Modeling of net ecosystem exchange and its components for a humid grassland ecosystem

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[1]   We measured the net ecosystem exchange (NEE) of a managed humid grassland in southwest Ireland from 2002 to 2004 with an eddy covariance (EC) system. In addition, a process-based biogeochemical model (PaSim) incorporating land management practices such as grazing and grass harvesting was used to simulate the carbon dynamics. The modeled NEE of 2.6, 2.7 and 3.4 t C ha^{-1} (uptake) for 2002, 2003 and 2004 compares well with the measured NEE of 1.9, 2.6 and 2.9 t C ha^{-1}. There is good agreement between the model output and the EC observations in the growing season but not so good in the winter period. The year-on-year increase in measured NEE is partly attributed to a circa 4% year-on-year increase in annual photosynthetic photon flux density (Q_{PPFD}). The year of lowest NEE (2002) was associated with highest rainfall (1785 mm) and lowest Q_{PPFD}. In the wettest year, grass harvesting was delayed by a month, resulting in a reduced NEE. The management of grassland in regions of high rainfall is dependent on weather conditions. If wet conditions become more prevalent (e.g., as a result of climate change), grasslands in such regions may shift from intensive to extensive management with further reductions in NEE. The reasonable agreement between the model predictions and the EC measurements demonstrates the potential of the model for applications such as upscaling EC measurements to regional scales and predicting responses of grasslands to climate change.

1. Introduction

[2] Increasing levels of greenhouse gases in the atmosphere are causing climate change [*Intergovernmental Panel on Climate Change*, 2001]. As a result, there is a need to understand the carbon (C) balance of terrestrial ecosystems. Grasslands cover approximately 3.5×10^9 ha globally [*Soussana et al.*, 2004a] and are estimated to store between 10% [*Eswaran et al.*, 1993] and 30% [*Anderson*, 1991] of the global soil C pool. As such they play a significant role in the global C cycle. Studies of CO_2 dynamics in grasslands have shown them to be both sinks and sources of C [e.g., *Barcza et al.*, 2003; *Byrne et al.*, 2005; *Flanagan et al.*, 2002; *Novick et al.*, 2004].

[3] The net CO_2 exchange of terrestrial ecosystems is determined by the difference between C uptake due to photosynthesis and C loss due to respiration. Many studies have utilized eddy covariance (EC) [*Novick et al.*, 2004; *Suyker et al.*, 2003; *Xu and Baldocchi*, 2004] to determine the seasonal and interannual variability of net ecosystem

exchange (NEE). Ecosystem respiration is usually estimated from a combination of: an extrapolation of nighttime fluxes under strong turbulence [*Falge et al.*, 2002] and an empirical regression model of nighttime fluxes with soil temperature [*Xu and Baldocchi*, 2004]. The variations in soil and ecosystem respiration are commonly linked with soil temperature and soil water content. Some relationships have also been found with soil organic carbon and plant growth rate [*Franzluebbers et al.*, 2002].

[4] Recognition of the role of terrestrial ecosystems in the global C cycle has stimulated the development of several biogeochemical models of the C cycle such as CENTURY [*Parton et al.*, 1987], RothC [*Coleman and Jenkinson*, 1996], DNDC [*Li et al.*, 1994] and PaSim [*Riedo et al.*, 1998]. When used with measured C fluxes these models can be used to interpolate and extrapolate C fluxes in time and space, and to simulate separately the constituents of the NEE (soil, plant and animal respiration and gross primary production) that cannot be directly measured by EC. Models can also be used to assess the effect of different land management strategies and climate change scenarios on the C balance of ecosystems.

[5] In this study we test the effectiveness of the grassland biogeochemical model PaSim in simulating the seasonal and interannual variability of net ecosystem exchange (NEE) and total respiration (R_{tot}) by comparing the model outputs to 3 years of eddy covariance (EC) data for an intensively managed grassland in southwest Ireland. A

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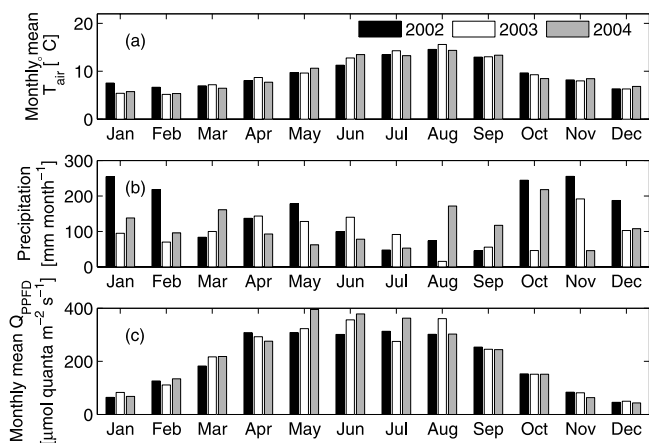
Figure 1. (a) Monthly average air temperatures for 2002–2004, (b) monthly totals of precipitation for 2002–2004, and (c) monthly average Q_{PPFD} for 2002–2004.

further aim of the study is to investigate the biogeochemical processes influencing the C dynamics of the ecosystem.

2. Materials and Methods

2.1. Site Description

[6] The study area (Latitude: 51°59″N, Longitude: 8°46″W) is situated in an area of intensively managed grassland in County Cork, southwest Ireland. The site has an average elevation of 200 m above sea level. The climate is temperate maritime with an average rainfall of 1470 mm yr^{-1} and an annual daily mean temperature of 6.2°C in January and 13.7°C in July. Air temperature was above 5°C on 331, 317 and 320 days during 2002, 2003 and 2004, respectively. Frost occurs on less than 10 days per year. Monthly averages of air temperature and photosynthetic photon flux density (Q_{PPFD}) and monthly precipitation totals are presented in Figure 1. Annual totals of precipitation and Q_{PPFD} are presented in Table 1.

[7] The dominant grass species is perennial ryegrass (*Lolium perenne* L.) and the site is in managed grassland for approximately 20 years. The dominant soil type is surface water gley [*Gardiner and Radford*, 1980] with low-lying areas having a shallow surface peat layer. The soil properties are summarized in Table 2. Nitrogen is typically applied at the annual rate of 200 kg of synthetic N ha^{-1} (mainly as NH_4NO_3) and approximately 130 kg organic N ha^{-1} (as farmyard slurry). The mean soil phosphorus concentration (Morgan's P) in 2002 was 10.2 mg P L^{-1} [*Scanlon et al.*, 2004]. Grass production rates are in the range 7.6–14 t DM ha^{-1} yr^{-1} [*Byrne et al.*, 2005]. The footprint is composed of fields that vary in size from 0.7 to 3.8 hectares. These are delineated by hedgerows (1.0–1.5 m high) and subdivided into paddocks by wire fence lines. The

Table 1. Annual Totals of Measured Precipitation, Photosynthetic Flux Density and Net Ecosystem Exchange

	Precipitation, mm	Q_{PPFD}, mol quanta m^{-2}	NEE, t C ha^{-1}
2002	1785	6725	1.91
2003	1178	6950	2.59
2004	1340	7221	2.95

nearest hedgerow in the prevailing wind direction (WSW) is 450 m from the EC sensors. Approximately 50% of the fields are grazed intensively by dairy and beef cattle at a density of 2.2 livestock units ha^{-1} between April and October each year. Cattle are housed for the remainder of the year. The remaining fields are harvested over two four-week periods, typically in June and again in September. LAI was calculated from PPFD transmission data that were measured in 2004 with a linear array of 80 quantum sensors (AccuPAR model PAR-80, Ceptometer, Decagon Instruments, Washington) and used to calculate gap fractions, which were inverted to derive LAI estimates [*Norman and Campbell*, 1989]. The area-weighted average measured LAI in the footprint area varied from 2 to 4 m^2 m^{-2} during the growing season. After a field is harvested its LAI is close to zero and after grazing periods paddocks typically have LAI values of circa 1 m^2 m^{-2}.

2.2. EC System and Gap-Filling

[8] In the EC system CO_2 and H_2O concentrations were measured with an open path infrared gas analyzer (LI-7500, Li-Cor, USA) and the wind speed was measured with a 3-D sonic anemometer (Model 81000, R. M. Young, USA). All concentrations and wind speeds were logged at 10 Hz and CO_2 flux values were calculated at 30-minute intervals. The CO_2 sensor was mounted 10 m above the ground during 2002 and 2003, and at 3 m during 2004. Management practices and soil types within the flux footprint area are largely homogeneous allowing comparisons between 2002, 2003 and 2004 to be made.

[9] Precipitation was measured using a tipping bucket rain gauge (ARG100, Environmental Measurements Ltd., UK). A net radiometer (CNR1, Kipp and Zonen, Netherlands) was used to measure the solar irradiance. Photosynthetic photon flux density (Q_{PPFD}) was measured using a PAR LITE sensor (Kipp and Zonen, Netherlands). Air temperature and humidity were measured at one minute intervals using a temperature and humidity probe (HMP45C, Campbell Scientific, UK) mounted 3 m above the ground and 30 minute averages were logged by a CR23X datalogger (Campbell Scientific, USA).

[10] All CO_2 fluxes were adjusted using Webb correction [*Webb et al.*, 1980]. As the EC system performed poorly during rain events, a precipitation filter was used to screen out unsatisfactory flux data. The data was partitioned into daytime and nighttime sets using an incoming solar radiation threshold of 20 W m^{-2}. The wind speeds from the

Table 2. Soil Parameters

Parameter	Unit	Value
Soil pH[a]	...	5.6
Main rooting depth[a]	m	0.25
Sand:Silt:Clay[a]	%	42:41:17
Depth of the three layers[a]	m	0.02; 0.20; 0.60
Bulk density[a]	g cm^{-3}	1.0; 1.0; 1.7
Saturated soil water content[b]	m^3/m^{-3}	0.60; 0.43; 0.40
Air entry potential[c]	mm	−50.0; −100.0; −100.0
Saturated hydraulic conductivity[c]	mm d^{-1}	188.0; 18.0; 18.0
Parameter b[d]	...	5.4

[a]Soil samples.
[b]Literature.
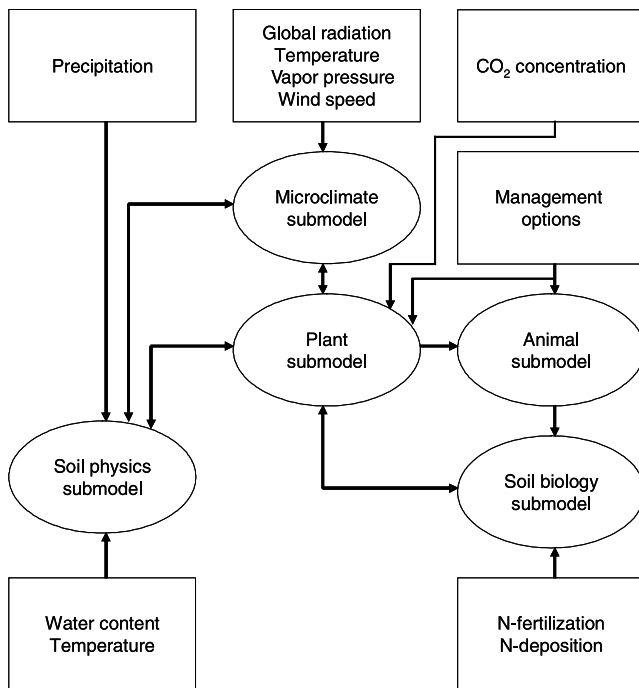[c]Model optimization.
[d]*Clapp and Hornberger* [1978].

Figure 2. Submodels, driving variables and internal fluxes of carbon (C), nitrogen (N) and water.

sonic anemometer were double rotated such that the mean vertical wind speed was set to zero. In periods of high atmospheric stability there is a lack of turbulent mixing near the soil surface and the EC technique does not always yield reliable results. Nocturnal fluxes corresponding to u_* (frictional velocity) less than 0.2 m s^{-1} were excluded [*Baldocchi*, 2003] and replaced by an exponential regression function of soil temperature [*Jaksic et al.*, 2006]. The daytime data was sorted bi-monthly and for each period a different regression relationship was developed between the good daytime CO_2 fluxes and Q_{PPFD}. The regression used the Misterlich formula [*Falge et al.*, 2001] for the relationship between CO_2 flux and Q_{PPFD}. These relationships were then used to gap-fill daytime CO_2 fluxes. An upper threshold (for daytime data) and a lower limit (for nighttime data) were set for the 30-min CO_2 flux measurements [*Jaksic*, 2004]. After post-processing and filtering of spurious data, 57% of the CO_2 flux data were suitable for analysis. The remainder was replaced by gap-filled data. The average flux footprint was estimated based on a fetch to sensor height ratio of 100:1 combined with the probability density distribution of the wind direction.

2.3. Model Description and Parameterization

[11] The model used in this study is PaSim 3.6 (v5) and was described in detail by *Riedo et al.* [1998] and has been used in a number of studies [*Riedo et al.*, 1999, 2000, 2001, 2002; *Schmid et al.*, 2001; *Soussana et al.*, 2004b]. PaSim is a mechanistically based ecosystem model which simulates the carbon, nitrogen and water balances of the atmosphere-plant-soil system and can be used to predict dry matter production of a fertilized and cut mixed perennial meadow. The model has five submodels: soil physics, soil biology, plant, animal and microclimate (Figure 2). PaSim is driven

with hourly meteorological input data for: radiation, air temperature, vapor pressure, wind speed, precipitation and atmospheric concentration of CO_2 and ammonia (NH_3). PaSim integrates the land management practices of grass cutting, grazing and the application of fertilizer and slurry.

[12] The plant submodel was developed on the basis of the Hurley Pasture model [*Thornley and Verbane*, 1989] and simulates shoot and root growth in relation to C and N uptake, energy fluxes and soil moisture conditions. The microclimate submodel is used to calculate the interception of radiation by the canopy and the energy balances of the canopy and soil surface. Canopy development is divided into two distinct stages, a reproductive stage and a vegetative stage. A transition from reproductive to vegetative growth is triggered after a sustained period of air temperatures above a base level. In addition, after the second cut the canopy is automatically assumed to be in the vegetative state. The soil biology submodel calculates plant available soil C and N and is derived from the CENTURY model [*Parton et al.*, 1987]. The animal submodel allows the effects of grazing animals to be incorporated.

[13] The initial state of the model was established using an equilibrium run. The model was run repeatedly with the meteorological and management data of 2002-2004 until the concentrations of C and N in the various soil pools had stabilized. This was taken to be when the change in the variables between two runs was less than 2.5%. The resulting soil C and N concentrations (Table 3) were used as the initial conditions for the simulations of 2002, 2003 and 2004.

[14] All the meteorological input data were measured on site, except for the concentrations of CO_2 and NH_3, which were taken as constants from the literature [*Intergovernmental Panel on Climate Change*, 2001; *Seinfeld*, 1986]. Some soil parameters were determined from surface soil samples taken within the flux tower footprint. Other soil parameters were set using values from the literature [*Clapp and Hornberger*, 1978] or determined by optimization of PaSim results. The vertical soil profile was divided into three layers: 0–2 cm; 2–20 cm and 20–60 cm. For modeling purposes the soil-bedrock interface was set at a depth of 2 m.

[15] The current version of the model is known to produce too much biomass in winter, even though an additional stress parameter has been included to account for enhanced mortality in autumn and winter (N. Vuichard et al., Estimating the greenhouse gas fluxes of European grasslands with a process driven model: Part 1. Model evaluation from in-situ measurements, manuscript in preparation, 2006). To compensate for

Table 3. Initial Conditions for Carbon and Nitrogen in the Various Pools

	Carbon, kg C m^{-2}	Nitrogen, kg N m^{-2}
Wstruct[a]	1.693	...
Wmetab[b]	0.109	0.010
Wactive[c]	0.305	0.043
Wslow[d]	5.701	0.378
Wpassive[e]	5.054	0.455

[a]Structural dead plant material.
[b]Metabolic dead plant material.
[c]Active soil organic matter.
[d]Slow soil organic matter.
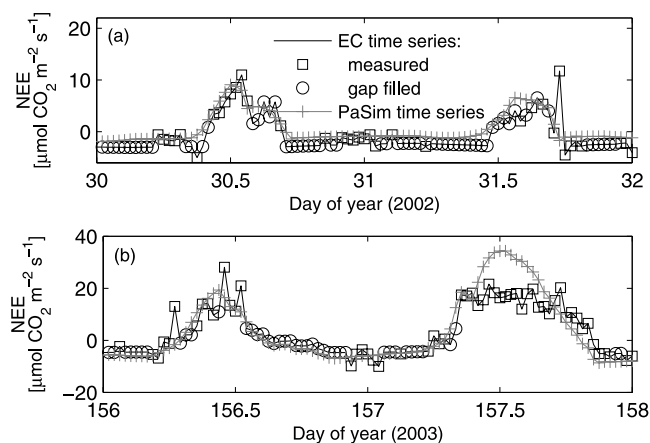[e]Passive soil organic matter.

Figure 3. Selected 2-day modeled and measured NEE time series from (a) winter 2002 and (b) growing season 2003.

Table 4. Slopes and Intercepts of Linear Regressions of Modeled to Measured Data and Coefficients of Determination, Excluding Gap-Filled Values

Data Set	Number of Values	Slope	Intercept, μmol CO_2 m^{-2}s^{-1}	Coefficient of Determination
All	28616	0.77	0.52	0.57
Growing season[a]	10876	0.77	1.06	0.56
Growing season, daytime[a]	7689	0.61	3.41	0.35
Growing season, nighttime[a]	3187	0.28	−3.65	0.15
Winter[b]	5183	0.35	0.42	0.45
Winter, daytime[b]	2338	0.26	1.12	0.18
Winter, nighttime[b]	2845	0.03	−0.59	0.01

[a]Growing season comparison period defined as in Table 5. All years have been combined.

[b]December, January and February of all years combined.

this we therefore include an extra cut at the end of each year to reset the biomass and leaf area index (LAI) to realistic values.

[16] PaSim was used to calculate the ecosystem gross primary production (GPP) and the respiration of the soil, plants and the grazing animals at 30-min time intervals. Here soil respiration is defined as heterotrophic respiration only. We define NEE as the difference between the modeled GPP and the sum of all the modeled respiration components (R_{tot}). We adopted the biological convention whereby fluxes from the atmosphere to the biosphere (uptakes) are positive (Figure 3).

[17] The variation in management practices (time of grass cutting and fertilizer and slurry applications) and productivity between fields implies a degree of heterogeneity (particularly in summer) that cannot easily be addressed directly by the model. In order to deal with this all fertilizer and slurry applications were temporally averaged in order to have 10 applications per year. In addition we simplified the

modeling exercise by using a single point simulation and representing each series of temporally and spatially distributed field harvests in the footprint with two cuts of increasing magnitude, separated by 7 days in the model. In the model, the net effect of the cuts is to set the LAI to 1.0 m^2 m^{-2} and the shoot dry matter to 0.15 kg m^{-2}. We also assume that all the nonharvested fields were continuously grazed during the summer time.

[18] Linear regressions were performed to evaluate the relationship between modeled and measured NEE (Figure 4 and Table 4). Gap-filled values were excluded from these analyses in order to test the model against quality controlled measurements only. The model performance was also evaluated on seasonal subsets of daytime and nighttime data (Table 4).

3. Results

[19] Figure 5 shows the cumulative NEE observed by EC and simulated by PaSim for the 3 years of the study. The growing season (roughly April to October) can be divided
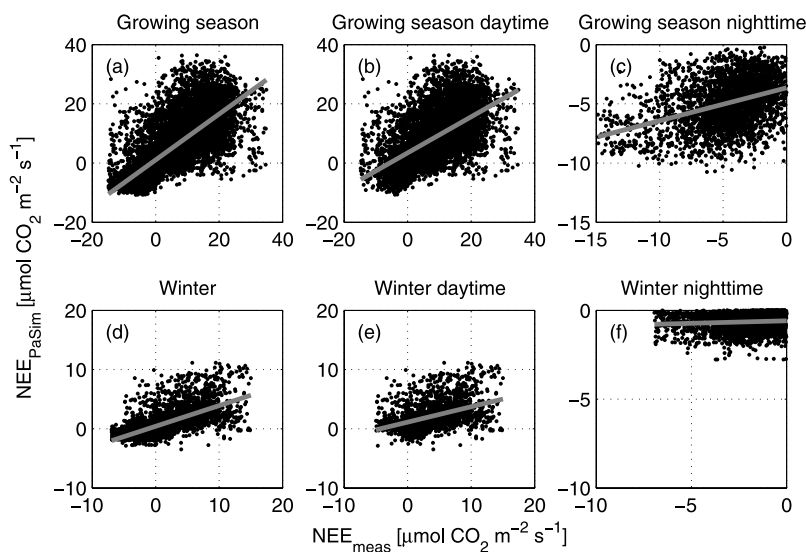

Figure 4. Comparison of modeled and measured NEE with linear regression lines for (a) all data during the growing season comparison period, (b) daytime data during the growing season comparison period, (c) nighttime data during the growing season comparison period, (d) all winter data, (e) winter daytime data, and (f) winter nighttime data.
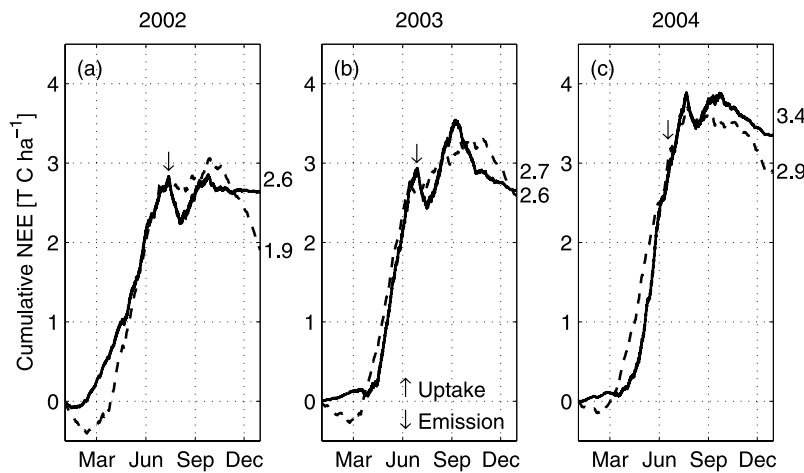
Figure 5. Modeled (solid line) and measured (dashed line) cumulative net ecosystem exchange for 2002, 2003 and 2004. The arrows indicate the timing of the first harvest.

into an active spring growing phase up to the first major grass harvest (illustrated by a downward arrow in Figure 5), typically in June, and a less active growing phase from July to October.

[20] The measured annual uptake (after gap filling) is 1.9, 2.6 and 2.9 t C ha^{-1} for 2002, 2003, 2004, respectively. The annual uptake modeled with PaSim is 2.6, 2.7 and 3.4 t C ha^{-1}, respectively (Table 5). For each year of the study, the modeled uptake is higher than the observed. Most of the C uptake occurs during the growing season in the months of April, May and June (Figure 5). The effects of the harvesting are visible as changes in the gradient of cumulative modeled NEE (Figure 5). From late October to year's end, the cumulative NEE decreases as respiration exceeds photosynthesis.

[21] In order to compare the measured and modeled values of NEE more closely we chose the period from the start of the grass growing season to the time of the first harvest (Table 5). This period is chosen for two reasons: (1) as this is the period of greatest C uptake (Figure 5); and (2) there is no harvesting during this period. For such a comparison it is first necessary to define the start of the growing season. As there is no standard definition, we chose a growing season start date when the measured soil temperature at 7.5 cm depth is consistently above 6°C (Table 5). We end the comparison period on the day of the first grass harvest (Table 5). The comparison period has a

duration ranging from 58 to 103 days, depending on the year. The gradient of the cumulative NEE curve represents the rate of change of NEE. During the spring period, the gradient of uptake for the cumulative NEE observed is 2.8, 3.1, 2.7 g C m^{-2} d^{-1} for the three consecutive years of the study. The gradient of uptake for the modeled NEE is similar to the observed in 2004 but higher in 2002 and 2003 (Table 5).

[22] Linear regressions of half-hourly modeled NEE values to measured NEE values were performed ($p < 0.0001$). Coefficients of determination (r^2) were also calculated (Table 4). The slope of the regression line to the entire data set was 0.77 with an intercept of 0.52 μmol m^{-2} s^{-1} (Figure 4 and Table 4). The intercepts of the linear regressions indicate that at low values of NEE, the model systematically over predicts the magnitude of NEE, whether it is uptake or release (positive intercepts for daytime NEE and negative intercepts for nighttime NEE). However, large values of both uptake and emission fluxes tend to be underestimated by the model, as evidenced by the slope values, which are all less than 1 (Table 4). The slope of the
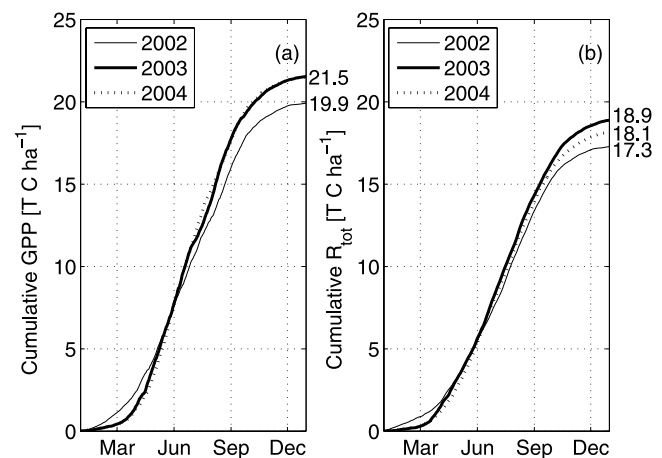
Table 5. Comparison of the Observed and Modeled Annual NEE and Gradient of Cumulative Observed and Modeled NEE During the Growing Season

	2002	2003	2004
Annual sum of NEE, t C ha^{-1} yr^{-1}			
Observed	1.91	2.59	2.95
Modeled	2.64	2.66	3.36
Growing season comparison period definition			
Starting date (julian day)	79	78	98
Finishing date (julian day)	182	166	156
Length (days)	103	88	58
Gradient of observed NEE during growing season, g C m^{-2} d^{-1}	2.8	3.1	2.9
Gradient of modeled NEE during growing season, g C m^{-2} d^{-1}	2.1	3.0	3.9

Figure 6. (a) Cumulative gross primary production (GPP). (b) Cumulative total respiration of the ecosystem (R$_{tot}$). GPP is positive in accordance with the biological sign convention.
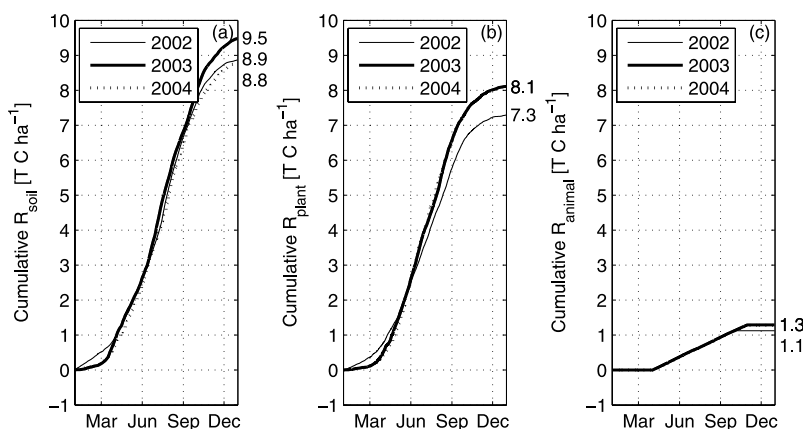
Figure 7. Cumulative sums of the modeled components of total respiration: (a) soil, (b) plant, and (c) grazing animal. Grazing animal respiration was lower in 2004 owing to the early ending of the grazing season caused by wet conditions in October.

regression line calculated on a subset of the data taken from the winter period (defined here as days 335–365 and 1–59 of each year) is only 0.35. The model performs worst on the winter nighttime data. Performance during the summer is better, with a slope of 0.77, an intercept of 1.06 μmol m^{-2} s^{-1} and r^2 = 0.56. The slopes of the linear regressions to the day-time subsets are higher than for the nighttime subsets, suggesting that, in this case, the model is a better predictor of GPP than of respiration.

[23] Figure 6 shows the accumulated model output of GPP and R$_{tot}$. The annual GPP increases from 19.9 t C ha^{-1} (2002) to 21.5 t C ha^{-1} for 2003 and 2004. The annual R$_{tot}$ increases from 17.2 t C ha^{-1} (2002) to 18.9 t C ha^{-1} (2003) and then decreases slightly to 18.2 t C ha^{-1} (2004). The modeled interannual changes in GPP and R$_{tot}$ are less than 9%. As NEE is the difference between GPP and R$_{tot}$ (and is small relative to both), small interannual variation in NEE needs to be interpreted with caution. Figure 7 shows the

modeled partitioning of R$_{tot}$ as: R$_{soil}$; R$_{plant}$; and R$_{animal}$. On average the soil respiration represents 55%, plants 40% and grazing animals 5% of R$_{tot}$. In order to illustrate the model performance over the daily range of values of Q$_{PPFD}$ in the late growing season, diurnal ensemble averages of measured and modeled NEE and measured Q$_{PPFD}$ were calculated over 14 days in August 2003 and are presented in Figure 8. The use of diurnal averaging smoothes the effects of daily variations in environmental parameters on NEE.

4. Discussion

4.1. Comparison of Modeled and Observed NEE

[24] Figure 5 and Tables 4 and 5 show that the modeled NEE broadly agrees with the observations. However, the model overestimates the annual NEE sums by between 3% and 38%. Although PaSim accurately models the observations during the growing season, it has limitations in the
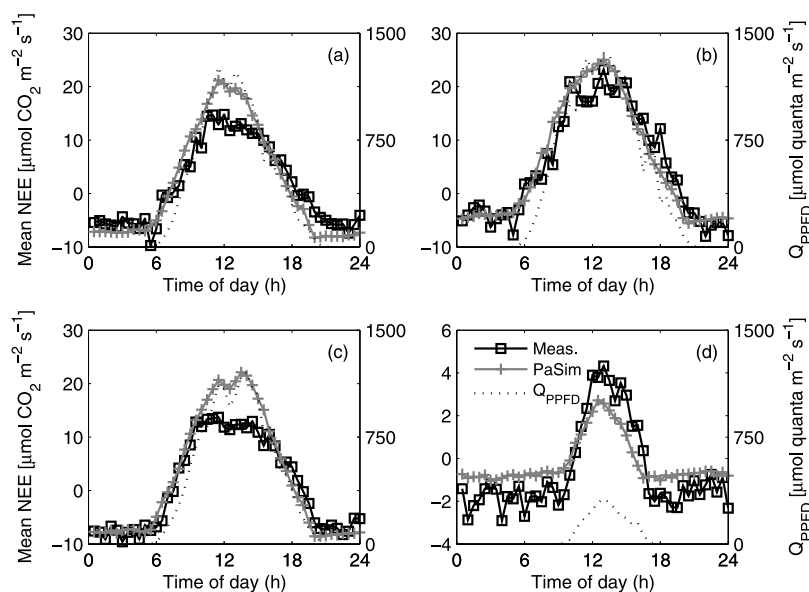

Figure 8. Half-hourly measured and modeled NEE and Q$_{PPFD}$ measured above the canopy for 14 days ensemble averaged from (a) 8–21 August 2002, (b) 1–14 May 2003, (c) 8–21 August 2003 and (d) 16–30 December 2003.

winter period where it over predicts the uptake. The shape of the curve for the cumulative modeled NEE in the first months of 2002 is different from that in 2003 and 2004 (Figure 5). This is due to the oversensitivity of PaSim to initial conditions, even when the ecosystem can be considered to be in equilibrium.

[25] The result of our approximation of the spatially and temporally heterogeneous management activities with a single point simulation is that the model captures the cumulative NEE but does not capture variations in NEE as the footprint becomes more heterogeneous after harvesting begins. In the autumn and winter period the observations show a decrease in the cumulative NEE (i.e., R_{tot} exceeds GPP). The model captures this trend better in 2003 and 2004 than in 2002.

[26] For both model and observations, there is a year-to-year increase in NEE with the lowest NEE associated with the wettest year. There was a 3.5% increase in integrated annual Q_{PPFD} from 2002 to 2003 and a 4% increase from 2003 to 2004. The average air temperature was similar for all 3 years. The environmental factor that varied the most between the 3 years was precipitation: 2002 was wetter than average (17% above the long-term annual average); 2003 was drier than average (19% below average); 2004 was 9% drier than average. The increase in NEE (from 2002 to 2003) is partly attributed to the decrease in precipitation and consequent earlier harvest of 2003. The earliest harvest [2004] has the smallest immediate effect on the cumulative NEE gradient (Figure 5) and the annual NEE of 2004 is the largest of the 3 years. Climate predictions for southwestern Ireland for the period 2021–2060 suggest a more seasonally extreme pattern of precipitation with a mean reduction of up to 20 mm in June and a mean increase of up to 20 mm in December, compared to the 1961–2000 average [*McGrath et al.*, 2005]. It is possible that the predicted increase in winter precipitation may lead to a more frequent occurrence of very wet conditions similar to those of early 2002, affecting the annual NEE indirectly by forcing management changes such as delaying of harvesting.

4.2. Analysis of Components of NEE

[27] GPP and R_{tot} are dependent on meteorological, hydrological, soil, vegetation and microbiological conditions. Both GPP and R_{tot} were lowest in 2002, the wettest year (Figures 6a and 6b; GPP = 19.9 t C ha^{-1}; R_{tot} = 17.3 t C ha^{-1}), suggesting that at this site productivity may be limited by wet soil conditions at the high end of the annual rainfall distribution.

[28] From the model study, the optimum NEE (largest difference between GPP and R_{tot}), corresponds to an annual precipitation close to the average annual precipitation (circa 1470 mm). Unlike the study of *Xu and Baldocchi* [2004] of a grassland in California, the variation in R_{tot} in our study cannot be linked to daily precipitation events because the climate in Ireland is humid and temperate all year round and consequently Irish soils are rarely subject to moisture deficit.

[29] The modeled photosynthetic response to incident Q_{PPFD} appears to be good during the active growth comparison season (Figure 4). However, at high values of incident Q_{PPFD} in the summer the measured photosynthetic response is observed to saturate while the modeled response continues to increase. This effect can be clearly seen in the ensemble-averaged diurnal NEE values from August 2002 and 2003 (Figures 8a and 8c), and also occurs in 2004. In the model the saturation leaf photosynthetic rate is controlled by the current development stage of the canopy. The rate of leaf photosynthesis during the reproductive stage is significantly greater than that during the vegetative state. As two grass harvests have been made by this time of year, the model is running in the vegetative growth stage. Therefore it seems that this lack of saturation in the modeled light response is due to too low a value of the light-saturated photosynthetic rate for the vegetative stage. Figure 8b illustrates the good agreement between measured and modeled fluxes during the growing season (14 days of May 2003 in this case). The underestimation of the magnitude of both daytime and nighttime fluxes during winter is clear from Figure 8d, with poorer accuracy for nighttime (respiration) fluxes. It is therefore likely that daytime respiration fluxes are also underestimated in winter, implying that some of the underestimation of winter daytime GPP is masked in Figure 8d.

[30] The average ratio of R_{soil} to R_{plant} during 2002–2004 was 1.16. Working at the same site, *Byrne and Kiely* [2006] estimated that during 2004 the average ratio of R_{soil} to R_{plant} was 1.27. Similar findings have been reported [*Kuzyakov et al.*, 2001, 1999] using $^{14}CO_2$ pulse labeling experiments of *Lolium perenne* L.

[31] On the basis of the measured and modeled values of NEE, this intensively managed grassland appears to be a sink for atmospheric CO_2. However, the apparent ecosystem (soil and grass) uptake of C is reduced by the removal of biomass through grazing and harvesting. For example, approximately half the annual biomass production of 3.8 to 7.0 t C ha^{-1} is removed by harvesting. On preliminary inspection this would suggest that these grasslands are net sources of CO_2. However, such a conclusion would ignore the final fate of the biomass C. Some may ultimately be exported from the farm as meat and milk and more will be emitted as CH_4 owing to enteric fermentation. Biomass C will also be returned to the soil as freshly deposited manure and in applications of animal slurry. Therefore a full appraisal of the C sink/source status of a managed grassland ecosystem must examine all the components of the farm C balance including belowground C cycling and the multiple pathways of C exchange over the annual cycle.

5. Conclusions

[32] PaSim shows promise as a tool for upscaling ecosystem-scale NEE measurements to the regional level and as a means of gap-filling EC time series. The use of a biogeochemical process-based model such as PaSim also allows the constituents of NEE, namely GPP and plant, animal and soil respiration to be estimated separately. By manipulating the model inputs, the effects of climate change scenarios and altered management regimes on ecosystem NEE and productivity can also be investigated.

[33] In this study, the modeled and observed NEE were in especially good agreement during the spring growing season when most of the C uptake occurs. However, some departures from the observations were apparent after the first harvesting had taken place. These may be attributed to the difficulty of adequately representing the heterogeneous nature of land management within the EC footprint in the

summer period with a single point simulation and the lack of saturation of the modeled photosynthetic response to solar radiation at the levels encountered in the late summer of each year. In the winter, the model mostly underpredicts the magnitudes of daytime NEE and nighttime respiration fluxes. The year of lowest NEE (2002) was associated with highest rainfall (1785 mm) and lowest Q_{PPFD}. In 2002, the wettest year, grass harvesting was delayed by a month resulting in a reduced NEE. The management of grassland in regions of high rainfall is very dependent on weather conditions. If wet conditions become more prevalent (e.g., as a result of climate change), grasslands in such regions may shift from intensive to extensive management with further reductions in NEE. The model simulations of GPP and R_{tot}, also showed that GPP and R_{tot} were higher in the drier years and lowest in the wet year.

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