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The effects of drought and timing of precipitation on the inter-annual variation in ecosystem-atmosphere exchange in a Mediterranean grassland

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ABSTRACT

We studied the seasonal and inter-annual variation in carbon, water and energy fluxes over a Mediterranean grassland ecosystem in Portugal, dominated by annual species, using the eddy-covariance technique. The study period, from 2004 to 2008, was characterised by high intra- and inter-annual precipitation variation: the hydrological years 2004–2005 and 2007–2008 had precipitation below average ('dry' years) whereas the other two hydrological years had precipitation above average ('wet' years).

The variation in energy partitioning into sensible heat (H) and latent heat (λE) fluxes was associated with changes in soil water content, coinciding with plant emergence and senescence. The ecosystem was λE-dominated in those periods with soil water content above 15%, and became H-dominated when soil water content fell below 15%.

Annually integrated net ecosystem carbon exchange (NEE) was highly sensitive to drought, varying from a carbon sink in 'wet' years (e.g., 2005–2006, $-190\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$), to a carbon source in 'dry' years (e.g., 2004–2005, $+49\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$). There was a negative correlation between annually integrated NEE and annual precipitation ($r^2 = 0.78$). However, timing of precipitation influenced NEE, with individual rain events in the dry season resulting in large pulses of ecosystem respiration (R_{eco}). Low precipitation at the peak of the growing season, as in the spring of 2007, decreased carbon sequestration. The best descriptor for inter-annual variation in NEE was leaf area duration (LAD), which explained 96% of the variance.

Average radiation-use efficiency (RUE) was $1.59\,\mathrm{g\,MJ^{-1}}$ and inherent water-use efficiency (IWUE) was $24.6\,\mathrm{g\,C\,hPa\,kg^{-1}}$ H_2O. RUE and IWUE had similar trends in inter-annual variation, reflecting differences in productivity and timing of precipitation.

Our study showed that carbon and energy fluxes in this Mediterranean environment depended strongly upon water availability.

1. Introduction

Accurately predicting the future feedback of the biosphere on atmospheric CO_2 partly depends on a better understanding of the carbon balance in major land-use classes. On the other hand, water resources are likely to be the major factor affecting humanity in this century. Therefore, long-term measurements of CO_2 and H_2O fluxes between the earth's surface and the atmosphere are important to understand the processes controlling carbon cycling across the globe (Baldocchi et al., 2001). Grassland ecosystems cover approximately 40% of the earth's terrestrial area. Yet, large uncertainties remain in resolving whether these ecosystems function as CO_2 sources or sinks (Baldocchi et al., 2001). This uncertainty is primarily attributable to the sensitivity of grasslands to climate variability, especially variation in annual precipitation (Flanagan et al., 2002; Knapp and Smith, 2001; Sala et al., 1988) and an incomplete understanding of the regulation of ecosystem respiration (Flanagan and Johnson, 2005).

Climate change may impact strongly on grasslands, as most future scenarios predict an increase in climate variability, with a concomitant higher frequency of drought periods. Paredes et al. (2006) showed that precipitation during March in western Iberia (including Portugal) has been decreasing since the early 1960s, and the PDSI drought index illustrates a clear trend for increasing drought in the same period (Pires, pers. comm.). Increasing drought may affect the potential of grasslands to act as carbon sinks, as droughts are the main source of inter-annual variation in terrestrial carbon sequestration, reducing both productivity and net ecosystem carbon exchange (Ciais et al., 2005). For example, the drought affecting Europe in 2003 reduced the sink capacity of a grassland in

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France by 6% (Ciais et al., 2005), and a grassland in Hungary changed from a carbon sink to a carbon source (Nagy et al., 2007). Similarly, a Mediterranean grassland was a carbon sink in a year with average precipitation, while this ecosystem changed to a moderate carbon source in a year with precipitation below the average (Aires et al., 2008a).

In the Mediterranean environment, water to support primary productivity and ecosystem respiration is limiting. Grasslands under this type of climate are adapted to seasonal drought, but are vulnerable to decreased precipitation since the soil water store accessible to grasses and herbs is limited. These grasslands are typically dominated by C3 annual species and drought-resistant perennials, with fluctuations in species composition and productivity between years due to changes in temperature, and amount and distribution of precipitation. The beginning of the growing season depends on the timing of the first precipitation in autumn, followed by rapid growth. Mediterranean grasslands are thus active in winter and early spring, with senescence starting generally in May. Variation in the timing and size of the precipitation event, and intervals between precipitation events, are crucial in determining the pulse effects on productivity and respiration.

Understanding which environmental variables control inter-annual variation in net ecosystem carbon exchange (NEE) requires long-term flux measurements. To date, published long-term carbon flux studies include reports on temperate, tropical and boreal forests (Barford et al., 2001; Barr et al., 2007; Carrara et al., 2003; Dunn et al., 2007; Saigusa et al., 2005), with the inter-annual variation in NEE in these ecosystems attributed to a variety of factors, such as the occurrence of summer drought, air temperature and solar radiation. Only a few long-term carbon flux studies have been conducted on grasslands (Flanagan et al., 2002; Gilmanov et al., 2003; Suyker et al., 2003). More specifically, only one study reports on long-term flux measurements in a Mediterranean grassland ecosystem in California (Ma et al., 2007), showing that inter-annual variation in NEE of the savanna and grassland components depended primarily on the timing of precipitation, rather than total annual precipitation.

In this paper we report a 4-year (2004–2008) flux study on a Mediterranean grassland ecosystem in Portugal, where grasslands, savannas and shrublands cover about 2.3 million ha, representing 25% of the total land area (EarthTrends, 2006). Data are reported in terms of hydrological years (i.e., the period from 1 October to 30 September of the next year), which correspond approximately to the annual cycle of the vegetation. The objectives of our study were (1) to describe the development of energy, water and carbon fluxes between the atmosphere and the ecosystem on the diurnal, seasonal and annual scales, (2) to quantify the extent to which environmental factors affect the diurnal and seasonal patterns observed in NEE, (3) to find the best descriptor for the inter-annual variation in NEE, (4) to relate carbon fluxes with evapotranspiration and absorbed radiation, to determine radiation- and water-use efficiencies.

2. Materials and methods

2.1. Site description

The study area was established in June 2004 on a 50-ha homogeneous semi-natural grassland located in *Monte do Tojal*, Évora, in southern Portugal (38°28′28″N; 8°01′25″W; 190 m a.s.l.). The soil is a Luvisol (FAO), with 71% sand, 20% clay and 9% silt, overlaying a fractured granodiorite. At the beginning of the experiment, the average organic carbon content of this soil up to a depth of 90 cm was 6.04 kg m^{-2} with 55% of this carbon (3.32 kg m^{-2}) in the top 35 cm. The bulk density of the upper 30 cm of the soil profile is 1.64 ± 0.08 g cm^{-3} ($n = 16$). The climate is Mediterranean with hot and dry summers and mild winters. Long-term (1951–1980) mean annual air temperature is 15.5 °C, and mean annual precipitation is 669 mm (INMG, 1991). Most of the precipitation is confined to the period between October and May. However, the Mediterranean climate is characterised by a high variability in annual precipitation and a high frequency of drought periods (Xoplaki et al., 2004). In Portugal, the frequency of droughts increased since the 1970s (Miranda et al., 2006).

The vegetation at the site consists of a mixture of C3 annual species and one C4 grass, *Cynodon dactylon*. With the exception of the latter, most of the species in this grassland community are annuals, emerging after the first rains in autumn and senescing in mid-spring. Species composition differed considerably between the growing seasons. In 2005, the dominant species were *Vulpia bromoides*, *Avena barbata*, *C. dactylon* and *Chamaemelum mixtum*. In 2006, dominant species were *Medicago sativa*, *V. geniculata* and *C. dactylon*, whereas in 2007 *V. bromoides*, *V. geniculata*, *C. dactylon*, *Tolpis barbata* and *Leontodon taraxacoides* were dominant. The site was occasionally grazed by sheep until October 2007 with an average stocking density of 60 animals/ha. In October 2007 agricultural practice changed, the site being ploughed and reseeded with *Lupinus luteus* at a density of 60 kg/ha. This had a profound effect on species composition in 2008, with dominant species being *Spergula arvensis*, *Rumex bucephalophorus*, *Chamaemelum fuscatum*, *L. luteus* and *Silene gallica*.

2.2. Field measurements and data treatment

The fluxes of carbon dioxide, water vapour and energy were continuously measured using an eddy-covariance system at a height of 2.5 m. The system consisted of a 3D sonic anemometer (model 1210R3, Gill Instruments Ltd., Lymington, UK) and an open-path infrared gas analyzer (IRGA, model LI-7500, LI-COR Inc., Lincoln, NE, USA) measuring the three components of the wind velocity, the sonic temperature and the concentrations of water vapour and CO_2. The raw data from the eddy-covariance measurements were processed using the software Eddyflux (Meteotools, Jena, Germany). For detailed information on the data processing, flux computation and data quality control see Aires et al. (2008a,b). Data were subjected to gap-filling and flux partitioning procedures, following the methodology proposed by Reichstein et al. (2005).

Uncertainties in the annually integrated values of NEE were calculated using the ‘daily-differencing’ approach, as described by Richardson et al. (2006). For each hydrological year, the random flux measurement error (standard deviation of the inferred random error) was calculated, with subsequent estimations of accumulated flux uncertainty using Monte Carlo simulations.

Continuous site measurements included standard climatological and soil parameters. Air temperature and relative humidity were measured using a temperature/humidity probe (MP300, Campbell Scientific Ltd., Shepshed, UK). Soil temperature was measured by platinum resistance thermometers placed at depths of 2, 10 and 20 cm. Soil heat flux measurements were obtained using a soil heat flux plate (HFT-3, Campbell Scientific Ltd., Shepshed, UK), buried at 8 cm depth. Soil volumetric water content was measured at depths of 2, 15 and 30 cm using frequency domain reflectometer probes (ML2x, Delta-T Devices, Burwell, Cambridge, UK). Precipitation was recorded by a tipping bucket rain gauge (ARG100, Environmental Measurements Ltd., Gateshead, UK).

Photosynthetic photon flux density was measured at 1.5 m above the ground with a quantum sensor (LI-190SA, LI-COR, Lincoln, Nebraska, USA). The all-wave radiation components, incoming and outgoing longwave radiation (CG-3, Kipp & Zonen, Delft, NL), incoming shortwave radiation (Casella solarimeter, Casella London

Ltd., Kempston, UK) and outgoing shortwave radiation (Starpyranometer 8101, Philipp Schenk, Wien, AT) were measured at a height of 1.5 m. The output signals of all measuring equipment were scanned by a data-logger (DT-605, Datataker Ltd., Cambridge, UK) and the 30-min averages were subsequently sent to and stored on a computer.

Aboveground biomass and leaf area index were determined at about monthly intervals from April 2005 to September 2008. Sampling frequency was dependent on season, with increased frequency in the growing season. On each sampling date, all aboveground plant material within six quadrats of 25 by 25 cm was harvested. Material was divided into live and senescent biomass. Green leaves were removed from the stems, with subsequent scanning to determine leaf area index (LAI), using WinRhizo software (Regents Instruments Inc.). All material was dried for 72 h at 65 °C before weighing. In addition, leaf area duration (LAD) was calculated as the integral of LAI over the year on a yearly basis.

2.3. Data analysis

Water-use efficiency (WUE) and inherent water-use efficiency (IWUE) at the ecosystem level are calculated following Beer et al. (2009). WUE (g C kg^{-1} H_2O) is the ratio between daily-integrated GPP and daily-integrated evapotranspiration (E). Multiplication of WUE with mean daylight vapour pressure deficit (VPD) leads to IWUE in g C hPa kg^{-1} H_2O. On an annual scale, WUE and IWUE are calculated using integrated values of GPP and E over the year, and averaging daylight VPD using data from available days within the growing season, which is from 1 January until 30 June. WUE and IWUE are first calculated annually and then averaged over the course of the study. On a daily scale, calculation of WUE and IWUE are based on daily sums of GPP and E and mean daylight VPD.

Radiation-use efficiency (RUE) is calculated as the slope of the linear regression between daily-integrated gross carbon assimilation (i.e., GPP) and the daily-integrated absorbed photosynthetically active radiation (APAR). The fraction of absorbed PAR (*f*APAR) was calculated using the Beer–Lambert law: $f\text{APAR} = 1 - e^{-k\text{LAI}}$, where LAI is the leaf area index and k is the light extinction coefficient, which is estimated to be 0.4 for herbaceous vegetation (Lambers et al., 1998). Analysis of covariance, to assess inter-annual variation of IWUE and RUE, was performed using the VasserStats statistical computations website (http://faculty.vasser.edu/lowry/VasserStats.html). Regression analysis was performed using the statistical package SigmaPlot 11.0 (Systac Software, Inc.).

3. Results and discussion

3.1. Climate

Fig. 1 shows the variation of the main meteorological conditions and soil water content over the course of the study. Mean air temperatures for the four consecutive hydrological years were 14.7, 14.5, 14.0 and 13.7 °C, respectively. Daily maximum temperatures of approx. 39 °C occurred in the summer of all years. Annual precipitation differed markedly between the four hydrological years. The first, 2004–2005, was extremely dry – it was the most severe drought episode in the last 140 years (Garcia-Herrera et al., 2007) with a total precipitation of 364 mm, 45% below the long-term (1951–1980) mean. Rain was especially scarce during the grass growing season, between January and April 2005. Soil water content was below 15% from the beginning of February 2005 onwards, and this led to severe plant water deficits early in the growing season. During the following two hydrological years total precipitation was normal to wet: 751 mm in 2005–2006 and 873 mm in 2006–2007 (12% and 30% above the long-term mean, respectively). Precipitation in both these years was more uniformly distributed between October and April, in comparison with hydrological year 2004–2005. Monthly precipitation was highest in October 2005 and October 2006, with values of 192 and 231 mm respectively. Total precipitation in the last hydrological year (2007–2008) was 12% below the long-term mean with a value of 586 mm, with low precipitation in October, November and December 2007. In this period total precipitation was 120 mm, with values of 355 and 481 mm for the same period in the hydrological years 2005–2006 and 2006–2007. Daily-integrated shortwave radiation (R_s) was similar in all hydrological years, with minima of 1–5 MJ m^{-2} d^{-1} in winter and maxima of 29–31 MJ m^{-2} d^{-1} in summer. Annual incident shortwave radiation was 6856, 6474, 6381 and 6654 MJ m^{-2} in the four hydrological years.

3.2. Biomass and leaf area index

At our site, leaf area index (LAI) and biomass production are primarily dependent on timing and quantity of precipitation (Figs. 1b and 2). Germination occurs in autumn after the first substantial precipitation event. On 1 December, aboveground biomass was 0.065 and 0.160 g m^{-2} in 2005 and 2006, respectively. This difference in biomass reflected the timing of precipitation, which occurred in mid-October in 2005, and in mid-September in 2006. Thus, the later onset of autumn precipitation in 2005 delayed sward development by a month. Low precipitation in the period of October to December 2007, with a concomitant change in agricultural practice as the experimental site was ploughed and reseeded, resulted in low biomass accumulation until February 2008. Seasonal dynamics of aboveground biomass and LAI showed a peak in late spring, followed by a rapid decline as the sward senesced. Maximum values for aboveground biomass were 0.14, 0.51, 0.80 and 0.67 kg m^{-2} in late spring 2005, 2006, 2007 and 2008, respectively. The LAI in these four consecutive years peaked at 0.40, 2.52, 2.31 and 2.26 m^2 m^{-2}. But maximum LAI provides limited information. A measure of how much leaf area was deployed throughout the year is given by leaf area duration (LAD). Highest estimates of LAD occurred in the hydrological years 2005–2006 and 2006–2007, with respective values of 0.88 and 0.70 m^2 × year m^{-2}. In the hydrological year 2007–2008, LAD was 0.44 m^2 × year m^{-2}, as a result of the later development of the sward. For this grassland (Pereira et al., 2007) reported a LAD of 0.3 m^2 × year m^{-2} in the hydrological year 2004–2005.

3.3. Seasonal and inter-annual patterns of energy exchange

Closure of the surface energy balance, by comparing daily total fluxes of net radiation (R_n) against the sums of sensible (H), latent (λE) and soil heat (G) flux, is often used to test eddy-covariance data quality (Wilson et al., 2002). The linear regression produced an intercept of −6.13 W m^{-2}, a slope of 0.94 and an r^2 of 0.87 (Fig. 3), hence the energy imbalance over the course of this study was 6%, which falls well within the range of values reported previously (Baldocchi et al., 2004; Flanagan et al., 2002; Meyers, 2001; Wever et al., 2002; Wilson et al., 2002)

Seasonal and inter-annual variation in daily energy fluxes (H, λE, G and R_n) are shown in Fig. 4. The seasonal variation of R_n closely followed the variation of R_s (Fig. 1), with maximum values of 13.8–19.7 MJ m^{-2} d^{-1} in May or June, and minimum values of close to zero in December. Seasonal variation in H was closely related to the pattern of change in R_n, although maximum values of R_n coincided with the summer solstice, while maximum values of H of between 8.3 and 11.5 MJ m^{-2} d^{-1} occurred mid-summer (July–August), as a result of maximum air temperatures. During most of the year, sensible heat energy was transferred from

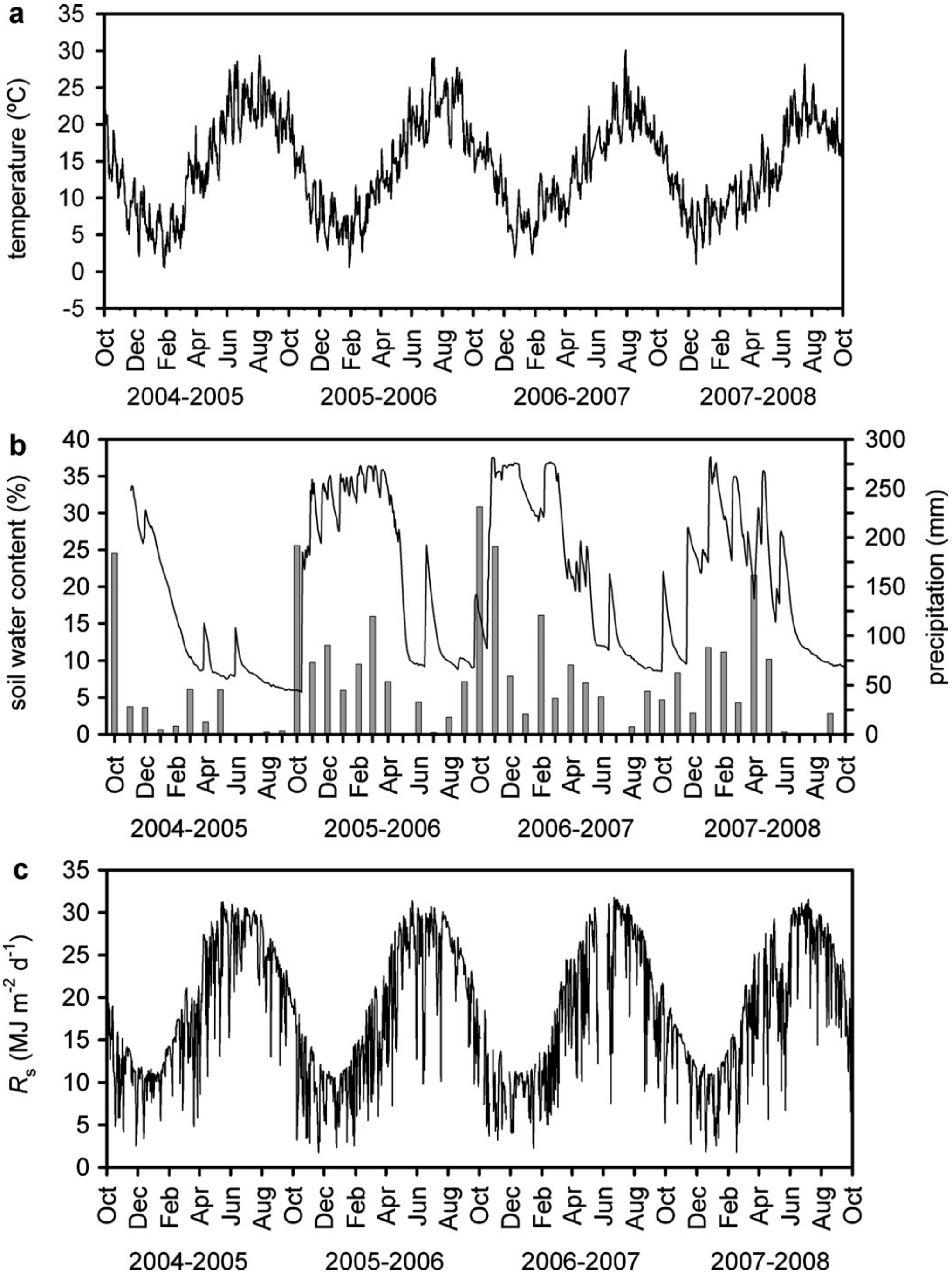

Fig. 1. Seasonal variation in (a) daily average temperature, (b) monthly total precipitation and daily average volumetric soil moisture content (θ_v) at a depth of 15 cm, and (c) daily-integrated shortwave radiation (R_s) over the course of the study.

the soil surface to the atmosphere. Soil heat flux (G) was negative in autumn and winter, with minimum values approaching -2 MJ m^{-2} d^{-1}. Highest values (1.5–2.0 MJ m^{-2} d^{-1}) were recorded in mid-summer, with the ecosystem storing energy in the soil. The variation in seasonal and inter-annual patterns of λE was more pronounced, as compared to R_n, H and G, with low values of λE (<2 MJ m^{-2} d^{-1}) in winter. However, from June to September 2005 values of λE were equally low, as a result of the drought conditions in late winter and early spring of 2005. Maximum value of λE in 2005 was 4.7 MJ m^{-2} d^{-1}, recorded after two rain events on the 26th and the 28th of March. In the subsequent three years of the study, maximum rates of λE occurred in April to May, with respective values of 8.8, 7.8 and 8.7 MJ m^{-2} d^{-1}, approximately twice the maximum rate observed in 2005. The Bowen ratio varied from approximately zero in winter to summer values of 3.4–8.5 (Fig. 5).

Seasonal and inter-annual fluctuations in H, G and λE resulted in large variations in energy partitioning at the site (Table 1). On an annual basis only a minor part of R_n was converted to G, with G/R_n ranging from 0.01 to 0.02. In the hydrological years 2004–2005 and 2007–2008, a major fraction of R_n was partitioned into H, with H/R_n being 0.55 and 0.43 respectively. The evaporative fraction ($\lambda E/R_n$) was dominant in 2005–2006 and 2006–2007, with respective values of 0.45 and 0.55, which is also reflected in the low Bowen ratio β (=$H/\lambda E$) for these two hydrological years. Annual values of evaporative fraction in this study (0.37–0.55) are comparable to the 0.48–0.58 reported for a tallgrass prairie (Burba and Verma,

Table 1
Meteorological and biometeorological parameters during the course of the study.

	T_a (°C)	θ_v (%)	R_n (MJ m^{-2})	G (MJ m^{-2})	H (MJ m^{-2})	λE (MJ m^{-2})	G/R_n	H/R_n	$\lambda E/R_n$	β
2004–2005 hydrological year	14.7	13.4	2120.9	40.2	1165.7	776.3	0.02	0.55	0.37	2.20
2005–2006 hydrological year	14.5	22.9	2615.1	13.4	911.4	1179.3	0.01	0.35	0.45	1.05
2006–2007 hydrological year	14.0	22.8	2481.4	56.8	919.8	1375.2	0.02	0.37	0.55	0.81
2007–2008 hydrological year	13.7	20.2	2889.0	65.6	1236.2	1158.3	0.02	0.43	0.40	2.09
2004–2005 wet period 08.10.2004–05.02.2005	9.3	24.9	270.7	−97.5	52.3	254.7	−0.36	0.19	0.94	0.24
2005 dry period 06.02.2005–10.10.2005	17.8	8.4	1843.7	135.2	1117.3	523.0	0.07	0.61	0.28	3.22
2005–2006 wet period 11.10.2005–04.05.2006	9.5	31.5	1027.0	−72.1	58.3	685.0	−0.07	0.06	0.67	0.02
2006 dry period 05.05.2006–21.09.2006	21.2	11.5	1488.1	89.0	803.2	454.8	0.06	0.54	0.31	2.31
2006–2007 wet period 22.09.2006–15.05.2007	10.8	29.0	1318.6	−30.6	145.7	829.2	−0.02	0.11	0.63	0.14
2007 dry period 16.05.2007–17.11.2007	18.2	11.8	1442.9	65.3	910.3	676.4	0.05	0.63	0.47	1.91
2007–2008 wet period 18.11.2007–20.06.2008	10.4	26.4	1363.7	8.2	290.2	900.4	0.01	0.21	0.66	0.30
2008 dry period 21.06.2008–30.09.2008	20.4	10.7	1326.0	77.0	834.9	162.0	0.06	0.63	0.12	6.00

T_a, average daily air temperature; θ_v, average volumetric soil water content at a depth of 15 cm; R_n, net radiation; G, soil heat flux; H, sensible heat flux; λE, latent heat flux; β, Bowen ratio. The wet period is defined as the period with daily $\theta_v > 15\%$; the dry period is defined as the period with $\theta_v < 15\%$.

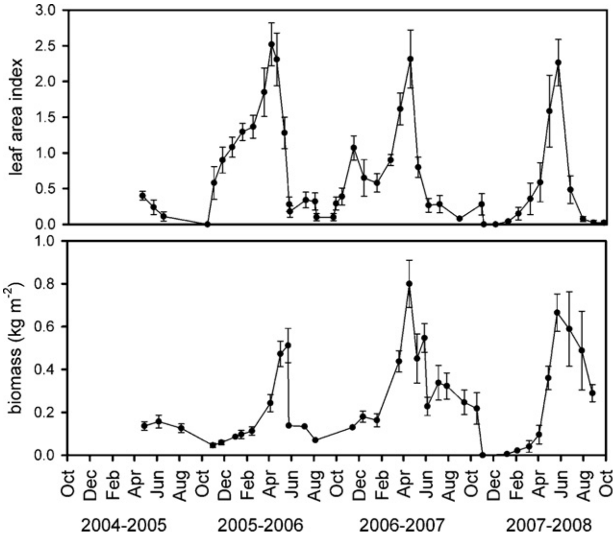

Fig. 2. Seasonal variation in aboveground biomass (kg m^{-2}) and leaf area index (LAI) over the course of the study.

2005), but higher than the 0.31–0.35 in a Mediterranean grassland (Baldocchi et al., 2004), probably reflecting differences in soil water content and the presence of the deep-rooted C4 grass (*Cynodon dactylon*) during the summer, enhancing soil water extraction (Aires et al., 2008b).

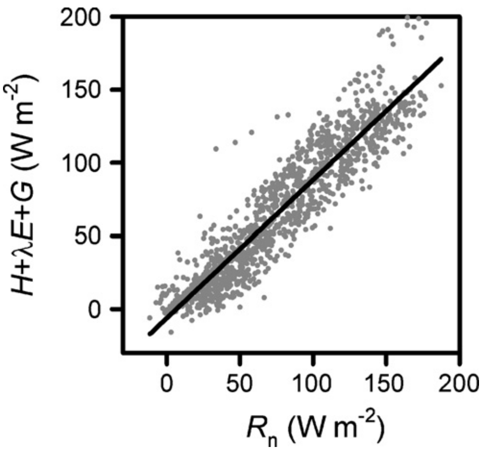

Fig. 3. Site energy balance closure for daily total fluxes during the course of the study. The net radiation (R_n) is compared with the sum of the sensible heat flux (H), the latent heat flux (λE) and the soil heat flux (G). Linear regression: $y = -6.13 + 0.94x$, $r^2 = 0.87$, $P < 0.001$, d.f. = 1244.

The energy partitioning into sensible heat flux (H) and latent heat flux (λE) showed large seasonal and inter-annual differences, with the differences being more pronounced when a distinction is made based on daily average volumetric soil water content at 15 cm depth (θ_v). The ecosystem was λE-dominated in those periods with soil water content above 15%, and became H-dominated when soil water content fell below 15% (Table 1). The timing of the switch from an H-dominated to a λE-dominated energy balance was dependent on the first precipitation event (>5 mm d^{-1}) in autumn, increasing the soil water content to values exceeding 15%, enabling seed germination. Likewise, the switch from a λE-dominated to an H-dominated ecosystem occurred when soil water content fell below 15%, which coincides with the start of biomass senescence. This switch in dominance from λE to H, is also reflected in the Bowen ratio β, with values ranging from 0.02 to 0.30 in the 'wet period' ($\theta_v > 15\%$), while in the 'dry period' ($\theta_v < 15\%$) values range from 1.91 to 6.00. Several other studies report on soil moisture being the controlling factor of variation in energy partitioning (Burba and Verma, 2005; Gu et al., 2005; Li et al., 2005; Wever et al., 2002). In the last three years of the study, the change in energy partitioning occurred in May–June. In the first hydrological year (2004–2005), however, a drought affecting Portugal led to the switch from λE to H occurring in mid-February. The presence of water stress in the ecosystem at that time was reflected in the Bowen ratio, which exceeded unity from the middle of February 2005 onwards.

3.4. Seasonal and inter-annual patterns of ecosystem carbon exchange

Seasonal trends in daily-integrated carbon fluxes over the course of the study are shown in Fig. 6. Considerable diurnal variation in NEE, GPP and R_{eco} was observed and was primarily attributable to the variation in incident solar radiation. Daily values for NEE ranged from −5.1 to 5.8 g C m^{-2} d^{-1}, with a net carbon uptake during the growing period and a net carbon loss for the remainder of the year.

In Mediterranean grasslands dominated by annual herb species, the onset of plant development is limited by water deficits. In autumn, the beginning of the growing season depends on the timing of the first precipitation. This allows seed germination and the onset of sward development, with increasing leaf area deployment. In the hydrological year 2004–2005, the first precipitation event occurred on 19 October 2004 and the ecosystem became a daily carbon sink in the beginning of December. However, low precipitation thereafter resulted in low GPP and R_{eco} until mid-March 2005, with values of 1–2 g C m^{-2} d^{-1}. In the subsequent two hydrological years (2005–2006 and 2006–2007), the first precipitation events occurred on 10 October 2005 and 21

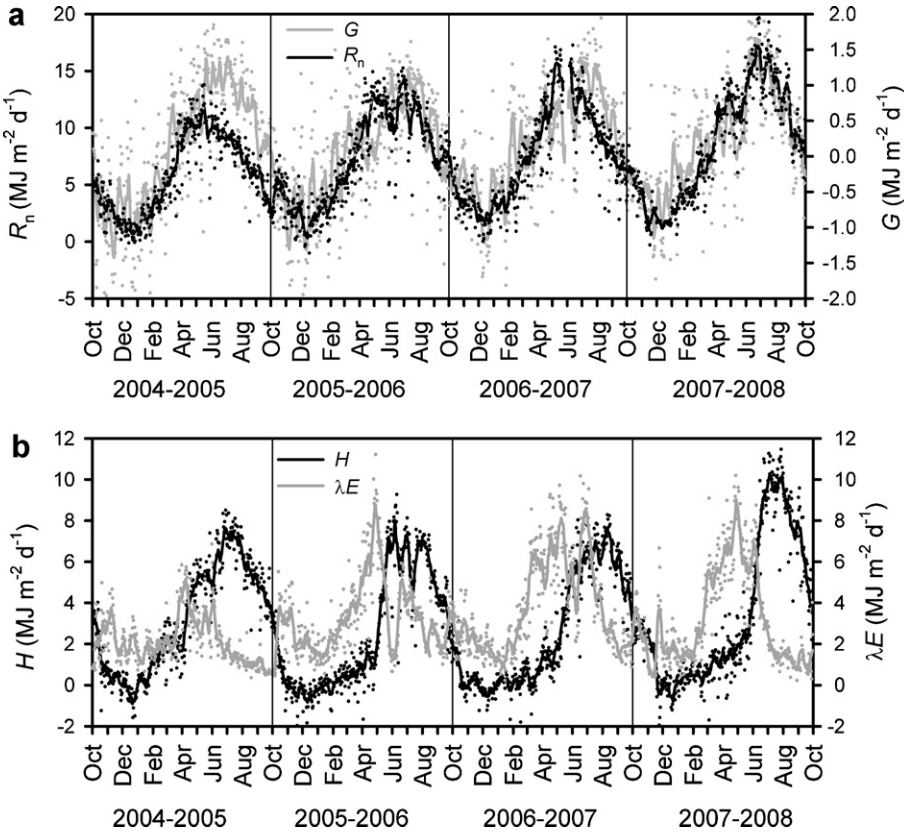

Fig. 4. Seasonal and inter-annual variation in daily-integrated (a) net radiation (R_n) and soil heat flux (G), and (b) sensible heat flux (H) and latent heat flux (λE) over the course of the study. The lines are 10-day running means.

September 2006. The early precipitation in the hydrological year 2006–2007 increased the length of the growing season. However, carbon sequestration did not occur at an earlier time as compared to the hydrological years 2004–2005 and 2005–2006, as a result of an increase in R_{eco}. Ecosystem respiration depends strongly on available water content and soil temperature, with an increase in respiration at higher temperatures, but only if available soil water is sufficient. Thus, in September–October 2006, the combination of increased soil water and high air temperatures facilitated an increase in R_{eco}. Since it rained “normally” in the hydrological years 2005–2006 and 2006–2007, GPP and R_{eco} increased steadily during the growing season, with an increasing dominance of GPP over R_{eco} (Fig. 6b). In the hydrological year 2007–2008, sward development, and consequently GPP, was affected by the change in agricultural practice, with the site being ploughed and reseeded in autumn 2007. Unusually low precipitation during the October–December period delayed seed germination. As a consequence, the ecosystem only started to sequester carbon in the beginning of 2008, with GPP only exceeding 2 g C m^{-1} d^{-1} from February 2008 onwards, while in the hydrological years 2005–2006 and 2006–2007, GPP of the established sward exceeded 2 g C m^{-1} d^{-1} from December onwards. Thus, although the first precipitation event marks seed

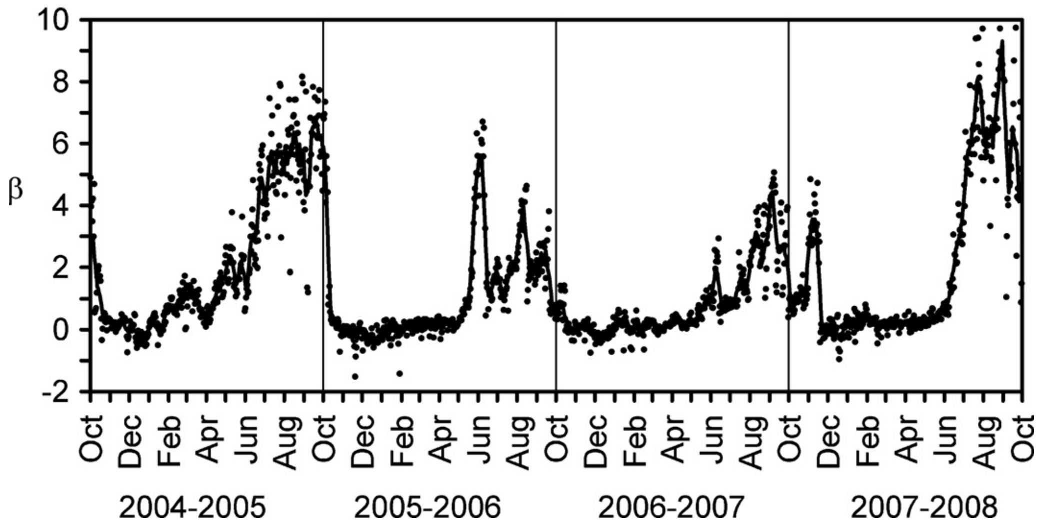

Fig. 5. Seasonal and inter-annual variation in β, the Bowen ratio, over the course of the study. The lines are 10-day running means.

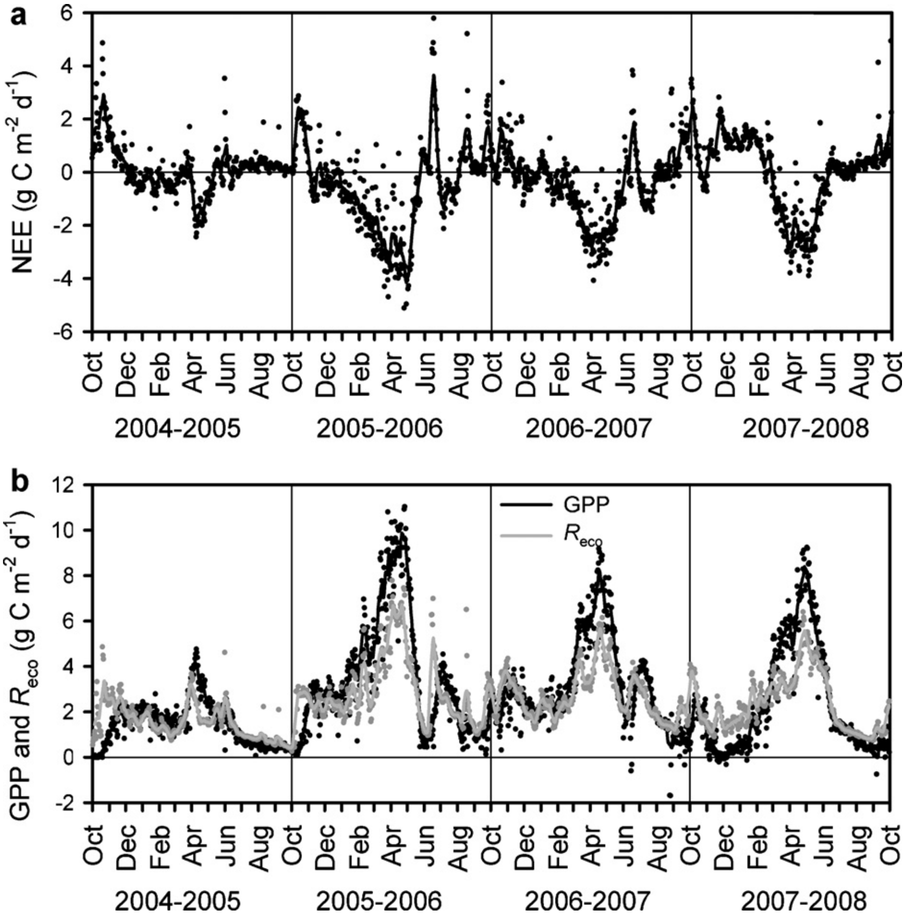

Fig. 6. (a) Seasonal and inter-annual variation in daily-integrated net ecosystem carbon exchange (NEE), and (b) gross primary productivity (GPP) and ecosystem respiration (R_{eco}) over the course of the study. The lines are 10-day running means.

germination and the subsequent increase in GPP, the onset of carbon sequestration depends on subsequent precipitation as well as on the magnitude of R_{eco}, through its responses to temperature and soil water.

Over the course of the growing season, variation in GPP and NEE was highly correlated with variation in LAI (Fig. 7), as the potential of this grassland to intercept light for photosynthesis is limited by leaf area. For this grassland, changes in LAI explained 70% of the variation in GPP, with the increase in GPP per unit LAI being 3.8 g C $\text{m}^{-2}\,\text{d}^{-1}$. The linear relationship between carbon fluxes and LAI has been demonstrated by others (Flanagan et al., 2002; Saigusa et al., 1998; Xu and Baldocchi, 2004). The increase in GPP per unit LAI of 3.8 g C $\text{m}^{-2}\,\text{d}^{-1}$ found in this study is consistent with the 3.9 g C $\text{m}^{-2}\,\text{d}^{-1}$ reported by Xu and Baldocchi (2004) for a Mediterranean grassland in California, and the 3.1 g C $\text{m}^{-2}\,\text{d}^{-1}$ for a steppe in Mongolia (Li et al., 2005).

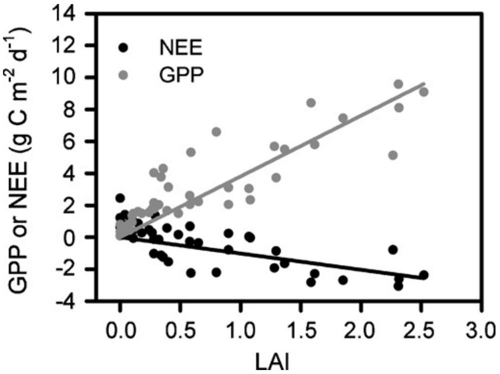

Fig. 7. The relationships between leaf area index (LAI) and net ecosystem carbon exchange (NEE) and gross primary productivity (GPP) over the course of the study. GPP and NEE data represent the 10-day running mean, centered on the day samples for LAI. Linear regression NEE: $y = -1.02x$, $r^2 = 0.49$, $P < 0.001$, d.f. = 43. Linear regression GPP: $y = 3.80x$, $r^2 = 0.70$, $P < 0.001$, d.f. = 43.

With the seasonal onset of canopy senescence, GPP and R_{eco} decreased, and by June, there was a net loss of carbon from the ecosystem, as the grassland continued to lose carbon via soil respiration. However, between May and October, R_{eco} was limited by the low availability of water. With the vegetation in a senescent state, precipitation pulses occurring in the dry season (June–October) increased available soil water, which stimulates microbial activity (Jarvis et al., 2007). As a result, R_{eco} increased, with the magnitude of response of R_{eco} depending on the change in soil water content (Fig. 8). Over the 3-day post-event period, precipitation pulses resulted in a carbon release of 2.39 ± 0.31 (s.d.) g C $\text{m}^{-2}\,\text{d}^{-1}$, with the increase in R_{eco} accounting for 82% of this change in NEE. The pulses of R_{eco} were sustained for 3–5 days and cease as soon as available soil water decreases to pre-pulse levels. In the last hydrological year of this study, four precipitation pulses (2 October 2007, 20 November 2007, 5 and 28 September 2008) resulted in an increased carbon release by about 40 g C m^{-2}, as compared to background values for NEE during these months. This carbon release resulted in the ecosystem being a net carbon source in this hydrological year, with the annual total value of NEE being 15 g C m^{-2} (Table 2), even though maximum daily-integrated NEE (-3.89 g C $\text{m}^{-2}\,\text{d}^{-1}$) was comparable to the hydrological year 2006–2007 (-4.07 g C $\text{m}^{-2}\,\text{d}^{-1}$).

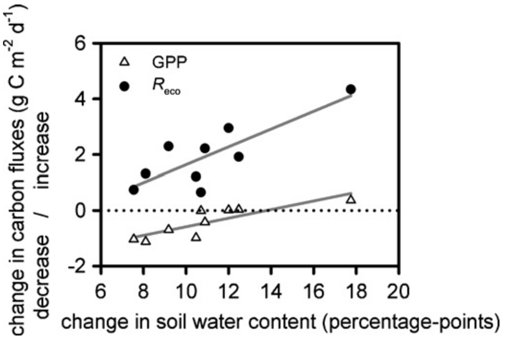

Fig. 8. Observed pulse effect on ecosystem respiration and gross primary productivity following all rain events exceeding 15 mm in the period June–September over the course of the study. Linear regression GPP: $y = -2.13 + 0.15x$, $r^2 = 0.71$, $P = 0.0042$, d.f. = 8. Linear regression R_{eco}: $y = -1.56 + 0.32x$, $r^2 = 0.67$, $P = 0.0067$, d.f. = 8.

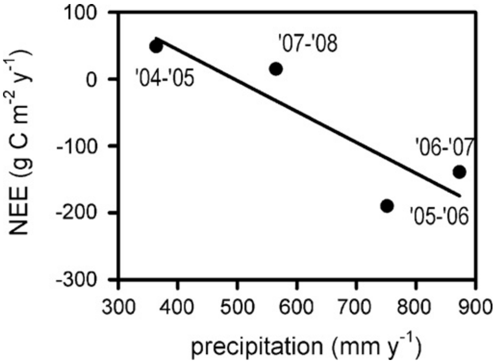

Fig. 9. Relationship between annual total net ecosystem carbon exchange (NEE) and annual total precipitation for the four years of the study. Linear regression: $y = 228.58 - 0.46x$, $r^2 = 0.78$, $P = 0.1148$, d.f. = 3.

Large pulses of R_{eco} immediately after individual rain events during the summer dry period, have also been observed in a Mediterranean grassland in California (Flanagan et al., 2002; Saigusa et al., 1998; Xu and Baldocchi, 2004). In a temperate grassland, Flanagan et al. (2002) reported on precipitation events acting to flush CO_2 from the soil, which resulted in high values for R_{eco}, and subsequently caused this ecosystem to be a source of carbon. Ultimately, several large precipitation pulses in the dry season can promote plant growth. Indeed, in June 2006 and 2007 large precipitation events enhanced the growth of the C4 grass (*Cynodon dactylon*). As a consequence, after the inherent pulses of R_{eco}, a second peak of carbon uptake was observed (Fig. 6). This can partly compensate for the carbon losses after the precipitation events.

The maximum GPP in the four years of this study was 4.8, 12.6, 9.2 and 9.2 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$, observed in April. Maximum values for R_{eco} were 4.9, 7.8, 6.2 and 6.4 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$. Maximum carbon sink capacity was recorded in April with peak NEE values of −2.4, −5.11, −4.07 and −3.89 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$, coinciding with high LAI of the fully developed sward. However, large inter-annual variation was found in maximum daily-integrated NEE. The low maximum value for NEE in the first hydrological year 2004–2005 (−2.4 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$) reflected the extreme drought that occurred in western Iberia (including Portugal) at that time. Low, comparable values of maximum daily-integrated NEE were found in several other studies with drought impacts: −1.58 to −1.74 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ for a sparse grassland in New Zealand (Hunt et al., 2004), −2.3 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ for a steppe in Mongolia (Li et al., 2005), −2.8 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ for a warm temperate grassland in North Carolina (Novick et al., 2004), and −3.3 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ for a mixed-grass prairie in Oklahoma during a year with low precipitation between January and May (Sims and Bradford, 2001). Maximum values of NEE for the last three years in our study are similar to the −4.8 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ reported for a Mediterranean grassland in California (Xu and Baldocchi, 2004), the −5.0 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ found during a wet year in a temperate grassland in Alberta (Flanagan et al., 2002), and the −4.9 and −5.5 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ in a mixed-grass prairie in Oklahoma (Sims and Bradford, 2001). Higher values of maximum daily NEE were found in several other studies; i.e., −5.5 and −8.2 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ in a tallgrass prairie in Texas (Dugas et al., 1999), −8.4 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ in a tallgrass prairie in Oklahoma (Suyker and Verma, 2001).

Annually integrated carbon fluxes (Table 2) ranged from +49 to −190 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$. During the first year of the study (2004–2005), low precipitation resulted in the ecosystem being a net carbon source of 49 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$. In the hydrological years 2005–2006 and 2006–2007 NEE was −190 and −139 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$, respectively. Although precipitation was higher in the third hydrological year (2006–2007) as compared to the second year (2005–2006), the ecosystem sequestered more carbon in 2005–2006 (190 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$), with higher total values for both GPP and R_{eco}. However, dominance of GPP over R_{eco} resulted in higher NEE in 2005–2006. In addition, precipitation at a crucial time, March and April, was considerably higher in 2006 (173 mm) as compared to 2007 (107 mm). This water input had a stronger effect on GPP than on R_{eco}, and resulted in an increased carbon sequestration. In 2007–2008 the ecosystem was a small carbon source, NEE being 15 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$. Our values of annually integrated carbon fluxes are in agreement with other studies in similar ecosystems. A Mediterranean grassland changed from a carbon sink (−132 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$) in the first year of the study, to a carbon source (+29 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$) in the following year (Xu and Baldocchi, 2004). The long-term study at the same Mediterranean grassland found annually integrated values of NEE ranging from +189 to −88 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$ (Ma et al., 2007).

Over the course of our study the amount of precipitation was the overall dominating factor in regulating the annual carbon exchange of this grassland (Fig. 9). NEE was linearly related to precipitation on a yearly basis ($r^2 = 0.78$), with increased carbon sequestration with increasing precipitation. However, timing of occurrence of precipitation influenced NEE. In the hydrological year 2006–2007, early precipitation in autumn increased R_{eco}, and low precipitation at the peak of the growing season decreased GPP, thereby lowering the carbon sequestration potential although total annual precipitation was high. In the hydrological year 2007–2008 precipitation pulses in the dry season (June–October) increased R_{eco}, with the ecosystem becoming a carbon source in this hydrological year. Inter-annual variation in aboveground productivity in grasslands is well corre-

Table 2

Net ecosystem carbon exchange (NEE), gross primary productivity (GPP), ecosystem respiration (R_{eco}), total precipitation and average volumetric soil water content in the top 15 cm (θ_v) for the four hydrological years. For annually integrated NEE, uncertainty values are given, calculated following Richardson et al. (2006).

Hydrological year	2004–2005	2005–2006	2006–2007	2007–2008
NEE ($\mathrm{g\,C\,m^{-2}}$)	49 ± 7.9	−190 ± 10.3	−139 ± 14.9	15 ± 9.5
GPP ($\mathrm{g\,C\,m^{-2}}$)	524	1261	1130	849
R_{eco} ($\mathrm{g\,C\,m^{-2}}$)	573	1071	990	864
Precipitation (mm)	363.6	751.2	872.8	585.9
θ_v	10.9	21.8	21.9	20.1

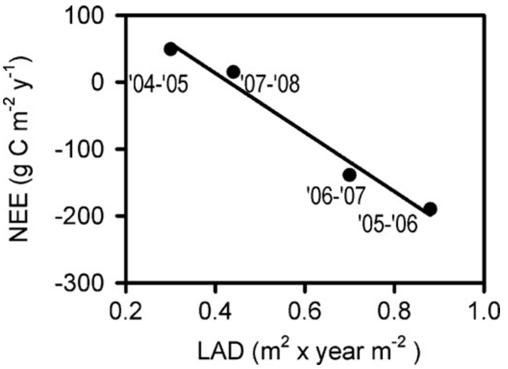

Fig. 10. Relationship between net ecosystem carbon exchange (NEE) and leaf area duration (LAD) for the four years of the study. Linear regression: $y = 190.22 - 442.19x$, $r^2 = 0.98$, $P = 0.114$, d.f. = 3.

lated with annual precipitation (Sala et al., 1988; Sims and Singh, 1978). In a northern temperate grassland, Flanagan et al. (2002) found a linear relationship between annually integrated NEE and precipitation, with carbon sequestration increasing with increasing precipitation, as was also found in our study. Similarly, moisture stress was the greatest source of inter-annual variation of NEE in a tallgrass prairie in Oklahoma (Suyker et al., 2003). However, for a Mediterranean grassland Xu and Baldocchi (2004) concluded that timing of precipitation rather than amount of precipitation had more impact on NEE, by influencing the length of the growing season and ecosystem respiration. Similarly, Ma et al. (2007) concluded that inter-annual variation in NEE was significantly related to the length of the growing season.

As shown in Fig. 7, day-to-day variations in GPP and NEE were correlated with LAI. In addition, integrated annual values for NEE were highly correlated with leaf area duration (LAD), with 98% of the variance in NEE being explained by changes in LAD (Fig. 10). Thus, the best descriptor for inter-annual variation in NEE in our study was LAD. Leaf area duration, the integral of LAI over time, reflects not only the length of the growing season but also the timing of precipitation and the influence of management and grazing on LAI.

3.5. Water-use efficiency

Water-use efficiency (WUE) – at the ecosystem level – measured as the ratio between daily-integrated GPP and daily-integrated evapotranspiration (E), is a useful indicator of the relationship between terrestrial water and carbon cycles. However, WUE varies with meteorology, specifically the vapour pressure deficit (VPD). Multiplying WUE by VPD yields the intrinsic water-use efficiency (IWUE), which reflects inherent capacity for carbon assimilation at a given stomatal conductance (Beer et al., 2007; Chaves et al., 2004; Pereira et al., 2006), enabling a better comparison across regions and ecosystems. Fig. 11 shows the relationship between GPP and E, and between the product GPP VPD and E over the course of the study. In our grassland, WUE was 2.53 g C kg^{-1} H_2O over the course of the study, which is in agreement with data reported by Beer et al. (2009). For grasslands in Italy and Hungary, with maximum LAI of 2 and 2.5 (similar to our site) WUE was 3.16 and 2.10 g C kg^{-1} H_2O, respectively (Beer et al., 2009). IWUE in our grassland over the course of the study was 24.58 g C hPa kg^{-1} H_2O. The improved correlation coefficient for the relation between GPP VPD and E, i.e., IWUE, as compared to the relation between GPP and E (Fig. 11) indicates that the intrinsic link between carbon and water fluxes through stomatal conductance exists at the ecosystem level and on the annual time scale, as also shown in Beer et al. (2009). In our study, 86% of the variation in GPP VPD could be explained by changes in evapotranspiration. For the above-mentioned grasslands in Italy and Hungary IWUE was 21.45 and 19.53 g C hPa kg^{-1} H_2O, somewhat lower than the 24.58 g C hPa kg^{-1} H_2O in our study, but well within the range of variability among ecosystems reported by Beer et al. (2009).

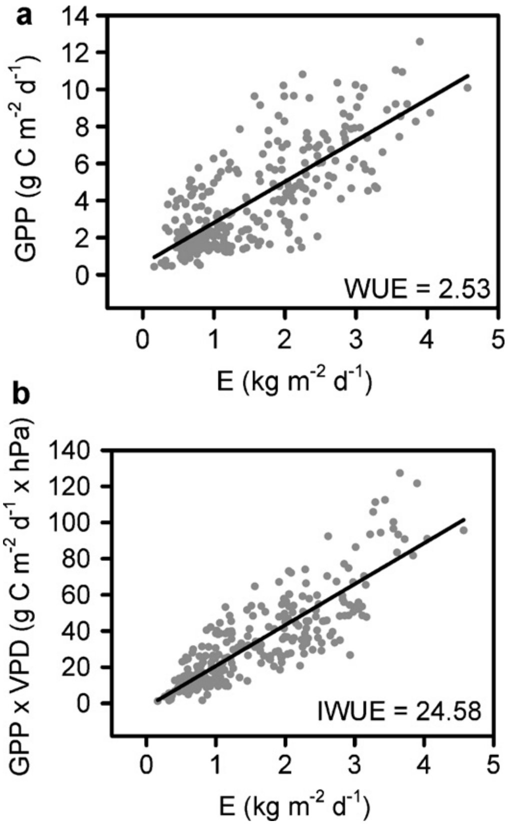

Fig. 11. Relationship between (a) GPP and E, and between (b) GPP VPD and E during the growing seasons for the four years of the study. Shown is the correlation coefficient, the slope of the linear fit between the variables and the ratio of annual sums (GPP, E) or means (daylight VPD) according to Beer et al. (2009). Linear regression GPP: $y = 0.58 + 2.22x$, $r^2 = 0.59$, $P > 0.0001$, d.f. = 299. Linear regression GPP VPD: $y = -1.97 + 22.64x$, $r^2 = 0.73$, $P > 0.0001$, d.f. = 299.

Analysis of covariance (ANCOVA) indicated a significant ($P = 0.006$) inter-annual variation in IWUE, with the highest value (in g C hPa kg^{-1} H_2O) in the highly productive 2005–2006 (28.07) and the lowest (21.44) in 2006–2007. The IWUE in 2004–2005 and in 2007–2008 were intermediate (24.67 and 24.16 g C hPa kg^{-1} H_2O, respectively). Higher IWUE may result from increased GPP, related to higher LAI and LAD, or higher photosynthetic capacity. The latter may result from differences in species composition and/or differences in nitrogen content of the leaves, increasing photosynthesis without altering stomatal conductance.

Daily values of IWUE during the growing season of the four consecutive years (Fig. 12) showed pronounced seasonal and inter-annual variation. Daily-integrated IWUE reached maximum values at the peak of the growing season in each year, coinciding with maximum GPP. In 2005, the impact of the drought is reflected in the high daily IWUE, reaching 46.75 g C hPa kg^{-1} H_2O in June, i.e., IWUE increases in response to water deficits, because drought-induced stomatal closure restricts water loss more than CO_2 uptake. This is consistent with Beer et al. (2009), who reports increasing IWUE on daily time scales during drought periods, at the ecosystem level. In 2008, the later peak of IWUE (June 2008) coincided with the later development of the sward as the result of the ploughing and reseeding of the experimental plot, and the subsequent low precipitation in the period of October to November 2007.

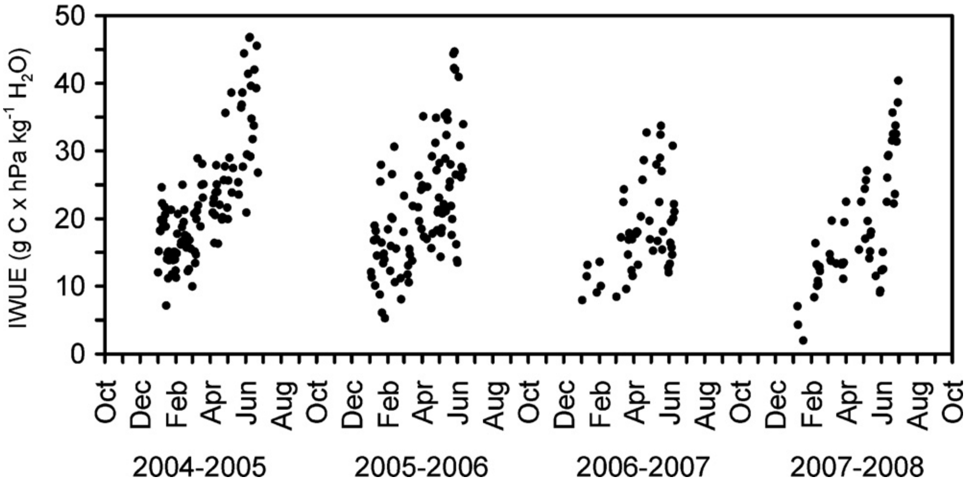

Fig. 12. Seasonal and inter-annual variation in inherent water-use efficiency (IWUE) during the growing seasons over the course of the study.

3.6. Radiation-use efficiency

Radiation-use efficiency (RUE), calculated as the slope of the linear regression between daily-integrated APAR and daily-integrated GPP, is an important parameter when calculating productivity using a light-use efficiency model (Monteith, 1972), which offers opportunities for landscape and global scale estimations of GPP and NPP. Fig. 13 shows the seasonal and inter-annual variation in APAR for the last three years of the study. Data on LAI is only available from April 2005 onwards; hence the first hydrological year (2004–2005) was excluded from this analysis. Maximum APAR coincided with the peak of plant growth, i.e., during the end of April. In our grassland, RUE for the three years was 1.32 g C MJ^{-1} ($r^2 = 0.81$). Average herbage carbon content was 42.8 ± 0.32%, thus RUE was 3.08 g DM MJ^{-1}. This value is based on calculations using gross primary productivity (GPP). Assuming that net primary productivity (NPP), the more commonly used measure of RUE, equals GPP/1.92 (Zhang et al., 2009), this results in a value of RUE (g DM MJ^{-1}, based on NPP) of 1.59 g DM MJ^{-1}.

Comparing our data with published data on RUE is difficult due to the wide range of experimental approaches used to estimate RUE and the wide range of units used to express RUE (Bonhomme, 2000). In our study, RUE was calculated using data on absorbed PAR, with the majority of published data based on intercepted PAR or intercepted solar radiation. For comparison, published data is converted to absorbed PAR, using conversion factors following Sinclair and Muchow (1999). For wheat (*Triticum aestivum*), pea (*Pisum sativum*) and mustard (*Brassica juncea*) in a field experiment in Australia, RUE was 2.13, 1.78 and 2.26 g DM MJ^{-1}, respectively (O'Connell et al., 2004). For soybean (*Glycine max*), mungbean (*Vigna radiata*) and cowpea (*Vigna unguiculata*), values of RUE were 2.07, 2.21 and 2.47 g DM MJ^{-1}, respectively (Muchow et al., 1993). These are values of RUE for crop species, grown under favourable conditions, which can explain the substantially higher RUE, as compared to RUE in our semi-arid grassland.

More extensive data on RUE in grassland ecosystems have been published, using an integrative approach of remote sensing, field measurements and meteorological data. For semi-arid grasslands in Kazakhstan, RUE ranged from 0.34 to 1.59 g C MJ^{-1} (Propastin and Kappas, 2009). For a semi-arid grassland in Arizona, with data based on net productivity for the summer growing season, Nouvellon et al. (2000) reported RUE values in the range of 0.20–1.72 g DM MJ^{-1}, with inter-annual variation mainly due to changes in precipitation. Mean RUE for temperate grasslands was 1.26 g DM MJ^{-1} in an extensive review by Ruimy et al. (1994). Our data is within the range of these reported values.

Analysis of covariance (ANCOVA) indicated an inter-annual variation in RUE, with a significant difference ($P < 0.0001$) in the slope of the regression lines between the three years (Fig. 14). RUE for the three hydrological years 2005–2006, 2006–2007 and 2007–2008

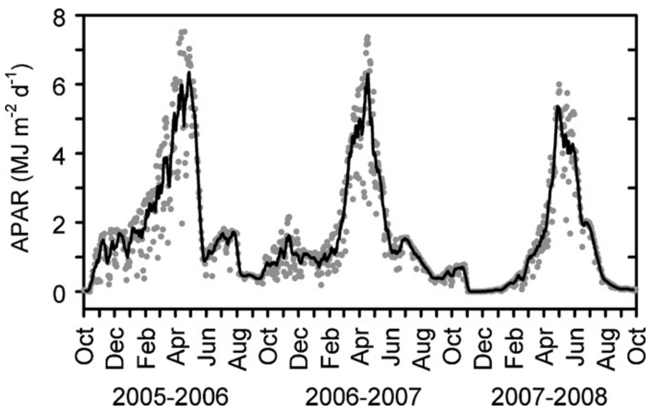

Fig. 13. Seasonal and inter-annual variation in absorbed photosynthetically active radiation (APAR) during the last three years of the study. The lines are 10-day running means.

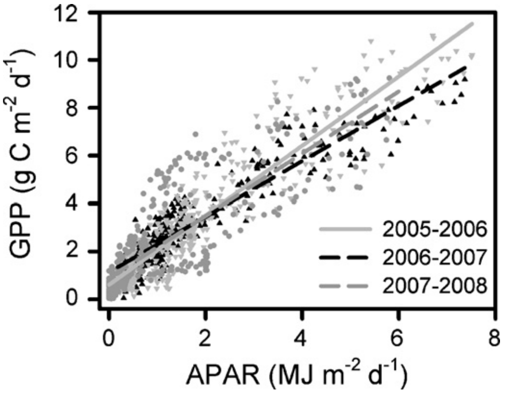

Fig. 14. Linear regression between daily-integrated absorbed photosynthetically active radiation (APAR) and gross primary productivity (GPP) over the last three years of the study. Linear regression 2005–2006: $y = 0.61 + 1.45x$, $r^2 = 0.86$, $P > 0.0001$, d.f. = 364. Linear regression 2006–2007: $y = 1.14 + 1.16x$, $r^2 = 0.87$, $P > 0.0001$, d.f. = 358. Linear regression 2007–2008: $y = 0.88 + 1.30x$, $r^2 = 0.70$, $P > 0.0001$, d.f. = 346.

was 1.45, 1.16 and 1.30 g C MJ^{-1} or 1.77, 1.41 and 1.58 g DM MJ^{-1} (based on NPP).

Inter-annual variation in RUE can result from changes in species composition and/or changes in crop ontogeny (Andrade et al., 2000; Fletcher et al., 2008), as well as several environmental variables (Sinclair and Muchow, 1999). In addition, specific leaf nitrogen (SLN, g m^{-2}) is known to affect RUE in different crops (Bange et al., 1997; Muchow et al., 1993). However, in our grassland, inter-annual variation in RUE cannot be accounted for by differences in SLN. Inter-annual variation in RUE reflected differences in productivity, as well as differences in IWUE. This can explain the maximum value of RUE (1.77 g DM MJ^{-1}) occurring in the hydrological year 2005–2006, when productivity was highest. In the hydrological year 2006–2007, RUE was lowest (1.41 g DM MJ^{-1}), as a result of lower IWUE and lower productivity, as low precipitation at the peak of the growing season decreased GPP. The intermediary value of RUE in the hydrological year 2007–2008 (1.58 g DM MJ^{-1}) cannot be related to the low values of annual accumulated GPP or LAD. In that year, the value of RUE probably reflects the change in species composition, with the field being ploughed and reseeded with *L. luteus*. Subsequent low precipitation resulted in a delay of sward development, and GPP only exceeded 2 g C m^{-1} d^{-1} from February 2008 onwards. Thus RUE in 2008 was primarily dependent upon the reduced length of the growing season – February to June – with favourable temperatures for grass growth resulting in relatively high RUE despite annual GPP being low.

4. Conclusions

Our results showed that Mediterranean grasslands, dominated by annual species, are extremely vulnerable to drought during the growing season. In the hydrological year 2004–2005 an extreme drought affected western Iberia, including Portugal. This was evident from our data, with maximum values for the Bowen ratio and daily IWUE at that time. In relation to carbon cycling, our grassland ecosystem was a source of carbon in this hydrological year, with a net release of 49 g C m^{-2}. The ecosystem was also a source of carbon in the hydrological year 2007–2008. The 15 g C m^{-2} emitted from the grassland in that year can be related to below average precipitation and the change in management practice that delayed sward establishment. In contrast, during the hydrological years 2005–2006 and 2006–2007, with precipitation above average, our ecosystem was a sink for carbon.

On an annual basis NEE correlated with total precipitation. The deviations from the regression line can be explained by management changes and the timing of precipitation, with precipitation in the dry season and early autumn promoting a release of carbon from the ecosystem through an increase in ecosystem respiration. In addition, lack of precipitation at peak growth resulted in a decrease of GPP, with a concomitant decrease in carbon sequestration. Changes in management, which are necessary to prevent fire or shrub encroachment or to renew the herbaceous plant community, may result in a setback of carbon sequestration by shortening the growing season and enhancing soil respiration following autumn precipitation events.

In contrast to NEE, annual IWUE and RUE did not correlate with total precipitation but were sensitive to the timing of precipitation. High IWUE with simultaneous high RUE, as occurring in the hydrological year 2005–2006, indicates high efficiency in photosynthesis, with respect to the capture of water and light.

The best descriptor for inter-annual variation in NEE was LAD. This parameter, through its dependence on LAI, integrates several variables that affect ecosystem growth and functioning, such as the length of the growing season, timing of precipitation, management and grazing. More studies are needed to validate the use of this parameter, and to understand how NEE of different ecosystems respond to LAD.

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