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Published in:
Global Biogeochemical Cycles
DOI:
10.1029/2005GB002611
Publication date:
2007
Citation for published version (APA):

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Estimating the greenhouse gas fluxes of European grasslands with a process-based model:
1. Model evaluation from in situ measurements

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Received 2 September 2005; revised 20 July 2006; accepted 28 August 2006; published 19 January 2007.

[1] We improved a process-oriented biogeochemical model of carbon and nitrogen cycling in grasslands and tested it against in situ measurements of biomass and CO2 and CH4 fluxes at five European grassland sites. The new version of the model (PASIM) calculates the growth and senescence of aboveground vegetation biomass accounting for sporadic removals when the grassland is cut and for continuous removals when it is grazed. Limitations induced by high leaf area index (LAI), soil water deficits and aging of leaves are also included. We added to this a simple empirical formulation to account for the detrimental impact on vegetation of trampling and excreta by grazing animals. Finally, a more realistic methane emission module than is currently used was introduced on the basis of the quality of the animals’ diet. Evaluation of this improved version of PASIM is performed at (1) Laqueuille, France, on grassland continuously grazed by cattle with two plots of intensive and extensive grazing intensities, (2) Oensingen, Switzerland, on cut grassland with two fertilized and nonfertilized plots, and (3) Carlow, Ireland, on grassland that is both cut and grazed by cattle during the growing season. In addition, we compared the modeled animal CH4 emissions with in situ measurements on cattle for two grazing intensities at the grazed grassland site of Laqueuille. Altogether, when all improvements to the PASIM model are included, we found that the new parameterizations resulted into a better fit to the observed seasonal cycle of biomass and of measured CO2 and CH4 fluxes. However, the large uncertainties in measurements of biomass and LAI make simulation of biomass dynamics difficult to make. Also simulations for cut grassland are better than for grazed swards. This work paves the way for simulating greenhouse gas fluxes over grasslands in a spatially explicit manner, in order to quantify and understand the past, present and future role of grasslands in the greenhouse gas budget of the European continent.


1. Introduction

[2] Cultivated grasslands cover 20% of the European continent and are distributed about equally between western Europe (80 Mha) and eastern Europe (60 Mha). Despite this contribution to land cover, very little is known about their greenhouse gas budget. Most of the grasslands in Europe are cultivated for feeding animals, either directly by grazing or indirectly by forage grass production. European grasslands are amongst the most productive in the world. The amount of grassland biomass harvested for forage production, a fraction of net primary productivity (NPP), is in the range of 2–8 t C ha⁻¹ yr⁻¹ [Corrall, 1988] which is similar to NPP of European temperate forests [Schulze, 2000]. To sustain a high productivity, European grasslands are gener-
ally supplied with N fertilizers and consequently they emit N₂O to the atmosphere [Jarvis et al., 2001]. N₂O is a powerful greenhouse gas, about 300 times more powerful than CO₂ (per unit mass) on a 100-years time horizon [Intergovernmental Panel on Climate Change, 1995]. Typical N₂O emissions from grassland soils, converted into CO₂ equivalent sources on a 100-years time horizon [Bouwman, 1996] range between 0.1 and 1 t eq C ha⁻¹ yr⁻¹ [Machefert et al., 2002; Sozanska et al., 2002]. Extrapolated to the entire area of European grasslands, this is equivalent to a CO₂ source of 0.14 GtC yr⁻¹, i.e., one sixth of the EU-15 fossil fuel emissions. European grasslands also sustain ~15% of the global ruminant population (150 millions of cows and 150 millions of sheep) (FAOSTAT data, 2004, available at faostat.fao.org). Animals are direct sources of CO₂ via their metabolic activity. A cow respires for example about 1 tC yr⁻¹, a flux which bypasses the soil and vegetation respiration but needs to be accounted for in closing the carbon budget of grassland ecosystems. Grazing animals emit CH₄ to the atmosphere (23 times more powerful than CO₂ [Intergovernmental Panel on Climate Change, 1995]), typically 0.05 to 0.25 tCH₄ per animal and per year (0.3 to 1.5 t eq C [Vernorel, 1995]). In addition, they have an impact on the cycling of C and N in pastures via grazing, urine and faecal returns, and mechanical disturbance (trampling). Overall, compared to the CO₂ fluxes in terms of radiative forcing, the fluxes of CH₄ and N₂O over grasslands are so important that they need to be accounted for in any evaluation of the European grasslands greenhouse gas budget [Soussana et al., 2004].

[3] The greenhouse gas budget of European grasslands is highly uncertain as there have been very few direct measurements of the fluxes with a sufficiently long-term continuity. However, a network of nine new sites was established as part of the GreenGrass project in 2002 (European Commission DG Research Vth Framework Programme, contract EVK2-CT2001-00105). There are also few continental-scale model-derived estimates of greenhouse gas budget of grasslands. Vleeshouwers and Verhagen [2002], further quoted by Janssens et al. [2003] developed a semi-empirical model of land use that induced soil carbon disturbances to the European continent, and they inferred a carbon sink of 101 TgC yr⁻¹ over grasslands (0.52 tC ha⁻¹ yr⁻¹) with uncertainties of similar magnitude to the mean. Regarding N₂O fluxes, Freibauer [2003] and Boeckx and VanCleemput [2001] estimated emissions of agricultural land using emission factors. They obtained a total N₂O emission of 442 ± 116 GgN₂O-N yr⁻¹ (0.056 Gt-eqCO₂-C), of which 165 ± 48 GgN₂O-N yr⁻¹ was emitted by grasslands. Other studies were made by Brown et al. [2002] for the United Kingdom and by de Vries et al. [2003] for the Netherlands which yielded national average estimates. Methane emissions due to animal enteric fermentation have been mainly determined at the animal level (Murray et al. [2001] for sheep; Vernorel [1995] for cattle) and then upscaled to the regional or continental level using statistical information on animal numbers by category [Crutzen et al., 1986].

[4] These studies have no doubt delivered improved quantification of individual components of grasslands greenhouse gas budget but they do not allow a comparison of sources and sinks of CO₂ with sources of CH₄ and of N₂O. To our knowledge, only the recent study of Freibauer [2003] has combined flux estimates for N₂O, CH₄ and CO₂. In that study, regional budgets are calculated using emission factors for each gas and the only flux component of the CO₂ budget is the one related to soil disturbance on farmed organic soils: a process which always was assumed to act as a net source to the atmosphere. When upscaled using emission factors, the fluxes of each gas are decoupled from each other and the process-related interactions between them cannot be properly accounted. For instance, increasing N fertilization leads to higher N₂O emissions, but there is a concurrent stimulation of NPP, which fosters CO₂ uptake. Current approaches lack consistent handling of management effects on greenhouse gas emissions from grasslands and therefore hinder any reliable predictions under future climate and management changes.

[5] In this paper we develop a new modeling approach with the objective of quantifying how climate and management conditions determine greenhouse gas emissions for grasslands in a spatially and temporally explicit manner. Several process-based models of grasslands have been developed [Sheehy and Johnson, 1988], and applied at different scales from plot [Gilmanov et al., 1997; Riedo et al., 1999] to region [Mougin et al., 1995; Schapendonk et al., 1998]. Some of these models describe vegetation for an agronomic purpose or for an economic one by predicting the amount of harvested forage grass [Riedo et al., 1999; Schapendonk et al., 1998]. Others account for the fate of carbon and nitrogen in the soils [Parton et al., 1988]. Few simulation models are designed to simulate simultaneously CO₂ fluxes exchanged with vegetation, soil and animals and the atmosphere, N₂O emissions produced by soil processes and CH₄ emissions due to animals. We improve a process-based model of grassland biogeochemistry called PASIM [Riedo et al., 1998]. The PASIM model was evolved from the Hurley-Pasture Model [Thornley, 1998] and has been to date only tested at Swiss grassland sites harvested for forage production, for simulating vegetation variables [Riedo et al., 2000] and N₂O emissions [Schmid et al., 2001a, 2001b]. Here we enhance the model and apply it to grazed sites and include CH₄ emissions by animals. We selected three temperate grassland sites (of which two compare two treatments) used within the GreenGrass project, located in Ireland, France and Switzerland, which represent contrasting soil and climate conditions for both grazing and cutting management schemes. Two of these sites include high- and low-nitrogen fertilizer applications regimes. We evaluate the PASIM model against in situ NEE measurements made on a continuous basis by the eddy covariance technique, and against shoot biomass and leaf area index measurements. In addition, we evaluate the modeled CH₄ emissions against flux data from Laqueille.
apply the same model to upscale the greenhouse gas budget of grasslands for the European continent.

2. Methods

2.1. Grassland Model

2.1.1. Key Processes

PASIM is a process-based grassland biogeochemical model derived by Riedo et al. [1998] from the Hurley Pasture Model (HPM) [Thornley, 1998]. The program contains 8000 lines and it is written in ACSL language [Mitchell and Gauthier Associates, 1993]. As for other advanced biogeochemical models, PASIM simulates the carbon and nitrogen cycles, the latter having been improved by Schmid et al. [2001b], who added a detailed description of the nitrification and denitrification processes leading to nitrous oxide emissions. In PASIM, the photosynthesis model is a multilayered one based on a nonrectangular hyperbola [Riedo et al., 1998]. This model takes into account sun and shaded leaf fractions. Carbon assimilated by photosynthesis on a time step of 30 minutes is allocated dynamically to 1 root and 3 different shoot biomass compartments (each of those being dissociated in 4 age compartments), or is respired by autotrophic processes (Figure 1).

Aboveground biomass is either cut for yield production, grazed by animals or accumulates on the soil surface owing to death and detachment. Typically 3 to 5% of the total carbon ingested by animals is emitted back to the atmosphere as CH$_4$. The nitrogen cycle in PASIM considers three different types of N inputs to the soil via atmospheric deposition, fertilizer addition, and symbiotic fixation by clover. A fraction of the added soil nitrogen is available for plant growth and subsequently taken up by roots, whereas another fraction of soil nitrogen is lost through leaching, volatilization and nitrification/denitrification, the latter processes being responsible for N$_2$O gas emission to the atmosphere. Three distinct management practices are treated as boundary conditions to the model: (1) grazing intensity estimated from the cattle stocking density (animals ha$^{-1}$), (2) harvesting as controlled by the prescribed timing of cuts and amount of harvested biomass, and (3) timing and amount of N fertilizer applications. We have used the PASIM model in its standard configuration [Riedo et al., 1998; Schmid et al., 2001b], with the same parameter values as in Riedo for all sites, except for the key changes described below (see also Appendix A).

2.1.2. Effects of Animals’ Diet on CH$_4$ Emissions

Methane emissions by animals were previously calculated as a fixed proportion of the ingested carbon. In reality, the main factors responsible for CH$_4$ production are not only the amount but also the quality of the diet [Blaxter and Clapperton, 1965]. We thus introduced a quality factor in the equation governing CH$_4$ emission from cattle. Thus we let the CH$_4$ production (hereafter called $m$) depend on the DNDFI, the amount of digestible fiber in the animal’s intake (hereafter called $q$). Regression model of Pinarés-Patino et al. [2007] gives

$$m = aq + b,$$  

where $m$ is the daily methane emission per kg of animal live weight (gCH$_4$ kg$^{-1}$ day$^{-1}$), $q$ is the amount of digestible

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![Figure 1. Flow diagram of PASIM model. The grey boxes represent management drivers, treated as boundary conditions for the model.](image-url)
fiber in the intake (kg day\(^{-1}\)). The slope and intercept values are \(a = 0.045\) gCH\(_4\) kg\(^{-1}\) day\(^{-1}\) and \(b = 0.287\) gCH\(_4\) kg\(^{-1}\) day\(^{-1}\). The intake \(q\) can further be expressed as the product

\[
q = dfi, \tag{2}
\]

where \(i\) is the amount of organic dry-matter biomass ingested per animal per day (kg DM day\(^{-1}\) animal\(^{-1}\)), \(f\) is the fraction of fiber in the intake, often called NDF (dimensionless) and \(d\) is the fraction of digestible fiber in total fibers, often called DNDN (dimensionless). In PASIM, we write \(f\) and \(d\) as the weighted means of the different leaf, sheath and ear pools of shoot biomass. This is expressed by

\[
f = \frac{\sum_i w_i f_i}{\sum_i w_i}, \tag{3}
\]

\[
d = \frac{\sum_i \sum_{j=1.4} w_i d_{i,j}}{\sum_i \sum_{j=1.4} w_i}, \tag{4}
\]

where \(w_i\) is the amount of the pool \(i\) (age \(j\)) ingested by the animal, and \(d_{i,j}\) is the fraction of digestible fibers for pool \(i\) (age \(j\)) defined according to Groot [1999]. The values of these parameters are given in Table 1.

### 2.1.3. Water and LAI Limitations on Vegetation Dynamics

[9] Vegetation growth is simulated for four biomass compartments of different ages. Biomass flows from a compartment to the next one at a turnover rate \(k\). Thus biomass in the \(i\)th age compartment \((w_i)\) follows a first-order differential equation given by

\[
\frac{dw_i}{dt} = w_i(1 - k + kw_{i-1}). \tag{5}
\]

[10] In the first age compartment, however, the input flux corresponds to the allocation of assimilates. In HPM, \(k = k_{30} f_t/f_w\), where \(f_t\) is a dimensionless stress factor relative to temperature, \(f_w\) a stress factor relative to soil water deficit and \(k_{30}\) the turnover rate at 20°C without any stress. In the initial version of PASIM, \(f_w\) was arbitrarily set to 1, thus ignoring water limitations effects on vegetation age dynamics. We introduce a simple formulation of \(f_w\) given by

\[
f_w = 0.5(1 + f_{w0}), \tag{6}
\]

where \(f_{w0}\) is the water stress effect on photosynthesis, and varies between 0 and 1 [Riedo et al., 1998]. With that new formulation, the turnover rate of vegetation exposed to strong water deficit conditions \((f_{w0} \approx 0)\) reaches up to twice the value in normal conditions.

[11] In addition, we also impose a limitation of vegetation turnover rates driven by leaf area index (LAI) values. As suggested by Bouman et al. [1996] in the LINGRA model, “with increasing LAI, the deeper layers of the crop become shaded, the low light intensities initiate remobilization of nitrogen from the shaded leaves and the leaves go through a stage of rapid senescence.” The LAI limitation factor \(f_L\), acts to increase the turnover rate at high LAI value. As in the work by Bouman et al. [1996], we assume \(f_L = 1\) for LAI < 4, and \(f_L\) increasing linearly with LAI to reach a maximum value of 2.5 for LAI = 8. The expression of \(f_L\) writes

\[
f_L = \max\left[1, 0.5\left(\min(8, \text{LAI})^3 - 1\right)\right]. \tag{7}
\]

[12] The effects of high LAI and of soil water deficit in increasing turnover rates (shortening turnover times) are not considered to be additive. In presence of both water and LAI limitations, the value of \(k\) is given by

\[
k = k_{30} f_t \max\left(\frac{1}{f_w}, f_L\right). \tag{8}
\]

### 2.1.4. Senescence Impacts on Vegetation Dynamics

[13] Both growth and senescence are governed by the allocation of assimilates and by the turnover rate \(k\) of the vegetation age cohorts. During mortality periods, when no new assimilates get allocated to the tissues, the mass of each age cohort follows an exponential decay with time. This formulation causes a delay in the mortality of each compartment and of the plant system as a whole. The half-life of a one-compartment system is \(\ln(2)/k\). Contrary to what we know on plant physiology [Thornley, 1998], with a cascade of 4 compartments of same turnover \(k\), the half-life of the system of pools is not \(4 \times \ln(2)/k\). For example, for \(k = 0.05\) day\(^{-1}\) (the nominal value in PASIM at 20°C and without any stress), the half-life of the 4 compartments system has been defined by numerical integration to 73.5 days, instead of 55.4 days if using the \(4 \times \ln(2)/k\). Thus the more age dependent the pools, the longer the turnover rate of the system will be. To correct for this bias, we introduce in the model a senescence term, which accelerates the turnover when the age of a compartment is above a certain threshold. This senescence term \(k_{si}\) is added to the turnover \(k\) of each compartment \(i\), according to the following formula suggested by Krinner et al. [2005],

\[
k_{si} = \min\left(1, \frac{1}{a_{c,i}(ac_{c,i}/ai)^{a_{c1}/2}}\right) \quad \text{if } a_i > a_{c1}/2; \tag{9}
\]

\[
k_{si} = 0 \quad \text{if } a_i < a_{c1}/2,
\]

where \(a_i\) is the age of biomass in the compartment \(i\) and \(a_{c1}\) is a critical age equals to multiples of the half-life of the first
Figure 2. Biomass dynamics for a system of one age compartment (pluses), two age-compartments (circles), three age compartments (crosses) and four age compartments (triangles). The thick lines represent the biomass dynamic with the added senescence term ($k_{\text{ss}, i}$, see text) and the thin ones represent that without. The curves were generated by a simple model using Scilab with a value of the turnover rate $k = 0.05 \text{ day}^{-1}$ and by injecting an arbitrary biomass input of 100 units on day 0 into the first age compartment and no input thereafter.

compartment: $a_{C,1} = \ln(2)/k$, $a_{C,2} = 2 \times \ln(2)/k$, $a_{C,3} = 3 \times \ln(2)/k$ and $a_{C,4} = 4 \times \ln(2)/k$. Using a turnover rate value of $k = 0.05 \text{ day}^{-1}$, we obtain for example $a_{C,1}$, $a_{C,2}$, $a_{C,3}$ and $a_{C,4}$ values of respectively 13.9, 27.7, 41.6 and 55.4 days.

(14) The age of biomass in the compartment $i$, $a_i$, is calculated at each step from the input of younger material issued from compartment $(i - 1)$ and the loss of material to $(i + 1)$ according to

$$\frac{da_i}{dt} = \frac{w_i a_i (1 - k_{\text{tot}, i}) + k_{\text{tot}, i-1} w_{i-1} a_{i-1} + 1}{w_i (1 - k_{\text{tot}, i}) + k_{\text{tot}, i-1} w_{i-1}}$$

(10)

where $k_{\text{tot}, i}$ is the total turnover rate, including the senescence term of (9), as given by

$$k_{\text{tot}, i} = k + k_{\text{ss}, i}\ (11)$$

(15) Figure 2 shows how adding a senescence term, which accelerates the turnover of aging biomass pools reduces the half-life of vegetation biomass. This change in the PASIM model prevents the half-life of the green material being overestimated, and avoids errors in the dynamics of carbon and nitrogen pools.

2.1.5. Grazing Impact on Vegetation Dynamics

(16) In the previous version of PASIM, the impact of defoliation and intake by animals was accounted for but the detrimental effects of trampling and of excretal returns (e.g., urine scorching) [Guthery and Bingham, 1996] was not. We simulate these extra processes by removing at each time step a fixed proportion $k_G$ of the above ground biomass, which flows to the litter compartment. The value of the rate of removal $k_G$ (day$^{-1}$) depends on animal stocking rate $s$ (Livestock Units per hectare and per day, LSU ha$^{-1}$ day$^{-1}$), and it is given by

$$k_G = gs,$$

(12)

where $g$ is expressed in (LSU ha$^{-1}$) and equals to 0.008, implying that an additional 0.8% of the aboveground herbage biomass is returned each day to litter for an instantaneous stocking rate of 1 LSU ha$^{-1}$.

2.2. Flux and Pools Data From Representative Sites

(17) The results of the model are compared to carbon fluxes and pools measurements from three grasslands, Oensingen (OEN), Laqueuille (LAQ) and Carlow (CAR) over the period mid-2002 to mid-2003. Two of these grasslands (OEN and LAQ) compare two experimental sites. Table 2 gives the timing and characteristics of grassland management for the five sites. Details on the site-specific parameters values may be found in auxiliary Table S1.

2.2.1. Oensingen, Switzerland (Cut)

(18) The OEN grassland has been newly sown in spring 2001 with grass and clover. It is intensively managed grassland, located in Switzerland (47° 17' N, 07° 44'E) at 450 m a.s.l., with an annual mean temperature of 9 °C and annual precipitation of 1100 mm yr$^{-1}$. The soil type on OEN is stagnic Cambisol (eutric) with a soil organic matter content of 3.5%. We use data from two distinct plots characterized by contrasted N treatments, OEN-HN (for High Nitrogen) and OEN-LN (for Low Nitrogen). The two plots were managed by cutting. At OEN-HN, five cuts were applied in 2002, together with five fertilizer applications, one in the early spring and one after each cut, summing up to a total amount of 210 kg N ha$^{-1}$. In 2003, an amount of 60 kg N ha$^{-1}$ fertilizer was applied in the early growing season. At OEN-LN, only three cuts were applied in 2002 and no fertilizer was supplied during the whole period.

2.2.2. Laqueuille, France (Grazed)

(19) The Laqueuille grassland, LAQ, is semi-natural grazed grassland located in central France (45°38'N, 02°44'E) at an elevation of 1040 m a.s.l. with an annual mean temperature of 8 °C and annual precipitation of 1000 mm yr$^{-1}$. These climate conditions are quite comparable with those of the Oensingen site. The LAQ grassland is an andosol developed on basaltic rocks. It has a loamy texture and a high soil organic matter content (18% with a C:N ratio of 10.5). As for OEN, two distinct plots have been established, characterized by contrasted N treatments and cattle grazing intensity. Those sites are called respectively LAQ-HN (high nitrogen and intensive grazing) and LAQ-LN (low nitrogen and extensive grazing). The two plots were managed by continuous grazing with heifers from day 141 until day 292 in 2002. The mean animal stocking rate during this grazing season reached 2.2 and 1.3 LSU ha$^{-1}$ for LAQ-HN and for LAQ-LN, respectively. Both plots received 80 kg N ha$^{-1}$ of organic
fertilizer on day 14 in 2002, before the start of the treatments, and the intensive plot received an additional 80 kg N ha\(^{-1}\) of ammonium nitrate on day 171 in 2002 (see Table 2).

### 2.2.3. Carlow, Ireland (Cut and Grazed)

[20] The Carlow grassland, CAR, has been resown with grass and clover in 2001. It is an extensively cut and grazed grassland located in Ireland (52\(^\circ\) 52\(^\prime\)N, 06\(^\circ\) 55\(^\prime\)W) at 56 m a.s.l.. The annual mean temperature is 9.5\(^\circ\)C and annual precipitation 820 mm yr\(^{-1}\). The soil is a medium to loamy textured grey/brown podsolic soil (4 % OM, C:N ratio of 9.4). During 2002–2003, the CAR grassland has been used for cutting and grazing. In 2002, the CAR grassland received two nitrogen fertilizer applications for an annual amount of 200 kg N ha\(^{-1}\) (Table 2). The main application of 150 kg N ha\(^{-1}\) occurred in spring. The CAR site has been cut once on day 155 in 2002 and it was subsequently grazed between day 197 and day 321 with a mean animal stocking rate of 1.6 LSU ha\(^{-1}\) (see Table 2).

### 2.2.4. In Situ Flux and Pool Measurements

[21] At each of the three sites, GreenGrass experimental researchers measured the Net Ecosystem Exchange of CO\(_2\) (NEE) on a quasicontinuous basis by the eddy covariance method (for Oensingen [Ammann et al., 2004]). These data are reported here on a daily basis. Further, at the grazed site LAQ, the CH\(_4\) emissions by cows were quantified in situ by the SF6 dual tracer method [Johnson et al., 1994]. Unlike NEE, these measurements of CH\(_4\) fluxes are noncontinuous, and they span over 4 weekly periods in 2002. The SF6 dual tracer method shows higher animal-to-animal variation than the net-ecosystem exchange module (equations (1) to (4)).

### 3. Results: Model Evaluation Against Observations

#### 3.1. Setup of Site-Specific Simulations

[22] We define a control simulation called S0, with the former version of the model without any of the changes presented in section 2.1 (version 3.5 [Riedo et al., 1998; Schmid et al., 2001b]). Then we increment successively LAI and water deficit limitations (simulation S1), age-dependent senescence (S2) and trampling impacts (S3). The model is driven at each site by observed gap-filled hourly time series of temperature, precipitation, and downwelling shortwave radiation. The soil texture is prescribed from measurements made on each site. The biomass and soil pools are always initialized to values closed to their steady state equilibrium values after a 50 years spinup during which climate and management practice of year 2002 are repeatedly cycled. Then we calculate the fluxes and biomass evolution for the period from mid-2002 to mid-2003. We provide a detailed comparison of the model output with observed shoot biomass, LAI and NEE for the three sites and for both N treatments at Oensingen and Laqueuille. In addition, we evaluate the model results against site measurements of herbivore CH\(_4\) emissions at Laqueuille. For herbivore methane emissions, we use the S3 version of the model, but with and without the changes in the methane production module (equations (1) to (4)).

#### 3.2. Oensingen Carbon Simulation

[23] For the cut and highly fertilized grassland of Oensingen, OEN-HN, the phase and amplitude of NEE, LAI and shoot biomass are well simulated by the control version S0 (Figure 3) when the observed dates of grass harvest are prescribed. All the S0-S2 runs are equally close to the measured data (Table 3). The model-data correlation coef-
ficients for NEE are $R^2_{S0} = 0.67$, $R^2_{S2} = 0.73$ (Figure 4 for S2, intercept of -4.4 kg C ha$^{-1}$ d$^{-1}$ and slope of 0.71). The root-mean squared difference between model and data values are RMS$_{\text{WSH},S0} = 0.1$ and RMS$_{\text{WSH},S2} = 0.1$ kg DM m$^{-2}$ for shoot biomass (26% and 22% of the mean observed shoot biomass, respectively). For LAI simulations, we obtain root mean squared differences of RMS$_{\text{LAI},S0} = 1.4$ and RMS$_{\text{LAI},S2} = 1.1$ m$^2$ m$^{-2}$ (50% and 40% of the mean observed shoot biomass, respectively). It can be seen in Figure 3 that the modeled NEE in both S0 and S1 has an over-early start of the net CO$\text{}_2$ uptake in 2003. This bias is reduced in S2 since the higher leaf mortality delays the growth of biomass in spring. Overall, we find that when N is not limiting and under intensive cutting, PASIM simulates well the carbon fluxes and biomass dynamic of the Oensingen grassland. In particular, the model captures very well the recovery of biomass after cutting (Figure 3). In contrast, when no fertilizers are applied at this site, we can see in Figure 5, that the simulation S0 grossly overestimates the LAI during the peak of the growing season, by up to 7 m$^2$ m$^{-2}$ as compared with the data (Table 3, RMS$_{\text{WSH,SL0}} = 3.9$) while NEE and shoot biomass at harvest dates are simulated well (Table 3, RMS$_{\text{WSH,SL0}} = 0.1$). Accounting for water and high LAI limitations on biomass growth in S1 decreases the maximum LAI values (RMS$_{\text{LAI},S1} = 3.6$) in the right direction, but still significantly overestimates the early season LAI. This is also reflected in the overestimated CO$\text{}_2$ uptake during the early season, up to May ($R^2_{S1} = 0.59$). This model bias is reduced in S2 where LAI drops to 0.5 in January–February (RMS$_{\text{LAI},S2} = 2.0$), causing NEE to be close to zero during the winter ($R^2_{S2} = 0.72$, Figure 4, intercept of -5.3 kg C ha$^{-1}$ d$^{-1}$ and slope of 0.89). This is because the added senescence effect induces enough leaf mortality to bring down LAI in the winter (Figure 5). In parallel, the simulation S2 reduces significantly the shoot biomass at the first harvest dates to 0.6 kg DM m$^{-2}$ (Figure 5 and Table 3, RMS$_{\text{WSH,SL2}} = 0.2$ kg DM m$^{-2}$). Finally, in the S2 version, the model still largely overestimates LAI but not the shoot biomass on OEN-LN (low N), while it calculates consistent LAI and shoot biomass values on OEN-HN (high N). At low N and low LAI leaves appear to have a lower area per unit mass than predicted by the model, which induces an overestimation of LAI for the OEN-LN site.

3.3. Laqueuille Carbon Simulation

[25] For the high-nitrogen and intensively grazed plot of Laqueuille, LAQ-HN, the simulation S0 gives unrealistically high values of LAI, with values of up to around 20 m$^2$ m$^{-2}$.\n
![Figure 3.](set) (a) Model-data comparison for the highly fertilized cut grassland of Oensingen, OEN-HN, of net ecosystem exchange in kgC-CO$_2$ ha$^{-1}$ d$^{-1}$. (b) Same for LAI (m$^2$ m$^{-2}$). (c) Same for shoot biomass (kg DM m$^{-2}$). Vertical dashed lines represent cut events. Each column correspond to the simulations with the initial version of the model (S0), to which are added water and LAI limitations on vegetation dynamics (S1), and senescence (S2).
Similarly, shoot biomass is overestimated by a factor of 9 (RMS$_{WSH,S0} = 1.3$ kg DM m$^{-2}$) when compared to the data (Figures 6b and 6c). In S0, the model-data correlation coefficient for NEE is also very low ($R^2_{S0} = 0.01$). Accounting for LAI and water limitations on vegetation dynamics in the simulation S1 greatly improves the fit to the data, with a gain of a factor of 2 (Table 3). Further, adding senescence in simulation S2 produces more realistic LAI values, especially in winter times. The best fit to the data for NEE, shoot biomass and LAI is finally obtained when adding the effect of trampling in the S3 simulation (Figure 6 and Table 3), albeit the model still overestimates LAI and shoot biomass from April to June. In the simulation S3, the NEE variability is reduced, in closer agreement with the flux data (Figure 4, $R^2_{S3} = 0.09$, intercept of 1.0 kgC ha$^{-1}$ d$^{-1}$ and slope of 0.39). Note that the NEE of the grazed Laqueuille grassland is nearly flat during the growing season because of the continuous biomass consumption by cows, in contrast with Oensingen which has large intraannual NEE variations due to the cuts (compare Figure 5 and Figure 6). This major difference between grazed and cut NEE, which determines the European patterns of NEE...

Figure 4. Scatterplots of the modeled versus measured NEE (in kgC-CO$_2$ ha$^{-1}$ d$^{-1}$) for the five sites of this study for the last version of the model (S2 for Oensingen sites and S3 for the grazed sites).

Figure 5. Same as Figure 3 for the nonfertilized cut grassland of Oensingen, OEN-LN.
(see companion paper) is correctly captured by the model. For the low-nitrogen and extensively grazed plot of LAQ-LN, the simulation S0 run has similar shortcomings to those at LAQ-HN (Figure 7), with overestimated LAI, shoot biomass and NEE variability during the growing season. We find that adding successively LAI and water limitations (S1 run), winter senescence (S2 run) and trampling (S3 run) in the model improves the fit to the data at LAQ-LN. The above conclusions regarding the model performances at LAQ-HN can thus be generalized to the low-nitrogen extensive conditions of LAQ-LN. This is illustrated by comparing Figure 6 and Figure 7. The best fit to the site data here again is

<table>
<thead>
<tr>
<th>Parameter</th>
<th>OEN-HN</th>
<th>OEN-LN</th>
<th>LAQ-HN</th>
<th>LAQ-LN</th>
<th>CARL</th>
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<tr>
<td>WSH, kg DM m⁻²</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Observed mean value</td>
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<tr>
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<td>1.1</td>
<td>0.5</td>
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<tr>
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<td>0.1</td>
<td>0.6</td>
<td>0.5</td>
<td>0.3</td>
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<tr>
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<td>0.4</td>
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<tr>
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<td>...</td>
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<td>0.1</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td>2.4</td>
<td>1.3</td>
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<tr>
<td>RMS S3</td>
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<td>...</td>
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<tr>
<td>R², NEE, %</td>
<td></td>
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<td></td>
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<td></td>
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<tr>
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<td>...</td>
<td>9</td>
<td>10</td>
<td>83</td>
</tr>
</tbody>
</table>

*RMS, root mean squared difference of model versus data; R², correlation coefficient of model versus NEE data.

**Table 3.** Evaluation of the Modeled Shoot Biomass (WSH), LAI and NEE at the Five Different Grasslands Versus In Situ Measurements

**Figure 6.** Same as Figure 3 for the fertilized and intensively grazed grassland of Laqueville, LAQ-HN. We added the results of Simulation S3 which accounts for animal trampling in reducing the growth of aboveground biomass. Horizontal thick lines represent the grazing period.
obtained in the simulation S3 giving \( R^2_{S3} = 0.10 \) for NEE (Figure 4, intercept of 1.9 kg C ha\(^{-1}\) d\(^{-1}\) and slope of 0.40), RMS for LAI of 2 m\(^2\) m\(^{-2}\) and RMS for shoot biomass of 0.3 kg DM m\(^{-2}\).

### 3.4. Carlow Carbon Simulations

[26] For the cut and grazed grassland site of Carlow, CAR, we observe in Figure 8 that NEE is correctly simulated in the simulation S0 (\( R^2_{S0} = 0.75 \)). However, the simulation S0 grossly overestimates both LAI and shoot biomass values at CAR (Figure 8 and Table 3) with a RMS for LAI of 9.6 m\(^2\) m\(^{-2}\) and a RMS for shoot biomass of 0.5 kg DM m\(^{-2}\). New parameterizations introduced in S1-3 tend to successively improve the NEE simulation (Figure 8 and Table 3), leading to a model-data correlation coefficient of 0.83 for S3 (Figure 4, intercept of 6.1 kg C ha\(^{-1}\) d\(^{-1}\) and slope of 1.07). Shoot biomass and LAI are also improved in S2 and S3 simulations. However, during the period of grazing, these versions of the model still overestimate the observed LAI and biomass, by up to a factor of 2.

### 3.5. Laqueuille \( \text{CH}_4 \) Flux Simulation

[27] At the intensively grazed and fertilized grassland, LAQ-HN, the animal methane emissions are well simulated (Figure 9a). The thin dashes in this figure represent the estimate obtained by applying the regression model of section 2.1.2. applied directly to the DNDFI data. The main source of misfit between the simulated and observed \( \text{CH}_4 \) flux is caused by errors in the prescribed values of NDF, DNDF or intake parameters as seen in Figures 9b–9d. The NDF is correctly simulated (Figure 9b) but the model is not able to represent the dynamics of the DNDF and intake (Figures 9c and 9d). At the extensively grazed and less fertilized grassland, LAQ-LN, more or less the same conclusions can be drawn that at LAQ-HN (Figure 10). This gives us confidence in the fact that the model can reproduce \( \text{CH}_4 \) emissions by grazing animals in the case of two contrasted N treatments, although the main driver (of the modeled \( \text{CH}_4 \) flux) remains the prescribed animal density. The DNDF data show a decrease from the second measurement period while the simulated DNDF increases at that period (Figure 10c). The intake is poorly simulated for the third measurement period (Figure 10d). In all cases, our new methane emission equations give better results than the former parameterizations. This is illustrated by comparing the dotted and dash-dotted lines for both LAQ-HN (Figure 9a) and LAQ-LN (Figure 10a).

### 4. Discussion and Concluding Remarks

[28] We first need to keep in mind that a very stringent evaluation of the model is hindered by rather large uncertainties on biomass measurements, typically with an error of 15%, due in part to spatial heterogeneity. Eddy covariance flux measurements, due to gaps and night time respiration problems are also accompanied by an uncertainty (which may reach 20% for day hourly data and 40% for night hourly data [Moncrieff et al., 1996]). The model is not
perfect either. Uncertainty analysis of the annual cumulated NEE (e.g., NEP) simulated by PASIM (using 50 version) has been performed by Gottschalk et al. [2007] for several European grasslands sites. They obtain a considerable variation of global uncertainty from site to site and between years (the standard deviation varying from 3% up to 100% of the mean NEP value) and conclude that the site specific combination and interaction of ecosystem parameters, driving forces and management make it impossible to define an absolute model output uncertainty. Regarding the simulated carbon balance of grasslands, it must also be kept in mind that all the runs are equilibrium calculations where the ecosystem is not disturbed. By construction the simulated long-term mean carbon balance, or Net Biome Productivity (NBP) equals zero. Thus the observed annual mean sink at LAQ-HN and LAQ-LN, or source at OEN-HN and OEN-LN cannot be simulated by PASIM. For this reason, we only discussed NEE variations during the year, but not the average annual NEE estimates.

[29] Generally, we found that (1) it is especially difficult to realistically simulate biomass dynamics, (2) the simulations for cut grasslands are better than for grazed ones, irrespective of the nitrogen treatments, and (3) accelerating the vegetation turnover during the growing season always improves the fit to the data. However, the model improvements benefit rather to shoot biomass and LAI than to NEE. Thus NEE improvements are loosely related to those made on LAI: for instance on LAQ-HN, the LAI is reduced by one order of magnitude among versions (from 20 to 2 m²m⁻², Figure 6b) while model-data correlation coefficient for NEE does not vary by more than 9% (Figure 6a). This counterintuitive result is explained by the fact that full light interception is obtained at LAI values below 10 m²m⁻². Hence the high LAI values calculated in the S0 version do not increase photosynthesis as the additional leaf layers are fully shaded. Moreover, the N content of leaves increases with the number of the version used, as nutrients are concentrated in a smaller number of leaf layers, which tends to increase the photosynthesis per unit leaf area in the higher versions. As a result of these two processes, the annual GPP does not vary by more than 15% (data not shown) between the different versions of PASIM for grazed sites. The difference in the model performances between cut and grazed grasslands may be explained by the fact that sporadic cutting events enables the model to reset the vegetation variables to values close to zero and thus prevents the model from drifting away from the data after the onset of growth. In contrast, continuous defoliation by grazing has a weaker impact on vegetation than defoliation by cutting and it is more difficult to account for such a permanent disturbance in models. Moreover, grazing induces complex animal-vegetation interactions, which have an impact on sward level but are not simulated by PASIM. Because of the development of spatial heterogeneity in grazed paddocks, the herbage growth varies spatially which makes it more difficult to simulate using a model such as PASIM which assumes a spatial homogeneity. The correlations between simulated and observed NEE at the different sites confirm

Figure 8. Same as Figure 6 for the mixed cut and grazed grassland of Carlow, CAR. Vertical dashed lines represent cut events and horizontal thick lines grazing periods.
Figure 9. (a) Model-data comparison of animals’ daily CH$_4$ fluxes at the intensive LAQ-HN plot in gC-CH$_4$ ha$^{-1}$ d$^{-1}$. (b) Proportion of fiber in the ingested biomass. (c) Proportion of digestible fiber in the total ingested fiber. (d) Animal intake (kg DM ha$^{-1}$ d$^{-1}$). The thin dashes mentioned as regression model are the CH$_4$ fluxes obtained when applying the empirical model of diet quality directly to the DNDFI data.

Figure 10. Same as Figure 9 but at the extensive LAQ-LN plot.
the fact that PASIM better simulates cut grasslands. The sawtooth shape of NEE due to harvest is well captured at both OEN and CAR cut sites, with an abrupt shift from CO₂ uptake to CO₂ release after harvest. In contrast, at the LAQ grazed site, the absence of cuts induces smaller amplitude NEE variations during the growing season, which the model does not capture very well.

Concerning animal CH₄ emissions, we found that the model of Pinares-Patino et al. [2007] can successfully be introduced in PASIM, yet with some difficulties to simulate some of the key input variables of the empirical model, such as the DNDF and intake. In PASIM, the intake is only driven by the shoot biomass averaged at the plot level. When sward spatial heterogeneity exists, the relation between intake and vegetation status may be much more complex and this may explain discrepancies between measurements and simulated intake. Moreover, to fully validate the model of Pinares-Patino et al., it will be necessary to test it across a large range of grasslands quality and with different types of animals.

Appendix A

Table A1 presents the variables and parameters of the equations of the PASIM model as modified in this paper.

Acknowledgment. This work was funded by the EC under the contract EVK2-CT2001-00105 “GreenGrass.”

References

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