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Summer drought influence on CO_2 and water fluxes of extensively managed grassland in Germany

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ABSTRACT

Net ecosystem CO_2 exchange (NEE) and water fluxes of extensively managed grassland in Germany were measured in a dry year, 2003 and a normal year, 2004 using eddy covariance. Empirical descriptions of canopy capacities (light utilization efficiency and canopy capacity for maximum carboxylation) and inherent water use efficiency (IWUE*) were computed to indicate the grassland's response to environmental and management conditions. Compared with 2004, 2003 was characterized by a 2.5 °C rise in summer mean temperature and an annual precipitation deficit of 286 mm, which was almost one-third below the average precipitation of the normal year 2004 and the long-term annual average (1959–2005). Annual net water balance (precipitation minus evapo-transpiration) in 2003 and 2004 were 85 mm and 361 mm, respectively. Slightly higher IWUE* in 2003 indicates the grassland's sensitivity to drought. The grassland provided an annual gross primary production (GPP) and ecosystem respiration (R_{eco}) of 1022 and 728 $g\,C\,m^{-2}$ respectively in 2003, as compared to their corresponding values of 1233 and 973 $g\,C\,m^{-2}$ in 2004. Drought-induced biomass senescence caused GPP reduction in 2003, which in turn affected the ecosystem respiration. Light explained more than 80% of NEE variability during canopy development and as a result, annual NEE in 2003 and 2004 were -295 and $-260\,g\,C\,m^{-2}$, respectively. Taking into account the exported carbon by biomass harvest, we calculated net biome productivity (NBP) of $-113\,g\,C\,m^{-2}\,yr^{-1}$. We conclude that this managed grassland acted as a moderate carbon sink, despite the difference in environmental and management conditions.

1. Introduction

Climate change projections forecast greater variability of precipitation and higher frequency of drought in the mid- and high latitudes (Houghton et al., 2001; IPCC, 2007). Some studies show that the variability in precipitation is already affecting ecosystem carbon exchange, even in temperate areas that are typically not considered drought-prone (Nagy et al., 2007; Noormets et al., 2008). The dynamics of precipitation and available soil water are the key factors that regulate carbon assimilation, ecosystem respiration and thus overall carbon balance. Long-term CO_2 flux monitoring initiatives such as FLUXNET have arisen to understand how the weather variables drive the carbon cycling in ecosystems across the globe (Baldocchi et al., 2001). Most of these investigations however, are based on fluxes of water and CO_2 in forests (Aubinet et al., 2000; Granier et al., 2007; Noormets et al., 2008). With an area increasing at the rate of $6\,M\,ha\,yr^{-1}$ due to deforestation (Goudriaan, 1992), grasslands are increasingly becoming important for the global carbon balance (Hunt et al., 2004; Novick et al., 2004; Xu and Baldocchi, 2004).

Increasing temperature trends over much of central and Western Europe have caused significant warming and drying periods in recent decade (Fink et al., 2004; Schaer et al., 2004). Climate data reveal that the year 2003 provided an exceptionally hot summer period, by far the hottest summer since at least 1500 AD (Luterbacher et al., 2004). The small buffering capacity with respect to available soil water made the grasslands very sensitive to the extreme hot and dry summer conditions in 2003, affecting the plant carbon uptake (Allard et al., 2007; Ammann et al., 2007; Nagy et al., 2007), and thereby leading to anomalous ecosystem/atmosphere

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exchange along the continental scale (Ciais et al., 2005; Reichstein et al., 2005). Schaer et al. (2004) showed that the temperature and rain characteristics of the summer 2003 in Central Europe are found in future climate simulations for 2070–2100 as average conditions. Considering that warmer and drier summers may be expected more often in the future, better knowledge of grassland response to such events is needed.

Besides the grassland carbon dynamics is being influenced by climatic factors, management factor such as harvesting and fertilization are also intimately linked to carbon dynamics of managed grasslands. Biomass harvesting directly affects CO_2 assimilation through the reduction in the amount of assimilating plant materials (Novick et al., 2004; Rogiers et al., 2005). The biomass thus exported is also not available for eventual decomposition and ecosystem respiration, and ultimately harvest influences the annual ecosystem carbon balance (Ammann et al., 2007).

We studied temperate grassland in east-central Germany, which is extensively managed, unfertilized and moderately warm. We present the results of carbon and water fluxes from eddy covariance measurements, during two contrasting years (2003, 2004) as a part of the CarboEurope-IP program. The year 2004 is considered as a "normal year" with no water deficit and moderate temperatures, while 2003 is considered as a dry year with potential water deficit and high temperatures. The main objectives of the study were (1) to examine how the summer drought during 2003 influences the components of ecosystem CO_2 and water fluxes, and (2) to examine how biomass harvesting affects the annual carbon budget of the grassland.

2. Materials and methods

2.1. Site characteristics

An eddy flux tower was established in a 60 ha area of temperate grassland located in Grillenburg (375 m a.s.l., 50°56′58.09″N, 13°30′45.09″E), near Dresden (30 km away) in east-central Germany. Mean annual precipitation and air temperatures (1959–2005) were 824 mm and 7.9 °C, respectively. The site was generally covered with snow between December and February. The soil pH was moderately acidic (5.7–6.2), and the soil type was pseudogley silt loam that was free from lime concretions up to a depth of 3 m. The sand, silt and clay fractions in the ploughed layer (Ap horizon, 0–23 cm) were 10, 81, and 9% respectively, whereas 13, 76 and 11% respectively in the next S horizon (23–70 cm). The bulk densities of these two horizons were 1.4 and 1.7 g cm^{-3}, respectively. The grassland meadow was extensively managed with 2 to 3 hay harvests per year. The meadow was dominated by the native fescue (*Festuca pratensis*), meadow foxtail (*Alopecurus pratensis*) and Timothy (*Phleum pratense*) grasses.

2.2. Biomass sampling, LAI and plant nutrients determination

Biomass sampling was conducted monthly using 10 random quadrats of 25 cm × 25 cm area, between February and December 2004. Sampled biomass was first separated into green and dead components. The green component (grass, forbs, and legumes) was then divided into three equal parts and one part was used as a subsample for leaf area (LA) determination using leaf area meter (LI-3100, LiCor, Nebraska, USA) and separately oven-dried at 70 °C for 48 h. Total LA was determined from the biomass: LA ratio of the sample biomass and total biomass. Leaf area index (LAI) was then determined from total LA and ground area. The remaining portions of green component along with dead ones were oven dried at 70 °C for 48 h and weighed to obtain the green biomass and total biomass (green plus dead biomass).

The monthly sampling of biomass and LAI determination were not carried out for 2003. LAI was however, derived from MODIS simple ratio (SR) index based on the regression with measured LAI in 2004 as detailed in Dinh (2008). The MODIS SR index corresponds well to the changes in LAI and a strong linear relationship between LAI and SR ($R^2 = 0.79$) indicates that SR alone could explain about 80% of change in LAI. The green biomass in 2003 was estimated using the regression between green biomass and green LAI established during 2004 ($R^2 = 0.70$).

Biomass export by harvest (H_{export}) was carried on 177, 217 and 300 DOY (day of year) during 2004. Harvest yield was estimated based on the ratio of the vegetation height before and after cutting in each harvest, and the corresponding yield from each harvest were 188, 87 and 58 g of dried biomass per square meter. During 2003, biomass export by harvest (H_{export}) was carried on 167 and 287 DOY, and the information about harvest yield from each harvest was not available.

Belowground biomass sampling was done in 2004 by extracting soil cores (8 cm diameter) from the same plots, where aboveground biomass sampling was done. The extracted soil columns were divided into three layers (0–3, 3–12 and 12–27 cm depths) and fresh weight of individual layers determined immediately in the field. Roots were carefully removed from each soil layer within 48 h, washed, oven-dried at 70 °C for 48 h, and weighed to obtain root biomass profiles.

A portion of the dried plant samples (shoots) was re-dried in the desiccators for carbon and nitrogen analysis. A known fraction of the dried samples was ground and about 4–5 g of sample was then analyzed to determine the foliar carbon and nitrogen concentrations (%) by means of elementary analysis (Markert, 1996). The amount of carbon to nitrogen in the plant samples was expressed as C/N ratio.

2.3. Soil nutrients determination

After root removal, the soil samples were divided into approximately three equal parts. One set of samples was used to determine the soil pH (1:2.5, v/v). The second set of samples was used for gravimetric moisture content, which was determined for all layers by drying the soil samples at 100 °C until a constant weight was obtained. The third set was used for determination of nitrate and ammonium ions in soil. The nitrate and ammonium ions were extracted by shaking fresh soil samples in 1 M KCl (solution to soil ratio 2.5:1, v/v) for one hour followed by filtering. The ammonium concentration was determined by Flow-Injection Analysis (FIA-Lab II, MLE, Dresden, Germany) and nitrate was determined by means of anion-exchange HPLC (Kontron, Germany, column type-VYDAC 302 IC) with UV detector 430.

2.4. Climate, micro-meteorology, CO_2 and water fluxes

Long-term climate data (1959–2005) were received from the nearby Tharandt Anchor Station (5 km, 380 m a.s.l., 50°58′00″N, 13°34′16″E). At the Grillenburg grassland site, CO_2 exchange, sensible heat, latent heat and momentum flux were measured using an open-path infra-red gas analyzer (IRGA; LI-7500, LiCor Inc., Lincoln, NE, USA); and wind velocity and air pressure using an ultrasonic anemometer (METEK, USA1, Elmshorn, Germany) at a height of three meter. Global and net radiation, air temperature, relative humidity, soil temperature and rainfall as well as fluxes of CO_2 (net ecosystem exchange; NEE), H_2O (evapo-transpiration; ET) and sensible heat (H) were available on half-hourly basis. The calculation and correction of the fluxes are described by Grünwald and Bernhofer (2007) based on the general EUROFLUX methodology (Aubinet et al., 2000). NEE was determined as the sum of CO_2 flux, F_C and CO_2 storage change, S_C. S_C was calculated using the temporal changes in the CO_2 concentration for the respective EC level. Gap filling and flux partitioning were performed by the "Online Eddy-Covariance Data Gap-Filling and Flux-Partitioning Tool" (Reichstein et al., 2005) including u^*-correction to replace unreliable data due to low-turbulence conditions. The gap filling algorithm is based on methods described by Falge et al. (2001) and merges the sensitivity of meteorological variables with the auto-correlation of fluxes in time (Reichstein et al., 2005). This procedure enables a consistent data treatment on measured night-time fluxes during sufficient turbulence condition. In case of frequent data gaps (as occurred in 2003 during the nights due to frequent dew formation on the open-path gas analyzer) the resulting gap-filled data were not consistent with periods of sufficient data availability and hence such measurements were not included in the records. Photosynthetic photon flux density (PPFD) was calculated from the corresponding global radiation values (Alados et al., 2002).

Net CO_2 exchange, NEE measured by eddy covariance is the arithmetic sum of gross ecosystem exchange, GEE (GEE = −GPP, gross primary productivity) and ecosystem respiration, R_{eco}.

$$\text{NEE} = \text{GEE} + R_{\text{eco}} \tag{1}$$

A negative sign indicates a carbon sink.

The partitioning of the measured NEE into GPP and R_{eco} was achieved via a stepwise procedure and algorithms discussed in detail by Reichstein et al. (2005) as modified by Owen et al. (2007). The procedure establishes a short-term temperature dependent ecosystem respiration from turbulent night-time data using the equation established by Lloyd and Taylor (1994) to estimate the daytime respiration (Eq. (2))

$$R_{\text{eco}} = R_{\text{ref}} \cdot e^{E_0((1/T_{\text{ref}}-T_0)-(1/T_{\text{air}}-T_0))} \tag{2}$$

where T_{ref} is 15 °C, T_0 is constant (−46.02 °C) and T_{air} is the air temperature. The free parameters are E_0, the activation energy, and R_{ref}, the reference ecosystem respiration at 15 °C. Initial estimates for E_0 were based on windows of 14 days and a step of 5 days (i.e., 9 days of overlap). As Reichstein et al. (2005), we assumed that E_0 is actually constant over the year, obtaining the value as the average E_0 weighted by the inverse of the standard error. Time dependent changes in R_{eco} were then fixed via estimation of R_{ref}, using a window of 8 days and a step of 4 days (i.e., 4 days of overlap). The final value of R_{eco} for each half-hour was calculated using the values of R_{ref} and constant E_0. GPP was then obtained as

$$\text{GPP} = R_{\text{eco}} - \text{NEE} \tag{3}$$

2.5. Calculation of annual carbon budget

Net biome productivity (NBP) explicitly takes into account carbon fluxes caused by disturbance (carbon export by harvest, carbon import by organic fertilization) and is normally taken as a measure of carbon source or sink strength. Therefore in managed grasslands according to Chapin et al. (2002)

$$\text{NBP} = \text{NEE} - F_{\text{manure}} + F_{\text{harvest}} \tag{4}$$

where F_{harvest} is the carbon exported from the ecosystem through biomass harvest, F_{manure} is the carbon imported into the ecosystem through organic fertilizer application. A negative sign indicates a carbon sink.

The grassland investigated in our study was unfertilized. Hence the Eq. (4) could be simplified to

$$\text{NBP} = \text{NEE} + F_{\text{harvest}} \tag{5}$$

2.6. Calculation of annual water balance and inherent water use efficiency

Daily water balance (P–ET) is the difference between the daily values of precipitation (P) and evapo-transpiration (ET) (Wever et al., 2002). Daily water balance was cumulated annually to indicate the vegetation period with water deficit or surplus. We assume that when cumulative P–ET decreases, there is a likelihood of water deficit. Water loss by surface run-off was not computed in both years and hence was not taken into account while calculating the daily water balance.

The ratio of gross primary production (GPP) and evapo-transpiration (ET) multiplied by vapor pressure deficit (VPD) at the ecosystem level on daily timescale gives inherent water use efficiency (IWUE*) (Beer et al., 2009).

$$\text{IWUE}* = \frac{\text{GPP} \cdot \text{VPD}}{\text{ET}} \tag{6}$$

where ET/VPD being a hydrological measure that approximates the canopy conductance at the ecosystem level. The usage of the star marker indicates that IWUE* is based on measures at the ecosystem level. For calculating inherent water use efficiency (IWUE*), we first plotted GPP · VPD against daily ET values ($R^2 = 0.75$ for both years, data not shown) that provided a good coupling between the carbon and water cycles. We then determined the daily pattern of IWUE* to indicate the grassland's response to environmental and management conditions. Since ET is the sum of transpiration (linked to GPP) from vegetation and evaporation from the soil surface (not linked to GPP), an analysis was performed for the exclusion of data from the rainy days as well as the two subsequent post-rainfall days that affect IWUE*. Several studies have highlighted the need for eliminating days with high evaporation and interception causing underestimated IWUE* which occurs basically on days after precipitation events (Grelle et al., 1997; Kuglitsch et al., 2008; Beer et al., 2009).

2.7. Hyperbolic light response model

An empirical hyperbolic model (Eq. (7)) was employed to determine the light response parameters (α, γ, $\beta+\gamma_{2000}$) in order to understand the canopy response to environmental and management conditions. Empirical descriptions of the daily NEE fluxes were accomplished via nonlinear least squares fit of the data to the hyperbolic light response model, also known as the rectangular hyperbola or the Michaelis–Menten type model (Gilmanov et al., 2003; Owen et al., 2007; Hussain et al., 2009).

$$\text{NEE} = -\frac{\alpha\ \beta Q}{\alpha Q + \beta} + \gamma \tag{7}$$

where α is the initial slope of the light response curve and an approximation of the canopy light utilization efficiency (μmol CO_2 m^{-2} s^{-1})/(μmol photon m^{-2} s^{-1}), β is the maximum CO_2 uptake rate of the canopy (μmol CO_2 m^{-2} s^{-1}), Q is the PPFD (μmol photon m^{-2} s^{-1}), γ is an estimate of the average daytime ecosystem respiration occurring during the observation period (μmol CO_2 m^{-2} s^{-1}), (α/β) is the radiation required for half-maximal uptake rate, and ($\beta+\gamma$) is the theoretical maximum uptake capacity (μmol CO_2 m^{-2} s^{-1}) as sometimes the rectangular hyperbola saturates very slowly in terms of light. Owen et al. (2007) evaluated $(\alpha\beta Q)/(\alpha Q+\beta)$ at a reasonable level of high light ($Q = 2000$ μmol m^{-2} s^{-1} is used in this study), which is an approximation of GPP and can be thought of as the average maximum canopy uptake capacity, notated here as $(\beta+\gamma)_{2000}$. Sigmaplot (version 11) was employed to estimate these parameters. Sigmaplot performed normality and constant variance tests from the data fit, and p value was computed to determine if there has been a significant improvement in the fit. Parameters were estimated for 5–10 days between growing and summer periods in each year, the period during which water stress potentially influenced the grassland physiology.

2.8. *Temperature dependence by an empirical model*

Ecosystem respiration is a function of temperature, and temperature sensitivity of respiration is affected by the variation in soil moisture. We first determined the relationship of ecosystem respiration and temperature using two parameters exponential fit for the selected days in the growing and summer periods where LAI and soil moisture was similar (Aires et al., 2008).

$$R_{\mathrm{eco}} = a \cdot \exp(b \cdot T_{\mathrm{air}}) \tag{8}$$

where a and b are the fitting parameters. We then determined the temperature sensitivity of R_{eco} (Q_{10}) using following equation described by Aires et al. (2008).

$$Q_{10} = \exp(10b) \tag{9}$$

3. Results

3.1. *Comparison of environmental conditions*

Long-term climate data from Tharandt Anchor Station reveals that the annual mean temperature and annual mean radiation in 2004 were close to the long-term annual means (1959–2005); whereas their respective values in 2003 were 1.2 °C and 20 W m^{-2} above the long-term annual mean. Annual precipitation in 2004 was 55 mm above the long-term mean; whereas in 2003 it was 312 mm below the long-term mean (Fig. 1).

Climate data from the Grillenburg study site reveals that the air temperature increased more rapidly during May in 2003 compared to 2004 (i.e., 13.6 °C compared to 9.7 °C, respectively). The summer mean temperature (June–August) in 2003 was 2.5 °C higher than in 2004. As a result, the annual mean temperature in 2003 and 2004 were 8.3° and 7.8 °C, respectively. Increasing temperature during summer led to a higher VPD value (40 hPa) in 2003 as compared to a relatively lower value (25 hPa) in 2004 (Fig. 2a and b). Radiation input was low during winter days and high during summer days (Fig. 2c and d). Rapid increase in radiation occurred from

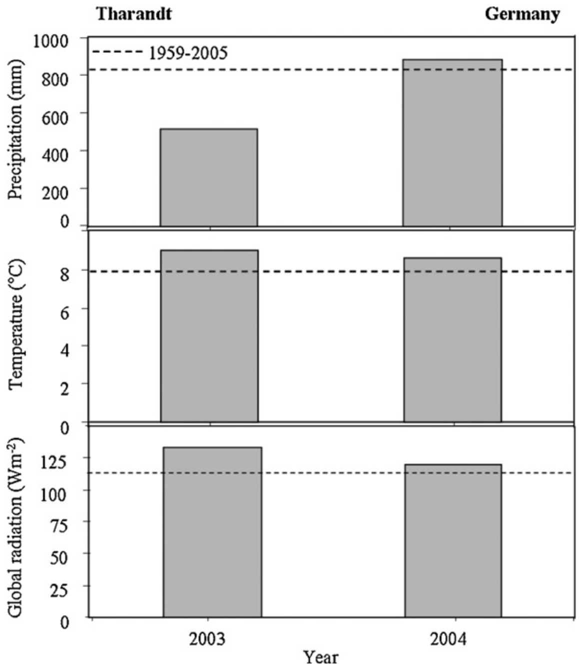

Fig. 1. Annual sum of precipitation, annual means of temperature and global radiation from the nearest Anchor Station at Tharandt for 2003 and 2004. The dotted line indicates long-term annual mean (1959–2005) for each climatic parameter.

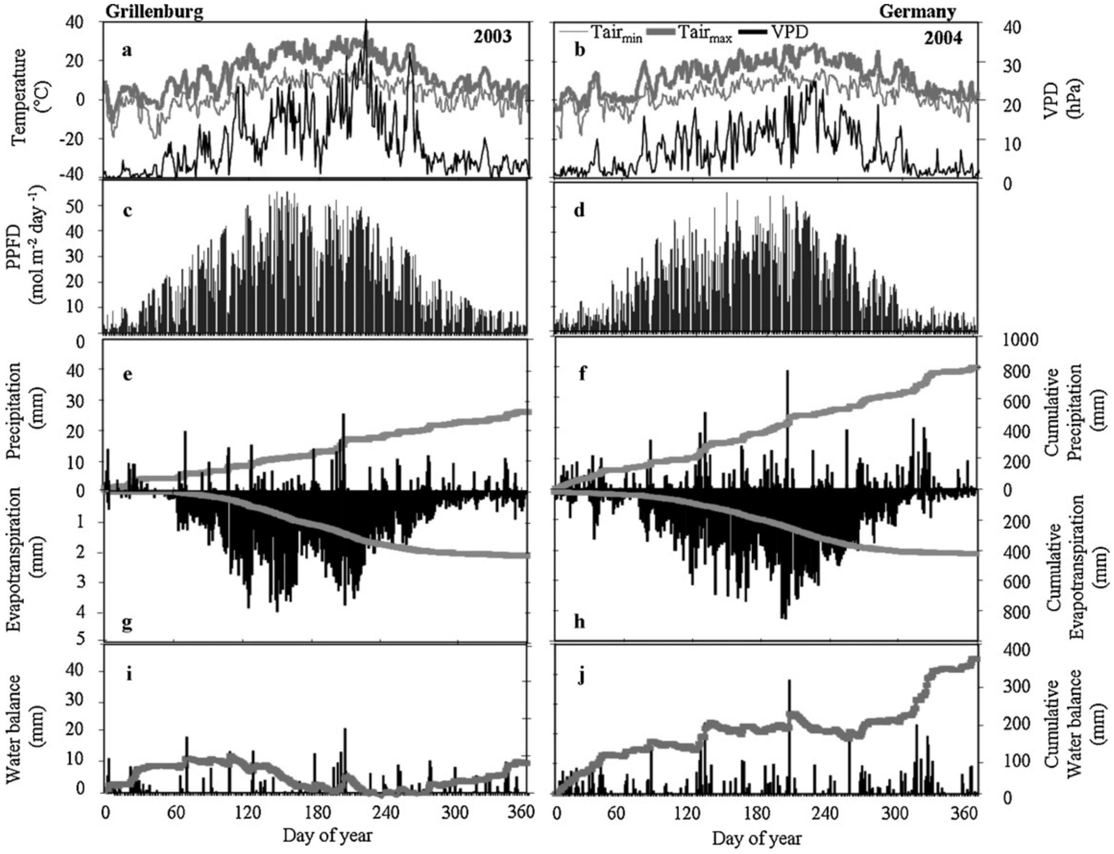

Fig. 2. Daily values of air temperatures (T_{min} and T_{max}) and vapor pressure deficit, VPD (a, b); photosynthetic photon flux density, PPFD (c, d); precipitation, P (e, f); evapotranspiration, ET in inverted axis (g, h) and net water balance or P–ET (i, j) for 2004 and 2003. Bold grey lines on the right side of panel indicate the annual cumulated values.

Table 1
Soil water content (SWC), soil nitrate and ammonium concentrations, and leaf tissue nitrogen and C/N contents in 2004 at the Grillenburg site.

Sampling (days of year)	SWC (%)	Soil		Plant tissue	
		NO_3^-–N (μmol l^{-1})	NH_4^+–N (μmol l^{-1})	N (%)	C/N
40	25.0 ± 2.5	5.1 ± 2.2	0.7 ± 0.7	–	–
68	29.2 ± 3.1	6.0 ± 2.1	1.0 ± 1.0	–	–
113	22.9 ± 3.1	4.0 ± 1.5	1.2 ± 0.9	3.7 ± 0.4	12.6 ± 1.5
133	27.0 ± 2.2	2.4 ± 1.2	2.5 ± 0.8	3.8 ± 0.6	13.0 ± 1.5
168	25.3 ± 2.1	3.2 ± 1.4	1.1 ± 0.9	2.9 ± 0.6	19.2 ± 2.8
189	23.6 ± 2.4	6.7 ± 2.6	1.3 ± 1.1	2.4 ± 0.7	31.1 ± 3.7
238	15.8 ± 1.8	3.9 ± 2.0	0.8 ± 0.7	2.9 ± 0.3	18.0 ± 2.2
285	20.6 ± 2.1	4.4 ± 1.9	0.9 ± 0.8	2.7 ± 0.5	21.4 ± 2.6
313	24.6 ± 2.3	–	–	2.8 ± 0.7	19.3 ± 2.5
348	26.4 ± 2.8	–	–	2.9 ± 0.6	14.4 ± 1.7

SWC is the average soil moisture content in 0–27 cm soil depth (±SE).

May in 2003; whereas from June in 2004. Radiation inputs in June and August 2003 showed about 22 and 42% respective increase over the values that occurred during the same periods in 2004. As a result of this difference, the annual radiation input was higher in 2003 (7940 mol m^{-2} yr^{-1}) than in 2004 (7200 mol m^{-2} yr^{-1}). Difference in spring precipitation (February) between years was substantial, where 2003 showed a characteristic precipitation deficit of 80% compared to 2004. Precipitation in July was maximum in both years; however, 15% less in 2003. Soil water content in the 0–27 cm soil profile was >25% between May and July in 2004 (Table 1) but declined to 15% in August. Soil water content was not measured in 2003. However, it is reasonable to expect a decline in soil water content at least as low as 15% or even lower in August 2003 since precipitation in August was much lower than 2004. The total rainfall amounts in 2003 and 2004 were 512 and 798 mm, respectively resulting in an annual deficit of 286 mm in 2003, which was almost one-third below the annual precipitation of 2004 (Table 4). Peak evapo-transpiration (ET) of 4 mm d^{-1} occurred in May during 2003, whereas similar values were reached only in late July during 2004 (Fig. 2g and h). A decrease in ET was however, observed during summer periods (except July) in 2003. Despite the large differences measured in total precipitation, annual ET from the grassland meadow was similar in both years (427 and 437 mm in 2003 and 2004, respectively, Table 4). Comparing environmental conditions in both years, our results indicate that June and August 2003 were extremely hot compared to 2004; and May and July were less extreme, but still warmer than 2004.

3.2. *Components of water balance and inherent water use efficiency*

The net water balance (P–ET) began to decrease from May 2003 indicating the onset of water deficit, which subsequently becomes stronger in summer as P–ET decreases further in June (Fig. 2i and j). Conversely, in 2004 P–ET increases throughout the spring and summer indicating sufficient water availability in normal year. It is noted in 2003 that large amounts of precipitation in July did not strongly influenced the cumulative P–ET as compared to 2004. The cumulative net water balance in 2003 and 2004 were 85 and 361 mm yr^{-1} respectively, showing a characteristic water deficit of 276 mm yr^{-1} in 2003, i.e., only 25% of water was available to the plants in 2003 (Table 4). The water deficit of 75% (276 mm yr^{-1}) was almost equal to the precipitation deficit (286 mm yr^{-1}) in 2003.

The patterns of IWUE* differed considerably between both years depending on biomass and environmental conditions. IWUE* in 2003 increased from spring reaching peak values as early as May; whereas in 2004 such peaks of lower magnitude were observed only in July. The occurrence of negative IWUE* peaks in both years coincided with the harvest periods. Increases in IWUE* after first and second harvests were apparent in 2004 due to biomass re-growth. However, such IWUE* increases were limited in 2003 due to biomass senescence. We assumed that July precipitation had no influence on IWUE* patterns in both years because data sets from rainy days and two subsequent post-rainfall days were already removed from the analysis. The springtime and summertime differences in IWUE* led to annual values of 23.5 and 21.6 g C hPa/mm H_2O in 2003 and 2004, respectively (Fig. 3).

3.3. *Biomass, LAI development and nutrient concentration*

Biomass began to develop rapidly in spring 2003 reaching LAI values close to four as early as May (Fig. 4a), whereas in 2004 rapid biomass development just started in May reaching a similar LAI only in June (Fig. 4b). The grassland biomass and LAI showed only a single peak in 2003 (in May) and then declined as senescence occurred in response to drought after harvest. Vegetation recovery after harvest was poor in 2003 compared to 2004.

Half of the root biomass was found in the first 3 cm of the soil profile and around 90% to a depth of 12 cm (Fig. 4c). Less than 10% occurred between 12 and 27 cm during mid-summer. Even during winter, substantial root biomass was maintained and appeared similar to those found during the summer. A short-term increase in root biomass was observed on 188 DOY, i.e., 10 days after the first harvest. Root biomass subsequently decreased as the season progressed.

During canopy development, there was a high percentage of nitrogen concentration and a low ratio of carbon to nitrogen (C/N) in grassland leaves (Table 1). Decreased nitrogen concentration and increased carbon to nitrogen ratio (C/N) in the leaves were apparent during summer after harvest. This period was also characterized by the accumulation of nitrates in the soil by the increased root biomass. The concentration of ammonium nitrogen in the soil started to increase from spring reaching a maximum during early summer, and declined thereafter (Table 1).

3.4. *Seasonal changes in net ecosystem CO_2 exchange and annual carbon budget*

Results reveal that high carbon fluxes occurred during the growing period and low fluxes during winter (Fig. 5). GPP began to increase with biomass from

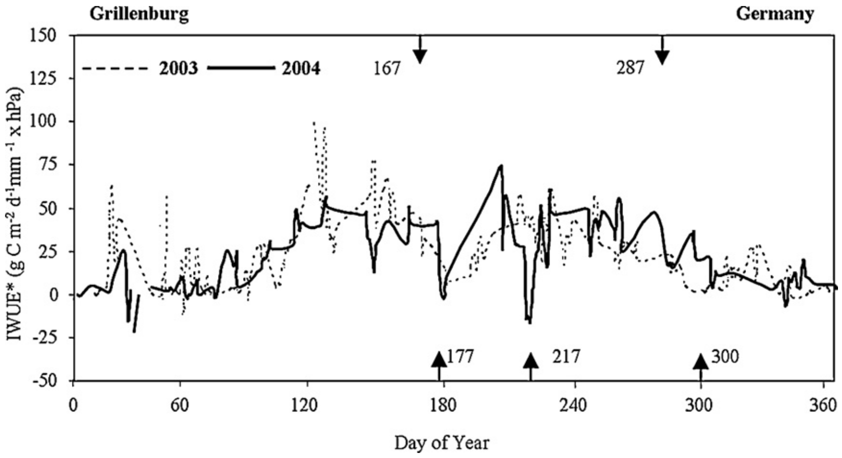

Fig. 3. Daily values of inherent water use efficiency (IWUE*) computed according to Eq. (6)) at the Grillenburg meadow during 2003 and 2004. Data from rainy days and two post-rainfall days were eliminated for analysis. Harvest periods in 2003 were indicated by downward arrows at the top, while upward arrows at the bottom of the panel indicates harvest periods in 2004.

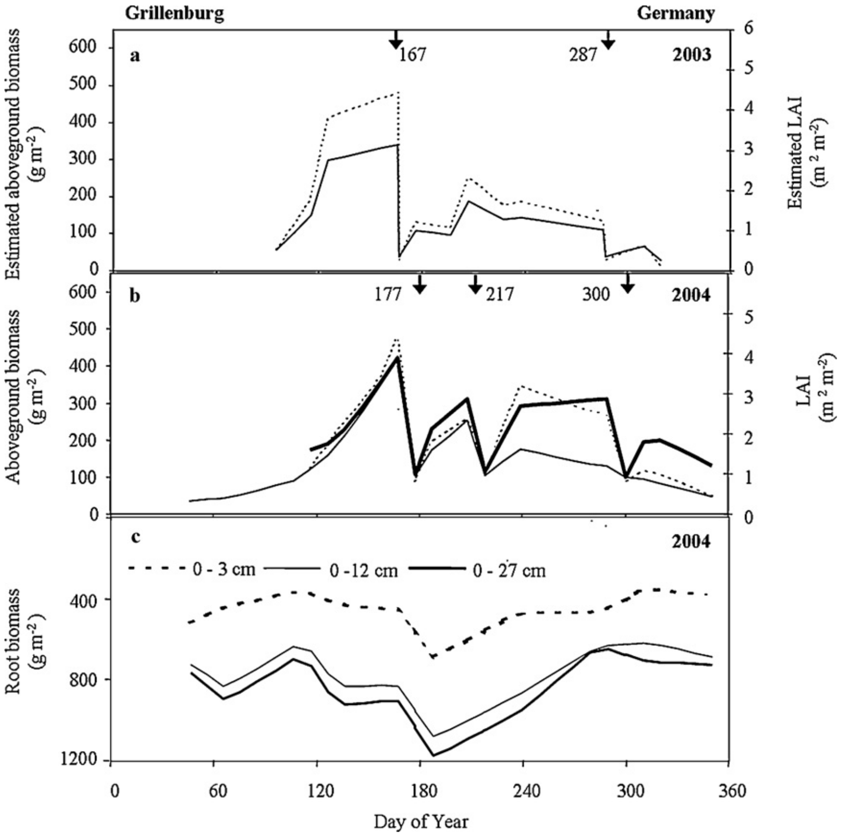

Fig. 4. Seasonal course of aboveground green biomass (thin line) and leaf area index (dotted line) in 2003 estimated by MODIS SR method from 2004 data (a); aboveground green biomass (thin line) and total biomass (bold line), and green leaf area index (dotted line) in 2004 (b); and root biomass integrated from the surface at different depths in 2004 (c) at the Grillenburg meadow site. Biomass harvests were carried out on DOY 167 (Jun 16) and 287 (Oct 14) in 2003, and DOY 177 (Jun 25), 217 (Aug 4) and 300 (Oct 26) in 2004 as indicated by arrows.

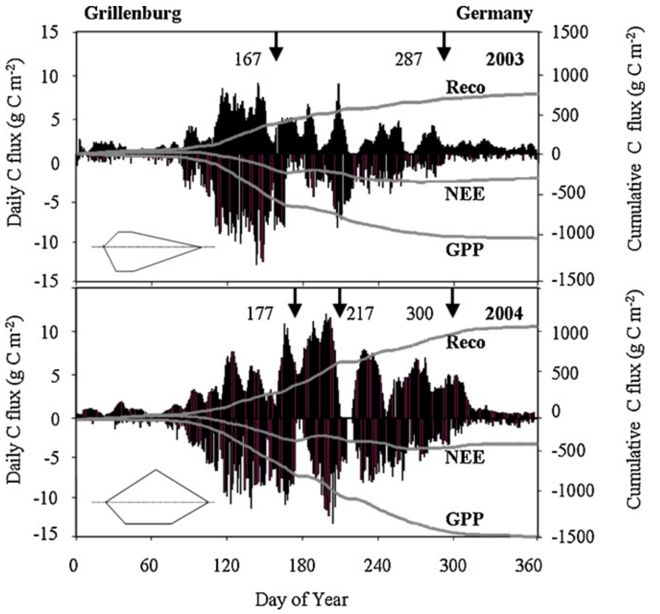

Fig. 5. Annual courses for daily carbon dioxide uptake (negative bars, GPP), carbon dioxide emission (positive bars, R_{eco}), and the cumulative fluxes for R_{eco}, GPP, and NEE at the Grillenburg meadow during 2004 and 2003. Harvests were carried out as indicated with arrows on DOY 177 (Jun 25), 217 (Aug 4) and 300 (Oct 26) in 2004; and 167 (Jun 16) and 287 (Oct 14) in 2003. Small insert figures in the lower left of each panel provide a simplified interpretation of changes in the maximal GPP and R_{eco} fluxes over the course of the season. The negative signs indicates carbon uptake by the ecosystem; and positive signs indicates the carbon release by respiration (NEE > 0 indicates carbon loss and NEE < 0 indicates carbon uptake and expressed in g C m^{-2}).

spring in both years with maxima occurring much earlier in 2003 (3.6 ± 0.7 g C m^{-2}) than in 2004 (2.5 ± 0.5 g C m^{-2}). GPP increase continued through May in 2003 with biomass development and high radiation resulting in 13.6 ± 0.6 g C m^{-2} as compared to 10.7 ± 0.8 g C m^{-2} in 2004. GPP then declined to 9.3 ± 0.5 g C m^{-2} in June 2003 as a result of drought-induced biomass senescence; whereas such a decrease in GPP was not apparent in 2004 (10.3 ± 0.8 g C m^{-2}). High precipitation in July 2003 did not augment the CO_2 uptake (GPP in July was 8.5 ± 0.8 g C m^{-2}). Decline in GPP during 2003 continued through the remainder part of the growing period (maxima GPP in August and September 2003 were 6.2 ± 0.4 and 4.5 ± 0.7 g C m^{-2}, respectively). Compared to 2003, much higher GPP values were observed in summer 2004 (maxima GPP in July, August and September were 12.4 ± 0.9, 8.0 ± 0.3 and 7.4 ± 0.7 g C m^{-2}, respectively). Ecosystem respiration increased with GPP during canopy development with maxima occurring in mid-season when the root biomass was greatest, and decreased with dry periods after harvest. Short-term CO_2 emissions in July due to major rain events were evident in both years. Thus, on an annual scale, the grassland provided annual GPP values of 1022 and 1233 g C m^{-2} respectively, and annual R_{eco} values of 728 and 973 g C m^{-2} respectively, in 2003 and 2004 (Table 4). The number of net sink days in 2003 and 2004 were 201 and 186 days, resulting in respective annual NEE values of −295 and −260 g C m^{-2} (Table 4).

The annual carbon budget of 2004 corresponding to the carbon sequestration of the grassland meadow was calculated according to the Eq. (5). The first harvest (on 177 DOY) during maximum canopy development exported 82.7 g C m^{-2} from the system (56%), while the second (217 DOY) and third harvests (300 DOY) exported 38.3 (26%) and 25.5 g C m^{-2} (17%), respectively. On an annual scale, the total carbon exported outside the grassland system ($F_{harvest}$) was 147 g C m^{-2} (Table 4). An estimate of net biome productivity (NBP) indicates an annual carbon sequestration rate of −113 g C m^{-2} (Table 4).

3.5. Environmental control on CO_2 exchange

3.5.1. NEE in response to PPFD

Considering that light intensity is certain to influence daytime NEE variation, we plotted NEE against PPFD for the selected periods and fitted to a rectangular hyperbola model (Eq. (7)) for the estimation of light response parameters (Table 2). NEE measured during canopy development in both years fitted the light-response function well (R^2 > 0.80, Table 2). Light utilization efficiency (α) of the canopy differed considerably between years with average annual values of 0.01 and 0.07

Table 2
Relationship between NEE and PPFD for the selected periods in 2003 and 2004 and the curves were fitted with hyperbolic light response model as described in Eq. (7).

Year	Periods (DOY)	n	α	γ	$(\beta+\gamma)_{2000}$	R^2	SE_α	SE_γ	p value
2003	151–156	125	−0.02	1.5	−15.0	0.79	0.004	0.61	0.0135
	159–166	195	−0.02	2.1	−20.0	0.83	0.002	0.46	<0.0001
	185–190	170	−0.01	3.3	−12.0	0.77	0.002	0.39	<0.0001
	192–196	107	−0.01	0.7	−11.3	0.84	0.002	0.45	0.1105
	199–207	225	−0.01	2.4	−11.5	0.80	0.002	0.41	<0.0001
	210–220	274	−0.01	1.5	−11.6	0.75	0.002	0.46	0.0012
	227–236	260	−0.01	1.6	−13.8	0.82	0.001	0.32	<0.0001
	239–247	201	−0.02	2.6	−16.1	0.86	0.002	0.29	<0.0001
	249–257	191	−0.01	1.1	11.4	0.87	0.002	0.27	<0.0001
	261–274	284	−0.01	1.5	−14.0	0.77	0.001	0.32	<0.0001
2004	150–162	282	−0.01	7.1	−12.0	0.82	0.010	0.99	<0.0001
	172–175	98	−0.05	6.4	−22.8	0.85	0.010	1.27	<0.0001
	189–193	124	−0.09	7.8	−13.0	0.76	0.020	0.81	<0.0001
	196–207	129	−0.06	6.3	−22.6	0.88	0.009	0.86	<0.0001
	229–238	215	−0.09	5.9	−17.6	0.77	0.015	0.79	<0.0001
	239–248	23	−0.07	5.6	−19.3	0.77	0.013	0.94	<0.0001
	254–264	221	−0.07	5.3	−16.6	0.83	0.017	0.64	<0.0001
	278–280	58	−0.09	5.4	−13.8	0.86	0.022	0.84	<0.0001

DOY are the selected periods; n is the number of half hourly NEE determinations included in empirical model fits; parameters α, is light utilization efficiency (μmol CO_2 m^{-2} s^{-1})/(μmol photon m^{-2} s^{-1}); γ is an estimate of the average daytime ecosystem respiration (μmol CO_2 m^{-2} s^{-1}); $(\beta+\gamma)_{2000}$ is an average maximum canopy uptake capacity, which is estimated at the light level of 2000 (μmol photon m^{-2} s^{-1}); p value indicate the level of significance.

(μmol CO_2 m^{-2} s^{-1})/(μmol photon m^{-2} s^{-1}) in 2003 and 2004, respectively. Interpreting $(\beta+\gamma)_{2000}$ as an estimate of GPP at maximum light, the photosynthetic potential of the canopy was 13.7 and 17.0 μmol m^{-2} s^{-1}, respectively; the estimated average respiration (γ) was 1.8 and 6.2 μmol m^{-2} s^{-1}, respectively for 2003 and 2004. After harvest, an increase in α and γ, and a decrease in $(\beta+\gamma)_{2000}$ explained the canopy response to cutting.

3.5.2. R_{eco} in response to temperature, soil moisture and gross photosynthesis

Ecosystem respiration increased exponentially with temperature (R^2 = 0.70–0.90, Table 3) and this relationship was affected by the changes in soil moisture. Results reveal that the temperature sensitivity coefficient (Q_{10}) of respiration decreased from growing season with abundant soil moisture, to dry summer with low soil moisture (Table 3).

The year 2004 showed strong positive correlations of ecosystem respiration with gross photosynthesis in growing and summer periods (R^2 = 0.90); whereas 2003 showed a weaker correlation in summer period (R^2 = 0.64) (Fig. 6a and b).

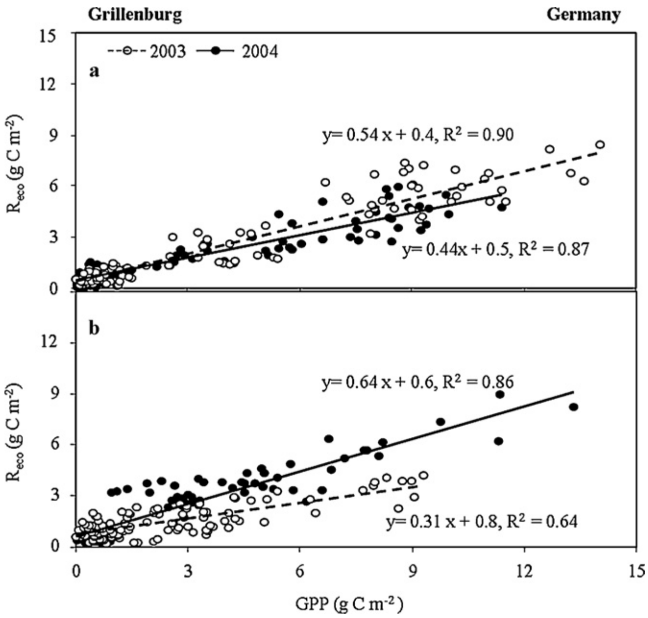

Fig. 6. Linear relationships between the daily values of ecosystem respiration (R_{eco}) and gross primary production (GPP). (a) Data from the growing season (n = 120 in 2003, n = 100 in 2004); (b) data from the summer season (n = 119 in 2003, n = 91 in 2004). Open circles shows the data for 2003 and closed circles for 2004. Rainy days were excluded from the analysis.

3.5.3. GPP in response to VPD and temperature

GPP response to VPD was linear in 2004 (R^2 = 0.66); whereas non-linear in 2003 (R^2 = 0.50). GPP reached a maximum at around 25 hPa in both years; however declined as VPD increased above 25 hPa as observed in 2003 (Fig. 7a). Gross photosynthesis responded linearly to the changes in daily mean temperature (R^2 = 0.50–0.65) in both years (Fig. 7b).

4. Discussion

4.1. Influence of summer drought on ecosystem CO_2 exchange

Climate data show that the year 2003 provided an exceptional drought with a characteristic deficit of 286 mm in annual precipitation, which was almost one-third below the average precipitation of normal year 2004 and long-term annual average (1959–2005). Drought and heat waves were extreme in summer 2003 particu-

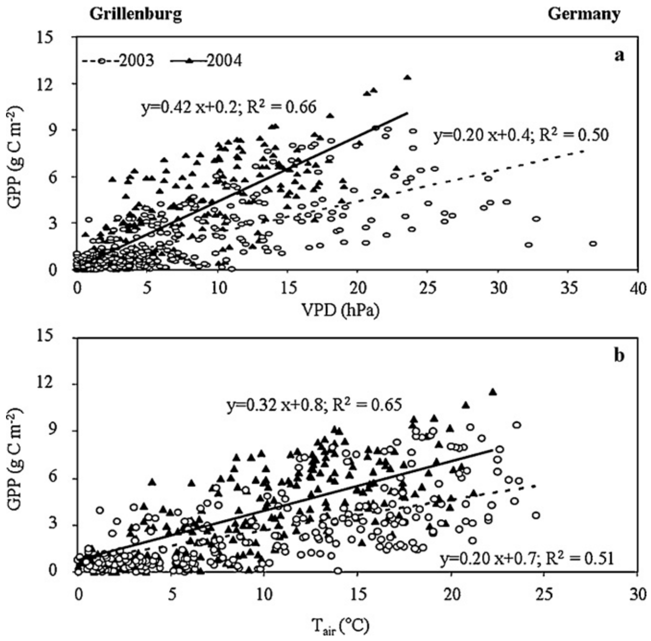

Fig. 7. Relationships of daily values of gross primary production with daily VPD (n = 314 in 2003, 2004) (a); and with daily air temperature (n = 320 in 2003, n = 322 in 2004) (b).

Table 3

Relationship between ecosystem respiration and air temperature for the selected periods in 2003 and 2004 and the curves were fitted with two parameters exponential function as described in Eq. (8).

Periods (DOY)	SWC	*n*	*a*	*b*	R^2	Q_{10}	*p* value
2003							
165–167	–	144	0.99	0.07	0.95	2.01	<0.0001
226–229	–	192	0.69	0.06	0.98	1.80	<0.0001
2004							
165–167	25.3 ± 2.1	145	3.08	0.05	0.85	1.68	<0.0001
226–229	15.8 ± 1.8	192	2.61	0.04	0.70	1.45	<0.0001

DOY are the selected periods, where LAI and soil moisture were similar; SWC is the average soil moisture content in 0–27 cm soil depth and taken from the nearest sampling periods (± indicates SE); *n* is the number of half hourly night-time R_{eco} measurements included in model fits; *a* and *b* are the regression coefficients; Q_{10} is temperature sensitivity coefficient as defined in the Eq. (9); *p* value indicates the level of significance.

larly during the periods of June and August. Many stations across central Europe have reported similar extremes in 2003 (Fink et al., 2004; Schaer et al., 2004; Rebetez et al., 2006).

Higher GPP during growing period occurred due to efficient use of water by high growth rates of plants (i.e., higher IWUE*, refer Fig. 3) resulting from increased leaf area (Fig. 4) and leaf nitrogen (Table 1). Evidence has shown that leaf nitrogen concentration greatly influences the CO_2 carboxylation, and about 50–80% nitrogen was reported to be allocated for the synthesis of photosynthetic protein i.e., Rubisco (Evans, 1989). Given a good linear relationship between GPP and LAI ($R^2 = 0.73$ in 2003, $R^2 = 0.80$ in 2004, data not shown; Flanagan et al., 2002; Xu and Baldocchi, 2004; Aires et al., 2008; Gilmanov et al., 2010), it is suggested that the photosynthetic area primarily influences the canopy capacity for maximum CO_2 assimilation. Abiotic variable like light explained more than 80% of daytime NEE variation during canopy development (Table 2), which is in agreement with studies of Aires et al. (2008); Wohlfahrt et al. (2008a); Schmitt et al. (2010), suggesting light as a good predictor of net carbon assimilation during growing periods.

Drought-induced biomass senescence caused LAI reduction in 2003 (Fig. 4) and as a consequence GPP was reduced considerably (Fig. 5). Our result shows that July rain did not augment the gross photosynthesis and as a result, 20% of GPP was suppressed due to a water deficit of 276 mm yr^{-1} (Table 4). Several abiotic variables such as light, temperature, soil moisture and VPD change simultaneously during summer drought and the effect of individual variables on CO_2 uptake were evaluated in the present study. Our analyses show that changes in temperature did not strongly affected the gross photosynthesis (Fig. 7b), despite the characteristic rise in mean summer temperature. However, the associated increase in VPD above 25 hPa (as observed in 2003) caused a substantial reduction in GPP (Fig. 7a), suggesting that stomatal closure in response to high VPD probably have affected the gross photosynthesis (Novick et al., 2004; Kjelgaard et al., 2008; Nakano et al., 2008). During summer 2003, the IWUE* decrease in response to high VPD and low ET (Fig. 3) confirm the strong control of stomata on transpiration in reducing the water cost of carbon gain (Wever et al., 2002). Slight increase in annual IWUE* values in 2003 further demonstrate the grassland's sensitivity to drought condition, which is in agreement with the results reported by Beer et al. (2009) for a dry year. Other significant changes in grassland physiology that occurred with the drought period were the reduction in light utilization efficiency (α) of the canopy impacting the canopy capacity for maximum CO_2 assimilation (Table 2).

The respiration increase during canopy development was explained by strong relationship with gross photosynthesis (Fig. 6a), which controls the substrate availability for the autotrophic and heterotrophic respiration through root exudates (Davidson et al., 2006). A strong dependence of ecosystem respiration on gross photosynthesis was also reported in Mediterranean and temperate grassland ecosystems (Xu and Baldocchi, 2004; Chimner and Welker, 2005; Aires et al., 2008; Schmitt et al., 2010). During summer 2003, ecosystem respiration fell in parallel with gross photosynthesis suggesting limiting supply of photosynthetic substrates for the rhizospheric activity under water deficit, and as a result about 25% of ecosystem respiration was suppressed in 2003 (Table 4). It is noted that the short-term CO_2 emission occurred in July 2003 after major rain events could be attributed to increase rhizospheric activity within hours of water addition, which soon ceases as the soil dries out (Hunt et al., 2002; Xu and Baldocchi, 2004). Abiotic factor such as temperature explained 70 to 98% variation in ecosystem respiration highlighting the significant role of temperature on the microbial and plant respiration (Wohlfahrt et al., 2005a). However, this temperature relationship was affected considerably by the variation in soil moisture and we found that the temperature sensitivity coefficient (Q_{10}) of respiration decreased from the growing period with abundant moisture to the summer period with low soil moisture content (Table 3). Based on the results from the present study and other grassland studies (Hunt et al., 2002; Xu and Baldocchi, 2004; Flanagan and Johnson, 2005), it is suggested that the ecosystem respiration is strongly limited by soil moisture availability.

Thus compared with the normal conditions in 2004, the summer drought in 2003 significantly affected the grassland productivity, where about 20 and 25% of GPP and R_{eco}, respectively were suppressed due to an annual water deficit of 276 mm (Table 4). Despite strong interaction with climatic factors, the average annual NEE indicates an apparent carbon sink activity in two years (−295 and −260 g C m^{-2} in 2003 and 2004, respectively; Table 4), in agreement with the results from other grassland sites reviewed by Allard et al. (2007) and Soussana et al. (2007).

4.2. Annual carbon budget of managed Grillenburg meadow

The carbon dynamics of managed grasslands are often closely related to biomass harvest. The immediate response of harvest were the reduction in biomass (Fig. 4), plant water use (IWUE*, Fig. 3) thus maximum CO_2 uptake (GPP), turning the meadow from

Table 4

Summary of water and carbon fluxes in 2003 and 2004 for the Grillenburg grassland.

Year	Annual precipitation (P) (mm)	Annual evapo-transpiration (ET) (mm)	Annual water balance (P–ET) (mm)	Annual GPP (g C m^{-2})	Annual R_{eco} (g C m^{-2})	Annual NEE (g C m^{-2})	$F_{harvest}$ (g C m^{-2})	Net biome productivity (NBP) (g C m^{-2})
2003	512	427	85	1022	728	−295	–	–
2004	798	437	361	1233	973	−260	147	−113

Negative sign indicates the carbon sink.

sink to a short-term source of CO_2. The Grillenburg grassland took an average of 21 days in 2003 and 19 days in 2004 after the first harvest to recover and become a net sink for CO_2 with re-growth of biomass (Fig. 5), compared to 11, 16 and 14 days reported by Novick et al. (2004); Jaksic et al. (2006); Schmitt et al. (2010), respectively for other temperate grasslands. This pattern repeated itself after the second and third harvest, but the daily average rates of net carbon gain and loss before and after harvest respectively, decreased from first harvest to the third harvest. The slope of the light response curve or light use efficiency of the canopy (α) was positively influenced by harvest since the newly developed leaves have higher α values than old leaves (Table 2), compensating for the loss of the leaf area (Owensby et al., 2006). Other changes that occurred after harvest were the decrease in leaf N content (Table 1), which may have likely attributed from low mineralization rates caused by high ratio of carbon to nitrogen in the leaf (Seneviratne, 2000). As a result, a short-term increase in carbon and biomass allocation into the roots occurred with high nitrates accumulation, which may have allowed the grassland to survive with low growth rates as a potentially adaptive mechanism under water deficit condition (Maron and Jefferies, 2001; Xu and Zhou, 2005b).

Besides exerting a short-term negative impact on daily NEE, biomass harvest exports carbon from the site switching carbon sink potential of an ecosystem to mere carbon source (Ammann et al., 2007). It is, therefore, essential to account this carbon fluxes exported by harvest while calculating the annual carbon balance of the grassland ecosystem. Our result for 2004 shows that the total annual carbon exported outside the grassland system (F_{harvest}) was 147 g C m^{-2} (56% of annual NEE) leading to an annual estimate of net biome productivity (NBP) of −113 g C m^{-2} (Table 4). The final estimate of NBP indicates that the capacity of the grassland to sequester carbon was still persistent, despite strong interactions with climate and management factors. Similar results of carbon sink activity were also reported for other managed grassland sites in Europe (Jaksic et al., 2006; Ammann et al., 2007; Zeeman et al., 2010). The net carbon storage of the investigated grassland is just 2% of the total soil organic carbon (SOC) content stored in the top layer of Grillenburg soil (5.8 kg C m^{-2}) suggesting that the turnover time of net carbon sequestration may be in the order of decades depending on climatic and management factors.

5. Conclusion

Climate data show that the year 2003 provided an exceptional drought as compared to a normal year 2004. Compared to 2004, about 20 and 25% of GPP and R_{eco}, respectively were suppressed by summer drought in 2003. Reduction in green biomass due to drought was likely to be attributed for GPP reduction, which in turn affected the ecosystem respiration. Despite the strong interaction with environmental factors, the average annual NEE indicated an apparent carbon sink activity in both years. The pattern of net carbon gain was interrupted by biomass harvest, turning the grassland from a sink to a short-term carbon source. Taking into account the total carbon exported by harvest, the estimated net biome productivity (NBP) of the grassland indicates an annual net sequestration rate of −113 g C m^{-2}, which is about 2% of total soil organic carbon (SOC) of the grassland site. Based on our NEE measurements and estimates of NBP, it is concluded that the grassland acted as a moderate carbon sink, despite strong interactions with environmental and management factors. Our presented results provided very valuable estimates of the carbon stock of this extensively managed temperate grassland. However, further investigations are required to improve the predictability of carbon cycling of grassland ecosystems in the future.

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