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CO_2 fluxes in adjacent new and permanent temperate grasslands

Kenneth A. Byrne *, Ger Kiely, Paul Leahy

Centre for Hydrology, Micrometeorology and Climate Change, Department of Civil and Environmental Engineering, University College Cork, Cork, Ireland

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Abstract

Carbon dioxide (CO_2) fluxes and grass production were measured in adjacent new and permanent intensively managed, *Lolium perenne* grasslands. Cumulative grass production during 2004 was 0.38 and 0.70 kg C m^{-2} $year^{-1}$ in the new and permanent sites, respectively. Chamber measurements were used to create site-specific statistical response functions of gross primary production (GPP) and total respiration (R_{TOT}) at the two sites. A 1-year time series of GPP and R_{TOT} was reconstructed by combining these functions with measurements of leaf area index (LAI) and continuous meteorological data. Net ecosystem exchange (NEE) was estimated by subtracting R_{TOT} from GPP. Seasonal variation in GPP closely followed the changes in grass production and LAI. R_{TOT} increased in summertime due to increased soil temperature and optimal soil moisture conditions. Both sites were net CO_2 sinks during the grass growing season. Cumulative values of GPP, R_{TOT} and NEE in the new grassland were 2.14, −1.98 and 0.15 kg C m^{-2} $year^{-1}$, respectively. In the permanent grassland cumulative values of GPP, R_{TOT} and NEE were 2.90, −2.52 and 0.38 kg C m^{-2} $year^{-1}$, respectively.

Keywords: *Lolium perenne*; Carbon balance; Leaf area index; Crop yield

1. Introduction

Terrestrial ecosystems in the northern hemisphere are net sinks for atmospheric carbon dioxide (CO_2) (Ciais et al., 1995; Fan et al., 1998; Janssens et al., 2003; Pacala et al., 2001). However, the size and spatial distribution of this sink remains uncertain (Pacala et al., 2001; Schimel et al., 2001). In attempting to quantify this sink, the scientific community has focused much of its attention on forest ecosystems which have been extensively studied in North America (Barford et al., 2001; Chen et al., 1999; Law et al., 2001) and Eurasia (Kolari et al., 2004; Kowalski et al., 2004; Schulze et al., 1999; Valentini et al., 2000). However, CO_2 exchange in grasslands has received much less attention even though grasslands are one of the world's most abundant land cover types and comprise approximately 40.5% of the earth's terrestrial land area, excluding areas of permanent ice cover (Adams et al., 1990; White et al., 2000). There is a growing body of research information regarding CO_2 dynamics both in C_4-dominated grasslands (Frank and Karn, 2003; Ham and Knapp, 1998; Meyers, 2001; Sims and Bradford, 2001; Suyker et al., 2003; Xu and Baldocchi, 2004) and temperate grasslands (Flanagan et al., 2002; Ham and Knapp, 1998; Hunt et al., 2004; Novick et al., 2004; Xu and Baldocchi, 2004). These studies show that grasslands can act as both a sink and source of CO_2. However, there is a need for information on the effect of management and environmental factors on CO_2 exchange in intensively managed grasslands.

In this study we have two sites: one is a recently established grassland (Site A), the second is a

* Corresponding author. Tel.: +353 21 490 3025; fax: +353 21 427 6648.
E-mail address: k.byrne@ucc.ie (K.A. Byrne).

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permanent grassland (Site B). We aim to (1) measure grass production at both sites; (2) assess the major biotic and abiotic factors controlling CO_2 dynamics in both grasslands; and (3) use chamber measurements to create statistical response functions for CO_2 exchange in order to reconstruct monthly and annual fluxes of gross primary production (GPP, kg C m^{-2}), net ecosystem exchange (NEE, kg C m^{-2}) and total respiration (R_{TOT}, kg C m^{-2}) at the two sites.

2. Materials and methods

2.1. Site description

The study was located in intensively managed and fertilised grassland in Co. Cork southern Ireland (latitude: 51°59′N, longitude: 8° 45′W). The average application of nitrogen in the area as fertiliser and slurry is approximately 300 kg N ha^{-1} $year^{-1}$. Site A was previously grassland and a new pasture was established, following ploughing and cultivation in Autumn 2003. Site B is a permanent 15-year-old pasture. The dominant grass species in both sites is perennial ryegrass (*Lolium perenne* L.) with smaller amounts of Meadow foxtail (*Alopecurus pratensis* L.) and Yorkshire-fog (*Holcus lanatus* L.) The study area is 180 m above sea level and the climate is temperate maritime with an average annual rainfall of 1470 mm. Climatic conditions during 2004 are shown in Fig. 1.

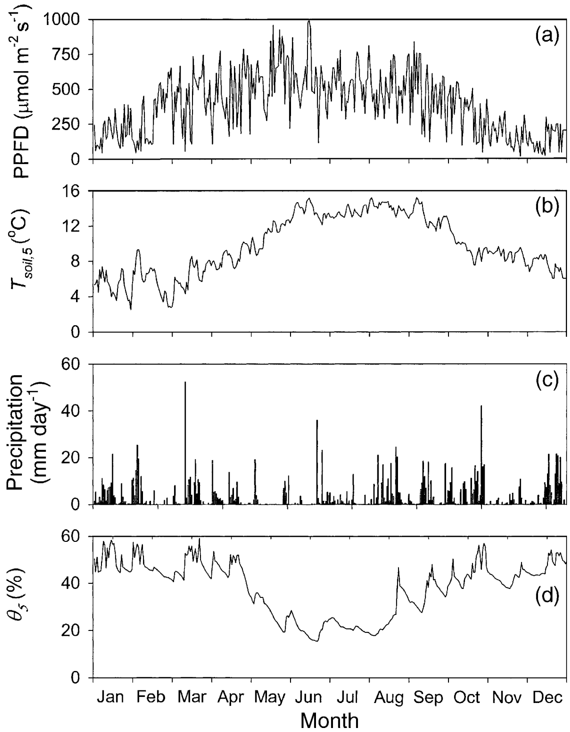

Fig. 1. (a) Average daytime photosynthetic photon flux density (PPFD); (b) average daily soil temperature at 5 cm depth ($T_{soil,5}$); (c) daily precipitation; and (d) average daily volumetric soil moisture content at 5 cm depth (θ_5) during 2004. All data were taken from the meteorological station located in Site B.

The soil type is surface water gley (Gardiner and Radford, 1980). Soil properties are similar in both sites. In Site A the surface soil (0–20 cm) is a loam (52% sand, 30% silt and 18% clay) and the subsoil (20–30 cm) is a sandy-clay loam (53% sand, 27% silt and 20% clay). The surface soil bulk density is 1.73 g cm^{-3} and the organic carbon content is 3.9%. In Site B the surface soil (0–20 cm) is a loam (39% sand, 44% silt and 17% clay) as is the subsoil (20–30 cm) (43% sand, 41% silt and 16% clay). The surface soil bulk density is 1.17 g cm^{-3} and the organic carbon content is 5.9%. The phosphorus content (Morgans P) of the surface soil is 17.6 mg P l^{-1} in Site A and 13.5 mg P l^{-1} in Site B. These are within the range of values observed at the same site by Scanlon et al. (2004). Soil pH in the top 20 cm is 5.9 and 5.4 in Sites A and B, respectively.

2.2. Grass growth measurements

In February 2004 eight samples plots were installed in each site (A and B) using stainless steel collars (60 cm × 60 cm × 15 cm). Grass production was measured by cutting the grass to a stubble height of 5 cm from two plots of each site every week on a 4-week cycle, i.e. all eight plots in each site were cut over a period of 4 weeks. The dry mass was measured after oven drying at 70 °C for 48 h. In order to simulate local management all plots received an equivalent fertiliser application of 300 kg N ha^{-1} divided into eight equal applications at intervals of 4 weeks from 1 March to 13 September. Grass height was measured weekly in all plots from 29 March to 15 November. Weekly, simultaneous measurements of grass height and one-sided leaf area index (LAI) were made in each site throughout the study period. LAI was calculated from PPFD transmission data that were measured with a linear array of 80-sensor series of quantum sensors (AccuPAR model PAR-80, Ceptometer, Decagon Instruments, WA, USA) and used to calculate gap fractions, which were inverted to derive LAI estimates (Norman and Campbell, 1989). Linear regression constrained to pass through the origin was used to develop site-specific relationships between grass height and LAI (Fig. 2).

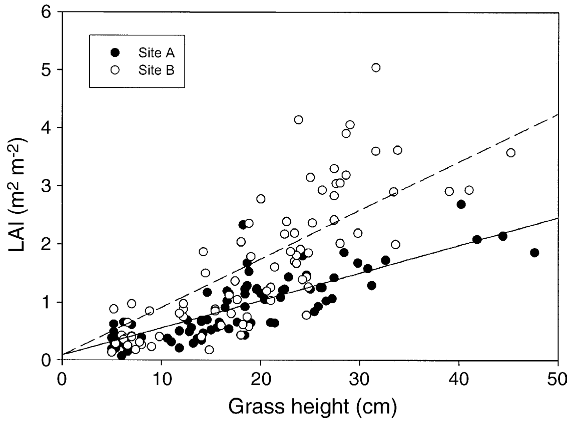

Fig. 2. Relationships between grass height and leaf area index (LAI) in Sites A and B. For Site A the equation for the fitted (solid) line is $L_A = 0.015(h_A)$; $R^2 = 0.69$; (L_A = LAI; h_A = grass height in cm); for Site B the equation for the fitted (dashed) line is $L_B = 0.087(h_B)$; $R^2 = 0.64$; (L_B = LAI; h_B = grass height in cm).

2.3. Measurement of CO_2 fluxes

CO_2 fluxes were measured from the same stainless steel collars (i.e. eight per site) as used for grass production measurements. Measurements were made one or two times per week from March 2004 to March 2005. CO_2 fluxes were measured using a vented and thermostatically controlled, transparent perspex chamber (60 cm × 60 cm × 30 cm). The chamber headspace was fitted with a fan to ensure good air mixing. During CO_2 measurement the chamber was placed over the stainless steel collar, which has a water channel at the top to allow air sealing. The CO_2 concentration in the chamber headspace was measured using a portable infra-red gas analyzer (EGM-4, PP Systems, UK) equipped with a vacuum pump (suction from chamber headspace 100–150 ml air min^{-1}). Analyser readings of CO_2 concentration in ppm were recorded at intervals of 15 s after closing the chamber. The instantaneous net CO_2 exchange was measured with the chamber exposed to ambient illumination for 60–120 s. After each measurement the chamber was removed to allow stabilisation of the CO_2 concentration. Following this the total respiration rate (R_{TOT}) was measured with the chamber covered with an opaque canvas cover. For description of the method see Alm et al. (1997) and Tuittila et al. (1999). In order to relate CO_2 fluxes to prevailing environmental conditions, the photosynthetic photon flux density (PPFD) and air temperature inside the chamber were recorded simultaneously with NEE measurements. At the same time, soil temperature at 5 cm depth ($T_{soil,5}$, °C) and volumetric soil moisture content in the top 6 cm (θ_6, m^3 m^{-3}), relative to the sample plot soil surface, were measured. Photosynthetic photon flux density (μmol m^{-2} s^{-1}) was measured with a photodiode-based sensor (PAR-1, PP-Systems, UK). Soil moisture content was measured using a portable soil moisture probe (Theta Probe MLx2, Delta-T Devices, UK) suitably calibrated for the study area.

Continuous meteorological data (PPFD, soil temperature at 5 cm depth and soil moisture content at 5 cm depth) was collected at half-hourly intervals by an adjacent weather station located in Site B.

2.4. Modeling of CO_2 fluxes

CO_2 fluxes were calculated from the linear rate of change in CO_2 concentration inside the chamber headspace. We adopt the sign convention where fluxes from the biosphere to the atmosphere are negative. Gross primary production was calculated as the difference between CO_2 fluxes measured in light and dark and it was always positive.

Using the measured CO_2 fluxes and associated values of PPFD, $T_{soil,5}$, θ_6 and LAI statistical response functions for GPP and R_{TOT} were developed separately for each site using the procedure described below.

GPP was related to PPFD using the Michaelis–Menten type relationship for the light dependence of the rate of photosynthesis (Stryer, 1988). GPP was related to LAI using the Michaelis–Menten type relationship. Both of these relationships were incorporated in a statistical response function of the following form:

$$P_G = a_1\left(\frac{Q_{PPFD}}{a_2 + Q_{PPFD}}\right)\left(\frac{L}{a_3 + L}\right) \quad (1)$$

where P_G is the gross primary productivity, Q_{PPFD} the photosynthetic photon flux density, and L is the leaf area index.

Site-specific equation parameters for Sites A and B (Table 1) were determined using least squares non-linear regression.

Table 1
Estimated parameters used in Eq. (1) to calculate half-hourly gross primary productivity (GPP) in Sites A and B during 2004

Site	Parameter	Estimate	Std. error	p	R^2
A	a_1	69.10	5.93	<0.0001	0.78
	a_2	503.72	51.23	<0.0001	
	a_3	0.99	0.15	<0.0001	
B	a_1	116.18	13.96	<0.0001	0.81
	a_2	498.51	62.01	<0.0001	
	a_3	2.66	0.51	<0.0001	

Table 2
Estimated parameters used in Eq. (2) to calculate half-hourly total respiration (R_{TOT}) in Sites A and B during 2004

Site	Parameter	Estimate	Std. error	p	R^2
A	a_1	3.64	0.32	<0.0001	0.86
	a_2	0.06	0.004	<0.0001	
	a_3	20.92	0.29	<0.0001	
	a_4	0.45	0.01	<0.0001	
B	a_1	4.27	0.48	<0.0001	0.83
	a_2	0.07	0.006	<0.0001	
	a_3	25.48	0.60	<0.0001	
	a_4	0.50	0.02	<0.0001	

R_{TOT} was related to $T_{soil,5}$ using an exponential function and to θ_6 using an exponential type equation. Both of these relationships were incorporated in a statistical response function of the following form:

$$R_{TOT} = -a_1\exp(a_2 T_{soil,5})\exp\left[-0.5\left(\frac{\ln(\theta_6/a_3)}{a_4}\right)^2\right] \quad (2)$$

R_{TOT} is limited at low and high values of θ therefore a function to describe the relationship should rise to a maximum value and then decay. The θ response incorporated in Eq. (2) has this property. Site-specific equation parameters for Sites A and B (Table 2) were determined using least squares non-linear regression.

GPP and R_{TOT} are influenced simultaneously by the controlling variables in Eqs. (1) and (2). The sensitivity of GPP and R_{TOT} to variation in each controlling variable was analysed by adjusting the measured exchange rates so that a single factor was allowed to vary and the other factors were kept constant. These adjusted values of GPP and R_{TOT} allow presentation of the trend in the data related to a single controlling factor (fitted lines in Figs. 5 and 6). Each measured value of GPP and R_{TOT} was partitioned into its predicted and residual components using Eqs. (1) and (2), respectively. In this way the component predicted by the model in prevailing conditions was replaced by a value predicted in selected conditions. The set values were LAI = 1.0 $m^2\,m^{-2}$, PPFD = 500 $\mu mol\,m^{-2}\,s^{-1}$, θ_6 = 20% and $T_{soil,5}$ = 15 °C. Using the same values in both sites allows the response of GPP and R_{TOT} to their respective controlling variables to be compared between Sites. Furthermore, by adding the residuals to the adjusted values the variation not explained by the models is also presented.

GPP and R_{TOT} dynamics during 2004 were reconstructed by including the half-hourly environmental data from the meteorological station on site into the statistical response functions for GPP and R_{TOT} (Eqs. (1) and (2), respectively). Average daily LAI was included in the GPP function and was estimated for each site as follows: the average daily grass height in Sites A and B was estimated by linear interpolation of the weekly measured grass height. These daily grass heights were converted to daily LAI using the grass height–LAI relationships (Fig. 2). Grass height was not measured outside of the grass growing season and therefore LAI in Sites A and B was assumed to be 0.5 and 1.0, respectively, during this time (Fig. 4).

NEE was calculated half-hourly for each site with the equation:

$$F_c = P_G + R_{TOT} \quad (3)$$

where F_c is the net ecosystem exchange.

As stated previously we use the sign convention in which fluxes into the atmosphere are negative and fluxes into the ecosystem are positive. Therefore, GPP is always positive and R_{TOT} is always negative. Using Eq. (3), NEE is positive when the magnitude of GPP exceeds that of R_{TOT}. GPP, NEE and R_{TOT} values were integrated over the study period and monthly and annual totals calculated.

3. Results

3.1. Environmental variables

Soil temperature showed a marked seasonal trend during 2004 with a minimum daily average in wintertime of 2.5 °C and a maximum daily average

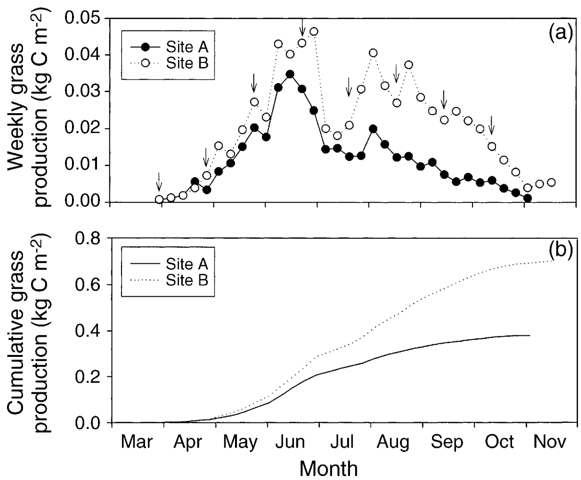

Fig. 3. (a) Weekly and (b) cumulative grass production in Sites A and B during 2004. The C content of grass is assumed to be 0.5. The arrows indicate the times of fertilizer application.

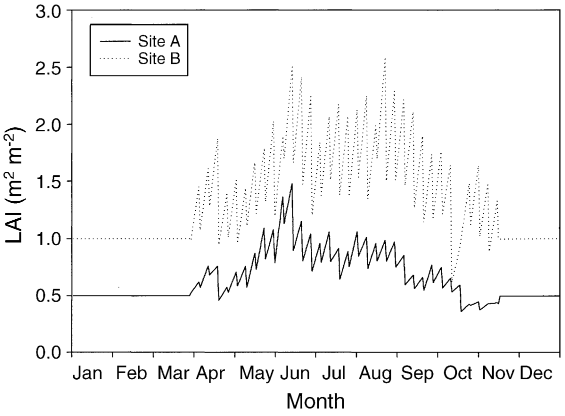

Fig. 4. Daily leaf area index (LAI) in Sites A and B during 2004. LAI was measured weekly in each site and daily values were calculated by linear interpolation.

in summer of 15.3 °C (Fig. 1). The total precipitation during 2004 was 1410 mm with rain days occurring throughout the year (Fig. 1(d)). There was a relatively dry period between Days 170 and 200. This is reflected in the annual trend in soil moisture content. Volumetric soil moisture content varied in the range 15–59% (Fig. 1).

3.2. Grass production

There was a clear difference in grass production between Sites A and B (Fig. 3). Grass production in Site A started to increase after the week ending 12 April and reached a peak of 0.03 kg C m^{-2} $week^{-1}$ in the week ending 14 June. Thereafter, it declined and although there was a brief increase in the week ending 2 August, production declined steadily hereafter. In contrast to Site A, grass production in Site B was consistently higher throughout the study period. Grass production increased after the week ending 12 April and, similarly to Site A, peaked between the weeks ending 31 May and 5 July. Subsequently grass production declined but increased after the week ending 12 July and reached ~0.04 kg C m^{-2} $week^{-1}$ in the weeks ending 2 August and 23 August, respectively. The cumulative grass production in Sites A and B was 0.38 and 0.70 kg C m^{-2}, respectively (Fig. 3(b)).

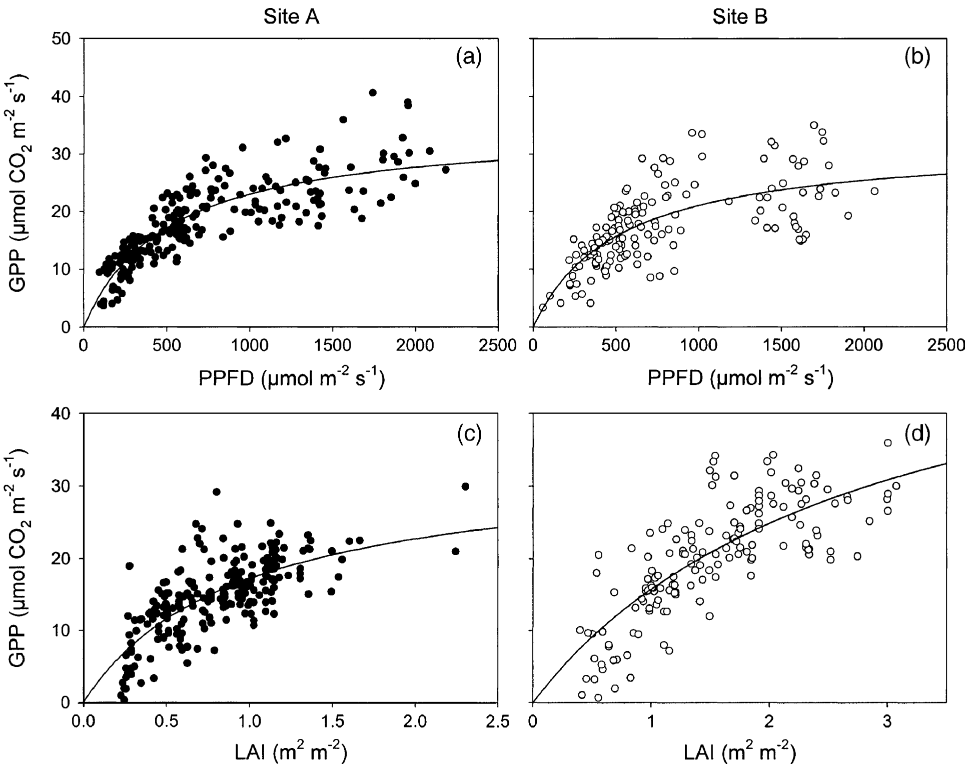

Fig. 5. (i) Adjusted response of gross primary production (GPP) to photosynthetic photon flux density (PPFD) in (a) Site A and (b) Site B. GPP values were adjusted to LAI = 1.0 m^2 m^{-2} using Eq. (1) and the parameter values in Table 1. (ii) Adjusted response of gross primary production (GPP) to leaf area index (LAI) in (c) Site A and (d) Site B. GPP values were adjusted to PPFD = 500 μmol m^{-2} s^{-1} using Eq. (1) and the parameter values in Table 1.

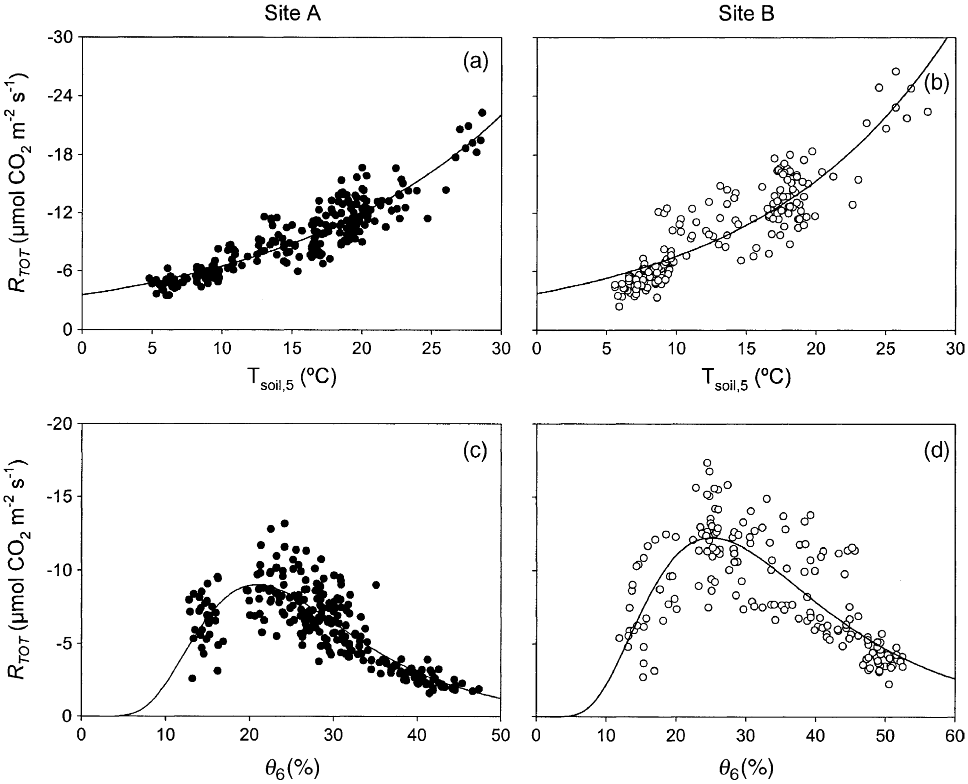

Fig. 6. (i) Adjusted response of total respiration (R_{TOT}) to soil temperature at 5 cm depth ($T_{soil,5}$) in (a) Site A and (b) Site B. R_{TOT} values were adjusted to soil moisture content in the top 6 cm (θ_6) = 20% using Eq. (2) and the parameter values in Table 2. (ii) Adjusted response of R_{TOT} to $T_{soil,5}$ in (c) Site A and (d) Site B. R_{TOT} values were adjusted to $T_{soil,5}$ = 15 °C using Eq. (2) and the parameter values in Table 2.

3.3. Leaf area index

Site averaged LAI ($m^2 m^{-2}$) in both sites varied in response to the 4-week grass cutting cycle (Fig. 4). LAI values in Site B were higher than in Site A. The highest LAI values occurred during periods of high grass production. Although LAI values in Site A were >1.25 between 5 June and 13 June, LAI was typically ~1.0 during the summer period. After this it declined to ~0.5. LAI in Site B followed a similar pattern to Site A, although the values were much higher. Typical summertime values were between 1.4 and 2.2.

3.4. Factors controlling GPP and R_{TOT}

PPFD and LAI controlled the rate of GPP in both sites. The GPP response to both PPFD and LAI was saturating (Fig. 5). Eq. (1) explained 78 and 81% of the variation in GPP and Sites A and B, respectively (Table 1). There was good agreement between measured and modelled GPP (Fig. 7(a, b)) although Eq. (1) may overestimate low GPP fluxes in Site B.

$T_{soil,5}$ and θ_6 controlled the rate of R_{TOT} in both sites (Fig. 6). Maximum R_{TOT} occurred when θ_6 was 20.1 and 25.5% at sites A and B, respectively. Eq. (2) explained 86 and 83% of the variation in R_{TOT} in Sites A and B, respectively (Table 2). There was good agreement between measured and modelled R_{TOT} (Fig. 7(c, d)) but Eq. (2) overestimates R_{TOT} fluxes below 5 µmol CO_2 m^{-2} s^{-1} in both sites.

3.5. Seasonal patterns of modeled GPP, R_{TOT} and NEE

In Sites A and B, GPP had a marked trend increasing from 0.06 and 0.08 kg C m^{-2} $month^{-1}$, respectively, in January to 0.36 and 0.47 kg C m^{-2} $month^{-1}$, respectively, in June. Thereafter, it declined from June to December. The high rates of GPP between May and August (Table 3) coincided with the period of highest grass production (Fig. 3) and LAI (Fig. 4) as well as high PPFD and better soil aeration (Fig. 1). Cumulative GPP for 2004 (Table 3) was higher in Site B (2.90 kg C m^{-2}) than in Site A (2.14 kg C m^{-2})

Table 3
Monthly and total values (kg C m^{-2}) of gross primary productivity (GPP), total respiration (R_{TOT}) and net ecosystem exchange (NEE) in Sites A and B during 2004

	Site A			Site B		
Month	GPP	R_{TOT}	NEE	GPP	R_{TOT}	NEE
January	0.06	−0.09	−0.03	0.08	−0.11	−0.03
February	0.09	−0.10	−0.01	0.12	−0.12	0.00
March	0.14	−0.10	0.04	0.20	−0.13	0.07
April	0.19	−0.12	0.07	0.26	−0.16	0.10
May	0.31	−0.21	0.10	0.38	−0.28	0.10
June	0.36	−0.26	0.10	0.47	−0.29	0.18
July	0.31	−0.26	0.05	0.43	−0.32	0.11
August	0.27	−0.25	0.02	0.38	−0.32	0.06
September	0.18	−0.21	−0.03	0.26	−0.30	−0.03
October	0.12	−0.14	−0.02	0.17	−0.18	−0.01
November	0.05	−0.14	−0.08	0.09	−0.18	−0.10
December	0.05	−0.11	−0.06	0.07	−0.4	−0.07
Total	2.14	−1.99	0.15	2.90	−2.52	0.38

although the difference was not as pronounced as the difference in grass production.

R_{TOT} varied seasonally in both sites with higher rates occurring in Site B (Table 3). The highest R_{TOT} rates occurred during the grass growing season when GPP and consequently R_{TOT} were high. This is because a large proportion of R_{TOT} is derived from root respiration that in turn is derived from recently assimilated CO_2. R_{TOT} rates were lowest outside the grass growing season (Table 3) when soil temperature was low and moisture content was high (Fig. 1). Cumulative R_{TOT} was 1.99 kg C m^{-2} in Site A and 2.52 kg C m^{-2} in Site B (Table 3).

NEE was positive (i.e. the site was a net sink for atmospheric CO_2) when GPP exceeded R_{TOT}. In Site A, monthly NEE was positive from March to August (Table 3) and coincided with the period of highest grass growth (Fig. 3). In the other months NEE was negative. The NEE in February, September and October was small relative to GPP and R_{TOT}. Overall, Site A was estimated to be a sink for 0.15 kg C m^{-2} in 2004 (Table 3).

NEE was higher in Site B than in Site A and was positive from March to August. Monthly NEE was highest during April to July (Table 3), the period of highest grass growth (Fig. 3). Overall Site B was estimated to be a sink for 0.38 kg C m^{-2} in 2004. As in Site A, there were months when modeled NEE was negative (i.e. September and October) although grass growth was relatively good (Fig. 3) and actual NEE is more likely to have been positive at this time.

4. Discussion

4.1. Grass production

The cumulative grass production in Site B is similar to the typical grass production rate of 0.65–0.75 kg C m^{-2} $year^{-1}$ in the south west of Ireland (Brereton, 1995). However, the cumulative grass production in Site A is approximately half of that in Site B. Given that reseeded *L. perenne* swards have similar grass production rates to permanent swards (Keating et al., 1995) this is contrary to expectation. Site A received regular applications of nitrogen and levels of soil phosphorus are adequate. We suggest that tiller density is low, due to insufficient grass-seeding, and consequently grass production is limited. Although tiller density was not measured, for a given grass height LAI in Site B is higher than in Site A (Fig. 2). This is most likely due to differences in tiller density.

4.2. The relationship between GPP and biotic and abiotic factors

GPP is commonly related to PPFD using the Michaelis–Menten function (Alm et al., 1997; Maljanen et al., 2001) and it was used here. While it provides a reasonable fit (Fig. 5(a, b)) such a relationship cannot capture variations in LAI that occur both seasonally and as a result of cutting. The GPP response to LAI was also modeled by incorporating a Michaelis–Menten function (Fig. 5(c, d)). The range of LAI during the CO_2 flux measurement period is much greater in Site B than in Site A and this is reflected in the relationship (GPP versus LAI, Fig. 5). The relationship between GPP and LAI has been reported elsewhere (Flanagan et al., 2002; Xu and Baldocchi, 2004) where a linear fit was used to describe the relationship. Given that self-shading is likely to occur as LAI increases a Michaelis–Menten function is considered to be more appropriate in this study.

4.3. The relationship between R_{TOT} and biotic and abiotic factors

R_{TOT} is the combination of autotrophic plant respiration (above- and below-ground) and heterotrophic microbial respiration. Temporal variation in R_{TOT} is commonly related to soil temperature and moisture content (Franzluebbers et al., 2002; Leiros et al., 1999; Orchard and Cook, 1983). Although there has been discussion and study of which exponential

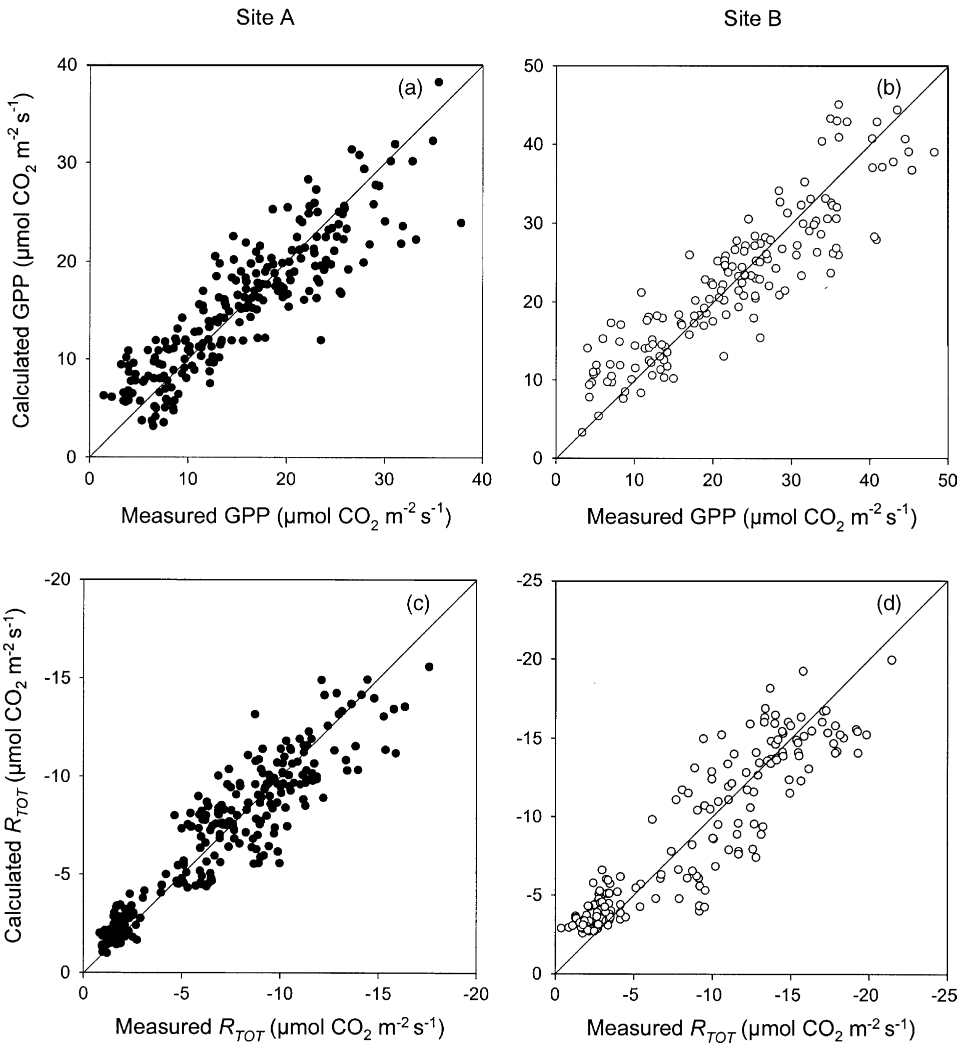

Fig. 7. Relationship between measured and calculated gross primary production (GPP) in (a) Site A and (b) Site B and, relationship between measured and calculated total respiration (R_{TOT}) in (c) Site A and (d) Site B.

formulation is best (Fang and Moncrieff, 2001; Lloyd and Taylor, 1994) the temperature effect in this study was best described by an exponential function. Although Fang and Moncrieff (2001) suggest that choosing an equation on the basis of a regression method does not ensure model suitability we feel that the exponential function is suitable for this study given that we have not extrapolated it beyond the temperature range to which the model was fitted.

Soil moisture content also exerts a strong influence on R_{TOT}. The relationship found here (Fig. 6) is similar to that found by Mielnick and Dugas (2000) although the R^2 in that study is lower (0.26). They found that maximum soil CO_2 efflux occurred at 25–30% soil moisture content, a value similar to this study (Fig. 6). Many studies demonstrate a positive relationship between soil moisture and CO_2 efflux (Epron et al., 1999; Leiros et al., 1999; Orchard and Cook, 1983). Others have found the opposite when soil moisture is high (Davidson et al., 1998; Gulledge and Schimel, 2000). Several functional forms have been used to describe the relationship, including linear functions with volumetric water content as an independent variable (Epron et al., 1999; Leiros et al., 1999; Orchard and Cook, 1983), exponential and logarithmic functions with water potential as an independent variable (Davidson et al., 1998; Davidson et al., 2000; Orchard and Cook, 1983). In this study an exponential type equation was found to provide the best fit for the relationship between R_{TOT} and θ_6 (Fig. 6(c, d)). R_{TOT} values increased with θ_6 reaching a maximum when θ_6 was 18.8 and 21.4% in Sites A and B, respectively (Fig. 6). At higher θ_6 values the relationship with R_{TOT} was negative. At high θ levels diffusion of O_2 is impeded which in turn retards decomposition and CO_2 production. At low θ levels decomposition is moisture limited.

Based on equations developed by Saxton et al. (1986) the permanent wilting point in both sites is estimated to occur when θ is 12%. θ_6 values approaching this were measured in both sites (Fig. 6(c, d)) and while the permanent wilting point may have been reached it is unlikely to have been maintained for long enough to be detrimental to grass growth.

4.4. Annual CO_2 flux

The annual NEE values in Sites A and B of 0.15 and 0.38 kg C m^{-2} $year^{-1}$, respectively, are within the range of those reported elsewhere for *L. perenne* grasslands. Working in the Netherlands, Jacobs et al. (2003) found a net C uptake of 0.68 kg C m^{-2} $year^{-1}$ in a grassland dominated by *L. perenne* and *Poa trivialis*, Also in the Netherlands, Schapendonk et al. (1997) found a NEE of 0.30 kg C m^{-2} $year^{-1}$. Using soil C analysis, Loiseau and Soussana (1999) found a C uptake of 0.6 and 0.8 kg C m^{-2} $year^{-1}$ in a *L. perenne* grassland fertilized with 160 and 530 kg N ha^{-1} $year^{-1}$.

In Site A NEE is 7% of GPP whereas in Site B it is 13%. The higher NEE in Site B is probably linked to the higher GPP and this is reflected in the grass production measured in both sites. Grass production in Site B is 85% higher than in Site A but GPP in Site B is only 26% higher than in Site A. This suggests that belowground transfer of C is higher in Site B.

The transfer of plant C to stable soil C was not measured in this study. If, as suggested by Follett et al. (1997), 10% of the annual C fixed by plants was stored in the soil as humus then Sites A and B would store about 0.015 and 0.038 kg C m^{-2} $year^{-1}$, respectively, in the soil. Rainfall in the study area is high (Fig. 1) and some of this may be lost as dissolved organic carbon in drainage water (Kalbitz et al., 2000).

Ploughing and cultivation, such as occurred during the reseeding of Site A in Autumn 2003, disturbs soil aggregates and may break soil structures. These changes and increased aeration can increase the rate of decomposition. During this phase, and in the absence of growing vegetation, the soil is a net source for CO_2. The sink function is restored when CO_2 uptake by the new grass crop exceeds respiration. The C content of the soil is low (4–6%) and any organic matter that accumulated at the soil surface during the previous rotation, which lasted approximately 15 years, may have been buried during ploughing. This would have limited the potential for C losses due to decomposition.

The aforementioned estimates of NEE assume that the grass was not removed from the sites. However, if the cumulative grass production (Fig. 3(b)) is subtracted from the NEE (Table 3) the NEE is reduced to −0.23 and −0.32 kg C m^{-2} $year^{-1}$ in Sites A and B, respect- ively. This assumes that all the C from the grass is immediately released back to the atmosphere. Under normal grassland management the grass would either be consumed on site by grazing animals or harvested and stored as winter feed. Some of this C would be returned to the site either in animal excreta or during slurry spreading. Therefore, the precise NEE of these intensively managed grasslands remains to be determined. Further studies on the farm level C balance and below ground C transfer and soil C cycling would help to address this question.

5. Conclusions

Our study shows that intensively managed and fertilized temperate grassland has the potential to act as a C sink. Chamber based CO_2 flux measurements found that GPP is strongly related to PPFD and LAI. R_{TOT} is both soil temperature and soil moisture dependent. These measurements provide a basis for developing statistical response functions that can be used to reconstruct seasonal and annual fluxes of GPP and R_{TOT}. The estimated NEE of 0.15 and 0.38 kg C m^{-2} $year^{-1}$ in Sites A and B, respectively, is within the range of those reported elsewhere for *L. perenne* grasslands. The difference in NEE between the two study sites is probably related to the difference in grass production and associated belowground translocation of C. While the results of this study suggest that increased productivity may lead to higher NEE knowledge of the influence of management factors such as grass cutting and grazing on grassland CO_2 exchange are required to determine the precise NEE.

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References

Adams, J.M., Faure, H., Fauredenard, L., McGlade, J.M., Woodward, F.I., 1990. Increases in terrestrial carbon storage from the last glacial maximum to the present. Nature 348, 711–714.

Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykänen, H., Martikainen, P.J., 1997. Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen Finland. Oecologia 110, 423–431.

Barford, C.C., Wofsy, S.C., Goulden, M.L., Munger, J.W., Pyle, E.H., Urbanski, S.P., Hutyra, L., Saleska, S.R., Fitzjarrald, D., Moore, K., 2001. Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. Science 294, 1688–1691.

Brereton, A.J., 1995. Regional and year-to-year variation in production. In: Jeffrey, D.W., Jones, M.B., McAdam, J.H. (Eds.), Irish Grasslands—Their Biology and Management. Royal Irish Academy, Dublin, pp. 12–22.

Chen, W.J., Black, T.A., Yang, P.C., Barr, A.G., Neumann, H.H., Nesic, Z., Blanken, P.D., Novak, M.D., Eley, J., Ketler, R.J., Cuenca, R., 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. Global Change Biol. 5, 41–53.

Ciais, P., Tans, P.P., Trolier, M., White, J.W.C., Francey, R.J., 1995. A large Northern hemisphere terrestrial CO_2 sink indicated by the $^{13}C/^{12}C$ ratio of atmospheric CO_2. Science 269, 1098–1102.

Davidson, A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biol. 4, 217–227.

Davidson, E.A., Verchot, L.V., Cattânio, J.H., Ackerman, I.L., Carvalho, J.E.M., 2000. Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. Biogeochemistry 48, 53–69.

Epron, D., Farque, L., Lucot, E., Badot, P.M., 1999. Soil CO_2 efflux in a beech forest: dependence on soil temperature and soil water content. Ann. Forest Sci. 56, 221–226.

Fan, S.M., Mahlman, J., Pacala, S., Sarmiento, J., Takahashi, T., Tans, P., 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. Science 282, 442–446.

Fang, C., Moncrieff, J.B., 2001. The dependence of soil CO_2 efflux on temperature. Soil Biol. Biochem. 33, 155–165.

Flanagan, L.B., Wever, L.A., Carlson, P.J., 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a Northern temperate grassland. Global Change Biol. 8, 599–615.

Follett, R.F., Paul, E.A., Leavitt, S.W., Halvorson, A.D., Lyon, D., Peterson, G.A., 1997. Carbon isotope ratios of Great Plains and in wheat-fallow systems. Soil Sci. Soc. Am. J. 61.

Frank, A.B., Karn, J.F., 2003. Vegetation indices, CO_2 flux, and biomass for Northern plains grasslands. J. Range Man. 56, 382–387.

Franzluebbers, K., Franzluebbers, A.J., Jawson, M.D., 2002. Environmental controls on soil and whole-ecosystem respiration from a tallgrass prairie. Soil Sci. Soc. Am. J. 66, 254–262.

Gardiner, M.J., Radford, T., 1980. Soil Associations of Ireland and Their Land Use Potential. An Foras Talúntais, Dublin, 143 pp.

Gulledge, J., Schimel, J.P., 2000. Controls on soil carbon dioxide and methane fluxes in a variety of taiga forest stands in interior Alaska. Ecosystems 3, 269–282.

Ham, J.M., Knapp, A.K., 1998. Fluxes of CO_2, water vapor, and energy from a prairie ecosystem during the seasonal transition from carbon sink to carbon source. Agric. Forest Meteorol. 89, 1–14.

Hunt, J.E., Kelliher, F.M., McSeveny, T.M., Ross, D.J., Whitehead, D., 2004. Long-term carbon exchange in a sparse, seasonally dry tussock grassland. Global Change Biol. 10, 1785–1800.

Jacobs, A.F.G., Heusinkveld, B.G., Holtslag, A.A.M., 2003. Carbon dioxide and water vapour flux densities over a grassland area in the Netherlands. Int. J. Climatol. 23, 1663–1675.

Janssens, I.A., Freibauer, A., Ciais, P., Smith, P., Nabuurs, G.J., Folberth, G., Schlamadinger, B., Hutjes, R.W.A., Ceulemans, R., Schulze, E.-D., Valentini, R., Dolman, A.J., 2003. Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO_2 emissions. Science 300, 1538–1542.

Kalbitz, K., Solinger, S., Park, J.-H., Michalzik, B., Matzner, E., 2000. Controls on the dynamics of dissolved organic matter in soil: a review. Soil Sci. 165, 277–304.

Keating, T., O'Kiely, P., Keane, G.P., 1995. Production from permanent and reseeded swards. In: Jeffrey, D.W., Jones, M.B., McAdam, J.H. (Eds.), Irish Grasslands—Their Biology and Management. Royal Irish Academy, Dublin, pp. 32–40.

Kolari, P., Pumpanen, J., Rannik, U., Ilvesniemi, H., Hari, P., Berninger, F., 2004. Carbon balance of different aged Scots pine forests in Southern Finland. Global Change Biol. 10, 1106–1119.

Kowalski, A.S., Loustau, D., Berbigier, P., Manca, G., Tedeschi, V., Borghetti, M., Valentini, R., Kolari, P., Berninger, F., Rannik, U., Hari, P., Rayment, M., Mencuccini, M., Moncrieff, J., Grace, J., 2004. Paired comparisons of carbon exchange between undisturbed and regenerating stands in four managed forests in Europe. Global Change Biol. 10, 1707–1723.

Law, B.E., Thornton, P.E., Irvine, J., Anthoni, P.M., Van Tuyl, S., 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biol. 7, 755–777.

Leiros, M.C., Trasar-Cepeda, C., Seoane, S., Gil-Sotres, F., 1999. Dependence of mineralization of soil organic matter on temperature and moisture. Soil Biol. Biochem. 31, 327–335.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Funct. Ecol. 8, 315–323.

Loiseau, P., Soussana, J.F., 1999. Elevated [CO_2], temperature increase and N supply effects on the accumulation of below-ground carbon in a temperate grassland ecosystem. Plant Soil 212, 123–131.

Maljanen, M., Martikainen, P.J., Walden, J., Silvola, J., 2001. CO_2 exchange in an organic field growing barley or grass in eastern Finland. Global Change Biol. 7, 679–692.

Meyers, T.P., 2001. A comparison of summertime water and CO_2 fluxes over rangeland for well watered and drought conditions. Agric. Forest Meteorol. 106, 205–214.

Mielnick, P.C., Dugas, W.A., 2000. Soil CO_2 flux in a tallgrass prairie. Soil Biol. Biochem. 32, 221–228.

Norman, J.M., Campbell, G.S., 1989. Canopy structure. In: Pearcy, R.W., Ehleringer, J., Mooney, H.A., Rundel, P.W. (Eds.), Plant Physiological Ecology. Chapman and Hall, New York, pp. 301–325.

Novick, K.A., Stoy, P.C., Katul, G.G., Ellsworth, D.S., Siqueira, M.B.S., Juang, J., Oren, R., 2004. Carbon dioxide and water vapour exchange in a warm temperate grassland. Oecologia 138, 259–274.

Orchard, V.A., Cook, F.J., 1983. Relationship between soil respiration and soil moisture. Soil Biol. Biochem. 15, 447–453.

Pacala, S.W., Hurtt, G.C., Baker, D., Peylin, P., Houghton, R.A., Birdsey, R.A., Heath, L., Sundquist, E.T., Stallard, R.F., Ciais, P., Moorcroft, P., Caspersen, J.P., Shevliakova, E., Moore, B., Kohlmaier, G., Holland, E., Gloor, M., Harmon, M.E., Fan, S.M., Sarmiento, J.L., Goodale, C.L., Schimel, D., Field, C.B., 2001. Consistent land- and atmosphere-based US carbon sink estimates. Science 292, 2316–2320.

Saxton, K.E., Rawls, W.J., Romberger, S.J., Papendick, R.I., 1986. Estimating generalized soil-water characteristics from texture. Soil Sci. Soc. Am. J. 50, 1031–1036.

Scanlon, T.M., Kiely, G., Xie, Q., 2004. A nested catchment approach for defining the hydrological controls on non-point phosphorus transport. J. Hydrol. 291, 218–231.

Schapendonk, A.H.C.M., Dijkstra, P., Groenwold, J., Pot, C.S., Vand de Geijn, S.C., 1997. Carbon balance and water use efficiency of frequently cut *Lolium perenne* L. swards at elevated carbon dioxide. Global Change Biol. 3, 207–216.

Schimel, D.S., House, J.I., Hibbard, K.A., Bousquet, P., Ciais, P., Peylin, P., Braswell, B.H., Apps, M.J., Baker, D., Bondeau, A., Canadell, J., Churkina, G., Cramer, W., Denning, A.S., Field, C.B., Friedlingstein, P., Goodale, C., Heimann, M., Houghton, R.A., Melillo, J.M., Moore, B., Murdiyarso, D., Noble, I., Pacala, S.W., Raupach, M.R., Rayner, P.J., Scholes, R.J., Steffen, W.L., Wirth, C., 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414, 169–172.

Schulze, E.-D., Lloyd, J., Kelliher, F.M., Wirth, C., Rebmann, C., Luhker, B., Mund, M., Knohl, A., Milyukova, I.M., Schulze, W., Ziegler, W., Varlagin, A.b., Sogachev, A.F., Valentini, R., Dore, S., Grigoriev, S., Kolle, O., Panfyorov, M.I., Tchebakova, N., Vygodskaya, N., 1999. Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink—a synthesis. Global Change Biol. 5, 703–722.

Sims, P.L., Bradford, J.A., 2001. Carbon dioxide fluxes in a southern plains prairie. Agric. Forest Meteorol. 109, 117–134.

Stryer, L., 1988. Biochemistry. Freeman, New York.

Suyker, A.E., Verma, S.B., Burba, G.G., 2003. Interannual variability in net CO_2 exchange of a native tallgrass prairie. Global Change Biol. 9, 255–265.

Tuittila, E.-S., Komulainen, V.-M., Vasander, H., Laine, J., 1999. Restored cut-away peatland as a sink for atmospheric CO_2. Oecologia 120, 563–574.

Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.-D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861–865.

White, R., Murray, S., Rohweder, M., 2000. Pilot Analysis of Global Ecosystems (PAGE): Grassland Ecosystems. World Resources Institute, Washington, DC.

Xu, L., Baldocchi, D.D., 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. Agric. Forest Meteorol. 123, 79–96.