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A model-data fusion approach to analyse carbon dynamics in managed grasslands

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Abstract

Grasslands are an important component of the global carbon (C) cycle, with a strong potential for C sequestration. However, an improved capacity to quantify grassland C stocks and monitor their variation in space and time, particularly in response to management, is needed in order to conserve and enhance grassland C reservoirs. To meet this challenge we outline and test here an approach to combine C cycle modelling with observational data. We implemented an intermediate complexity model, DALEC-Grass, within a probabilistic model-data fusion (MDF) framework, CARDAMOM, at two managed grassland sites (Easter Bush and Crichton) in the UK. We used 3 years (Easter Bush, 2002-2004) of management data and observations of leaf area index (LAI) and Net Ecosystem Exchange (NEE) from eddy covariance to calibrate the distributions of model parameters. Using these refined distributions, we then assimilated the remaining 7 years (Easter Bush, 2005-2010 and Crichton, 2015) of LAI observations and evaluated the simulated NEE, above and below-ground biomass and other C fluxes against independent data from the two grasslands. Our results show that fusing model predictions with LAI observations allowed the CARDAMOM MDF system to diagnose the effects of grazing and cutting realistically. The overlap of MDF-predicted

34 and measured NEE (both sites) and ecosystem respiration (Easter Bush) was
35 92% and 83% respectively while the correlation coefficient (r) was 0.79 for
36 both variables. This study lays the foundation for using MDF with satellite
37 data on LAI to produce the spatially and temporally-resolved estimates of
38 C cycling needed in shaping and monitoring the implementation of relevant
39 policies and farm-management decisions.

40 *Keywords:* UK grasslands, primary production, carbon sequestration,
41 model-data fusion

42 Ecosystem carbon accounting abbreviations

43 Gross Primary Production : GPP

44 Autotrophic Respiration : AR

45 Heterotrophic Respiration : HR

46 Ecosystem Respiration : $ER = AR + HR$

47 Net Primary Production : $NPP = GPP - AR$

48 Net Ecosystem Exchange : $NEE = ER - GPP$

49 Net Ecosystem Production : $NEP = GPP - ER$

50 1. Introduction

51 Grasslands cover a third of the earth's surface and are a major compo-
52 nent of the terrestrial biosphere's carbon (C) cycle and a major contributor to
53 global annual fluxes and C stores (Hungate et al., 2017; Friedlingstein et al.,
54 2019; Sollenberger et al., 2019). Temperate grasslands, because of edapho-
55 climatic conditions and their botanical composition, can transfer and accu-
56 mulate C in their soils more efficiently than grasslands in warmer and drier
57 regions (Gibson, 2010). Based on this premise, and considering the rise in
58 atmospheric CO₂ concentration, European grasslands have the potential for
59 increased CO₂ sequestration (Chang et al., 2017). Estimates of grassland C
60 balance and its variation in space and time are essential for shaping evidence-
61 informed climate policies and monitoring progress on Nationally Determined
62 Contributions (NDCs) following the Paris agreement (De Oliveira Silva et al.,
63 2018). Livestock grazing and grass harvesting affect grassland C stocks, typ-
64 ically removing >50% of vegetation C on an annual basis (Erb et al., 2018).
65 In addition to sustaining livestock farming by providing biomass energy to
66 livestock directly from grazing or as fodder, vegetation also provides inputs
67 to the soil C pool in the form of litter and exudates, as well as indirectly from
68 excrement produced by grazers (Soussana and Lemaire, 2014; Chen et al.,
69 2015; Conant et al., 2017; Abdalla et al., 2018). Because of its dynamic
70 nature, the C balance of vegetation in managed grasslands (i.e. assimila-
71 tion, allocation, removal and loss) is complex and challenging to monitor
72 and assess.

73 Detailed, continuous measurements of the C dynamics of grasslands are
74 limited to a few sites globally. Computational approaches are therefore used
75 to extrapolate observed relationships across landscapes. Such computational
76 methods include (1) statistical models that relate climate data and selected

77 national statistics to grassland productivity and removals (e.g. Smit et al.,
 78 2008; Herrero et al., 2013; Qi et al., 2017, 2018); (2) process-based grassland
 79 models that simulate C uptake and turnover (e.g. Vuichard et al., 2007;
 80 Chang et al., 2013; Snow et al., 2014; Chang et al., 2015; Kipling et al., 2016;
 81 Rolinski et al., 2018; Puche et al., 2019; Sándor et al., 2020; van Oijen et al.,
 82 2020); and (3) processed earth observation (EO) data that map and track
 83 key ecological variables, such as leaf area index (e.g. Franke et al., 2012;
 84 Dusseux et al., 2014; Asam et al., 2015; Xu and Guo, 2015; Ali et al., 2016;
 85 Gómez Giménez et al., 2017; Punalekar et al., 2018). Each method has its
 86 strengths and weaknesses. Statistical approaches are strongly grounded on
 87 measured data but have low sensitivity to the spatial and temporal variation
 88 of system drivers (e.g. climate, management) and have limited explanatory
 89 depth (Smit et al., 2008). Process models describe most of the underlying
 90 biogeochemical processes, which gives them greater explanatory depth than
 91 purely statistical approaches and the capacity to explore the consequences
 92 of different management and soil-climate conditions. But process models
 93 require observational data for parameter calibration and output error evalu-
 94 ation (Ma et al., 2015; Ehrhardt et al., 2017). Model-based studies tend to
 95 present deterministic results, ignoring the role of uncertainties around model
 96 inputs, parameters and structure, and observed data (Smith et al., 2012;
 97 Kipling et al., 2016). Earth observations increasingly provide snapshots at
 98 high temporal and spatial resolution on certain drivers and proxies of C dy-
 99 namics (e.g. vegetation structure, soil moisture). But these products do
 100 not consider the full C budget, particularly below ground, nor diagnose how
 101 grassland ecosystems C storage evolves (Ali et al., 2016).

102 Model-data fusion (MDF) is a hybrid approach that combines aspects of
 103 the three aforementioned computational approaches (Raupach et al., 2005).
 104 MDF uses probabilistic methods to calibrate model parameters and/or to
 105 quantify model predictive uncertainty (Gottschalk et al., 2007; Patenaude
 106 et al., 2008; Ben Touhami and Bellocchi, 2015; Oenema et al., 2015; van
 107 Oijen, 2017). From an ecosystem modelling perspective, MDF can be under-
 108 stood as a framework in which model parameter distributions are calibrated
 109 according to a set of observations (observed data assimilation) and model
 110 output uncertainty is quantified. The behaviour of simulated fluxes and
 111 pools is constrained according to certain rules. For instance, ancillary data
 112 from national statistics, land surveys and scientific literature can be inte-
 113 grated in a MDF framework. The strong linkage to observations means that
 114 MDF is suitable for quantifying the existing situation and for explaining the

115 mechanisms that underlie the functioning of a grassland. Model-data fusion
 116 can accommodate models of varying complexity (e.g number of parameters,
 117 modules, calculation nodes) but increasing complexity increases the compu-
 118 tational cost and can reduce the robustness of the MDF process. The MDF
 119 approach has been used in studies focusing on various aspects of terrestrial
 120 ecosystem C dynamics (e.g. productivity, biomass, fire emissions) in the past
 121 (Wang et al., 2009; Fox et al., 2009; Keenan et al., 2012; Kuppel et al., 2014;
 122 Xiao et al., 2014; Kuppel et al., 2014; Bloom and Williams, 2015; Peylin
 123 et al., 2016; Smallman et al., 2017; Scholze et al., 2017; Peaucelle et al.,
 124 2019). Model-data fusion is actively benefiting from the increasing quality
 125 and range of EO data and can be used to monitor terrestrial ecosystem C
 126 balance at various spatial and temporal scales (Guo et al., 2014; Bloom et al.,
 127 2016; Ramapriyan and Murphy, 2017; Chen and Wang, 2018).

128 Here, for the first time to our knowledge, we apply MDF to analyse
 129 ecosystem C cycling in managed grasslands. Previous probabilistic model-
 130 based studies have focused on plant functional type identification and have
 131 not considered the role of management on C cycling (Kuppel et al., 2014;
 132 Peylin et al., 2016; Peaucelle et al., 2019). In this study, we present a devel-
 133 opment of the Data Assimilation Linked Ecosystem Carbon model (DALEC)
 134 that is tailored for use in MDF for grasslands (DALEC-Grass). DALEC is a
 135 C-budget model that is integrated into the Carbon Data Model Framework
 136 (CARDAMOM) (Bloom and Williams, 2015; Bloom et al., 2016; Smallman
 137 et al., 2017). DALEC and the CARDAMOM MDF framework have been used
 138 before in MDF studies on forests and croplands (Revill et al., 2016; Small-
 139 man et al., 2017). The aim of the present study is to demonstrate MDF
 140 with DALEC-Grass and test its ability to quantify C dynamics in grasslands
 141 under variable grazing and cutting regimes. As a first step, we calibrate the
 142 distribution of DALEC-Grass parameters using 3 years of measured data on
 143 leaf area index (LAI) and net ecosystem exchange (NEE) from a grassland
 144 in eastern Scotland (UK). LAI data are routinely estimated from EO sys-
 145 tems at fine spatial (<1 ha) and temporal resolutions (\approx days). Therefore,
 146 time series of satellite LAI data have the potential to inform and constrain
 147 grassland models effectively at sub-field scales and during critical growth
 148 changes and management interventions. As a second step, we tested this
 149 assumption by evaluating our model’s predictive skill when a limited number
 150 of field-measured LAI data are assimilated through the CARDAMOM MDF
 151 framework. We assess the model’s performance by comparing its outputs
 152 to independent eddy flux data on NEE of CO_2 , above and below-ground

153 biomass and soil respiration from chambers. Six additional years of data
 154 from the core study site and one year of data from another UK site are used
 155 for the validation process. The materials and methods section describes the
 156 DALEC-Grass model, the CARDAMOM framework, the characteristics of
 157 the grassland sites that are modelled and the methodology that is followed.
 158 Finally, we discuss the potential for DALEC-Grass and CARDAMOM to
 159 produce landscape analyses of grassland C cycling under varied management
 160 systems using earth observation.

161 **2. Materials and methods**

162 *2.1. DALEC-Grass*

163 DALEC-Grass is a development of the DALEC model in which a number
 164 of processes related to grass growing, cutting and grazing have been intro-
 165 duced (Smallman et al., 2017). The model is written in fortran and its code
 166 is available online at <https://github.com/GCEL/DALEC-Grass>. DALEC-
 167 Grass is a parsimonious terrestrial ecosystem C cycling model of intermedi-
 168 ate complexity which tracks the dynamics of three plant C pools and two
 169 dead organic matter pools. DALEC-Grass does not resolve explicitly mix-
 170 tures of grasses and biodiversity, and water and nitrogen (N) cycling are
 171 not described. The model is driven by temperature, short-wave radiation,
 172 vapour pressure deficit and CO₂ concentration (Table 1). Carbon enters the
 173 ecosystem via gross primary production (GPP) which is partitioned into au-
 174 totrophic respiration or allocated to various plant pools (Fig. 1). The model
 175 simulates the turnover of plant C pools to litter and soil organic matter
 176 based on both mortality and grazing/cutting. The mineralisation (i.e. het-
 177 erotrophic respiration) and decomposition of litter and soil organic C pools
 178 are temperature dependent first order processes.

179 DALEC-Grass has 25 parameters impacting photosynthesis, litter pro-
 180 duction and decomposition, fractional allocation of C, and climate sensitiv-
 181 ity of phenology and decomposition. A further 8 parameters relate to initial
 182 conditions of C pools and to management impacts of grazing and cutting
 183 (see Table 5 in supplementary material). The calculations in DALEC-Grass
 184 are performed on a daily basis by default. A component of DALEC-Grass is
 185 the Aggregated Canopy Model (ACMv1); a photosynthesis model that emu-
 186 lates a detailed mechanistic model, and that uses daily meteorological data
 187 to estimate GPP (Williams et al., 1997). The duration and intensity of the
 188 grass growing period is calculated following the growing season index (GSI)

189 approach (Jolly et al., 2005). The GSI method uses information on vapour
 190 pressure deficit (VPD), daylength and daily minimum temperature to adjust
 191 the plant's physiological progress (Smallman et al., 2017).

192 The net primary productivity (NPP) C, which remains after accounting
 193 for C losses via autotrophic respiration, is allocated to root, stem and leaf
 194 tissues. In DALEC-Grass, the above- to below-ground C allocation balance is
 195 dynamic and is calculated on a daily basis using the architecture-dependent
 196 strategy presented in Reyes et al. (2017). According to this approach, the C
 197 that is transferred to the fine root C pool is linked to above-ground biomass
 198 and increases after the plant has grown a sufficient quantity of leaves. This
 199 linkage is achieved by the following equation :

$$F_{root_t} = 1 - \exp(-1 * P4 * LAI_t) \quad (1)$$

200 where F_{root_t} is the fraction of NPP C that goes to the root C pool on day t ,
 201 LAI_t is the LAI of the sward on day t and $P4$ is a model parameter. The
 202 remaining NPP C is allocated to above-ground biomass. Its partitioning to
 203 the stem and leaves C pools is based on the idea that increasing stem mass is
 204 needed to support increasing leaf mass but the stem to leaf ratio is dynamic
 205 and not constant. The C allocation to leaves and stems is calculated using
 206 parameter $P29$ within the following equations :

$$F_{leaf_t} = NPP_t * (1 - (P29 * (LAI_t / LAI_{max}))) \quad (2)$$

$$F_{stem_t} = NPP_t * (P29 * (LAI_t / LAI_{max})) \quad (3)$$

207 where F_{leaf_t} is the fraction of NPP allocated to the leaf C pool on day t ,
 208 F_{stem_t} is the fraction of NPP allocated to the stem C pool on day t , LAI_t is
 209 the LAI of the sward on day t and LAI_{max} (set to $6 \text{ m}^2 \text{ m}^{-2}$) is a maximum
 210 LAI for managed grasslands.

211 Animal grazing and grass cutting is imposed as a time series forcing.
 212 The number of livestock units (LSU) per ha per day determines the animal
 213 grazing intensity. The amount of C that one LSU removes from the grassland
 214 via grazing is estimated by multiplying the LSU value by a "dry matter
 215 demand per weight of 1 LSU" parameter ($P31$); with the standard weight
 216 of one LSU being equal to 650kg. The resulting dry matter (DM) value
 217 (in kgDMha^{-1}) is converted to gCm^{-2} and removed from the C pool of the
 218 foliage. DALEC-Grass has a set of internal mechanisms through which it

219 can accept/perform or reject/skip a grazing instance. These mechanisms
220 reflect the logical assumption that there is a minimum amount of above-
221 ground biomass that has to remain after grazing for grass to be able to grow
222 the following days; i.e. grazing is not simulated when the simulated above-
223 ground biomass is below a threshold. This minimum biomass threshold is
224 a model parameter (P27) and a similar parameter and concept is applied
225 for cutting (P28); i.e. cutting cannot take place when the simulated above-
226 ground biomass is below a threshold. These mechanisms exist to ensure
227 there are no unrealistic combinations of livestock density and simulated grass
228 biomass.

229 DALEC-Grass uses a simple scheme to convert the amount of C in grass
230 into (1) C in animal-respired CO_2 ; (2) C in methane (CH_4) produced via di-
231 gestion; and (3) C in animal excrement. Of the total amount of C ($\text{gCm}^{-2}\text{d}^{-1}$)
232 that is grazed : (1) 54% is lost to the atmosphere as CO_2 ; (2) 4% is lost to
233 the atmosphere as CH_4 ; (3) 32% returns to the soil as C in excrement; and
234 (4) the remaining 10% stays in the animal's body. In reality the conversion
235 factors of grazed C are dynamic, they depend on animal type, weight and age
236 and vary even between animals that have the same aforementioned character-
237 istics (Vertès et al., 2018; Snow et al., 2014). The grazed C conversion factors
238 used in DALEC-Grass are generic in order to reflect different estimates for
239 beef/dairy cattle and sheep and were extracted from the relevant literature
240 (Bell et al., 2016; Lee et al., 2017; Worrall and Clay, 2012; Parsons et al.,
241 2009). In terms of modelling soil C dynamics, DALEC-Grass uses a simple
242 soil C scheme, in which plant residue and excrement-contained C go into a
243 single litter pool. Litter C undergoes temperature-dependent decomposition
244 with part of the C lost as heterotrophic respiration while the remainder is
245 moved into a single slowly-decomposing soil C pool that represents the soil's
246 organic matter.

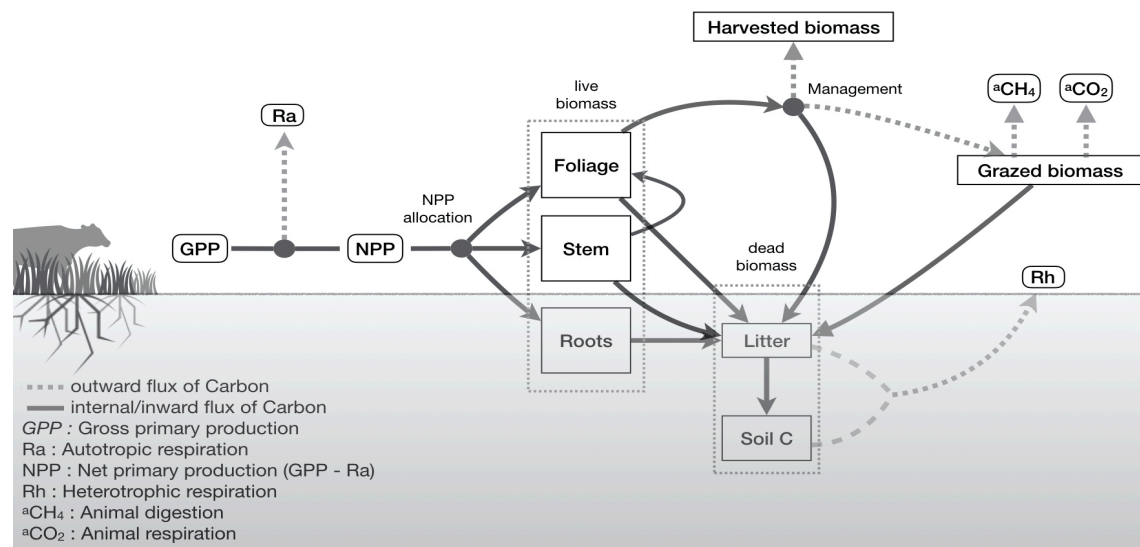


Figure 1: Diagram of the DALEC-Grass model. Daily GPP is calculated by the ACM model. DALEC has 5 pools: leaves, stem, roots, litter and soil organic matter.

Table 1: DALEC meteorological and management inputs

Variable	units
Minimum daily temperature	°C
Maximum daily temperature	°C
Short-wave radiation	MJm ⁻² day
Atmospheric CO ₂ concentration	ppm
21-day average minimum temperature	C
21-day average photoperiod	sec
21-day average vapour pressure deficit	Pa
Animal density	livestock units per ha

2.2. Carbon Data Model Framework

DALEC-Grass is integrated into the Carbon Data Model Framework (CARDAMOM) (Bloom et al., 2016). CARDAMOM is a MDF framework that uses Bayesian inference to approximate the joint distribution of model parameters. This approximation is done using a function of the likelihood of each sampled parameter vector. The Bayes’ theorem forms the basis Bayesian inference:

$$P(\theta|D) = \frac{P(D|\theta)P(\theta)}{P(D)} \quad (4)$$

where θ represents the parameters, D the observed data, $P(\theta|D)$ the posterior distribution of parameters, $P(D|\theta)$ the likelihood of θ given D , $P(\theta)$ the prior distribution of parameters and $P(D)$ the marginal distribution of D (normalisation constant). The effectiveness of Bayesian inference stems from the fact that the posterior distribution of parameters is proportional to the likelihood:

$$P(\theta|D) \propto P(D|\theta)P(\theta) \quad (5)$$

Markov Chain Monte Carlo (MCMC) is a group of algorithms that are used to sample from probability distributions (Chib and Greenberg, 1995). For a discussion on MCMC theory we refer to van Ravenzwaaij et al. 2018 and for a description of different MCMC algorithms we refer to Houska et al. 2015. In our implementation of CARDAMOM, the Metropolis-Hastings (MH) MCMC algorithm is used. Metropolis-Hastings creates a Markov chain

260 by deciding whether each sampled θ is accepted or rejected after comparing
 261 its likelihood to that of the last accepted θ . This comparison is done using
 262 the acceptance ratio (A) :

$$A = \frac{f(\theta')}{f(\theta)} \quad (6)$$

263 where θ' is the sampled θ under examination and f is a function proportional
 264 to $P(\theta|D)$. For this study, MH used a metric that describes the model's pre-
 265 dictive skill against observed variables as a surrogate likelihood. This metric
 266 is named *accuracy* and is described in Myrgeiotis et al. (2016). Accuracy
 267 quantifies the number of simulated data points that fall within the respec-
 268 tive measured range (i.e. standard deviation assuming normal distribution
 269 for D) while it also considers possible time lags between measured and sim-
 270 ulated time series. Accuracy can take any value between 0 (no simulated
 271 points within the observed range) and 1 (all simulated points within the ob-
 272 served range). The consideration of time lags when calculating the metric
 273 allows CARDAMOM to capture some of the impacts that possible temporal
 274 uncertainties in model inputs can have on model outputs (Myrgeiotis et al.,
 275 2018). Similarly, delayed responses of the grassland's physiology and/or bio-
 276 geochemistry to driving variables, which could appear due to model for-
 277 mulation uncertainty and/or parametric uncertainty, can also be captured.
 278 Moreover, the model's internal mechanisms can lead to instances when e.g.
 279 a day's grazing, even though it is specified in the inputs, is not modelled
 280 because there is not sufficient simulated grass biomass on that day. This
 281 can lead to time lags in LAI fluctuation and affect the level of fit between
 282 modelled and measured data.

283 For each assimilated variable (LAI and NEE) we provide an estimate of
 284 uncertainty around the measured data points. For LAI the uncertainty is set
 285 equal to $\pm 15\%$ of the mean measured value (Van Wijk and Williams, 2005).
 286 Attributing uncertainty levels around measured NEE data is more compli-
 287 cated because most measured datasets depend on a single flux tower and do
 288 not provide uncertainty estimates. In this study the uncertainty around the
 289 measured NEE data is set equal to $\pm 1 \text{ gCm}^{-2}$ (Hill et al., 2012; Revill et al.,
 290 2016). The overall setup of the implementation of MH in CARDAMOM is
 291 the following :

- 292 • 10 chains are run in parallel

- 293 • Each chain has 100 million steps
- 294 • The initial 10% of all accepted steps is used as burn-in
- 295 • At each step of the Markov chain the MH algorithm:
 - 296 1. obtains a sampled parameter vector
 - 297 2. calculates the objective function (i.e. accuracy metric)
 - 298 3. calculates A and :
 - 299 – If $A > 1$ then θ' is accepted
 - 300 – If $A >$ a uniform random number $[0.3 - 1]$ then θ' is accepted
 - 301 – If $A <$ a uniform random number $[0.3 - 1]$ then θ' is rejected

302 A list of ecological and dynamic constraints (EDCs) is used in CAR-
 303 DAMOM to refine the parameter space that the MH sampling explores
 304 (Bloom et al., 2016). EDCs are checks of the mathematical, ecological and
 305 biogeochemical sanity of the sampled model parameter combinations and
 306 model outputs (pools, fluxes). These checks are performed in CARDAMOM
 307 before and/or after each run of DALEC-Grass, which is performed to esti-
 308 mate the likelihood of each sampled parameter vector in MH. Altogether,
 309 EDCs reflect existing knowledge on grassland ecosystem functioning. Table
 310 2 outlines the EDCs that were used with CARDAMOM in this study. Eco-
 311 logical and dynamic constrains are a key feature of the CARDAMOM MDF
 312 framework. Retrieving posterior parameter distributions that are mathemat-
 313 ically and theoretically sound depends on the use of appropriate EDCs. In
 314 this regard, the present study is a test of CARDAMOM’s grassland-specific
 315 EDCs.

316 The assessment of if and when a MCMC algorithm has converged to the
 317 stationary distribution of parameters is an essential part of its implementa-
 318 tion. The difficulty of convergence assessment increases with the number of
 319 parameters and no single convergence diagnostic is generally accepted as be-
 320 ing suitable for every application (Brooks and Gelman, 1998). When multiple
 321 chains are explored, such as in CARDAMOM, convergence diagnostics based
 322 on the comparison of inter and intra-chain variances are appropriate. The
 323 Gelman-Rubin (GR, see supplementary material) is one of the most widely
 324 used convergence diagnostics of this type and was used to assess chain con-
 325 vergence in this study (Gelman and Rubin, 1992). The equations used for
 326 calculating the potential scale reduction factor (PSRF) of the GR method

327 and the results of chain convergence assessment are presented in the supple-
328 mentary material.

329 2.3. Field measured data

330 Measured data from two managed grassland sites, of contrasting soil and
331 climatic conditions, in eastern (Easter Bush) and southern (Crichton) Scot-
332 land are used in this study.

333 2.3.1. Easter Bush

334 Easter Bush is located in South East Scotland, 10 km south of Edin-
335 burgh (03°02'W, 55°52'N, 190 m above sea level). The mean annual rainfall
336 between 2002 and 2010 was 947 ± 234 mm and the mean annual temperature
337 was 9.0 ± 0.4 °C. The field has been under permanent grassland management
338 for more than 20 years with a species composition of >99% perennial rye-
339 grass (*Lolium perenne*) and < 0.5% clover (*Trifolium repens*). The soil type
340 is an imperfectly drained Eutric Cambisol (FAO classification) with a pH of
341 5.1 (in H₂O), a clay fraction of 20-26% (Clayey Loam to Sandy Loam) and
342 a soil organic carbon content of 4% (0-10 cm depth). The grassland was
343 grazed continuously by heifers in calf, ewes and lambs at different stocking
344 densities. The grass was cut for silage in June and August 2002 and in May
345 2003. Ammonium nitrate fertiliser was applied to the field 3-4 times per
346 year, usually between March and July at an average of 56 kg N ha⁻¹ per
347 application. An additional fifth mineral N application was applied as urea in
348 2008 and organic manure was applied in September 2004 and March 2005 as
349 cattle slurry. Vegetation for above ground biomass and LAI measurements
350 were collected from 4 to 6 quadrats (0.0625 m²) per sampling occasion. The
351 leaf area was analysed using a Li3100 Area meter (LI-COR inc. Lincoln,
352 Nebraska, USA). Fresh weight of biomass samples were recorded before sam-
353 ples were dried at 80°C for 24 hours and dry weight was measured. NEE
354 was measured by an eddy covariance system consisting of a fast response
355 3D ultrasonic anemometer (Metek USA-1, Metek GmbH, Elsmhorn, Ger-
356 many) and a fast closed path CO₂-H₂O analyser (LI-COR 7000 infra-red gas
357 analyzer, LI-COR, Lincoln, NE, USA). Quality control of the eddy covari-
358 ance data followed the procedure proposed by Foken and Wichura (1996).
359 Missing NEE data were gap-filled using the online tool developed by Reich-
360 stein et al. (2005). Soil respiration rates were measured weekly (297 times
361 between 2003 and 2010) at 4 locations using a closed dynamic chamber (vol-
362 ume 1334 cm³, cover area 78.5 cm², PP-Systems, Hitchin, UK), which was

Table 2: Ecological and Dynamic Constraints

Index	Description
1	Fluxes cannot be negative
2	Pools cannot be negative
3	GSI-related minimum parameters cannot be larger than maximum parameters
4	Turnover rate of soil organic matter cannot be larger than that of litter
5	Initial SOM pool cannot be smaller than the sum of all other pools
6	Annual GPP cannot be more than 2000 g C m ⁻² (Xia et al., 2017; Gilmanov et al., 2007)
7	Annual GPP cannot be less than 500 g C m ⁻² (Xia et al., 2017; Gilmanov et al., 2007)
8	Daily GPP cannot be more than 20 g C m ⁻² (Xia et al., 2017; Gilmanov et al., 2007)
9	Annual ecosystem respiration cannot be more than 2000 g C m ⁻² (Xia et al., 2017; Gilmanov et al., 2007)
10	Annual ecosystem respiration cannot be less than 500 g C m ⁻² (Xia et al., 2017; Gilmanov et al., 2007)
11	Daily ecosystem respiration cannot be more than 15 g C m ⁻² (Xia et al., 2017; Gilmanov et al., 2007)
12	LAI cannot exceed 6 m ² m ⁻²
13	Minimum daily estimated root to shoot ratio cannot be less than 1 (Mokany et al., 2006)
14	Daily cut grass biomass cannot be more than 300 g C m ⁻² or less than 50 g C m ⁻² (Qi et al., 2017)

placed onto soil and vegetation. The CO₂ increase within the chamber was monitored over 30-180 s by a portable sensitive infrared gas analyser (EGM 2, PP-Systems). It should be noted that the area covered for the soil respiration measurements also included vegetation and, therefore, measurements are effectively equivalent to ecosystem respiration (the sum of autotrophic and heterotrophic respiration). The data were converted from $\mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1}$ to $\text{g CO}_2\text{-C m}^{-2} \text{ d}^{-1}$ using the daily minimum and maximum temperatures and a Q10 equal to 2 (Meyer et al., 2018; Barba et al., 2018).

2.3.2. Crichton

The field experiment was located at Crichton Royal Farm, Dumfries (55° 2'3"N, 35° 35'1" W) in South-West Scotland, on a long-term permanent grassland site (6.53 ha) used for intensive dairy production (Bell et al., 2016). The landscape was open grassland dominated (proportion of total harvested biomass > 99%) by perennial ryegrass (*Lolium perenne*) with white clover (*Trifolium repens*), creeping buttercup (*Ranunculus repens*) and chickweed (*Stellaria media*) being minor sward constituents. The Crichton site is representative of a wet climate zone, with a 30 year (1971-2000) long-term average rainfall of 1140 mm, and mean annual temperature of 9.3 °C. The soil was a Eutric Cambisol (FAO classification) and had a free-draining sandy to sandy-loam light texture. The soil organic C concentration (0-10 cm) was 5.25% (4.3-6.2%), and the pH varied between 5-6.3 at this site. The long term management of the site involved a rotation between cutting (with three cuts per year) and summer grazing. Between March and July 2015, 226 kg N ha⁻¹ were applied as slurry (4 applications) and synthetic fertiliser (2 applications). A sampling grid (20m * 20m) was marked out in the field at the beginning of the measurement campaign in June 2015. Leaf area index (LAI), aboveground biomass and respiration at soil surface (Rs) were made on four occasions, and root biomass on two occasions during June and July 2015. LAI was measured using a LAI-2200C Plant Canopy Analyzer (Licor Biosciences, Lincoln NE) at each point of the sampling grid. Aboveground biomass was measured using a rising plate meter calibrated against destructive biomass sampling. Root biomass was destructively sampled by taking replicate 2 cm diameter soil cores and dividing into 0-10 and 10-20 cm depths from positions adjacent to the collars used for Rs measurements. Soil respiration (Rs) was measured, at midday, on four dates, using a portable PP Systems Infra-red EGM4 Gas Analyser linked to a SRC-1 soil respiration chamber. The chamber (10 cm of diameter and 15 cm height) was equipped

400 with a fan, and was inserted into bare soil with a basal cutting ring to a
 401 depth of 2 cm during measurements. The air from the chamber was send to
 402 the analyser at flow rate of 0.2 l min^{-1} . After the chamber equilibrated the
 403 CO_2 concentration was measured every 5 seconds and the flux was calculated
 404 from the concentration increase over approximately 60 seconds time using a
 405 linear regression. Net ecosystem exchange of CO_2 was measured using an
 406 eddy covariance tower (EC) sited within the field (11 m height), with a Gill
 407 R3 sonic anemometer (Gill Instruments, Lymington UK) and a Licor LI700
 408 CO_2 analyser (Licor Biosciences, Lincoln NE). Velocity measurements were
 409 rotated to minimize the mean vertical velocity. A site specific cospectral
 410 model was developed, based on sensible heat fluxes. Similarly, sensor specific
 411 models of sensor frequency response attenuation were developed and com-
 412 bined with the cospectral models to determine, and then apply, frequency
 413 response corrections. The resulting fluxes were screened for plausibility in-
 414 strument diagnostics and for individual deviations from the group mean by
 415 more than two standard deviations.

416 *2.4. Methodology*

417 The volume of field-measured data and the range of measured variables at
 418 Easter Bush and Crichton allows us to test DALEC-Grass and CARDAMOM
 419 in detail. In designing the methodology of the study we considered two main
 420 aspects: (1) the efficient use of the available field-measured data and (2)
 421 the ability to relate our computational experiments with the envisioned ap-
 422 plication of DALEC-Grass in MDF studies. For these reasons, the use of
 423 LAI observations has a particular importance. LAI is a physiology-related
 424 variable, for which data can be collected rather easily and frequently at the
 425 different spatial scales that DALEC-Grass can be applied i.e. farm, land-
 426 scape, region. This contrasts with what is the case for the other measured
 427 variables examined in this study with the possible exception of aboveground
 428 biomass for which satellite data are increasingly available. Because of the
 429 lack of accurate satellite-based LAI data for Easter Bush during the simu-
 430 lated period, field-measured LAI data were used in this study.

431 Initially, all DALEC-Grass parameters have a uniform distribution i.e.
 432 only a realistic minimum and maximum value is known for each of them.
 433 In order to refine these uniform distributions we drive DALEC-Grass with 3
 434 years of climate and management data for the Easter Bush site while assim-
 435 ilating in-situ NEE and LAI observations (step 1). Through this parameter

calibration step we expect parameter distributions to become more representative of managed (cut and grazed) grasslands. It should be clarified that the term calibration is used to refer to the refinement of the prior distribution of parameters and not the parameters themselves. During calibration, the calculated accuracy metric is the mean of the accuracy for LAI and the accuracy for NEE. In order to test the MDF framework we, then, run DALEC-Grass (step 2) for 6 additional years at Easter Bush, this time assimilating only the available LAI observations. We assess the model's performance at Easter Bush by comparing model outputs with independent in-situ data on NEE (flux tower based) and ecosystem respiration (ER, chamber based). Moreover, we run DALEC-Grass with one year of climate and management data from Crichton while assimilating the available field-measured LAI data (step 3). The model's performance at Crichton is assessed by comparing model outputs with independent in-situ data on NEE, above and below-ground biomass and soil respiration. The four steps of our computational experiment are :

1. Calibration of DALEC-Grass parameters: Implementation of CARDAMOM at Easter Bush by assimilating 3 years (2002-2004) of LAI and NEE observations.
2. MDF at Easter Bush: Using the calibrated distributions (step 1), implementation of CARDAMOM at Easter Bush for 6 years (2005-2010) by assimilating the corresponding LAI observations.
3. MDF at Crichton: Using the calibrated distributions (step 1), implementation of CARDAMOM at Crichton for 2015 by assimilating LAI observations.
4. Quantitative assessment of MDF at steps 1,2 and 3 against the assimilated data and against independent data.

In order to assess model accuracy and precision we calculate, for each variable examined, the percentage of observed data points (i.e. mean of observations) that fell within the 95% confidence intervals (CI) produced by the model runs. We refer to this metric as *overlap* and present it as a percentage that can take a value between 0 and 100. We also calculate (1) the Root Mean Squared Error (RMSE) to quantify the difference between measured and modelled data; (2) the bias in model predictions; and (3) the Pearson correlation coefficient (r) to quantify how well the trends in measured

470 data are captured by the model (for equations see Myrgeiotis et al. (2016)).
 471 It should be noted that –where mentioned– estimates of the uncertainty of
 472 measurements come from using the RMSE equation after replacing base of
 473 the exponent with the sum of 2 standard deviations of each measured data
 474 point.

475 3. Results

476 3.1. *Easter Bush*

477 Three years (2002-2004) of measured LAI and NEE data were assimilated
 478 by CARDAMOM to calibrate the distributions of DALEC-Grass parameters.
 479 For the calibration period, 25 % of LAI observations and 90 % of NEE
 480 observations fell within the 95 % confidence interval of the CARDAMOM
 481 analysis while r was 0.25 and 0.56 respectively (Table 3). The calibrated
 482 parameter distributions were used to run DALEC-Grass for the subsequent 6
 483 years of measurements (2005-2011); this time assimilating available measured
 484 LAI data only.

485 For the 2005 to 2011 MDF period, 85% of the measured weekly-mean
 486 NEE and 82% of the daily LAI data points lied within the 95% CIs. The
 487 variation in NEE ($r = 0.70$) and LAI ($r = 0.74$) was well captured. DALEC-
 488 Grass tended to overestimate both NEE (bias=0.38 gCm⁻²) and LAI (bias =
 489 0.47 m²m⁻²). We used a 15% relative uncertainty around the measured LAI
 490 data during the MDF process with CARDAMOM. We found that the RMSE
 491 of the measured against modelled LAI data was 10% lower than the mean
 492 uncertainty of the measured LAI data. We repeated this process for NEE,
 493 and found that the estimated RMSE was equal to the uncertainty attributed
 494 to the measured data during the MDF process (i.e. 1 gCm⁻²).

495 DALEC-Grass was able to capture the patterns and magnitudes in mea-
 496 sured ER (Fig. 4). The comparison of modelled and measured ER estimates
 497 produced a r of 0.79, which reflects the model’s skill in representing ER pat-
 498 terns. In terms of the relative size of ER, 83% of the mean measured ER
 499 data were within the modelled 95% CI. The estimated RMSE (1.5 gCm⁻²)
 500 was smaller than the average uncertainty of the measured data (1.65 gCm⁻²)
 501 (Table 3). The inter-annual patterns in MDF-estimated NEE, ER and GPP
 502 mirror the measured data as presented in Jones et al. 2017 (Fig. 5).

503 The mean simulated harvest (283 gCm⁻²a⁻¹) was just 3% higher than
 504 the measured harvest (270 gCm⁻²a⁻¹) in 2002 and 30% lower than the 2003
 505 measured harvest (170 gCm⁻²a⁻¹) (Jones et al., 2017). However, both in

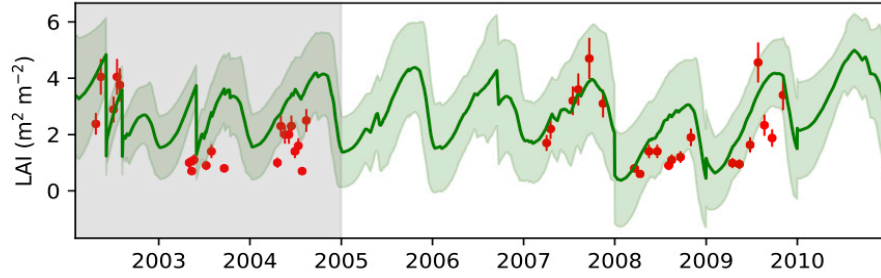


Figure 2: Modelled and measured daily Leaf Area Index (LAI) at the Easter Bush site. Grey-shaded area (2002-2004) shows the parameter calibration period. The unshaded area (2005-2011) represents the LAI data assimilation period. The mean modelled LAI and the CARDAMOM-estimated 95% confidence intervals presented in green. The measured LAI and its 15% relative uncertainty presented in red.

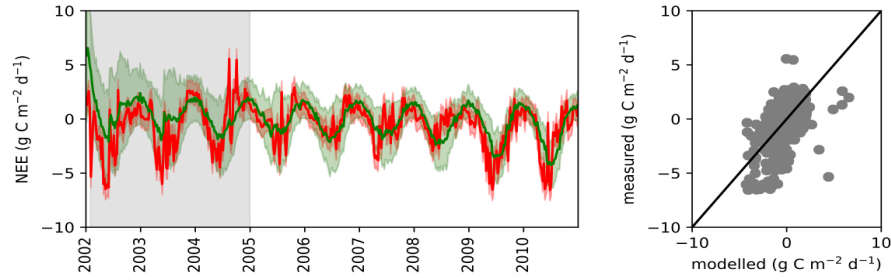


Figure 3: Weekly mean Net Ecosystem Exchange (NEE) at the Easter Bush site. From left to right: (1) Time series of measured (red) and modelled (green) weekly mean NEE. The green-shaded area represents the 95% confidence intervals and the red-shaded area represents the uncertainty around the measured NEE ($1\text{gCm}^{-2}\text{d}^{-1}$). The parameter calibration period (2002-2004) is shown as grey-shaded area. (2) Scatter plot of measured and corresponding modelled weekly mean NEE.

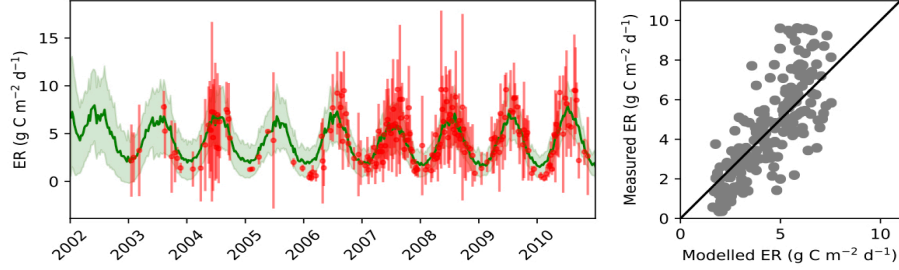


Figure 4: Weekly mean Ecosystem Respiration (ER) at the Easter Bush site. From left to right: (1) Time series of measured (red) and modelled (green) weekly mean ER. The green-shaded area represents the 95% confidence intervals and the red error bars the uncertainty around the measured ER. (2) Scatter plot of measured and corresponding modelled weekly mean ER.

Table 3: Model performance metrics for Easter Bush

Variable	Time period	r	Bias	Overlap	RMSE
LAI	2002-2004	0.34	1.33	25 %	1.6
	2005-2010	0.74	0.47	82 %	1.0
NEE	2002-2004	0.56	0.95	90 %	2.11
	2005-2010	0.70	0.38	85 %	1.00
ER	2002-2010	0.79	-0.07	83 %	1.5

Weekly mean data used for Net Ecosystem Exchange (NEE) and ecosystem Respiration (ER). Overlap shows the percentage of observed data that lie within the model-based 95% CIs. Bias and RMSE in gCm^{-2} for ER and NEE and in m^2m^{-2} for LAI.

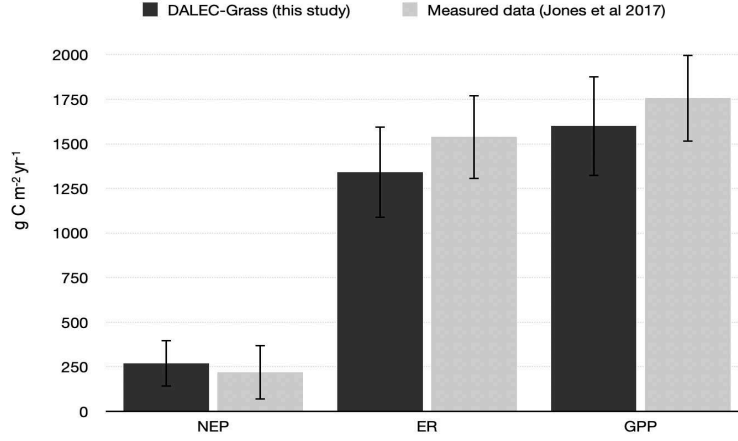


Figure 5: Comparison of MDF-based and measurements-based (after Jones et al. 2017) annual Net Ecosystem Production (NEP), Gross Primary Productivity (GPP) and Ecosystem Respiration (ER). Bars show the mean $\text{gCm}^{-2}\text{yr}^{-1}$ between 2002 and 2010 and error bars show the inter-annual standard deviation.

2002 and 2003 the measured annual harvest was within the CARDAMOM estimated 95% CIs. The simulated Easter Bush grassland behaved as a typical UK permanent grassland producing an average of 262 gCm^{-2} (5.6 tDMha^{-1}) of grass biomass per year. This level of biomass availability and removal is within the expected range ($353 \pm 96 \text{ gCm}^{-2}\text{a}^{-1}$) as estimated in a recent study by Qi et al., 2017. Finally, DALEC-Grass estimated a mean annual input to soils of $710 \text{ gCm}^{-2}\text{a}^{-1}$ in the form of root and leaf litter.

3.2. Crichton

The calibrated parameter distributions retrieved for Easter Bush (2002-2004) were used as priors for the CARDAMOM analysis at the Crichton site. Four field-measured LAI data points were available for assimilation (Fig. 6). The assimilation of measured LAI data also affected the fit between measured and modelled aboveground biomass and grass harvest. All four measured LAI data points were within the modelled 95% CIs. However, the model did not capture the first of four aboveground biomass measurements. It should be noted that neither the quantity of grass harvested nor the amount of aboveground biomass (at any point in time) were provided to the model during the LAI data assimilation in CARDAMOM. Despite this discrepancy, the two simulated harvests removed 276 gCm^{-2} (5.8 tDMha^{-1}) from the

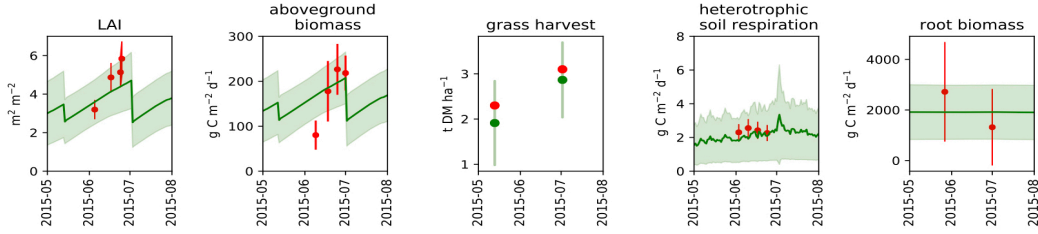


Figure 6: Modelled (green) and measured (red) LAI, aboveground biomass, grass harvest, root biomass and heterotrophic respiration at the Crichton site. The red error bars represent the uncertainty around the measured data. The CARDAMOM-estimated 95% confidence intervals are presented in green shading

525 grassland, and each measured harvest yield was within the corresponding
 526 CARDAMOM's 95 % CI (Fig. 6).

527 DALEC-Grass was successful in reproducing the measured patterns and
 528 magnitudes of NEE. The estimated correlation coefficient was 0.88, the mean
 529 bias was 0.25 gCm⁻², the RMSE was 0.96 gCm⁻² and all the of the measured
 530 data were within the 95% CIs (Fig. 7). Notwithstanding the large variability
 531 among the collected samples of root biomass, the mean simulated amount
 532 of C contained in grass roots was within the respective measured ranges
 533 (Fig. 6). DALEC-Grass currently does not separate autotrophic respiration
 534 C into above and belowground fluxes. In order to allow for a comparison
 535 between measured and simulated respiration data we assumed that between
 536 40% and 60% of total surface respiration can be attributed to heterotrophic
 537 sources (Li et al., 2018). While not directly measured we, henceforth, refer to
 538 heterotrophic respiration data as measured data. The comparison between
 539 measured and modelled heterotrophic respiration showed that all four mea-
 540 sured data points lied within the 95% CI (Fig. 6). Finally, DALEC-Grass
 541 estimated that 780 gCm⁻²y⁻¹ were added to Crichton's soil in 2015 in the
 542 form of root and leaf litter.

543 3.3. MDF-retrieved distributions

544 Model parameter distributions were calibrated using 3 years of LAI and
 545 NEE data from Easter Bush (calibration period). This calibration process
 546 led to reductions in the length of the uniform prior distributions that var-
 547 ied according to parameter. The average prior length reduction was 47%
 548 with achieved reductions being between 3% and 99%. Details on the appli-
 549 cation of CARDAMOM for parameter distribution calibration include pos-

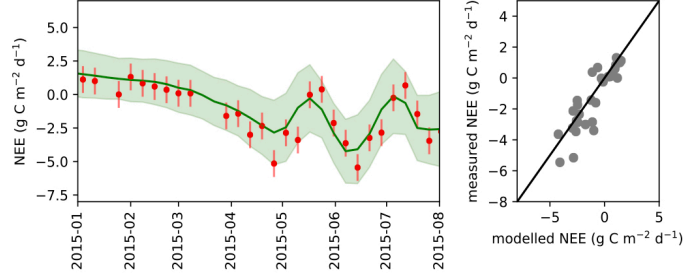


Figure 7: Weekly average Net Ecosystem Exchange (NEE) at Crichton. From left to right: (1) Time series of measured (red) and modelled (green) weekly mean NEE. The green-shaded area represents the 95% confidence intervals and the red error bars represent the uncertainty around the measured NEE ($1\text{gCm}^{-2}\text{d}^{-1}$). (2) Scatter plot of measured and corresponding modelled weekly mean NEE.

Table 4: Model performance metrics for Crichton

Variable	r	Bias	Overlap	RMSE
NEE (weekly mean)	0.88	0.25	100 %	0.96

Weekly mean data used for Net Ecosystem Exchange (NEE). Overlap shows the percentage of observed data that lie within the model-based 95% CIs. Bias and RMSE in gCm^{-2} .

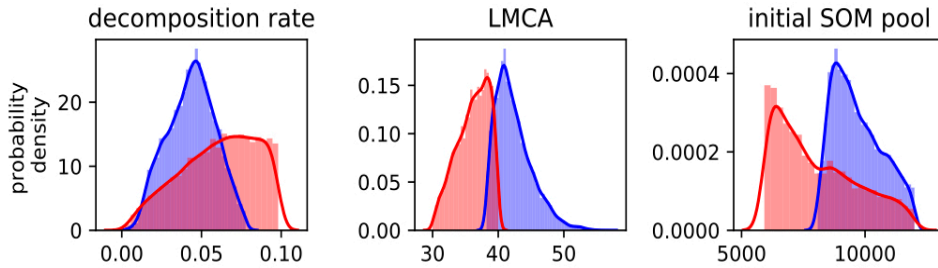


Figure 8: Probability densities of the posterior distributions for three selected DALEC-Grass parameters based on MDF results at Easter Bush (in red) and Crichton (in blue).

terior means, maximum-a-posteriori-probability and prior length reduction, and are presented in Table 5 in supplementary material along with information on MCMC chain convergence assessment (Fig. 9).

4. Discussion

The results of this study show how MDF can quantify C dynamics in grasslands under variable grazing and cutting regimes. A limited number of in-situ LAI observations were assimilated through the CARDAMOM MDF framework in order to test the predictive skill of DALEC-Grass against 7 years of data at two Scottish grasslands. At the grazed Easter Bush grassland 21 in-situ LAI observations were assimilated to produce time series of C fluxes (NEE and ER) that closely matched corresponding measurements (eddy covariance and chamber-based fluxes, respectively). At the harvested Crichton site 4 in-situ LAI observations were assimilated and CARDAMOM produced robust estimates of above and below-ground biomass C pools and NEE C fluxes. The use of CARDAMOM also allowed us to handle observational and model parametric uncertainty and provide a level of predictive uncertainty for the examined variables.

4.1. Model performance

Our MDF approach provides a probabilistic solution to the parameter identification problem. Among the factors that affect the robustness of model analyses are how measurement uncertainty and model parameter identification are assessed. In this study, measured data uncertainty has been considered at the parameter retrieval stage, through the use of the accuracy metric as the cost function, and at the model evaluation stage, through the use of the CIs in quantifying and expressing model prediction skill. As a consequence, the results of simulations are distributions of parameter values and provide a quantitative analysis of the parameter-induced uncertainty around the model's results. The average uncertainty around predicted C fluxes (NEE, ER) was less-than-or-equal to that attributed to NEE ($1 \text{ gCm}^{-2}\text{d}^{-1}$ based on literature) and estimated from ER measurements ($1.65 \text{ gCm}^{-2}\text{d}^{-1}$) (Hill et al., 2012; Revill et al., 2016).

CARDAMOM's key novelty is the use of ecological and dynamical constraints (EDCs) as conditions imposed on the parameter retrieval process. The aim of including EDCs is to ensure that the MDF process respects a set of mathematical, ecological and biogeochemical rules. In practice, the

585 success of the MDF process can be judged by the level of fit between the
586 outputs of DALEC-Grass and the assimilated measured data. However, in
587 this study, we wanted to have a stricter assessment of DALEC-Grass and
588 CARDAMOM. We used 3 years of measured data on LAI and NEE (Easter
589 Bush) to calibrate the parameter distributions and, thereafter, used the re-
590 fined prior distributions and LAI data assimilation for the remaining 6 years
591 of data in Easter Bush and the one year of data in Crichton. The evaluation
592 of MDF performance against NEE (Easter Bush and Crichton), ER (Easter
593 Bush), biomass (Crichton) and heterotrophic respiration (Crichton) showed
594 that DALEC-Grass was able to describe the examined C dynamics in man-
595 aged grasslands with good accuracy. The mean overlap for NEE, ER and LAI
596 during the MDF implementation was equal to 88% and RMSE was less than,
597 or equal to, the respective measurement uncertainty (for NEE and ER). We
598 argue that calculating the overlap along with the RMSE is an effective way
599 to express the level of agreement between modelled and measured data for
600 which uncertainty is quantified.

601 *4.2. Retrieved parameter distributions*

602 The MDF application at Easter Bush and Crichton adjusted the distribu-
603 tions of model parameters to fit the observed LAI at each site. CARDAMOM
604 was able to retrieve parameter distributions that led to model outputs that fit
605 with the available observations while being conceptually and mathematically
606 sound, as proven by the stability of the CIs for all the variables examined in
607 the two grasslands. The parameter distributions obtained for each grassland
608 did not differ for most parameters. However, for three parameters CAR-
609 DAMOM produced informatively different distributions at the two grasslands
610 (Fig. 8). For the "litter decomposition rate" parameter, the addition of an-
611 imal excrement C to the soil's litter C pool led CARDAMOM to retrieve
612 a higher decomposition rate (i.e. more litter C goes into the SOC pool) in
613 Easter Bush compared to Crichton, where there was no grazing during the
614 measurement period. A higher leaf C per area (LMCA) was retrieved for
615 Crichton compared to Easter Bush. This result suggests that the vegetation
616 of cut Crichton grassland is more C dense than that of the grazed Easter Bush
617 grassland, something that relevant studies confirm (Liu et al., 2017; Zheng
618 et al., 2015; Laliberté et al., 2012). We argue that the ability to infer the
619 relative difference in vegetation C density between grasslands is an important
620 outcome produced by the combination of the model's management related
621 processes and the CARDAMOM EDCs. Moreover, DALEC-Grass depends

on a simple soil C scheme and CARDAMOM is given a wide prior range for initial SOC pool size parameter. Despite this, CARDAMOM suggests that, considering productivity levels, allocation patterns and EDCs, Easter Bush had a lower soil C content than Crichton. These results are confirmed by field-measured data, which show that SOC in Easter Bush is around 30% less than SOC in Crichton (COSMOS-UK, 2019).

Based on the DALEC-Grass simulations and the corresponding measured data Easter Bush and Crichton were net sinks of C during the simulated periods. Both grasslands had a simulated annual aboveground biomass productivity that is within the observed limits (i.e. 238-429 gCm⁻²yr⁻¹). The parsimonious mechanisms used in DALEC-Grass to describe grazing and cutting were effective and the retrieved parameter distributions for the relevant parameters are in agreement with relevant observations (Genever and Buckingham, 2016). For Easter Bush, CARDAMOM inferred from the data and modelling that grazing occurs when the total aboveground biomass is > 38-47 gCm⁻² (0.8-1.0 tDMha⁻¹). The distribution of the minimum pre-cutting aboveground biomass for Easter Bush showed that ≈ 120 gCm⁻² (2.8 tDMha⁻¹) is the most likely value for this parameter. The minimum pre-cutting and pre-grazing aboveground biomass parameters (P27 and P28) also define how much biomass will be left standing immediately after each cutting and their posterior distributions suggest a minimum harvest of 86 gCm⁻² (1.8 tDMha⁻¹). This is a realistic, albeit low, minimum harvest yield for the UK where grasslands can be cut up to three times per year Qi et al., 2017. Finally, DALEC-Grass results showed that the annual amount of C added to the soil as root and leaf litter is $\approx 10\%$ more in Crichton compared to that estimated for Easter Bush. This difference is a result of the adaptation of C allocation patterns in response to the presence of grazing animals which also leads to a lower leaf C content in the grazed ecosystem (Easter Bush) (Hao and He, 2019; Chen et al., 2015; Mcsherry and Ritchie, 2013).

4.3. Limitations

Our analysis highlights areas for potential improvement in both the model and the MDF framework. DALEC-Grass is frugal with its number of parameters and therefore the processes it incorporates. The results of this study showed that there is still a margin for improvement, which can be inferred from the different evaluation metrics. Moreover, the model requires information on grassland management as forcing. This requirement currently limits the applicability of DALEC-Grass to the areas with detailed management

659 data. The ACMv1 model (i.e. the module used to estimate GPP) used in
 660 DALEC-Grass does not consider the impact of plant water availability, and
 661 thus drought stress, on GPP. This likely has a limited effect on simulations
 662 in Scotland but DALEC-Grass can be updated if needed using a recently
 663 developed version of ACM that explicitly considers water cycling on estima-
 664 tion of GPP (Smallman and Williams, 2019). Furthermore, DALEC-Grass
 665 does not, at this stage, have a detailed description of the role of N for grass
 666 growth and C allocation. Because Easter Bush and Crichton are amply fer-
 667 tilised grasslands the results of this study are premised on non N-limited
 668 conditions. However, the lack of N cycling representation also means that
 669 soil C to N ratio and its role in litter and organic matter decomposition is not
 670 considered. The conversion of grazed biomass to C returned to the soil, in the
 671 form of excrement, depends on generic conversion factors but the assumption
 672 that all the daily-produced animal excrement is deposited on the soil is not
 673 realistic. Nevertheless, all livestock-related constants can be converted to
 674 parameters with appropriate respective priors, which can, in turn, be refined
 675 by CARDAMOM. Finally, in this study, we used field data from two sites in
 676 Scotland. These grasslands are representative of grasslands in the UK, and
 677 northwest Europe, but testing DALEC-Grass at grasslands across the world
 678 is needed for broader application.

679 4.4. *Future development*

680 Notwithstanding the aforementioned limitations, DALEC-Grass has a
 681 range of potential applications that vary from gap-filling time-series of C
 682 fluxes from micrometeorological towers to farm-level grassland C budgeting
 683 and validation of large-scale terrestrial ecosystem models. With appropriate
 684 development and testing the model can handle spatially resolved satellite-
 685 based data on LAI, which will allow the quantification of grassland pro-
 686 ductivity and C dynamics at landscape, regional and even national scales.
 687 To this end, DALEC-Grass will have to be developed in a way that allows
 688 the inference of management at grass-covered pixels of satellite images of the
 689 land’s surface. Such a spatially-resolved version of DALEC-Grass, when used
 690 in CARDAMOM, will allow us to better understand how key factors such as
 691 livestock density and cutting intensity affect ecosystem productivity and C
 692 sequestration.

693 5. Conclusions

694 We demonstrated how a model of C dynamics linked by a model-data
695 fusion framework to observations of LAI generated constrained analyses of
696 grassland ecosystem functioning under management. The results of this
697 study suggest that landscape grassland C cycling can be constrained using
698 LAI data at relevant resolutions and accuracy. An initial parameter calibration
699 using eddy flux data constrained key C cycle parameters, leading to a
700 better understanding of grassland productivity and C sequestration capacity.
701 Once this calibration was completed, assimilation of LAI data over time allowed
702 the model to make robust estimates of the effects of grass grazing and
703 cutting on net CO₂ exchanges. The data assimilation approach meant that
704 the effects of parametric and observation uncertainties could be considered
705 and quantified. We showed that the forecast uncertainty in our predictions
706 was comparable to that of independent observations. We provide evidence
707 that DALEC-Grass is a conceptually sound, structurally robust and computationally
708 lightweight model. In the era of EO satellites, and the associated
709 availability of swathes of data, the attributes of the model show its potential
710 to provide in-depth monitoring of managed grasslands across temporal and
711 spatial scales. Our aim is to realise this potential by further appropriate
712 development and testing at landscape scales.

713 6. Acknowledgements

714 VM and MW devised the study concept. VM developed DALEC-Grass
715 , implemented the MDF and undertook the analysis with support from all
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1173 **Supplementary material**

Table 5: DALEC-Grass parameters. Description, units and calibration results.

Code	Description	Unit	Prior _{min}	Prior _{max}	Posterior _{mean}	Posterior _{SD}	MAP	Prior length reduction (%)
P1	Decomposition rate	fraction d ⁻¹	1.00e-05	0.3	0.06	0.03	0.08	97
P2	Fraction of GPP that is respired	-	0.4	0.51	0.4427	0.0298	0.4158	3
P3	GSI sensitivity for leaf growth	-	0.75	9	3.968	0.767	4.637	61
P4	NPP belowground allocation	-	0.01	1	0.330	0.068	0.352	60
P5	Maximum GSI for leaf turnover	-	1.00e-07	3	0.214	0.230	0.173	50
P6	Turnover rate of roots	fraction d ⁻¹	1.00e-06	0.1	3.45e-03	1.98e-03	5.38e-03	91
P7	Turnover rate of litter	fraction d ⁻¹	1.00e-06	0.1	4.39e-03	2.66e-03	3.07e-03	90
P8	Turnover rate of soil organic matter	fraction d ⁻¹	1.00e-10	0.01	3.84e-05	2.75e-05	2.44e-06	99
P9	Temperature Q10 factor	-	0.008	0.15	0.0416	0.0162	0.0418	57
P10	Photosynthetic N use efficiency (PNUE)	g C per g N per leaf m ² per day	7	25	15	3	18	31
P11	Maximum GSI for labile/stem turnover	-	0.0001	2	0.634	0.137	0.603	68
P12	Minimum GSI temperature threshold	K	225	330	251	16	264	27
P13	Maximum GSI temperature threshold	K	225	330	304	20	303	17
P14	Minimum GSI photoperiod threshold	seconds	3600	30000	12283	5191	6892	23
P15	Leaf Mass C per Area (LMCA)	g C per m ² of leaf	20	60	46	6	46	56
P16	Initial C in stem/labile pool	g C m ⁻²	1	300	151	75	52	4
P17	Initial C in foliar pool	g C m ⁻²	1	300	132	68	43	13
P18	Initial C in roots pool	g C m ⁻²	1	5000	893	800	284	40
P19	Initial C in litter pool	g C m ⁻²	1	5000	793	561	486	52
P20	Maximum GSI photoperiod threshold	seconds	3600	64800	31917	6262	28880	42
P21	Minimum GSI VPD threshold	Pa	1	5500	1209	929	186	27
P22	Maximum GSI VPD threshold	Pa	1	5500	3376	1156	1457	16
P23	Critical GPP for LAI increase	g C m ⁻² d ⁻¹	1.00e-05	1	0.30	0.13	0.26	53
P24	GSI sensitivity for leaf senescence	-	0.96	1	0.99	0.00	1.00	52
P25	GSI growing stage indicator	-	0.3	3	1.27	0.13	1.13	82
P26	Initial GSI value	-	0.5	3	1.61	0.23	1.83	61
P27	Minimum vegetation DM for grazing	kg DM ha ⁻¹	500	2000	995	197	1114	30
P28	Minimum vegetation DM for cutting	kg DM ha ⁻¹	1000	6000	3232	611	2896	52
P29	Leaf to stem allocation parameter	-	0.05	0.9	0.61	0.11	0.66	45
P30	Initial C in SOM pool	g C m ⁻²	5000	15000	9912	2513	9240	31
P31	DM demand (as % of animal weight)	-	0.01	0.03	0.02	0.01	0.03	2
P32	Post grazing labile/stem loss	-	0.001	0.75	0.16	0.06	0.19	67
P33	Post cutting labile/stem loss	-	0.001	0.75	0.18	0.15	0.08	34

GSI: Growing Season Index, VPD: Vapour Pressure Deficit, SOM: Soil Organic Matter,
DM: Dry Matter, GPP: Gross Primary Productivity, NPP: Net Primary Productivity
MAP: Maximum a posteriori probability estimate
Prior length reduction: $100 * (1 - (\text{posterior}_{max} - \text{posterior}_{min}) / (\text{prior}_{max} - \text{prior}_{min}))$
Estimates for the prior range for parameter P30 come from (Bradley et al., 2006)

1174 *Chain convergence assessment*

1175 The Gelman-Rubin potential scale reduction factor (PSRF) was calculated
1176 using the following equations :

$$B = \frac{N}{M-1} \sum_{m=1}^M (\overline{\theta}_m - \bar{\theta})^2 \quad (7)$$

$$W = \frac{1}{M} \sum_{m=1}^M \sigma_m^2 \quad (8)$$

$$\overline{V} = \frac{N-1}{N} W + \frac{M+1}{MN} B \quad (9)$$

$$PSRF = \sqrt{\frac{\overline{V}}{W}} \quad (10)$$

1177 where θ is a model parameter, σ^2 is the variance, M is the number of chains
1178 and N is the length of each chain. A PSRF ≈ 1 shows that chain convergence
1179 was achieved. The use of EDCs in CARDAMOM means that N was not the
1180 same for all chains. For this reason we used the last 10000 values retrieved by
1181 the MH algorithm for each chain to calculate the PSRF. The PSRF for each
1182 parameter as estimated from results from the calibration period (2002-2004)
1183 are presented in Figure 9.

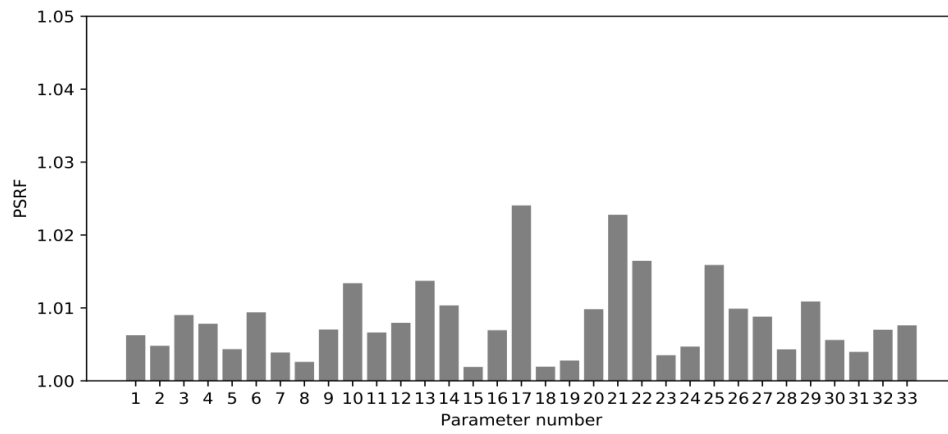


Figure 9: Estimated potential scale reduction factor (PSRF) for each model parameter after parameter calibration. The names (and other information) of each model parameter number are presented in Table 5

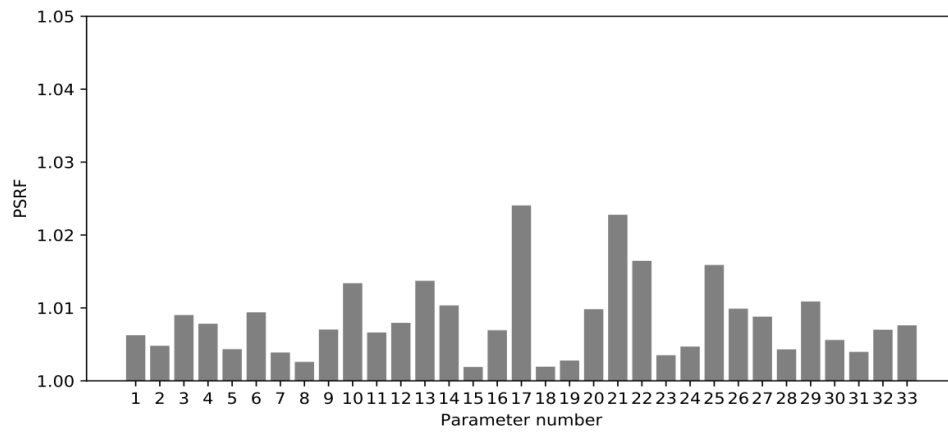


Figure 9: Estimated potential scale reduction factor (PSRF) for each model parameter after parameter calibration. The names (and other information) of each model parameter number are presented in Table 5