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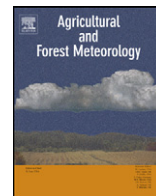
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Interpreting post-drought rewetting effects on soil and ecosystem carbon dynamics in a Mediterranean oak savannah

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ABSTRACT

A transient increase in soil carbon dioxide efflux after rewetting of previously dry soils, termed the Birch effect, can significantly influence the ecosystem carbon balance. This has generally been related to increased soil microbial respiration in response to a temporal increase in labile soil carbon. In order to quantify ecosystem carbon losses by the Birch effect and to trace the underlying biogeochemical processes, we monitored the effects of first natural rain pulses on soil and ecosystem carbon dioxide fluxes and their isotopic composition ($\delta^{13}\text{C}$) after an extended summer drought in a Mediterranean oak woodland. While GPP was affected negatively, rain largely enhanced soil respiratory processes, which increased their relative contribution to NEE by up to 95%, resulting in a significant net carbon loss from the ecosystem. This was reflected by high correlation ($r=0.91$) between the two fluxes. Further, isotopic composition of soil respiration ($\delta^{13}\text{C}_s$) explained on average 71% of the isotopic composition of ecosystem respiration ($\delta^{13}\text{C}_R$). We found a strong relationship between soil moisture and the increase in soil respiration (R_s) and NEE, indicating that the Birch effect observed during this study did not result from a transient increase in labile soil carbon but from a gradual (several days) moisture response of size and/or activity of the soil microbial community. We also observed large variation in $\delta^{13}\text{C}$ of soil and ecosystem respired CO_2 that corresponded to the rain pulses with enrichment of up to 8 and 6‰, respectively, and a subsequent depletion to initial values during the following dry days, which might be explained by increased relative contribution of soil microbial communities from deeper soil layers to overall soil respiration, a switch in the respired carbon source (e.g. anaplerotic carbon) and changes in apparent fractionation during the mineralization of soil organic matter after the depletion of labile carbon pools.

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1. Introduction

Respiratory carbon fluxes constitute one of the major determinants of the carbon balance in terrestrial ecosystems (Valentini et al., 2000; Rambal et al., 2004), and have been shown to compensate or even exceed annual gross primary productivity in seasonally dry ecosystems (e.g. Xu and Baldocchi, 2004; Pereira et al., 2007; Jongen et al., 2011), such as in the Mediterranean Basin. In these ecosystems, high evaporative demand, low soil water availability and the temporal unpredictability of rainfalls restrict ecosystem carbon gain mainly to the spring time (Xu and Baldocchi, 2004; Pereira et al., 2007; Unger et al., 2009; 2010b; Bugalho et al., 2011; Jongen et al., 2011). This results in a general net carbon loss by

respiration processes during summer drought (Pereira et al., 2007; Jongen et al., 2011).

Ecosystem respiration is controlled by a multitude of environmental factors (Werner et al., 2006; Unger et al., 2010b). Besides the supreme climatic controls of respiratory processes by e.g. temperature (e.g. Lloyd and Taylor, 1994) and moisture (e.g. Davidson et al., 2000; Reichstein et al., 2003; Cook and Orchard, 2008), autotrophic respiration of leaves, stems and roots (including the microbial and fungal rhizosphere) depends mainly on recent photosynthetic carbon assimilation, whereas heterotrophic respiration of soil microorganisms and non-mycorrhizal fungi is a function of the amount of labile soil carbon (Scott-Denton et al., 2006; Subke et al., 2006). Consequently, different respiration sources have different temporal dynamics (Werner and Gessler, 2011). Autotrophic soil respiration follows periods of growth- and carbon assimilation cycles throughout the year whereas heterotrophic soil respiration depends on temporal events of carbon input such as litter fall, priming and other processes (e.g. Kuzyakov and Cheng, 2001).

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Thus, temporal availability of respiratory substrates is a dominant factor determining respiration rates, which can be difficult to distinguish from climatic effects particularly under natural conditions (Davidson et al., 2006; Kuzyakov and Gavrichkova, 2010).

It has been shown that in seasonally dry ecosystems the so-called Birch effect (Birch, 1964), a rapid transient increase in soil carbon dioxide efflux in response to rewetting of previously dry soils can have a significant influence on annual ecosystem carbon balance (Pereira et al., 2004, 2007; Jarvis et al., 2007). This effect has been attributed to rapidly increasing mineralization rates of soil microorganisms in response to changing moisture conditions (Inglis et al., 2009; Borken and Matzner, 2009; Unger et al., 2010a). However, a complete understanding of the processes underlying the Birch effect has not yet been achieved (Borken and Matzner, 2009). Length and severity of the drought period prior to rewetting probably play a key role in how soil microbes respond to the sudden changes in soil water status (Xu et al., 2004; Cable et al., 2008; Unger et al., 2010a). Various studies have shown that the Birch effect can increase carbon losses from dry soils by magnitudes between the 6- up to the 80-fold (e.g. Xu et al., 2004; Unger et al., 2010a). The overall effect of rain pulse events during summer drought on ecosystem carbon sequestration will, however, depend on how gross primary productivity (GPP) is affected by the rain events in comparison to the respiratory carbon losses. Under future climate scenarios, the Mediterranean Basin is predicted to experience increased length and irregularity of summer droughts (Miranda et al., 2002) and therefore a change in both occurrence and magnitudes of the Birch effect and its importance for ecosystem carbon sequestration (Unger et al., 2010a). Moreover, the predicted increase in soil water content variability could substantially lower carbon sequestration in such ecosystems on the long-term (Fierer and Schimel, 2002). Thus, it is highly desirable to quantify the impact of the Birch effect on ecosystem carbon exchange and to investigate the origin of the carbon losses. Stable carbon isotopes are of potential use to trace the underlying biogeochemical processes (Werner and Gessler, 2011) and may allow for distinguishing between carbon sources respired during the Birch effect, as soil respiration fluxes after rain pulses have been shown to exhibit large temporal variability in isotopic composition (up to 10‰, Unger et al., 2010a).

In order to quantify ecosystem carbon losses by the Birch effect and to trace its underlying biogeochemical processes, we monitored the responses of soil respiration and net ecosystem exchange fluxes and their stable carbon isotope compositions (soil respiration: $\delta^{13}\text{C}_s$; ecosystem respiration: $\delta^{13}\text{C}_R$) along with GPP and photosynthetic parameters of oak trees (*Quercus ilex*) following the first natural rainfall after a long summer drought in a Mediterranean evergreen oak woodland. Our aims were (a) to quantify the direct and indirect effects of the rain events after drought on soil and ecosystem carbon dynamics, (b) to analyze the driving climate parameters of rapid and intermediate changes in magnitude and isotopic compositions of ecosystem and soil respiration fluxes, and (c) to investigate the origins of the Birch effect under natural conditions.

2. Materials and methods

2.1. Study site

The site Herdade da Mitra is located in the centre of the Portuguese Alentejo 12 km south of Évora, Portugal (38°32'27"N, 8°00'01"W, 264 m a.s.l.). The stand is a savannah-type evergreen oak woodland ("montado", with tree density of 30 ha⁻¹, 21% tree crown cover, leaf area index of 0.55; Carreiras et al., 2006) in a very homogeneous, slightly undulated landscape, which shows the signs of a typical silvo-pastoral system (Werner and Correia,

1996; Bugalho et al., 2011). Plant community is composed of sparse canopy forming *Quercus ilex* ssp. *ballota* L. (syn. *Q. rotundifolia* Lam.) in mixture with *Quercus suber* L. and a grass layer dominated by herbaceous annuals (e.g. *Tuberaria guttata* (L.) Fourr.), some drought deciduous graminea and a few shrubs (e.g. *Cistus salvifolius* L.). The soil type is Dystric Cambisol with a maximum soil depth of around 1 m and a low water retention capacity, overlying a granitic rock (David et al., 2007). The climate is Mediterranean with a precipitation/potential evapotranspiration ratio (P/PET) of 0.3–0.5, with hot dry summers and mild wet winters. Mean annual temperature is 15.5 °C and mean annual precipitation is 669 mm. 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, Rhyll, 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.

2.2. Net ecosystem exchange measurements

Continuous records of CO₂-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 a closed-path gas analyzer (LI-7000, LI-COR, Lincoln, NE, USA).

The raw data from the eddy covariance measurements were processed off-line using Eddyflux software (Meteotools, Jena, Germany). Following the Carboeurope-IP recommendations a planar fit coordinate rotation (Wilczak et al., 2001) for wind components was performed. The CO₂-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 concentration 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 CO₂-storage term, calculated for one point measurements at 0.75 m height as in Greco and Baldocchi (1996), was added to the estimated carbon dioxide flux.

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 absolute limits violations exceeded 1% of the total records of any of the three components of wind velocity and/or CO₂-concentration. Gap filling and flux-partitioning methods proposed by Reichstein et al. (2005) were used to fill data gaps and to calculate gross primary productivity (GPP) from NEE data.

2.3. Soil respiration measurements

On 9 October 2005 after a long summer drought a succession of days with natural precipitation pulses began. Concurrently soil respiration (R_s) was monitored in the morning, at midday and at midnight during a period of 15 days and additionally in diurnal cycles during three selected days (typically every 2–4 h) with a closed system soil respirometer (PP-System EGM2 soil respiration

system with SRC-1 chamber; PP-Systems, Amesbury, MA, USA) on five plots with three replicates each. Soil temperature (T_{soil}) and soil water content (SWC) were recorded in 5–10 cm depth alongside soil respiration measurements using the temperature sensor of the soil respiration system and a moisture probe (Theta Meter HH1, Delta-T Devices, Cambridge, UK), respectively.

2.4. Tree physiological measurements

Diurnal courses (every 2 h between 9:00 and 17:00) of leaf gas exchange (net photosynthesis (A), stomatal conductance (g_s), leaf internal to external CO_2 mixing ratios (c_i/c_a)) on five *Q. ilex* trees with three replicates per tree were recorded on 10, 13, 14, 16, 17, 18, 20, 21, 23 and 24 October using a LI-6400 open-flow gas exchange system (LI-COR, Lincoln, NE, USA). Predawn (4:00) and midday (12:00) leaf water potentials were measured during the same days on five *Q. ilex* with three replicates per tree using a Scholander-type pressure chamber (Manofrigido, Portugal). Standard deviations were calculated through error propagation procedure.

2.5. CO_2 -sampling for isotope analyses

Isotopic signatures of both soil and ecosystem respiration were calculated using the Keeling plot method (as described below). For sampling we used 12 mL soda glass vials (Exetainer, Labco, High Wycombe, UK) capped with pierceable septa for atmospheric air sampling (Werner et al., 2007). Gas samples for ecosystem Keeling plot analyses were collected at midnight:

Air was collected at nine heights: 24, 20, 16, 12, 8, 4, 2, 1 and 0.5 m (the heights between 16 and 24 m were above the tree canopy). Air was pumped at 10 L min^{-1} (pump Capex V2X, Charles Austen Pumps, Byfleet, Surrey, UK) through Dekabon (Synflex) tubing (25 m length, inner diameter 6.9 mm; Sertoflex, Serto Jacob, Fuldabrück, Germany), which was fixed at the eddy flux tower. A simple sampling system consisting of an Exetainer vial pierced by two needles connected to the pump and an infrared gas analyzer (IRGA, BINOS 100 4P, Rosemount Analytical, Hanau, Germany; precision for $\text{CO}_2 \pm 1 \text{ ppm}$) was mounted, pumping air through the tubing until stable CO_2 mixing ratios were reached and then sampled for 1 min. For 30 min samples were repeatedly collected from the top to the bottom resulting in two to three samples per height.

$\delta^{13}\text{C}_s$ was monitored along with the soil respiration fluxes in diurnal cycles on three of the soil plots using chamber Keeling plots. A custom-made, well ventilated and gas tight Plexiglas chamber (17 L; University of Bielefeld, Germany) was connected by Dekabon tubing in a closed system to the pump and the gas analyzer described above. Samples were taken between chamber outlet and gas analyzer. Climatic conditions inside the chamber were controlled with two thermocouples fixed at different heights and a photosynthetic active radiation quantum sensor (LI-190, LI-COR, Lincoln, NE, USA) connected to a datalogger (CR10; Campbell Scientific, Inc., Utah). The chamber was tightly fitted on a permanently installed soil collar (diameter of 0.3 m) and sealed with acryl rubber mastic. Once the chamber was placed on the plot and CO_2 mixing ratios inside the air stream were rising, air was sampled every minute over 10 min, collecting 10 samples in total per measurement series.

Additionally, five vials of known $\delta^{13}\text{C}$ and CO_2 mixing ratios were filled in the field at each sampling date and used as reference. Samples were analyzed (UAI, ICAT, Lisbon, Portugal) within 12–20 h after collection on a stable isotope ratio mass spectrometer (IsoPrime, GV Instruments, Manchester, UK) operating in continuous-flow coupled to a Multiflow prep-system (GV Instruments). A laboratory gas of known isotopic composition was

measured to correct for any drift ($n=5$, during the analysis of 100 samples). Repeated measurement precision was $<0.1\%$.

2.6. Statistics and Keeling plot calculations

The Keeling plot approach was used to assess the isotopic composition of ecosystem and soil respired CO_2 . Assuming that both source and background CO_2 remain constant during the sampling period ($<30 \text{ min}$), the isotopic signature of ecosystem respiration ($\delta^{13}\text{C}_R$) can be calculated as the y-intercept of a linear regression of $\delta^{13}\text{C}$ vs. the inverse of the CO_2 -mixing ratio obtained from vertical profiles (Keeling, 1958):

$$\delta^{13}\text{C}_a = c_T(\delta^{13}\text{C}_T - \delta^{13}\text{C}_R)(1/c_a) + \delta^{13}\text{C}_R \quad (1)$$

where $\delta^{13}\text{C}$ denotes isotopic composition and c denotes CO_2 -mixing ratios. The subscripts indicate sample air from several heights above and within the canopy (a), tropospheric air (T) and air respired from the ecosystem (R).

$\delta^{13}\text{C}_s$ was estimated from mixing ratio gradients of soil respired CO_2 by an adaptation of Eq. (1):

$$\delta^{13}\text{C}_m = c_b(\delta^{13}\text{C}_b - \delta^{13}\text{C}_s)(1/c_m) + \delta^{13}\text{C}_s \quad (2)$$

Subscripts indicate sample air mixing ratios in the chamber (m), atmospheric background air (b) and soil respiration (s).

We calculated model I regressions following Zobitz et al. (2006). Data points were removed from the regression when the residual of an individual data point was three times higher than the standard deviation. Regressions were rejected when not significant ($p \leq 0.01$). Uncertainties in the Keeling plot intercepts were expressed as standard errors of the intercept.

Regression analyses between climate factors, flux- and isotope data were performed with calculation of Pearson product-moment correlation coefficients (r) for comparison of results and tests for the significance of correlations ($p \leq 0.05$). Temporal variability in soil respiration and $\delta^{13}\text{C}_s$ and tree physiological parameters was tested for significance by applying a one-way ANOVA (combined with a Tukey honest significance post hoc test, $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$). All statistical analyses were performed using STATISTICA (StatSoft, Tulsa, OK, USA).

3. Results

3.1. Climate

Mean air temperatures between September and October 2005 ranged between 20 and 25°C (Fig. 1). Two small rainfall events, each of them less than 2 mm occurred on 4 and 5 September 2005, did, however, not impact net ecosystem carbon exchange (NEE). The wet autumn season started on 9 October 2005, when first significant rainfall was observed (4.8 mm). This was followed by a series of precipitation pulses (most significant on 10 October, daily total 34 mm and maximum rainfall intensity of 18.8 mm h^{-1} ; Fig. 2c). Concomitantly net radiation was strongly reduced (Fig. 2a) by cloud cover. Vapor pressure deficit (VPD) and air temperature (T_{air}) (Fig. 2b) dropped instantly after the initial rainfall to on average 0.5 kPa and 15°C , respectively, and remained low even during the short precipitation-free periods (e.g. 13–15 October). Soil temperature in 10 cm depth followed the general course of air temperature but with smaller diel fluctuations. Soil moistures in the upper 10 cm increased from ~ 0.1 to $\sim 0.17 \text{ m}^3 \text{ m}^{-3}$ in response to the initial rainfall on 9 October and afterwards increased gradually up to maximum values of $\sim 0.31 \text{ m}^3 \text{ m}^{-3}$ on 12 October. Interestingly, the large 34 mm rainfall of 10 October resulted only in a soil moisture increase of $\sim 0.9 \text{ m}^3 \text{ m}^{-3}$. After the period between 9 and 12 October soil moisture decreased to minimum values of ~ 0.15

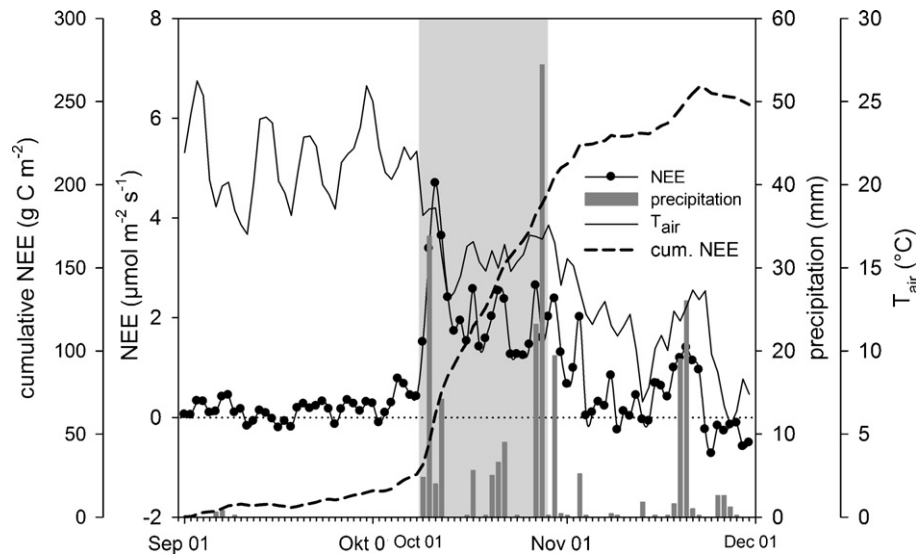


Fig. 1. Mean daily net ecosystem exchange (NEE, black circles); cumulative NEE (dashed line), air temperature (T_{air} , line) and daily sums of precipitation (bars) during the summer to autumn transition in 2005. The observation period in October 2005 is framed by a grey box.

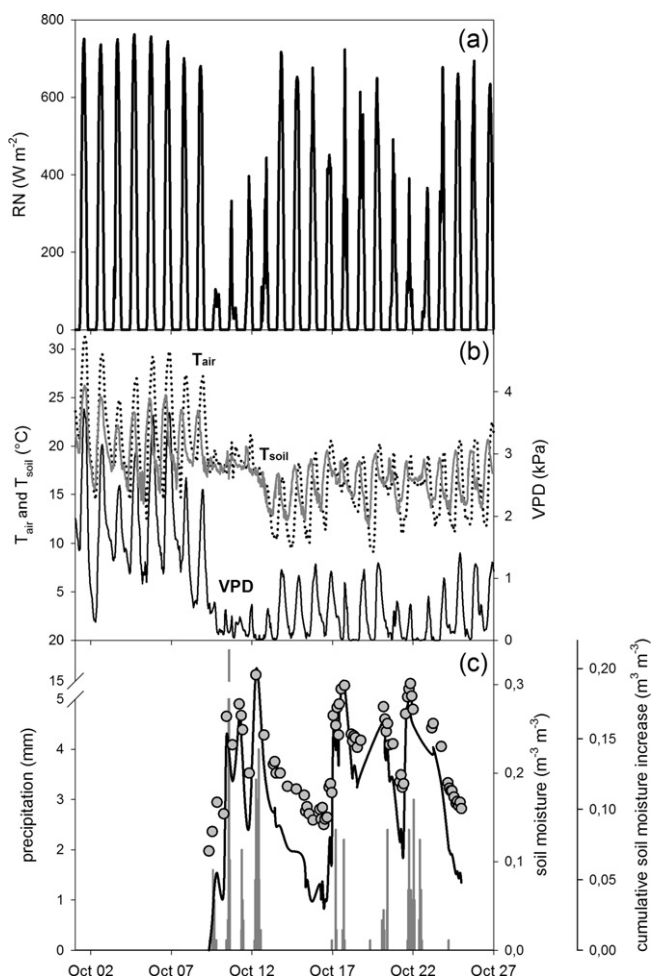


Fig. 2. Variation in (a) net radiation; (b) air temperature (dotted), soil temperature in 10 cm depth (grey line) and VPD (black line); (c) precipitation (grey bars); soil moisture in 5–10 cm depth (grey circles) and cumulative soil moisture increase (black line) during October 2005, pre- and post-soil rewetting upon first autumn rains.

during dry days, while new rainfalls above 2 mm on 17, 19 and 21 October resulted in immediate soil moisture increases to maximum values of $\sim 0.3 \text{ m}^3 \text{ m}^{-3}$ similar to 12 October. After the thorough field observation period between 8 October and 25 October 2005, mean air temperatures steadily decreased to minimum values of $5\text{--}10^\circ\text{C}$, while further major rain events occurred throughout the end of November (Fig. 1).

3.2. Tree physiological variables

Gas exchange parameters and water potentials of *Q. ilex* trees responded only gradually to increasing water availability (Table 1). Until 21 October daily averages of net photosynthesis rates (A) ranged between 2.6 and $5.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and then increased in response to higher light levels to 6.6 and $9.4 \mu\text{mol m}^{-2} \text{ s}^{-1}$ on 23 and 24 October, respectively (Table 1). Beneficial light conditions during the sunny days of 13 and 14 October, however, did not result in increased net photosynthetic uptake and significantly higher A than the initial value on 10 October was only observed on 24 October. Stomatal conductance increased gradually from ~ 21 to $\sim 170 \text{ mmol m}^{-2} \text{ s}^{-1}$ during the observation period (Table 1) and was only after 17 October significantly increased. The ratio of leaf internal to external CO_2 mixing ratio (c_i/c_a) was lowest directly after the first rains (0.48) and increased significantly to values around ~ 0.7 after 13 October (Table 1). Predawn water potentials exhibited a slight though highly significant increase ($p \leq 0.001$) after the initial precipitation pulses (-0.9 to -0.3 MPa), whereas midday water potentials showed a strong increase ($p \leq 0.001$) in response to first rains (-3.6 to -1.1 MPa) and thereafter exhibited large variations (-2.4 to -1.1 MPa) corresponding to rainy and sunny periods (Table 1).

3.3. Soil and ecosystem carbon dioxide fluxes

At the end of the severe summer drought both net ecosystem exchange (NEE) and soil respiration were close to zero (Figs. 1, 3a, and 4a). While the small rain pulses in September did not affect NEE (Fig. 1) rewetting in October caused major changes in both soil and ecosystem carbon dynamics (Figs. 1, 3a, and 4a). After the first precipitation pulses both mean nighttime (20:00–6:00) and daytime (8:00–18:00) NEE increased to 5 and $4 \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively (Fig. 3a), indicating a significant net carbon loss of the

Table 1

Leaf gas exchange parameters (stomatal conductance (g_s), net carbon assimilation (A), leaf internal over external CO_2 mixing ratio (c_i/c_a) and leaf water potentials at predawn (Ψ leaf PD) and midday (Ψ leaf MD) for *Quercus ilex* trees during the time between 9 October and 24 October 2005; $n = 5 \pm \text{SD}$.

| Date | g_s ($\text{mmol m}^{-2} \text{s}^{-1}$) | A ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | c_i/c_a | Ψ leaf PD (MPa) | Ψ leaf MD (MPa) |
|----------|--|--|----------------------|-----------------------|-----------------------|
| 09.10.05 | – | – | – | -0.9 ± 0.07 | -3.4 ± 0.23 |
| 10.10.05 | 21.5 ± 0.8 | 2.7 ± 0.5 | 0.48 ± 0.03 | $-0.7 \pm 0.09^{***}$ | $-1.1 \pm 0.17^{***}$ |
| 11.10.05 | – | – | – | -0.8 ± 0.05 | $-1.4 \pm 0.07^{***}$ |
| 12.10.05 | – | – | – | – | – |
| 13.10.05 | 59.9 ± 25.5 | 3.6 ± 1.8 | $0.69 \pm 0.09^*$ | $-0.6 \pm 0.08^{***}$ | $-1.4 \pm 0.11^{***}$ |
| 14.10.05 | 73.3 ± 4.9 | 5.4 ± 1.6 | $0.66 \pm 0.09^*$ | – | $-2.0 \pm 0.30^{***}$ |
| 15.10.05 | – | – | – | – | – |
| 16.10.05 | 67.8 ± 25.3 | 3.4 ± 2 | $0.74 \pm 0.13^{**}$ | $-0.4 \pm 0.08^{***}$ | $-1.9 \pm 0.04^{***}$ |
| 17.10.05 | $84.3 \pm 52.7^*$ | 4.5 ± 3.2 | 0.72 ± 0.17 | $-0.3 \pm 0.04^{***}$ | $-2.1 \pm 0.18^{***}$ |
| 18.10.05 | $93.1 \pm 30.7^*$ | 5.6 ± 2.4 | $0.66 \pm 0.1^{**}$ | $-0.3 \pm 0.08^{***}$ | $-2.1 \pm 0.17^{***}$ |
| 19.10.05 | – | – | – | – | – |
| 20.10.05 | 72.7 ± 18.3 | 3.8 ± 1.4 | $0.72 \pm 0.08^{**}$ | $-0.4 \pm 0.04^{***}$ | $-1.2 \pm 0.15^{***}$ |
| 21.10.05 | $114.15 \pm 78^{**}$ | 2.6 ± 1.8 | $0.82 \pm 0.12^{**}$ | – | $-1.1 \pm 0.05^{***}$ |
| 22.10.05 | – | – | – | – | – |
| 23.10.05 | $111.4 \pm 30.7^{**}$ | 6.6 ± 2.9 | $0.68 \pm 0.1^{**}$ | – | – |
| 24.10.05 | $170.6 \pm 54.9^{***}$ | $9.4 \pm 2.7^{***}$ | $0.68 \pm 0.09^*$ | $-0.5 \pm 0.15^{***}$ | $-2.4 \pm 0.17^{***}$ |

* Significant differences from start value $p \leq 0.05$.

** Significant differences from start value $p \leq 0.01$.

*** Significant differences from start value $p \leq 0.001$.

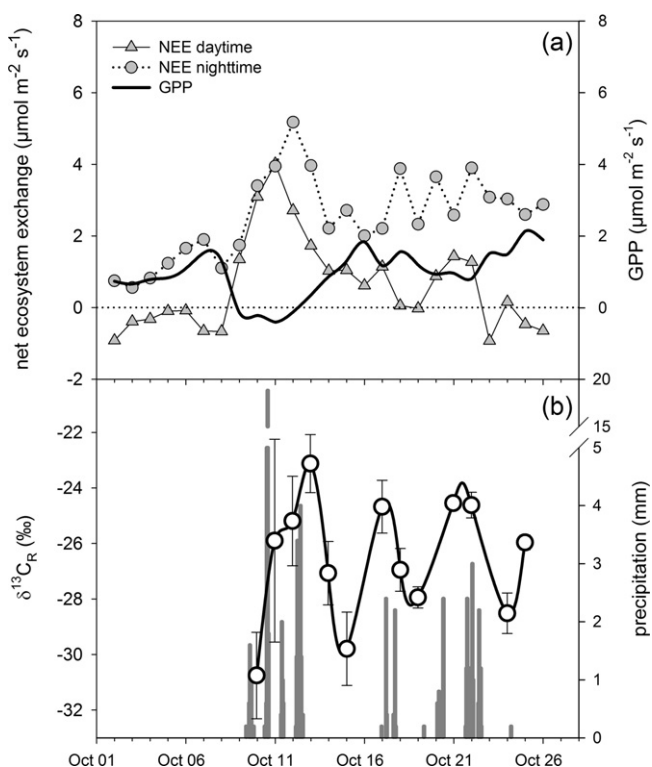


Fig. 3. (a) Mean nighttime (circles) and daytime (triangles) net ecosystem exchange (NEE) and mean diurnal gross primary productivity (GPP, line); (b) precipitation (bars) and nighttime $\delta^{13}\text{C}_R$ during October 2005. Error bars represent standard errors of Keeling plot intercepts for ordinary least square (OLS) regressions.

ecosystem by respiratory processes. The main respiration pulse occurred on 11 October, one day after the largest rainfall. Thereafter nighttime NEE dropped to $\sim 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ and increased slowly towards the end of October with short pulse-like increases to $4 \mu\text{mol m}^{-2} \text{s}^{-1}$ in response to subsequent rainfalls on 17, 19 and 21 October. Daytime NEE, on the other hand, started to decrease continuously after the first heavy rains but returned to pre-rain levels on 23 October (Fig. 3a). Mean daily NEE was highest on October 11 ($\sim 5 \mu\text{mol m}^{-2} \text{s}^{-1}$) and dropped steadily to small net carbon uptake rates of $\sim -0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ as the wet season progressed and new understory vegetation started to develop in November 2005 (Fig. 1). Mean daily GPP was low ($\sim 1 \mu\text{mol m}^{-2} \text{s}^{-1}$) after summer drought

and was affected negatively by the rain pulses ($\sim 0 \mu\text{mol m}^{-2} \text{s}^{-1}$) as tree photosynthesis was negatively affected by reduced radiation, temperatures and VPD (Fig. 2a, b). GPP returned to pre-rain values only on October 15 and did not increase significantly above these throughout October as trees did not seem to benefit from the increasing soil moistures. Cumulative NEE indicated a significant carbon dioxide loss from the system between 1 September and 30 November 2005. This net carbon dioxide loss amounted in total to 248 g C m^{-2} , of which 195 g C m^{-2} occurred during October (Fig. 1).

Soil respiration reflected the results observed at the ecosystem scale and significantly increased up to the 12-fold in response to the first rain events, following the pattern of nighttime NEE (Fig. 4a). After the first rains soil CO_2 -efflux increased its contribution to nighttime NEE by $\sim 30\%$ resulting in a total contribution of up to $\sim 95\%$. Moreover, the patterns of nighttime NEE and R_s were well-matched (Fig. 4a) and R_s was found to explain 91% of nighttime NEE variability ($r = 0.91$, Fig. 5b; Table 2).

Key climatic drivers of soil and ecosystem carbon dioxide fluxes after the rain were mainly soil climatic variables, which were directly affected by the rain pulse. Variations in R_s were directly influenced by soil moisture changes ($r = 0.69$ – 0.88 ; Table 2), while nighttime NEE was better related to soil temperature ($r = 0.74$; Table 2). From all other climatic variables VPD ($r = -0.37$ to -0.74) and predawn water potentials of *Q. ilex* ($r = 0.21$ – 0.44) correlated best, though not significantly, with soil and ecosystem fluxes.

3.4. $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_S$

Isotopic signature of ecosystem respiration ($\delta^{13}\text{C}_R$) was highly variable (Fig. 3b) and ranged between -30.7% (i.e. on 9 October) and -23.1% (i.e. on 12 October). We found that generally $\delta^{13}\text{C}_R$ followed the precipitation pattern with enrichment after days with heavy rainfalls and subsequent depletion during dry days (Fig. 3b). Similar to the fluxes (see Section 3.3) $\delta^{13}\text{C}_S$ followed the temporal pattern of $\delta^{13}\text{C}_R$ (Fig. 4c) and increased significantly within the first two days of rain from -27.4% to -23% on 12 October. Reflecting the changes in $\delta^{13}\text{C}_R$, $\delta^{13}\text{C}_S$ showed increasing depletion during dry days and enrichment ($p \leq 0.01$ on 12 and 21 October) during days with precipitation. Combining all plots, $\delta^{13}\text{C}_S$ was found to explain 61% in the variation observed in $\delta^{13}\text{C}_R$ ($r = 0.61$; Fig. 5a; Table 2), confirming that ecosystem respiration during this time was driven largely by soil respiration (see Section 3.3). However, there was spatial heterogeneity as $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_S$ of soil plot 2 ($r = 0.71$) and 3 ($r = 0.79$) were well correlated, while the correlation was weaker for soil plot 1 ($r = 0.35$).

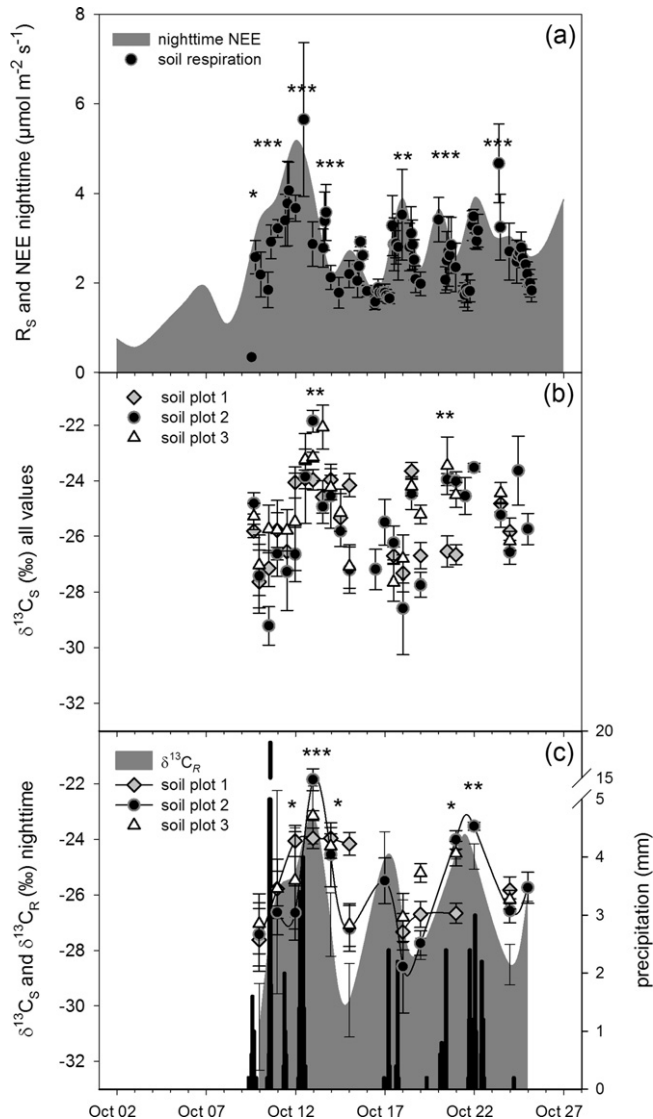


Fig. 4. (a) soil respiration (black circles) and nighttime NEE (shaded area); (b) daytime and nighttime values and (c) exclusively nighttime values of $\delta^{13}\text{C}_s$ from soil plot 1 (grey diamonds); 2 (black circles) and 3 (white triangles), precipitation (bars) and nighttime $\delta^{13}\text{C}_R$ (shaded area) during October 2005. Error bars of $\delta^{13}\text{C}$ represent standard errors of Keeling plot intercepts for ordinary least square (OLS) regressions. Error bars of soil respiration represents standard deviations for $n=5$. Asterisks mark significant differences from start value (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$) for soil respiration and $\delta^{13}\text{C}_s$.

The good linear relationships of soil respiration and nighttime NEE with soil climate parameters were confirmed by their isotopic compositions. $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_s$ were weakly correlated with soil moisture (r 0.24–0.55) and well correlated with predawn water potentials of canopy forming *Q. ilex* (r 0.67–0.77). Daily average R_s was significantly correlated with nighttime $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_s$ (r 0.60–0.70). However, direct relationships between R_s and nighttime NEE fluxes with their isotopic compositions were weak (Table 2).

4. Discussion

4.1. Effects of post-drought rewetting on soil and ecosystem carbon dynamics

Although rain is essential for primary productivity, it can have negative effects on carbon sequestration by increasing

carbon-losses from soils, a phenomenon termed the Birch effect (e.g. Birch, 1964; Jarvis et al., 2007; Inglima et al., 2009; Unger et al., 2010a). The 2005 summer drought in Portugal was exceptionally severe (Pereira et al., 2007). However, autumn precipitation was ca. 40 mm higher than the long-term mean (Pereira et al., 2007). The beginning of the wet season was thus expected to cause major changes in soil and ecosystem carbon dynamics. Corresponding to this hypothesis we observed a five-fold increase in nighttime NEE (Fig. 2a), which was the 1.5-fold of mean monthly GPP in October (Fig. 1; Pereira et al., 2007), highly dependent on soil respiration and well related to soil moisture. The Birch effect in Mediterranean ecosystems has been shown to increase soil respiration by the 15-fold (Jarvis et al., 2007), the 24-fold (Unger et al., 2010a) up to the 60–80 fold (Xu et al., 2004). Compared with these studies the observed increase in soil respiration of about 12 times above the baseline was moderate. Nevertheless, mean NEE did not return to pre-rain values until 3 November (Fig. 1) and the cumulative CO_2 loss from the system in October was 195 g C m^{-2} , which is considerable as compared to an annual GPP of $-756 \text{ g C m}^{-2} \text{ y}^{-1}$ (Tenhunen et al., 2009) in the studied system.

Soil respiration increased its relative contribution to NEE from 64 to 95%, a value substantially higher than the normal range (50–68%, Unger et al., 2009, 2010b). As in the current study only heterotrophic soil respiration was measured a possible increase in tree root respiration (e.g. Tang and Baldocchi, 2005) might have been missed out and soil contribution to NEE fluxes was potentially underestimated and even higher than 95%.

In contrast to soil respiration, carbon uptake by trees was not increased after rain (Table 1, Fig. 3a) reflected by only small changes in GPP throughout October (Fig. 3a). Although single leaf stomatal conductance and assimilation rates slightly increased (Table 1) initial rainfalls had a negative effect on GPP (Fig. 3a). Such low rain use efficiency during summer drought is typical for *Q. ilex* (Pereira et al., 2007) limiting a counterbalance to carbon loss from the soils by a Birch effect respiration pulse during and directly following summer rain events.

The Birch effect has been shown to occur in two stages: (i) an immediate increase in soil respiration that rapidly passes within minutes to hours and is not related to either soil moisture or soil temperature (henceforth called “immediate Birch effect”) (Xu et al., 2004; Unger et al., 2010a) and (ii) a subsequent longer-term increase in soil respiration above the pre-rain values (henceforth called “gradual Birch effect”) which is strongly related to soil moisture and which duration correlates with the amount of rainfall (Xu et al., 2004; Unger et al., 2010a). We expected a large immediate Birch effect in response to the first rain event and that the CO_2 -pulses after succeeding precipitation events would become less pronounced, as has been shown before (e.g. Bottner, 1985; Denef et al., 2001; Fierer and Schimel, 2002, 2003). However, we found that first strong rain events on 9 and 10 October, did not cause a pulse-like and transient increase in soil respiration and nighttime NEE. Both fluxes increased strongly but gradually and peaked on 12 October (Fig. 4a) after three days of increasing soil moistures (Fig. 2c). Thus, in contrast to other studies (Borken et al., 2003; Fierer and Schimel, 2003; Xu et al., 2004; Butterfly et al., 2009; Inglima et al., 2009; Unger et al., 2010a), an immediate Birch effect was lacking and the maximum response of soil respiration towards natural rain pulses was time-lagged by three days. The same time-lag was observed for soil moisture and the soil moisture pattern during the observation period was consistent with soil respiration (r 0.69–0.88) and nighttime NEE (r 0.45), as has also been reported by other studies (e.g. Lee et al., 2004; Jarvis et al., 2007; Pereira et al., 2007; Inglima et al., 2009).

The occurrence of immediate Birch effects is related to both the drought status of the system prior to rewetting and the

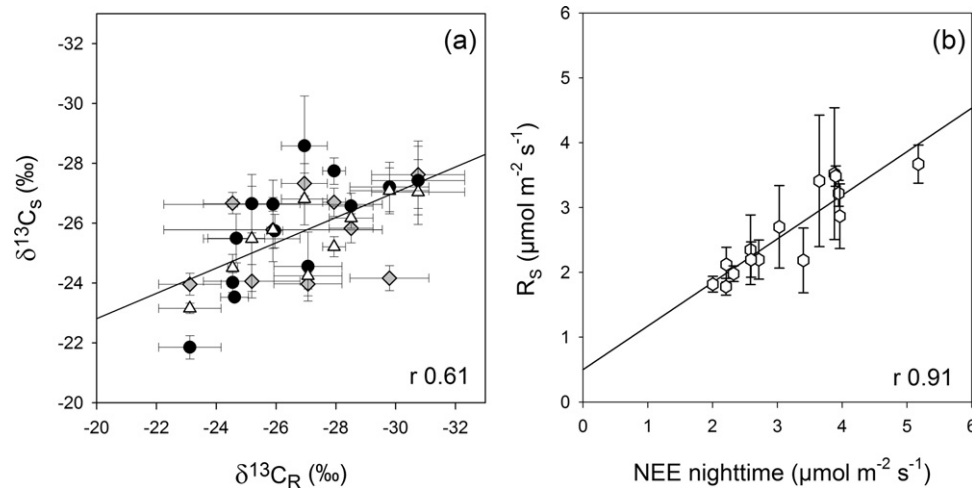


Fig. 5. Regressions between (a) $\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_S$ of soil respiration from three different soil plots 1 (grey diamonds); 2 (black circles) and 3 (white triangles), regression line covers all plots ($n=33$; $r=0.61$) and (b) soil respiration and ecosystem respiration at nighttime ($n=14$; $r=0.91$).

magnitude of the rewetting pulse (e.g. Xu et al., 2004; Cable et al., 2008; Unger et al., 2010a). Cable et al. (2008) showed that rewetting pulses of less than 7 mm did not enhance soil respiration significantly and that the magnitude of the carbon pulse depended largely on antecedent soil moistures. Similarly, Fischer (2009) showed that the occurrence of large and transient CO_2 -pulses depends on the magnitude of soil water potential change during rewetting. We hypothesize that the initial rainfall after drought was too small (4.8 mm) to cause an immediate Birch effect. However, it was sufficient to initiate a significant soil moisture increase (Fig. 2c) reflecting on soil microbial activity.

Thus, wetting rate and infiltration to a soil seem to play a major role in determining the microbial response to changing soil water potentials. For example, surface runoff and rapid infiltration through deep soil cracks might explain the observed delay in soil moisture response to initial rains. Further, rain interception of the canopy may delay the release of a significant amount of water to the soil (Lee et al., 2004), although this effect is not likely to be relevant in the open Mediterranean woodland, where canopy interception plays a much smaller role than in dense forest systems (e.g. David et al., 2006; Limousin et al., 2008).

4.2. Effects of post-drought rewetting on $\delta^{13}\text{C}$ of soil and ecosystem respiration

In concurrence with the increases in ecosystem and soil respiration we observed large fluctuations in $\delta^{13}\text{C}_R$ ($\sim -31\%$ to -23%) and $\delta^{13}\text{C}_S$ ($\sim -28\%$ to -22%), indicating shifts in the carbon source respired by the soil microbial community. With increasing soil moistures both $\delta^{13}\text{C}_S$ and $\delta^{13}\text{C}_R$ exhibited a significant enrichment of up to 8‰ and 6‰, respectively (Fig. 4b, c) and subsequently decreased to previous values during the following dry days. Similar to the increase in nighttime NEE and soil respiration but gradual and peaked days after the initial rainfall (in the night of 12–13 October), confirming the lack of an immediate Birch effect.

Enrichment in $\delta^{13}\text{C}_S$ up to -20% directly after rewetting of dry soils has been reported before (Unger et al., 2010a). The increase in $\delta^{13}\text{C}_S$ was discussed with a rapid and transient change in the respired carbon source in direct response to the rainfall. The extent of this enrichment was reported to be smaller after severe ($\sim -3\%$) than after mild drought ($\sim -9\%$) (Unger et al., 2010a), which was hypothesized to be due to increased relative contributions of

Table 2

Pearson coefficients (r) for linear regressions between diel, daytime (DT) and nighttime (NT) values of soil and ecosystem fluxes (R_S , NEE) and their isotopic compositions ($\delta^{13}\text{C}_R$ and $\delta^{13}\text{C}_S$) with climatic variables (net radiation (RN), air temperature (T_{air}), vapour pressure deficit (VPD), predawn water potentials of *Q. ilex* (WP_{PD}), soil moisture (SM) and soil temperature (T_{soil})) for the period between 9 October and 24 October 2005. Shaded areas indicate regression parameters exclusively for nighttime. Direction of relationships is indicated. Significant relationships ($p < 0.05$) are marked in bold, $n = 10$ –16.

| | NEE diel | NEE DT | NEE NT | R_S diel | R_S DT | R_S NT | $\delta^{13}\text{C}_R$ NT | $\delta^{13}\text{C}_S$ DT | $\delta^{13}\text{C}_S$ NT |
|----------------------------|--------------|--------------|-------------|--------------|--------------|-------------|----------------------------|----------------------------|----------------------------|
| RN | -0.62 | -0.54 | -0.34 | 0.24 | 0.58 | -0.23 | 0.00 | 0.42 | 0.26 |
| T_{air} | 0.27 | 0.21 | -0.10 | -0.62 | -0.70 | -0.11 | -0.36 | -0.42 | -0.61 |
| VPD | -0.74 | -0.65 | -0.49 | 0.03 | 0.44 | -0.37 | -0.06 | 0.44 | 0.15 |
| WP_{PD} | 0.21 | 0.16 | 0.21 | 0.54 | 0.42 | 0.44 | 0.77 | -0.19 | 0.67 |
| T_{soil} | 0.77 | 0.58 | 0.74 | 0.29 | 0.16 | 0.54 | -0.04 | -0.05 | -0.23 |
| SM | -0.21 | -0.31 | 0.45 | 0.73 | 0.88 | 0.69 | 0.24 | 0.47 | 0.55 |
| NEE diel | - | - | - | -0.06 | -0.22 | 0.37 | 0.07 | -0.55 | -0.12 |
| NEE DT | - | - | - | -0.10 | -0.20 | 0.33 | 0.01 | -0.51 | -0.04 |
| NEE NT | - | - | - | 0.55 | 0.31 | 0.91 | 0.17 | -0.03 | 0.21 |
| R_S diel | -0.06 | -0.10 | 0.55 | - | - | - | 0.61 | 0.29 | 0.70 |
| R_S DT | -0.22 | -0.20 | 0.31 | - | - | - | 0.57 | 0.39 | 0.61 |
| R_S NT | 0.37 | 0.33 | 0.91 | - | - | - | 0.25 | 0.08 | 0.30 |
| $\delta^{13}\text{C}_R$ NT | 0.07 | 0.01 | 0.17 | 0.63 | 0.57 | 0.25 | - | 0.01 | 0.71 |
| $\delta^{13}\text{C}_S$ DT | -0.55 | -0.51 | -0.03 | 0.29 | 0.39 | 0.08 | 0.01 | - | 0.46 |
| $\delta^{13}\text{C}_S$ NT | -0.12 | -0.04 | 0.21 | 0.70 | 0.61 | 0.30 | 0.71 | 0.46 | - |

microbial communities from deeper soil layers under severe drought conditions (Theis et al., 2007; Joos et al., 2010).

We found initially depleted values in both $\delta^{13}\text{C}_\text{R}$ and $\delta^{13}\text{C}_\text{S}$ corresponding to the results for mild drought conditions found by Unger et al. (2010a). However, while Unger et al. (2010a) found the enrichment in $\delta^{13}\text{C}_\text{S}$ to be pulse-like and transient, occurring only in the first hours after irrigation, the changes in both $\delta^{13}\text{C}_\text{S}$ and $\delta^{13}\text{C}_\text{R}$ observed in this study occurred to be gradual with a delay of 3 days to initial rewetting. A recent study of Gavrichkova et al. (2011) related strong variability of $\delta^{13}\text{C}_\text{S}$ in a beech forest (up to 10‰) to variations in the contribution of root respiration to total soil CO_2 -efflux. However, the contribution of autotrophic respiration and recent photosynthetic substrates (such as root exudates) to the respiration pulse during the Birch effect can be assumed to be negligible, as the initial effect of the rain on plant productivity was not beneficial (Fig. 4a). Although seed germination of understory plants started in the second half of October, there was no living understory during the time of observation and soil plots were fairly distant from trees. Unger et al. (2010a) showed further, that respiration pulses in plots with and without understory roots were similar. Thus, the increase in soil respiration during the Birch pulse stemmed predominantly from heterotrophic sources.

Direct relationships between isotopic compositions of soil and ecosystem respired CO_2 were strong both at fortnight and diurnal scales (Table 2). Although, the Keeling plot method at the ecosystem scale is a well accepted tool to integrate the isotopic composition of all ecosystem respiration components we cannot completely exclude a potential influence of the sampling method (sampling over all heights) on $\delta^{13}\text{C}_\text{R}$ calculations by a bias towards lower heights and thus, a stronger influence of soil respiratory signature on ecosystem respiration. However, as soil respiration contributed to more than 90% to ecosystem respiration, the observed similarity between $\delta^{13}\text{C}_\text{R}$ and $\delta^{13}\text{C}_\text{S}$ was expected. The strong correlation between $\delta^{13}\text{C}_\text{S}$ and $\delta^{13}\text{C}_\text{R}$ thus lends additional support to the finding that heterotrophic soil respiration controlled ecosystem respiration after the first rains.

In direct comparison neither $\delta^{13}\text{C}_\text{S}$ nor $\delta^{13}\text{C}_\text{R}$ were correlated to the variations in NEE and R_S , but were well correlated with diel averages of NEE and R_S , suggesting a time-integrated response between the flux increases and the change in respired carbon source.

4.3. Origin of the Birch effect under natural conditions

The Birch effect underlying processes still remain largely debated (Borken and Matzner, 2009). It has been shown that rewetting does not enhance CO_2 -fluxes from inorganic carbon pools, as often hypothesized, but rather induces rapidly increased mineralization rates in response to changing moisture conditions (Inglima et al., 2009; Borken and Matzner, 2009; Unger et al., 2010a). Several hypotheses have been proposed: (i) a spontaneous increase in fungal and microbial biomass in response to water availability (Griffiths and Birch, 1961; Jager and Bruins, 1974; Orchard and Cook, 1983; Scheu and Parkinson, 1994); (ii) shattering of soil aggregates by rain fall impact exposing previously unavailable organic substrates for decomposition (e.g. Denef et al., 2001); (iii) a drought-induced increase in dead microbial biomass (e.g. Bottner, 1985) or labile litter (e.g. Joos et al., 2010), becoming available for decomposition after rewetting; (iv) mineralization of hypotonic substances (e.g. polyols, amino acids and amines), which are released by soil microbes upon rewetting in order to adapt cell water status to the changes in soil water potential (Kieft et al., 1987; Halverson et al., 2000; Fierer and Schimel, 2002, 2003; Jarvis et al., 2007; Unger et al., 2010a). Unger et al. (2010a) found that the substrates involved in this rapid Birch pulse most probably stem from

increased mineralization of microbial carbon upon rewetting (e.g. hypotheses iii; iv). The gradual and longer term increase in soil respiration upon rewetting on the other hand was explained by a soil moisture response of soil microbial activity with increased mineralization of soil organic matter carbon (SOM-C) (hypothesis i).

Although we observed large variability in $\delta^{13}\text{C}_\text{S}$ and $\delta^{13}\text{C}_\text{R}$ the gradual increase in both nighttime NEE and soil respiration in response to natural rewetting and their consistent correlation with soil moisture indicate that the Birch effect observed in this study was rather due to a positive effect on soil microbial activity (hypothesis i) than to priming by temporarily increased labile substrates. Further, changes in the CO_2 -fluxes were well related to soil moisture, while there were no consistent relationships between soil climatic drivers and $\delta^{13}\text{C}_\text{R}$ or $\delta^{13}\text{C}_\text{S}$ in direct response to rain-falls. This lends further support that rapid transient changes in the respired carbon sources (e.g. hypotheses iii and iv) did not occur. Nevertheless, the observed changes in $\delta^{13}\text{C}_\text{R}$ and $\delta^{13}\text{C}_\text{S}$ indicated a gradual shift in the respired carbon source with increasing soil moistures, which was well correlated to diel integrations of NEE and R_S . Saetre and Stark (2005) found that bacterial and fungal growth peaked two days after rewetting, thereby largely depleting labile soil carbon, and then rapidly perished. This finding matches our results, as the growing microbial community is likely to change substrate, when the amount of labile soil carbon decreases.

One hypothesis for such a switch in the respiratory carbon source might be increased respiration of anaplerotic carbon after the depletion of labile carbon pools. Anaplerotic carbon is provided by phosphoenol pyruvate carboxylase (PEPc) and has been shown to make up to 10% of bacterial biomass (Perez and Matin, 1982). This carbon is substantially enriched compared to carbon fixed by C_3 -plants which results from intermixing of enriched atmospheric CO_2 with respired CO_2 in the soil air spaces. Further, fractionation against ^{12}C by carbonic anhydrase during hydration of CO_2 prior to C-fixation by PEPc plays an important role (Mook et al., 1974). Additionally, the carbon cycle of deeper soil layers is largely sustained by soil microbial biomass alone due to decreased input of plant assimilates (Tu and Dawson, 2005), and thus the relative contribution of anaplerotic carbon to the overall signal is enhanced. Consequently, the substrate for mineralization becomes progressively enriched with increasing soil depth (e.g. Nadelhoffer and Fry, 1988; Ehleringer et al., 2000).

Despite the severity of the summer drought, pre-wetting soil moistures of more than $0.1 \text{ m}^3 \text{ m}^{-3}$ suggested that drought conditions were mild before the first rainfalls in October 2005, which might be explained by already moderate temperatures and VPD and nighttime dew formation. Corresponding to these conditions both $\delta^{13}\text{C}_\text{S}$ and $\delta^{13}\text{C}_\text{R}$ were rather depleted prior to rewetting, indicating that the sources for soil respiration stemmed initially to a large part from the upper soil layers (e.g. decaying litter and root material). A temporal delay in infiltration of rain water into deeper soil layers might therefore explain the time-integrated response of soil respiration and $\delta^{13}\text{C}_\text{S}$ to initial rewetting as microbial communities in deeper soil layers might have become active later. Thus, both accelerated turn-over of anaplerotic carbon with increasing microbial growth as well as increased microbial contribution from deeper soil layers might explain the observed enrichment in response to the gradual soil moisture increase (see also Unger et al., 2010a).

Additionally, recent studies reported apparent fractionation during the mineralization of soil organic matter, resulting in enriched soil respiration above the substrate, ranging between 3 and 5‰ (e.g. Cotrufo et al., 2005; Paterson et al., 2009; Werth and Kuzyakov, 2010; Lerch et al., 2010; Ngao and Cotrufo, 2011). This has been explained by selective substrate utilization of soil

microbes preferentially mineralizing enriched substrates such as sugars, cellulose, and starch rather than depleted sources such as lignins and lipids. Thus, although the observed enrichment in $\delta^{13}\text{C}_s$ was substantially higher than might be explained by this effect, increasing microbial mineralization of SOM in response to gradually rising soil moistures has likely contributed. However, measurements of soil moisture and soil respiration development in different soil layers after rain are needed to backup these hypotheses.

5. Conclusions

Precipitation pulses after drought negatively affected GPP and largely enhanced soil respiratory processes, which increased their contribution to nighttime NEE by up to more than 95%. This was reflected in significant correlations between nighttime NEE and soil respiration as well as their isotopic compositions. The strong relationship between soil moisture and the increase in soil respiration indicated that the Birch effect observed during this study did not result from a transient increase in labile soil carbon but from a moisture response of size and/or activity of the soil microbial community. Variability in isotopic composition of soil and ecosystem respiration that occurred after the rain pulses can be hypothesized to be due to increased relative contribution of soil microbial communities from deeper soil layers to overall soil respiration, a switch in the respired carbon source (e.g. anaplerotic carbon) and changes in apparent fractionation during the mineralization of soil organic matter after the depletion of labile carbon pools. However, further studies on the impact of rain events after drought on soil heterotrophic organism's metabolism are needed to confirm these hypotheses. Quantifying the impact of the Birch effect on ecosystem carbon dynamics and analyzing the mechanisms behind it will be a major aim of future research, as carbon losses from seasonally dry soils are expected to become more important in the perspective of prolonged droughts and an increasing number of extreme weather events.

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