic anemometer (*CSAT-3*, *Campbell Scientific*, Logan, UT, USA).

Air temperature and humidity were measured by a thermohygrometer (*HMP 35C*, *CSI*, USA) at 1.5 m above the surface, and used to calculate vapour pressure deficit (VPD). Soil water content (SWC) was measured by a water content reflectometer (*CS615*, *CSI*) at 15 cm depth. Rainfall was measured by a tipping bucket (0.2 mm) rain gauge (model *785 M*, *Davis Instruments Corp.*, Hayward, CA, USA). Fluxes of incident and reflected photons in photosynthetic wavelengths, measured by two quantum sensors (*Li-190*, *Li-Cor*, Lincoln, NE, USA) at 1.5 m over a representative ground surface (with mixed plant cover and bare soil/rock) were used to determine F_P.

A data-logger (*CR23X*, *CSI*) managed the measurements and recorded the data. Means, variances, and covariances of 10 Hz data were calculated and stored every 15 min. Environmental and soil measurements made every 10 s were stored as 15 min averages. Eddy flux corrections for density perturbations (Webb *et al.* 1980) and coordinate rotation (McMillen 1988) were carried out in post-processing, as was the conversion to half-hour means following Reynolds' rules (Moncrieff *et al.* 1997).

The one-sided leaf area index (LAI) was estimated for the five most abundant species from reflectance measurements with an Agricultural Digital Camera (*ADC*, *Dycam*, Woodland Hills, CA, USA). The ADC records images with 495×365 pixels using an 8.5 mm lens and 8.5 mm focal length. Brightness values were measured with a charge-coupled device (CCD) consisting of a colour filter array sensitive to red and near-infrared wavelengths. The images were processed with specific software delivered with the camera that allows selection of a training area for the canopy species and calculation of NDVI or other vegetation indices. In our study, LAI values were calculated from an NDVI-LAI relationship obtained by correlating NDVI values from the ADC camera with LAI values from destructive sampling.

Data analysis: To examine the influence of environmental variables (T_a, SWC, and VPD) on daytime ecosystem gas exchange, representative data were selected as one "complete" week (few gaps in eddy covariance measurements) for each month from May 2004 to February 2005. The 3rd week of each month was selected except for July 2004 and December 2004 when, because of data gaps, the 1st and the 4th week were selected, respectively.

The relationship between F_C and F_P was explored for half-hour data from complete weeks belonging to representative months of the four seasons: June, August, and October 2004 and January 2005. Night time flux data are not presented here.

Empirical model: Daytime half-hour data were fitted using an empirical hyperbolic model (Hunt *et al.* 2002, Kowalski *et al.* 2003, Hasting *et al.* 2005) to test the ability of the following model to describe the anticipated dependence of F_C [μmol m^{-2} s^{-1}] on F_P [μmol m^{-2} s^{-1}]:

$$F_C = \frac{a_1 F_P}{a_2 + F_P} + R_D \quad (1)$$

where a_1 and a_2 [μmol m^{-2} s^{-1}] are constants and R_D [μmol m^{-2} s^{-1}] represents daytime respiration. The ecophysiological interpretation of fitted model parameters describes a_1 as the maximum photosynthetic uptake, and a_1/a_2 the initial slope of the irradiance response, sometimes termed apparent quantum yield or efficiency (Suyker and Verma 2001). This model has been used to fill daytime gaps in the estimation of long-term NEE (net ecosystem exchange) in grasslands (Hunt *et al.* 2002), temperate forest ecosystems (Kowalski *et al.* 2003), and even for desert shrubs (Hasting *et al.* 2005).

Results

Seasonal variation in environmental conditions: Over the study period, rainfall and F_P were strongly asynchronous (Fig. 1*A,B*). With the exception of a rainy May 2004, rain fell mostly in late autumn and winter, when F_P reached its minimum value. Light rainfall events (*ca.* 1 mm) were observed during summer, whereas winter events were more frequent and substantive (*ca.* 5 mm), mostly during cool spells in December 2004 and February 2005. The absorbed photon flux (F_P) showed maximum values during summer (*ca.* 1 050 μmol m^{-2} s^{-1}), decreased through autumn, and fell to 50 % of the summer maximum by winter (*ca.* 550 μmol m^{-2} s^{-1} in February 2004). Snowfall was prominent during the 2004/2005 winter. Nevertheless, winter precipitation was very low (96 mm) during this cold dry period, which was followed by a dry spring. Despite proximity to the coast, the temperature variability was near-continental, ranging from a maximum of 33 ºC at midday in August 2005 to a minimum of –14 ºC during one night in January 2005 (Fig. 1*C*).

Seasonal variation in carbon and water fluxes: The mean daytime *E* decreased constantly after June 2004, when it showed its maximum (*ca.* 2.06 mmol m^{-2} s^{-1}) and reached a minimum of *ca.* 0.20 mmol m^{-2} s^{-1} in December 2004 (Fig. 1*D*). Thereafter it began to increase again through the winter, reaching spring values in February 2005 (*ca.* 1.19 mmol m^{-2} s^{-1}). Unlike *E*, the daytime F_C did not vary smoothly across the seasons (Fig. 1*D*). In early summer, relatively humid air (VPD <17 hPa) and higher SWC (*ca.* 11 % vol.) corresponded to a mean daytime carbon uptake, with NEE of *ca.* –2.11 μmol m^{-2} s^{-1} (Fig. 1*E*). By August and September 2004, when VPD reached the highest values (*ca.* 23 and 19 hPa, respectively) and SWC the lowest ones (*ca.* 9 % vol.), the mean daytime NEE represented a source of

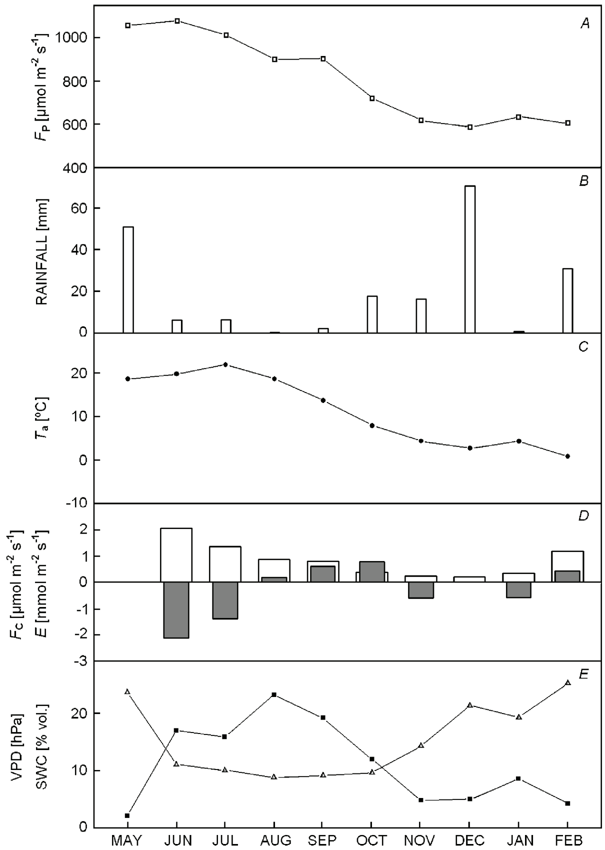

Fig. 1. Mean daytime environmental conditions and gas exchange in the montane shrubland "*El Llano de los Juanes*" from May 2004 to February 2005. (*A*) The absorbed flux of photosynthetically active photons, F_P. (*B*) Total (day and night) rainfall [mm]. (*C*) Air temperature, T_a. (*D*) Evapotranspiration, *E* (*white bars*) and CO_2 flux, F_C (*gray bars*). (*E*) Soil water content, SWC (*white triangles*) and vapour pressure deficit, VPD (*black squares*).

ca. 0.20 and 0.61 μmol m^{-2} s^{-1}, respectively. The shrubland also was a source of CO_2 during October 2004, even though VPD was less than 15 hPa and soil moisture was *ca.* 11 % vol. after the first light rain events. Not until well into the rainy period (November 2004) when SWC reached 14 % vol., did uptake again characterise the daytime F_C (*ca.* –0.60 μmol m^{-2} s^{-1}). During cold spells in winter (December 2004 and February 2005), when daytime temperatures fell near freezing, the ecosystem turned into a daytime carbon source (*ca.* 0.01 and 0.43 μmol m^{-2} s^{-1}, respectively). However, during January 2005, daytime temperatures increased remarkably exceeding 10 ºC, and the ecosystem became for this period a daytime CO_2 sink (NEE of *ca.* –0.60 μmol m^{-2} s^{-1}).

Functional relationships between environmental variables and daytime carbon exchange: Fig. 2 presents relationships between F_C and F_P over a week for every season. As shown in Fig. 2*A*, the empirical hyperbolic model (light response) that we used described the data well in June 2004 (with R_D = 0.73±0.27 μmol m^{-2} s^{-1}, a_1 = –4.5±0.2 μmol m^{-2} s^{-1}, and a_2 = 330±80 μmol m^{-2} s^{-1}), when daytime NEE changed rapidly from release of *ca.* 0.73 μmol m^{-2} s^{-1} in the dark to uptake of *ca.* 1.21 μmol m^{-2} s^{-1} at F_P of only 250 μmol m^{-2} s^{-1}; with further increasing irradiance, uptake increased more slowly and reached saturation at F_P of *ca.* 1 500 μmol m^{-2} s^{-1}. However, during other periods the model was clearly inadequate. In August 2004 (Fig. 2*B*), when SWC was less than 9 % vol. and mean daytime T_a was *ca.* 19 ºC, although F_P reached its maximum levels, the ecosystem was neither a daytime source or a sink of CO_2 for VPD <20 hPa, but it became an increasing daytime source of CO_2 for F_P values higher than 1 000 μmol m^{-2} s^{-1} and VPD >20 hPa. In October 2004 (Fig. 2*C*), when SWC was *ca.* 10 % vol. and mean daytime T_a was *ca.* 8 ºC, the ecosystem was a CO_2 source for values of F_P higher than 500 μmol m^{-2} s^{-1}. Finally, in January (Fig. 2*D*), when SWC was higher than 19 % vol. and mean daytime T_a was *ca.* 4 ºC, the ecosystem was again a daytime CO_2 sink but the correlation between F_C and F_P indicated that a linear empirical model would fit the data better than the empirical hyperbolic model (linear model r^2 = 0.67; hyperbolic r^2 = 0.64).

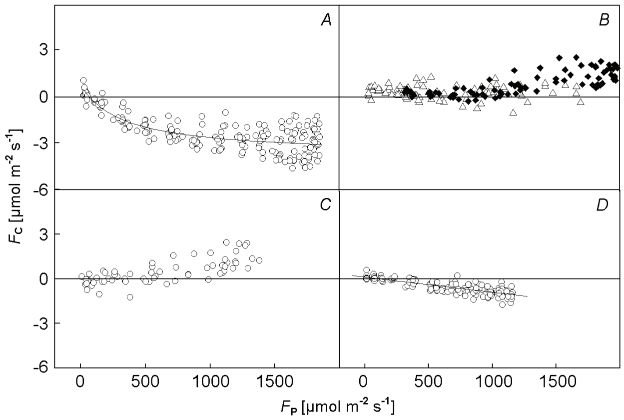

Fig. 2. Ecosystem irradiance response; daytime CO_2 flux, F_C *versus* the absorbed flux of photosynthetically active photons, F_P for representative weeks during different months corresponding to the seasons of the year: (*A*) June (spring), (*B*) August (summer), (*C*) October (autumn), and (*D*) January (winter). In August, data are presented for HUMID (VPD < 20 hPa) (*white triangles*) and DRY (VPD >20 hPa) (*black diamonds*) conditions.

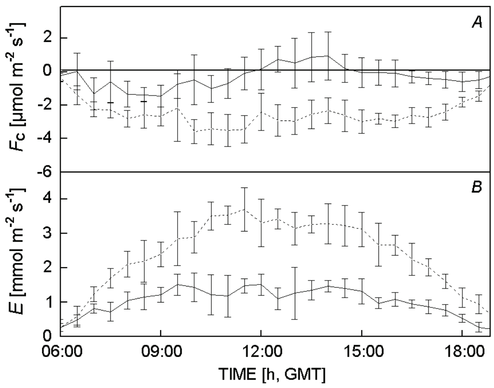

Fig. 3. Mean daytime trends in (*A*) CO_2 flux, F_C and (*B*) evapotranspiration, E for the same week in June: 2004 (*dashed line*) *versus* 2005 (*solid line*).

Table 1. Environmental conditions for a representative week in June 2004 and June 2005: the absorbed flux of photosynthetically active photons (F_P); air temperature (T_a), soil water content (SWC), and Leaf Area Index (LAI). Daytime means and standard deviations are presented (n > 100).

Date	F_P [μmol m^{-2} s^{-1}]	T_a [ºC]	SWC [% volume]	LAI [m^2 m^{-2}]
June 2004	998 ± 480	21.5 ± 2.3	12.02 ± 0.05	1.45
June 2005	1240 ± 582	19.9 ± 2.0	10.31 ± 0.05	1.16

Interannual variability: Fig. 3 shows the daytime course of half-hour gas exchange over the same complete week during June 2004 *versus* 2005. In 2004 the ecosystem was a strong CO_2 sink throughout daytime (Fig. 3*A*), whereas daytime CO_2 uptake was dramatically reduced (by 85 %) in June 2005 due to afternoon CO_2 release. Likewise, for the compared week E was reduced by two thirds in 2005 *versus* 2004 (Fig. 3*B*).

Compared to the same week of June in 2004, F_P was 24 % higher and the mean daytime T_a was nearly 2 ºC cooler in June 2005 (Table 1). No rain was detected during either week. The mean SWC in the week of June 2004 was *ca.* 2 % vol. higher than that measured in June 2005. Ecosystem LAI, calculated as the weighted sum of leaf area of all species, was 1.45 m^2 m^{-2} for the 2004 growing season, but it was reduced by 20 % in 2005; this decrease was consistent across plant species.

Discussion

The semiarid, montane climate of the *Sierra de Gádor* includes particular environmental conditions whose effects on F_C and E are not yet fully understood. The main characteristic is that rainfall and F_P are strongly asynchronous. Other remarkable environmental characteristics that contrast with what has been observed in other studies on semiarid ecosystems (Scott *et al.* 2003, Gorissen *et al.* 2004, Huxman *et al.* 2004) are a temperature range approaching 50 ºC and extremely low rainfall.

Similar to previous studies (Rey *et al.* 2002), the interaction between SWC and T_a in this semiarid shrubland ecosystem was crucial in determining whether the ecosystem acted as sink or as source. During the growing season F_P was elevated but the ecosystem turned from a daytime CO_2 sink to source when SWC fell below 10 % vol., probably because photosynthesis was water-limited while the warm temperatures allowed strong soil respiration. Similarly, during winter and despite high SWC, the ecosystem turned into a daytime CO_2 source when daytime T_a fell below 4 ºC, likely because photosynthesis was more affected than soil respiration by cold temperatures.

The empirical hyperbolic model examined in this study failed to describe F_C over most of the year. This contrasts with numerous sites including some in Mediterranean climates (Kowalski *et al.* 2004), where the model was usually adequate. This is perhaps because of the complexity of this ecosystem, where several environmental variables are continuously interacting to determine extreme changes in the NEE. The wintertime failure of the hyperbolic model to describe the data better than a simple linear model is not new, but simply indicates insufficient irradiance to even approach saturation; ecophysiological interpretations of the model parameters are inappropriate in such cases.

In our ecosystem there was mounting evidence that the seasonal timing of precipitation can fundamentally affect ecosystem function. Although water is a critical limiting factor to plant growth in semiarid environments (Hunt *et al.* 2004), not only the amount of precipitation, but also the timing (with respect to the growing season) can be crucial (Rey *et al.* 2002, Schwinning *et al.* 2004). During daytime, both E and F_C were dramatically reduced in June 2005 compared to the same period in June 2004 despite enhanced F_P and SWC conditions. The more obvious differences between the two years appeared in the timing and amount of spring rains, and in the phenological development of vegetation. While the last rainfall event (1.20 mm) before the week selected in 2004 was only 8 d prior, no precipitation was observed for two months prior to the selected week in 2005. It is likely that abundant rainfall in late spring 2004 led to the profound development of *Festuca scariosa* that dominated the ecosystem, giving it the appearance of grassland.

Evidence for the importance of precipitation timing was also observed in the fall. Following early autumn rains, conditions of high values of F_P and mild temperatures were favourable to photosynthesis; however, our ecosystem acted like a daytime CO_2 source. Moreover, in October 2004, when SWC had already recovered to the late spring levels after the summer drought, visual observations revealed the yellow colour of virtually all plants, suggesting that plants had not recovered yet.

We conclude that semiarid shrublands are widespread ecosystems of the world, particularly in the Mediterranean climates, but few estimates of their carbon sequestration potential have been made so far, and likewise of the environmental variables that control them (Rambal *et al.* 2003). Furthermore, data loss is inevitable in such long-term integrations of direct NEE measurements, implying the need for gap filling (Falge *et al.* 2001). As a result, there is great interest in defining the relationship between CO_2 uptake and environmental variables that could allow us to reliably quantify NEE from meteorological measurements. In the present study the model describing carbon exchange during daytime as a function of the absorbed flux of photosynthetically active photons (F_P) could not be used over the whole year. Depending on the season, daytime carbon exchange was determined by the interaction of several environmental variables such as temperature, SWC, VPD, and F_P. It is therefore clear that further studies of semiarid ecosystems are needed in order to develop improved models accounting for interactions among several environmental variables to reliably predict the long-term NEE of these complex ecosystems and estimate their contribution to the global carbon balance.

Similar to previous studies (UNEP 1997, Reichstein *et al.* 2002, Rey *et al.* 2005), our results suggest that the timing of rainfall events may play a fundamental role in determining inter-annual variations in ecosystem productivity. Spring rainfalls (amount and timing) are likely to affect the phenological development of vegetation during the growing season and, in turn, determine inter-annual differences in daytime carbon and water vapour exchange.

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