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Partitioning of respiration in an intensively managed grassland

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Abstract

Total (R_{TOT}) and heterotrophic (R_H) respiration were measured in an intensively managed perennial ryegrass (*Lolium perenne* L.) grassland. The overall aim of the study was to partition R_{TOT} into R_H and autotrophic respiration (R_A). This was achieved as follows: (1) analyse the effect of air temperature, soil moisture content and leaf area index on R_{TOT} and the influence of soil temperature and soil moisture content on R_H; (2) combine these effects into separate empirical models for R_{TOT} and R_H and; (3) use these models to determine temporal trends in R_{TOT} and R_H and to assess the relative contribution of R_H and R_A to R_{TOT}. CO_2 fluxes were measured using a vented and thermostatically controlled perspex chamber in conjunction with a portable infrared gas analyser. R_{TOT} was measured in plots with grass and R_H in plots with bare soil. R_{TOT} was related to air temperature and R_H to soil temperature using exponential relationships. Both R_{TOT} and R_H were related to soil moisture content using lognormal relationships. R_{TOT} was related to leaf area index using a linear relationship. These relationships were combined to produce statistical response functions that explained 87% and 84% of the variation in R_{TOT} and R_H, respectively. These relationships were combined with meteorological and leaf area index data to reconstruct daily and seasonal fluxes. R_{TOT} values in wintertime were ~4 g C m^{-2} day^{-1} increasing to ~10 g C m^{-2} day^{-1} in summertime when temperatures and leaf area index were higher and soils were drier. R_H has a similar seasonal trend to R_{TOT} but was consistently lower. Wintertime values were ~2 g C m^{-2} day^{-1} and increased to ~5 g C m^{-2} day^{-1} in summertime. Before day of year 143, and after day of year 259 R_H and R_A represented 62% and 38% of R_{TOT}, respectively. In the period between these days R_H and R_A both accounted for 50% of R_{TOT}. In total during 2004 R_{TOT}, R_H and R_A were 2.34, 1.31 and 1.03 kg C m^{-2}, respectively.

Introduction

Grasslands cover approximately 40.5% of the Earth's terrestrial land area, excluding areas of permanent ice cover (Adams et al., 1990; White et al., 2000). Estimates of the amount of soil carbon (C) stored in these grasslands vary from 10% (Anderson, 1991) to 30% (Eswaran et al., 1993) of the global total. Studies have found that grasslands can act as both a sink and a source for atmospheric CO_2 (Barcza et al., 2003; Flanagan et al., 2002; Jacobs et al., 2003; Novick et al., 2004).

Carbon (C) fluxes in terrestrial ecosystems are dominated by two processes: (1) biochemical uptake of CO_2 through photosynthesis and (2) biochemical loss of CO_2 through respiration (R_{TOT}). R_{TOT} is the principal pathway of C loss from the ecosystem to the atmosphere and is a major determinant of the net uptake of C from the atmosphere. For instance, eddy covariance studies have shown that annually 80% of the C taken up during photosynthesis is respired back to the

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atmosphere (Law et al., 2002). Understanding R_{TOT} and its component processes is therefore vital to understanding C cycling and sequestration in soils.

R_{TOT} integrates two distinct processes, namely autotrophic (R_A) and heterotrophic (R_H) respiration. R_A is produced by growth-associated processes that require respiration and accounts for about half of soil respiration (Hanson et al., 2000; Hogberg et al., 2001). R_H is derived from microbial decomposition of recently produced organic matter (Giardina et al., 2004; Trumbore, 2000). Decomposition of older, more recalcitrant C compounds represents only a small fraction (10%) of soil respiration (Gaudinski et al., 2000; Giardina et al., 2004; Trumbore, 2000). The contribution of R_A and R_H to R_{TOT} can vary seasonally and between ecosystems (Hanson et al., 2000).

Soil respiration is commonly related to soil temperature using an exponential function (Leiros et al., 1999; Mielnick and Dugas, 2000; Xu and Baldocchi, 2004) although there has been discussion of which exponential function is best (Lloyd and Taylor, 1994). The relationship of R_{TOT} to soil moisture has been described by numerous equations, including linear (Leiros et al., 1999) logarithmic (Orchard and Cook, 1983), quadratic (Mielnick and Dugas, 2000) and parabolic (Raich and Potter, 1995). Soil respiration has also been related to the quantity and quality of soil organic carbon (La Scala et al., 2000). Other studies have shown soil pH to influence soil respiration (Andersson and Nilsson, 2001; Sitaula et al., 1995) since microbial activity is increased with rising pH values (Ellis et al., 1998). The link between primary production and R_A, (and thereby R_{TOT}), has been demonstrated in forest (Hogberg et al., 2001), cropland (Kuzyakov and Cheng, 2001) and grassland (Craine and Wedin, 2002) ecosystems. A number of studies have combined response functions for the relationship between CO_2 and its controlling factors to develop empirical models of soil respiration (Bremer and Ham, 2002; Lohila et al., 2003; Reth et al., 2005a).

Our understanding of the relative contribution of R_H and R_A to R_{TOT} in intensively managed grasslands remains limited and therefore the overall aim of the study is to partition R_{TOT} into R_H and R_A. This is achieved as follows: (1) analyse the effect of air temperature, soil moisture content and leaf area index on R_{TOT} and the influence of soil temperature and soil moisture content on $R_{H;}$ (2) combine these effects into separate empirical models for R_{TOT} and R_H and; (3) use these models to determine temporal trends in R_{TOT} and R_H and to assess the relative contribution of R_H and R_A to R_{TOT}.

Materials and methods

Site description

The study was located in an area of intensively managed grassland located 180 m above seas level in County Cork, southern Ireland (Latitude: 51°59′ N, Longitude 8°45′ W). The climate is temperate maritime and the average annual rainfall is 1470 mm. The total rainfall in 2004 was 1340 mm and the average daily mean temperature was 9.5° C. Approximately 300 kg N ha^{-1} $year^{-1}$ is applied as fertiliser and slurry. The soil is an Aqualf (Soil Survey Staff, 1975) and the surface soil (0–20 cm) is a loam (39% sand, 44% silt and 17% clay) with a bulk density of 1.17 g cm^{-3} and an organic carbon content of 5.9%. The phosphorus content of the surface soil is 11.5 mg P kg^{-1} (Morgans P) and is within the range of values observed at the same site by Scanlon et al. (2004). The dominant grass species is perennial ryegrass (*Lolium perenne* L.) with smaller amounts of Meadow foxtail (*Alopecurus pratensis* L.) and Yorkshire-fog (*Holcus lanatus* L.).

Experimental design

In February 2004, 10 sample plots were installed in the site using stainless steel collars ($0.6 \times 0.6 \times 0.15$ m). In eight of these plots the grass was cut to a height of 0.05 m in two plots every week on a four-week cycle i.e. all eight plots were cut over a period of 4 weeks. Grass cutting began on day of year 89 and ended on day of year 320. Grass height was measured weekly in all eight plots during the same period. Weekly, simultaneous measurements of grass height and two-sided leaf area index (LAI) were made in the study 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 a site-specific relationship between grass height and LAI ($\mathrm{LAI} = 0.087 \times \mathrm{h}$; $R^2 = 0.64$; h = grass height in m). Using this relationship, LAI for each sample plot at the time of CO_2 measurements was estimated. All plots received an equivalent fertiliser application of 300 kg N ha^{-1} divided into eight equal applications at four weekly intervals from day of year 61 to day of year 257.

Two plots (of the 10 installed in February 2004) were kept completely free of grass by regular clipping. Three additional plots were installed in January 2005 and also kept free of grass by regular clipping.

Measurement of CO_2 fluxes

CO_2 fluxes were measured one or two times per week during the period March 2004 to March 2005. CO_2 fluxes were measured using a vented and thermostatically controlled, transparent perspex chamber ($0.6 \times 0.6 \times 0.3$ m). The chamber headspace was fitted with a fan to ensure good air mixing and the vent ensured that pressure within the chamber headspace was the same as in ambient conditions. 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 infrared gas analyser (EGM-4, PP Systems, UK) equipped with a vacuum pump (suction from chamber headspace 0.01–0.015 L air min^{-1}). After closing the chamber, analyser readings of CO_2 concentration in ppm and air temperature (T_{air}, °C) were recorded at intervals of 15 s for a period of 60–120 s. During CO_2 measurements the chamber was covered with an opaque canvas cover. R_{TOT} was measured in the eight plots with grass cover and R_H was measured in the five plots with grass removed. For a description of the method see Alm et al. (1997) and Tuittila et al. (1999). CO_2 flux rates were calculated from the linear rate of change in CO_2 concentration inside the chamber headspace.

After each measurement, the soil temperature at 0.05 m depth ($T_{soil,5}$, °C) and volumetric soil moisture content ($m^3\ m^{-3}$) in the top 0.06 m (θ_6), relative to the sample plot soil surface, were measured in each plot. Soil moisture content was measured using a portable soil moisture probe (Theta Probe MLx2, Delta – T Devices, UK) calibrated for the study area. Soil temperature and soil moisture content at 0.05 m depth were measured at half-hourly intervals by a weather station located on site.

Modelling of CO_2 fluxes

In order to identify the major factors controlling R_{TOT} and R_H and to integrate these fluxes on a daily, seasonal and annual basis the relationships between the flux rate and the controlling factors were determined. For both R_{TOT} and R_H, a subsample of 70% of the flux measurements was randomly selected for regression modelling and the remaining 30% were used for validation of the models.

R_{TOT} was related to T_{air} using an exponential function, to θ_6 using an exponential type equation and to LAI using a linear equation. These relationships were incorporated in a statistical response function of the following form:

$$R_{TOT} = a_1 \exp(a_2 T_{air}) \exp\left[-0.5\left(\frac{\ln\left(\frac{\theta_6}{a_3}\right)}{a_4}\right)^2\right] \times (\mathrm{LAI} + \mathrm{a}_5) \quad (1)$$

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

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

The parameters (a_i) of the statistical response functions for R_{TOT} and R_H (Table 1) were estimated using the non-linear Levenberg–Marquardt technique. This technique uses an iterative approach to minimise the sum of squares error

Table 1. Parameter estimates, standard errors, *p*-values and coefficient of determination (R^2) for models used to construct half-hourly total respiration (R_{TOT}) and heterotrophic respiration (R_H) using Equations (1) and (2), respectively.

	Parameter	Estimate	Std. error	p	R^2
R_{TOT}	a_1	0.41	0.16	0.0116	0.87
	a_2	0.05	0.004	<0.0001	
	a_3	24.45	0.52	<0.0001	
	a_4	0.54	0.02	<0.0001	
	a_5	10.17	4.27	<0.0188	
R_H	a_1	2.43	0.37	<0.0001	0.84
	a_2	0.06	0.007	<0.0001	
	a_3	27.89	0.78	<0.0001	
	a_4	0.47	0.03	<0.0001	

function, where the initial parameters are adjusted until the most likely parameter values are reached when no further reduction in the sum of squares takes place (Motulsky and Christopoulos, 2003).

R_{TOT} and R_H are influenced simultaneously by the controlling factors in Equations (1) and (2). The response of R_{TOT} and R_H to variation in each individual controlling factor was analysed as follows. The measured values of R_{TOT} and R_H were adjusted so that a single controlling factor was allowed to vary and the other factors were kept constant. The constant values for each controlling factor were LAI = 1.0 $m^2\ m^{-2}$, $\theta_6 = 20\%$, $T_{air} = 15$ °C and $T_{soil,5} = 15$ °C. For example, the dependence of R_H on $T_{soil,5}$ was tested by combining the measured values of R_H and $T_{soil,5}$ with Equation (2) (and the parameters in Table 1) while keeping $\theta_6 = 20\%$. This procedure allows presentation of the response of R_{TOT} and R_H to variation in each individual controlling factor (fitted lines in Figures 2–4). Each measured value of R_{TOT} and R_H was partitioned into its predicted and residual components using Equations (1) and (2), respectively. Furthermore, by adding the residuals to the adjusted values the variation not explained by the models is also presented.

R_{TOT} and R_H dynamics during 2004 were reconstructed by including the half-hourly environmental data from the meteorological station into the statistical response functions for R_{TOT} and R_H (Equations (1) and (2), respectively). Average daily LAI was included in the R_{TOT} function and was estimated as follows: the average daily grass height 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 relationship already described. Grass height was not measured outside of the grass-growing season and therefore LAI was assumed to be 1.0 during this time (Figure 1d).

R_A (μmol $CO_2\ m^{-2}\ s^{-1}$) was calculated half-hourly with the equation:

$$R_A = R_{TOT} - R_H \tag{3}$$

R_{TOT}, R_H and R_A values were integrated over the study period and daily and annual totals calculated.

Results

T_{air} and $T_{soil,5}$ showed a marked seasonal trend during 2004 with a minimum daily average in wintertime of 0.3 and 2.5 °C, respectively and a maximum daily average in summer of 17.2 and 15.3 °C, respectively (Figure 1a). Total precipitation during 2004 was 1410 mm with rain days occurring throughout the year (Figure 1b). Soil moisture content was between 40% and 60% for much of the year with drier conditions during summertime. LAI varied in response to grass cutting with values between 1.1 and 2.5 $m^2\ m^{-2}$ (Figure 1d). Values were greater between days 150 and 250 when grass production was higher.

R_{TOT} was controlled by T_{air} (Figure 2a), θ_6 (Figure 3a) and LAI (Figure 4). The maximum R_{TOT} occurred when θ_6 was 24.4%. Equation (1) explained 87% of the variation in R_{TOT} (Table 1). There was good agreement between the measured and modelled R_{TOT} (Figure 5a)

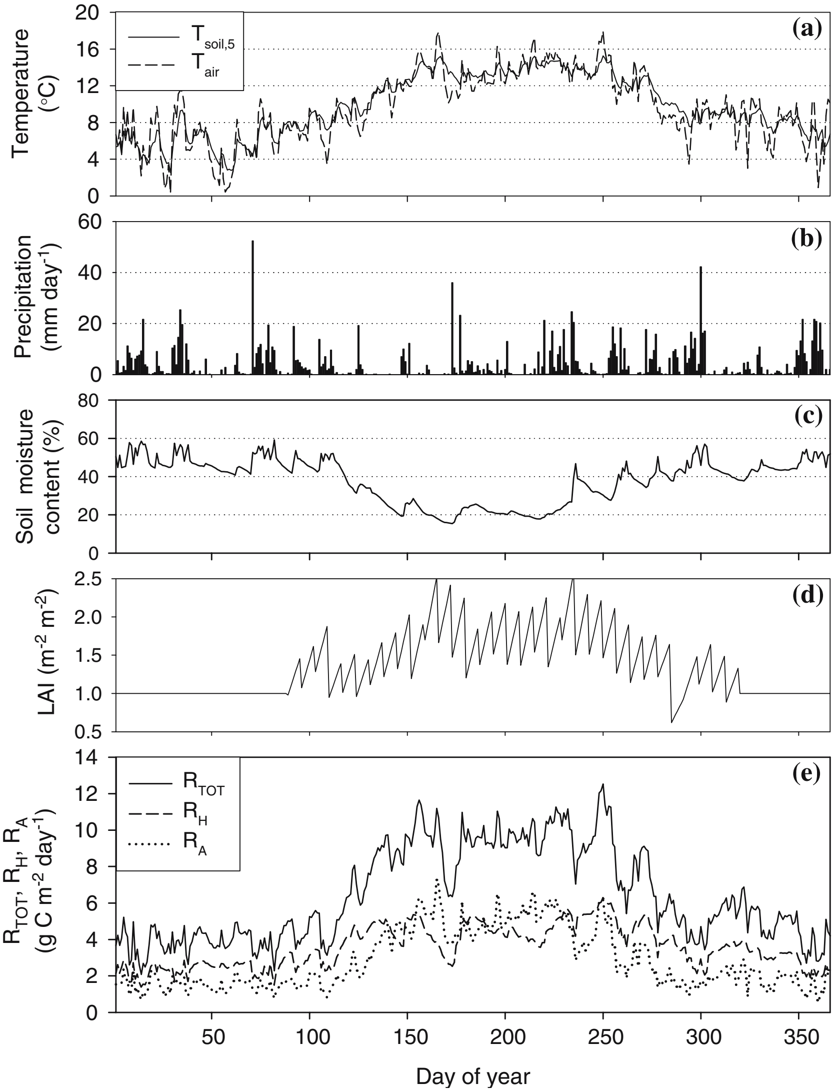

Figure 1. (a) Average daily soil temperature at 5 cm depth ($T_{\mathrm{soil,5}}$) and air temperature (T_{air}), (b) daily precipitation, (c) average daily volumetric soil moisture content at 5 cm depth (θ_5) and (d) daily leaf area index, (e) average daily total respiration (R_{TOT}), heterotrophic respiration (R_{H}) and autotrophic respiration (R_{A}), during 2004.

although the R_{TOT} model (Equation (1)) overestimates R_{TOT} fluxes below 5 μmol CO_2 m^{-2} s^{-1}. In the 30% independent data set Equation (1) explained 91% of the variation in R_{TOT} and there was good agreement between measured and modelled data (Figure 5a).

R_{H} was related to $T_{\mathrm{soil,5}}$ (Figure 2b) and θ_6 (Figure 3b) and maximum R_{H} occurred when θ_6 was 27.8%. Equation (2) explained 84% of the variation in R_{H} (Table 1) and there was good agreement between measured and modelled R_{H} (Figure 5b). In the 30% independent data set Equation (1) explained 87% of the variation in R_{H} and there was good agreement between measured and modelled data (Figure 5b).

There was a marked seasonal trend in R_{TOT} (Figure 1e) with low values in winter (~4 g C m^{-2} day^{-1}) when the air temperatures was lower (Figure 1a) and the soil moisture content was higher (Figure 5c). R_{TOT} increased during the grass-growing season (~10 g C m^{-2} day^{-1}) as the soil became warmer (Figure 1a) and drier

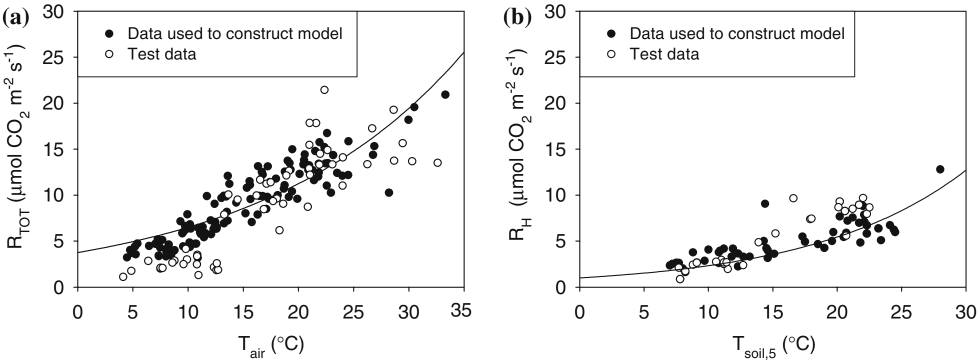

Figure 2. (a) Dependence of R_{TOT} on air temperature ($T_{soil,5}$) and, (b) dependence of R_H on soil temperature at 5 cm depth ($T_{soil,5}$). Using Equation (1) and the parameter values in Table 1, the measured R_{TOT} values were adjusted to soil moisture content in the top 6 cm (θ_6) = 20% and LAI = 1 m^2 m^{-2}. Using Equation (2) and the parameter values in Table 1, the measured R_H values were adjusted to soil moisture content in the top 6 cm (θ_6) = 20%. The data used for regression models (70% of measurements) and the independent test data (30% of measurements) are shown separately.

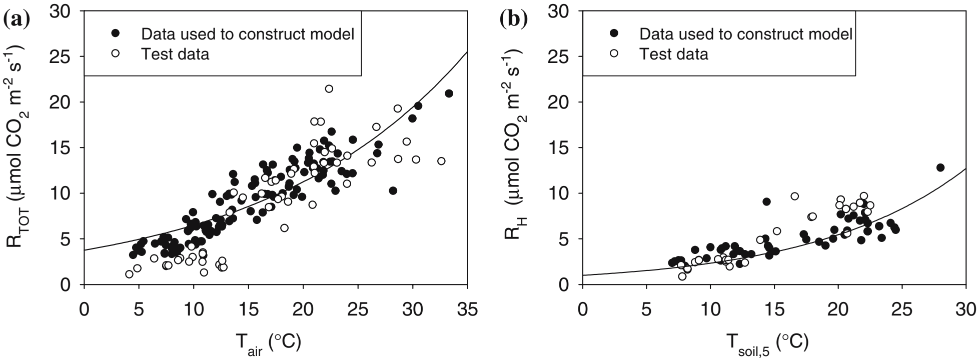

Figure 3. (a) Dependence of R_{TOT} on soil moisture content in the top 6 cm (θ_6) and, (b) dependence of R_H on soil moisture content in the top 6 cm (θ_6). Using Equation (1) and the parameter values in Table 1, the measured total respiration values were adjusted to air temperature (T_{air}) = 15 °C and LAI = 1 m^2 m^{-2}. Using Equation (2) and the parameter values in Table 1, the measured R_H values were adjusted to soil temperature at 5 cm depth ($T_{soil,5}$) = 15 °C. The data used for regression models (70% of measurements) and the independent test data (30% of measurements) are shown separately.

(Figure 1c) and LAI increased (Figure 1d). R_H has a similar seasonal trend to R_{TOT} but was consistently lower. Wintertime values of R_H were ~2 g C m^{-2} day^{-1} and increased to (~5 g C m^{-2} day^{-1} in summertime (Figure 1e). Changes in R_{TOT} and R_H were closely associated with changes in T_{air} and $T_{soil,5}$ such as occurred after day of year 143 and day of year 250.

The relative contribution of R_H and R_A to R_{TOT} varied throughout the year (Figure 1e) and three periods are evident: (i) in the period up to day of year 143 R_H and R_A represented 62% and 38% of R_{TOT}, respectively; (ii) between day of year 144 and day of year 228 R_H and R_A both accounted for 50% of R_{TOT}; (iii) after day of year 259 R_H and R_A accounted for 62% and 38% of R_{TOT}, respectively. In total during 2004 R_{TOT}, R_H and R_A were 2.34, 1.31 and 1.03 kg C m^{-2}, respectively.

Discussion

This study confirmed the relationship between R_{TOT} and R_H and a number of controlling factors. The strong correlation between temperature and soil CO_2 efflux has been well demonstrated (Fang and Moncrieff, 2001; Reth et al., 2005b).

Both R_{TOT} and R_{H} showed an exponential response to increasing air temperature and soil temperature, respectively with the variability in R_{TOT} and R_{H} indicating the influence of other factors.

The response of respiration to increasing soil moisture content was observed to follow the three phases identified by Reichstein et al. (2003); (1) in dry conditions metabolic activity increases strongly with increasing soil moisture content (Howard and Howard, 1993) (2) at near optimum soil moisture content changes in soil moisture have little effect on respiration (Qi and Xu, 2001) and (3) when the moisture content exceeds field capacity and the soil begins to saturate respiration is inhibited (Davidson et al., 2000) due to the inhibition of aerobic decomposition by oxygen deficiency (Skopp et al., 1990). Based on the equation developed by Saxton et al. (1986) the soil is at field capacity when the volumetric soil moisture content is 26%. This is very close to the soil moisture content at which maximum R_{TOT} and R_{H} occurs (Figure 3).

Although soil temperature and soil moisture are important regulators of R_{TOT} and R_{H}, R_{A} (and therefore a large part of R_{TOT}) is derived from recently fixed C. We found that as LAI (and therefore aboveground biomass) increased so did the rate of R_{TOT}. Given that a large proportion of R_{TOT} is derived from R_{A} this suggests that respiration is linked to photosynthesis. Evidence for this is provided by Craine and Wedin (2002), who found that soil CO_2 flux declined with increased time since grass clipping. Elsewhere Kuzyakov and Cheng (2001) found that root-derived CO_2 was sensitive to changes in photosynthesis.

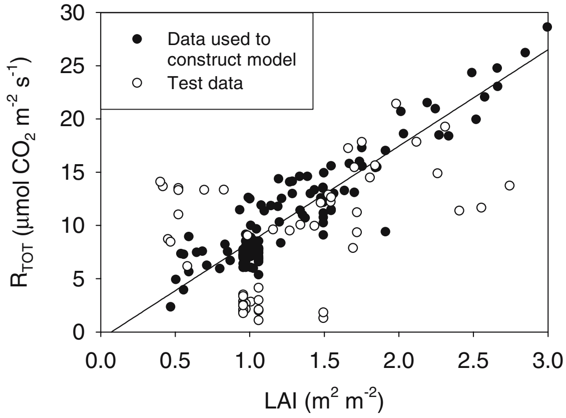

Figure 4. Dependence of R_{TOT} on LAI. Using Equation (1) and the parameter values in Table 1, the measured R_{TOT} values were adjusted to air temperature (T_{air}) = 15 °C and soil moisture content in the top 6 cm (θ_6) = 20%. The data used for regression models (70% of measurements) and the independent test data (30% of measurements) are shown separately.

The empirical models provided a robust means of modelling R_{TOT} and R_{H} and compare well to other studies. For instance, Reth et al.

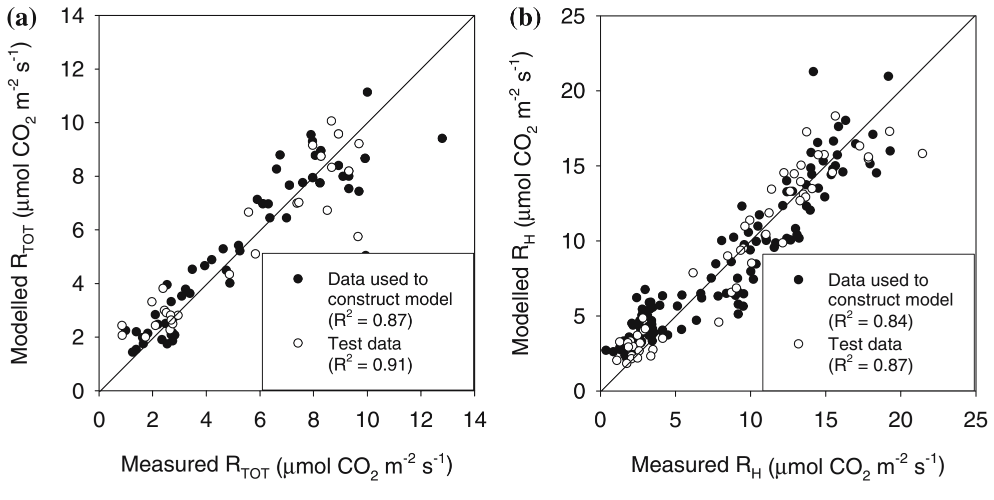

Figure 5. Comparison of measured and modelled (a) R_{TOT} and (b) R_{H}. The data used for regression models (70% of measurements) and the independent test data (30% of measurements) are shown separately. The solid line represents the 1:1 relationship.

(2005b) explained 60% of the variance in soil CO_2 efflux using soil temperature, relative soil water content, soil pH and relative root mass. Bremer and Ham (2002) explained 77% of the variance in soil respiration in a temperate grassland under mowed and burned regimes using soil temperature, soil moisture content and LAI.

The range of values of R_{TOT} (1–22 μmol CO_2 m^{-2} s^{-1}) and R_H (1–13 μmol CO_2 m^{-2} s^{-1}) observed in this study compare well with other studies in grasslands. Working in a northern temperate grassland, Flanagan and Johnson (2005) measured R_{TOT} values of ~4 to 32 μmol CO_2 m^{-2} s^{-1} while Craine and Wedin (2002) measured fluxes of ~1 to 16 μmol CO_2 m^{-2} s^{-1} in a Minnesota grassland.

During the summer months the contribution of R_A to R_{TOT} exceeded that of R_H. This is due to the higher LAI during this time, which leads to higher respiration rates (Figure 4). The contribution of R_A to R_{TOT} is within the range of 40–60% reported by Raich and Schlesinger (1992). The findings of $^{14}CO_2$ pulse labelling experiments using *L. perenne* L. support this (Kuzyakov et al., 1999, 2001). The presence of fine roots in the bare soil plots may have led to an over-estimation of R_H, however given the similarity between our estimate of the contribution of R_A to R_{TOT} and other studies we consider our method to be reasonably robust.

We have shown that empirical regression models provide a robust means of modelling CO_2 fluxes and reconstructing daily fluxes. Further improvements could be made by investigating the response of respiration to drying and wetting of soil, differences between daytime and nighttime respiration and incorporating factors such as fine root biomass and soil properties. This would increase the range of conditions under which such models are valid.

Conclusions

In this study we developed empirical regression models that allow estimation of R_{TOT} and R_H in intensively managed grassland. Air temperature, soil moisture content and leaf area index are the most important factors controlling R_{TOT}. The principal factors controlling R_H are soil temperature and soil moisture content. R_A accounted for 50% of R_{TOT} during the summer months and approximately 38% during the rest of the year.

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