Drought impact on carbon and water cycling in a Mediterranean *Quercus suber* L. woodland during the extreme drought event in 2012

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Abstract

Savannah-type ecosystems account for 26–30 % of global gross primary productivity GPP with water being one of the major driving factors. In Europe, savannah-type woodlands cover an area of about 1.5 million ha. Here, the recent past has shown a significant decrease of precipitation

P in winter and spring as well as decrease of total annual precipitation. Strong effects on local water balance and carbon sink strength have thus been reported due to changes in precipitation regime.

The objective of this study is to quantify the impact of the extreme drought event in 2012 on the water balance, gross primary productivity and carbon sink strength of a typical Portuguese

cork-oak woodland (*montado*) compared to the wet year 2011. Physiological responses of the dominant tree species *Quercus suber* (L.) are disentangled, employing combined photosynthesis and stomatal conductance modelling.

Precipitation effectiveness ET/P increased from 86 % in 2011 to 122 % in the dry year 2012 due to deep soil or ground water access of the *Q. suber* trees leaving no water for ground wa-

ter replenishment. Understorey and overstorey GPP were strongly reduced by 53 % and 28 %, respectively, in 2012 compared to 2011 due to the late onset of the autumn rains in 2011 and an additional severe winter/spring drought. However, the ecosystem was still a carbon sink in both years but with a 38 % reduced sink strength under extreme drought in 2012 compared to 2011. The combined photosynthesis-stomatal conductance model yielded best results if it was

allowed to adjust photosynthetic and stomatal parameters simultaneously. If stomatal response was modelled with the Leuning approach, which allows for a different sensitivity to vapour pressure deficit, the stomatal model parameters were highly coupled. A change in either of the parameters needed to be compensated by the other to guarantee a stable sensitivity of stomatal conductance to assimilation, independently from variations in vapour pressure deficit. The

Q. suber trees showed a 37 % reduced stomatal conductance during the drought period 2012 compared to 2011 due to water supply limitations. In response to reduced leaf internal CO_2 availability, the trees strongly reduced apparent maximum carboxylation rate by 43 % in 2012 compared to 2011. Unexpectedly, the optimum temperature T_{opt} of maximum electron trans-

port rate decreased during the drought period, enhancing the susceptibility of the trees to high temperature stress during the summer.

Our results suggest that, if the trend of decreasing annual precipitation and changed precipitation pattern on the Iberian Peninsula continues, sustained effects on local ground water reservoirs, understorey species composition and tree mortality have to be expected in the long term. To successfully model the effect of drought on the *montado* ecosystem, variable apparent maximum carboxylation rate $V_{c,max}$, stomatal conductance parameter m and vapor pressure deficit sensitivity parameter D_0 need to be incorporated in photosynthesis-stomatal conductance modelling.

1 Introduction

One of the typical semi-arid ecosystem in Europe is a savannah-type woodland (*montado*), consisting of a sparse overstorey tree layer and a herbaceous understorey layer. During the biomass peak of the herbaceous plants in spring, the understorey layer can provide a large contribution to the whole ecosystem water and carbon balance and thus, can play a significant role in the annual carbon and water budgets (Unger et al., 2009; Paco et al., 2009; Dubbert et al., 2014b). However, each layer responds differently to changes in precipitation depending on their life form (chamaephyte or therophyte) and access to different water reservoirs throughout the year (Paco et al., 2009) including deep soil or ground water (David et al., 2004).

Montado ecosystems (span.: *dehesa*) cover an area of about 1.5 million ha in Europe (Bugalho et al., 2011) and contribute together with savannah-type ecosystems on other continents about 30 % to global gross primary productivity GPP (Beer et al., 2010; Grace et al., 2006). The major driving factor of GPP in *montado* ecosystems is water (Vargas et al., 2013; Pereira et al., 2007; David et al., 2004), since annual precipitation patterns show periodical summer droughts and evapotranspiration losses are high (Krishnan et al., 2012; Huxman et al., 2005).

In the recent past, precipitation shows a significant decrease of rain amount in February and March as well as a decrease of total annual rainfall on the Iberian Peninsula (Guerreiro et al., 2013; García-Barrón et al., 2013; Mourato et al., 2010; Paredes et al., 2006). A trend towards

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extreme events in the form of droughts is observed due to a more heterogeneous distribution of precipitation throughout the year (García-Barrón et al., 2013). These type of changes in precipitation regime have been reported to strongly affect local water balance (Rodrigues et al., 2011; Vaz et al., 2010; Grant et al., 2010) and carbon sink strength (Pérez-Ramos et al., 2013; Pereira et al., 2007; Granier et al., 2007; Ciais et al., 2005) of ecosystems in semi-arid regions and are expected to increase with proceeding climate change (Bussotti et al., 2013; Guerreiro et al., 2013).

Species in semi-arid environments have developed vast structural and functional adaptations to regulate carbon assimilation and respiratory water loss (e.g. Tenhunen et al., 1987; Werner et al., 1999). Considerable knowledge has been acquired on leaf-level physiological processes in the last three decades (e.g. Beyschlag et al., 1986; Sala and Tenhunen, 1996; Tenhunen et al., 1985, 1990; Werner et al., 2001), emphasizing the role of ecophysiological adaptations to seasonality and summer drought in Mediterranean climate conditions. In these environments lack of precipitation often interacts with excessive irradiance and high temperature further constraining leaf carbon fixation through photoinhibition during drought (Werner et al., 2001, 2002). Cork oaks strongly reduce transpirational water loss by stomatal closure in response to drought to avoid a critical level of dehydration and hydraulic failure (Oliveira et al., 1992; Tenhunen et al., 1984, 1987; Werner and Correia, 1996; Kurz-Besson et al., 2006).

To investigate the influence of drought on carbon sink strength at the ecosystem level, combined stomatal conductance-photosynthesis models can be used in order to disentangle regulatory processes from effects of micro-climatic variations. Different descriptions of the underlying processes exist in the literature, though. For example, stomatal conductance can be modelled either reacting to relative humidity (Ball et al., 1987) or to vapour pressure deficit (Leuning, 1995). Also the determination of parameters in individual descriptions is different among different authors. The sensitivity of stomatal conductance to vapor pressure, for example, is often taken as a fixed value while determining only the other parameters in the coupled stomatal conductance-photosynthesis model time-variant, although the sensitivities of stomatal conductance to photosynthesis and to vapour pressure are highly correlated. Recent studies could consequently demonstrate that changes of one single parameter, e.g. only maximum carboxylation

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rate or only stomatal conductance sensitivity, does not explain drought-induced reductions in both GPP and T simultaneously (Egea et al., 2011; Reichstein et al., 2003; Zhou et al., 2013). Further, different temperature dependencies of e.g. maximum carboxylation or electron transport rate have been proposed (Medlyn et al., 2002; von Caemmerer, 2000; June et al., 2004).

5   In the present study, we report on drought effects on a Portuguese *montado* ecosystem using the unique opportunity of two consecutive years of very contrasting hydrological conditions. 2011 being a wet year with regular drought pattern occurring in summer, and 2012 being an extremely dry year with strongly reduced precipitation amount. Particularly, 2012 showed a severe additional winter/spring drought characteristic for precipitation pattern changes in recent
10 past on the Iberian Peninsula (2nd driest year since 1950, Costa et al., 2012; Santos et al., 2013; Trigo et al., 2013). This study is focussing on: (1) quantifying the effects of drought on the local ecosystem water balance, overstorey and understorey GPP, as well as differences in net ecosystem carbon exchange NEE between both years. (2) Identifying physiological responses in the drought year 2012 of the *Q. suber* trees using a combined photosynthesis-stomatal conductance
15 model and testing the model performance with different process descriptions.

2   Material and methods

2.1   Site description

The study was conducted at the savannah-type flux observation site "PT-Cor" (Fig. 1) of the European Integrated Carbon Observation System (ICOS) ca. 100 km north-east of Lisbon, Por-
20 tugal (latitude: $39°8'20.7''$ N, longitude: $8°20'3.0''$ W, altitude: 162 m a.s.l.). The site is planted with evergreen *Quercus suber* (L.) trees of 209 individuals ha^{-1} on a Luvisol soil (Jongen et al., 2011). The tree canopy has a leaf area index LAI of 1.05 ± 0.07 $m_{leaf}^2 m_{ground}^{-2}$, a midday gap probability $P_{gap}(0)$ of 0.76 ± 0.03 and an average tree canopy height of 9.7 m (Piayda et al., 2014). The *Q. suber* trees likely have deep soil water and ground water access. Native annual
25 grasses and herbs build the understorey vegetation (Jongen et al., 2013b; Dubbert et al., 2014a), which emerges after the first rains in autumn, has a peak stand height in spring (March–April)

and becomes senescent at the beginning of the summer period (late May) with a maximum LAI of $0.70 \pm 0.05\,\mathrm{m^2_{leaf}\,m^{-2}_{ground}}$. The understorey vegetation density and LAI are spatially highly variable due to the heterogeneous topography and hence, differences in soil moisture regime. The whole region is under forest management.

2.2 Climate conditions

The site is characterised by a Mediterranean climate with moist and mild winters and dry and hot summers. The long term mean annual temperature is about $15.9\,^{\circ}\mathrm{C}$ and the annual sum of precipitation is about $680\,\mathrm{mm}$ (Jongen et al., 2013b), with a characteristic annual pattern of high winter precipitation (November to January) and summer drought during June to September (Paredes et al., 2006). The relevance of the winter precipitation for the Portuguese hydrological cycle can be easily explained by the prevailing Mediterranean-type climate that concentrates most of precipitation during the winter half of the year, with little to no precipitation in summer. Hence, the following data treatment is based on the hydrological year beginning with first autumn precipitation (October to September).

2.3 Overstorey eddy covariance measurements

The overstorey tower (Fig. 1, point 1) is set up with a Gill R3A-50 ultrasonic anemometer (Gill Instruments Ltd., Lymington, UK) in combination with a LI-7000 closed path CO_2/H_2O analyzer (LI-COR, Lincoln, USA). The inlet tube has a length of $8.5\,\mathrm{m}$, is attached to one of the anemometer arms and operated with an average flow rate of ca. $8\,\mathrm{L\,min^{-1}}$. The reference cell is flushed with N_2. The measurement height is about $23.5\,\mathrm{m}$ above ground. Data is continuously acquired and processed live on a field laptop with the eddy covariance data acquisition and processing software package EddyMeas (meteotools, Jena, Germany; Kolle and Rebmann, 2007).

At a height of $20\,\mathrm{m}$ above ground, two up- and downward facing LI-190 Quantum sensors (LI-COR, Lincoln, USA) and a NR-LITE net radiometer (Kipp and Zonen, Delft, the Netherlands) are attached. A radiation shielded HMP 155 probe measures air temperature T_a and

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relative humidity rH (Vaisala, Helsinki, Finland). Precipitation P is measured with an ARG100 aerodynamic rain gauge (Environmental Measurements Ltd., North Shields, UK) at the tower top. The meteorological parameters are logged on a CR10X datalogger (Campbell Scientific, Logan, USA).

2.4 Understorey eddy covariance measurements

The understorey tower was located about 286 m north-west of the overstorey tower (Fig. 1, point 2). It was equipped with a Gill R3-50 ultrasonic anemometer (Gill Instruments Ltd., Lymington, UK) in combination with a LI-7500A open path CO_2/H_2O analyzer (LI-COR, Lincoln, USA). The gas analyzer was tilted $45°$ from the vertical and the sensor separation was about 30 cm. The measurement height of both sensors was 3.15 m above ground. EddyMeas was used for data acquisition here as well.

At 2 m height above ground, two PAR LITE quantum sensors facing up- and downward were attached to a CNR1 net radiometer (Kipp and Zonen, Delft, the Netherlands). Air temperature T_a and relative humidity rH were measured with a HMP 155 probe covered by a radiation shield and atmospheric pressure p was measured with a PTB 110 barometer at 1.5 m above ground (Vaisala, Helsinki, Finland). The meteorological parameters were logged on a CR1000 datalogger (Campbell Scientific, Logan, USA).

A third eddy covariance system consisting of an Gill R3-50 ultrasonic anemometer in combination with a LI-7500A open path CO_2/H_2O analyzer was used to test comparability of over- and understorey tower systems. For a period of one week each it was mounted on the overstorey and the understorey tower and measured in parallel. Both systems showed high Bravais–Pearson correlation coefficients of 0.78 to 0.91 as well as small normalized root mean squared errors of 0.01 to 0.06 for water and carbon fluxes in comparison with the portable eddy system.

2.5 Soil temperature and moisture

Soil temperature T_s and soil moisture θ were measured at open and tree-shaded locations between the two towers. T_s was measured with PT100 PRT temperature probes (Campbell Sci-

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entific, Logan, USA) in 2, 4, 8, 16, 30, and 60 cm depth, with two replicates at the open and two replicates at the shaded location. θ was measured with 10hs sensors (Decagon Devices, Inc., Washington, USA) at 5, 15, 30 and 60 cm depth, with four replicates at the open and four replicates at the shaded location. The meteorological parameters were logged on CR1000
5 dataloggers (Campbell Scientific, Logan, USA).

2.6 Data treatment

Eddy flux data were post-processed using EddySoft and Python 2.7. Half-hourly means were calculated by block-averaging the 20 Hz data, time lags between CO_2/H_2O signals and vertical wind velocity were determined via cross correlation analysis following Aubinet et al. (1999).
10 Whenever the cross correlation failed for the closed path analyzer signals of the overstorey tower, the dependency on rH was used to determine the lag for the H_2O signal according to Ibrom et al. (2007). High frequency losses were compensated with the use of inductances derived from co-spectral analysis (Eugster and Senn, 1995). The sectorial planar fit method was used for the coordinate rotation of wind vectors (Rebmann et al., 2012; Wilczak et al., 2001).
15 For both towers, the moisture and cross wind correction according to Schotanus et al. (1983) was applied and the WPL correction for flux density fluctuations was used for the CO_2/H_2O signals of the open path understorey sensor only (Leuning, 2007; Webb et al., 1980). The storage term of CO_2 was calculated after Hollinger et al. (1994) and added to the turbulent CO_2 flux.
20   For the purpose of quality control, flags were determined for every half-hourly flux value including the following tests: the 20 Hz data were scanned for exceeded physical limits, change rates and variances. The stationary test of Foken and Wichura (1996) was applied to the high frequency data based upon a 50 % deviation criterion. On a half-hourly basis, the integral turbulence characteristics (ITC) were calculated following Thomas and Foken (2002) with a 30 %
25 deviation criterion. For the understorey tower, the parametrisation of the ITC was recalculated according to the observations. A spike detection routine was used on the half-hourly data based on the absolute median deviation (Papale et al., 2006). All quality control tests were summed up in a simplified flag system referring to Mauder and Foken (2011).

The partitioning of the net CO_2 fluxes NEE into gross primary productivity GPP and ecosystem respiration R_{eco} followed Lasslop et al. (2010) and the flux gap-filling was made according to Reichstein et al. (2005). Gaps only filled up to a maximum gap length of 6 days.

The measured wind speed was used to calculate aerodynamic conductance $g_a = u_*^2/u$ with
the measured friction velocity u_*^2 and horizontal wind speed u. Leaf temperature is estimated using measured air temperature T_a and measured sensible heat flux H via $T_l = T_a + H/(g_a\rho_a c_p)$ with ρ_a being the density and c_p the heat capacity of the air.

T_s and θ were integrated over the respective depths and the replicates of each site (open and shaded) are averaged. To calculate ecosystem representative T_s and θ, the open and the shaded
site were weighted using time-dependent P_{gap}, modelled from the daily course of sun inclination angle and the view zenith angle distribution of P_{gap} (Piayda et al., 2014).

The soil heat flux G was calculated from the averaged T_s profiles. To estimate the energy balance closure of the towers, the storage terms due to changes in T_a and rH were added to the energy balance equation and plotted against the turbulent energy fluxes for daytime values with
global radiation $R_g > 20\,\mathrm{W\,m^{-2}}$ (Mauder et al., 2013; Foken, 2008; Twine et al., 2000). The ratio was used to correct sensible heat H, latent heat λE and evapotranspiration ET flux with the bowen ratio being preserved.

2.7 Photosynthesis and stomatal conductance modelling

The Farquhar model for photosynthesis (Farquhar et al., 1980) combined with the Leuning
model for stomatal conductance (Leuning, 1995) was used in a two-leaf scheme to model gross primary productivity and evapotranspiration GPP_o and ET_o measured at the overstorey tower for the summer months May to September of 2011 and 2012. The separation into sunlit and shaded leaves follows De Pury and Farquhar (1997) and could directly derived by measured leaf projection function and LAI from (Piayda et al., 2014). For model comparison, stomatal
conductance was modelled as well with the approach of Ball et al. (1987). The model was fitted to a 31 day long moving window of GPP_o and ET_o to gain stable median daily cycles. These were cropped to the time from sunrise to 15:00. Model fitting was done using a Nelder–Mead simplex algorithm (Nelder and Mead, 1965) with a higher order multi objective cost function

for GPP$_o$ and ET$_o$ according to Duckstein (1981) under varying apparent maximum carboxylation rate $V_{c,max}$ (no separate modelling of mesophyll conductance), assimilation sensitivity m, vapour pressure deficit sensitivity D_0 of stomatal conductance g_s and optimum temperature T_{opt} of maximum electron transport rate J_{max}. Three different T_{opt} descriptions were used for
5 model comparison. The uncertainty of inferred parameters was estimated using bootstrap. See Appendix A for detailed model equations.

3 Results and discussion

Ecosystem fluxes for the hydrological years 2011 and 2012 (October 2010 to September 2012) are discussed in the following. Flux time series are only compared when data availability is
10 given for both hydrological years, but not on an annual sum basis.

The dominant wind direction changes during the season. Absolute values of flux measurements of the overstorey tower are thus not directly comparable to the absolute values of the understorey tower due to changing footprint area and the heterogeneity of the ecosystem. However, comparisons of the intra-annual pattern of ecosystem fluxes between both towers and
15 inter-annual changes between both years 2011 and 2012 are possible and conducted in the following.

3.1 Meteorological and environmental conditions

Water scarcity is the most important factor for ecosystem productivity in savannah-type ecosystems (Pereira et al., 2007). Drought severity and impact on vegetation depends on timing and
20 amount of precipitation P (Peñuelas et al., 2004). The hydrological years 2011 and 2012 mark, therefore, exceptional years on the Iberian Peninsula. Precipitation P was 34 % higher in 2011 and 39 % lower in 2012 compared to the long term average precipitation of about 680 mm (Jongen et al., 2013a) (Fig. 2a and b). In particular, the winter 2011/2012 was very dry over Soutwestern Iberia, with only about 20 % of the long term precipitation (Santos et al., 2013;
25 Trigo et al., 2013). 2012 was the second driest year since 1950. The last negative P anomaly of

comparable severity occurred in the drought year 2004/2005 (Paredes et al., 2006; Santos et al., 2007).

The intra-annual pattern of precipitation has especially changed in 2012. Total annual reduction to the previous year 2011 was 495 mm of which 68 % occurred during a long drought event in winter and early spring (December–March). The beginning of autumn precipitation was also delayed by almost a month in 2012. Winter precipitation is the most important for replenishing the soil and ground water reservoirs after the summer drought. But the winter precipitation period was shortened and interrupted for about four months in the hydrological year 2012. These phenomena, i.e. reduced annual P, additional winter/spring drought, and prolonged summer drought, are characteristic for observed P extremes in the last decades (e.g. Guerreiro et al., 2013; Paredes et al., 2006).

We address first the question of changes in environmental and climatic components between both years, which may have caused significant changes in ecosystem functioning. The distributions of most relevant climatic and environmental variables for plant functioning are therefore analysed in quantile-quantile (Q-Q) plots in Fig. 3. Air temperature T_a (Fig. 3a) and incoming photosynthetically active radiation PAR (data not shown) showed only minor changes between the two years so that plant available energy in both years was comparably high. In contrast, moisture related variables showed large deviations from the on-to-one line in the Q-Q plots (Fig. 3b–d). All precipitation P intensities of 2012 stayed well below the ones in 2011 (Fig. 3b). Air vapour pressure deficit vpd was considerably increased at high deficits in 2012 compared to 2011 (Fig. 3c). This comes from lower absolute humidity because air temperature T_a did not change substantially. Possible reasons are either diminished local ecosystem evopotranspiration ET due to diminished soil moisture (Fig. 3d) and plant transpiration or less air moisture input by incoming air masses from the ocean. Soil moisture was significantly decreased in 2012 compared to 2011 (Fig. 3d), which is exhibited especially in the missing medium soil moisture amounts. The contribution of local ET to the observed reduction in vpd was estimated by approximating the average contribution of local ET to absolute humidity of the atmospheric boundary layer. 50 % of absolute humidity reduction in 2012 compared to 2011 could be explained by a reduced contribution of local ET. This illustrates the strong influence of ET on

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local hydrological conditions and the reinforcement of plant drought stress due to increased vpd.

The ecosystem, therefore, faced increased transpirational demand from higher atmospheric vpd combined with strongly decreased soil water availability, which resulted in high water stress 5 for the trees but also for understorey vegetation in 2012 compared to 2011. In the following, the effect of decreased water availability on the ecosystem water budget is discussed.

3.2 Drought influence on ecosystem water balance

Evapotranspiration ET is the major component of total water efflux in Mediterranean ecosystems on annual basis (Huxman et al., 2005). A comparably small amount of precipitation is left 10 for ground water recharge and runoff. ET usually peaks in May before the onset of drought in the beginning of June in Mediterranean ecosystems (Vargas et al., 2013). But ecosystem evapotranspiration measured here at the overstorey tower ET_o (Fig. 4b) peaked within the summer drought period in June to July in 2011. This behaviour is typical for *montado* ecosystems with ground water access of the trees (Paco et al., 2009; Pereira et al., 2007; David et al., 2007, 2004). 15 ET_o showed a slight peak shift towards spring in 2012 and was diminished by 26 % compared to 2011. The major decrease occurred in late spring and summer (March to September) although the major reduction in precipitation P occurred in winter and early spring (December to March) (Fig. 2b). When atmospheric demand (Fig. 4a) and energy input into the system increased in spring 2012, the *Q. suber* trees were not able to maintain transpiration T as high as in 2011. This 20 indicates, that most likely the deep soil and/or ground water reservoirs were not refilled after summer 2011 due to the dry winter as displayed by soil moisture observations in 60 cm depth (Fig. 5b). However, the strongly diminished transpiration T led to a non-significant increase in maximum daily leaf temperature $T_{l,max}$ of only 1.7 °C during the summer period of 2012. The small influence of the reduced transpirational cooling on leaf temperature could be attributed to 25 the high aerodynamic conductance g_a in this open canopy, enabling a comparably high energy transport by sensible heat.

Evapotranspiration measured at the understorey tower ET_u peaked in March to April 2011 before the beginning of the summer die back of the understorey vegetation, which is rather

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typical in savannah-type ecosystems (e.g. Paco et al., 2009). ET_o was reduced, though, by 38 % in 2012 compared to 2011. The peak was slightly delayed under drought conditions in 2012, in contrast to ecosystem ET_o. The late onset of autumn precipitation P in October and additionally the missing recharge of upper soil moisture in winter (Fig. 5a) had an immediate impact on

5 ET_u inhibiting plant growth and herbaceous transpiration (see Sect. 3.3). ET_o, on the other hand, was influenced from March onwards only. The precipitation events occurring in April and March 2012 (Fig. 2a) were not able to increase ET_u up to the level of 2011 even though the atmospheric demand was slightly higher in 2012 (Fig. 3c). This can be explained on the one hand by very low soil moistures up to 20 cm depth in October and from March onwards

10 (Fig. 5a), which prevented soil evaporation, and on the other hand, by the strong reduction in plant cover leading to a reduced contribution of herbaceous plant transpiration to ET_u (see Sect. 3.3).

Precipitation effectiveness ET_o/P indicates the amount of total precipitation P used for actual ecosystem evapotranspiration ET_o. $ET_o/P = 86\%$ in 2011, which is high but comparable

15 to other studies (Sala and Tenhunen, 1996; Piñol et al., 1991). However, the strong reduction of ecosystem evapotranspiration ET_o of 26 % in 2012 was vastly exceeded by the reduction in precipitation P of 54 %. This confirms recent results from Besson et al. (2014) showing a certain resilience of *Q. suber* tree transpiration to annual water shortages. This led to ET_o/P of 122 % in 2012, which is to our knowledge, the highest value reported for *montado* ecosystems so far.

20 Hence more water evaporated from the soil and was transpired by the trees than was brought into the ecosystem by precipitation. This was possible due to the deep soil or ground water access of the trees maintaining a relatively high transpiration rate throughout the summer. But it left also no water for ground water replenishment or runoff generation (cf. Sala and Tenhunen, 1996).

25 Ecosytem productivity was markedly changed in 2012 due to the strong alterations in the water balance, which will be discussed in the following.

3.3 Understorey growth inhibition

The local understorey vegetation consists of native annual grasses and herbs (Jongen et al., 2013b; Dubbert et al., 2014a). The species are adapted to regular summer droughts by seed formation in spring before the onset of the summer droughts. They survive the dry periods
5 as seeds and germinate again at the onset of autumn precipitation. Species abundance during spring depends thus on the amount of previous winter precipitation (Figueroa and Davy, 1991). The timing of the first autumn rains and rewetting of the soils is thereby of great importance for germination success, number of individuals and plant productivity (Jongen et al., 2013c; de Dios Miranda et al., 2009).

10 The understorey showed a typical annual cycle of gross primary productivity GPP_u in 2011 (Fig. 6c) for savannah-type understorey vegetation with the growth onset at the end of October (Ma et al., 2007). Carbon uptake peaked in February to March and ended with the complete die back at the end of May. GPP_u was strongly reduced by 53 % in 2012 compared to 2011. A small GPP_u peak occurred along with precipitation P in April and May (Fig. 2). The reduction of
15 GPP_u can be explained by the very low soil moisture $\theta_{20\,cm}$ during October 2011 (Fig. 5a) due to the late onset of autumn precipitation P inhibiting seed germination. $\theta_{20\,cm}$ was lower during the entire year 2012 in comparison to 2011, particularly over the main growth period of the understorey vegetation from January to April. It was up to 52 % lower in March 2012, inhibiting further growth during winter/spring and probably caused higher seedling mortality.
20 Dubbert et al. (2014a) reported a maximum understorey vegetation cover in this ecosystem of about 80 % for 2011 that was reduced to about 25 % during the same period in 2012 (data for 2012 not shown). Similar effects on seedling germination and mortality were shown by others (Peco and Espigares, 1994; Espigares and Peco, 1995, 1993) under artificial rainfall treatments and could be shown here under natural conditions.

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3.4 Ecosystem productivity reduction

Most European, Mediterranean savannah-like ecosystems show a severe drop in gross primary productivity during summer (June to August) framed by a major peak in early spring (April to May) and a minor peak at the onset of autumn rain (Baldocchi et al., 2009).

In our ecosystem, gross primary productivity measured at the overstorey tower GPP_o showed an in this respect atypical annual behaviour with a very late peak during June–July (Fig. 6b). The amount of carbon gained was also higher compared to other Mediterranean evergreen woodlands in particular during the drought period in summer (Baldocchi et al., 2009; Ma et al., 2007). This annual pattern is rather characteristic for temperate than semi-arid ecosystems. The *Q. suber* trees must have deep soil water or ground water access in "regular" hydrological years, as shown in Sect. 3.2. This enabled them to maintain high productivity during the summer period despite high atmospheric water demand and low topsoil soil moisture.

Gross primary productivity GPP_o showed almost the same seasonal timing in 2012 compared to 2011 but was strongly reduced by 28 % (Fig. 6b). The major reduction took place in spring and summer (April to September) together with the reduction in evapotranspiration ET_o (Fig. 4b) when atmospheric demand was high and the emptied deep soil and ground water reservoirs were unable to supply sufficient water (see Sect. 3.2) in 2012 compared to a regular year. This confirms the results of Pereira et al. (2007) who showed that drought effects on sclerophyllous trees became apparent only after the depletion of the deep soil and ground water reserves. Despite a delayed bud burst in spring, a significant difference in leaf area index LAI could not be observed during the summer period by long-term leaf area index observations of Costa e Silva et al. (2014). Reductions in GPP_o and ET_o can hence be attributed solely to leaf physiological responses discussed in Sect. 3.6.

3.5 Net ecosystem carbon exchange reduction

The net ecosystem carbon flux NEE_o was strongly reduced by 38 % in the drought year 2012 compared to the wet year 2011 (Fig. 6a). The ecosystem was, however, a carbon sink in both years on annual basis even though reductions in precipitation P (Fig. 2) and gross primary pro-

ductivity GPP$_o$ (Fig. 6b) were severe in 2012. Pereira et al. (2007) found a similar behaviour in another montado ecosystems in Portugal. It still demonstrates here once more that precipitation is the dominant environmental variable for inter-annual change of NEE in semi-arid ecosystems even in ecosystems with ground water access. The reduction in carbon sink strength took place

5 mainly in summer (May to September) along with the strongest reduction in gross primary productivity GPP$_o$ (Fig. 6b) caused by the lack of water availability for the *Q. suber* trees (cf. Sect. 3.2). GPP$_o$ exhibited a reduction of 28 % in 2012 compared to 2011 while R_{eco} showed only a reduction of 16 %. R_{eco} is mainly reduced in summer (July to September, data not shown) where soil moisture in the upper soil layer $\theta_{20\,cm}$ is low in both years due to the regular summer

10 drought (Fig. 5a) and inter-annual differences are small. NEE$_o$ is therefore much more driven by GPP$_o$ than by R_{eco} in the ecosystem studied here. Reichstein et al. (2002) hypothesized that gross primary productivity GPP$_o$ should be less affected by drought than ecosystem respiration R_{eco} in ecosystems with large subsoil water reservoirs because R_{eco} depends on soil moisture and soil temperature. But it is hot and dry almost every summer in the Mediterranean so that

15 the lack of soil moisture in the upper soil inhibits soil respiration during summer and reduces largely the contribution of R_{eco} to inter-annual variations (e.g. Unger et al., 2009). This could also be the reason for the controversial findings of Valentini et al. (2000) that R_{eco} becomes less important for variations of NEE with decreasing latitude on the Northern Hemisphere. It is, however, clear that vastly different GPP$_o$ and R_{eco} cannot be sustained over long time; R_{eco}

20 base rates have to adapt in the long-term.

3.6 Drought impact on tree physiology

Multiple physiological mechanisms of plant responses to drought, excessive irradiance and high temperatures have been recognized on the leaf-level such as reduction of exposed leaf area or leaf shedding (Beyschlag et al., 1986; Sala and Tenhunen, 1996; Tenhunen et al., 1985, 1990;

25 Werner et al., 2001). To avoid hydraulic failure or photodamage, carboxylation efficiency $V_{c,max}$ and/or stomatal conductance g_s can be down-regulated restricting water loss and carbon assimilation and hence increasing photorespiration as a protective electron sink (Farquhar and Sharkey, 1982; Cowan, 1977; Tenhunen et al., 1987; Matthews and Boyer, 1984; Ehleringer

and Cook, 1984). The photosynthesis apparatus can further adapt to altered environmental conditions by changing the rigidity of the membranes altering thus the temperature optimum of, for example, electron transport rates (Kattge and Knorr, 2007; von Caemmerer, 2000; Berry and Björkman, 1980).

There are different levels of complexity on how to describe photosynthesis in the literature. We focus here on Farquhar-type models of photosynthesis (Farquhar et al., 1980). There are three mechanisms that differ strongly between the different models of vegetation-atmosphere exchange: (1) the reactions to soil water stress, (2) the formulations used for the description of stomatal conductance and (3) the reactions to heat stress. How plants react to water stress is probably the least well-described mechanism in photosynthesis models. The different ecosystem and land surface models differ strongly on how they react to soil water stress. The widely used community land model CLM, for example, reduces apparent carboxylation efficiency $V_{c,max}$ under drought (Oleson et al., 2010), which then indirectly reduces stomatal conductance as well, while the land surface scheme ORCHIDEE down-regulates stomatal conductance directly leaving $V_{c,max}$ unchanged (Krinner et al., 2005; Verbeeck et al., 2011).

There is also a great variety of descriptions of stomatal conductance (cf. Damour et al., 2010). Most large-scale models apply the formulation of Ball et al. (1987) though, the so called Ball–Berry or sometimes Ball–Woodrow–Berry model (cf. Eq. A12). Leuning (1995) argued that stomata under controlled conditions react to vapour pressure deficit rather then relative humidity and proposed and alternate form of the Ball–Berry model (cf. Eq. A11), the so-called Leuning model or sometimes Ball–Berry–Leuning formulation. But the photosynthesis models also differ in their reactions to heat stress. It is still discussed in the physiological literature if heat is only changing thylakoid membrane properties limiting electron transport (von Caemmerer, 2000; June et al., 2004) or if heat is also inhibiting enzyme activities, i.e. also carboxylation rates (Medlyn et al., 2002; Kattge and Knorr, 2007).

Gross primary productivity GPP_o and evapotranspiration ET_o were modelled here for the period May to September to investigate drought impact on *Q. suber* tree physiology on the ecosystem scale and further test different model formulations described above. Differences be-

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tween both years were most prominent during May to September, understorey vegetation had already vanished and soil evaporation was low compared to tree transpiration (Fig. 4c).

The following discussion includes (1) whether a down-regulation of only carboxylation efficiency $V_{c,max}$ or only stomatal sensitivity m is sufficient to describe the ecosystem behaviour in both years. (2) It evaluates the performance of the two prominent stomatal conductance formulations. (3) It compares different representations of photosynthetic temperature dependencies. (4) It discusses possible reasons for down-regulation of stomatal conductance g_s and carboxlation $V_{c,max}$, (5) disentangling the causes for down-regulation of stomatal conductance g_s. (6) The unexpected change in optimal temperature T_{opt} between the two years is discussed.

First, GPP_o and ET_o were modelled with either allowing the model to adapt each day only $V_{c,max}$ or only the slope m of the Ball–Berry stomatal conductance formulation (Ball et al., 1987) (Eq. A11). The model was not able to reproduce the observations with sufficient performance in both cases, especially in 2012. The goodness of fit to the observed data steadily decreased with ongoing summer drought. GPP_o and ET_o could be successfully modelled if both, $V_{c,max}$ and m were allowed to adapt daily to changing environmental conditions, leading to constantly high Nash–Sutcliffe model efficiencies of $\overline{\varepsilon_{GPP_o}} = 0.81$ and $\overline{\varepsilon_{ET_o}} = 0.89$ for 2011 and $\overline{\varepsilon_{GPP_o}} = 0.80$ and $\overline{\varepsilon_{ET_o}} = 0.76$ for 2012.

Second, the same model calibration experiment was performed with the Leuning model of stomatal conductance (Leuning, 1995) (Eq. A11). The Leuning model has, however, an additional model parameter D_0 which describes the sensitivity of the stomata to changes in vapour pressure deficit vpd. The Leuning model showed comparable high model performances to the Ball–Berry model in both years. When the Leuning model was used in earlier studies (e.g. Wang and Leuning, 1998), D_0 was fixed to a constant value. This implies that stomatal conductance sensitivity to vpd needs to change always similar to the sensitivity to assimilation. Model performance decreased considerably if D_0 was fixed here. This is because m and D_0 are highly correlated in the Leuning model (cf. Fig. 7b and d). This strict coupling is likely incorrect here since daily maximum vpd during the summer drought period was not significantly different between both years (only 1.3 hPa increase on average) but a strong decrease in $V_{c,max}$ could be observed (see below). Consequently, a decrease in model performance occurred, when D_0 was

set constant. Enabling the *Q. suber* trees to regulate stomatal response to vpd and assimilation A separately was necessary to explain observed GPP_o and ET_o.

The two first points illustrate that the plants needed to regulate their potency of possible carbon assimilation but wanted to increase how swift stomata react to changes. The reduction in maximum carboxylation rate $V_{c,max}$, though, was about 43 % while the increase in the slope m was about 9 % or 29 % whether calculation followed Ball et al. (1987) or Leuning (1995), respectively. The increase in m is not significant when the bootstrapped uncertainty is considered. Still, a significant, overall decrease in stomatal conductance g_s of about 37 % was observed.

Third, the temperature dependency of photosynthetic activity has generally been attributed to two different processes in previous publications. Medlyn et al. (2002) and Kattge and Knorr (2007) described the temperature dependency of both, maximum carboxylation rate $V_{c,max}$ of the Rubisco enzyme and maximum electron transport rate J_{max} by a peaked function, according to Johnson et al. (1942) (Eq. A7). An increase in enzyme activity with temperature is followed by a decrease above an optimum temperature T_{opt} due to enzyme deactivation (Case 1). Von Caemmerer (2000), among others, attributed possible decrease of activity of the photosynthetic apparatus at high temperatures rather to thylakoid membrane properties only, limiting electron transport, thus changing with leaf temperature. So only J_{max} is down-regulated above an optimum temperature T_{opt} (Eq. A7), but $V_{c,max}$ increases monotonically with a typical Arrhenius-type function (Eq. A6, Case 2). This was simplified by June et al. (2004) using a gaussian temperature dependency instead of the original formulation (Eq. A9, Case 3). Here all cases showed comparable model performances and no apparent differences in GPP_o and ET_o could be noticed. Thus, neither Case 1 nor Case 2 could be falsified here. Case 1 to case 3, however, show a decreasing demand for parametrization (Case 1: 6, Case 2: 4, and Case 3: 3 parameters). Despite the entropy factors of carboxylation ΔS_V and electron transport ΔS_J (Case 1 and Case 2) and optimum temperature T_{opt} (Case 3), all parameters were fixed to literature values (Table 1). Case 3, although containing only one parameter for optimization like Case 2, showed a more robust computational performance with fastest optimization by the Nelder–Mead algorithm (Nelder and Mead, 1965) among all cases.

Fourth, multiple reasons for down-regulation of photosynthesis under drought conditions are known, ranging from damage of involved enzymes due to high leaf temperatures, inhibition of the photosynthetic apparatus to avoid excess energy in the leaves, to insufficient availability of nitrogen inside the leaves (Tenhunen et al., 1987; Werner et al., 1999). But protection of the photosynthetic apparatus during environmental stress comes at the cost of reduced carbon sequestration (Tenhunen et al., 1990; Werner et al., 1999; Werner and Correia, 1996). Excessive radiation and high temperatures provide the risk of photoinhibition and photodamage under reduced CO_2 supply due to stomatal closure and low water potentials (Werner et al., 2002). Stomatal conductance g_s was strongly reduced by 37 % in 2012 compared to 2011 (Fig. 7f) although differences in daily maximum vpd during the summer drought period were not significant (only 1.3 hPa increase on average) between both years (Fig. 4a). It is thus very likely that the trees suffered from depleted deep soil or groundwater reservoirs due to the missing recharge by winter precipitation, since upper soil water content values were comparable during summer (Fig. 5a and b). This is an evidence that plant water status of *Q. suber* trees is strongly influenced by access to groundwater here and a down-regulation of transpiration occurred to avoid hydraulic failure (David et al., 2007; Oliveira et al., 1992). Although transpirational cooling of leaves should have been reduced due to limited stomatal conductance, the daily maximum leaf temperature $T_{l,max}$ increased by only 1.7 °C in 2012 compared to 2011 (Sect. 3.2) so that a temperature-based damage of enzymes relevant for photosynthesis is unlikely. The CO_2 influx into the leaves was, however, heavily reduced under the drought conditions in 2012. Energy utilization is thus limited while incoming photosynthetically active radiation PAR in 2012 was comparably high to 2011 (see Sect. 3.1). It is therefore very likely that the main cause for the *Q. suber* trees to down-regulate maximum carboxylation rate $V_{c,max}$ by 43 % (Fig. 7a) was to avoid over-excitation and photodamage (Demmig-Adams and Adams, 1992; Long et al., 1994; Werner et al., 2002). However, this effect may have been enforced by a decreased nitrogen availability during the leaf development phase in late spring caused by reduced soil water, and thus nitrogen solubility in 2012 (Fig. 5a and b) potentially changing leaf nitrogen status and permanently reducing photosynthetic capacity in 2012 compared to 2011 (Vaz et al., 2010). A possible indication for a permanent reduction of $V_{c,max}$ is that g_s tends to converge to the same value at

the end of the drought period in both years (Fig. 7f) so that leaf internal CO_2 availability should have approached comparable values as well. $V_{c,max}$ remained, however, down-regulated permanently. A simultaneous reduction of $V_{c,max}$ by 37 % (Fig. 7a) and an increase of m (9 % or 29 % whether g_s was calculated following Ball et al. (1987) or Leuning (1995), Fig. 7b and c) was observed. In case of a drought spell like 2012, the *Q. suber* trees responded with both, stomatal limitation as well as down-regulation of assimilation strongly altering entire ecosystem functioning, which was observed in different semi-arid ecosystems before (Reichstein et al., 2003; Egea et al., 2011; Zhou et al., 2013).

Fifth, the use of the Leuning (1995) model with variable D_0 allowed to disentangle the different impacts on g_s. Intra-annually, stomatal conductance showed a much stronger sensitivity to vpd (Fig. 7d) than to variations in assimilation (Fig. 7e). Between both years, $m/(1+(\overline{\text{vpd}}/D_0))$ increased only slightly by 10 % as a consequence of a slightly stronger reduction in $V_{c,max}$ than in g_s (43 % and 37 %, respectively). This displays the strong resilience of sclerophyllous tree species like *Q. suber* to drought, maintaining a water use efficiency comparable to regular years (Zhou et al., 2013). The impact of vpd on g_s was, however, weakened in 2012 (reduction of D_0 by 37 %, not significant) since g_s was generally reduced at comparable vpd. m compensated fluctuations in D_0 (Fig. 7b and d) to yield the observed robustness to assimilation. The observed high intra-annual robustness indicates that these Mediterranean species are adapted to maintain a stable operational point (Werner and Máguas, 2010).

Sixth, all three model descriptions (Case 1–3) showed a decrease in the optimum temperature of photosynthesis T_{opt} by 4–8 °C from 2011 to 2012 (Fig. 7g). Leaf renewal in 2012 occurred under strong drought conditions due to the additional winter drought and under increased temperatures due to the bud burst occurring more than one month later than in 2011 Costa e Silva et al. (2014). So carbon uptake in 2012 was further weakened due to a higher susceptibility of the photosynthesis apparatus to high temperatures in addition to the already discussed reduction of carboxylation efficiency $V_{c,max}$ by 43 %. Kattge and Knorr (2007) and von Caemmerer (2000), among others, showed for different plant species the opposite trend of increasing T_{opt} with increasing growth temperature. A possible explanation is that not only growth tempera-

ture but also nutrient availability and plant water status have changed strongly here affecting thylakoid membrane properties more than growth temperature.

In summary, the *Q. suber* trees responded to the drought year 2012 with a down-regulation of carboxylation efficiency and a decreased optimal temperature of photosynthesis. They coun-
teracted this reduced carbon sequestration with a better responsiveness of the stomata. These plant responses were caused neither by a higher vapour pressure deficit nor by leaf temperatures nor by a depletion of upper soil moisture. But they were most probably triggered by a strong depletion of deep soil or ground water due to the additional winter drought.

The combined model of photosynthesis and stomatal conductance was unable to reproduce
the observed carbon assimilation and evapotranspiration if only one reaction was considered, i.e. either in the photosynthetic apparatus or in stomatal conductance. It needed to adapt parameters in both sub-modules, i.e. a strong reduction in carboxylation efficiency and a smaller increase in stomatal sensitivity. Earlier model-data approaches had shown that combined photosynthesis-stomatal conductance models need to adapt both parts in times of drought but they always pre-
dicted decreases in carboxylation efficiency and stomatal sensitivity. However, the modelling performed here could not distinguish between different model formulations found in the liter-ature, i.e. the stomatal conductance formulations of Ball–Berry vs. Leuning and the different formulations of optimal photosynthetic temperatures.

3.7 Future development

It is expected that the trend of decreasing total annual precipitation and alteration of precipita-tion patterns on the Iberian Peninsula, namely occurrences of additional winter/spring droughts, will continue with proceeding climate change (Bussotti et al., 2013; Guerreiro et al., 2013; Hulme et al., 1999). Such severe drought periods might occur at higher frequency (Field et al., 2012; Heimann and Reichstein, 2008; Granier et al., 2007; Miranda et al., 2002) thereby af-
fecting the ecosystem water balance and productivity (Chaves et al., 2002; Fischer et al., 2002). If precipitation patterns similar to 2012 will occur more often then a sustainable depletion of local ground water reservoirs as well as water storage basins might be expected. This will affect strongly local agriculture that relies on ground water for the deep-rooted cork-oak trees and

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otherwise uses irrigation water from storage basins. The soil seed bank of native understorey plants may also deplete on the long term due to a shorter life cycle and reduced seed formation (Jongen et al., 2013c; Peñuelas et al., 2002, 2004; Gordo and Sanz, 2005). A shift of species composition is likely de Dios Miranda et al. (2009) but could not be observed in this ecosystem in a study by Dubbert et al. (2014a, 2012 data not shown) during the drought year 2012 itself. However, some effects such as tree mortality may only be evident in the long term after multiple, consecutive drought years (David et al., 2004; Bussotti et al., 2013).

4 Conclusions

We reported on the ecosystem fluxes of a savannah-type cork oak woodland under extreme hydrological conditions and altered precipitation P pattern. We analysed the effects of drought in the year 2012 compared to the wet year 2011 on evapotranspiration and gross primary productivity of a *montado* ecosystem and its overstorey and understorey components. We additionally analyzed physiological reactions of the *Q. suber* trees.

We conclude the following results: (1) the precipitation effectiveness ET_o/P increased up to 122 % in the dry year 2012 possible due to the ground water access of *Q. suber* trees leaving no water for ground water replenishing and runoff generation. If trends of decreasing annual P continue, sustainable effects on local ground water reservoirs and storage basins may be expected. (2) The understorey gross primary productivity GPP_u and the overstorey gross primary productivity GPP_o were reduced by 53 % and 28 %, respectively, in 2012 compared to 2011 due to a late onset of 2011 autumn rains and an additional severe winter/spring drought. Long term changes in understorey species composition and tree productivity are likely if prolonged summer droughts and additional winter/spring droughts become more frequent. (3) A combined photosynthesis and stomatal conductance model worked best if it was able to adapt the apparent maximum carboxylation rate $V_{c,max}$ and the stomatal conductance parameters simultaneously. The slope m of the stomatal conductance model had to be increased to compensate partly for the strong decrease in carboxylation rate. The model adjusted also the sensitivity of the stomata D_0 to vapour pressure deficit vpd in the Leuning model because both stomatal parameters, m

and D_0 are strongly correlated. The model performance was similar to the Ball–Berry approach. (4) The combined photosynthesis and stomatal conductance model also adjusted the optimum temperature of electron transport T_{opt} to lower values. This decreases carbon sequestration under higher temperatures but makes the photosynthetic apparatus also more vulnerable to heat stress in dry years. (5) The ecosystem was a carbon sink in both years with a 38 % reduced sink strength in the dry year 2012 compared to 2011. Gross primary productivity GPP was thereby a much stronger driver than ecosystem respiration R_{eco} of the inter-annual variations of the carbon sink.

Appendix A

Photosynthesis-stomatal conductance model

The entire canopy was separated in a sunlit and shaded part with the fraction of sunlit leaves as:

$$f_s = \frac{1 - \exp(-K\text{LAI})}{K\text{LAI}} \tag{A1}$$

where LAI $[\text{m}^2_{\text{leaf}} \text{m}^{-2}_{\text{ground}}]$ is leaf area index and $K = G(\beta)/\cos(\beta)$ with G being the angular dependent leaf projection function and β [°] being the sun zenith angle. The shaded fraction of the canopy equals $(1 - f_s)$. Carbon assimilation A $[\text{mol}(\text{CO}_2)\,\text{m}^{-2}\,\text{s}^{-1}]$ was modeled for each fraction with the Farquhar et al. (1980) model in the form of Knorr (2000) and enhanced by a smooth minimum function smin:

$$A = \text{smin}\{J_C; J_E; \eta\} - R_d \tag{A2}$$

with the carboxylation-limited rate J_C $[\text{mol}(\text{CO}_2)\,\text{m}^{-2}\,\text{s}^{-1}]$, the electron transport-limited rate J_E $[\text{mol}(\text{CO}_2)\,\text{m}^{-2}\,\text{s}^{-1}]$ and mitochondrial respiration R_d $[\text{mol}(\text{CO}_2)\,\text{m}^{-2}\,\text{s}^{-1}]$. The smoothing parameter η was set to 0.9. The Rubisco-limited rate J_C was described by:

$$J_C = V_{c,\max} \frac{C_i - \Gamma_\star}{C_i + K_C \left(1 + \left(\frac{O_i}{K_O}\right)\right)} \tag{A3}$$

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with maximum carboxylation rate $V_{c,max}$ [mol(CO_2) m^{-2} s^{-1}], CO_2 concentration inside the stomatal cavity C_i [mol(CO_2) mol(air)$^{-1}$], CO_2 compensation point $\Gamma_\star$ [mol(CO_2) mol(air)$^{-1}$] (set to leaf temperature $T_l \times 1.7 \times 10^{-6}$), Michaelis–Menten constants for CO_2 K_C [mol(CO_2) mol(air)$^{-1}$] and O_2 K_O [mol(O_2) mol(air)$^{-1}$], respectively. O_i [mol(O_2) mol(air)$^{-1}$] is the stomatal cav-

5 ity O_2 concentration taken as 21 %. The RuBP-limited CO_2 assimilation rate J_E was described by:

$$J_E = J \frac{C_i - \Gamma_\star}{4(C_i + 2\Gamma_\star)} \tag{A4}$$

with the rate of electron transport J [mol m^{-2} s^{-1}] as:

10 $$J = J_{max} \frac{\alpha PAR}{\sqrt{J_{max}^2 + \alpha^2 PAR^2}} \tag{A5}$$

with maximum electron transport rate J_{max} [mol(CO_2) m^{-2} s^{-1}], quantum yield of electron transport α and incident photosynthetically active photon flux density PAR [mol(quanta) m^{-2} s^{-1}]. The sunlit fraction of leaves f_s receives direct as well as diffuse incoming radiation where the

15 shaded fraction of leaves $(1 - f_s)$ only receives diffuse radiation. The temperature dependencies of K_C, K_O and R_d were modelled using Arrhenius functions:

$$f(T_l) = K_{25} \exp\left(\frac{E_K(T_l - 25)}{298R(T_l + 273)}\right) \tag{A6}$$

with the base rates K_{C25} [mol(CO_2) mol(air)$^{-1}$], K_{O25} [mol(O_2) mol(air)$^{-1}$], Rd$_{25}$ [mol(CO_2) m^{-2}]

20 at 25 °C and activation energies E_C, E_O, E_{Rd} [J mol^{-1}], respectively. T_l [°C] is leaf temperature and R [J mol^{-1} K^{-1}] is universal gas constant.

Temperature dependencies of $V_{c,max}$ and J_{max} were treated by three test cases with decreasing complexity and computational demand. Case 1 according to Medlyn et al. (2002) and Kattge and Knorr (2007): $V_{c,max}$ and J_{max} were both modelled using a modification of the Arrhenius

function (Eq. A6) showing a peak at optimum temperature followed by a decline with increasing T_l:

$$f(T_l) = K_{max25} \exp\left(\frac{E_K(T_l - 25)}{298R(T_l + 273)}\right) \frac{1 + \exp\left(\frac{298\Delta S_K - Hd_K}{298R}\right)}{1 + \exp\left(\frac{(T_l + 273)\Delta S_K - Hd_K}{(T_l + 273)R}\right)} \tag{A7}$$

with base rates $V_{c,max25}$ and J_{max25} at 25 °C, respectively. ΔS_V and ΔS_J $[\mathrm{J\,mol^{-1}\,K^{-1}}]$ are the entropy factors and Hd_V and Hd_J $[\mathrm{J\,mol^{-1}}]$ are the deactivation energies of $V_{c,max}$ and J_{max}, respectively. Case 2 according to von Caemmerer (2000): only the temperature dependency of J_{max} was modelled with the peaked function (Eq. A7), but $V_{c,max}$ was modelled with the simple Arrhenius function (Eq. A6). Case 3 according to June et al. (2004): $V_{c,max}$ was modelled with the simple Arrhenius function but J_{max} was modelled with a simple gaussian temperature dependency:

$$\begin{aligned} J_{max} &= J_{opt} \exp\left(-\frac{(T_l - T_{opt})^2}{\Omega^2}\right) \\ &= J_{max25} \exp\left(\frac{(25 - T_{opt})^2 - (T_l - T_{opt})^2}{\Omega^2}\right) \end{aligned} \tag{A8}$$

with optimum temperature T_{opt} [°C] and the empirical parameter $\Omega = 18$ °C.

Leaf surface CO_2 concentration C_s $[\mathrm{mol(CO_2)\,mol(air)^{-1}}]$ and H_2O concentration W_s $[\mathrm{mol(H_2O)\,mol(air)^{-1}}]$ were calculated via:

$$C_s = C_a - A\left(\frac{1}{g_a} + \frac{1.3}{g_b}\right) \tag{A9}$$

$$W_s = W_a - ET_{mod}\left(\frac{1}{g_a} + \frac{1}{g_b}\right) \tag{A10}$$

with the atmospheric CO_2 concentration C_a $[\mathrm{mol(CO_2)\,mol(air)^{-1}}]$, aerodynamic conductance g_a $[\mathrm{mol(air)\,m^{-2}\,s^{-1}}]$, leaf boundary layer conductance g_b $[\mathrm{mol(air)\,m^{-2}\,s^{-1}}]$, atmospheric H_2O concentration W_a $[\mathrm{mol(H_2O)\,mol(air)^{-1}}]$, modelled transpiration ET_{mod} $[\mathrm{mol(H_2O)\,m^-}$

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and stomatal conductance for water vapour $g_{s,h}$ $[\text{mol}(H_2O)\,m^{-2}\,s^{-1}]$. g_a was measured (see section 2.6) and g_b was estimated with the approach of Bonan (2002) via $g_b = 200\sqrt{d/u}$ where d is the measured leaf size and u is the observed wind speed.

Stomatal conductance for water vapour $g_{s,h}$ was calculated with the formulation of Leuning (1995):

$$g_{s,h} = m\,\frac{A}{(C_s - \Gamma_\star)\left(1 + \frac{W_i - W_s}{D_0}\right)} + b \tag{A11}$$

with the slope m $[\text{mol}(H_2O)\,\text{mol}(\text{air})^{-1}]$, the sensitivity parameter of vapour pressure deficit D_0 $[\text{mol}(H_2O)\,\text{mol}(\text{air})^{-1}]$ and the offset b $[\text{mol}(H_2O)\,m^{-2}\,s^{-1}]$. The description of Ball et al. (1987) was also tested:

$$g_{s,h} = m\,\frac{A\,\text{rH}_s}{C_s} + b \tag{A12}$$

with relative humidity at the leaf surface rH_s [–]. Total conductance for CO_2 $g_{c,c}$ and H_2O $g_{c,h}$ were then derived by:

$$g_{c,c} = \frac{1}{\left(\frac{1.56}{g_{s,h}} + \frac{1}{g_a} + \frac{1.3}{g_b}\right)} \tag{A13}$$

$$g_{c,h} = \frac{1}{\left(\frac{1}{g_{s,h}} + \frac{1}{g_a} + \frac{1}{g_b}\right)} \tag{A14}$$

CO_2 concentration in the stomatal cavity was thus calculated by:

$$C_i = C_a - \frac{A}{g_{c,c}} \tag{A15}$$

and modelled transpiration ET_{mod} $[\text{mol}(H_2O)\,m^{-2}\,s^{-1}]$ and gross primary productivity GPP_{mod} $[\text{mol}(CO_2)\,m^{-2}\,s^{-1}]$ for both, the sunlit and shaded fraction of the canopy, could be derived

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by:

$$\text{ET}_{\text{mod}} = g_{\text{c,h}} \left(W_i - W_a \right) \tag{A16}$$

$$\text{GPP}_{\text{mod}} = g_{\text{c,c}} \left(C_a - C_i \right) + R_d \tag{A17}$$

The optimum temperature T_{opt} of maximum electron transport rate J_{max} was calculated in Cases 1 and 2 according to von Caemmerer (2000):

$$T_{\text{opt}} = \frac{\text{Hd}_J}{\Delta S_J - R \log \left(\frac{E_{J_{\text{max}}}}{\text{Hd}_J - E_{J_{\text{max}}}} \right)} - 273.15 \tag{A18}$$

The entire calculation was iterated with initial values for $\text{ET}_{\text{mod}} = 0$, $g_{\text{s,h}} = 1$ and $C_i = 0.8\,C_a$, until a conversion of C_i was achieved for every time step. The modeled was ET_{mod} and GPP_{mod} of the sunlit and shaded part of the canopy were averaged using f_s and fitted against measured ET and GPP under variation of $V_{\text{c,max25}}$, ΔS_J, m and D_0. Constant relationships of $J_{\text{max25}} = 1.67\,V_{\text{c,max25}}$ and $\text{Rd}_{25} = 0.011\,V_{\text{c,max25}}$ were assumed (Medlyn et al., 2002; Kattge and Knorr, 2007). All other parameters used can be found in Table 1.

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Appendix B

Nomenclature.

A	$[\mathrm{mol\,m^{-2}\,s^{-1}}]$	carbon assimilation
b	$[\mathrm{mol\,H_2O\,m^{-2}\,s^{-1}}]$	Leuning model parameter (offset)
D_0	$[\mathrm{hPa}]$	Leuning model parameter (vpd sensitivity)
$\mathrm{ET_o}$	$[\mathrm{mm\,d^{-1}}]$	evapotranspiration measured at the overstorey tower
$\mathrm{ET_u}$	$[\mathrm{mm\,d^{-1}}]$	evapotranspiration measured at the understorey tower
$\mathrm{ET_o}/P$	$[\%]$	precipitation effectiveness
$\overline{\varepsilon_{\mathrm{GPP_o}}}$	$[-]$	average Nash–Suttcliff model efficiency for $\mathrm{GPP_o}$
$\overline{\varepsilon_{\mathrm{ET_o}}}$	$[-]$	average Nash–Suttcliff model efficiency for $\mathrm{ET_o}$
f_s	$[-]$	fraction of sunlit leaves
GPP	$[\mathrm{g\,C\,m^{-2}\,d^{-1}}]$	gross primary productivity
$\mathrm{GPP_o}$	$[\mathrm{g\,C\,m^{-2}\,d^{-1}}]$	gross primary productivity measured at the overstorey tower
$\mathrm{GPP_u}$	$[\mathrm{g\,C\,m^{-2}\,d^{-1}}]$	gross primary productivity measured at the understorey tower
$g_{s,h}$	$[\mathrm{mol\,H_2O\,m^{-2}\,s^{-1}}]$	stomatal conductance for water vapour
$g_{s,c}$	$[\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}]$	stomatal conductance for carbon
LAI	$[\mathrm{m^2_{leaf}\,m^{-2}_{ground}}]$	leaf area index
m	$[\mathrm{mol\,H_2O\,mol\,air^{-1}}]$	Leuning model parameter (slope)
NEE	$[\mathrm{g\,C\,m^{-2}\,d^{-1}}]$	net ecosystem carbon exchange
$\mathrm{NEE_o}$	$[\mathrm{g\,C\,m^{-2}\,d^{-1}}]$	net ecosystem carbon exchange measured at the overstorey tower
$\mathrm{NEE_u}$	$[\mathrm{g\,C\,m^{-2}\,d^{-1}}]$	understorey + soil net carbon exchange
P	$[\mathrm{mm}]$	precipitation
p	$[\mathrm{hPa}]$	atmospheric pressure
PAR	$[\mathrm{\mu mol\,m^{-2}\,s^{-1}}]$	photosynthetically active radiation
P_{gap}	$[-]$	tree canopy gap probability
R_{eco}	$[\mathrm{g\,C\,m^{-2}\,d^{-1}}]$	ecosystem respiration
rH	$[\%]$	relative air humidity
$\mathrm{rH_s}$	$[\%]$	relative air humidity at the leaf surface
θ	$[\%]$	soil moisture
T	$[\mathrm{mm\,d^{-1}}]$	transpiration
T_a	$[^\circ\mathrm{C}]$	air temperature
T_l	$[^\circ\mathrm{C}]$	leaf tempearture
$T_{l,\mathrm{max}}$	$[^\circ\mathrm{C}]$	maximum daily leaf tempearture
T_{opt}	$[^\circ\mathrm{C}]$	optimum temperature of electron transport
T_s	$[^\circ\mathrm{C}]$	soil temperature
$V_{c,\mathrm{max}}$	$[\mathrm{\mu mol\,m^{-2}\,s^{-1}}]$	apperent maximum carboxylation rate
vpd	$[\mathrm{hPa}]$	air vapour pressure deficit
$\mathrm{vpd_{max}}$	$[\mathrm{hPa}]$	maximum daily air vapour pressure deficit

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Table 1. Parameters used in the photosynthesis-stomatal conductance model. The offset parameter b was estimated first with an optimization on the entire data set and then set constant in following model runs.

| parameter	value	unit	source
α	0.28	[–]	(Beerling and Quick, 1995)
b	4300×10^{-6}	[mol(H$_2$O) m^{-2} s^{-1}]	site average
E_C	59356	[J mol^{-1}]	(Farquhar et al., 1980)
$E_{J_{max}}$	35870	[J mol^{-1}]	(Medlyn et al., 2002)
E_O	35948	[J mol^{-1}]	(Farquhar et al., 1980)
E_{Rd}	50967	[J mol^{-1}]	(Collatz et al., 1992)
$E_{V_{c,max}}$	58520	[J mol^{-1}]	(Farquhar et al., 1980)
Hd_J	220000	[J mol^{-1}]	(von Caemmerer, 2000)
Hd_V	200000	[J mol^{-1}]	(Medlyn et al., 2002)
K_{C25}	460×10^{-6}	[mol(CO$_2$) mol(air)$^{-1}$]	(Farquhar et al., 1980)
K_{O25}	0.33	[mol(O$_2$) mol(air)$^{-1}$]	(Farquhar et al., 1980)
O_i	0.21	[mol(O$_2$) mol(air)$^{-1}$]	(Farquhar et al., 1980)
Ω	18	[°C]	(June et al., 2004)
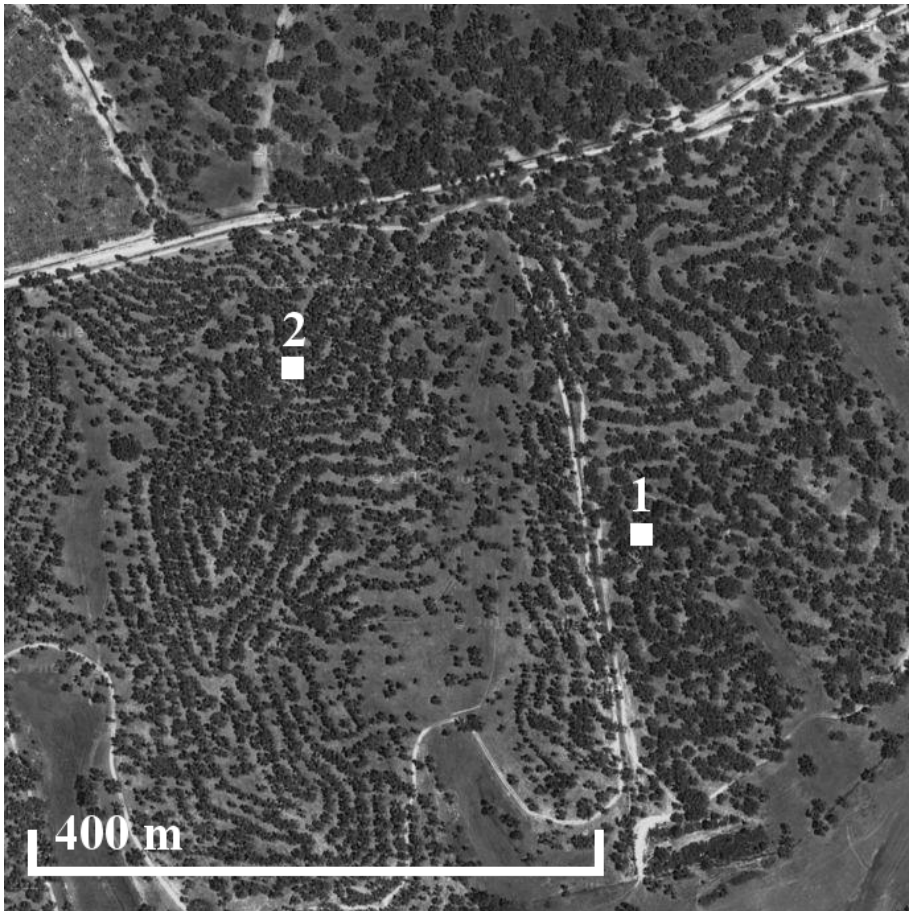
Fig. 1. Satellite image of the study site (©Google Maps, 2013). 1: position of the overstorey tower. 2: position of the understorey tower.
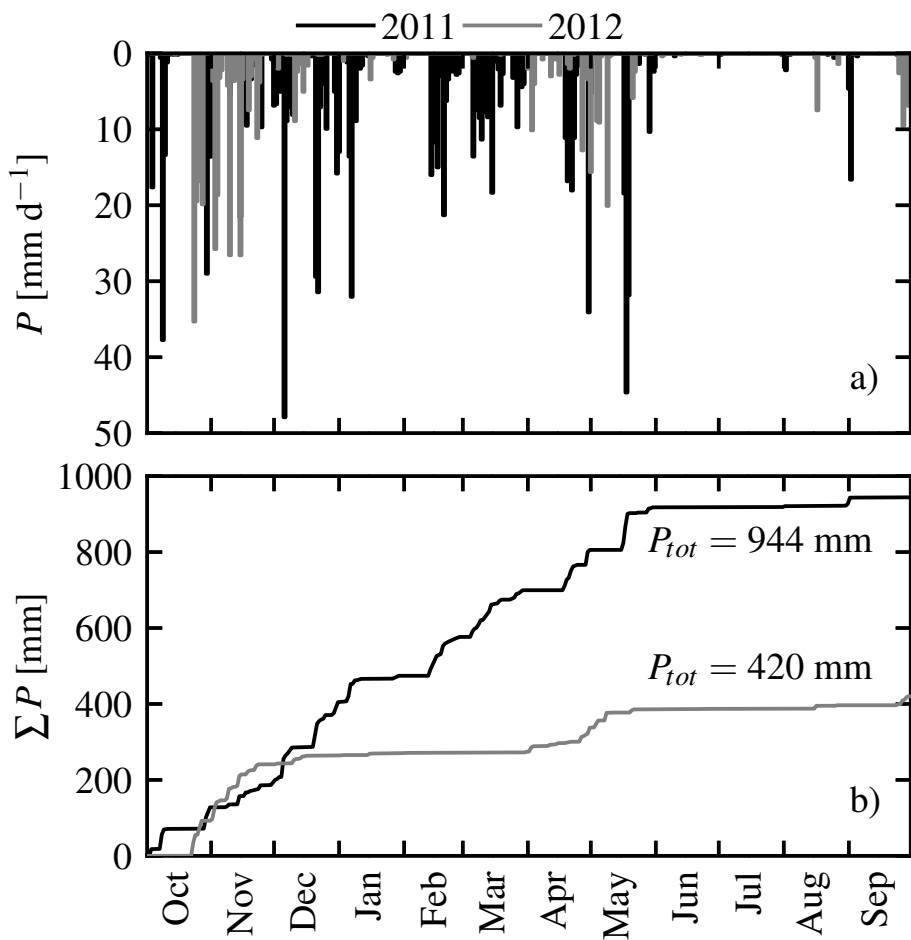
43

Fig. 2. (a) Daily sum of precipitation P for 2011 (black) and 2012 (grey). **(b)** Cumulative precipitation P for 2011 (black) and 2012 (grey) based on half hourly data.
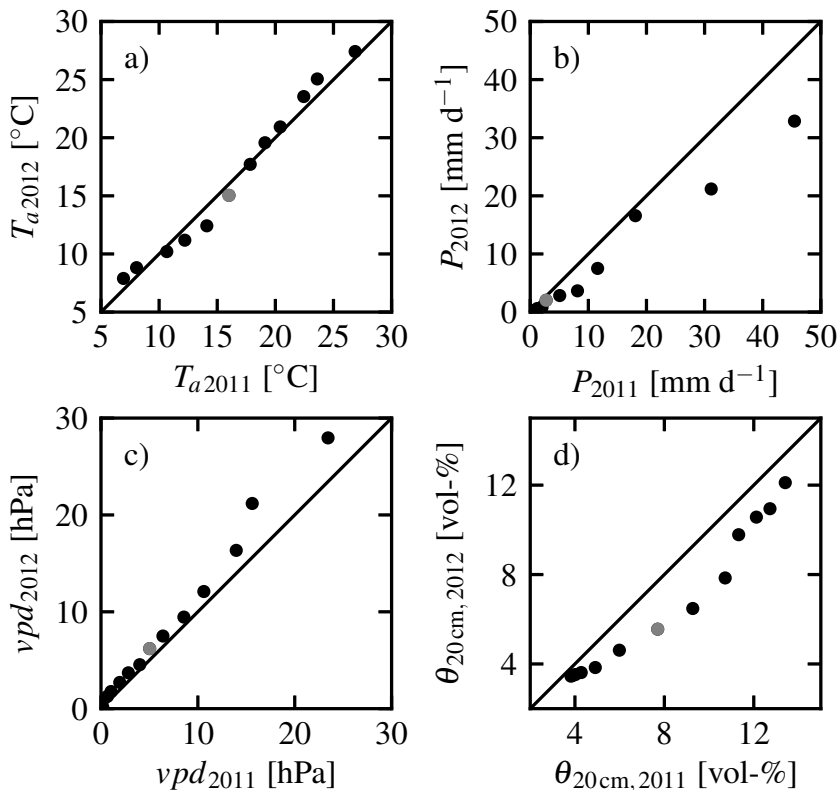
44

Fig. 3. Quantile-Quantile plot of important climate and environmental parameters for the years 2011 and 2012 based on daily averages. Black dots represent the 0.01, 0.05, 0.1, 0.2, 0.3, 0.4, 0.6, 0.7, 0.8, 0.9, 0.95, and 0.99 quantiles of the respective distribution. Grey dots represent the 0.5 quantile. **(a)** Air temperature T_a, **(b)** precipitation P, and **(c)** vapour pressure deficit of the air vpd, each measured at 20 m height above ground. **(d)** Soil moisture in the first 20 cm $\theta_{20\,cm}$ (root zone of understorey vegetation).
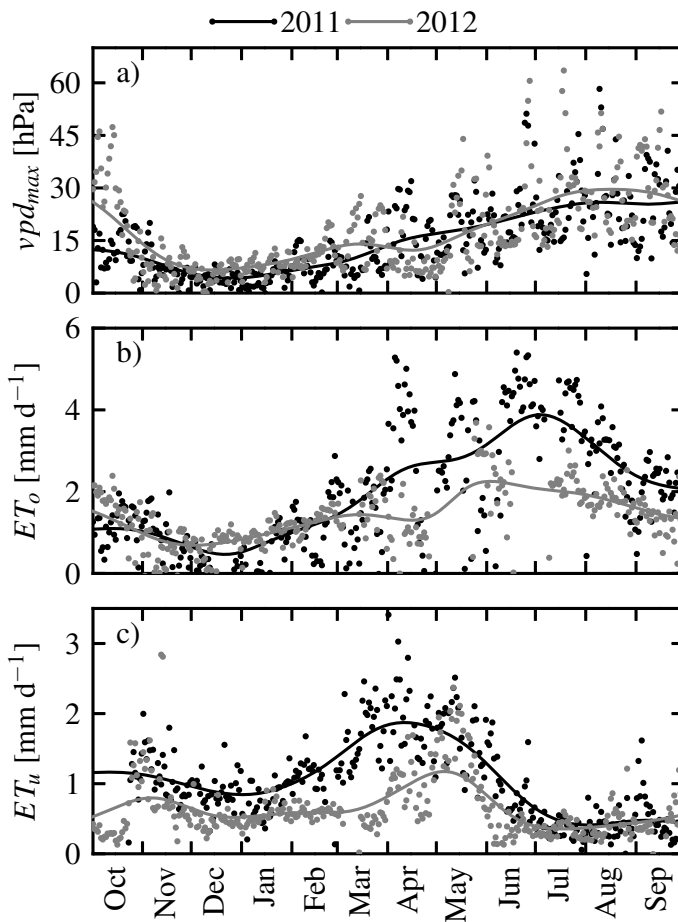
Fig. 4. (a) Maximum daily vapour pressure deficit vpd_{max}, **(b)** daily sum of ecosystem evapotranspiration ET_o and **(c)** daily sum of understorey transpiration + soil evaporation ET_u for 2011 (black) and 2012 (grey). Lines mark kernel regressions.
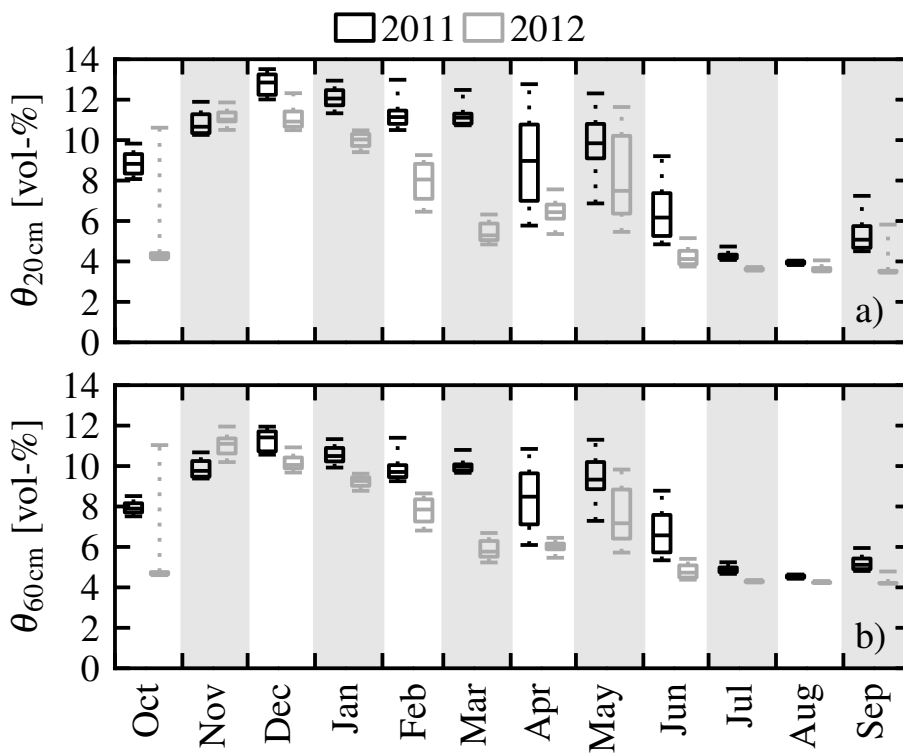
Fig. 5. Box plot of monthly volumetric soil moisture **(a)** down to 20 cm depth $\theta_{20\,cm}$ (root zone of understorey vegetation) and **(b)** down to 60 cm depth $\theta_{60\,cm}$ for the years 2011 (black) and 2012 (grey). Central line marks the median, box marks the 0.25 and 0.75 quantiles. Dashed lines mark the 0.05 and 0.95 quantiles. Data within a two day interval after a rain event were excluded.
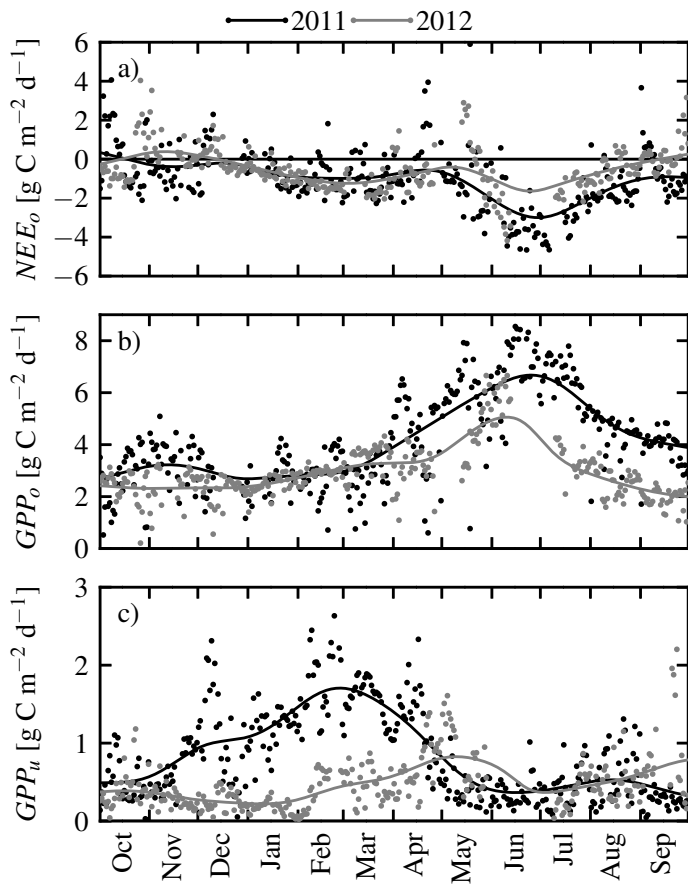
Fig. 6. (a) Ecosystem net carbon exchange NEE_o, **(b)** ecosystem gross primary productivity GPP_o, **(c)** understorey gross primary productivity GPP_u for 2011 (black) and 2012 (grey). Dots mark daily sums, lines are kernel regressions.
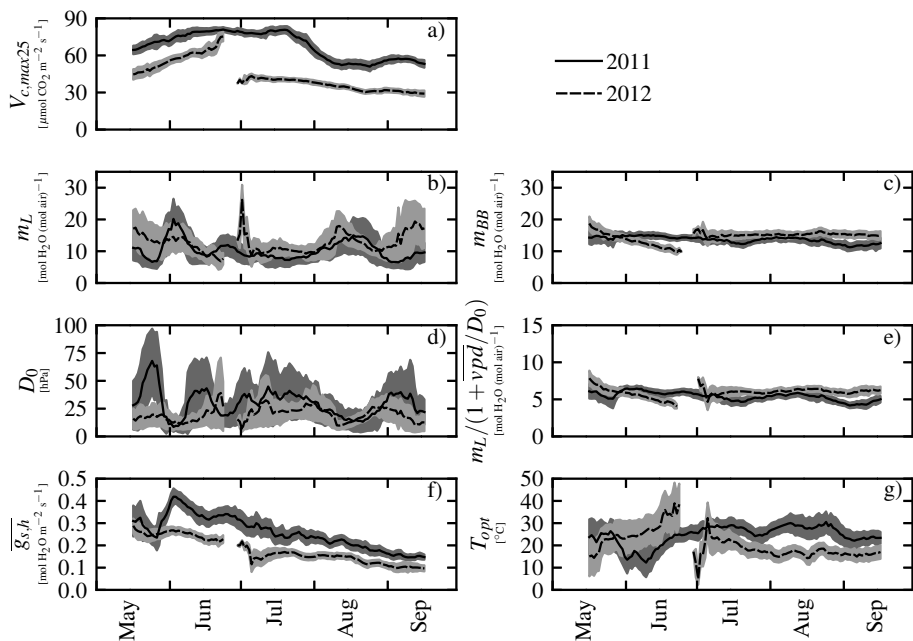
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Fig. 7. Daily values for **(a)** apparent maximum carboxylation rate at 25 °C $V_{c,max25}$, **(b)** assimilation sensitivity parameter m_L of the Leuning model, **(c)** assimilation sensitivity parameter m_{BB} of the Ball–Berry model, **(d)** vapour pressure deficit sensitivity parameter D_0, **(e)** fraction $m_L/(1+(\overline{vpd}/D_0))$ relating assimilation A and stomatal conductance g_s, **(f)** daily median stomatal conductance for water vapour $\overline{g_{s,h}}$ during daytime, **(g)** optimal temperature of electron transport T_{opt}. The model is fitted to median daily cycles of gross primary productivity GPP_o and evapotranspiration ET_o of the *Q. suber* trees in a 31 day long moving window for the summer period of 2011 (solid line, dark uncertainty band) and 2012 (dashed, light uncertainty band).

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