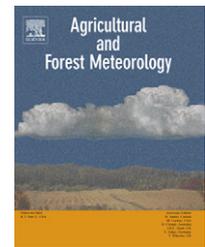


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Assessment and up-scaling of CO₂ exchange by patches of the herbaceous vegetation mosaic in a Portuguese cork oak woodland

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ABSTRACT

Long-term eddy covariance measurements over a montado oak woodland in southern Portugal have documented a vulnerability to predicted decreases in springtime rainfall, since water availability during spring limits annual CO₂ gain, the growth of fodder for animals, and the production of cork by *Quercus suber*. The current study examined CO₂ exchange of three different herbaceous vegetation components distributed over montado landscapes and within the footprint of long-term landscape eddy covariance monitoring studies. Simultaneous measurements with eddy covariance at two sites and with manually operated chambers at multiple locations revealed that slow drainage of shallow basins, the onset of drying at higher sites and a high release of CO₂ below tree canopies significantly influenced the overall course of montado ecosystem gas exchange during the spring.

Hyperbolic light response models were employed to up-scale and compare herbaceous gas exchange with landscape net ecosystem CO₂ flux. The up-scaling demonstrates the importance of the herbaceous understory in determining annual carbon balance of the montado and suggests a relatively small additional CO₂ uptake by the tree canopies and boles, i.e., by the aboveground tree compartment, during springtime. Annual flux totals obtained during the extremely dry year 2005 and a normal precipitation year 2006 for the oak woodland and a nearby grassland were essentially the same, indicating that both ecosystems similarly exploit available resources. Based on comparisons with additional temperate grasslands, we can visualize the montado herbaceous cover as a typical European grassland canopy, but where temperature fluctuations in winter control uptake, and where total production depends on springtime rainfall as it controls phenological events and eventually dieback of the vegetation. On the other hand, tree canopies remain active longer during late spring and early summer, modifying the montado response from that of grassland. Uncertainties in flux estimates via both chamber and eddy covariance methodologies currently prevent a full understanding of vegetation/atmosphere coupling, of the recycling of CO₂

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between the understory communities and trees, and of relationships between exchange rates of individual components of the vegetation mosaic and overall carbon and water balances in montado landscapes.

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1. Introduction

The montado (dehesa in Spain), often referred to as an open oak savanna (Pinto-Correia, 1993), is a unique Mediterranean-type ecosystem with an agro-silvo-pastoral origin characteristic of the Alentejo region of Portugal and extending throughout the dry regions of S.W. Iberia (Joffre and Rambal, 1988; Joffre et al., 1999). Generally, the tree cover does not follow a regular pattern, and the densities vary from 10 to 80 trees/ha (Joffre and Lacaze, 1993). The dominant tree species are the evergreen cork and holm oaks (*Quercus suber* and *Quercus rotundifolia*), and locally also deciduous mountain oaks (*Quercus pyrenaica*). The continuous layer of grasses and herbs or shrubs in the understory is influenced by gradients in habitat factors and by human activities such as grazing by animals, ploughing to reduce fire risk, and re-seeding with drought resistant cultivars (cf. Montoya, 1983). The herbaceous layer directly under trees may have a species composition different from that found outside the tree crowns (e.g., Gonzalez-Bernaldez et al., 1969; Parker and Muller, 1982) as the result of long-term changes in soil quality (Joffre and Rambal, 1988) and a different microclimate. In particular, perennial grasses are usually located only under trees.

Eddy covariance monitoring of carbon dioxide exchange over montado vegetation (Pereira et al., 2007) demonstrates that low winter temperatures and summer dry soils limit carbon uptake; the maximum in plant productivity and CO₂ uptake is found in the spring; and net ecosystem CO₂ exchange (F_{NEE}) varies inter-annually depending on rainfall (Fig. 1). Rapid development of the herbaceous layer during spring is extremely important with respect to annual carbon balance, since the total leaf area of this actively photosynthesizing surface during spring is twice or more than that of the trees. Future climate scenarios for the Mediterranean region indicate a longer dry season with less rain in spring and summer (Giorgi, 2006). Paredes et al. (2006) demonstrate that rainfall during March has decreased already since the early 1960s. The herbaceous component of the montado is particularly vulnerable to decreased springtime rainfall, since the soil water store accessible to grasses and herbs is limited (Aires et al., 2008).

One method of examining directly the CO₂ exchange characteristics of herbaceous vegetation is to employ large chambers that enclose “ecosystem monoliths”. Chamber measurements of CO₂ fluxes permit us to evaluate spatial variation in exchange fluxes that are dependent either on local habitat factors or due to herbaceous vegetation composition. A second possibility is to utilize eddy covariance methodology in favorable locations, e.g., where large open areas allow for appropriate conditions and where the measurement footprint is clearly related to defined herbaceous elements. During the springtime rapid growth period of 2006, we applied both

methods simultaneously at the Mitra montado site near Evora, Portugal. Chamber measurements were carried out both under trees and in open areas away from trees. Since the topography is undulating, with higher dry areas including trees, and low open areas without trees where water accumulates in springtime, we assessed both open situations separately. Eddy covariance measurements of CO₂, latent heat and energy exchange were made for the entire area at a 30 m tower (Pereira et al., 2007), but for the herbaceous component only in large low, open areas via a 2.25 m mast. Similar information was also obtained for an open grassland located 8 km distant from Mitra at Tojal (Pereira et al., 2007; Aires et al., 2008).

Results of the chamber measurements of net ecosystem CO₂ (F_{NEE}) exchange at three locations and from the 2.25 m eddy covariance station were analyzed with an empirical model in dependence on environmental factors and developing biomass, e.g., leaf area index (LAI). The goals of the study

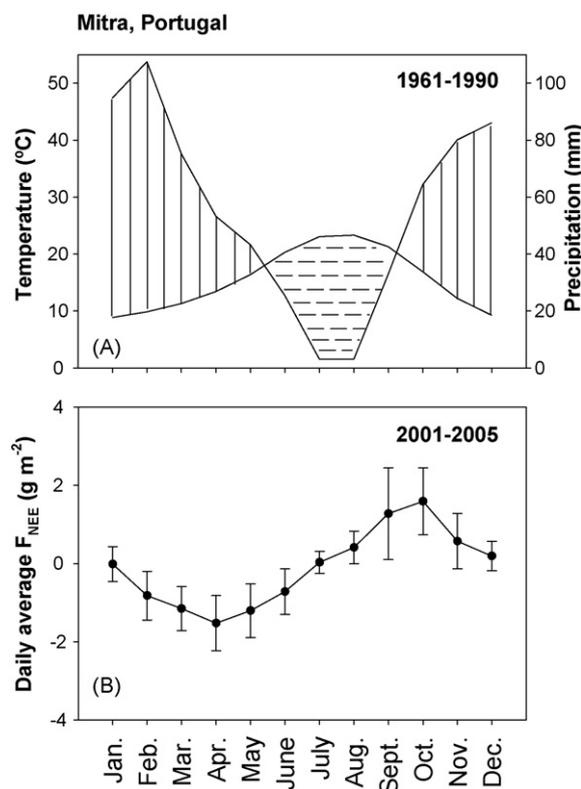


Fig. 1 – (A) Climate diagram according to Walter (1979) for the Mitra campus of the University of Evora, Portugal (Herdada da Mitra meteorological station 38°32'N, 7°54'W, 230 m a.s.l.). (B) Mean annual course obtained for F_{NEE} from the 30 m eddy covariance tower during the period 2001–2005 in Herdade de Mitra as reported by Pereira et al. (2007). Error bars indicate the monthly standard deviation.

were (1) to compare the carbon exchange dynamics during springtime of the three herbaceous layers studied, i.e., under trees, outside of trees in elevated locations of the landscape, and in open low areas, in their sensitivity to environmental factors and LAI development, (2) to examine in low areas the differences in carbon exchange that were estimated by chambers and eddy covariance methodology, (3) to estimate total springtime CO₂ uptake by the herbaceous component of the montado in relation to cover by different plant communities and with respect to total exchange fluxes, and (4) to develop concepts related to ecosystem function that will aid in the evaluation of climate change impacts on the montado.

2. Materials and methods

2.1. Site description

The experimental sites were located in the center of the Alentejo Province, Portugal, at Herdade da Mitra (38°32'N, 8°00'W, 243 m a.s.l.) near the Mitra campus of the University of Evora. The climate is Mediterranean, with a hot and dry summer; most precipitation occurs between October and April. Monthly mean temperature and precipitation for the period 1961–1990 for the Mitra campus (Herdade da Mitra meteorological station 38°32'N, 7°54'W, 230 m a.s.l.) located ca. 1 km away from the study site are shown in Fig. 1.

The vegetation is typical for the montado (Fig. 2). The dominant tree species are *Quercus suber* (cork oak) and *Quercus rotundifolia* (holm oak) at a density of 40–50 trees ha⁻¹, comprising an overstory with ca. 35% of tree canopy cover in the footprint of the 30 m long-term eddy covariance tower

at the site (Siebicke, 2007). Below and between the trees, the continuous herbaceous layer was dominated by forbs, legumes and grasses, such as, *Coleostephus myconis*, *Echium plantagineum*, *Tuberaria guttata*, *Arum italicum*, *Geranium molle*, *Rumex bucephalophorus*, *Bellardia trixago*, *Plantago coronopus*, *Raphanus raphanistrum*, *Ornithopus sativus*, *Trifolium dubium*, *Poa annua*, and *Bromus* sp. Approximately 70% of the herbaceous community consists of annuals, while 30% were perennials. The soil is a very shallow (ca. 30 cm deep) sandy Cambisol (FAO, 1988) overlying a fractured gneiss rock.

2.2. F_{NEE} measurements via eddy covariance methodology

An open-path eddy covariance system consisting of an LI-7500 open path CO₂ analyzer (LiCor; Lincoln, Nebraska) and CSAT3 sonic anemometer (Campbell Scientific, Inc.) was installed at 2.25 m height. Air temperature, CO₂ and water vapour concentrations as well as the wind velocity were sampled at 20 Hz frequency from the beginning of March to mid-May 2006 in a low open grassland site (see Fig. 2) to measure energy, latent heat and carbon dioxide exchange. We calculated the net ecosystem CO₂ exchange rate (F_{NEE}) directly from flux data following the EUROFLUX methodology (Aubinet et al., 2000; including also updates by Lee et al., 2004; Mauder and Foken, 2006). Covariance of the vertical velocity component and of the CO₂ concentration was computed every half hour. Planar fit rotation (Wilczak et al., 2001) and quality tests (Foken and Wichura, 1996) in the updated flux methodology (Foken et al., 2004) were applied. The procedure of gap filling, as well as the method for calculating ecosystem respiration (F_{RE}) and gross photosynthesis (F_{GPP}) from net CO₂ fluxes (F_{NEE}) were carried out as described by Reichstein et al. (2005) and Owen et al. (2007).

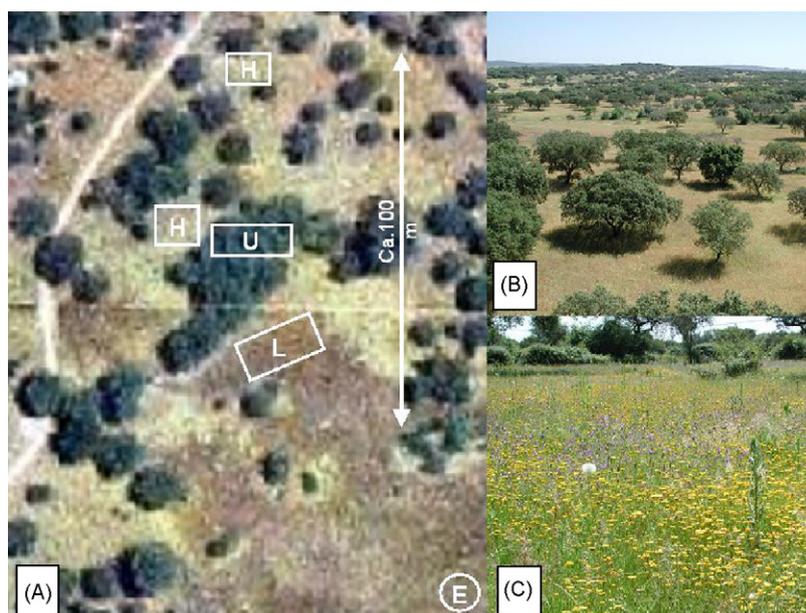


Fig. 2 – (A) Location of the chamber measurement plots within the montado vegetation mosaic—L: indicates low open plots; H: high open plots; and U: under canopy plots; E indicates the eddy covariance 2.25 m mast. North is the vertical direction in the figure. The main wind direction is from northwest. Measurements of the landscape gas exchange from the 30 m tower (Fig. 1) were conducted ca. 300 m to the northeast of the scene. (B) View of the montado vegetation from the 30 m eddy covariance tower. (C) View of dense low open site vegetation in late spring.

Similar measurements were carried out as reported by Pereira et al. (2007) ca. 300 m from the sites shown in Fig. 2 at a measurement height of 29 m. Sensors were an R3 Gill sonic anemometer (Gill Instruments, Hampshire, UK) and LiCor 7000 closed path analyzer. Measurements were also conducted at the Tojal grassland site (38°28'N, 8°01'W, 190 m a.s.l.) ca. 8 km distant from Mitra with an R3 Gill sonic anemometer and LiCor 7500 open path analyzer at 2.5 m. Details of all measurement methods, the seasonal and annual flux sums for F_{GPP} , F_{NEE} and F_{RE} , and radiation and rain use efficiencies for the Mitra landscape and Tojal grassland are described in Pereira et al. (2007) and Aires et al. (2008). For the measurement period during springtime of 2006, an atmospheric stability and wind direction-dependent footprint analysis was carried out on a half-hour basis for data obtained for the Mitra landscape at 29 m height (Siebicke, 2007), identifying the time dependent flux contributions from landscape components that were characterized individually via large chamber flux determinations (next section). The footprint analysis was used together with chamber fluxes to obtain a “bottom-up” estimate of landscape level fluxes within the footprint of the tall tower over the course of the measurement period in spring.

2.3. F_{NEE} measurements with chambers

Sites with replicated measurement plots were set up for chamber measurements at the locations indicated in Fig. 2. Local topographic variation within the area shown in Fig. 2 was only 3–4 m. Nevertheless, this variation leads to a repeating vegetation mosaic characteristic of the region, where trees are established in high drained areas, and meadows free of trees are found where flooding and water-logging occurs during winter and spring. Thus, the gas exchange behaviour of three major herbaceous components of the land cover of the region was sampled. These were designated as low open moist grassland (“L”); high open relatively dry grassland (“H”); and vegetation occurring under oaks (“U”). The eddy covariance 2.25 m mast was located in the low open vegetation as indicated in Fig. 2 with circled letter “E”. It provides a direct comparison with the set of the chamber measurements at the “L” site, and an important reference for the measurements further away as discussed in Section 3. Soil characteristics differed between sites, with significantly greater sand content at H and U and greater silt content at L. A maximum available water storage in the 30 cm soil profile of 24 mm was reported by David et al. (2004).

F_{NEE} and F_{RE} were directly measured with a systematic rotation during seven campaigns over all site locations, using manually operated, closed gas exchange chambers modified from the description given by Droesler (2005; <http://www.wzw.tum.de/vegoek/publikat/dissdipl.html>), Wohlfahrt et al. (2005), and Li et al. (2008) as used in Central European bogs and alpine grasslands. The 38 cm × 38 cm × 54 cm chambers of our system were constructed of transparent plexiglass (3 mm XT type 20070; light transmission 95%). Dark chambers, for measuring ecosystem respiration (F_{RE}) were constructed of opaque PVC, and covered with an opaque insulation layer and with reflective aluminum foil. Using extensions, chamber height was adjusted to the canopy height, which was up to ca. 65 cm on the meadows. Chambers were placed on frames

made of polyethylene that were inserted 4 cm into the ground 2–3 days before measurements were conducted. They were sealed to the chamber with a flexible rubber gasket. Tests indicated that leakage did not occur (see Droesler, 2005 for details), however, this could not be examined regularly in the case of systematic field measurements.

Increased pressure in the chamber was avoided by (i) a 12 mm opening at the top of the chamber which was closed after the chamber had been placed onto the frame and (ii) a vent inserted at the bottom of the chamber. Circulation of air within the chamber was provided by fans yielding a wind speed of 1.5 m s⁻¹. Change in chamber CO₂ concentration over time was assessed with a portable, battery operated IRGA (LiCor 800 and 820). Measurements were carried out in most cases within 3 min of placing the chamber on the frames, except at rates of F_{NEE} close to 0, when they lasted as long as 5 min. Depletion of CO₂ in the chamber during measurement was ca. 20–30 ppm. Influence of the concentration change on estimated gas exchange rates was ignored. By mounting frozen ice packs inside and at the back of the chamber in the air flow, temperature during measurements could be maintained within 1 °C relative to ambient (air and soil temperatures inside and outside of the chambers are monitored during measurement). Comparisons of F_{NEE} determined via chamber methods and via eddy covariance methodology are reported for the low open moist grassland in Section 3.

During each measurement campaign, light and dark chamber measurements were conducted cyclically from sunrise to sunset over single days, with six observations per cycle and comparing two herbaceous vegetation types (three replicates at each site). Eight to 11 measurement cycles were accomplished on individual days. A campaign was completed after three sets of site comparisons (six vegetation locations compared), and after which the rotation over the sites was begun again. A data base was compiled with the observed environmental conditions, F_{NEE} , F_{RE} and estimated F_{GPP} . To estimate F_{GPP} , ecosystem respiration was estimated for each F_{NEE} observation time by linearly extrapolating between dark chamber observations (F_{RE}) and then adding it to F_{NEE} . As seen in Fig. 5, the measurements of F_{NEE} and F_{RE} were closely associated in time, thus the errors made in F_{RE} estimations were very small. Chamber measurements were conducted from the beginning of March until mid-May over the course of the springtime, in order to develop a picture of the seasonal changes in CO₂ exchange occurring during this period. Limitation in manpower to carry out the labor intensive chamber measurements prevented continuation of the observations with chambers during nighttime periods.

2.4. Estimation of model parameters describing gas exchange response

Empirical description of the measured F_{NEE} fluxes was accomplished via a non-linear least squares fit of the data to a hyperbolic light response model, also known as the Michaelis-Menten or rectangular hyperbola model (cf. Owen et al., 2007):

$$F_{NEE} = -\frac{\alpha\beta Q}{\alpha Q + \beta} + \gamma \quad (1)$$

where F_{NEE} is net ecosystem CO_2 exchange ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$), α is the initial slope of the light response curve and an approximation of the canopy light utilization efficiency ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1} / \mu\text{mol photon m}^{-2} \text{ s}^{-1}$), β is the maximum F_{NEE} of the canopy ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$), Q is the photosynthetic photon flux density ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$), γ is an estimate of the average ecosystem respiration (F_{RE}) occurring during the observation period ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$), (α/β) is the radiation required for half maximal uptake rate, and $(\beta + \gamma)$ is the theoretical maximum uptake capacity. Since the rectangular hyperbola may saturate very slowly in terms of light, the term $\alpha\beta Q/(\alpha Q + \beta)$ evaluated at a reasonable level of high light ($Q = 2000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ is used in this study) approximates the maximum F_{GPP} and can be thought of as the average maximum canopy uptake capacity during each observation period, notated here as $(\beta + \gamma)_{2000}$.

The parameters α , β , β_{2000} (e.g., F_{NEE} at $Q = 2000$) and γ were estimated for each site using F_{NEE} data for each measurement campaign. Data were pooled for each site and campaign, including measurements in three replicate plots on each separate day. A generalized model was obtained for each site by regressing the determined parameter values on measured environmental variables. The purpose of the generalized model was to carry out “gap filling”, i.e., to estimate a continuous record of ecosystem CO_2 exchange over the course of the measurement period for each location. Given that there are strong changes during this period in environmental driver variables, the best gap filling is obtained by including information from all measurement days into the model parameter regression analysis.

3. Results

3.1. Habitat conditions and seasonal development of the vegetation mosaic

Daily maximum air temperature continuously monitored at the 2.25 m eddy covariance station increased rapidly with increasing radiation input from 11.6 °C in early March to 31.1 °C at the end of the measurement period (Fig. 3). Minimum temperature was initially low and frost occurred in the area on one occasion. Recorded minima at the eddy covariance station increased from 1.3 °C to 16.8 °C. Soil temperature at the eddy station (10 cm depth) was influenced by the higher than normal precipitation during January through March. This led to high water tables and surface standing water in the low open meadow, a condition that extended to the eastern fringe where the eddy station was located. After water tables receded, soil temperature at the eddy station increased and remained near 16 °C. Soil temperatures recorded at the low open and high open chamber measurement sites agreed well with those at the eddy covariance station after water tables receded, while soil temperature at sites under tree crowns were consistently cooler. With increasing temperature, maximum VPD increased as did evapotranspiration measured via eddy covariance (Fig. 3).

Soil water content at the low open site remained high and relatively constant over the entire measurement period (17–20% of dry weight). The site was located at the western fringe of the meadow, and standing water did not occur, although this was apparent 10 m distant from the site in the direction of

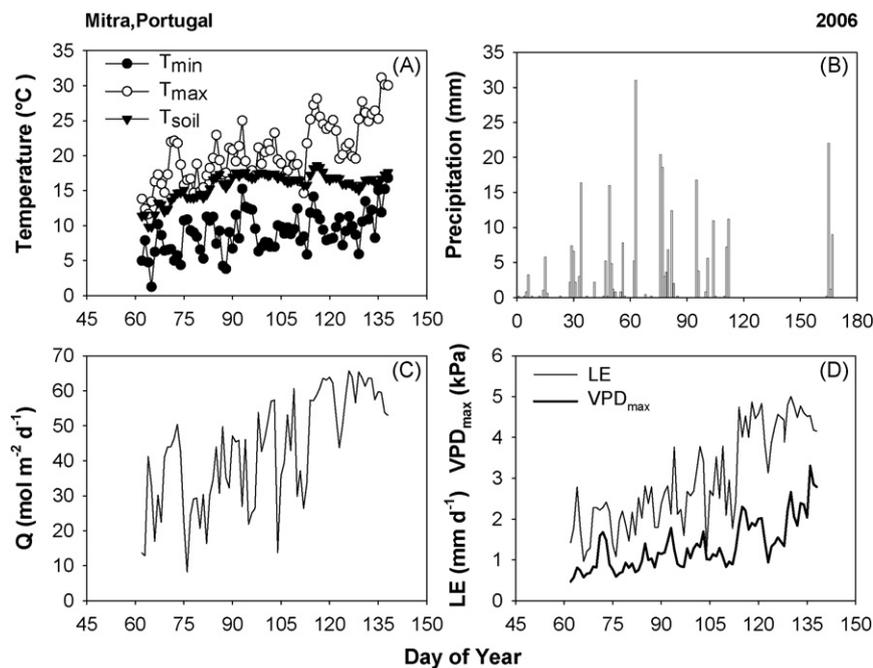


Fig. 3 – Spring season time courses for (A) maximum and minimum temperatures and daily average soil temperature at 10 cm measured at the 2.25 m mast of the understory eddy covariance station, (B) daily precipitation, (C) daily total photosynthetic photon flux, and (D) maximum vapor pressure deficit of the air and latent heat flux of low open herbaceous vegetation as determined at the 2.25 m mast station.

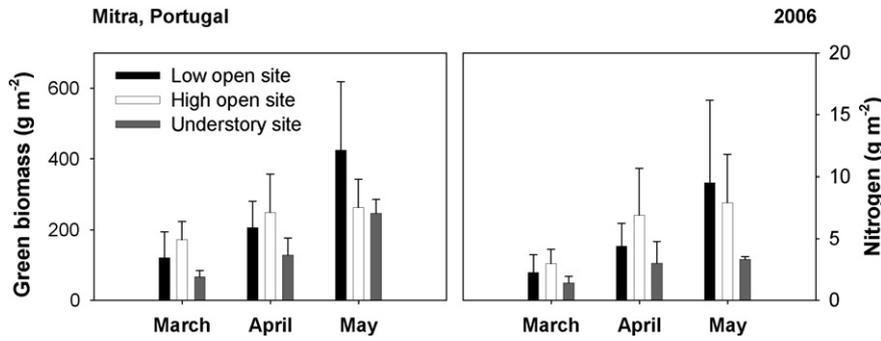


Fig. 4 – Average monthly green biomass and total aboveground nitrogen content on a ground area basis at the three herbaceous vegetation study locations.

the center of the meadow. In contrast, soil water content at the H and U locations decreased strongly in May, especially during the last 10 days of the measurement period. With respect to the footprint areas of the eddy station, soil water content and water table depth were monitored along a transect from the L chamber measurement site to the tower (see Fig. 2A). Average water table along the transect was at the surface on day of year

(DOY) 70 and was recorded at ca. 15 cm below the surface on DOY 110.

Herbaceous green biomass increased moderately from March to mid-May at the H site, and strongly (a factor of 3–4) at the L and U sites (Fig. 4). The maximum for herbaceous biomass was 540 g m^{-2} observed in May for the low open meadow. Similar patterns as for biomass occurred for

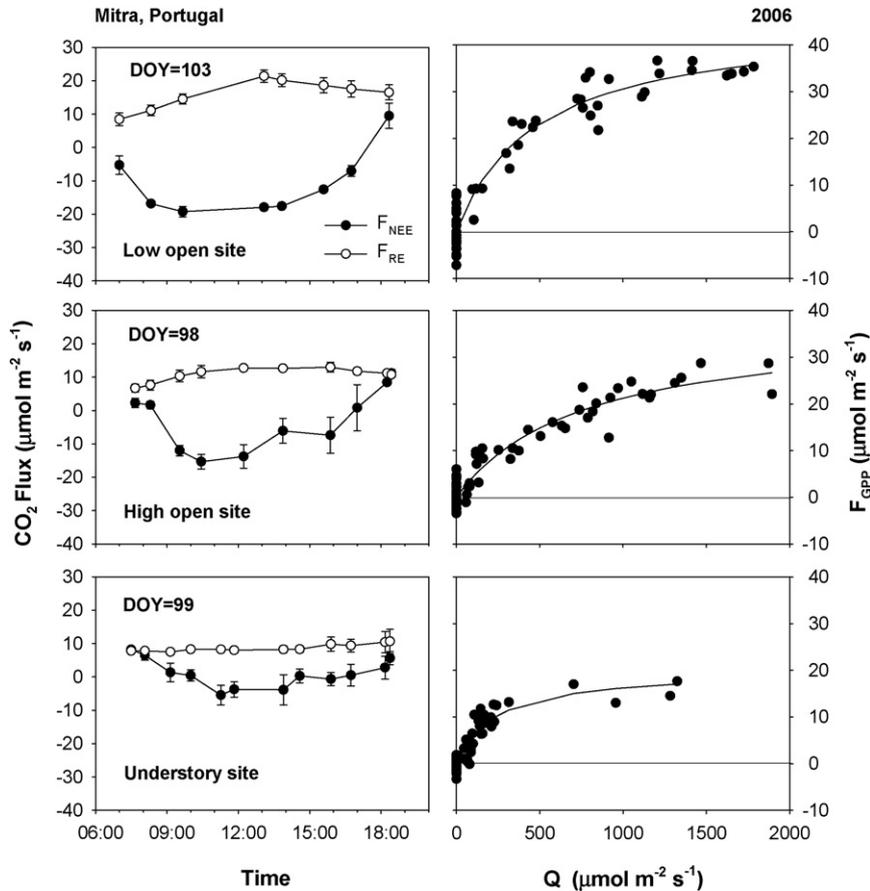


Fig. 5 – Examples of fluxes (F_{NEE} and F_{RE} in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) measured with transparent and darkened chambers over the course of 1 day at each of the herbaceous vegetation study sites and plotted as a function of incident photosynthetic photon flux density, Q . Also shown are the predicted light response curves obtained in fitting of the hyperbolic light response model. Both measured and predicted data in the right hand panels are corrected with average ecosystem respiration (parameter γ) to obtain the estimates of F_{GPP} shown. DOY is day of year. R^2 values for the model fits are 0.92, 0.93 and 0.89 for the low, high and shade sites, respectively.

aboveground total nitrogen at the H and L sites, but aboveground N remained low in the U site and concentration in biomass actually decreased during May (cf. biomass versus nitrogen m^{-2}), potentially indicating an N limitation on activity and flux rates. The composition of the plant community changed during the course of the spring, with an increase in legumes at the L and H sites, enriching the aboveground N pool and potentially contributing to greater photosynthetic activity, while grasses with low N increased at the U site.

3.2. Quantifying gas exchange characteristics of landscape elements

An example of the type of data obtained with chambers is illustrated in Fig. 5, comparing response on sunny days during the middle of the measurement period in the three herbaceous vegetation types. Although environmental conditions are different on each day, a high capacity for uptake (F_{NEE}) and respiratory loss (F_{RE}) of CO_2 at the L and H sites in comparison to the U site is apparent. Variation in gas exchange response among plot replicates is small. Results of inverting the simple hyperbolic light response model for the same data are shown in the right hand panels of the figure. The measured F_{NEE} data have been adjusted to F_{GPP} by adding the value of F_{RE} to observed fluxes. While some unexplained scatter around the predicted response curves is found due to temperature change, diurnal hysteresis (Gilmanov et al., 2003, 2005), or simply measurement errors, Q is a very good predictor of response. Points at $Q = 0$ scatter, depending on the variation in temperature over the course of each day, which influences the dark chamber fluxes. Considering all campaigns at three sites, R^2 ranged between 0.79 and 0.98, and was greater than 0.8 in 97% of all cases (a case includes the flux rate observations during a campaign at a single location as in the examples in Fig. 5).

Seasonal trends for $(\beta + \gamma)_{2000}$, α and γ for all sites are shown in Fig. 6. Average standard errors for α , β and γ were 0.008, 3.62 and 0.52, respectively, including all days and measurement sites. Interpreting $(\beta + \gamma)_{2000}$ as an estimate of maximum F_{GPP} , the photosynthetic potential of the three sites continually increased along with biomass development (from ca. 8 to $44 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ ground area s}^{-1}$). Differences between the L and H sites were not large, while the U sites exhibited lower photosynthetic potential due to lower LAI (biomass) and apparent reduced specific activity (low N content). Light utilization efficiency of the vegetation increased with development of the herbaceous vegetation in a similar manner at all sites, approaching a maximum of ca. $0.065 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \mu\text{mol photon m}^{-2} \text{ s}^{-1}$. Seasonal patterns observed for γ were similar to those for $(\beta + \gamma)_{2000}$, in part due to increments in respiration as biomass increased, but presumably also due to increased delivery of photosynthate-derived substrates to the microbial communities as canopy photosynthetic capacity increased.

The results described in Fig. 6 allow us to obtain a generalized set of empirical equations, applicable to the measurement period, that describe seasonal change in F_{NEE} and F_{RE} . Considering that LAI (biomass) and temperature are certain to influence both flux components, we examined both linear and curvilinear regressions employing these as pre-

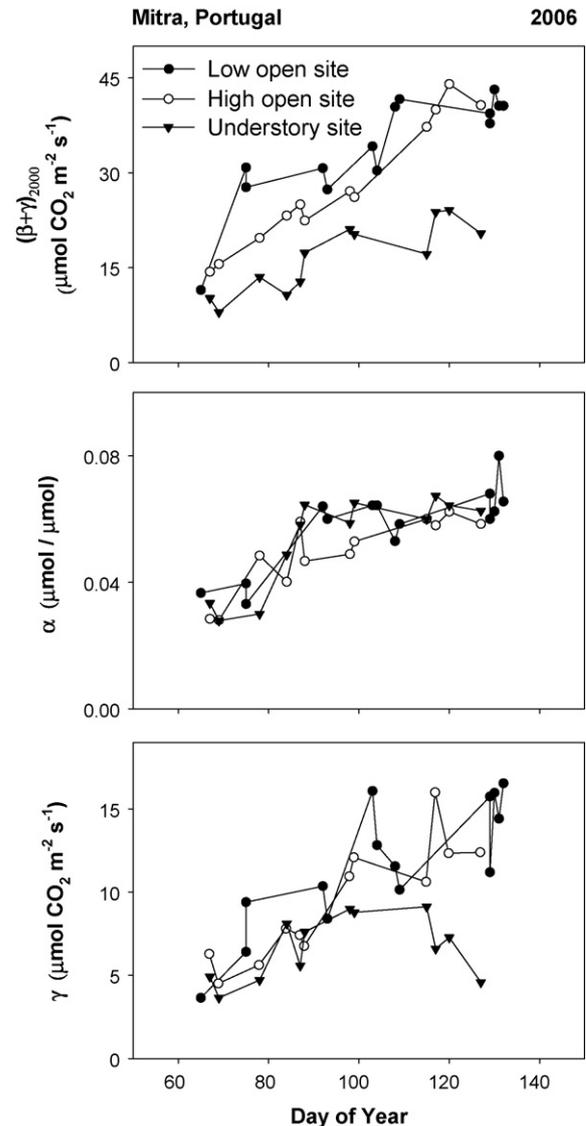


Fig. 6 – The springtime seasonal courses estimated for the empirical model parameters $(\beta + \gamma)_{2000}$, α , and γ as determined with chamber flux measurements at the three herbaceous vegetation study sites. Points organized according to day of year are connected with lines only to help with visualization of the trends.

dictors for the parameters of Eq. (1). The results are presented in Tables 1 and 2. Curvilinear regressions (e.g., exponential) did not provide a better description of α , β , γ or F_{RE} than the linear equations shown. Residual analysis also did not lead us to expect that a curvilinear description would be more appropriate. In the case of α , LAI and temperature alone did not provide much predictive power, but including β into the equation improved prediction to the levels shown. As a test, parameters obtained with these equations were used with information on LAI development to estimate F_{NEE} for all chamber measurements (Fig. 7). The results demonstrate that the empirical models provide reasonable descriptions of CO_2 exchange at each of the herbaceous vegetation sites, in order to estimate a continuous record of ecosystem gas exchange

Table 1 – Coefficients and statistics of the multiple linear regression $Y = a(LAI) + b(T_{air}) + c\beta + d$; applied in the analysis of model parameters at different sites (L = low open, H = high open, U = understory)

Site	Y	a	b	c	d	R ²
L	β	12.78*	2.21**	–	–27.83	0.66
	α	0.0397*	0.0059	–0.0023*	–0.0382	0.46
	γ	0.67	0.86***	–	–8.83*	0.82
H	β	1.86	1.35**	–	–0.89	0.52
	α	0.0058	–0.0001	0.0019*	–0.0195	0.65
	γ	0.24	0.73**	–	–6.28	0.62
U	β	4.91	0.39	–	2.92	0.29
	α	0.0277*	–0.0015	0.0007	0.0186	0.42
	γ	0.66	0.22	–	1.57	0.18

Units for parameters are those given in the methods section and T_{air} is in °C. *Significant at $P = 0.05$, **Significant at $P = 0.01$, ***Significant at $P = 0.001$.

behaviour during the springtime of 2006. Nevertheless, a large scatter remains that is in part caused by additional factors influencing ecosystem gas exchange, e.g., changing light quality, vpd, physiological adjustments over time, etc.

Multiple linear regressions for F_{RE} (Table 2) indicated a strong influence of temperature on respiration at the low open and high open sites, while F_{RE} at the U site was very weakly correlated with temperature. A possible reason for this has been provided by Tang et al. (2005) for similar oak savanna in California. The dark chamber measurements at the U sites are different from those at the other sites, since it is impossible to separate herbaceous community respiration from that of tree roots and microbial activity, which may be stimulated by tree root exudation. Tang et al. (2005) determined that photosynthate from the tree canopy increases soil respiration with a 7–12 h time lag. Thus, due to compensating effects, as temperatures decrease in the afternoon and evening, respiration may nevertheless increase. LAI provided additional explanation of respiration response only at the low open location. At the U site, F_{RE} was negatively correlated with LAI, perhaps indicating a slowly diminishing activity of the surface layer tree roots over time and a shift in activity to lower soil layers.

3.3. Spatial and temporal estimates of vegetation CO₂ exchange

The models for site level CO₂ exchange were used with information on LAI development and site specific temperature

Table 2 – Coefficients and statistics of the multiple linear regression $F_{RE} = a(LAI) + b(T_{air}) + c$ applied at different sites (L = low open, H = high open, U = understory)

Site	a	b	c	R ²
L (F_{RE})	0.471**	0.449***	0.297	0.41
H (F_{RE})	–0.002	0.382***	1.836*	0.35
U (F_{RE})	–1.297***	0.087***	6.640***	0.19

F_{RE} is in $\mu\text{mol m}^{-2} \text{s}^{-1}$ and T_{air} is in °C. *Significant at $P = 0.05$, **Significant at $P = 0.01$, ***Significant at $P = 0.001$.

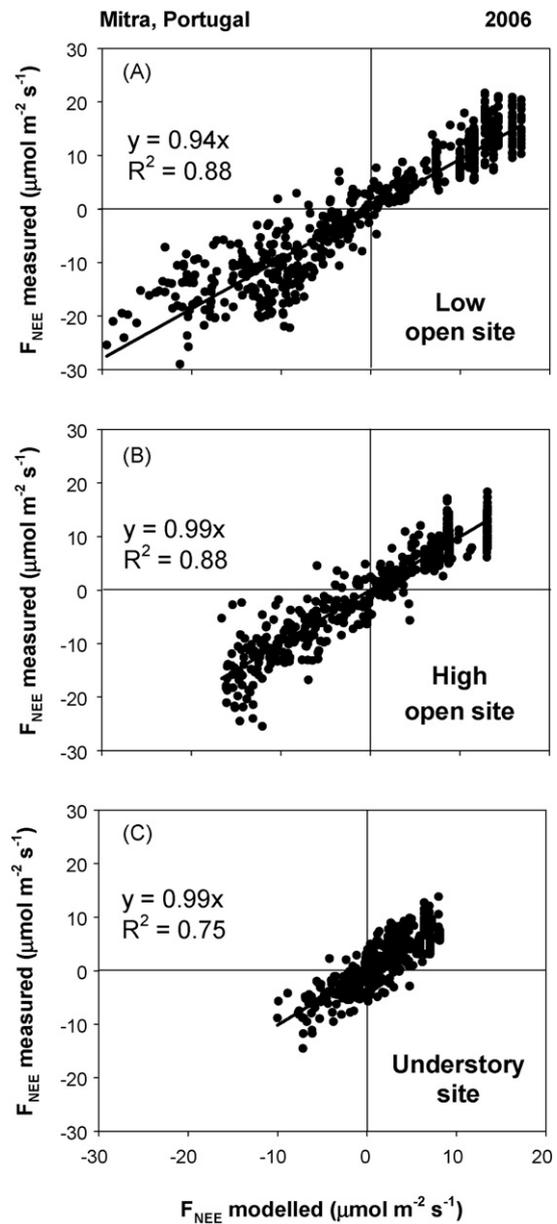


Fig. 7 – Comparison of predicted and measured F_{NEE} for the generalized hyperbolic light response models applied over the period of springtime measurements at the three herbaceous vegetation study sites according to Eq. (1). Three sets of equations for α , β and γ are given in Table 1, which according to prevailing air temperature and existing LAI, are included into Eq. (1) to predict F_{NEE} .

to estimate F_{NEE} for each daylight half hour during the measurement period. Integrating F_{NEE} over the daytime hours, the seasonal time course comparisons shown in Fig. 8 were estimated for the three herbaceous vegetation sites. These can be compared further with measurements from the 2.25 m eddy covariance tower. As seen in Fig. 8C and D, comparisons of F_{NEE} for the low open area, obtained either as direct momentary measurements (3–5 min view for the chambers versus half-hour averaging from the eddy station), or as the modeled F_{NEE} flux versus measured eddy flux integrated over

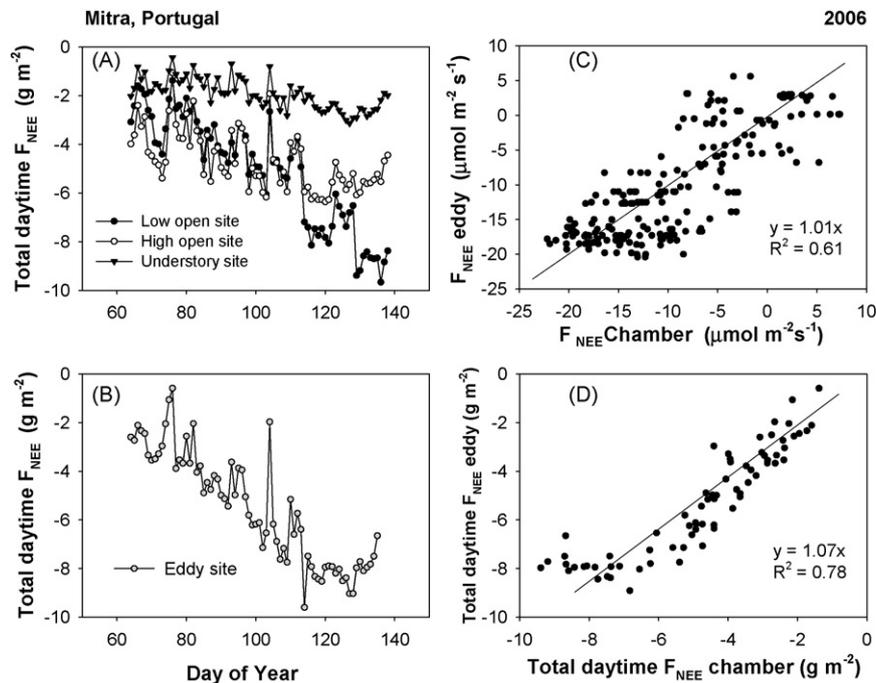


Fig. 8 – Summary of daytime carbon exchange by herbaceous vegetation at three study sites as characterized by chamber and eddy covariance measurements. (A) Modelled seasonal course in daytime carbon gain (integrated F_{NEE}) at each chamber study site. (B) Measured seasonal course in daytime carbon gain observed at the 2.25 m eddy covariance mast. (C) Direct comparison for low, open herbaceous vegetation (“L” site) of momentary chamber F_{NEE} measurements during daytime with measured F_{NEE} at the 2.25 m eddy covariance mast (location “E” in Fig. 2). (D) Comparison for low, open herbaceous vegetation (“L” site) of the total daytime carbon gain estimated from the chamber-based model and from measurements at the 2.25 m eddy covariance mast (location “E” in Fig. 2).

the daytime period agree reasonably well. Large scatter in Fig. 8C may be explained by differences in radiation between the point location of the chamber measurements versus the footprint of the flux tower, differences in the objects that are being viewed, and environmental modifications caused by the chambers (see also Wohlfahrt et al., 2005). The scatter may mask seasonal shifts in the correlation shown. Apparent systematic deviations from the regression line in Fig. 8D seem primarily due to differences in the water balance status of the objects viewed by chambers and the eddy covariance system (see discussion of Fig. 9 below). A similar behavior is observed for daytime F_{NEE} trends at the L and H sites during most of the observation period, while in the last weeks, decreased water availability (6.5% water content) as well as restricted development of biomass at H (cf. Fig. 4) apparently led to a slow decrease in CO_2 uptake. F_{NEE} of the low open area in contrast continues to increase with moist soil and continuing vegetation growth. F_{NEE} at the U site is predicted to remain low due to reduced light, the apparent influence of low nitrogen availability (low values of $(\beta + \gamma)_{2000}$), and again at the end of the study period, decreased soil moisture (9% water content).

Since direct measurements with chambers could not be carried out during the nighttime period, we assumed that the temperature response of respiration determined during the daytime period is the same as at night, in order to derive estimates of nighttime CO_2 losses and daily F_{NEE} . Thus, the regression models from Table 2 were used to estimate F_{RE} over the nighttime period of each day during the measurement

period. The comparison of herbaceous vegetation sites based on modelled chamber data and the observations from the low open meadow eddy covariance tower are presented in Fig. 9A through D. Considering first the low open site, a very good agreement was found for the modelled nighttime flux and nighttime eddy covariance measurements during the time period DOY 98 until 133. Before day of year 98, F_{RE} measured by eddy during nighttime was much less than estimated with chambers. This occurred because of flooding of the meadow in the footprint of the tower, whereas the chamber measurements were conducted at higher sites with a non-water-logged soil profile. With a water table at the surface on DOY 70 and subsequent decreasing rainfall, the meadow dried and the sites became comparable. At the end of the measurement period, soil drying at H and U may have an influence, again separating the flux estimates. The long period of agreement found between modelled and measured nighttime fluxes at the low open site supports the hypothesis that the comparison shown in Fig. 9B provides a good first approximation of the nighttime gas exchange of the L, H, and U vegetation stands. Nighttime respiration at the L and H sites is estimated to be essentially the same (Fig. 9B). In contrast, the nighttime respiration at the U site was lower except very early in the spring. It decreased continually as the season progressed, possibly due to changing tree root activity, change in the quality of respiration substrates, and soil drying.

Modelled daytime F_{NEE} and nighttime F_{RE} ($=F_{NEE}$) can be combined to provide daily F_{NEE} as shown in Fig. 9C and D.

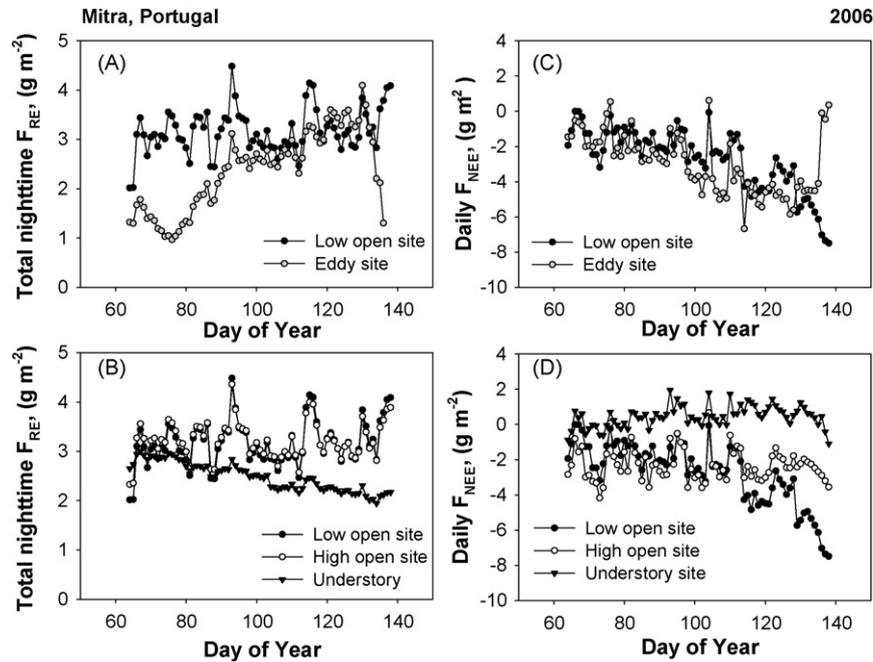


Fig. 9 – Nighttime respiration and daily integrated F_{NEE} estimates (day plus night) by herbaceous vegetation at three study sites as determined by up-scaling from the chamber and eddy covariance measurements described in the text.

Considering the comparison of eddy to the chamber-based model at the low open site, a generally good agreement is found. Since the nighttime integrated F_{RE} fluxes during early season are quite different (Fig. 9A), compensatory influences must occur to achieve this agreement. Daytime carbon gain estimated via eddy covariance for a large area of water-logged meadow are in fact lower than estimated at the chamber measurement site (Fig. 8). Periods with relatively large deviations between modelled chamber data and eddy covariance estimates are found in Fig. 9C (ca. DOY 107 and 128), suggesting that systematic errors may occur with the empirical models under certain conditions. Daily maximum temperatures during these periods are much lower than normal. The L and H sites exhibit similar daily F_{NEE} until DOY 115 (Fig. 9D), after which carbon uptake capacity of the low open site continues to increase while high open remains constant. A loss of carbon occurs under the trees. The understory locations seem to act overall as a net CO_2 vent in the montado landscape, despite the development of herbaceous vegetation under the crowns and daytime CO_2 uptake.

Siebicke (2007) carried out a detailed analysis of the eddy covariance footprint of the 30 m tower during the measurement period on a half-hour basis. From this work, an estimate for weighting of contributions from different vegetation patches may be derived. In summary, the analysis indicated that ca. 33% of the landscape flux originates at low open, 36% at high open and 31% from tree canopy locations and below the crowns at night, respectively. For the daytime period, average contributions from the same vegetation units were 33, 34 and 33%. When considering the current location of the tower, the greatest variation in flux contribution to the “measured landscape flux” came from the low areas,

particularly during the daytime (27–41%). The tall tower site was chosen in order to examine a high area with trees. In this context, the low area may be viewed as a disturbance factor for the tall tower experiment, one which has a relatively large variation in magnitude.

The weighted average daily F_{NEE} for the entire herbaceous layer within the tower footprint was estimated from the hourly modelled chamber CO_2 exchange rates that are summarized in Fig. 9. This daily F_{NEE} is compared to flux rates of the montado landscape as observed at the 30-m tower in Fig. 10B (lower panel). Additionally, the upscaling was conducted by substituting eddy flux estimates for the chamber-derived values at L sites (Fig. 10A, upper panel). Two periods are differentiated in these comparisons, the month of March shown as open circles and the period of April to mid-May shown as solid circles. Generally, we found a very good coincidence in the time dependent variation in flux estimates (not shown) throughout the observation period. However, it can be seen from Fig. 10 that the herbaceous ecosystem component progressively explains more of the landscape level carbon gain as the aboveground vegetation develops, and as the magnitude of carbon gain increases to maximum. Thus, the comparison supports strongly the importance of the herbaceous component in determining carbon exchange of the montado during springtime.

On the other hand, alternative upscaling with estimates from the chambers or from the eddy flux measurements to represent the low open vegetation provides us with differing impressions of the role played by herbaceous vegetation in overall ecosystem carbon exchange. Using chambers, the average difference between landscape versus understory diurnal carbon gain, that potentially might be ascribed to aboveground boles and tree canopies, is ca. $1.4 \text{ g C m}^{-2} \text{ day}^{-1}$

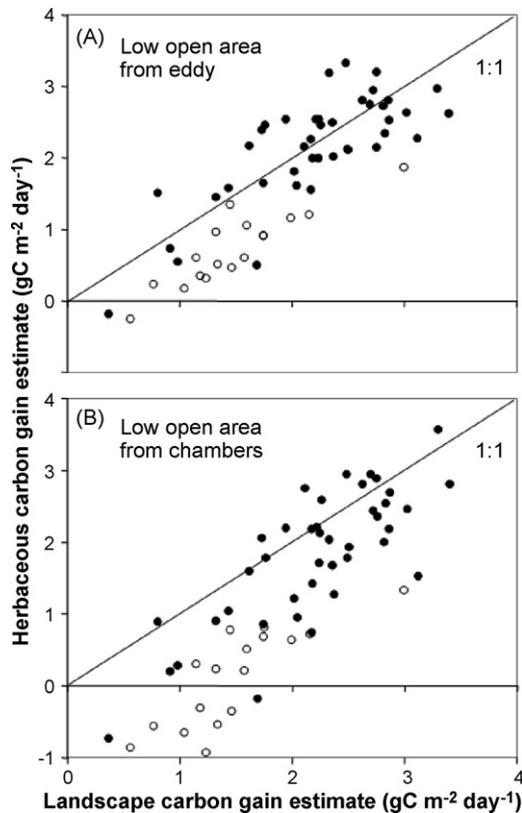


Fig. 10 – (A) Daily carbon gain (the daily integrated F_{NEE} as a positive number), estimated by up-scaling with herbaceous vegetation models for the H and U sites and via eddy measurements for the L site, compared to measured landscape carbon gain estimated from the 30 m tower during springtime in Mitra. Observations during March shown as open circles, during April to mid-May as solid circles. (B) The same comparison where up-scaling for the herbaceous H, U and L sites is based on the models developed from the chamber measurements.

in March, and 0.4 in April to mid-May. Assuming instead that the low open areas function as observed via eddy, the carbon gain that can be ascribed to the aboveground component of the trees is on average ca. $0.75 \text{ g C m}^{-2} \text{ day}^{-1}$ in March and essentially zero during April to mid-May. Better insight with respect to flux contributions from different components of the vegetation mosaic will require a more detailed spatial monitoring of water distribution in the landscape, since this is primarily responsible for the differences found in Fig. 10A and B. Net uptake by the boles and tree canopies of $1.4 \text{ g C m}^{-2} \text{ day}^{-1}$ in March seems large, but a value near zero during April and May seems too small. Progressive drying of the low open areas is not the only problem confronted in this exercise, rather spatial patterns in LAI development and in drying of the high areas may similarly be important. The relatively large time dependent changes in contributions from low open areas mentioned above will probably add to the difficulty in obtaining a clear understanding of contributions to landscape CO_2 exchange. Nevertheless, the comparison in Fig. 10 suggests that F_{NEE} of the tree canopies and the boles,

e.g., those components aboveground and not assessed in chamber experiments, in a landscape one-third covered by older trees results during springtime in only a small net carbon gain. This conclusion is discussed further below.

4. Discussion

4.1. Function of the montado herbaceous vegetation

Eddy covariance studies of carbon balance have been applied during the last decade in a variety of ways, e.g., to study “homogeneous vegetation on a flat surface”; by establishing observation towers at clear transitions between two vegetation types in order to monitor both depending on wind direction; and by using multiple towers in a three dimensional design to clarify advection phenomena (cf. <http://www.carboeurope.org/> publications). In the current study, we have employed a design with two eddy covariance towers coupled with distributed chamber measurements, such that new insight into the function of the tree and grassland mosaic of the montado is achieved. At the level of herbaceous mosaic components (e.g., at the low open site, L), our results demonstrate that very similar flux rates are obtained via continuous eddy covariance monitoring and chamber measurements when habitat conditions within the tower footprint and at plot locations converge (cf. the nighttime respiration comparison in Fig. 9 when water tables for both sampling locations are similar). Use of both eddy and chambers in the low open areas at Mitra provide us not only with a comparison of CO_2 exchange via different methodologies, but also a picture of how the contributions of low areas to overall landscape fluxes change over time, as water drains from the basins and increasingly larger areas have aerated soils. Chamber measurements also suggest that as springtime progresses, a second slow change in flux contribution occurs as the soil at high locations (H) begins to dry out. Better spatial sampling of these changes in landscape water status remain as a large challenge, as well as a limitation with respect to understanding and interpretation of the landscape flux measurements.

The time series observations reported here allow one to consider whether the montado herbaceous component as a grassland exhibits unusual or unique traits. We compared the time dependence for F_{NEE} shown in Fig. 9C and D with springtime increases in F_{NEE} at other grassland sites of the CarboEurope network (cf. www.carboeurope.org). Strong increases in CO_2 uptake occurred at the low and high open sites during the period DOY 90 until ca. day 130, controlled by increasing radiation and temperature at this time. Springtime increases at Laqueuille in Central France and at Grillenburg in Central Germany near Dresden occur during the same period (cf. Gilmanov et al., 2007). The maximum values reached for F_{NEE} at these sites in late spring are ca. $7\text{--}8 \text{ g C m}^{-2} \text{ day}^{-1}$, essentially the same as in open locations at Mitra. On the other hand, at the Central European sites, F_{NEE} is negative during winter, while in Mitra a small net gain in CO_2 may occur. At Carlow in Ireland (Gilmanov et al., 2007) and at Easter Bush in Scotland (Calanca et al., 2007), e.g., sites influenced by oceanic conditions, CO_2 uptake during winter may similarly occur.

With mild temperatures and continued precipitation, continuous CO₂ uptake leads to very high F_{GPP} , while cold periods result in respiratory CO₂ loss. Thus, we can visualize the situation in Mitra as one with a typical European grassland canopy, but where temperature fluctuations in winter control uptake just as in Ireland, and where total production depends on springtime rainfall (Giorgi, 2006) as it controls phenological events and eventually dieback of the vegetation. With invasion of C4 species into the montado, the response to low water availability will differ from northern grassland communities (Aires et al., 2008).

The up-scaling with empirical models and comparison with landscape level flux measurements as reported in Figs. 8–10 demonstrates the importance of the herbaceous understory in determining springtime as well as annual carbon balance of the montado, and suggests low additional CO₂ uptake and possibly at times net CO₂ loss by the tree canopies and boles (Fig. 10). While the up-scaling exercise provides a first important impression about the separation of contributions from the understory and from trees, better definition of the phenomena involved will require additional new approaches. Wohlfahrt et al. (2005) discussed in a case study of a mountain meadow, the reasons for disagreement in flux estimates obtained via eddy covariance, ecosystem chambers, and up-scaling from ecophysiological measurements, and they attempted to estimate errors associated with each method. In general, the uncertainties due to differences in footprint as well as chamber influences on the enclosed vegetation may be large, and, thus, prevent stronger definition of the role played by herbaceous vegetation versus trees. Furthermore, analyses of flux contributions recently carried out by Göckede et al. (2007) for tall vegetation suggest that the degree and manner of coupling between atmosphere and the surface changes, such that the layers of the montado cannot always be considered as separate and additive. Instead a changing degree of internal recycling must occur. Definition of tree contributions to montado CO₂ exchange will require the application of additional new modelling approaches combined with measurements of tree water use and water use efficiency.

In the current up-scaling study, further difficulties are confronted, since the empirical models provide an extremely simple description of ecosystem behaviour, and there will be no predicted response to relevant factors other than radiation, temperature and LAI. Quality of radiation is not considered, for example, and in the case of vegetation under trees, the light environment used in our modelling cannot be representative. The general spatial patterning and time-dependent changes in soil water content across the montado landscape are also not considered. We have assumed that respiration during day and night remains the same, consistent with approaches that have been taken in the treatment of eddy covariance CO₂ flux data when trying to obtain estimates of F_{GPP} and F_{RE} (cf. Reichstein et al., 2005). This may not be the case as assimilates are redistributed among leaves, roots and the soil. Finally, grazing influences the contributions of the herbaceous vegetation at Mitra to landscape F_{NEE} fluxes (cf. Allard et al., 2007; Ammann et al., 2007), although grazing did not occur within the tower footprint during the period of this study.

4.2. Function of the montado ecosystem

Comparison of landscape level CO₂ fluxes from Mitra with those obtained from the Tojal grassland eddy station located 8 km distant from Mitra support the conclusions made above, but also demonstrate that several additional dimensions must be considered. On the one hand, annual flux totals obtained for the two sites during the extremely dry year 2005 and a normal precipitation year 2006 are essentially the same, indicating that both ecosystems similarly exploit available resources (Pereira et al., 2007). The maximum in uptake of CO₂ for the normal precipitation year (NEE) at Tojal was $-4.8 \text{ g C m}^{-2} \text{ day}^{-1}$ (Aires et al., 2008), similar to the values reported for a Mediterranean C3 grassland in California (Xu and Baldocchi, 2004; Baldocchi et al., 2004).

However, maximum CO₂ uptake occurred during May and June at the montado site during both 2005 and 2006 as opposed to April in the grassland. Thus, the observations suggest that both at Tojal and at Mitra, carbon uptake by the herbaceous vegetation is high and dominates ecosystem gas exchange during March and April, while it decreases rapidly during May. The tree canopies remain active much longer at Mitra due to deep rooting. The observations are compatible with optimal conditions for photosynthesis in the elevated tree canopies during May and June. Maximal leaf photosynthesis of cork oaks in Portugal was found in other studies to occur during May and June, and high photosynthesis rates occur up to 30 °C leaf temperature, when the water supply to plants is adequate (Tenhunen et al., 1987). A similar prolonged activity was reported by Baldocchi et al. (2004) for an oak-grass savanna in comparison with grassland in California. Low uptake of CO₂ by the tree crowns during March and April could result from long-term low temperature exposure of the evergreen leaves during winter. Leaf flushing and flowering which occurs during this period may reduce the aboveground tree carbon gain by increasing overall canopy respiration. These factors must be examined in future field studies.

Locations below the tree crowns are sites for net CO₂ release. This is due to low carbon assimilation rates by the herbaceous canopy in the shade (low incident PAR) as well as low leaf N, and to relatively high observed rates of ecosystem respiration (Fig. 8D). The observed correlation of temperature with respiration (Table 2) is compatible with the ideas advanced by Tang et al. (2005), e.g., that CO₂ efflux due to root activity and time-dependent transport of photosynthates to the roots confuses the direct effect of temperature on respiration. In contrast to the results of Tang and Baldocchi (2005), F_{RE} during the springtime period at Mitra was lower than in open areas. The low concentration of N in leaf tissues of the herbaceous layer under the trees is contradictory to other findings, e.g. Moreno et al. (2007), who found significantly higher soil organic matter and total N beneath trees than beyond tree crown projection. In the low fertility soils of Mitra, we can explain this by the decrease in importance of nitrogen fixing species below the crowns and the competition between trees and herbs for the scarce nitrogen. The effect of CO₂ efflux from locations below the crowns is an essential consideration if a correct description of ecosystem flux partitioning is to be achieved (cf. Tang and Baldocchi, 2005). Further study of spatial and temporal variation in respiration

fluxes from under the trees, the apparent competition of trees and herbs for nutrients, and the activity of microbes is needed. Until now, situations below the crowns have been viewed as advantageous for understory plants, since high radiation and temperature stress are avoided.

The results of the study demonstrate that variations in experimental design with the simultaneous use of multiple eddy covariance towers and chambers provides new insight with respect to the functioning of the patterned montado landscape. Additional modelling and simultaneous measurements are required to fully understand vegetation/atmosphere coupling, to quantify mixing and recycling of CO₂ between the understory and trees, and to better define relationships between flux components from individual components of the vegetation mosaic and overall carbon and water balances in montado landscapes. The vegetation structure found in the montado with competition for resources between trees and the herbaceous layer is one of general interest both in terms of atmosphere/land-surface coupling and global change ecology. Similar structure occurs, for example, in arid rangelands where *Juniperus*, *Larrea* or *Artemisia* shrubs are mixed with sub-shrubs and perennial and annual grasses; in savannas, including the oak savannas of western North America (Grove and Rackham, 2001; Baldocchi et al., 2004); and at temperate forest to grassland transitions. Vegetation composition at these locations is a mosaic where structure gradually changes along gradients in natural environmental factors, primarily water availability, and in human-induced stresses. These locations deserve greater attention in the future, since they are likely sensitive to climate change which will impact the services that can be derived from such a vegetation mosaic.

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