

Six-year Stable Annual Uptake of Carbon Dioxide in Intensively Managed Humid Temperate Grassland

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ABSTRACT

Variability and future alterations in regional and global climate patterns may exert a strong control on the carbon dioxide (CO₂) exchange of grassland ecosystems. We used 6 years of eddy-covariance measurements to evaluate the impacts of seasonal and inter-annual variations in environmental conditions on the net ecosystem CO₂ exchange (NEE), gross ecosystem production (GEP), and ecosystem respiration (ER) of an intensively managed grassland in the humid temperate climate of southern Ireland. In all the years of the study period, considerable uptake of atmospheric CO₂ occurred in this grassland with a narrow range in the annual NEE from -245 to -284 g C m⁻² y⁻¹, with the exception of 2008 in which the NEE reached -352 g C m⁻² y⁻¹. None of the measured environmental variables (air temperature (Ta), soil moisture, photosynthetically active radiation, vapor pressure deficit (VPD), precipitation (PPT), and so on) correlated with NEE on a seasonal or annual scale because of the equal responses from the component fluxes GEP and ER to variances in these variables. Pronounced reduction of summer PPT in two out of the six studied years correlated with

decreases in both GEP and ER, but not with NEE. Thus, the stable annual NEE was primarily achieved through a strong coupling of ER and GEP on seasonal and annual scales. Limited inter-annual variations in Ta ($\pm 0.5^\circ\text{C}$) and generally sufficient soil moisture availability may have further favored a stable annual NEE. Monthly ecosystem carbon use efficiency (CUE; as the ratio of NEE:GEP) during the main growing season (April 1–September 30) was negatively correlated with temperature and VPD, but positively correlated with soil moisture, whereas the annual CUE correlated negatively with annual NEE. Thus, although drier and warmer summers may mildly reduce the uptake potential, the annual uptake of atmospheric CO₂ in this intensively managed grassland, may be expected to continue even under predicted future climatic changes in the humid temperate climate region.

Key words: carbon use efficiency; climate change; eddy-covariance; flux; inter-annual variability; Ireland; *Lolium perenne* L.; net ecosystem exchange of carbon dioxide.

Received 23 June 2010; accepted 8 October 2010;
published online 12 November 2010

Author Contributions: MP wrote the paper, analyzed and interpreted the data. PL contributed to data analysis, commented on paper. GK conceived and designed the study, assisted in writing of paper, supported the research.

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INTRODUCTION

Grasslands cover about 40% of the Earth's terrestrial ice-free area and constitute an important component in the Earth climate system and global

carbon (C) balance, storing approximately one third of the global terrestrial C stock (Scurlock and Hall 1998; White and others 2000; IPCC 2007). In addition, grassland ecosystems are important ecological and socio-economical resources through their contribution to biodiversity and their use for food, forage, and livestock production (Sala and Paruelo 1997; White and others 2000). Thus, understanding grassland ecosystem dynamics is imperative to secure resource sustainability and to evaluate the role of grasslands in the global C cycle under future climate and management regimes.

Temperate grasslands are commonly considered to be close to C-neutral or a weak C sink, with mean C sequestration rates for North American and European grasslands ranging from 0.2 to 0.6 Mg C ha⁻¹ y⁻¹ (Jones and Donnelly 2004; Janssens and others 2005). In general, intensively managed grasslands may show enhanced uptake of atmospheric carbon dioxide (CO₂) (Allard and others 2007; Gilmanov and others 2010). In a recent review of global grasslands, Gilmanov and others (2010) reported mean annual ecosystem CO₂ uptake rates of 1.9 Mg C ha⁻¹ y⁻¹ for intensively managed grasslands, compared to 0.7 Mg C ha⁻¹ y⁻¹ for extensively managed grasslands. In addition to the net ecosystem CO₂ exchange (NEE), however, the net C sequestration rate of managed grasslands is highly affected by additional C fluxes due to management activities. For European grasslands, the net biome production (NBP) adjusting NEE by additional C inputs (for example, manure, feed concentrate, and so on) and outputs (for example, biomass and milk export, C losses via dissolved organic C, methane (CH₄), and respiration from cattle in stables) was recently estimated to average from 0.74 to 1.04 Mg C ha⁻¹ y⁻¹ on the farm scale (with the majority being intensively managed) (Soussana and others 2007; Ciais and others 2010), and at 101 Tg C y⁻¹ on the European scale (Janssens and others 2003).

In the past, several studies have shown that the annual CO₂ exchange of grasslands may vary in response to climate variability. Variations in precipitation (PPT) patterns, drought, and heat stress have been reported to result in prolonged suppression of both net primary and net ecosystem production (Heitschmidt and others 2005; Arnone and others 2008), and to cause a net release of CO₂ from grassland to the atmosphere (Kim and others 1992; Flanagan and others 2002; Gilmanov and others 2006, 2007; Ma and others 2007; Nagy and others 2007; Zhang and others 2010). Thus,

alterations in temperature and PPT regimes due to climatic changes may considerably affect the grassland C balance.

Variations in NEE result from differences in its two component fluxes: gross ecosystem production (GEP) and ecosystem respiration (ER). GEP is mainly controlled by the amount of photosynthetically active radiation (PAR), modified by effects from temperature and water availability, and further dependent on biotic controls such as vegetation biomass and leaf area, whereas ER is primarily driven by soil microbial activity and plant growth which themselves depend on temperature, moisture availability, and the supply of assimilates from photosynthetic activity (Bond-Lamberty and others 2004; Bahn and others 2008; Gilmanov and others 2010). Thus, ER is linked to GEP through its dependency on production and belowground allocation of photosynthetic assimilates. Considering these multiple controls, it is important to understand responses of the individual component fluxes GEP and ER to changes in environmental parameters to estimate the impacts of climatic conditions on the NEE.

To date, a limited number of multi-year (> 5 years) studies of grassland ecosystem CO₂ exchange exist, with the majority of them conducted in regions characterized by pronounced seasonal droughts and/or extensive grassland management. These multi-year studies altogether reported large inter-annual variability as well as the potential for the same site to exhibit annual net uptake and emission of CO₂ depending on climatic conditions (Frank 2004; Gilmanov and others 2006; Ma and others 2007; Wohlfahrt and others 2008). Meanwhile, less information is available on the long-term dynamics of grassland CO₂ exchange and response to climate variation in humid temperate regions. However, to evaluate the long-term CO₂ exchange capacity of grassland ecosystems and to predict its potential modification under a changing climate, multi-year observations are necessary to separate natural inter-annual variability in climate and ecosystem CO₂ exchange from the additional effects due to a changing climate.

In this study, we used 6 years of eddy-covariance (EC) data to determine the effects of environmental variables on the NEE, GEP, and ER of intensively managed grassland in the humid temperate climate of southern Ireland. Our primary objectives were (i) to determine the long-term annual CO₂ uptake/emission potential and (ii) to identify the main environmental drivers of inter-annual variability in CO₂ exchange.

MATERIALS AND METHODS

Site Description

This study was conducted at the Dripsey grassland research station which is located about 25 km northwest of Cork City in southern Ireland (51°59'N; 8°45'W; 195 m above sea level). The regional 30-year normal for annual mean air temperature (T_a) and total PPT are 9.4°C and 1207 mm, respectively (Met Eireann, 1960–1990 climate norms at Cork Airport Meteorological Station). Although, throughout the study period, annual PPT measured at the Dripsey grassland exceeded the annual amount measured at the Cork Airport Station by approximately 150 mm. Growing season length may extend from mid-March to mid-October; however, we define the main growing season in this study as from April 1 to September 30 based on measurements and observations of grass growth and production rates. The prevailing wind direction (Wd) is from the southwest.

The grassland is classified as a high quality pasture and meadow, with perennial ryegrass (*Lolium perenne* L.) being the dominant plant species, mixed with smaller amounts of Meadow foxtail (*Alopecurus pratensis* L.) and Yorkshire-fog (*Holcus lanatus* L.). The soil type is a gleysol with loamy soil texture (42% sand, 41% silt, 17% clay) (Lawton and others 2006). The soil organic C (SOC) concentration of the 0–20 cm soil layer was estimated at 5.9% in 2004 (Byrne and others 2005). The plant available soil moisture content ranges from 0.12 m³ m⁻³ (wilting point) to 0.32 m³ m⁻³ (field capacity), with the saturation level being estimated at 0.46 m³ m⁻³. The leaf area index (LAI) ranges between 0.5 and 1.0 m² m⁻² during the autumn and winter months and reaches 2.0–2.5 m² m⁻² during the summer months, with maximum grass heights in the summer recording approximately 20 and 45 cm in pasture and meadow fields, respectively (Byrne and others 2005; Byrne and Kiely 2006).

The grassland surrounding the EC flux tower consists of a mosaic of individual paddocks (the EC footprint may include ~15–50 fields depending on sensor height and atmospheric conditions) which vary in size between 1 and 3 ha and belong to three (2004–2009) or eight different farmers (2003). Thin wire-and-post fences separate most of these paddocks and thus exert no major obstruction to the wind flow. These paddocks differ in their management regimes but are all intensively managed for either silage/hay (1 or 2 cuts per year, typically in June and August, with an annual yield

of 7–10 t dry matter ha⁻¹ y⁻¹) or grazing of dairy and beef cattle (stocking density ranges between 1.7 and 2.2 livestock units ha⁻¹). Occasionally, some fields get mowed before grazing, and the cut grass is left on the field. From late March to early October, grazing events occur at different times for individual fields, with weekly to monthly rotational grazing cycles among fields belonging to the same farm, which introduces spatial and temporal heterogeneity in the footprint during this period. Cattle are housed for the remainder of the year (November–February). Fertilizer, including a variety of industrial inorganic fertilizers, slurry, and manure, was applied at various times to fields throughout the year totalling about 300–350 kg nitrogen (N) ha⁻¹ y⁻¹ between 2003 and 2004 and about 175–250 N ha⁻¹ y⁻¹ since 2005, with inorganic N fertilizer contributing about 60–90%. Although the spatial and temporal variability of these management activities causes considerable heterogeneity of the footprint within each year, averaged over the year, the management intensity and the proportion of grazed versus harvested fields was similar for all years. Furthermore, to evaluate the functioning of this farming system as a whole, our flux measurements represent an estimate of average CO₂ exchange of a managed grassland landscape (rather than of a single paddock ecosystem) which in this region is typically characterized by a combination of several small and individually managed paddock ecosystems.

In early 2005, a sector (5.25 ha in size) located southwest of the flux tower was ploughed and afforested with broadleaf trees. In this study we therefore disregarded fluxes if the mean Wd originated from this sector (230°–270°) for all years, including 2003 and 2004 for consistency.

Instrumentation for Micrometeorological Measurements

The net ecosystem exchange (NEE) of CO₂ was determined with the EC technique using a LI-7500 open path infrared gas analyzer (IRGA) (LICOR Inc., Lincoln, Nebraska, USA) in combination with a RM Young 3-D sonic anemometer (RM Young, model 81000, Traverse City, Michigan, USA) up to 2005 and with a Campbell Scientific (CS) 3-D sonic anemometer (CSAT3; CS, Logan, Utah, USA) in the following years. High frequency data (10 Hz) were averaged to 30 min averages.

The EC sensor height varied among years with 10, 3, and 6 m in 2003, 2004, and 2005–2009,

respectively. For the three different measurement heights, the mean distances for the peak flux source area and the 75% fetch were 191, 65, and 104 m and 1330, 449, and 724 m respectively, based on the Hsieh footprint model (Hsieh and others 2000).

Measurements of meteorological variables included Ta and relative humidity (RH) (HMP45A; Vaisala, Helsinki, Finland), PAR (PAR LITE sensor, Kipp & Zonen, Delft, The Netherlands), 2-dimensional wind speed (Ws) and Wd (RM Young). Vapor pressure deficit (VPD) was calculated based on Ta and RH. PPT was measured using a CS-ARG100 rain gauge. Soil temperature was determined with CS 107 temperature probes at 2.5, 5, and 7.5 cm depth. Volumetric soil water content (SWC) was measured at depths of 5, 10, 25, and 50 cm with CS 615 time domain reflectometers set horizontally in the soil, and for an average of 0–30-cm depth (root zone) with a vertically installed CS 615 probe. All meteorological measurements were sampled at 1 min intervals and averaged over 30 min. Gaps in the meteorological data due to power failure were filled with data from a nearby weather station (Met Eireann, Cork Airport Meteorological Station). Further details of instrument set up for micrometeorological measurements were previously given by Jaksic and others (2006).

Data Processing, Gap-Filling, and Flux Partitioning

Data processing followed standard protocols outlined by Aubinet and others (2000) and was previously described in detail by Jaksic and others (2006). In brief, we removed outliers in the dataset following Papale and others (2006), double rotated the wind vectors to align the coordinate system into the mean wind streamlines (Wilczak and others 2001), and applied a correction for variations in air density (Webb and others 1980). Data collected during and up to 1 h following rain events were rejected. Fluxes were also discarded for periods when friction velocity (u_*) was below the critical threshold of 0.2 m s^{-1} which was determined based on a regression of night time fluxes against u_* (Massman and Lee 2002).

Sensor malfunctioning resulted in an extended data gap in 2007. Owing to the large uncertainty associated with the gap-filling of longer periods during the growing season as a result of the spatial and temporal variability in management activities, we excluded the entire year of 2007 from our further analysis. Gaps of 3 to 4 weeks occurred in late March/early April 2005 and December 2009. These

gaps however were gap-filled (as described below) and included in the annual sum because interfering effects from management practices (that is, harvest) were minimal during these periods. In total, data gaps as a result of sensor malfunctioning, exclusion of data from the afforested sector, and data filtering during post-processing steps required gap-filling of 64, 58, 74, 68, 56, and 63% of the annual datasets in 2003, 2004, 2005, 2006, 2008, and 2009, respectively.

We developed a general exponential relationship between night time ER (above u_* threshold) and soil temperature at 5 cm depth based on data from all years. The additional effect of soil moisture was determined through residual analysis and added as a second scalar. To account for seasonal changes in the ER–Ts–SWC relationship, we then applied a time-varying correction factor determined by the comparison of modeled to observed values over a 100-points moving window (using a fixed number of measured (non-missing) data points rather than a fixed period of time) to adjust modeled values based on current conditions following Barr and others (2004). This final model was used to fill gaps in night time fluxes and to estimate daytime ER.

GEP was determined as the difference between daytime estimates of measured NEE and modeled ER. We developed a model that related GEP to environmental parameters including PAR, Ts, VPD, and SWC through residual analysis following Richardson and others (2007). A time-varying correction factor (Barr and others 2004) was also added to the final GEP model to account for seasonal variations in the general environmental response due to changes in phenology and short-term impacts from management events (that is, biomass removal via grazing and cutting; growth stimulation via fertilization) throughout the year. Previous studies used daily to monthly relationships between fluxes and environmental variables to account for these effects (Reichstein and others 2005; Gilmanov and others 2007; Chen and others 2009a; Zeeman and others 2010). However, high spatial and temporal heterogeneity of land management activities within the footprint caused random effects that in combination with fluctuations of the flux source area often hampered the development of robust relationships between component fluxes and environmental variables on daily to monthly scales throughout the summer months. Therefore, using a general robust multi-environmental-parameter relationship adjusted by a high temporal resolution correction factor proved best to account for these complex short-term management effects (model evaluation based on

comparison of root mean square errors). The correction factor however was considered unsuitable during the multi-week gaps (see above) and during autumn 2005 when good data coverage was sparse. These periods were therefore filled using the gap-filling models that related ER to Ts and SWC and related GEP to PAR, Ts, SWC, and VPD as described above. Gaps in daytime NEE were filled with the difference of modeled GEP and ER estimates. We use the micrometeorological sign convention in which fluxes from the atmosphere to the ecosystem are negative and emission fluxes are positive. For illustrative purposes however, GEP is presented in absolute values (|GEP|) where appropriate to facilitate the direct comparison with flux magnitudes of ER.

Uncertainty in Gap-Filled Flux Estimates

We estimated the uncertainty in monthly, seasonal and annual NEE, GEP, and ER estimates introduced by the gap-filling models by aggregating their mean absolute error (MAE) and bias error (BE) over the respective number of filled data points. Because MAE and BE varied on a seasonal scale, we derived MAE and BE separately for winter (December–February), spring (March–May), summer (June–August), and autumn (September–November)

periods. In addition, MAE was also added to and aggregated over the respective number of observed values to simulate random flux measurement errors (Richardson and others 2008).

RESULTS

Environmental Conditions

The seasonal patterns of monthly mean air and soil temperatures were similar for all years with the 6-year averages peaking in July/August (Figure 1). The 6-year average of monthly mean PAR peaked in June. On average, monthly PPT during autumn and winter months (October–January) was about 50 mm higher compared to the other months. The greatest deviation in soil moisture dynamics from the 6-year average was observed in 2006 when monthly mean SWC remained exceptionally high and close to the saturation level ($\sim 0.46 \text{ m}^3 \text{ m}^{-3}$) throughout the winter and early spring, followed by minimum monthly values of $0.21 \text{ m}^3 \text{ m}^{-3}$ in the summer coinciding with reduced rainfall. It is noteworthy, however, that diurnal SWC never dropped below the wilting point of $0.12 \text{ m}^3 \text{ m}^{-3}$ during this exceptional drought period. The summer of 2006 also included months with highest VPD and Ta among all years.

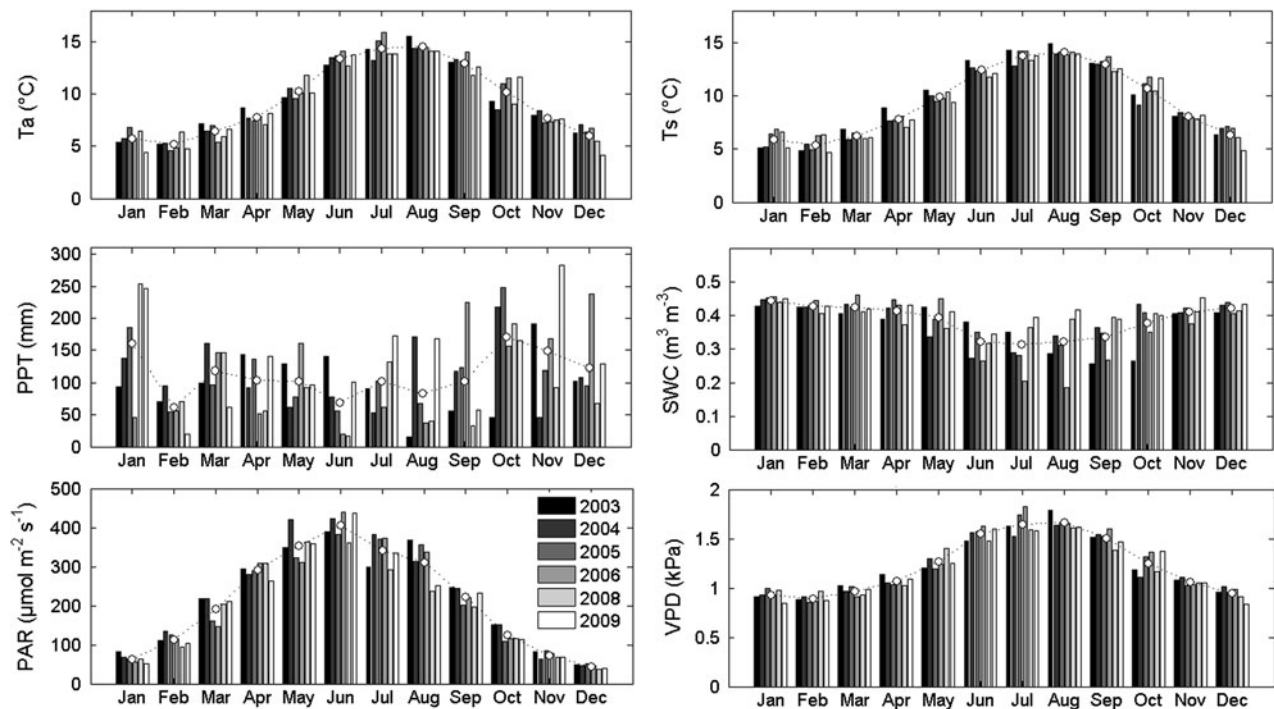


Figure 1. Monthly averages of air temperature (Ta), soil temperature (Ts) at 5-cm depth, photosynthetically active radiation (PAR), volumetric soil water content (SWC) from 0 to 30 cm depth (root zone), atmospheric water vapor pressure deficit (VPD), and monthly totals of precipitation (PPT) at the Dripsey grassland. Circles connected with dotted line indicate 6-year average for each month.

On a growing season and annual scale, the year 2008 was characterized by lowest mean temperatures (T_a and T_s), PAR, VPD and above average SWC, whereas highest annual mean temperature and VPD combined with lowest SWC were measured in 2006 (Table 1). Overall, the inter-annual variability was small for annual mean T_a and T_s ($< \pm 0.5^\circ\text{C}$), PAR ($212 \pm 17 \mu\text{mol m}^{-2} \text{s}^{-1}$), VPD ($1.26 \pm 0.08 \text{ kPa}$), and SWC ($0.38 \pm 0.03 \text{ m}^3 \text{ m}^{-3}$), whereas annual totals of PPT covered a wide range from 1178 to 1642 mm during 2003–2009.

Seasonal and Inter-Annual Patterns in Ecosystem CO_2 Fluxes

Minimum monthly NEE occurred in April and May suggesting the greatest net CO_2 uptake during this period (Figure 2A). Continuous CO_2 uptake occurred from February to July in all years, whereas net uptake or emission of CO_2 alternated for the remaining months among the study years, with the 6-year average suggesting a net CO_2 loss from the ecosystem to the atmosphere for the 5 months from September to January.

The 6-year average of monthly GEP was the greatest in May and July (Figure 2B). The intermittent reduction of GEP in June was most likely the result of the first harvest cut commonly being carried out during this month. Monthly GEP from May to August was the highest in 2004. In contrast, monthly GEP was considerably reduced in spring (March and April) and late summer (August) of 2006, compared to the other years.

The 6-year average of monthly ER was the greatest from July to September (Figure 2C). The shift in the timing of maximum ER and GEP explains the patterns observed for NEE including maximum net CO_2 uptake in spring and net CO_2 loss throughout autumn. Similar to GEP, the monthly ER from May to August was the greatest in 2004, whereas ER was considerably lower during those months of 2006 in which GEP was reduced (that is, March, April, and August). This indicates coupling of GEP and ER on a monthly scale.

The annual NEE remained within a narrow range from -245 to $-284 \text{ g C m}^{-2} \text{ y}^{-1}$ for 5 out of 6 years, given an uncertainty of $\pm 39\text{--}52 \text{ g C m}^{-2} \text{ y}^{-1}$ (Table 1). The exception was the year 2008 in which NEE reached $-352 \text{ g C m}^{-2} \text{ y}^{-1}$. Annual ER and GEP were considerably higher in the years 2003 and 2004 compared with other years.

Strong positive relationships were observed between GEP and ER on a seasonal and annual scale (Figure 3). The linear regression slope switched from less than 1 in spring to greater than 1 in

summer, while being approximately 1 in autumn. Linear regression slopes close to unity over the period March–August as well as for the entire year demonstrate the strong coupling of GEP and ER on these temporal scales and may explain the small variations in annual NEE. This dependency is further confirmed by similar directions and magnitudes in annual anomalies of GEP and ER in all years, except for 2008 in which anomalies were found diverted in opposite directions (Figure 4). Furthermore, although statistically not significant ($P > 0.05$), there was an apparent trend of spring GEP and summer ER being positively correlated (coefficient of determination (R^2) = 0.38).

Environmental Controls on Ecosystem CO_2 Fluxes

In general, short-term relationships between fluxes and environmental parameters were weak and most likely masked by grazing and silage cutting events which caused spatial and temporal heterogeneity of biomass and leaf area primarily during the harvesting period (June–August). Owing to the concurrent variations of these management events and the predominant flux source area, a clear signal from environmental variables was, therefore, not always apparent for the entire flux footprint.

Nevertheless, peaks in the 5-day averages of GEP and NEE commonly coincided with peaks in T_a and PAR (Figure 5, showing the representative years 2003, 2006, and 2008). Furthermore, peaks in GEP were often accompanied by simultaneous or slightly delayed (by 1 or 2 weeks) peaks in ER indicating a dependency of ER on GEP.

There were no related patterns between the time series of CO_2 fluxes and PPT events or fluctuations of soil moisture contents (Figure 5). However, residual analysis showed that both ER and GEP started to decrease as SWC either approached values beyond the saturation levels (above $\sim 0.46 \text{ m}^3 \text{ m}^{-3}$) or below about $0.25 \text{ m}^3 \text{ m}^{-3}$ (data not shown). Thus, higher soil moisture levels during the early spring 2006, for instance, may explain lower ER and GEP during this period compared with other years (Figure 5: also recall Figures 1 and 2).

There were two pronounced drought periods occurring within the study period which had varying effects on ecosystem CO_2 fluxes. The first drought event in late summer 2003 showed no apparent effect on ecosystem CO_2 fluxes (Figure 5, I). The effect of the second drought period in summer 2006, however, can be subdivided into three phases ($\text{II}_{a,b,c}$). During the first phase (II_a , first

Table 1. (a) Annual (A) and Main Growing Season (GS; April 1–September 30) Environmental Conditions and (b) Ecosystem CO₂ Fluxes (g C m⁻² y⁻¹; ±uncertainty as Described in the Text) for each of the Six Study Years at the Dripsey Grassland Site

		2003	2004	2005	2006	2008	2009	6-Year mean
(a) Environmental variables								
Air temperature (°C)	A	9.6	9.5	9.9 ^{max}	9.8	9.4 ^{min}	9.5	9.6 [9.4]
	GS	12.3	12.1	12.2	12.7 ^{max}	11.9 ^{min}	12.1	12.2 [12.1]
Soil temperature (°C)	A	9.7	9.3	9.8	9.9 ^{max}	9.3 ^{min}	9.3	9.5
	GS	12.5 ^{max}	11.6	11.9	12.0	11.5 ^{min}	11.6	11.8
Photosynthetically active Radiation (μmol m ⁻² s ⁻¹)	A	220	229 ^{max}	211	213	195 ^{min}	206	212
	GS	324	344 ^{max}	321	332	293 ^{min}	313	321
Vapor pressure deficit (kPa)	A	1.24	1.22	1.26	1.41 ^{max}	1.21 ^{min}	1.22	1.26
	GS	1.46	1.43	1.44	1.58 ^{max}	1.41 ^{min}	1.43	1.46
Soil water content (m ³ m ⁻³ ; 0–30 cm)	A	0.37	0.38	0.39	0.36 ^{min}	0.39	0.42 ^{max}	0.38
	GS	0.35	0.34	0.35	0.30 ^{min}	0.37	0.40 ^{max}	0.35
Precipitation (mm)	A	1178 ^{min}	1341	1362	1366	1194	1642 ^{max}	1347 [1207]
	GS	574	574	563	557	369 ^{min}	735 ^{max}	562 [475]
(b) Ecosystem CO₂ fluxes								
Net ecosystem exchange (NEE) ¹	A	-264 ± 52	-245 ± 39 ^{max}	-268 ± 52	-249 ± 49	-352 ± 36 ^{min}	-284 ± 45	-277 ± 46
Gross ecosystem production (GEP) ¹	A	-1810 ± 26	-1894 ± 25 ^{max}	-1709 ± 22	-1568 ± 25 ^{min}	-1752 ± 26	-1697 ± 26	-1738 ± 25
Ecosystem respiration (ER) ¹	A	1502 ± 51	1632 ± 49 ^{max}	1433 ± 58	1287 ± 55 ^{min}	1394 ± 49	1403 ± 50	1442 ± 52
Carbon use efficiency (CUE) ²	A	0.15	0.13 ^{min}	0.16	0.16	0.20 ^{max}	0.17	0.16

Values in [] indicate 30-year averages (1962–1991) from the Cork Airport Weather Station (Met Eireann).

min/max highlights minimum/maximum value among study years, respectively.

¹ Negative sign indicates CO₂.

² CUE derived from the ratio NEE:GEP.

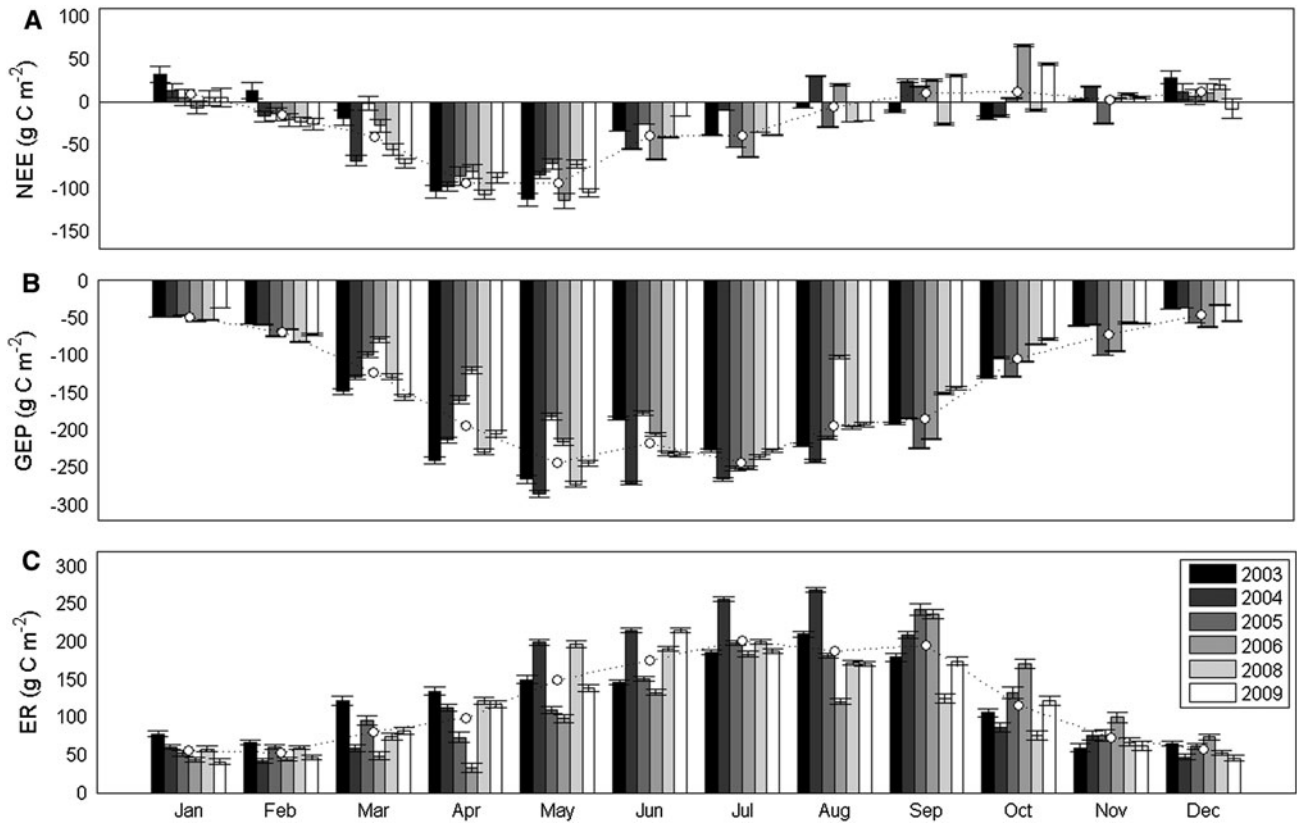


Figure 2. Monthly totals of **A** net ecosystem exchange (NEE), **B** gross ecosystem production (GEP), and **C** ecosystem respiration (ER) at the Dripsey grassland. *Circles* connected with *dotted line* indicate 6-year average for each month. *Error bars* represent uncertainty estimates as described in the text.

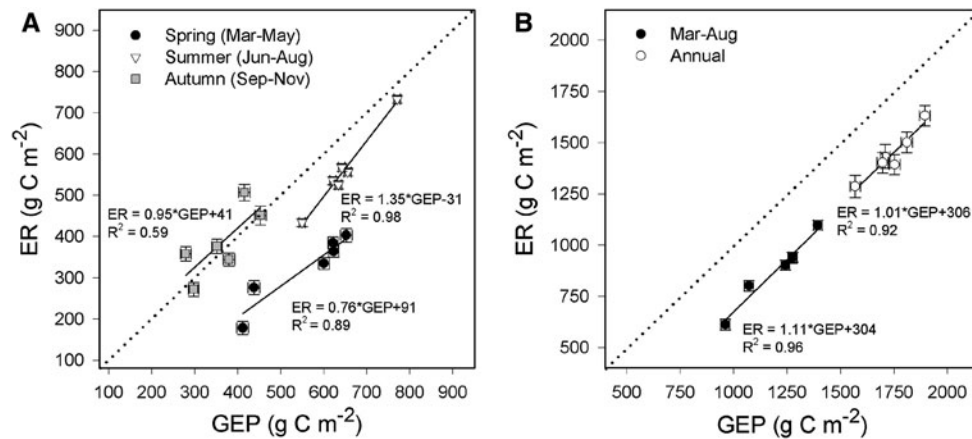


Figure 3. Correlation between totals of ecosystem respiration (ER) and gross ecosystem production (GEP) on **A** seasonal (spring = March 1–May 31; summer = June 1–August 31; autumn = September 1–October 31) and **B** early growing season (that is, spring and summer) and annual scale; *dotted line* indicates 1:1 relationship; GEP is shown in absolute values ($|GEP|$) for illustrative purposes. *Error bars* represent uncertainty estimates as described in the text.

week of June to mid-July), ecosystem CO_2 fluxes remained initially unaffected by the drop in SWC and continued to be primarily driven by variations

in T_a and PAR. The end of this phase was characterized by a drop in GEP, possibly because of a combination of harvesting events and/or drops in

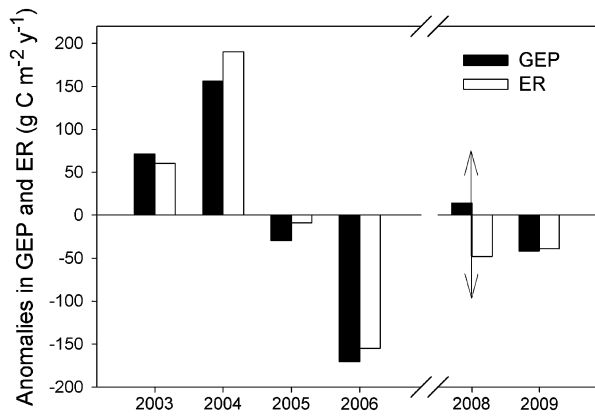


Figure 4. Anomalies in annual gross ecosystem production (GEP) and ecosystem respiration (ER). *Double arrow* highlights divergence of GEP and ER anomalies.

Ta and PAR, resulting in a net CO₂ loss. In the second phase (II_b; mid-July until mid-August), SWC further decreased to less than 0.20 m³ m⁻³. During this period, a simultaneous rapid decrease in both GEP and ER occurred, whereas NEE remained unaffected. The third phase terminating this drought period (II_c, mid-August until mid-September) showed large net CO₂ losses because the onset of heavy rainfall events resulted in an immediate increase of ER, whereas the recovery of GEP was delayed by 1 or 2 weeks.

Mean spring GEP and ER were positively correlated with mean spring Ta and PAR; however, owing to the simultaneous increase of both GEP and ER with higher TA and PAR, spring NEE did not correlate with these two environmental parameters

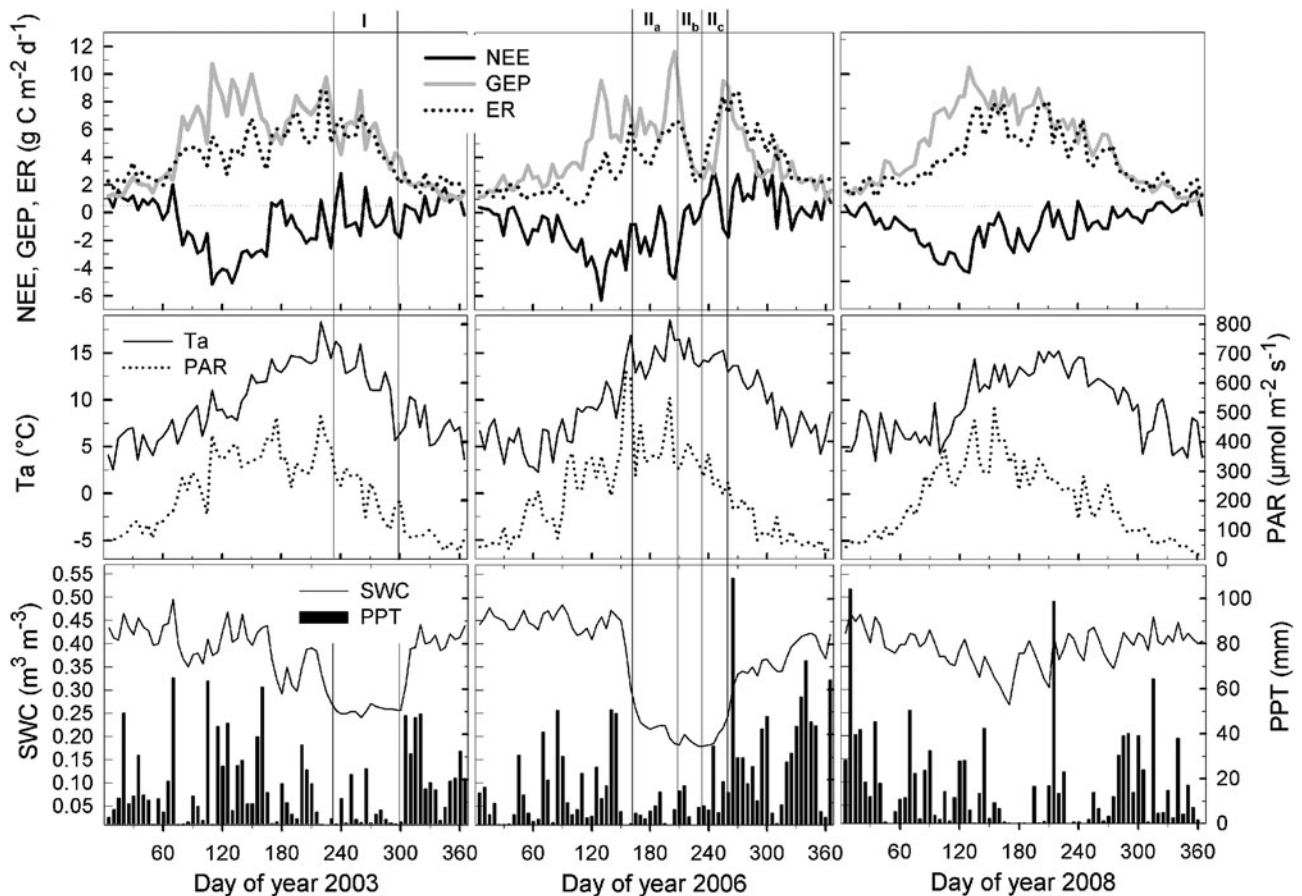


Figure 5. Five-day averages for daily totals of net ecosystem exchange (NEE), gross ecosystem production (GEP), ecosystem respiration (ER), and for daily means of air temperature (Ta), photosynthetically active radiation (PAR), soil water content (SWC, 0–30-cm depth) and 5-day totals of precipitation (PPT; shown as *horizontal bars*) in the selected years 2003, 2006, and 2008. *Roman numbers* (I and II_{a,b,c}) indicate various drought phases; note that GEP is shown in absolute values (|GEP|) for illustrative purposes.

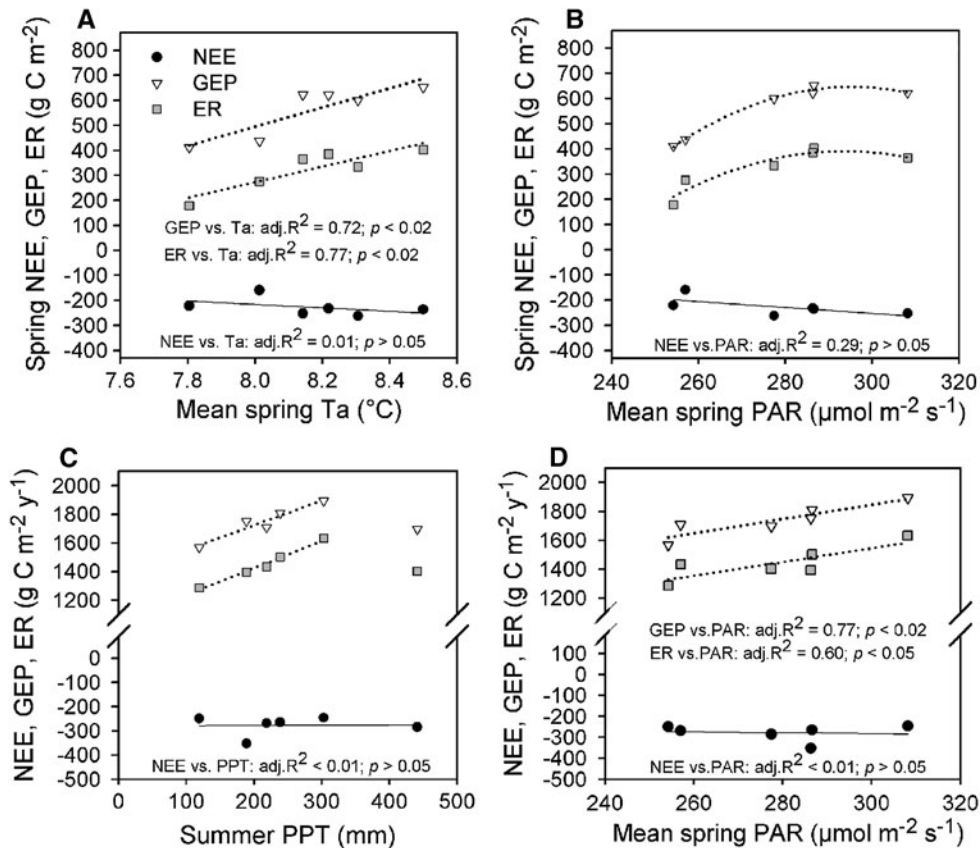


Figure 6. Correlations of net ecosystem exchange (NEE), gross ecosystem production (GEP), and ecosystem respiration (ER) with mean air temperature (Ta), photosynthetically active radiation (PAR), and totals of precipitation (PPT) on seasonal (spring = March 1–May 31; summer = June 1–August 31) and annual scales; note that GEP is shown in absolute values ($|GEP|$) for illustrative purposes.

(Figure 6A, B). Similarly, despite a positive correlation of annual GEP to summer PPT (up to a threshold of ~ 300 mm) and spring PAR, no effect on annual NEE was apparent because the simultaneous response in ER counter-balanced the differences in GEP (Figure 6C, D). We did not find any statistical relationship between any of the measured environmental controls and NEE on an annual scale.

Monthly ecosystem C use efficiency (CUE) defined as the ratio of NEE:GEP was negatively correlated with temperature (Ta and Ts) and VPD, and positively correlated with SWC (Figure 7A–C). Monthly CUE was not related to PAR (Figure 7D). A stepwise regression further suggested that anomalies in monthly CUE may be sufficiently explained by temperature and SWC, whereas the explanatory power of VPD was eliminated because of its correlation with temperature. The correlations of CUE to these environmental parameters explained the highest annual CUE in 2008, which was the year with the lowest annual mean temperatures and VPD, combined with relatively high annual mean SWC (recall Table 1), and produced a negative relationship between annual CUE and NEE (see inset in Figure 7D). Thus, while variations in individual environmental parameters did not directly result in

inter-annual differences in NEE, they indirectly affected annual NEE through their control on CUE.

DISCUSSION

Stable Inter-Annual NEE Due to Coupling of GEP and ER

The 6-year averages of NEE, GEP, and ER in this grassland were at the upper end of respective ranges reported for intensively managed grasslands in a recent review of global non-forest ecosystems by Gilmanov and others (2010), indicating its potential for high productivity and C turnover. Compared to previous long-term studies primarily conducted in drier and more extensively managed grasslands, the range of approximately $100 \text{ g C m}^{-2} \text{y}^{-1}$ between minimum and maximum annual NEE observed in this study was less than the range of 88 to $-141 \text{ g C m}^{-2} \text{y}^{-1}$ over 6 years in a Californian grassland site (Ma and others 2007), and 170 to $-116/236$ to $-32 \text{ g C m}^{-2} \text{y}^{-1}$ over 6/7 years in two sagebrush–steppe ecosystems (Gilmanov and others 2006), but comparable to the range from 69 to $-42 \text{ g C m}^{-2} \text{y}^{-1}$ over a 6-year study period in a temperate mountain meadow (Wohlfahrt and

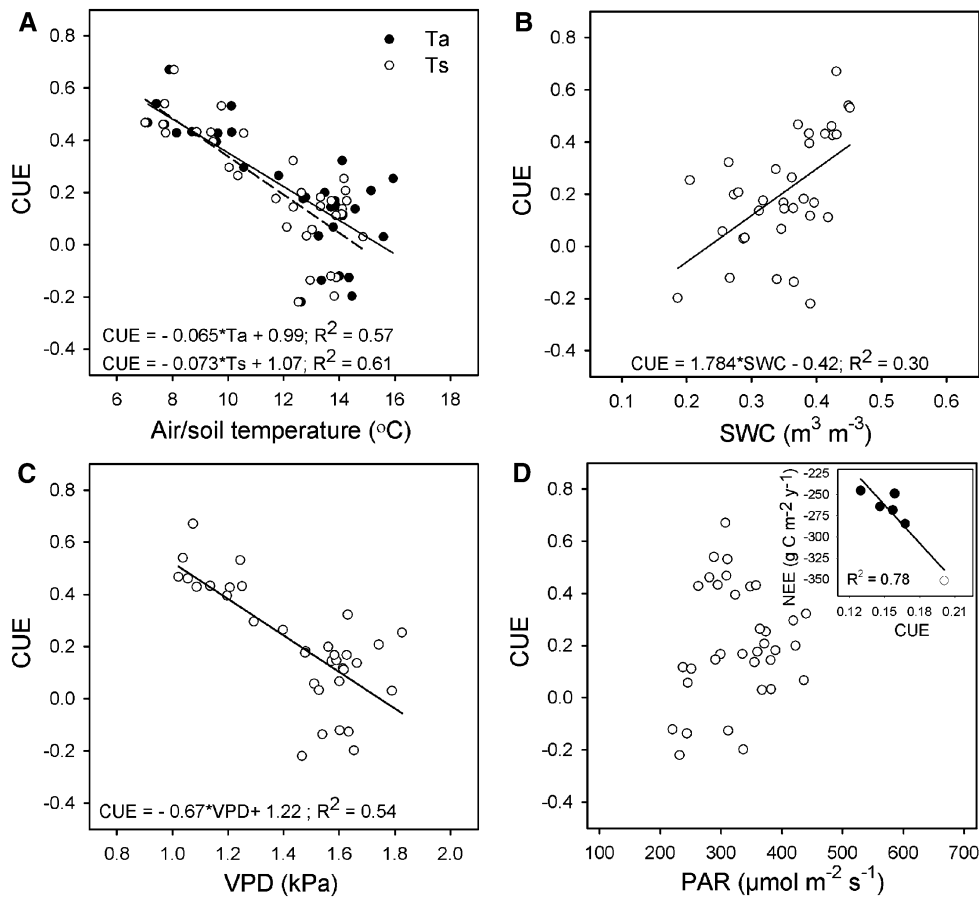


Figure 7. Correlations of monthly ecosystem carbon use efficiency (CUE; =NEE:GEP) with monthly means of **A** air/soil temperature (Ta; Ts), **B** volumetric soil water content (SWC, 0–30-cm depth average), **C** vapor pressure deficit (VPD), and **D** photosynthetically active radiation (PAR) during the main growing season. *Inset* figure shows relationship between annual net ecosystem exchange (NEE) and CUE (with 2008 highlighted as unfilled symbol).

others 2008) and from 4 to 70 g C m⁻² y⁻¹ over 6 years in a moderately grazed mixed-grass prairie (Frank 2004). In contrast to these other long-term studies, however, our grassland provided consistent and strong annual CO₂ uptake throughout the entire study period. A longer (from mid-March until mid-October) and more humid growing season compared to global grasslands may generally favor the CO₂ uptake potential in humid temperate grasslands. Thus, the strong capability for atmospheric CO₂ uptake might be a unique and distinguishing feature for intensively managed humid temperate grasslands compared with more extensively managed grasslands in dry temperate, continental, or Mediterranean climates.

Based on our results, we suggest that the stable inter-annual NEE was primarily due to a strong coupling of GEP and ER in this grassland. Numerous studies have previously suggested a tight relationship between GEP and ER in grassland ecosystems. For instance, Bahn and others (2008) found that soil respiration was positively correlated with assimilate supply over a range of European grassland sites. There is evidence in the literature that reduced assimilate supply following clipping

events may induce a negative effect on both autotrophic (root) and heterotrophic respiration (Bond-Lamberty and others 2004; Bahn and others 2006, 2008). Kaštovská and Šantrůčková (2007) reported rapid belowground allocation of fixed CO₂ and soil microbial biomass turnover in pasture plant–soil systems.

The approximate 1:1 linear GEP–ER response observed on the growing season and annual scale in our study, however, is in contrast to other studies which commonly observed linear response slopes less than 1 (Ma and others 2007; Fu and others 2009; Schmitt and others 2010). A recent synthesis of non-forest ecosystems, however, indicated that a slope of less than 1 occurs primarily for lower productivity ecosystems, whereas the slope for high productive grasslands appeared to be close to 1 (Figure 10b in Gilmanov and others 2010), suggesting that the strength of GEP–ER coupling increases with grassland productivity. To achieve a 1:1 linear GEP–ER response, similar absolute changes in GEP and ER are required. This condition was met in this study, possibly because of greater biomass production during the early growing season resulting in greater heterotrophic respiration

from increased availability of decomposable material during the later parts of the growing season. This hypothesis is supported by the positive relationship of spring GEP and summer ER in our study, suggesting that changes in spring productivity lead to corresponding changes in summer ER, thereby maintaining a similar net CO₂ balance. Thus, fast C allocation and turnover rates resulting in tight coupling of GEP and ER may favor a stable annual uptake of atmospheric CO₂ in this intensively managed grassland.

Besides the coupling mechanism between GEP and ER, limited inter-annual variation in temperature and generally abundant and sufficient soil moisture availability may have been the additional factors contributing to a stable and narrow range of annual NEE in this grassland. Studies in drier regions more prone to soil water stress have reported net CO₂ loss during drought events, commonly because of greater reductions in GEP compared with ER during these periods (Kim and others 1992; Novick and others 2004; Nagy and others 2007; Aires and others 2008; Arnone and others 2008; Zhang and others 2010). Thus, a consistent annual CO₂ uptake may be a feature more common for grasslands in humid temperate regions.

Environmental Controls on Grassland Ecosystem CO₂ Exchange

The lack of an individual environmental driver for inter-annual variability in NEE observed in this study was due to the compensating effects of environmental variables (for example, Ta, PAR, PPT, and so on) on the component fluxes GEP and ER, combined with a masking effect from management practices. Similar observations were previously made by Wohlfahrt and others (2008) for a repeatedly cut temperate mountain meadow.

Interestingly, two prolonged periods with reduced summer PPT showed contrasting effects on short-term CO₂ flux dynamics in 2003 versus 2006. We propose that, in this grassland, the effect of reduced summer PPT on CO₂ fluxes may depend on (i) the timing of the drought event (mid-summer versus late summer), and/or (ii) SWC falling below a threshold level of less than about 0.20 m³ m⁻³. In the first case, the combined effects from harvest and drought during mid-summer may have greater impact on ecosystem CO₂ fluxes than the sole drought effect during the late summer season (after the main harvesting season). The second possibility implies that soil moisture levels below a SWC threshold of about 0.20 m³ m⁻³ are necessary in this grassland to observe negative effects on GEP

and ER as a result of incipient soil water stress. It is noteworthy, however, that NEE was less affected during this period of minimum SWC. Instead, it was the onset of the rainy period following the drought which led to positive NEE and CO₂ losses due to an immediate pulse in ER whereas the recovery of GEP lagged behind by 1 or 2 weeks. The timing and interaction of drought and rain pulse events have been previously highlighted as important controls on grassland CO₂ fluxes (Kim and others 1992; Xu and others 2004; Gilmanov and others 2006; Ma and others 2007; Chen and others 2009b).

Despite the apparent lack of a single environmental control on annual NEE, temperature, VPD, and SWC indirectly affected annual NEE through their correlation with CUE in our study. This implies that despite generally coupled component fluxes, environmental variables may affect GEP and ER in a different manner. For instance, higher temperature may increase ER while the concurrent high VPD may constrain GEP, which, therefore, reduces CUE. However, our results suggested that only the continuous combination of low temperature, low VPD, and high SWC or vice versa may cause significant deviations from the otherwise stable and narrow range of annual CUE and NEE in this intensively managed temperate grassland landscape. Thus, drier and warmer summer periods predicted for Ireland by future scenarios (McGrath and Lynch 2008) might possibly result in a moderate reduction of the CO₂ uptake potential but are unlikely to lead to a net CO₂ loss from this grassland on an annual scale.

Effect of Management Practices on Ecosystem CO₂ Exchange

Owing to the spatial and temporal heterogeneity in management practices combined with additional effects from environmental variables (that is, Ta and PAR), it was not possible to clearly isolate the effects of management practices in this study. Nevertheless, our results indicated that management practices have a limited effect on annual NEE at this grassland because of the strong coupling of GEP and ER. For instance, we observed that sudden drops in GEP throughout the summer season, likely as a result of enhanced harvesting and/or grazing intensity were usually accompanied by simultaneous or somewhat delayed decreases in ER. This is in agreement with previous studies that reported significant and immediate impacts of harvest/grazing on soil respiration due to the link between photosynthetic supply and respiratory processes (Bremer and Ham 2002; Bahn and others 2006, 2008). In contrast,

studies in mountainous grassland sites reported that management events (harvesting, grazing, and so on) negatively affected NEE primarily via their impact on GEP (Rogiers and others 2005; Wohlfahrt and others 2008; Schmitt and others 2010). Other studies suggested that an initial reduction of NEE following harvest may be restored within the time-scale of a week because of the fast recovery of leaf biomass, with weak effects on annual NEE (for example, Novick and others 2004).

Moreover, greater GEP in 2003 and 2004 was likely the result of higher N fertilizer application rates compared to the following years. However, owing to a simultaneous increase in ER, the net CO₂ uptake potential of those 2 years with higher N fertilizer application rates remained similar to that in following years with comparably lower N fertilizer application rates. It is known that intensive N fertilization may, besides increasing gross plant production, also enhance mineralization rates and subsequently lead to greater soil C losses from stimulated respiratory processes (Hatch and others 2000; Jones and Donnelly 2004). In contrast, Shimizu and others (2009) found that relative to a non-fertilized control site, inorganic fertilizer application rates of approximately 175 kg N ha⁻¹ y⁻¹ (thus slightly lower compared to ~175 to 250 kg N ha⁻¹ y⁻¹ applied at our grassland during 2005–2009) led to a greater net ecosystem CO₂ uptake in a less intensively managed meadow located in a humid continental climate. Thus, our study indicates that the response of NEE to management practices may diminish for intensively managed (inorganic N fertilization rates > ~200 kg N ha⁻¹ y⁻¹) and highly productive grasslands.

Grassland C Balance

An important characteristic of managed grasslands is the additional C input (via manure fertilization, concentrate feed, and CH₄ oxidation) and output (in silage, milk, animal respiration during winter housing, dissolved organic C, and CH₄ losses from enteric fermentation and dung/slurry storage tanks) beyond ecosystem boundaries. Accounting for these fluxes provides an estimate of the net C balance on the farm scale, also defined as the NBP (Soussana and others 2007). For the Dripsey grassland, previous studies estimated the additional annual C import and export to be in the magnitude of 125–169 and 40–68 g C m⁻² y⁻¹, respectively (Jaksic and others 2006; Byrne and others 2007). Thus, the long-term mean NBP of our grassland based on the 6-year average NEE and these additional farm scale C fluxes (ignoring additional C

losses via volatile organic compounds and dissolved inorganic C) is estimated at -184 ± 57 g C m⁻² y⁻¹ (negative NBP indicating net C sink). This is more than twice a recent estimate of average NBP of -74 ± 10 g C m⁻² y⁻¹ (Ciais and others 2010) and at the upper end of the range from 266 to -231 g C m⁻² y⁻¹ reported for intensively managed European grasslands (Soussana and others 2007; Ciais and others 2010). Assuming that most of the C sequestration occurs within the upper 30-cm soil layer, we estimate that C sequestration at that rate would result in an annual increase in the SOC concentration of 0.061%. Unfortunately, it was not possible to confirm such small changes with repeated soil C measurements given the natural spatial variability of SOC. Nevertheless, these findings indicate that under the current management practices, this grassland may also be considered as a considerable and consistent C sink on the farm scale.

CONCLUSIONS

This study investigated 6 years of CO₂ flux data measured with the EC technique in an intensively managed grassland in the humid temperate climate of southern Ireland. A wide range in annual N fertilization and PPT rates, as well as contrasting amounts of summer PPT occurred throughout the study period. Based on findings from these long-term measurements, we conclude that this grassland landscape provided a consistent and strong annual uptake of CO₂ with a 6-year mean of 277 ± 46 g C m⁻² y⁻¹. The consistency in the CO₂ uptake capacity might be a distinguishing feature of grasslands in humid temperate regions compared to those in drier climate regions. Our findings further imply that the strength of CO₂ uptake in this grassland may not be very sensitive to predicted alterations in future climate (that is, warmer and drier summers).

Inter-annual variability in NEE was limited mainly by a strong coupling of the component fluxes GEP and ER, which showed similar responses to changes in environmental variables and/or management practices on a seasonal and annual scale. We propose that enhanced coupling of component fluxes could be an important characteristic for intensively managed grasslands. An estimate of the NBP, in which NEE was adjusted by additional C input and output fluxes because of management activities, indicated that this grassland may also function as a C sink on the farm scale. Thus, under the current management regime, this intensively managed grassland is able to provide

long-term beneficial effects within both economical and climate change related context.

ACKNOWLEDGMENTS

This study was financed by the Irish Government under the National Development Plan 2000–2006 (Grant No. 2001-CC/CD-(5/7)), and the STRIVE program 2007–2013 (Grant No. 2008-CCRP-1.1A) which is managed by the Environmental Protection Agency. We would like to thank Kilian Murphy and Nelius Foley for their support in instrument maintenance and data collection. We also express our gratitude to the local farmers for granting access to their private land to conduct this study. Helpful comments from the reviewers are greatly appreciated.

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