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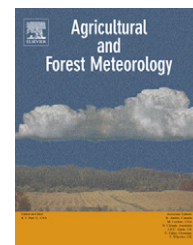
Partitioning carbon fluxes in a Mediterranean oak forest to disentangle changes in ecosystem sink strength during drought

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ABSTRACT

Net carbon flux partitioning was used to disentangle abiotic and biotic drivers of all important component fluxes influencing the overall sink strength of a Mediterranean ecosystem during a rapid spring to summer transition. Between May and June 2006 we analyzed how seasonal drought affected ecosystem assimilation and respiration fluxes in an evergreen oak woodland and attributed variations in the component fluxes (trees, understory, soil microorganisms and roots) to observations at the ecosystem scale. We observed a two thirds decrease in both ecosystem carbon assimilation and respiration (R_{eco}) within only 15 days time. The impact of decreasing R_{eco} on the ecosystem carbon balance was smaller than the impact of decreasing primary productivity. Flux partitioning of GPP and R_{eco} into their component fluxes from trees, understory, soil microorganisms and roots showed that declining ecosystem sink strength was due to a large drought and temperature-induced decrease in understory carbon uptake (from 56% to 21%). Hence, the shallow-rooted annuals mainly composing the understory have a surprisingly large impact on the source/sink behavior of this open evergreen oak woodland during spring to summer transition and the timing of the onset of drought might have a large effect on the annual carbon budget. In response to seasonal drought R_{eco} was increasingly dominated by respiration of heterotrophic soil microorganisms, while the root flux was found to be of minor importance. Soil respiration flux decreased with drought but its contribution to total daily CO_2-exchange increased by 11.5%. This partitioning approach disentangled changes in respiratory and photosynthetic ecosystem fluxes that were not apparent from the eddy-covariance or the soil respiration data alone. By the novel combination of understory vs. overstory carbon flux partitioning with soil respiration data from trenched and control plots, we gained a detailed understanding of factors controlling net carbon exchange of Mediterranean ecosystems.

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1.   Introduction

The carbon balance of ecosystems is controlled by inputs via photosynthetic assimilation, storage in various pools (e.g. plant biomass, soil carbon) and loss of carbon by autotrophic and heterotrophic respiration as well as leaching, physical demineralization of inorganic soil carbon, erosion and forest fires (e.g. Schulze et al., 2000; Law et al., 2002; Trumbore, 2006). Carbon cycling in forest ecosystems involves complex inter-actions between numerous C-pools, which vary both spatially and temporally and may also be differentially affected by environmental variables (e.g. Schimel et al., 2001; Law et al., 2002; Valentini et al., 2003). In order to understand large scale effects of global warming on ecosystem productivity a process-based understanding of carbon sequestration is needed.

Partitioning net carbon fluxes into assimilatory and respiratory components provides an important tool for analyzing abiotic and biotic processes driving carbon cycling. Various methods for measuring and modeling the opposing fluxes emerged within recent years. One common method uses eddy-covariance data in empirical models which apply temperature corrections to the nighttime CO_2-fluxes to calculate ecosystem respiration (R_{eco}) and to partition daytime fluxes (e.g. Aubinet et al., 2000; Reichstein et al., 2002b; Reichstein et al., 2005).

The interplay between ecosystem primary productivity and respiration processes determines the source/sink capacity of an ecosystem for atmospheric CO_2. Although many terrestrial ecosystems (e.g. forests) are net carbon sinks, changes in climate and phenology can result in a transformation of ecosystems to net carbon sources (Lindroth et al., 1998; Valentini et al., 2003; Ma et al., 2007; Pereira et al., 2007). It has been shown that ecosystem respiration (R_{eco}) is a main determinant of carbon balance in most ecosystems (e.g. Valentini et al., 2000; Rambal et al., 2004), particularly in low productive ecosystems such as the studied Mediterranean oak woodland (Pereira et al., 2007).

Temporal variation in ecosystem respiration was observed to be substantial in various studies across different biomes (e.g. Baldocchi, 1997; Valentini et al., 2000; Xu et al., 2004; Reichstein et al., 2005). This variability is mainly due to concomitant temporal changes in driving climatic factors such as temperature and soil moisture (e.g. Huxman et al., 2003; Xu et al., 2004; Davidson et al., 2006b; Jarvis et al., 2007). Autotrophic respiration of leaves and roots as well as mychorrizal respiration depends mainly on photosynthetic assimilation whereas heterotrophic respiration of soil micro-organisms and fungi is a function of the amount of labile soil carbon (Scott-Denton et al., 2006; Subke et al., 2006). Conse-quently, different respiration sources have different temporal dynamics. Autotrophic soil respiration follows periods of growth- and carbon-assimilation cycles throughout the year, whereas heterotrophic soil respiration also depends on pulse-like carbon inputs, such as litterfall, priming and other processes (e.g. Kuzyakov and Cheng, 2001).

The complex interplay between assimilatory and respira-tory sources and their responsiveness to abiotic changes such as drought and temperature remain poorly understood. Hence, there is a need to disentangle component fluxes for a better comprehension of changes in source/sink behavior of ecosystems in response to climate. Increasing scientific effort was made to partition ecosystem carbon fluxes into all major component fluxes (e.g. Goulden et al., 1996; Lavigne et al., 1997; Law et al., 1999, 2001; Davidson et al., 2006a; Ma et al., 2007).

Due to marked annual dynamics in their source/sink behavior and a simple two-layer structure, Mediterranean oak woodlands (*montado*) are very suitable for studying climate impacts on ecosystem and component carbon fluxes. They represent one of the most typical land use types in south-west Europe (Joffre et al., 1999). Slow growth rates and difficult land recovery after degradation make them especially vulnerable to global climate change (Giorgi, 2006). In these winter rain climate ecosystems, the upper layer is an open tree canopy (savanna-type), consisting mostly of deep rooted evergreen oaks standing over a low vegetation understory consisting largely of shallow-rooted herbaceous annuals that vanish by the end of spring when soil water in the upper soil layers has been depleted. Summer drought constitutes a period of high evaporative demand and low soil water availability (e.g. Tenhunen et al., 1990). Increasing frequency and severity of drought as well as changes in the precipitation pattern can cause large reductions in ecosystem carbon exchange of these ecosystems (Ciais et al., 2005; Giorgi, 2006; Granier et al., 2007; Pereira et al., 2007). The change from the productive spring period to summer drought is generally very rapid and turns the Mediterranean woodland from a carbon sink into a carbon source within only a few weeks. Since most of the annual net carbon assimilation in the Mediterranean occurs between March and June (Allard et al., 2008), timing and length of this event might strongly influence the annual carbon budget (Werner et al., 2006; Ma et al., 2007; Pereira et al., 2007; Allard et al., 2008).

In this partitioning study we took advantage of this rapid transition period to identify the factors driving changes in ecosystem source/sink behavior in the Mediterranean oak-savanna in southern Portugal. We aimed at identifying (i) changes in sink strength in a short-term response to drought; (ii) the component fluxes responsible for these changes and (iii) their dependencies on environmental factors. We hypothesized that some ecosystem components would be more sensitive to water deficits and rising temperature than others and thus, are likely to significantly influence ecosystem carbon budgets under future climate scenarios.

2.   Materials and methods

2.1.   Field site and environmental conditions

The experimental site Mitra is located near Évora in southern Portugal, at 38° latitude N and 8° longitude W and is part of the CarboEurope-IP project (see Pereira et al., 2007). The climate is typically Mediterranean, with a hot and dry summer. More than 80% of annual precipitation occurs between October and April. The long-term (1961–1990) mean annual temperature is 15–16 °C and average annual precipitation is ca. 669 mm. The site is on the "Alentejana" plain, with low altitude (220–250 m) and gentle slopes with soils derived from granite rock. It is in the middle of a homogeneous landscape dominated by

evergreen oak-savanna-like woodlands with *Quercus ilex* ssp. *rotundifolia* and *Quercus suber* trees. The understory consists of grazed pasture dominated by herbaceous annuals, which die out by the end of spring (e.g. *Tuberaria guttata* (L.) Fourr.), and also some drought deciduous graminea and a few shrubs (*Cistus salvifolius* L.). It has a two-layer plant cover with scattered trees (ca. 7.5 m height, stem diameter ca. 35 cm) and ca. 21% tree canopy cover (Carreiras et al., 2006), and leaf area index of ca. 0.55 (Jarvis et al., 2007). The vegetative period of the mostly herbaceous understory (ca. 0.5 m height) lasts from the autumn rains until May–June when soil water content generally decreases strongly. In 2006 between 20 May and 3 June an intensive field campaign was conducted at the study site:

Continuous records of CO_2 and H_2O fluxes and climate variables were taken on top of a 28-m-high metal tower (at the Mitra site of the CARBOEUROPE-IP consortium) equipped with sonic anemometer (Gill R3, Gill Instruments, Lymington, Hampshire, England) and gas analyzer (LI-7000, LI-COR, Lincoln, NE, USA). Weather conditions were continuously recorded by a solar-powered meteorological station (datalogger CR10X, Campbell Scientific, Logan, UT, USA), with a Q7 REBS net radiometer (Campbell Scientific), aspirated psychrometer H301 (Vector Instruments, Rhyl, Denbighshire, UK) and a rainfall recorder (tipping-bucket rain gauge Casella, Bedford, UK). Air temperatures (T_{air}), wind speed (anemometer A100R, Vector Instruments), net radiation (RN) and precipitation were measured in 10 s intervals and were automatically stored as half-hourly and daily means or totals. Vapor pressure deficit (VPD) was calculated from dry and wet bulb temperatures of the aspirated psychrometer. For carbon flux partitioning between understory and tree canopy we used data from a small eddy-covariance system at a height of 2.5 m (3D sonic anemometer, 1210R3, Gill Instruments Ltd., Lymington, UK; IRGA. LI-7500, LI-COR, Lincoln, NE, USA) installed at *Tojal*, a grassland field site (CARBO EUROPE IP) within 8 km distance and similar conditions.

The raw data from the eddy-covariance measurements were processed off-line using the software *Eddyflux* (Meteotools, Jena, Germany). Following the Carboeurope-IP recommendations a planar fit coordinate rotation (Wilczak et al., 2001) for wind components was performed. The CO_2-fluxes were determined, on a half-hourly basis (block averaging). A time-lag for each averaging period was determined in order to maximize the covariance between vertical wind velocity and carbon dioxide signal from the gas analyzer. The fluxes were corrected for the damping loss of the closed-path analyzer at high frequencies, according to Eugster and Senn (1995). In general, the correction factors varied between 1.05 and 1.30. A CO_2-storage term, calculated for one point measurement as in Greco and Baldocchi (1996), was added to the estimated carbon flux. In the grassland this storage term was negligible.

The quality of all primary data was guaranteed by a routine of equipment calibration and, for meteorological data, a comparison with data from close stations. To exclude non-representative 30 min measurements of carbon dioxide flux, the following screening criteria were applied: fluxes were removed if the mean vertical velocity deviation to zero was higher than what would be considered as normal for the site, following the same principle as in Rebmann et al. (2005); fluxes

were excluded if the high frequency spikes replaced or the absolute limits violations exceeded 1% of the total records of any of the three components of wind velocity and/or CO_2-concentration.

Total data gaps during the whole study period, due to missing and rejected data, were about 57% and 42% for *Mitra* and *Tojal* (Aires et al., 2008), respectively. Gap filling and flux-partitioning methods proposed by Reichstein et al. (2005) were used to fill data gaps and to separate the net ecosystem exchange (NEE) into gross primary production (GPP) and ecosystem respiration (R_{eco}), respectively.

2.2. Plant-scale observations

Diurnal and nocturnal courses of leaf gas exchange (LI-6400 open-flow gas exchange system, LI-COR, Lincoln, NE, USA) were recorded in 24-h cycles every 2–4 h on marked branches. Leaf gas exchange was measured on three *Q. ilex* trees in at least three sun-exposed leaves per tree and in 10 sun-exposed leaves of different *T. guttata* plants. During daytime a black plastic shield was used to cover the cuvette after each measurement in light to obtain dark respiration rates for each leaf. Predawn and midday leaf water potentials (pressure chamber, Manofrigido, Portugal) were also obtained for the same species.

2.3. Soil respiration measurements and trenching

Soil respiration (R_{soil}) was measured in 24-h cycles every 2–4 h using a closed-path chamber system (PP-System EGM2 Soil Respiration System with SRC-1 chamber; PP-Systems, Amesbury, MA, USA). Measurements were conducted on: (i) three plots of bare soil without further treatment and (ii) three plots with root exclusion with three measurements per plot.

Root exclusion was achieved by inserting metal rings from 0 to 20 cm depth 1 year prior to measurements (trenching) and solarization treatment during 2 weeks with black foils to avoid a resprout from the remaining root biomass or seed bank. We regarded trenching up to 20 cm depth as sufficient for the studied oak woodland, since the largest fraction of root biomass can be found in the upper soil layer (Kurz-Besson et al., 2006; Otieno et al., 2006), which was confirmed by own observations. We used a long time interval between trenching plot installation and measurements to avoid disturbance or decomposition of decaying root material, which can have pronounced effects on soil respiration (e.g. Lee et al., 2003). Three weeks before measurements a few new seedlings which had germinated inside the trenching plots were carefully removed with their roots and solarization was repeated to ensure root-free plots.

Soil temperature (T_{soil}) and soil water content (SWC) were recorded in 5–10 cm depth alongside soil respiration using the temperature sensor of the soil respiration system and a moisture probe (Theta Meter HH1, Delta-T Devices, Cambridge, UK), respectively.

2.4. Mass balance approach and flux partitioning

For nighttime flux partitioning mass balance equations were applied, assuming that the sum of component fluxes equals

the ecosystem flux and that no other component fluxes than soil flux (roots and soil microorganisms) and canopy flux (leaves of trees and herbs) contribute to the ecosystem flux.

$$f_R = f_S + f_C = f_r + f_{SMO} + f_T + f_U \qquad (1)$$

where f denotes CO_2-flux per m^2 ground. Subscripts indicate respired CO_2 from ecosystem (R), soil (S), canopy (C), roots (r), soil microorganisms (SMO) as well as from tree (T) and understory leaves (U).

Respiration from non-mychorrizal fungi and bacteria is included in heterotrophic soil respiration, whereas autotrophic soil respiration flux comprises root respiration and associated rhizospheric components (e.g. mychorrizal respiration). Here, we will refer to heterotrophic soil respiration as soil microorganism respiration flux (f_{SMO}) and to autotrophic soil respiration as root respiration flux (f_r).

Nighttime ecosystem respiration data (f_R) minus the soil flux (f_S) yields the canopy respiration flux (f_C, comprising trees and understory). Daytime respiration and photosynthesis of the canopy can be calculated by subtracting soil efflux during daytime from R_{eco} and R_{eco} from the net flux, respectively.

Subtracting soil respiration of trenching plots (f_{SMO}) from the total soil flux (f_S) yields the root flux (f_r). The nighttime respiration flux from the below canopy eddy-covariance system was used to partition the understory respiration (f_U) from f_S. Tree respiration (f_T) was then calculated by subtracting f_U from f_C. We assumed that proportionate contributions of trees and understory to canopy respiration remain constant between day and night and thus, used nighttime canopy respiration to partition daytime net flux of trees and understory into respiration and gross photosynthesis.

3. Results

3.1. Variation in climate parameters and CO_2-fluxes

Meteorological conditions during the spring of 2006 were characteristic for Mediterranean regions with highest precipitation in March (104 mm) and April (57 mm) and increasing air temperature and VPD (Fig. 1b, Fig. 2a–d). The study period was chosen between late May and early June when most significant changes in ecosystem source/sink behavior occur. During this transition period mean daily net ecosystem exchange (NEE) approached zero (Fig. 1a). Last rainfall event was on 22 April (Fig. 1b). Hence, when measurements were conducted during the end of May, the ecosystem already showed signs of drought stress. Midday values of air temperatures and VPD increased from 24 to 31 °C and from 19 to 36 hPa, respectively (Fig. 2a–d). Most days were sunny, except 22 May with rather cloudy conditions.

The upper soil layer (at 10 cm depth) was already very dry on 20 May (ca. 0.1 m^3 H_2O m^{-3} soil) and soil moisture at this depth did not exhibit a further decrease during the study (Fig. 2e–h).

Net ecosystem CO_2 uptake decreased from -11 to -3 μmol m^{-2} s^{-1} with highest uptake rates in the morning and midday hours (Fig. 2i–l). Ecosystem respiration (R_{eco}) decreased from 3.5 to 1.5 μmol m^{-2} s^{-1} with a clear diurnal cycle of increasing respiration rates during daytime and a
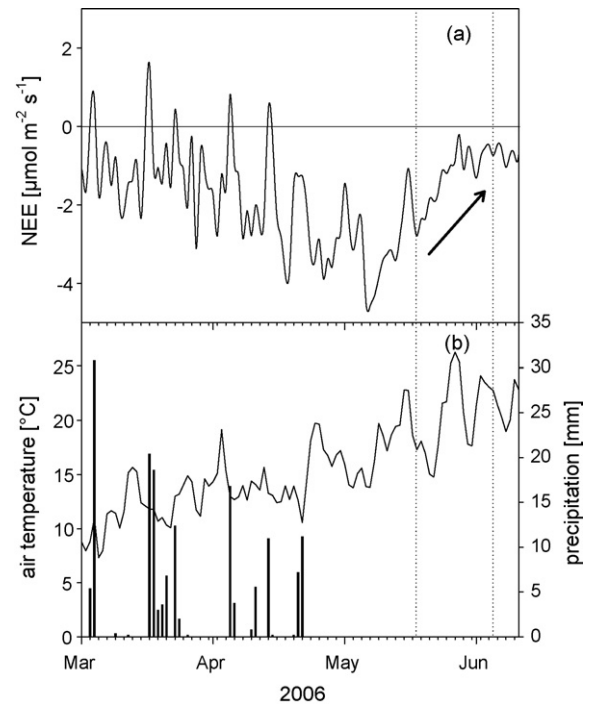

Fig. 1 – Temporal pattern of (a) mean daily net ecosystem exchange (NEE) and (b) daily precipitation sums (black bars) and mean daily air temperatures (black line) during the spring to summer transition in 2006. Arrow marks the rapid changes in NEE during the study period indicated by the dotted frame.

subsequent decrease at night (Fig. 2q–t). Soil efflux showed a similar pattern as R_{eco} though exhibiting lower rates (2.5–1 μmol m^{-2} s^{-1}).

Heterotrophic respiration of soil microorganisms (SMO) showed slightly smaller rates and a similar pattern as total soil efflux (2–1 μmol m^{-2} s^{-1}) whereas autotrophic soil respiration exhibited little variation over the observed period with very low rates of about 0.1–0.2 μmol m^{-2} s^{-1} (Fig. 2u–x).

Using Eq. (1) we calculated the canopy flux (Fig. 2i–l). Given the small contribution of soil efflux to daytime net ecosystem exchange, the pattern of the calculated canopy flux was very similar to the pattern of the net ecosystem flux.

The net canopy flux of the understory showed a constant decrease in both daytime CO_2 uptake (-7 to -0.5 μmol m^{-2} s^{-1}) and in nighttime respiration (0.5–0.1 μmol m^{-2} s^{-1}) reflecting the effects of water deficit on understory plants (Fig. 2m–p). Daytime net canopy flux of Q. ilex varied between -3 and -7 μmol m^{-2} s^{-1} exhibiting lowest values in the morning and midday hours of 20 May (Fig. 2m) and 30 (Fig. 2o). 22 May being rather cloudy with lower light intensities (see Fig. 2f) and 3 June with exceptionally high VPD (Fig. 2d) revealed a higher daytime canopy flux for Q. ilex (Fig. 2n, p). Nighttime respiration decreased only slightly.

Single leaf measurements of photosynthesis (Fig. 3a–d) were consistent with the canopy net fluxes shown in Fig. 2, whereas single leaf respiration measurements (Fig. 3i–l) were in contrast to canopy scale results. Photosynthesis and respiration measurements (Fig. 3) on foliage of trees (Q. ilex)
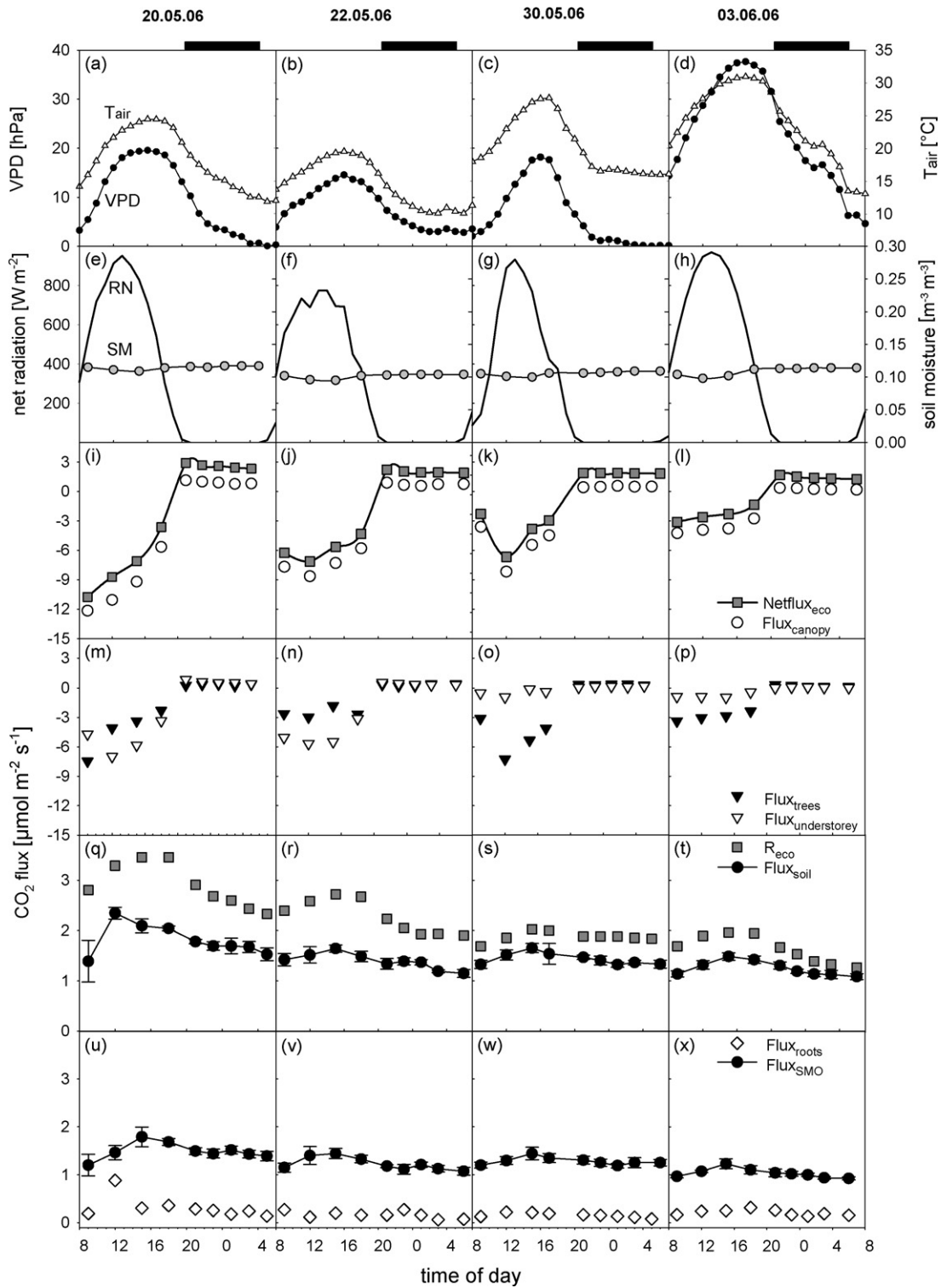
Fig. 2 – Temporal variation in (a–d): air temperature (T_{air}, white triangles) and VPD (black circles), (e–h): net radiation (RN, lines) and soil moisture (grey circles), (i–l): ecosystem CO_2 netflux (grey squares, lined) and foliage-derived flux (white circles), (m–p): tree- (black reversed triangles) and understory-derived (white triangles) fluxes, (q–t): R_{eco} (grey squares) and soil CO_2 efflux (black circles, lined), (u–x): soil microorganisms- (black diamonds, lined) and root-derived (white diamonds) respiration for four diurnal cycles with increasing summer drought (May–June 2006). Please note that foliage flux values are referred to m^2 ground and not leaf area, all measured values are lined. Carbon uptake is denoted as negative flux, whereas respiration is denoted as positive flux. Black bars indicate nighttime, $n = 3 \pm$ SD.

and understory plants (e.g. *Tuberaria guttata*) reflected different responses to increasing drought. Even with decreasing water availability and increasing temperature stress *Q. ilex* was able to maintain predawn leaf water potentials around −0.5 MPa (Fig. 3m–p) and maximum daytime photosynthetic carbon uptake did not vary much (4–6 μmol m^{-2} s^{-1}, Fig. 3a–d). Daytime transpiration (Fig. 3e–h) increased with temperature from 1 to 3.5 mmol m^{-2} s^{-1}, indicating sufficient water supply for transpirational cooling. In contrast, understory plants like *T. guttata* were severely affected by the changing environmental conditions and died during the study period. Despite the low predawn leaf water potentials (−1.5 MPa, Fig. 3m–p) transpiration rates (Fig. 3e, f) of *T. guttata* were in a similar range as *Q. ilex* between 1.5 and 3 mmol m^{-2} s^{-1}. *Q. ilex* increased transpiration rates up to 5 mmol m^{-2} s^{-1} in response to increasing air temperatures while *T. guttata* did not (Fig. 3 g, h). The low net photosynthetic assimilation on 20 May still being about 2.5 μmol m^{-2} s^{-1} decreased on 3 June below 0, since carbon loss by respiration, especially in the afternoon (up to −6 μmol m^{-2} s^{-1}), was higher than carbon gain by photosynthesis (Fig. 3a–d, i–l). Single leaf respiration in *Q. ilex* also increased throughout the study, but with a

lower magnitude (Fig. 3i–l). Please note that you cannot directly compare single leaf and ecosystem scale measurements of the understory plants, since there was a large decrease in understory leaf area throughout the study, as discussed below.

3.2. Response of component fluxes to drought and relative contribution to ecosystem flux

Daytime net ecosystem exchange rate was dominated by CO_2-uptake through the canopy (up to 86%), whereas nighttime ecosystem exchange was mainly due to soil respiration (up to 82%). Decreases in both ecosystem respiration and carbon assimilation were mainly caused by a strong decline in understory activity with progressive water deficit (Fig. 4a, b). Canopy respiration decreased by ca. 77% (1.3–0.3 μmol m^{-2} s^{-1}), whereas soil respiration decreased by ca. 32% (1.9–1.3 μmol m^{-2} s^{-1}), mainly due to a loss in root respiration of about 0.2 μmol m^{-2} s^{-1}. As to expect from the well-known temperature dependence of respiratory processes, nighttime respiration was generally smaller than daytime respiration (Fig. 4a).
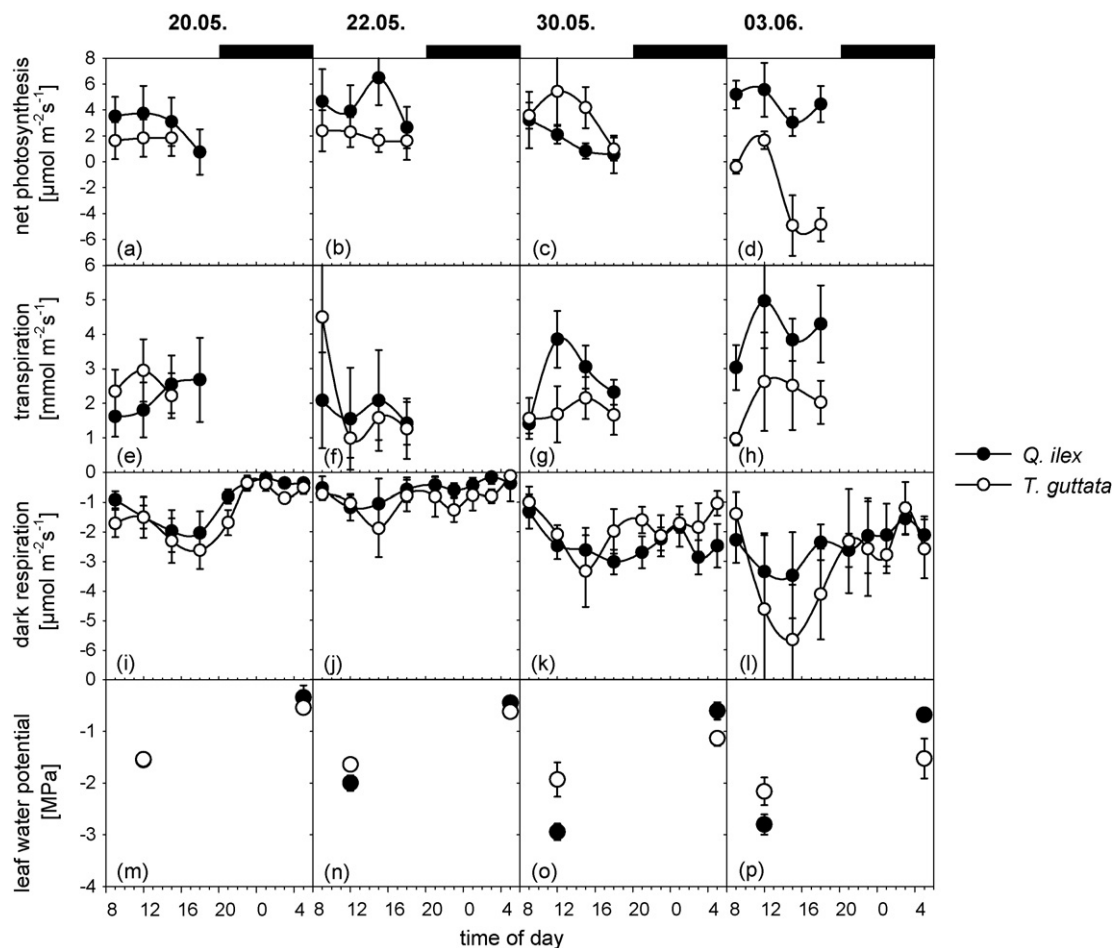

Fig. 3 – Diurnal cycles of net carbon assimilation (a–d), dark respiration (e–h) and water potentials (i–l) from single leaf measurements of *Q. ilex* (tree, black circles) and *T. guttata* (understory species, white circles) during May and June 2006. Please note that net photosynthesis (positive rates) and respiration (negative rates) are referred to m^2 leaf area. Black bars indicate nighttime, n = 3–10 ± SD.
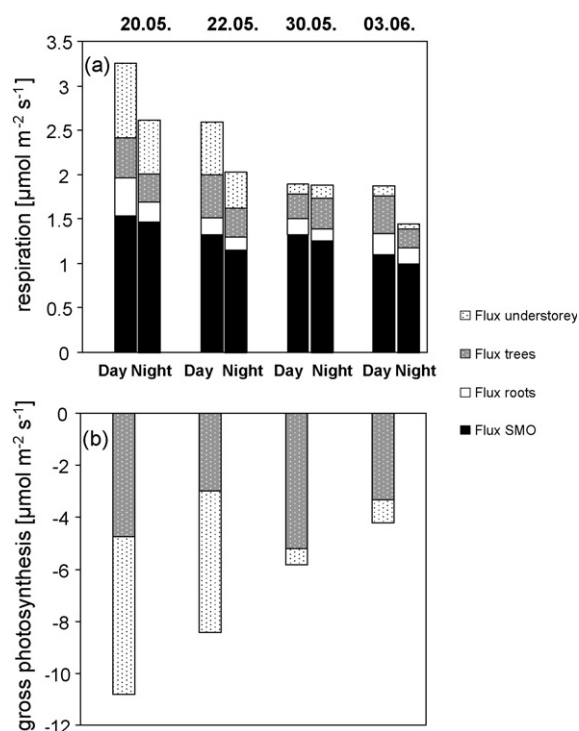
Fig. 4 – Mean diurnal and nocturnal respiration fluxes (a) and gross carbon assimilation (b) from understory (dotted), trees (grey), roots (white) and soil microorganisms (black) during May and June 2006. Please note that foliage flux values are referred to m^2 ground and not leaf area. Carbon uptake is denoted as negative flux, whereas respiration is denoted as positive flux.

Gross CO_2 uptake (Fig. 4b) remained more or less constant in trees (-3 to -5 μmol m^{-2} s^{-1}) but decreased strongly in the understory (-6 to -0.8 μmol m^{-2} s^{-1}) as drought progressed.

Fig. 5 shows the relative contributions of component fluxes to the total ecosystem flux. During the study contribution of tree respiration to daytime and nighttime ecosystem respiration increased about 3% and 9%, respectively. In contrast, the influence of understory respiration decreased dramatically from 33.2% to 3.5% and from 25.7% to 5.7% for night and day, respectively (Fig. 5a). Heterotrophic soil respiration was the main respiratory source in the ecosystem and exhibited an increase of ~12%, whereas the generally small contribution of autotrophic soil respiration only showed small changes (+4.3% and −0.2% for night and daytime, respectively; Fig. 5a). Canopy respiration varied more between day and night (30–50%) than soil respiration (10%).

Gross ecosystem CO_2-uptake on 20 May was still dominated by the understory (56%), with a marked reduction to only 21% at the beginning of June (Fig. 5b). While understory plants were still the main contributors to total daily CO_2-exchange (45%) on 20 May, trees (52.8%) and soil microorganisms (27.6%) became most significant contributors to NEE on 3 June. Although the system still remained a small net sink for CO_2, in early June it was on the verge of becoming a net source (Fig. 5c; see also Fig. 4).

4. Discussion

4.1. Partitioning of component fluxes from the ecosystem carbon flux

With ongoing transition from wet and mild spring period to dry and hot summer conditions we observed a constant decrease of more than 50% in both NEP and R_{eco} within a single fortnight resulting in an overall increase in NEE (see Figs. 1a, 2). Increasing NEE towards the summer is generally due to reduced carbon assimilation by the vegetation with decreased water availability (e.g. Beyschlag et al., 1987; Pereira et al., 2007) and is a characteristic of Mediterranean type ecosystems (Reichstein et al., 2002b; Rambal et al., 2003). Accordingly, strong declines in gross primary production in response to drought have been reported in many other studies (e.g. Pereira and Chaves, 1995; Baldocchi, 1997; Reichstein et al., 2002b; Xu and Baldocchi, 2004; Ma et al., 2007; Allard et al., 2008) and were also observed in previous years at the same site (Jarvis et al., 2007; Pereira et al., 2007).

Recent studies have shown the relevance of ecosystem productivity during the spring period for annual carbon budget in Mediterranean ecosystems (e.g. Xu and Baldocchi, 2004; Pereira et al., 2007; Ma et al., 2007). Allard et al. (2008) found that 83% of annual GPP occurred between March and June in a Q. ilex forest in southern France. Their work showed that decreased precipitation between April and June, as can be expected from global climate change (Giorgi, 2006), may largely influence annual carbon budget.

In a long-term partitioning study between overstory and understory fluxes in a Californian oak forest and a grassland Ma et al. (2007) demonstrated that both GPP and R_{eco} depended primarily on the amount of seasonal precipitation during periods of simultaneous activity of grass and tree canopies rather than on annual precipitation. They also found that spring-time precipitation is the predominant factor driving inter-annual differences in NEE. Our data support the results from Ma et al. (2007), as the drought sensitive understory species were the most important regulators of the ecosystem source/sink behavior during spring time, largely decreasing in their contribution to overall CO_2-uptake (56–21%, Fig. 4b) and ecosystem respiration (23–4%, Fig. 4a) with the onset of summer drought. Likewise, in our site, gross primary productivity as well as ecosystem respiration was highly correlated with the amount of rainfall during the spring months (March to June; Pereira et al., unpublished).

Trees (Q. ilex) did not strongly respond to warming and drought, indicating an apparent ability to extract sufficient water from deeper soil layers (e.g. Kurz-Besson et al., 2006) and thus, did not contribute to the observed rapid shift in the systems source/sink behavior. Although the system still remained a small net sink for CO_2, in early June it was on the verge of becoming a net source (Figs. 1a, 5c). Data from previous years for this system showed that net fluxes turn positive between the middle of June and the beginning of July (DOY 170–200), depending on the last significant rain events (data not shown). Since the length of the growing season is the main determinant for the magnitude of annual carbon uptake (Ma et al., 2007), the timing of summer drought-induced understory senescence can markedly influence the annual
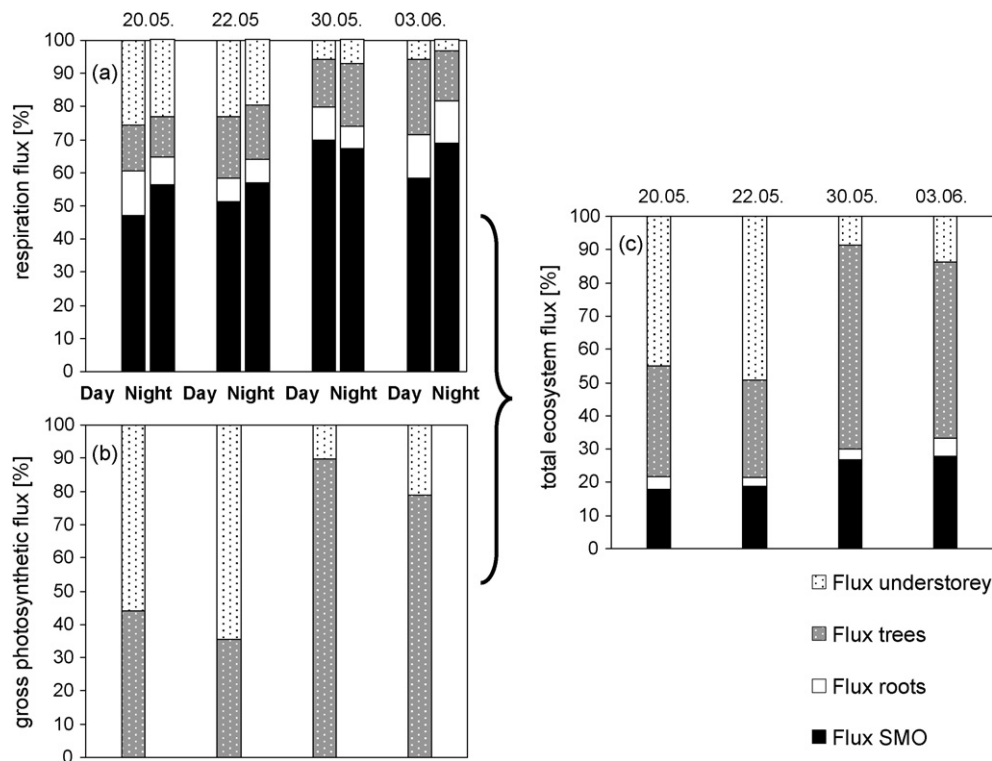
Fig. 5 – Relative contributions of component fluxes (%) to (a) total ecosystem respiration, (b) total ecosystem carbon assimilation and (c) to total daily CO_2-exchange during day and nighttime; calculated from absolute values of GPP and respiration data shown in Fig. 4; understory (dotted), trees (grey), roots (white) and soil microorganisms (black).

carbon budget. These findings match a recent study on water flux partitioning at the same site where the understory contributed by over 50% to total ecosystem transpiration in spring time, whereas in summer tree transpiration constituted ca. 90% of total ecosystem water fluxes (Paço et al., submitted for publication). Further, it was found that total leaf area index (LAI) in this system decreases by up to 70% with summer drought (Pereira et al., 2007), while instantaneous canopy-scale water use efficiency (WUE_i) increases, which can also be explained by the disappearance of the *water spending* understory plants.

Ecosytem respiration (R_{eco}) exhibited similar values as observed in studies by Rambal et al. (2004) and Reichstein et al. (2002a,b) for late spring in other Mediterranean *Q. ilex* dominated sites. Soil CO_2 efflux was the most important contributor to R_{eco} (∼70%, e.g. Goulden et al., 1996; Lavigne et al., 1997; Law et al., 2001; Davidson et al., 2006a), and comparable to other studies in Mediterranean and semiarid sites (e.g. Irvine et al., 2005; Tang and Baldocchi, 2005). The major component of soil respiration was heterotrophic respiration, i.e. from soil microorganisms (ca. 60% of R_{eco}), while autotrophic soil respiration was rather small (ca. 10% of R_{eco}), however, within the reported range for low productive ecosystems (Hanson et al., 2000; Subke et al., 2006). Roots generally contribute to a larger extent in systems with high soil CO_2 effluxes which was explained by lower carbon allocation to the roots and subsequent smaller autotrophic respiration fluxes in low productive ecosystems (Subke et al.,

2006). Our results for the low-productive Mediterranean oak-savanna fit this theory: low soil respiration rates coincided with low root contribution (15–28%) of R_{soil}.

Towards June R_{eco} and R_{soil} became increasingly similar, as found by Davidson et al. (2006a), where summer drought effects were visible in an initial increase in R_{soil}/R_{eco}, followed by stabilization with severe drought. In accordance to our study this observed increase in R_{soil}/R_{eco} was due to the strong drought-induced reduction of canopy respiration. The scaled proportions of canopy respiration to R_{eco} (Fig. 4, 19–40%) were slightly lower than contributions observed by Lavigne et al. (1997) in a boreal forest but in the range of studies from Goulden et al. (1996) and Law et al. (1999) for a temperate deciduous and a dry climate ponderosa pine forest, respectively.

It became evident that the total ecosystem response to changing environmental conditions can be substantially different from the response of single component fluxes, because it depends on the interplay of all sources: although absolute flux rates of soil microorganisms decreased in response to drought, they increased by 12% in their relative contribution to R_{eco} (see Fig. 5a). Similarly trees became most significant contributors to ecosystem carbon uptake although their absolute flux did not change (Fig. 5c). Since changes in relative contributions of tree- and root-fluxes to the ecosystem flux are negligible, these increases can be attributed entirely to the decrease in relative contribution of the understory flux, as discussed above.

4.2. Environmental drivers regulating changes in ecosystem carbon fluxes during drought

A wide range of studies has shown that R_{eco}, as respiration processes in general, is positively correlated with temperature. Moreover it depends on soil moisture, which under drought conditions can have a substantial influence and mask the temperature response (e.g. Davidson et al., 2000; Reichstein et al., 2002a,b; Xu et al., 2004; Gaumont-Guay et al., 2006; Jarvis et al., 2007). Temperature dependence (Q10) of R_{eco} increases with soil moisture (e.g. Reichstein et al., 2002a,b; Flanagan and Johnson, 2005). Hence, in systems without water limitation R_{eco} is generally determined by temperature (e.g. Huxman et al., 2003; Griffis et al., 2004). In our system soil moisture was limiting, as predawn water potentials of shallow-rooted understory species (T. guttata, see Fig. 3m–p) experienced a large decrease throughout the study period, indicating a drastic reduction in water availability. Drought-induced changes in heterotrophic soil respiration showed a positive relationship with predawn water potentials of understory foliage (T. guttata) but no significant correlation with temperature, which supports that the effects of soil moisture on respiration processes under seasonal drought overlaid the temperature effects (Table 1). However, on the diurnal scale temperature was positively correlated with both ecosystem and soil respiration (data not shown). Tang et al. (2005a,b) showed similar results for another Mediterranean oak-grass savanna, concluding that the seasonal pattern of soil respiration was driven mainly by soil moisture but that the diurnal pattern was controlled by temperature and in root rich patches (under tree crowns) also by photosynthesis.

A strong relationship between aboveground carbon assimilation and belowground allocation and, therefore, respiration has been observed in several studies (e.g. Ekblad and Högberg, 2001; Bowling et al., 2002; Mortazavi et al., 2005; Werner et al., 2006). Hence, diminishing substrate supply by photosynthesis to autotrophic and heterotrophic soil respiration (compare Verburg et al., 2004; Davidson et al., 2006b; Hartley et al., 2006) might have been another important factor affecting temporal changes in R_{eco} and R_{soil} with increasing water deficit.

A recent study by Tang et al. (2005b) showed that a diurnal pattern occurred in the soil CO_2 efflux on trenched plots but not on control plots. They explained this finding with either a shading effect by trees on the control plots or an offset of the temperature response in soil respiration created by a time-lag of several hours between photosynthetic fixation and translocation of photosynthate to root respiration. Contrastingly, our results suggest that there was no strong influence of recent photosynthate on soil respiration, as both trenched and control plots showed a diurnal pattern, which was well correlated with soil temperature (data not shown).

Root respiration was generally found to be less susceptible to drought than heterotrophic soil respiration (Borken et al., 2006; Scott-Denton et al., 2006), which might explain that the observed decrease in R_{SMO} was considerably stronger than in autotrophic soil respiration.

Root respiration rates were low and remained stable even with senescence of aboveground biomass. Carbohydrates stored in roots may buffer effects of reduced assimilate supply and sustain root metabolism for several days or even weeks after removal of aboveground biomass (Pregitzer et al., 2000; Högberg et al., 2001). This was confirmed by another study, where clipping did not affect root respiration for several days but soil microbial respiration responded strongly to short-term changes in assimilate supply (Bahn et al., 2006).

These observations lead to the conclusion that in our study decreasing soil respiration, rather than from decreased assimilation patterns, might have resulted from temperature acclimatization of soil heterotrophs (e.g. Zhang et al., 2005), which can be caused by simple substrate depletion of labile C-pools with increasing temperature, as found by Eliasson et al. (2005) in combination with decreasing assimilate supply from the understory plants.

Further, root respiration was positively correlated to net radiation (Table 1), which is a driver of photosynthesis, while understory foliage respiration was not. Thus, we might hypothesize that remaining assimilated carbon in senescent plant foliage was transferred to the root system in order to conserve energy for a possible resprout when conditions

Table 1 – Pearson-coefficients for linear regressions of temporal changes in component fluxes from soil microorganisms, roots, understory and tree foliage with daytime averages of climate variables and predawn water potentials of T. guttata.

		RN	T_{air}	T_{soil}	VPD	SWC	$WP_{predawn}$
Trees	Nighttime CO_2-release	**−0.86**	−0.70	−0.68	**−0.99**	−0.06	0.67
	Daytime CO_2-release	0.60	−0.41	−0.44	0.14	0.05	0.44
	Daytime CO_2-uptake	0.42	0.15	0.16	−0.38	0.55	0.1
Understory	Nighttime CO_2-release	0.04	**−0.72**	**−0.74**	−0.52	0.51	**0.94**
	Daytime CO_2-release	0.15	**−0.72**	**−0.74**	−0.43	0.46	**0.92**
	Daytime CO_2-uptake	0.12	**−0.79**	**−0.82**	−0.44	0.29	**0.92**
SMO	Nighttime CO_2-release	−0.24	−0.42	−0.42	−0.61	0.70	**0.73**
	Daytime CO_2-release	−0.26	−0.64	−0.64	**−0.71**	0.57	**0.88**
	Daytime CO_2-uptake	–	–	–	–	–	–
Roots	Nighttime CO_2-release	**0.81**	0.16	0.13	0.42	**0.84**	0.22
	Daytime CO_2-release	**0.73**	0.00	−0.03	0.10	**0.95**	0.43
	Daytime CO_2-uptake	–	–	–	–	–	–

Correlations that explain more than 50% of variability ($R^2 > 0.5$) are in bold.

change, especially as many Mediterranean understory plants including *T. guttata* have tuberous roots.

Respiration of foliage from understory plants was controlled by both increasing temperatures and decreasing water availability, severely affecting assimilation rates and therefore, as noted by Amthor (1994), the substrate pool for respiration. In spite of the canopy scale decrease, dark respiration of single leaves of the understory species *T. guttata* increased with temperature to extraordinarily high rates of up to 6 μmol m^{-2} s^{-1} (see Fig. 3i–l), which can be attributed to accelerated metabolism in dying tissue (Law et al., 1999). The decrease in understory respiration at the canopy scale was therefore entirely due to a decrease in leaf area by senescence with the onset of drought.

As discussed above, trees did not suffer from drought during the study period. Assimilation rates were mainly controlled by radiation and VPD, rather than temperature and soil moisture and respiration rates did not change significantly. Hartley et al. (2006) suggested that canopy photosynthesis regulates leaf respiration to a much larger extent than temperature. Rambal et al. (2004) found large changes in *Q. ilex* foliage respiration between May and June and attributed them to leaf growth. In our system, leaf growth and development of *Q. ilex* were already accomplished by the end of May thus trees exhibited low and stable respiration rates.

4.3. Strength and limitations of the partitioning approach

Partitioning ecosystem scale carbon fluxes into their component fluxes has become an important tool (e.g. Goulden et al., 1996; Lavigne et al., 1997; Law et al., 1999, 2001; Davidson et al., 2006a; Ma et al., 2007). Our partitioning techniques comprise a novel combination of understory vs. overstory eddy-covariance data with chamber-retrieved soil respiration measurements on trenched plots with and without root exclusion to separate all major component fluxes (canopy, soil, understory, overstory, roots and SMO) from the net ecosystem exchange.

A recent study by Misson et al. (2007) evaluated the limitations of combining understory and overstory eddy-covariance techniques to partition canopy fluxes. They showed that in open canopy forests, such as the oak-savanna investigated here, a nighttime temperature inversion layer can built up below the canopy causing problems estimating understory carbon fluxes especially in direct comparison to daytime values, where the inversion layer is smaller. On the other hand, footprints above and below the canopy are more similar in open forests, which is advantageous for combining overstory and understory eddy-covariance.

Some studies reported large spatial variations in soil respiration, mainly due to ample carbon translocation from trees (e.g. Tang and Baldocchi, 2005; Søe and Buchmann, 2005). In our study understory measurements were conducted in a grassland ecosystem close to the oak forest with similar conditions, which might have introduced some bias in the partitioning, due to the lack of carbon flux from tree roots to soil respiration. However, we do not expect this bias to be very pronounced, since the site has a low tree density with marked open patches and the tree influence on overall soil respiration might be relatively small.

Trenching methods for soil efflux partitioning do also contain some limitations. The long-term trenching approach (1 year prior to measurements) was chosen to buffer the well-known effects of decaying root materials on heterotrophic respiration (e.g. Hanson et al., 2000; Lee et al., 2003; Subke et al., 2006). However, many studies suggest that 1 year may not be enough to allow root material to decay completely, especially organic matter of large lateral roots (e.g. Epron et al., 1999; Hanson et al., 2000; Silver et al., 2005). However, our trenching plots did not contain bulky tree roots, but mostly fine roots from grasses which have been found to rapidly decompose within approximately 4 months after trenching (Ewel et al., 1987; Bowden et al., 1993).

Trenching depth of 20 cm is not large especially regarding tree root respiration, thus the approach probably underestimated the autotrophic soil respiration flux to some extent. However, to account for the entire root respiration of the deep-rooted *Q. ilex* trenching should have been several meters deep. This is difficult to achieve in practice, since incipient rock occurs already at about 30 cm depth, not comparable to long grown soils of other, more productive ecosystems. Thus, respiration from deep tree roots could probably not be accounted for. Nevertheless the largest fraction of root biomass is found in the upper soil layers (Kurz-Besson et al., 2006; Otieno et al., 2006). Soil respiration plots were fairly distant from trees, thus effects of tree root respiration are expected to be negligible. Furthermore, soil respiration was not decoupled from diurnal temperature correlation as in Tang et al. (2005b). Hence, root respiration data in our study may mostly reflect severe drought effects on understory plants, unaffected by canopy gas exchange of trees. For this partitioning study we therefore expect tree root as well as trunk respiration to be included in the tree foliage flux.

Apart from the above discussed problems, the use of two independent techniques (eddy-covariance and chamber measurements) in comparison with ecophysiological measurements brings major advantages in disentangling the relative and differential controls imposed by the ecosystem components on the carbon cycle.

5. Conclusions

Here, we present novel data disentangling abiotic and biotic drivers of all important component fluxes influencing the overall sink strength of a Mediterranean ecosystem during a rapid spring to summer transition. Decreasing soil water availability rather than increasing air temperature largely affected both assimilation and respiration fluxes of understory plants and in consequence R_{eco} and R_{soil}.

The drought sensitive understory plant species were found to play the most important role, determining the rapid decrease in CO_2 uptake of the open *Q. ilex* forest with increasing water deficit, since their contribution to total daily CO_2-exchange exhibited the most significant decrease (from 45% to 14%). This surprisingly high importance of the understory is crucial for the source/sink behavior of the whole ecosystem and the timing of the onset of drought may markedly influence the annual carbon budget.

Further, the partitioning approach revealed that total ecosystem respiration was increasingly dominated by heterotrophic soil respiration with decreasing water availability, even though the associated respiration rates of soil microorganisms decreased. Similarly, the relative contribution of tree carbon assimilation to daily ecosystem CO_2-uptake increased, although absolute rates did not change. Hence, chamber measurements of all major component fluxes (soil, roots, understory) of an ecosystem can be of large benefit to achieve a more process-based interpretation of eddy-covariance data.

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