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[1]*INRA, UR0874 Grassland Ecosystem Research, F-63039 Clermont-Ferrand, France*

[2] UMR 5505 IRIT, CNRS, University of Toulouse, France

[3] UMR 1248 AGIR, INRA-INPT, Castanet-Tolosan, France

[4] INRA – Agrocampus Ouest, UMR 1348 PEGASE, Domaine de la Prise, 35590 Saint-Gilles, France

Abstract:

Predicting regional and global carbon (C) and water dynamics on grasslands has become of major interest, as grasslands are one of the most widespread vegetation types worldwide, providing a number of ecosystem services (such as forage production and C storage). The present study is a contribution to a regional-scale analysis of the C and water cycles on managed grasslands. The mechanistic biogeochemical model PaSim (Pasture Simulation model) was evaluated at 12 grassland sites in Europe. A new parameterization was obtained on a common set of eco-physiological parameters, which represented an improvement of previous parameterization schemes (essentially obtained via calibration at specific sites). We found that C and water fluxes estimated with the parameter set are in good agreement with observations. The model with the new parameters estimated that European grassland are a sink of C with 213 g C m^{-2} yr^{-1}, which is close to the observed net ecosystem exchange (NEE) flux of the studied sites (185 g C m^{-2} yr^{-1} on average). The estimated yearly average gross primary productivity (GPP) and ecosystem respiration (RECO) for all of the study sites are 1220 and 1006 g C m^{-2} yr^{-1}, respectively, in agreement with observed average GPP (1230 g C m^{-2} yr^{-1}) and RECO (1046 g C m^{-2} yr^{-1}). For both variables aggregated on a weekly basis, the root mean square error (RMSE) was ~5-16 g C $week^{-1}$ across the study sites, while the goodness of fit (R^2) was ~0.4-0.9. For evapotranspiration (ET), the average value of simulated ET (415 mm yr^{-1}) for all sites and years is close to the average value of the observed ET (451 mm yr^{-1}) by flux towers (on a weekly basis, RMSE~2-8 mm $week^{-1}$;

R^2=0.3-0.9). However, further model development is needed to better represent soil water dynamics under dry conditions and soil temperature in winter. A quantification of the uncertainties introduced by spatially generalized parameter values in C and water exchange estimates is also necessary. In addition, some uncertainties in the input management data call for the need to improve the quality of the observational system.

Key word:

Carbon flux, eddy flux measurements, model evaluation, Pasture Simulation model (PaSim), water balance

Software availability

Name of Software: Pasture Simulation model (PaSim)

Developer: INRA, UR0874 initiative; contact: Raphaël Martin

Contact Address: INRA, UR0874 Grassland Ecosystem Research, 63039 Clermont-Ferrand, France

Telephone: +33-4-73624872

E-mail: raphael.martin@clermont.inra.fr

Availability: On request to the authors

Cost: free for no-profit use

Program language: Fortran

1. Introduction

Accurate quantification of ecosystem carbon (C) and water fluxes over regions, continents, or the globe is essential for understanding the feedbacks between the terrestrial biosphere and the atmosphere in the context of global change and climate policy-making (Xiao et al., 2012; Ciais et al., 2013). In the last decades, significant progresses have been made in quantifying regional to global C and water fluxes by using ecosystem modelling (Jung et al., 2007; Xiao et al., 2009), atmospheric inverse modelling (Butler et al., 2010) and upscaling of flux observations from eddy covariance towers (Jung et al., 2011). In particular, integrated environmental modelling (Laniak et al., 2013) provides effective tools for studying C and water cycles in agricultural and natural systems. Ecosystem models have been intensively developed and used to estimate C and water exchanges between the atmosphere and biosphere (Bondeau et al., 1999; Churkina et al., 1999; Huntzinger et al., 2012; Warszawski et al., 2014). They represent the key processes (such as plant photosynthesis, ecosystem respiration and evapotranspiration) and climatic and management drivers (e.g. grazing, cutting and fertilization) that regulate energy and matter exchanges. However, most of the modelling efforts have focussed on forests (Bondeau et al., 1999; Schaefer et al., 2012; Wu et al., 2012) and croplands (Palosuo et al., 2011; Roetter et al., 2012; Wattenbach et al., 2010), while lesser attention was given to grasslands (Ciais et al., 2010).

Grasslands are a widespread vegetation type worldwide, covering nearly one-fifth of the world's land surface (24 million km^2) (Suttie et al., 2005) and playing a significant role in the global C cycle (Scurlock and Hall, 1998; Ciais et al., 2010). At global scale, grasslands were estimated to be a net C sink of about 0.5 Pg C per year (Scurlock and Hall, 1998), but with high spatial heterogeneity and considerable uncertainty on the estimate of C exchange. Janssens et al. (2005) estimated that grasslands provide a C sink of 66±90 g C m^{-2} yr^{-1} over Europe. From an extensive network of flux towers, Schulze et al. (2009) inferred a net C sink: net biome production (NBP) in European grasslands of 57±34 g C m^{-2} yr^{-1}. However, grassland ecosystems are the most uncertain components of the Europe-wide C balance in comparison to forests and croplands because only few data and grassland-specific models are available (Ciais et al., 2010). As a consequence, it is urgent to improve and evaluate grassland models based on recently-available eddy flux data.

Over the last decades, grassland models were developed with different research foci. CENTURY model was developed to simulate soil C, N, P, and S dynamics on a monthly time step (Parton, 1988), with an updated version (DayCent) working on a daily basis (Parton et al., 2007). The Grassland Ecosystem Model (GEM) (Chen et al., 1996) linked biochemical, biophysical and ecosystem processes in a hierarchical approach to simulate C and N cycles, with focus on natural grasslands. The LINGRA model (Schapendonk et al., 1998) has been extensively applied to simulate growth of grasses, including perennial ryegrass (Rodriguez et al., 1999) and timothy (van Oijen et al., 2005) under northern and western European conditions. The Hurley Pasture Model (Thornley, 1998) describes the fluxes of C, N and water in a grazed soil-pasture-atmosphere system. DairyMod was designed to simulate not only biophysical, but also dairy management options (Johnson et al., 2008). Several integrated or whole farm system models were also available to simulate the biogeochemical processes and also include decision support system, such as Whole Farm Model (Bright et al., 2000), GP-FARM (Ascough et al., 2007), Integrated Farm System Model (http://www.ars.usda.gov/Main/docs.htm?docid=8519) and FASSET (Chirinda et al., 2011). An overview of the state of the art and the developments needed for process-based modelling of grazed agricultural systems were addressed by Snow et al. (2014).

Recently, attempts have also been made to introduce management options into global dynamic vegetation and crop models in order to extend functionalities for grasslands on regional and global scales. Biome and global dynamic vegetation models such as LPJmL (Bondeau et al., 2007), Biome-BGC (Hidy et al., 2012), ORCHIDEE (Krinner et al., 2005) and CARAIB (Warnant et al., 1994) were improved with mowing and grazing options. At the same time, widely used crop models, such as STICS (Brisson et al., 2003; Ruget et al., 2009), EPIC (Williams et al., 1989), CropSyst (Stöckle et al., 2003), DNDC (Rafique et al., 2011; Wang et al., 2012), DSSAT (Giraldo et al., 1999) and the APSIM platform (Holzworth et al., 2014) have also been adapted to simulate grasslands. These efforts have made great contributions to the overall development of grassland models (yet with a different detail in representing processes). However, model evaluation was limited in scope to specific goals (e.g. not all grassland models simulate biogeochemical cycles). A detailed evaluation of model performance against observational flux data from a variety of grassland sites is therefore desirable. In particular, for a process-based model representing in detail the mechanisms driving the functioning of grassland systems, evaluation is needed with extended datasets, which include different grassland observational sites with a diversity of climatic, management and soil conditions.

The process-based biogeochemical Pasture Simulation model (PaSim) is the focus of this study. It was originally developed by Riedo et al. (1998), based on the Hurley Pasture Model (Thornley, 1998), to simulate managed grasslands (clover-ryegrass swards). PaSim includes both grazing and cutting management options and is able to simulate a variety of temperate grassland ecosystems. Over the last decade, the model has been continuously improved to simulate C, water and N cycles. New approaches were integrated into the modelling structure to simulate, for instance, nitrous oxide (N_2O) emissions from soils (Schmid et al., 2001a) and methane (CH_4) emissions from animals (Vuichard et al., 2007a) as well as the performances (i.e. milk and meat production) of grazing animals (Graux et al., 2011). The model has been used in the climate-change impact studies (Graux et al., 2013; Vital et al., 2013), including an assessment of the contribution of forage-based systems to the global warming (Graux et al., 2012) with focus on France. However, PaSim has only been evaluated against a few European grassland sites using short periods of observed C fluxes and biomass production data, and based on limited parameterization (Vuichard et al., 2007a; Calanca et al., 2007). A full documentation and an extended evaluation of the model over a large number of sites are required.

A monitoring network consisting of a total of 12 grassland sites was established in

2002 and eddy-covariance flux measurements were made on this network within the European projects of the 5th, 6th and 7th framework programs，such as GREENGRASS (Soussana et al., 2007b), CARBOMONT (Bahn et al., 2008; Wohlfahrt et al., 2008), CarboEurope (Gilmanov et al., 2010) and CARBO-Extreme (Reichstein et al., 2013). This dataset provides a good opportunity to evaluate grassland model performances because these sites cover a variety of grassland types with contrasting management practices and representing different climate conditions.

The present study assesses the ability of PaSim to reproduce C and water fluxes of a number of European long-term eddy flux measurement sites. To do so, three sets of eco-physiological vegetation parameters (i.e. from permanent grassland, sown grassland, and an adjusted set, which is the calibrated parameter values based on flux measurements data and their plausible ranges) were applied in order to test whether a common set of vegetation parameters is appropriate to represent model outputs at European scale (regardless of the possible physiological dissimilarities among grasslands species in different places in Europe). Model calibration was not applied separately to each observational site. This did not make it possible to explore the spatial variability of model parameters. Testing such a scenario appeared beyond the scope of this paper since it implied too strong a deviation from the initial hypothesis of this regional study. Rather, we calibrated the model simultaneously on all datasets to find parameter values that would be applicable at regional scale. Multi-site calibration can be characterized by lower uncertainty than site-specific calibration, because more data are involved in the calibration process (e.g. Minunno et al., 2014).

The availability of a variety of detailed flux data from multiple sites offers the possibility of a genuine multi-location calibration of the model, holding to the assumption that a uniform calibration across sites is appropriate under these conditions. The results are discussed with respect to the strengths and weaknesses of the model in estimating C and water balances in Europe before presenting conclusions and avenues for future research.

2. Materials and Methods

2.1 Study sites and climate data

Twelve grassland sites with long-term eddy flux measurements were included in the study to evaluate model performances. The study sites cover a broad gradient of geographic and climatic conditions (Table 1) as well as a variety of soil types and management practices (Table 2). The sites are located in Central and Western Europe (Fig. 1, left), distributed over a range of latitudes from United Kingdom (Easter Bush) to Portugal (Mitra), of longitudes from Ireland (Dripsey) to Hungary (Bugac-Puszta), and of elevations from sea level up to mountain sites located at about 1800 m a.s.l. (Table 1). Along these ranges, the mean annual temperature varies from 5.2 (Monte Bondone, Italy) to 14.3 °C (Mitra, Portugal) with mean annual precipitation rates from 520 (Bugac-Puszta, Hungary) to 1271 mm (Dripsey, Ireland). With respect to management, the dataset covers the gradient from semi-natural to intensively managed mixed grass species swards (in the presence of clover) and essentially includes vegetation types representative of the zone. Semi-natural grasslands are typified by extensive systems either grazed (with a stocking rate of ~0.5-1.0 LSU ha^{-1} yr^{-1}) or not grazed (where forage production is limited to one cutting per year). Otherwise, the other sites are intensively managed by grazing and/or cutting and are supplied with relative large amounts of N fertilizer (>200 kg N ha^{-1}). It should be noted that the distinction between extensive and intensive grasslands may not be clear-cut. For instance, the unfertilized site of Amplero, grazed by a limited number of livestock units (0.5 LSU ha^{-1} yr^{-1}), qualifies as an intensive production system because it is grazed for a long period of time in the year (200 days), with intensive utilization of the sward and gain of N from returns by animals. At Easter Bush, the low impact of grazing pressure (in number of animals and duration) is instead compatible with an extensive system because the N fertilization treatment does not exceed the threshold (>200 kg N ha^{-1}) conventionally set for intensively managed grasslands (e.g. Bos et al., 2005).

Monthly and yearly summaries for the average temperature and total precipitation were obtained from the hourly weather data available for each site. The yearly reference evapotranspiration (ET_0, mm) was also calculated, using the Penman–Monteith method, which uses an hourly time step (Allen, 2005). These weather summaries were the basis for calculating two bioclimatic indicators.

The aridity pattern (Fig. 1, right) is characterized by semi-arid to humid conditions, with the average value of De Martonne-Gottmann index (*b*) ranging from 10-20 at Mitra (Portugal) and Bugac-Puszta (Hungary) to 45 at Dripsey (Ireland). The climate of Mitra is typically warm and dry for a large part of the year, with hot summers. Bugac-Puszta represents a continental climate, with hot summers, rain showers and mildly cold winters. The site is characterized by annual water deficit, as well as the Mediterranean upland site of Amplero (Central Italy). The other sites are mostly humid, with values of the aridity index around 30-50.

2.2 Flux measurements

Each study site was equipped with an eddy covariance system to determine the net ecosystem exchange (NEE) of CO_2. For each site, details of the materials and software used are provided by published papers (Table 1). The eddy covariance system consisted of a fast response 3D sonic anemometer coupled with fast CO_2–H_2O analyzers measuring fluxes of CO_2, latent and sensible heat, and momentum fluxes every 30 minutes. The flux data used in this study were downloaded from the European Fluxes Database Cluster (http://www.europe-fluxdata.eu). These data, previously filtered(quality checking and gap-filling) using methods based on friction velocity (u* filtering), contain inherent uncertainty (as detected by bootstrapping approach, after Reichstein et al., 2005 and Papale et al., 2006). We acknowledge that the random and systematic errors of eddy flux measurements could induce uncertainty and affect interpretation of data when eddy flux data were used for model calibration and validation (Lasslop et al., 2008). Random errors caused by poor measurement and sampling variability can be quite large at half-hourly time resolution, while systematic errors (biases) can be corrected (Aubinet et al., 2012). It is known that the correction can be insufficient to avoid propagation of uncertainties in the gap-filling procedure and in the partitioning of C exchanges into assimilation and respiration (Richardson et al., 2012). However, the absolute uncertainty in half-hourly measurements is reduced (down to ~10%) with daily or higher (monthly to annual) timescales and often equals the inter-annual variability of the measured fluxes (Hagen et al., 2006; Desai et al., 2008; Kroon et al., 2009).

2.3 Model description

The Pasture Simulation model (PaSim, version 5.3, https://www1.clermont.inra.fr/urep/modeles/pasim.htm) simulates C and N cycling in grassland ecosystems (mixed swards) at a sub-daily time step. The model has evolved over time, starting as a simulator of dry matter production and associated flows of C, N and water in productive pastures (Riedo et al., 1998). The biological N fixation by clover is simulated by assuming that clover fraction in the sward is fixed for the specific location (after Riedo et al., 1998). PaSim was later improved by Schmid et al. (2001b) with respect to the production and diffusion of N_2O (Riedo et al., 2002) the exchange of NH_3 with the atmosphere by Vuichard et al. (2007a, b), the animal herbage selection and intake, and the effects of diet quality on the emissions of CH_4 from grazing animals. More recently, Graux et al. (2011) further improved functionalities to estimate the forage production and dry matter intake taking into account selective grazing between vegetation compartments and the effect of high temperatures on animals, while also simulating ruminant performance and enteric CH_4 emissions during grazing according to the energy content of the intake. The livestock system considers change in body weight of the grazing livestock and simulates the level of milk and meat production with heifers, dairy and suckler cows during the grazing period.

The model consists of five interacting modules: microclimate, soil, vegetation, herbivores and management. The soil biophysical module simulates soil temperature and moisture profiles for different soil layers based on soil physical properties and hourly weather inputs and simulated plant water use. The soil biogeochemical module, adapted by monthly time-step CENTURY's organic decomposition approach (Parton, 1988), evenly distributes litter into the whole soil profile. The litter is segregated into its structural and substrate components, respectively supplying the structural and metabolic soil pools. In addition, the soil organic matter is further separated into three compartments (active, slow and passive) according to different decomposition rates. Soil pools are interlinked to represent C and N first-order kinetics. The N cycle considers N inputs to the soil via atmospheric deposition, fertilizer addition, symbiotic fixation by legumes and animal faeces and urine. The inorganic soil N is available for root uptake and is lost through the processes (leaching, volatilization and nitrification/denitrification) leading to N_2O and N2 emissions to the atmosphere. The vegetation module estimates the assimilated C by photosynthesis and allocates it dynamically to one root and three shoot compartments, each of which consisting of four age classes. The transition from one age category to the next is done using threshold time values to calculate the age of biomass in a compartment from the input of younger material and the loss of older material. C losses from the system are through animal milking, enteric CH_4 emissions and from animal returns, and ecosystem respiration. Accumulated aboveground biomass is either cut or grazed, or enters a pool after senescing. Herbivores are considered during the time they were at pasture (not during indoor periods). Management includes organic and mineral N fertilizations, mowing and grazing, setting by the user or optimized within the model to achieve some objectives.

2.4 Parameterization and Simulation

2.4.1 Parameterization strategies

In previous studies (Calanca et al., 2007; Vuichard et al., 2007b), PaSim was evaluated for a temporary grassland at Oensingen (Switzerland) and an upland permanent grassland at Laqueuille (France) based on a set of 26 parameters (Table 3). We assumed that a common set of eco-physiological model parameters can be established to simulate C_3 grasslands (including grasses, forbs and legumes) under contrasting climate and management regimes in Europe, while site-specific climate and management conditions provide supplementary factors driving the actual production of grasslands. Based on the set of parameters given in Table 3 and sensitivity analysis results (Ben Touhami et al., 2013), the following two steps were carried out to explore the parameter space and identify a common set of eco-physiological model parameters for PaSim. First, the model was run at all sites with two sets of default parameter values: temporary sown grassland (P_temp) and upland permanent grassland (P_perm). Second, manual calibration was carried out for these parameters, which were identified as influential parameters by Ben Touhami et al. (2013). The values of some of these parameters were modified within their plausible ranges (as from the published literature, documented by Graux, 2011) to ensure realistic representation of a variety of outputs. The calibration work was performed at all study sites together through a trial-and-error process comparing the model predictions with observational data. The solutions obtained constitute a satisfactory performance for all output variables according to the metrics of Table 4. Even though optimization methods are available (Trudinger et al., 2007; Wang et al., 2009), the manual calibration is useful for modellers to get a reference parameter set reflecting expert knowledge and simple adjustment strategies. It was proven that optimization methods may be problematic in confronting the interaction between parameters of complex models (Hollinger and Richardson, 2005; Richardson et al., 2010). The model performance was evaluated for each site separately and with all sites combined, by comparing the simulated C and water fluxes with data from eddy flux towers.

2.4.2 Model simulation and evaluation

For each site, simulations were carried out with three sets of parameter values described above for all available years in each site

PaSim was initialized via a spin-up process using the current weather input. In particular, soil C pools were initialized to steady-state by running the model over 100 years by looping the available meteorology at each site following Lardy et al. (2011). The results of the spin-up process matched the supplied soil C measurements with a relative error of about 10% on average (± ~2% standard error).

The agreement of model outputs against the following five plant and soil variables was examined, gross primary productivity (GPP, kg C m^{-2} d^{-1}), ecosystem respiration (RECO, kg C m^{-2} d^{-1}), net ecosystem exchange (NEE, kg C m^{-2} d^{-1}), soil water content (m^3 m^{-3}) and actual evapotranspiration (ET, mm d^{-1}). Ecosystem respiration (RECO) plays an important role in estimating global C balances of terrestrial ecosystems, and its knowledge is required to assess the GPP of such ecosystem (as a sum of NEE, and RECO, equations in appendixes A, B, C and D). Soil water content (SWC) and soil temperature (ST) were estimated for each of the six layers that make up the soil profile in PaSim (equations in appendixes E and F).

Different performance indices and threshold criteria (Bennett et al., 2013) were used to evaluate the model (Table 4). In particular, the goodness-of-fit R^2 (coefficient of determination) was calculated to assess the linear dependence between modelled and observed data and the variance explained by the model. The modelling efficiency (ME), the index of agreement (IA) and the root mean square error (RMSE) were derived to assess quantitative differences. The mean bias (MB) is a measure of the overall tendency of the model to under- or over-estimate (the systematic error) the observations. The performance of the model was assessed on daily, weekly and monthly time scales.

3. Results

This section first describes the study sites. Then, the comparison between PaSim results obtained with three sets of parameter values (two previously established and one established in this study) and observed C and water fluxes is illustrated. The model improvement gained with the new parameterization is presented. As well, the impact of both site-specific characteristics and management options on model performances is illustrated, followed by a detailed analysis of the model performances with focus on C and water balances. Only exemplary results (selected output variables and sites) are reported graphically and the main outcomes discussed hereafter, while the full set of results is provided online supplementary material.

3.1 The improvement of the model performance with the redefined parameter values

The adjusted parameters (denoted P_new) essentially reflect that previously used at the permanent grassland site of Laqueuille (P_perm) (Table 3). This indicates that Laqueuille site resembles the European grasslands used in this study, with the exception of four parameters: light-saturated leaf photosynthetic rate for reproductive stage, light-saturated leaf photosynthetic rate for vegetative stage, maximum specific leaf area, and temperature dependence factor of the soil respiration. Even though a formal sensitivity analysis was not undertaken in this study, these parameters had a significant impact on model outputs in a previous study (Ben Touhami et al., 2013). For three parameters, the new values lie between those in the previous studies. For the parameter governing soil respiration, previous modelling studies supported a default value equal to 2, which was substantially decreased (down to 0.7) to obtain simulated respiration values closer to observations. Given its impact on the modelled RECO, characterization of this parameter will require further studies.

The estimation of GPP and RECO was improved (Fig. 2) with the redefined common set of eco-physiological parameters (Table 3). GPP was overestimated at all sites using the P_temp parameter set with the exception of Oensingen (the site where that parameter set was originally derived) and, to a lesser extent, of Amplero. Using P_perm parameter set (permanent grassland), the bias of GPP was reduced at seven out of 12 sites. Applying the redefined P_redif parameter set (Table 3), the bias of GPP was further reduced for most of the sites except Oensingen, Bugac-Puszta and Amplero (Fig. 2).

With both P_temp and P_perm parameter sets, RECO was overestimated for most of the sites, with the exception of Oensingen and Amplero (Fig. 2). With P_perm, a slight underestimation was also obtained at intensively-managed Laqueuille (Fig. 2). When the redefined parameter set was used, the bias of RECO was reduced at all sites but Oensingen and Amplero. Overall, the estimated ET has a good agreement with the observed values with no real improvement with the redefined parameter values (Fig. 2 and Fig. A1).

3.2 The site variability of model performances with the redefined parameter values

Model performance in predicting GPP, RECO and ET (data aggregated on a weekly basis) is closely linked with site-specific conditions such as soil moisture (e.g. dry sandy soils versus humid soils). The model simulated well GPP and RECO for nine out of 12 sites. The exceptions were the sites of Amplero, Mitra and Bugac-Puszta (Fig. 3, Fig. 4 and Table 5), which are characterized by drier conditions than the other sites. The R^2 for the estimated versus observed GPP was greater than 0.8 for most of the sites and was lower than 0.5 at Amplero only (R^2=0.40) (Fig. 3). Similar results were found when other indices, such as the slope of the regression, IA, ME and RMSE were taken into account (Table. 5). Compared with GPP estimations, similar model performances were found for RECO across sites, but R^2 values for RECO were relatively lower than those obtained when simulating GPP. For RECO, R^2 values were generally greater than 0.7 for most of the sites, but lower than 0.5 at Amplero (R^2=0.39) and Mitra (R^2=0.46) (Fig. 4). At Oensingen, the model underestimated RECO during winter time and there were also periods (e.g. 2007) when summer modelled RECO was below of that measured (Fig. 5). However, winter RECO underestimation was common to most of the sites (online supplementary material). The model performance was satisfactory for predicting ET at most of the sites. Exceptions were dry sites such as Amplero, Bugac-Puszta and Mitra (Fig. A1).

3.3 The impact of site characteristics and management practices

Site characteristics and management practices were observed to have an important impact on the model ability to estimate RECO (Fig. 6), but they were less important when predicting GPP, NEE, ET, and soil temperature (data not shown). Concerning management practices, the model tended to underestimate or overestimate RECO, respectively for intensively and extensively managed grasslands (Fig. 6). The occurrence of cutting or grazing had no significant impact on the model performance in predicting RECO. The model tended to slightly underestimate RECO for temporary-sown grasslands, while simulations of permanent grasslands were in good agreement with measured data (Fig. 6). Concerning site-specific conditions, RECO was underestimated for non-montane grasslands (<800 m a.s.l.) and overestimated for mountain sites (Fig. 6).

An analysis of the normalized residuals (where each residual is the difference between the predicted and observed values divided by the standard deviation) showed seasonal patterns, which differed by site (Fig. 7). On average, the model slightly underestimated weekly-aggregated RECO in winter in most sites, but significantly overestimated it in summer time on Laqueuille extensive, Monte Bondone, Alinya, Bugac-Puszta, and Cabauw (Fig. 7). However, most of the residuals fall within the upper limit of the 95% confidence interval.

3.4 C and water balances

The mean annual C fluxes (NEE, GPP and RECO) are meant as a synthesis and a complement to the model performances of PaSim presented in this study. They showed a good agreement with observations using the redefined parameter set (Fig. 8). With these parameter values, the estimated NEE flux was on average 213 g C m^{-2} yr^{-1}, which indicates a sink of C approaching the average NEE flux observed at the studied sites (185 g C m^{-2} yr^{-1}) (Fig. 8). The estimated yearly average values of GPP (1220 g C m^{-2} yr^{-1}) and RECO (1006 g C m^{-2} yr^{-1}) are in agreement with the observed mean values (1230 g C m^{-2} yr^{-1} for GPP and 1046 g C m^{-2} yr^{-1} for RECO) across all sites (Fig. 8). As a consequence, the model overestimated the C sink by 15%. This is mainly due to RECO, which is underestimated while GPP is in good agreement with observations. The average value of simulated ET (415 mm yr^{-1}) for all sites and years was close to the average value of the observations (451 mm yr^{-1}), which corresponded to an underestimation by 8% (Fig. 9).

4. Discussion

4.1 Model performance over European grasslands

By evaluating PaSim at a variety of European sites, an improvement of model performances was obtained with using a common set of parameter values to estimate C and water fluxes at weekly and yearly time scales (Fig. 2, Fig. 8 and Table 3). The discrepancy between the observed and estimated GPP and RECO values was reduced compared with previous studies making us of parameter values obtained at specific conditions (Calanca et al., 2007; Ciais et al., 2010). For instance, Calanca et al. (2007) overestimated GPP of about 50% at Laqueuille (France).

4.2 The spatial variability of the model performance

The agreement between the observed and estimated GPP on arid sites (Bugac-Puszta, Amplero) is not as good as on other sites (Fig. 3). The mismatch between observed and estimated GPP values on these dry sites can be partially attributed to the fact that the model did not simulate soil water content fluctuations during summer time well (see effect of drought conditions for Bugac-Puszta, Fig. 2A and Amplero, Italy, Fig A3). Previous studies confirmed that extreme drought events may have a significant effect on C and water cycles (Ciais et al., 2005; Hussain et al., 2011). With all the slope coefficients less than 1, the range of the simulated soil water content was smaller than the observed range, while the intercept was well above 0 (Fig. A4), indicating that the model overestimated the soil water content during dry periods and underestimated it the rest of time. As a consequence, the overestimated soil water content during drought periods could explain the slight overestimation of GPP (Fig. A2). In contrast, at Mitra (Portugal), the underestimated GPP can be partially attributed to the underestimated soil water content during the growing season (Fig. A5) as water is the limitation factor of plant growth in arid regions. Underestimation of GPP was also obtained at Amplero (Italy), but the incomplete information available for this site (Fig. A3) about starting and ending dates of grazing (constant dates were used) makes interpretation of results difficult.

Comparing with GPP, a similar model performance for RECO was found, but R^2 for RECO is relatively lower than GPP (Fig. 3). The lower R^2 for RECO on most of the sites is mainly due to the underestimated RECO during winter as, for instance, at Bugac-Puszta (Fig.7, A2). On one hand the underestimated RECO during winter can be attributed to underestimation of soil temperature in the same period as soil respiration is sensitive to temperature. Soil respiration, one of the main components of RECO, depends on soil moisture, clay content, soil organic matter and C assimilation (Bahn et al., 2008; Balogh et al., 2011; Migliavacca et al., 2011) and these are also the drivers of PaSim. On another hand, the overestimated RECO at Bugac-Puszta is partially due to overestimated GPP as more C substrate is available. A third reason might be that the model overestimated soil moisture content (Fig. A2 and Fig. A5) since soil moisture is one of the most important limiting factors of soil respiration especially in arid and semi-arid regions (Balogh et al., 2011). At Amplero and Mitra, RECO underestimation follows GPP underestimation (Fig. A3 and Fig. A5). Indeed, RECO is intimately related to C supply (Bahn et al., 2008; Migliavacca et al., 2011).

4.3 Effect of site-specific conditions and management practices

Management practices affect grassland production and greenhouse gas emissions from grassland systems (Schmitt et al., 2010; Zeeman et al., 2010; Luo et al., 2012; Peichl et al., 2012). In this study, PaSim underestimated RECO for intensively-managed grasslands such as Oensingen and Amplero and overestimated it for extensively-managed grasslands (Fig. 6, 7). It is known that intensive management practices can introduce pronounced changes to soil physical structure, which in turn impact the soil water transport processes and the soil heterotrophic respiration (Moyano et al., 2012; Ball, 2013). It is the case for the present study as PaSim did not simulate adequately soil water fluctuations (Fig. 5, Fig. A2 and Fig. A3). At Oensingen (Switzerland), the model did not represent well the soil temperature (Fig. 5. This can be mainly attributed to the disturbance of management, which changed the soil structure when converting cropland into grassland at Oensingen in 2001, considering that tillage changes soil physical structure and, in turn, water and energy transport processes (Acharya et al., 2012). The human management could also modify microbial component and diversity (Cantarel et al., 2012), which significantly impacts on the soil respiration (Allison et al., 2010; Wieder et al., 2013). Moreover, the possibility to introduce more uncertainties is high due to imprecise input management information such as grazing, cutting, and fertilization rate and timing.

4.4 Limitations and further improvement

Referring to the model performance discussed above, certain modules of PaSim were identified as worthy of further development. One is the soil energy balance module because the model underestimated soil temperature when air temperature was high in summer (Fig. A5) and overestimated soil temperature in winter when air temperature is low (Fig. 5, Fig. A2, Fig. A3 and Fig. A5). The soil water transport module is also critical because soil water fluctuations were not well captured by the model (Fig. 5, Fig. A2, Fig. A3 and Fig. A5), especially on arid and semi-arid grasslands. Moreover, the effect of standing biomass on the energy balance (with shading and albedo) has not been investigated.

The choice of eco-physiological parameters used and calibrated manually in this study also requires a forma quantification of the parameter uncertainties introduced in regional studies. The interaction between model parameters is also an issue. For example, specific leaf area (*sla*), which depends on the maximum value set for it (*slam*), interacts in PaSim with C allocation-parameters across different organs of the plant. A higher *sla* could induce a lower allocation of assimilated C to leaf, which may be not the case in reality.

5. Conclusions and perspectives

5.1 Summary of findings of the regional-scale analysis

A regional-scale analysis of C and water cycles was performed on a variety of European grassland sites using a process-based model (PaSim) with a single set of eco-physiological parameters. It was shown that: 1) variables of C and water cycles (mainly GPP, RECO and ET) can be reasonably simulated by PaSim at European scale using a common set of parameter values; 2) better model performances are obtained at more humid sites; 3) RECO tends to be underestimated in intensively-managed grasslands and overestimated at sites when extensive management practices are adopted.

The parameterization for mechanistic simulation of grasslands (with biogeochemical capabilities) is a general way to facing regional studies. We have pursued in this study the question of to what extent calibration can improve the parameterization of a complex grassland model for regional-scale simulations in Europe. Acting upon the most influential parameters of PaSim, we have derived a set of parameter values of general validity in Europe. Even if for specific purposes process-based models need to be parameterized on a site-specific basis, our multi-dataset procedure demonstrates that it is possible to find global estimates for those parameters that encompass a wide range of conditions. The accurate estimation of C and water fluxes relies on the mechanistic representation of key ecosystem processes, with parameters that can be related to physical quantities, thus the perspective of using a regionally calibrated model regulating energy and matter exchanges is more interesting than applying statistical models (Laniak et al., 2013). In addition, statistical model estimations may involve significant levels of collinearity among predictor variables such as temperature and precipitation. They also rely on the assumption of stationarity (e.g. assuming that past relationships will hold in the future, even if factors such as climate and management evolve) and are subject to problems of low signal-to-noise ratios in yield or weather records in many locations (Lobell and Burke, 2010). The main finding is that the satisfactory performance obtained over contrasting climate conditions and management options justify the use of PaSim in regional studies on C and water fluxes in Europe. In C-water flux studies, this is especially relevant when daily-resolution outputs are mainly analysed in temporally-aggregated form - that is, the interest is in weekly, monthly or higher timeframes (e.g. Wallach and Thorburn, 2014).

5.2 Future work on grassland modelling

Our results indicate further model development is needed to address specific needs and this is critical under the pressure of a changing climate and related extreme weather events, potentially altering the C cycles at different scales (Field et al., 2011). A first issue is that heat waves and dry spells have (favouring conditions of aridity) a direct effect on CO_2 fluxes because warmer temperatures and soil moisture shortage affect both photosynthesis and respiration. Moreover, as changes in seasonal water availability have pronounced effects on individual species, a prominent role is suggested for species interactions in ecosystem responses to climate changes (Suttle et al., 2007). Adaptation and functional biodiversity would dampen down the effect of climate extremes on the C cycle, but the bases for biological adaptation and the role of biodiversity are still unclear (Reichstein et al., 2013b). The use of functional traits of plants, for which plant species are classified into functional types based on vegetative and reproductive traits, proposed by Cruz et al. (2002) can be a promising avenue for future research (Duru et al., 2013). But the level of detail of this study is too low to draw conclusions about the relationship between model parameters and phenotypic traits.

To obtain reliable estimates of the sign (source or sink) and magnitude of C-cycle feedbacks, future research should provide a mechanistic basis for inferring effects of extreme meteorological events on the C cycle. This would also help capturing the impacts of drought events on grasslands because drought avoidance of grassland plants mainly depends on rooting depth and soil water reserves. Concepts by Baker et al. (2008) and Sheikh et al. (2009), which consider root access to the stored water in the deep soil water during the drought season, could be integrated into PaSim.

The soil temperature module is another area of the model to be improved to better predict soil temperature over winter. This is especially critical for high-altitude grasslands, where vegetative growth restarts at snowmelt. This would also improve the estimation of soil respiration, for which soil temperature is a key driver.

Moreover, we acknowledge that the dynamics of aboveground biomass accumulation (either cut for yield production or grazed by animals) were not considered in the study design. Biomass data are mostly discontinuously measured and rather large uncertainties on biomass measurements (mainly owing to spatial heterogeneity) may hinder model evaluation (Vuichard, 2007b). A better model performance (yet integrating biomass measurements) could be attained by optimizing model parameters through model-data fusion methods such as Bayesian calibration (van Oijen et al., 2011). Studies of this type are underway on PaSim (Ben Touhami et al., 2012a, b) with attention given to the interaction among parameters.

The improvements of PaSim also include the development of scalable solutions with fundamental plant science research (a broad range of basic impact processes, open to a wide range of plant types) and transition of software engineering technology into modelling practice (Martin et al., 2011; Lardy et al., 2014), while addressing re-usability issues and inter-linking of model components (Donatelli et al., 2012).

For managed grasslands, complete management information is often unavailable for regional studies. High-quality grassland management data are needed to better understand their effects on the soil physical structure and C storage (Flechard et al., 2007; Schmitt et al., 2010; Chang et al., 2013).

The model improvement actions are ongoing under the guidance and conditions laid down by a number of international projects and initiatives (e.g. AgMIP, http://www.agmip.org), and will be expanded by the EU-FP7 project MODEXTREME (http://modextreme.org).

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APPENDICES

Appendix A - Primary production

Gross primary production (GPP) is the rate at which the plant captures and stores a given amount of chemical energy as biomass in a given length of time. Some fraction of this fixed energy is used for cellular respiration and maintenance of existing tissues (growth respiration and maintenance respiration). The remaining fixed energy (as mass of photosynthate) is referred to as net primary production (NPP):

$$NPP = GPP - R_{pl,tot} \quad (1)$$

where $R_{pl,tot}$ is the total plant respiration (autotrophic).

Plant residues deposited to the soil are subject to biological degradation. During this process, soil organic C is respired to CO_2 while providing energy to the decomposers (microorganisms and soil fauna). Heterotrophic C fluxes can also include respiratory losses of CO_2 by grazing ruminants. The combined autotrophic and heterotrophic ecosystem respiration (RECO) is the CO_2 release from the plants ($R_{pl, tot}$), soil (R_{soil}) and animals (R_{an}).The ensemble of instantaneous inward and outward flows of C within the ecosystem is the Net Ecosystem Exchange (NEE), given by:

$$NEE = RECO - GPP \quad (2)$$

with positive values indicating the system is a source of C losses, and negative values indicating that the system sequestrates C from the atmosphere.

Appendix B - Total plant respiration

A single process of respiration is associated with growth (Thornley, 1998). A component of this respiratory flux is deemed to be maintenance respiration (generally associated with the re-synthesis of degrading tissue), while also taking into account the energy required for mineral uptake. The dependence of respiratory components on C substrate supply is represented by separating C substrate from structure and coupling the respiration flux to photosynthesis. This allows simulating variation in the fractions of total plant respiration associated with different processes during plant development.

Total plant respiration, $R_{pl,tot}$ (kg C m^{-2} d^{-1}), is given by:

$$R_{pl,tot} = R_{m,rt} + R_{m,sh} + R_{G,rt} + R_{G,sh} + R_N \quad (3)$$

R_G and R_m stand for growth and maintenance respiration, respectively, referred to shoot (index *sh*) and root (index *rt*). R_N is the respiratory flux associated with uptake of N from the soil solution. The terms $R_{m,rt}$, $R_{G,rt}$ and R_N are soil respiratory fluxes from the biological activity of roots (autotrophic soil respiration).

Growth respiration rates

The two respiration fluxes needed to produce energy for the growth of shoots and roots, $R_{G,sh}$ and $R_{G,rt}$ (kg C m^{-2} d^{-1}), respectively, are calculated as:

$$R_{G,sh} = I_{C,G_{sh}} \cdot \left(\frac{1}{Y_{G,pl}} - 1\right) \quad (4)$$

$$R_{G,rt} = I_{C,G_{rt}} \cdot \left(\frac{1}{Y_{G,pl}} - 1\right) \quad (5)$$

The term $1/Y_{G,pl}$ is an efficiency measure representing the kg of C required to create 1 kg of structural C, $Y_{G,pl}$ being the photosynthetically-assimilated C initially allocated to substrate C reserves and then used for growth and maintenance of tissues. For the fraction required for growth, growth rates (kg C m^{-2} d^{-1}) are calculated for aboveground ($I_{C,G_{sh}}$) and belowground ($I_{C,G_{rt}}$) biomass, based on allocation values occurring during the vegetative stage ($I_{C,G_{sh,veg}}$ and $I_{C,G_{rt,veg}}$, kg C m^{-2} d^{-1}), modified in favour of aboveground biomass during the reproductive stage. The coefficient $Y_{G,pl}$ is set equal to 0.75 to represent plant growth efficiency (kg C (kg C)$^{-1}$).

C allocation fluxes into roots ($I_{C,G_{rt}}$) and aboveground ($I_{C,G_{sh}}$) plant parts are as follows:

$$I_{C,G_{rt}} = I_{C,G_{rt,veg}} - f_{devstage} \cdot I_{C,G_{rt,veg}} \quad (6)$$

$$I_{C,G_{sh}} = I_{C,G_{sh,veg}} + f_{devstage} \cdot I_{C,G_{rt,veg}} \quad (7)$$

Where $f_{devstage}$ is a factor depending on the plant development stage.

The terms $I_{C,G_{sh,veg}}$ and $I_{C,G_{rt,veg}}$are calculated on a constant growth rate at 20 °C ($I_{C,G20}$, usually set equal to 150 kg^2 (kg C)$^{-1}$ (kg N)$^{-1}$), applied to the cumulative structural biomass of roots and shoots (W_{sh}, W_{rt}, kg DM m^{-2}) and modulated by factors of temperature ($f_{T,G}$) and substrate C and N concentrations in shoots and roots (C_{sh}, C_{rt}, kg C (kg DM)$^{-1}$; N_{sh}, N_{rt}, kg N (kg DM)$^{-1}$), as follows:

$$I_{C,G_{sh,veg}} = I_{C,G20} \cdot f_{T,G} \cdot C_{sh} \cdot N_{sh} \cdot W_{sh} \quad (8)$$

$$I_{C,G_{rt,veg}} = I_{C,G20} \cdot f_{T,G} \cdot C_{rt} \cdot N_{rt} \cdot W_{rt} \quad (9)$$

Maintenance respiration rates

The respiration fluxes to maintain metabolic processes (those that do not result in a net increase in plant dry matter) of roots ($R_{m,rt}$) and shoots ($R_{m,sh}$) are a function of substrate C concentration (C, kg C kg DM^{-1}), structural biomass ($W_{sh} \cdot f_{C,sh}$, $W_{rt} \cdot f_{C,rt}$) and a temperature-dependent stress factor (Table 3):

$$R_{m,sh} = \frac{C}{C + K_{C,mai}} \cdot R_{m,sh,temp} \quad (10)$$

$$R_{m,rt} = \frac{C}{C + K_{C,mai}} \cdot R_{m,rt,temp} \quad (11)$$

where $K_{C,mai}$ is a maintenance respiration parameter, set equal to 0.03 kg substrate C (kg structural DM)$^{-1}$ d^{-1}. The terms $R_{m,sh,temp}$ and $R_{m,rt,temp}$ are temporary shoot and root maintenance respiration, respectively, as follows:

$$R_{m,sh,temp} = f_{T,sh} \cdot \sum_{j=1}^{4} k_{mai,j,20} \cdot W_{sh,j} \cdot f_{C,sh} \quad (12)$$

$$R_{m,rt,temp} = f_{T,rt} \cdot \sum_{j=1}^{4} k_{mai,j,20} \cdot W_{rt,j} \cdot f_{C,rt} \quad (13)$$

These maintenance respiration factors are transient in nature since they apply to temporary values. Both shoot and root biomasses are indeed divided into four state variables representing four age categories (j=1, ..., 4), for which the following values are given for the maintenance respiration parameter at 20 °C, $k_{mai,j,20}$ (kg C kg^{-1}structural C d^{-1}): 0.020 (j=1), 0.020 (j=2), 0.015 (j=3), 0.010 (j=4).
The terms $f_{C,sh}$ and $f_{C,rt}$ (kg C kg^{-1} DM) are fractional C content in shoot and root structural dry matter, respectively (reference values are 0.50 and 0.39, respectively).

N uptake respiration rate

The respiration flux associated with N uptake (R_N, kg C m^{-2} d^{-1}) is:

$$R_N = k_N \cdot IN_{soil,rt} \quad (14)$$

where $IN_{soil,rt}$ (kg Nm^{-2}) is the mineral N (NO_3^--N and NH_4^+-N) uptake by the sward, and k_N is the respiratory cost of N uptake (the reference value being 0.45 kg C kg^{-1} N).

Appendix C – Heterotrophic soil respiration

Apart the biological activity of roots and associated micro-organisms, the flux of CO_2 from the soil to the atmosphere is the result of the production of CO_2 from the activity of heterotrophic bacteria and fungi living on litter and in the root-free soil (after Parton, 1988). The soil organic carbon (SOC) pool is divided into five pools with different turnover times ranging from 0.5 to 1500 years. An additional component is given by the amount of C released as exudates (*exu*) from roots into the soil, estimated as a fraction of plant substrate C. The litter in decomposition over the total soil depth splits into its structural and substrate components, supplying the structural (*str*) and metabolic (*met*) soil pools respectively. Other three compartments with different decomposition rates include active (*act*), slow (*slo*) and passive (*pas*) pools of SOC, consisting of the microbial biomass, refractory components of litter and highly humified organic compounds respectively.

Total heterotrophic soil respiration, R_{SOC} (kg C m^{-2} d^{-1}), is given by:

$$R_{SOC} = R_{str} + R_{met} + R_{exu} + R_{act} + R_{slo} + R_{pas} \quad (15)$$

Soil respiration from structural organic matter

The respiration flux associated with structural SOC (R_{str}, kg C m^{-2}d^{-1}) is:

$$R_{str} = \left(1 - f_{lig,str}\right) \cdot f_{r,str} \cdot f_{C,str} + f_{lig,str} \cdot f_{r,str,lig} \cdot f_{C,str} \quad (16)$$

The microbial respiration parameter for the decomposition of the structural pool, $f_{r,str}$, and of lignin, $f_{r,str,lig}$, are set equal to 0.55 and 0.3, respectively. The term $f_{lig,str}$ is the fraction of lignin in structural soil organic matter. The fraction of C in the structural plant residue, $f_{C,str}$, is as follows:

$$f_{C,str} = k_{str} \cdot W_{C,str} \quad (17)$$

where k_{str} (kg C m^{-2} d^{-1}) is the decomposition rate for the structural pool and $W_{C,str}$ (kg C m^{-2}) is the C content in structural fraction of plant residue (depending on temperature, lignin, texture and water content).

Soil respiration from metabolic organic matter

The respiration flux associated with metabolic SOC (R_{met}, kg C m^{-2}d^{-1}) is:

$$R_{met} = f_{r,met} \cdot f_{C,met} \quad (18)$$

The microbial respiration parameter for the decomposition of the metabolic pool, $f_{r,met}$, is set equal to 0.55. The fraction of C in metabolic pool, $f_{C,met}$ (kg C m^{-2}), is calculated assuming linear kinetics.

Soil respiration from exudates

The respiration flux associated with root exudates (R_{exu}, kg C m^{-2} d^{-1}) is:

$$R_{exu} = f_{r,exu} \cdot f_{C,exu} \quad (19)$$

The parameter $f_{r,exu}$ is set equal to 0.75. The term $f_{C,exu}$ (kg C m^{-2}) is C substrate output for root exudation.

Soil respiration from active organic matter

The respiration flux associated with active SOC (R_{act}, kg C m^{-2}d^{-1}) is:

$$R_{act} = f_{r,act} \cdot f_{C,act} \quad (20)$$

The fraction of C in active pool, $f_{C,act}$ (kg C m^{-2}), is calculated as follows:

$$f_{r,act} = 0.85 - 0.68 \cdot (f_{clay,ah} + f_{silt,ah}) \quad (21)$$

where f_{clay} and f_{silt} are fractions of clay and silt, respectively.

Soil respiration from slow organic matter

The respiration flux associated with slow SOC (R_{slo}, kg C m^{-2}d^{-1}) is:

$$R_{slo} = f_{r,slo} \cdot f_{C,slo} \quad (22)$$

The microbial respiration parameter for the decomposition of the slow pool, $f_{r,slo}$, is set equal to 0.55. The fraction of C in slow fraction, $f_{c,met}$(kg C m^{-2}), is calculated as follows.

$$f_{r,slo} = k_{slo} \cdot W_{C,slo} \quad (23)$$

$$k_{slo} = k_{slo,20} \cdot k_{dec,t} \cdot k_{dec,\theta} \quad (24)$$

$W_{C,slo}$ (kg C m^{-2}) is the C content in slow pool (depending on temperature, lignin, texture and water content). The term $k_{slo,20}$ (d^{-1}) is the turnover rate for slow C pool at

20 °C, equal to 0.00027. The terms $k_{dec,t}$ and $k_{dec,\theta}$, are factor activities of soil organic matter for temperature and water content, respectively.

Soil respiration from passive organic matter

The respiration flux associated with active SOC (R_{pas}, kg C m^{-2}d^{-1}) is:

$$R_{pas} = f_{r,pas} \cdot f_{C,pas} \quad (25)$$

The microbial respiration parameter for the decomposition of the passive pool, $f_{r,pas}$, is set equal to 0.55. The fraction of C in passive pool, $f_{Cp,as}$ (kg C m^{-2}), is calculated assuming linear kinetics.

Appendix D - Respiration from grazing animals

Half of the C in plant material consumed by grazing animals ($I_{C,veg\rightarrow ani}$, kg C m^{-2} d^{-1}) is assumed to be respired (R_{ani}, kg C m^{-2}d^{-1}):

$$R_{ani} = 0.5 \cdot I_{C,veg\rightarrow ani} \quad (26)$$

The amount of ingested C is estimated as follows:

$$I_{C,veg\rightarrow ani} = \left(f_{C,sh} + C\right) \cdot \frac{W_{sh}}{W_{sh,tot}} \cdot I_{veg\rightarrow ani} \quad (27)$$

where ($I_{veg\rightarrow ani}$, kg DM m^{-2} d^{-1}) is the amount of ingested dry matter, which increases with the aboveground plant biomass ($W_{sh,tot}$, kg DM m^{-2}) available for the animals (W_{sh}, kg DM m^{-2}, is the cumulative structural aboveground biomass), limited by the maximum ingestion capacity the animal is able to maintain (I_{max}, whose reference value is 16 kg DM d^{-1} animal^{-1}).

Appendix E - Soil temperature

The calculation of temperature in each soil layer is based on the energy balance equations for the different soil layers (Campbell, 1985; Monteith, 1965; Shuttleworth and Wallace, 1985):

$$T_S^*(h) = 0.6 \cdot T_S(h) + (1 - 0.6) \cdot T_S'(h) \quad (28)$$

Where $T_s(h)$ (K) is the soil temperature at the midpoint of the i^{th} layer in the present time step, $T'_s(h)$(K) is soil temperature in the same layer but one time step in the past, and $T^*_s(h)$(K) is temperature in the i^{th} layer at some time between the two time steps.

Appendix F - Soil water balance

The water content in the different soil layers determines photosynthesis and stomatal conductance, soil evaporation, and rates of soil biological processes, and is used to calculate soil temperature in the different layers, which influences belowground plant processes, soil heat flux, and soil biological processes. Values of the soil matrix potential in soil layer *h*, $\psi(h)$ (m), is related to the water content in the same layer, $\theta_s(h)$ (m^3 m^{-3}) by the soil moisture characteristic (Campbell, 1985):

$$\theta_S(h) = \theta_{s,sat}(h) \cdot \left[\frac{\psi_e(h)}{\psi(h)}\right]^{\frac{1}{b(h)}} \quad (29)$$

where $\theta_{s,sat}(h)$ (m^3 m^{-3}) is the saturation soil water content in soil layer *h*, $\psi_e(h)$is the air entry water potential (m) in soil layer *h*, $b(h)$ is a physical parameter for soil layer *h*.

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Tables

Table 1. Location, climate and management of the grassland study sites.

Country	Site	ID	Years	Geographical settings			Climate		Source
				Latitude	Longitude	Elevation(m a.s.l.)	Mean air temperature (°C)	Precipitation total (mm yr^{-1})	
France	Laqueuille	FRLaq1 FRLaq2	2004-2010 2004-2010	45° 38’ N	02° 44’ E	1040	7.8	1072	Klumpp et al. (2011)
Germany	Grillenburg	DEGri	2004-2008	50° 57’ N	13° 30’ E	375	8.5	946	Prescher et al. (2010)
Hungary	Bugac-Puszta	HUBug	2003-2008	46° 41’ N	19° 36 ’E	140	10.2	520	Pintér et al. (2008)
Ireland	Dripsey	IEDri	2003-2005	51° 59’ N	08° 45’ W	195	9.6	1271	Byrne and Kiely (2006)
Italy	Amplero	ITAmp	2003-2007	41° 52’ N	13° 38’ E	884	9.4	781	Wohlfahrt et al. (2008)
	Monte Bondone	ITMbo	2003-2007	46° 00’ N	11° 02’ E	1550	5.2	1003	Wohlfahrt et al. (2008)
Portugal	Mitra	PTMi2	2005-2007	38° 32’ N	08° 00’ W	190	14.3	627	Aires et al. (2008)
Spain	Vall d’Alinya	ESVDA	2004-2008	42° 12’ N	01° 26’ W	1770	6.2	908	Wohlfahrt et al. (2008)
Switzerland	Oensingen	CHOe1	2002-2009	47° 17’ N	07° 44’ E	450	9.3	1197	Ammann et al. (2007)
The Netherlands	Cabauw	NLCa1	2004-2007	51° 57’ N	04° 54’ W	0.7	10	800	Jacobs et al. (2007)
United Kingdom	Easter Bush	UKEBu	2002-2008	55° 52’ N	03° 02’ W	190	9.0	956	Soussana et al. (2007a)

Table 2. Soil properties and management of the grassland study sites (ID as in Table 1)

ID	Management (average)						Soil properties for the whole soil profile[1]					
	Utilization[2]	Cuts (yr^{-1})	Nitrogen fertilization		Grazing		Clover fraction	Soil depth (m)	Soil texture			Bulk density ($t\ m^{-3}$)
			Events (yr^{-1})	Total amount (kg N ha^{-1} yr^{-1})	Stocking rate (LSU^3 ha^{-1} yr^{-1})	Duration (d yr^{-1})			Sand (%)	Silt (%)	Clay (%)	
FRLaq1	Intensive	-	3	210	1.10	160	0.12	0.7	27	53	20	0.87
FRLaq2	Extensive	-	-	-	0.60	160						
DEGri	Intensive	2-3	-	-	-	-	0.20	0.7	13	79	8	1.06
BUG	Extensive	-	-	-	0.30	180	0.10	0.6	85	6	9	1.08
IEDri	Intensive	-	3	280	0.72	150	0.17	0.7	52	27	21	1.19
ITAmp	Intensive	-	-	-	0.50	200	0.20	0.7	12	33	55	0.92
ITMbo	Extensive	1	-	-	-	-	0.20	0.7	44	39	17	1.04
PTMi2	Extensive	-	-	-	1.46	70	0.00	0.7	55	35	10	1.12
ESVDA	Extensive	-	-	-	0.18	120	0.10	0.6	15	50	35	0.87
OEN	Intensive	3-4	4	214	-	-	0.25	1.0	24	33	43	1.15
UKEBu	Extensive	-	4	200	0.65	160	0.00	0.7	12	24	62	1.47
NLCa1	Intensive	-	3	225	0.60	180	0.00	0.7	45	25	30	1.19

[1] Soil properties were obtained as the mean of six layers. Simulations make use of basic information for each layer.
[2] The classification into "extensive" or "intensive" grasslands was based on fertilizing intensity, the number of cuts, cattle density and/or grazing duration, which reflect the socio-economic environment in each country.
[3] Livestock Standard Unit: standard measurement unit allowing the aggregation of various categories of livestock (species, sex and age) in order to enable them to be compared, related to the animals' feed requirements, using as a reference unit (=1 LSU) a dairy cow producing 3000 kg of milk annually, without additional concentrated foodstuffs (EC, 2008).

Table 3. Summary of the PaSim eco-physiological parameters considered in this study. For each parameter, three sets of values are reported: two from the calibration obtained in previous studies (P_temp, Oensingen and P_perm, Laqueuille, after Calanca et al., 2007 and Vuichard et al., 2007b) and one from the calibration performed in this study (P_redef). Greyed areas indicate the recalibrated parameters.

Parameters		Values			Description
Name	Unit	P_temp (Oensingen)	P_perm (Laqueuille)	P_redef	
Fractional C content of root structural dry matter ($f_{C,rt}$)	kg C kg^{-1} DM	0.5	0.43	0.43	These parameters multiply the root and shoot growth rates, respectively, to obtain the C substrate variation.
Fractional C content of shoot structural dry matter ($f_{C,sh}$)	kg C kg^{-1} DM	0.39	0.435	0.435	
Parameter of the fractional N content of new plant structural dry matter (f_{nref})	kg N kg^{-1} DM	0.022	0.018	0.018	This parameter is used to derive the nitrogen concentration of newly produced structural dry matter.
Maximum canopy height	m	0.35	0.707	0.707	It determines the canopy height to calculate the latent and sensible heat fluxes from the canopy and the soil surface.
Shoot turnover rate at 20 °C (γ_s)	d^{-1}	0.03	0.012	0.012	They represent the leaf and root life-spans at a constant temperature, used to calculate the flow of plant residue.
Root turnover rate at 20 °C (γ_r)	d^{-1}	0.05	0.048	0.048	
Fraction of fibres in ingested ears (NDF_{ear})	-	0.8	0.742	0.742	These parameters represent the proportion of fibre (*NDF*) in the ingested tissues (ear, lamina, sheath/stem).
Fraction of fibres in ingested blades (NDF_{lam})	-	0.6	0.542	0.542	
Fraction of fibres in ingested stems and sheaths (NDF_{stem})	-	0.7	0.642	0.642	
Maximum plant N concentration ($F_{N,max}$)	kg N kg^{-1} DM	0.045	0.03	0.03	This parameter limits N absorption by plant.

Digestible neutral detergent fibres of leaf blades - age 1 ($DNDF_{lam1}$)	kg digestible fibres kg^{-1} fibres	0.92	0.91	0.91	These parameters influence the daily amount of digestible neutral detergent fibre (*DNDF*) from different plant components (ear, lamina and sheath/stem) in the animal's intake, depending on the age of tissues (four classes).
Digestible neutral detergent fibres of leaf blades - age 2 ($DNDF_{lam2}$)	kg digestible fibres kg^{-1} fibres	0.82	0.77	0.77	
Digestible neutral detergent fibres of leaf blades – age 3 (DNDFlam3)	kg digestible fibres kg^{-1} fibres	0.76	0.63	0.63	
Digestible neutral detergent fibres of leaf blades - age 4 (DNDFlam4)	kg digestible fibres kg^{-1} fibres	0.74	0.35	0.35	
Digestible neutral detergent fibres of stems and leaf sheaths – age 1 (DNDFstem1)	kg digestible fibres kg^{-1} fibres	0.84	0.92	0.92	
Digestible neutral detergent fibres of stems and leaf sheaths – age 2 ($DNDF_{stem2}$)	kg digestible fibres kg^{-1} fibres	0.65	0.79	0.79	
Digestible neutral detergent fibres of stems and leaf sheaths – age 3 ($DNDF_{stem3}$)	kg digestible fibres kg^{-1} fibres	0.53	0.66	0.66	
Digestible neutral detergent fibres of stems and leaf sheaths – age 4 ($DNDF_{stem4}$)	kg digestible fibres kg^{-1} fibres	0.5	0.4	0.4	

Digestible neutral detergent fibres of ears - age 1 ($DNDF_{ears1}$)	kg digestible fibres kg^{-1} fibres	0.76	0.93	0.93	
Digestible neutral detergent fibres of ears - age 2 ($DNDF_{ears2}$)	kg digestible fibres kg^{-1} fibres	0.48	0.68	0.68	
Digestible neutral detergent fibres of ears - age 3 ($DNDF_{ears3}$)	kg digestible fibres kg^{-1} fibres	0.3	0.44	0.44	
Digestible neutral detergent fibres of ears - age 4 ($DNDF_{ears4}$)	kg digestible fibres kg^{-1} fibres	0.26	0.38	0.38	
Light-saturated leaf photosynthetic rate for reproductive stage (*pmco2rep*)	µmol C m^{-2} s^{-1}	22.6666	16.723	19.723	They represent the influence of developmental stage (the end of ear emergence marking the transition from the reproductive to the vegetative stage) on the light-saturated leaf photosynthetic rate (defined at standard conditions of temperature, atmospheric CO_2 concentration and plant nitrogen concentration), which is a component of the rate of canopy photosynthesis.
Light-saturated leaf photosynthetic rate for vegetative stage (*pmco2veg*)	µmol C m^{-2} s^{-1}	15	11.099	13.099	
Maximum specific leaf area (*slam*)	m^2 kg^{-1}	33.5	25	29	This is the maximum value of specific leaf area, defined as the ratio of leaf area to dry weight, used to derive canopy leaf area from leaf biomass.
Temperature dependence factor of the soil respiration (m_{fT})	-	2	2	0.7	It multiplies the temperature-dependent function[1] to estimate soil respiration.

[1]

$$f(T_a) = \begin{cases} \frac{(T_a - T_0)^{q_{fT}} \cdot (T_0' - T_a)}{(T_{ref} - T_0)^{q_{fT}} \cdot (T_0' - T_{ref})}, & T_0 \le T_a \le T_0' \\ 0 & otherwise \end{cases}$$

where T_a (°C) is air temperature; T_0 (°C), T_0' (°C), T_{ref} (°C) are, respectively, the base air temperature, the ceiling air temperature at which processes cease, and reference air temperature at which the maximum rate of respiration occurs; q_{fT} (unitless) is a shape parameter. Reference values for soil respiration are: T_0=0 °C, T_0'=45 °C, T_{ref}=20 °C, q_{fT}=2.

Table 4. Model performance measurement indices.

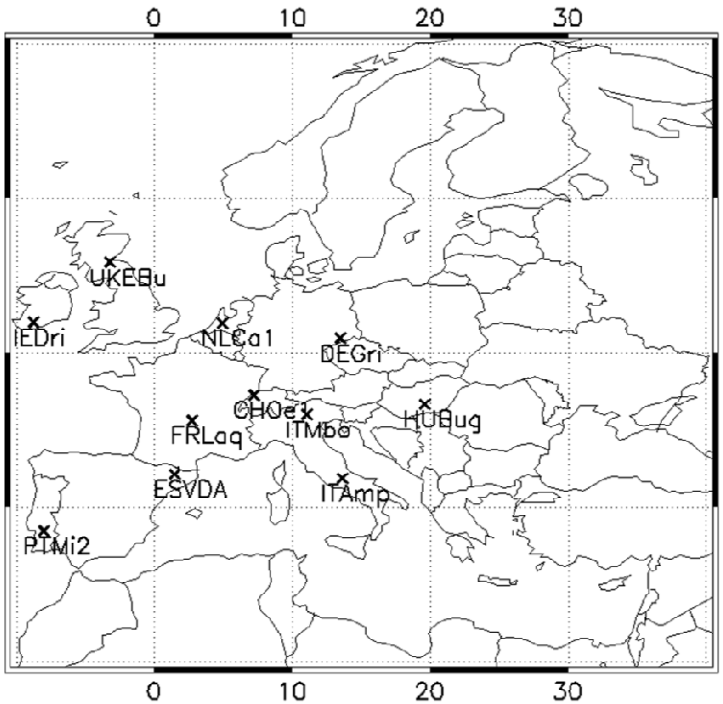
Performance measure	Equation	Unit	Value range and purpose	Reliability	
				criterion	source
Coefficient of determination (R^2) of the linear regression estimates versus measurements (Addiscott and Whitmore, 1987)	$\mathbf{R}^2 = \frac{\sum_{i=1}^{n}(\mathbf{P}_i - \mathbf{O}_i)\cdot(\mathbf{O}_i - \overline{\mathbf{O}})}{\sqrt{\sum_{i=1}^{n}(\mathbf{P}_i - \overline{\mathbf{P}})^2 \cdot \sum_{i=1}^{n}(\mathbf{O}_i - \overline{\mathbf{O}})^2}}$	-	0 (absence of fit of the regression line) to 1 (perfect fit of the regression line): the closer the values are to 1, the better the model	>0.8	De Jager (1994)
IA, index of agreement (Willmott and Wicks, 1980)	$\mathbf{IA} = \mathbf{1} - \frac{\sum(\mathbf{P}_i - \mathbf{O}_i)^2}{\sum_{i=1}^{n}(\lvert \mathbf{P}_i - \overline{\mathbf{O}} \rvert + \lvert \mathbf{O}_i - \overline{\mathbf{O}} \rvert)^2}$	-	0 (absence of agreement) to 1 (perfect agreement): the closer the values are to 1, the better the model	>0.8	De Jager (1994)
RMSE, root mean square error (Fox, 1981)	$\mathbf{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}(\mathbf{P}_i - \mathbf{O}_i)^2}{\mathbf{n}}}$	unit of the variable	0 (optimum) to positive infinity: the smaller RMSE, the better the model performance	-	-
MB, mean bias (Addiscott and Whitmore, 1987)	$\mathbf{MB} = \frac{\sum_{i=1}^{n}(\mathbf{P}_i - \mathbf{O}_i)}{\mathbf{n}}$	unit of the variable	negative infinity (underestimation) to positive infinity (overestimation): the closer the values are to 0, the better the model	-	-
ME, modelling efficiency (Nash and Sutcliffe, 1970)	$\mathbf{ME} = \mathbf{1} - \frac{\sum_{i=1}^{n}(\mathbf{P}_i - \mathbf{O}_i)^2}{\sum_{i=1}^{n}(\mathbf{O}_i - \overline{\mathbf{O}})^2}$	-	negative infinity to 1 (optimum): the closer the values are to 1, the better the model	>0.5	Moriasi et al. (2007)

Table 5. Model performances across grassland sites (ID as in Table 1) based on different evaluation indices (as in Table 4) calculated on weekly aggregated data.

Site ID	GPP					RECO					ET				
	BIAS	RMSE	IA	ME	R^2	BIAS	RMSE	IA	ME	R^2	BIAS	RMSE	IA	ME	R^2
	g C week^{-1}.m^{-2}	g C week^{-1}.m^{-2}	-	-	-	g C week^{-1}.m^{-2}	g C week^{-1}.m^{-2}	-	-	-	mm week^{-1}	mm week^{-1}	-	-	-
CHOe1	-6.07	15.83	0.91	0.69	0.73	-10.35	12.90	0.88	0.58	0.88	-1.69	3.14	0.96	0.84	0.891
ITMbo	-2.22	10.89	0.96	0.85	0.86	0.89	12.22	0.93	0.59	0.86	-1.26	2.67	0.97	0.89	0.926
DEGri	-0.10	9.13	0.95	0.81	0.83	-1.53	11.74	0.88	0.44	0.63	1.23	3.45	0.92	0.60	0.827
UKEBu	-1.85	10.53	0.95	0.79	0.81	-2.88	10.44	0.91	0.68	0.72	0.66	3.95	0.82	0.37	0.465
IEDri	5.03	13.40	0.93	0.66	0.83	2.27	12.58	0.91	0.61	0.70	-1.84	2.65	0.94	0.76	0.887
HUBug	9.24	16.79	0.83	-0.02	0.64	7.95	15.12	0.80	-0.59	0.70	1.74	6.03	0.86	0.24	0.645
ITAmp	-9.06	16.18	0.74	0.10	0.40	-9.03	14.44	0.61	-0.07	0.39	-2.31	5.08	0.88	0.57	0.676
ESVDA	0.94	6.59	0.92	0.58	0.77	1.43	5.04	0.91	0.52	0.82	0.78	2.82	0.95	0.73	0.864
FRLq1	-2.94	10.07	0.96	0.85	0.87	-2.87	11.42	0.93	0.65	0.80	-4.12	5.93	0.86	0.47	0.728
FRLq2	5.35	14.84	0.93	0.59	0.85	4.51	13.66	0.90	0.35	0.84	-1.49	3.97	0.94	0.75	0.799
PTMi2	-3.89	11.21	0.82	0.47	0.53	-2.14	8.39	0.78	0.43	0.46	3.79	8.21	0.61	-2.04	0.316
NLCa1	4.27	14.04	0.92	0.57	0.80	6.55	16.23	0.88	0.27	0.76	-1.18	2.87	0.96	0.82	0.888
Site ID	NEE					SWC					SoilT				
	BIAS	RMSE	IA	ME	R^2	BIAS	RMSE	IA	ME	R^2	BIAS	RMSE	IA	ME	R^2
	g C week^{-1} m^{-2}	g C week^{-1} m^{-2}	-	-	-	%	%	-	-	-	°C	°C	-	-	-
CHOe1	-4.10	12.27	0.80	0.25	0.43	5.04	7.78	0.69	0.21	0.72	-3.19	4.06	0.91	0.71	0.91
ITMbo	3.11	17.13	0.48	-0.92	0.02	-15.84	16.89	0.41	-5.20	0.26	-0.80	3.88	0.94	0.64	0.89
DEGri	-1.43	7.72	0.83	0.44	0.50	-4.24	6.23	0.83	0.50	0.80	-3.63	4.35	0.92	0.55	0.94
UKEBu	-1.03	8.90	0.74	0.21	0.31	1.69	5.36	0.75	0.48	0.68	-3.06	4.00	0.87	0.34	0.82
IEDri	-2.76	8.03	0.81	0.25	0.47	-1.60	2.64	0.82	0.49	0.72	-1.24	1.73	0.94	0.71	0.93
HUBug	-1.29	6.27	0.84	0.45	0.52	7.10	8.44	0.55	-1.34	0.34	-0.93	2.06	0.98	0.92	0.96
ITAmp	0.19	9.81	0.72	0.14	0.27	3.52	7.55	0.70	0.21	0.38	-0.94	5.96	0.90	0.39	0.77
ESVDA	0.49	6.04	0.65	-0.81	0.19	4.47	6.05	0.68	-0.14	0.48	1.95	2.46	0.97	0.88	0.96

FRLq1	0.08	9.88	0.76	0.32	0.35	4.45	6.06	0.60	-0.57	0.29	-1.36	2.42	0.96	0.85	0.911
FRLq2	-0.83	9.34	0.76	0.34	0.37	5.03	7.69	0.60	-0.24	0.29	-1.75	2.53	0.95	0.79	0.905
PTMi2	1.75	7.90	0.68	-0.51	0.25	0.28	8.83	0.61	0.39	0.78	-1.45	2.86	0.97	0.91	0.944
NLCa1	2.29	10.68	0.68	-0.79	0.28	-16.50	19.98	0.49	-1.67	0.29	NA	NA	NA	NA	NA

Figures:



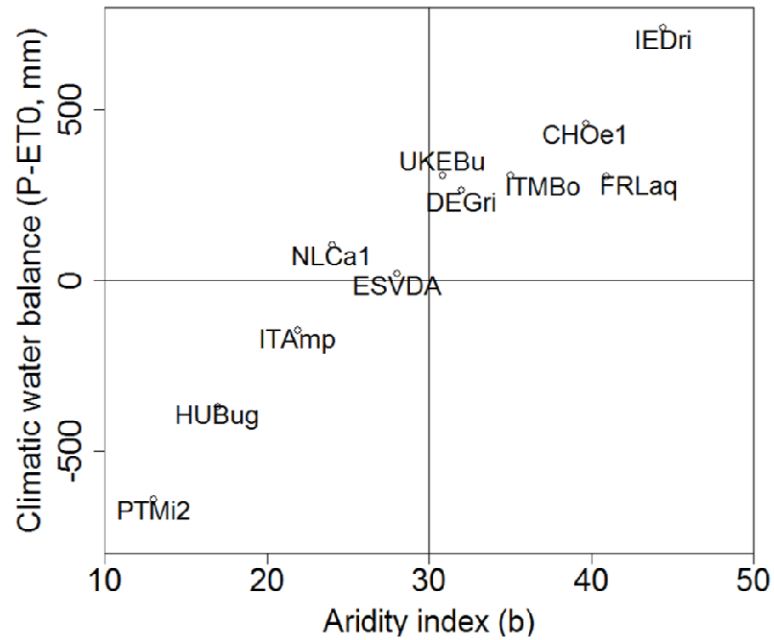


Fig 1. Geographic location (left) and classification (right) of grassland sites (ID as in Table 1) with respect to two indices (climatic water balance and De Martonne-Gottmann aridity index) of water availability. For the aridity index b, (De Martonne, E, 1942), the following range limits discriminate between thermo-pluviometric conditions associated with aridity gradients: $b<5$: extreme aridity; $5\leqslant b\leqslant 14$: aridity; $15\leqslant b\leqslant 19$: semi-aridity; $20\leqslant b\leqslant 29$: sub-humidity; $30\leqslant b\leqslant 59$: humidity; $b>59$: strong humidity (Diodato and Ceccarelli, 2004).

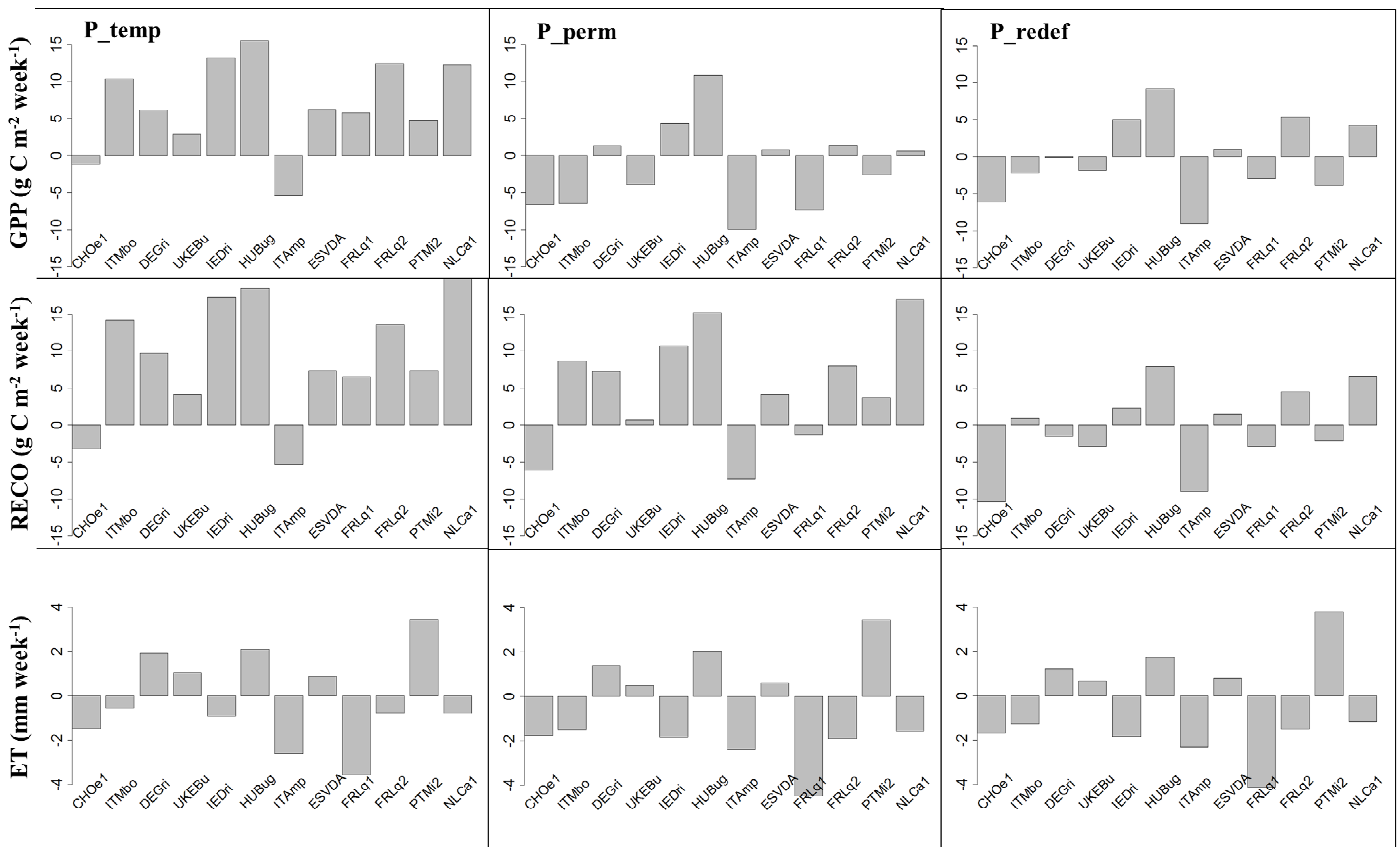


Fig 2. The mean bias of weekly values of GPP, RECO (g C m^{-2} $week^{-1}$) and ET (mm $week^{-1}$), using three sets of parameter values: for temporary grasslands as established at Oensingen, Switzerland (P_temp, left), for permanent grasslands as established at Laqueuille, France (P_perm, middle), and the common set established in this study (P_redef, right).

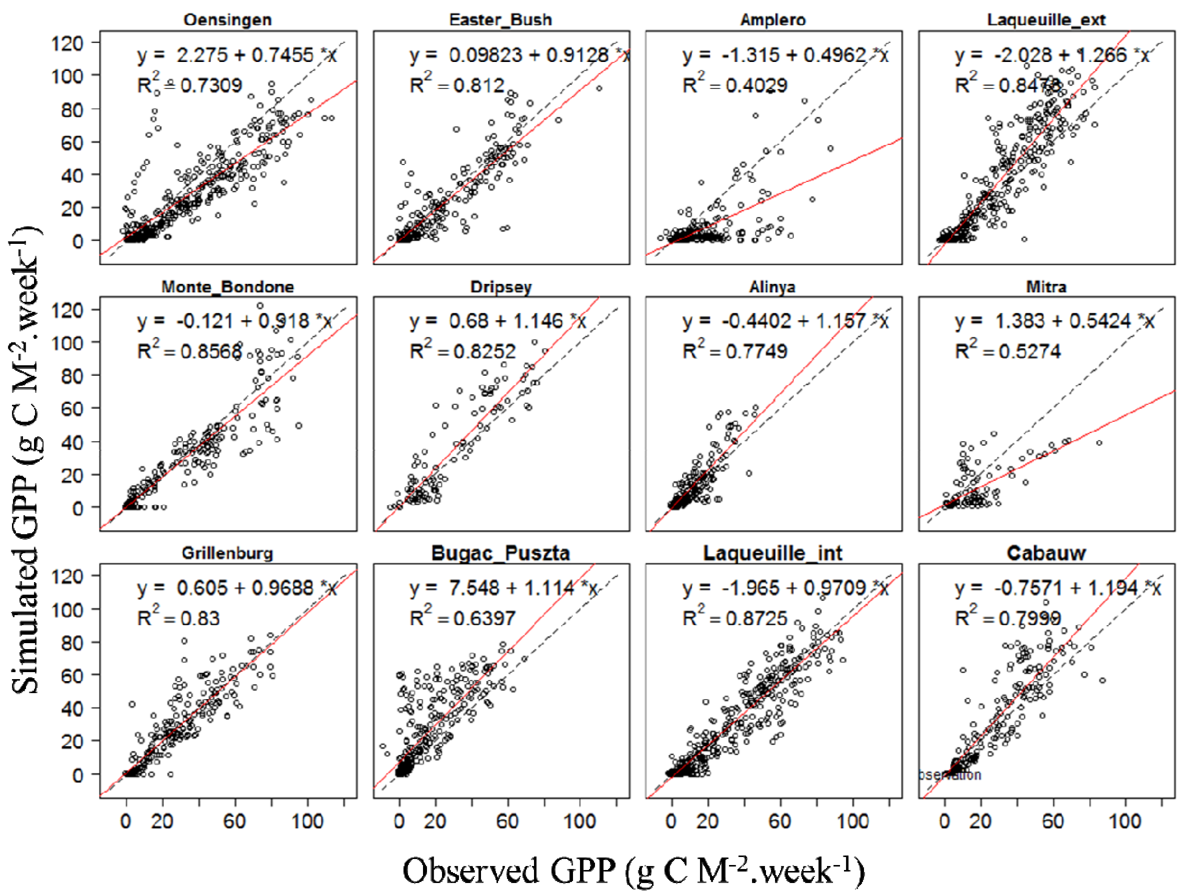


Fig. 3. Scatter plots of simulated versus measured GPP weekly values.
The dashed line is the 1:1 line. The solid red line represents the regression equation. The goodness-of-fit R^2 is the coefficient of determination of the regression equation.

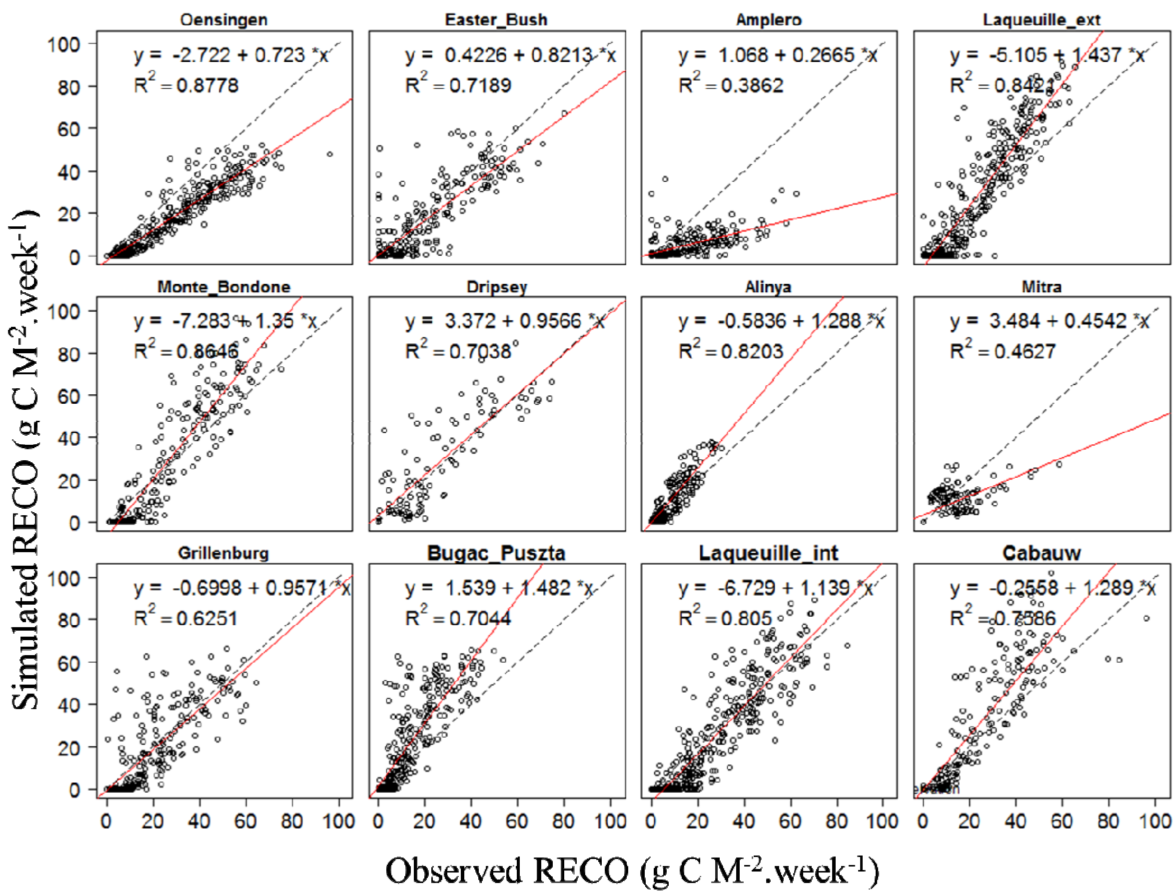


Fig. 4. Scatter plots of simulated versus measured RECO weekly values.
The dashed line is the 1:1 line. The solid red line represents the regression equation. The goodness-of-fit R^2 is the coefficient of determination of the regression equation.

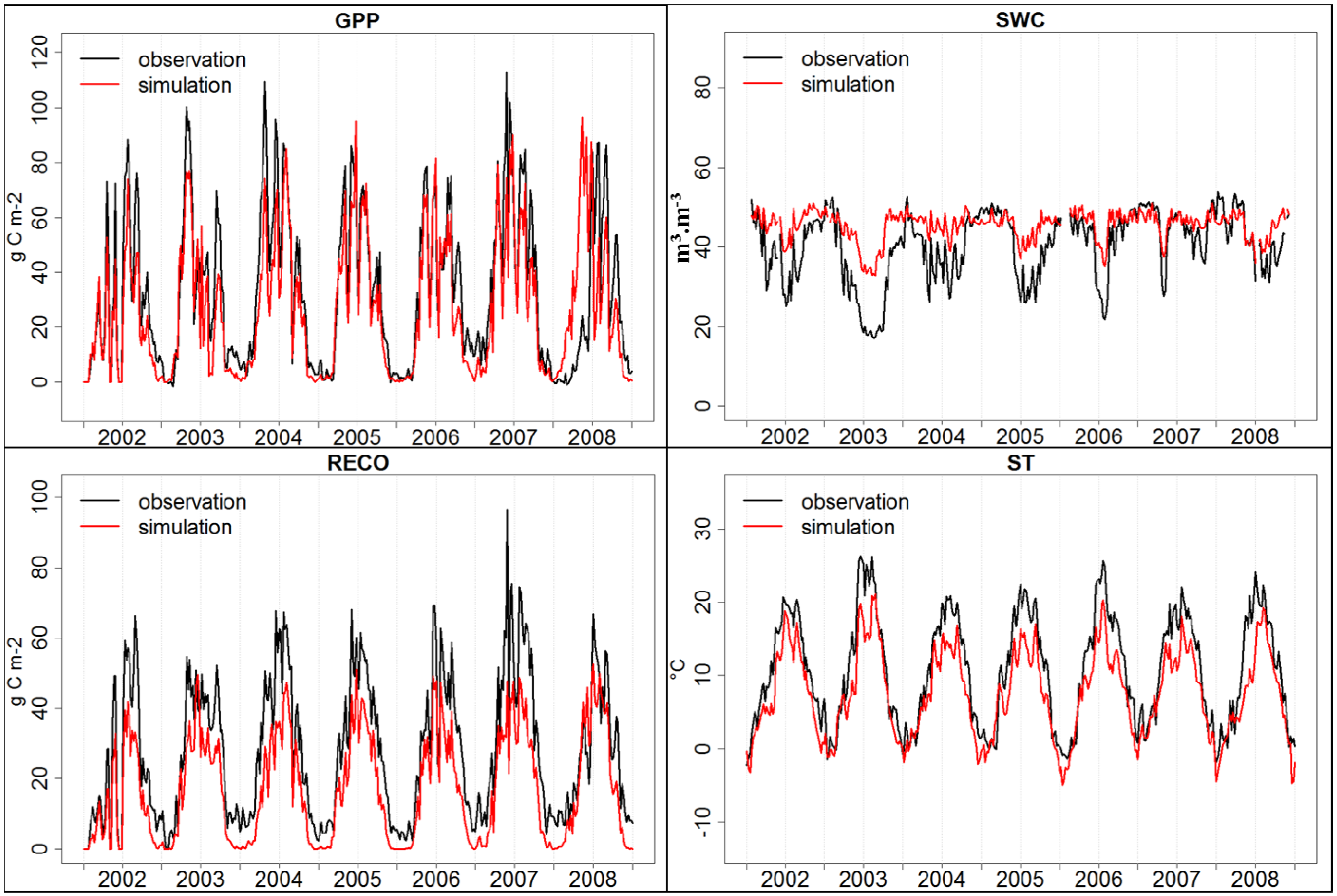


Fig. 5. The variability of simulated GPP, RECO, soil temperature (ST) and soil water content (SWC) against the observed data for Oensingen (Switzerland) weekly values.

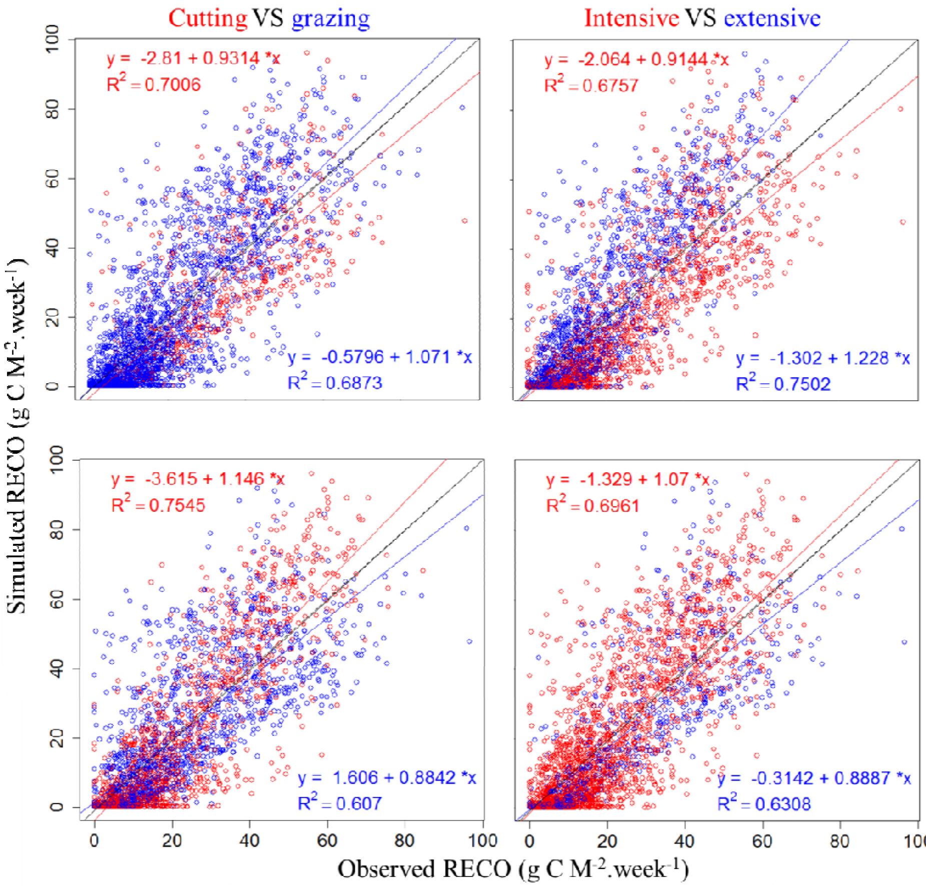


Fig. 6. Scatter plots of simulated with the redefined parameters versus measured RECO values (g C M^{-2}.$week^{-1}$) according to site characteristics and management practices. The goodness-of-fit R^2 is the coefficient of determination of the regression equation.

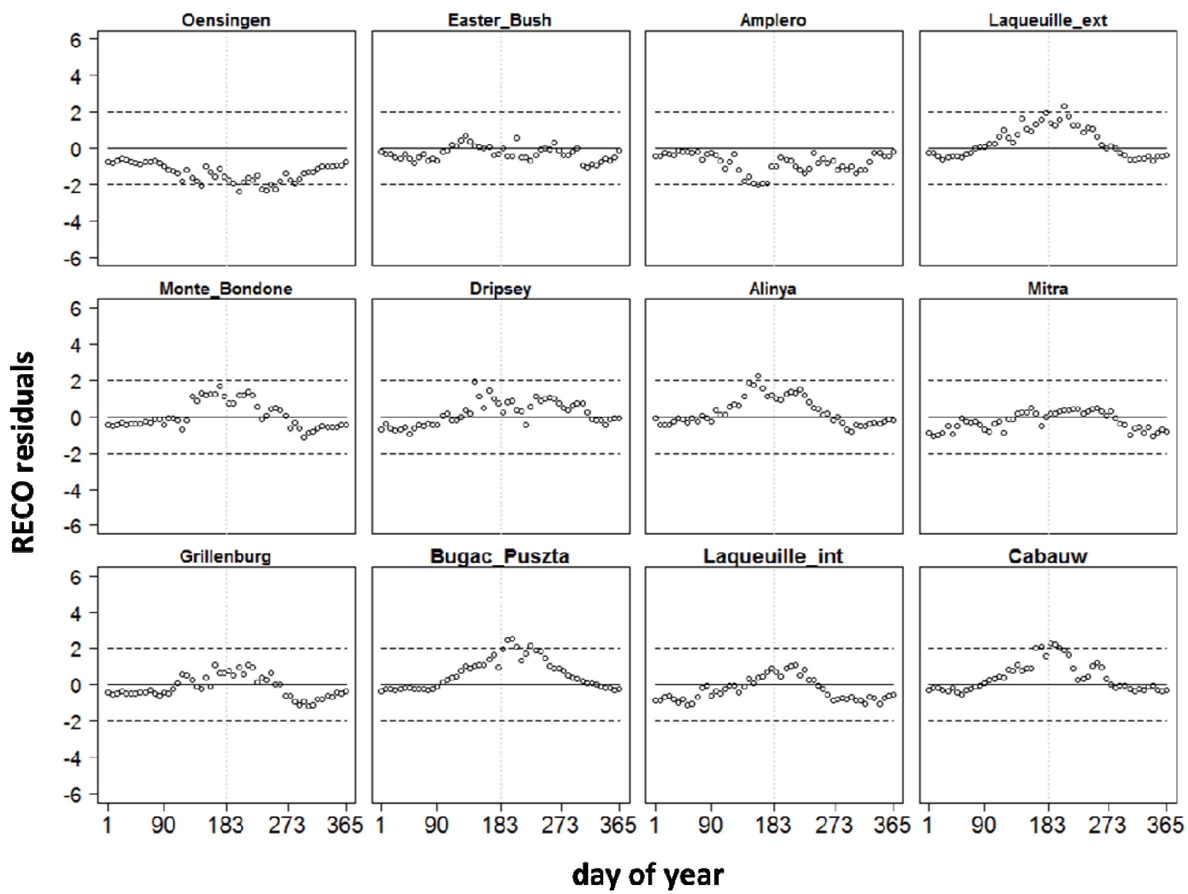


Fig. 7. Normalized residuals of RECO plotted versus day of year for each grassland site. Each point is the average of residuals for all years divided by the standard deviation. Horizontal lines represent the 95% confidence limits.

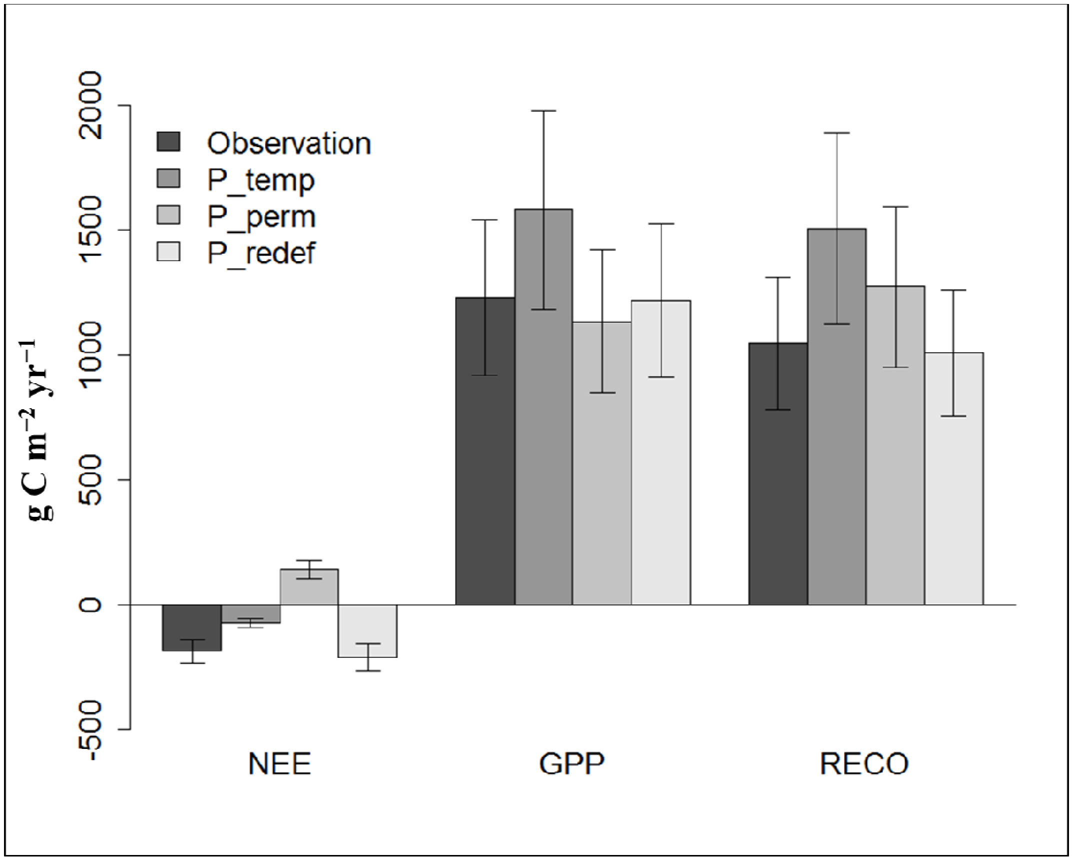


Fig. 8. Comparison of observed and simulated carbon fluxes (NEE, GPP, RECO; g C m^{-2} yr^{-1}) with different parameter values (default for Oensingen (P_temp) and Laqueuille (P_perm), and new parameter values (P_redef)). The values are averaged across all grassland sites.

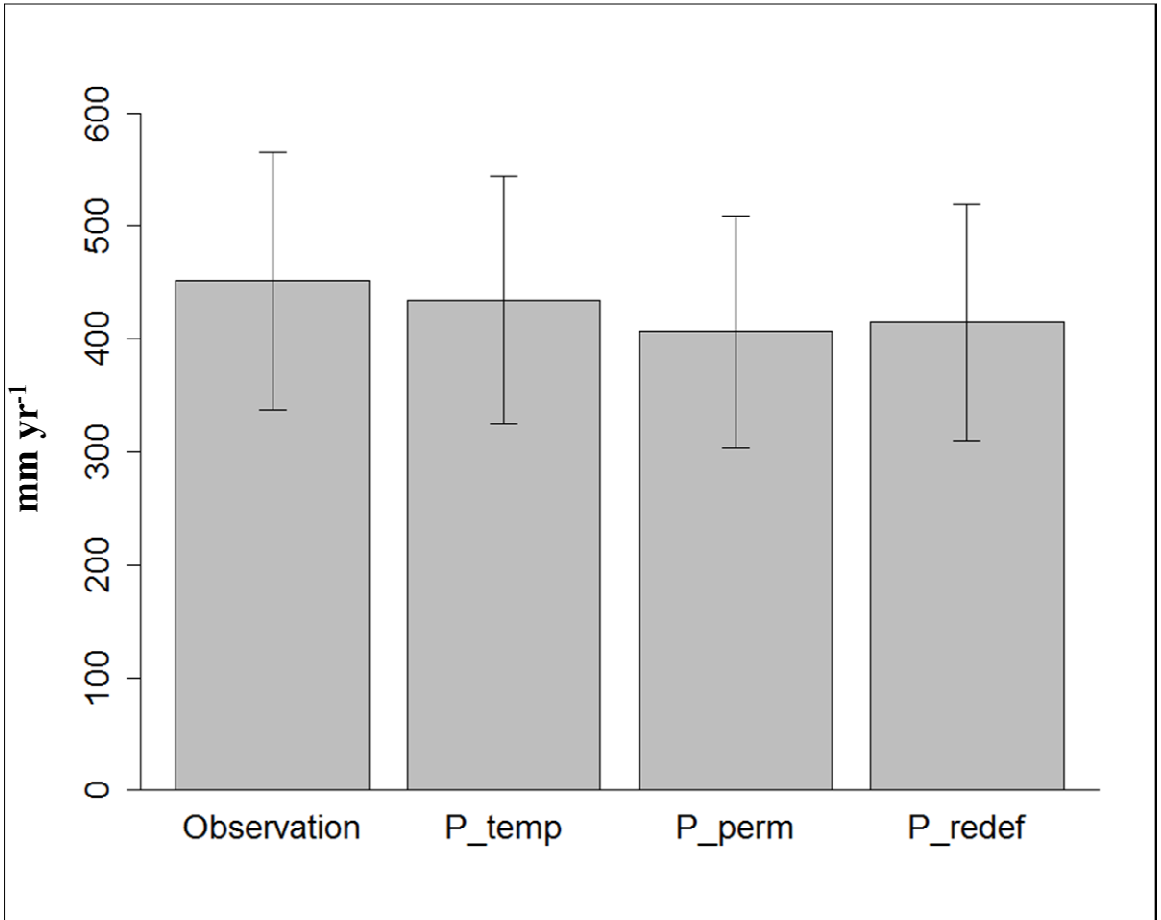


Fig. 9. Comparison of observed and simulated water fluxes (mm yr^{-1}) with different parameter values (default for Oensingen (P_temp) and Laqueuille (P_perm), and new parameter values (P_redef)). The values are averaged across all grassland sites.

Appendix G: support figures

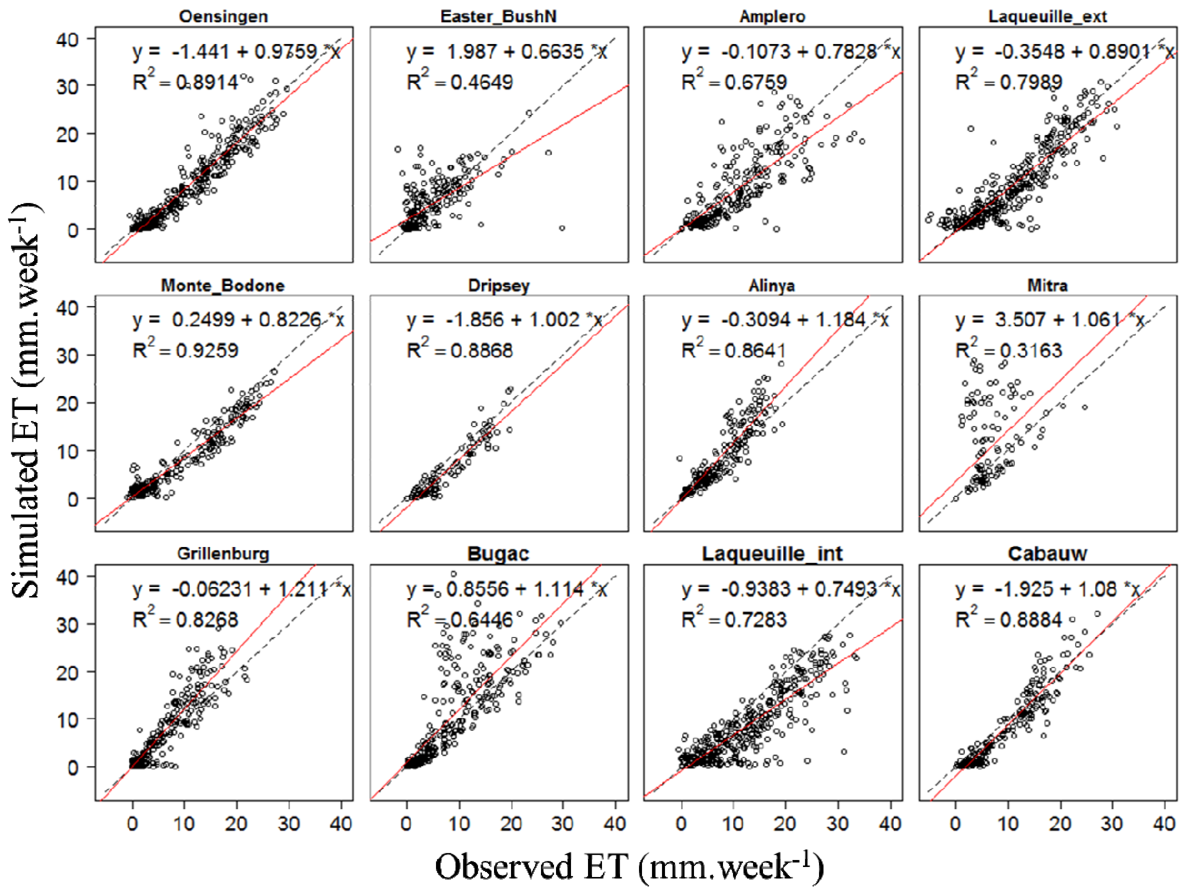


Fig. A1. Scatter plots of simulated versus measured ET weekly values.

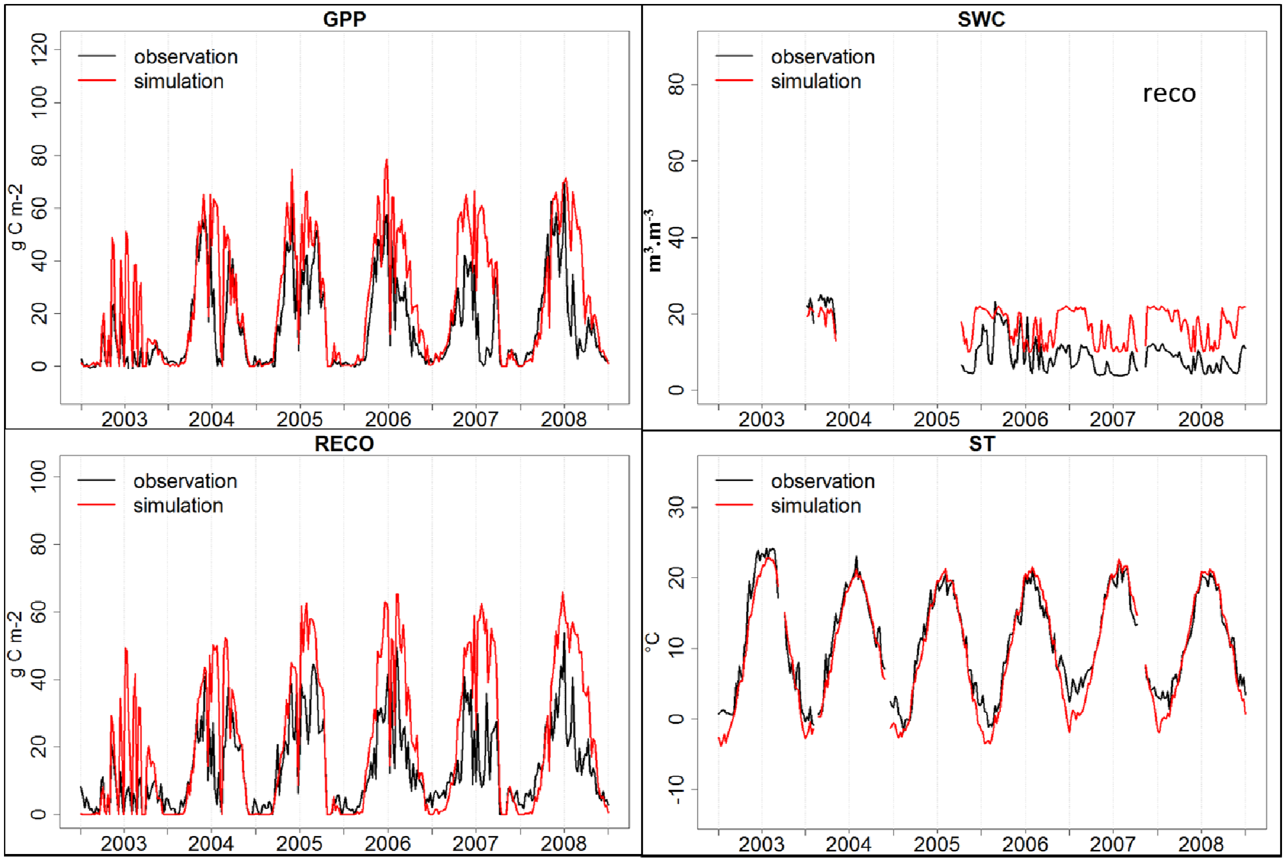


Fig. A2. The variability of simulated GPP, RECO, soil temperature (ST) and soil water content (SWC) against the observed data for Bugac-Puszta (Hungary) weekly values.

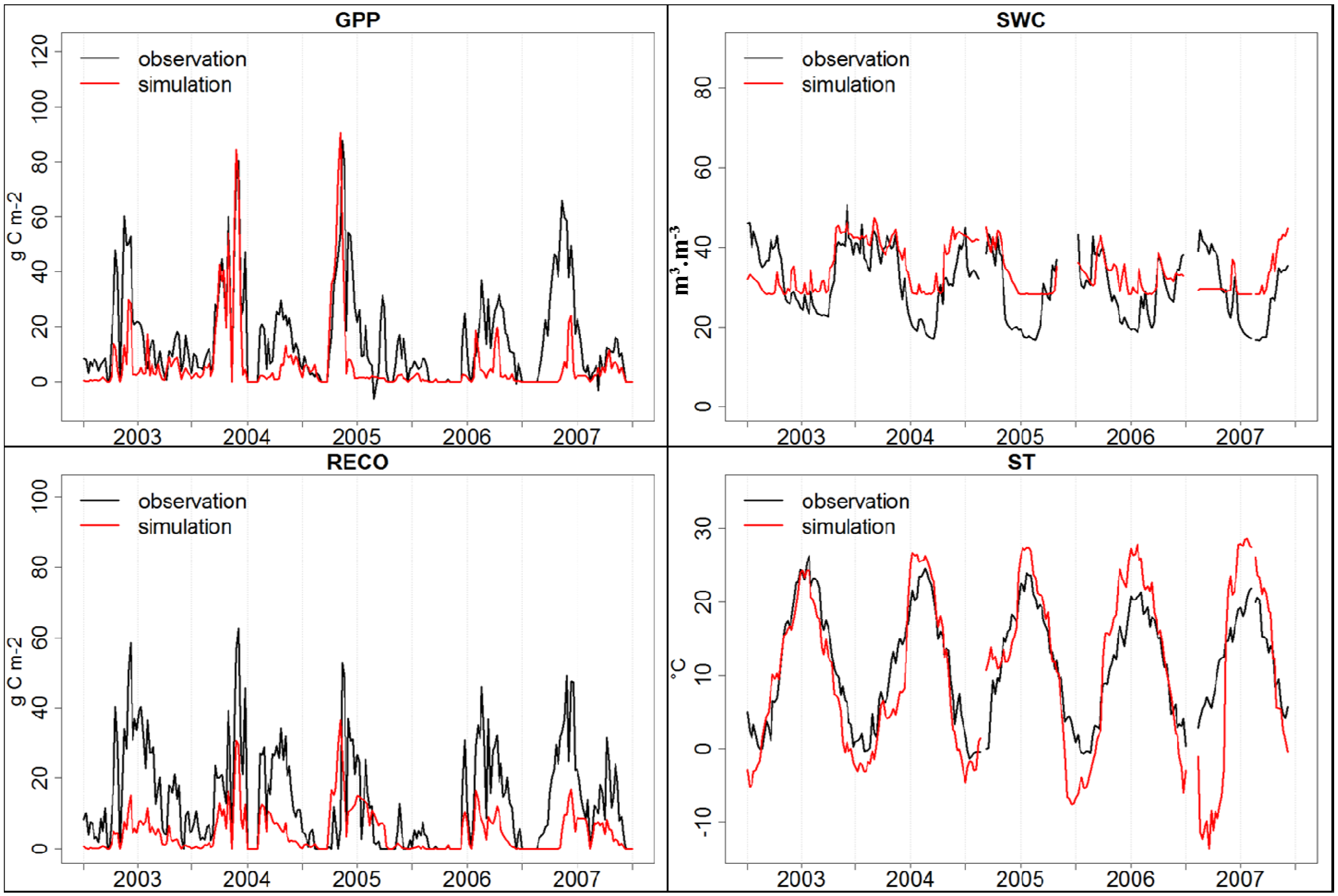


Fig. A3. The variability of simulated GPP, RECO, soil temperature (ST) and soil water content (SWC) against the observed data for Amplero (Italy) weekly values.

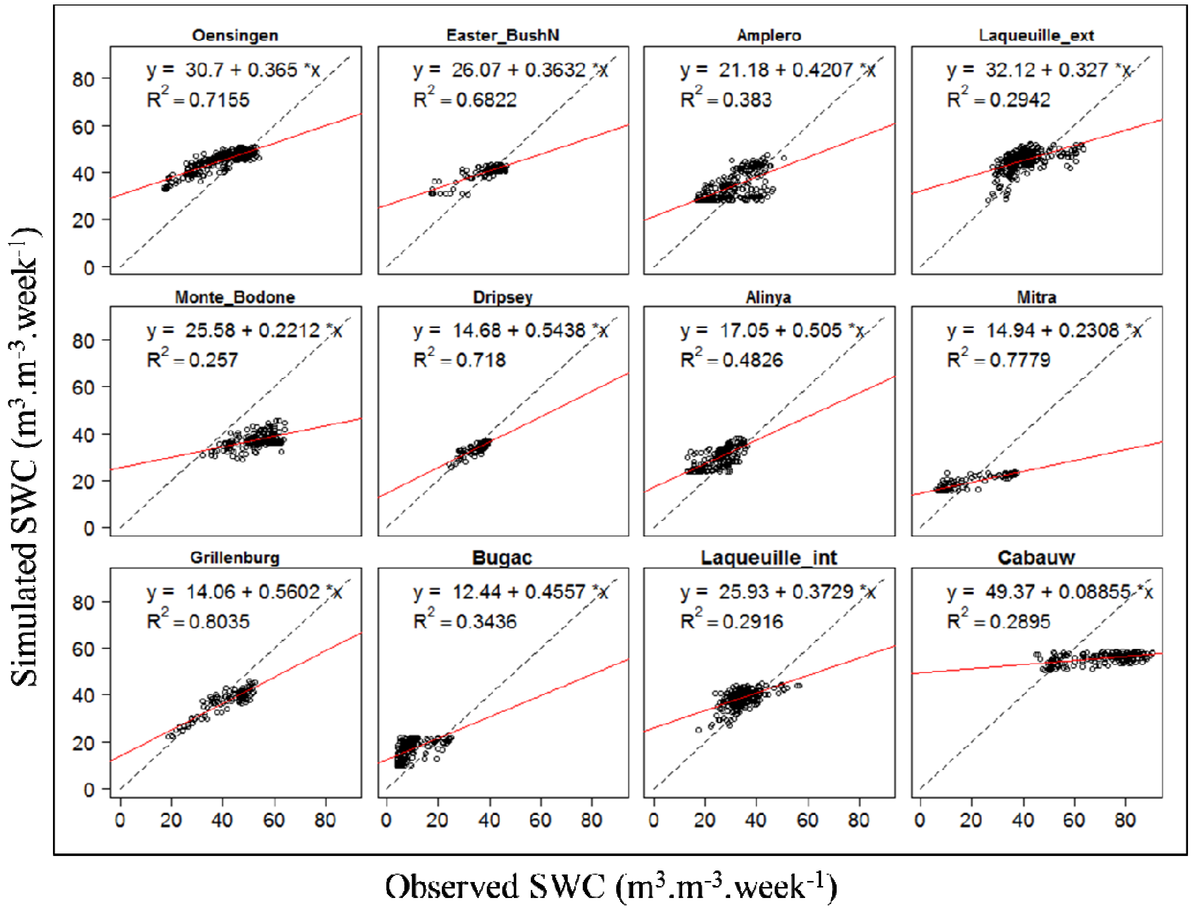


Fig. A4. Scatter plots of simulated versus measured soil water content in the top 10 centimetres.

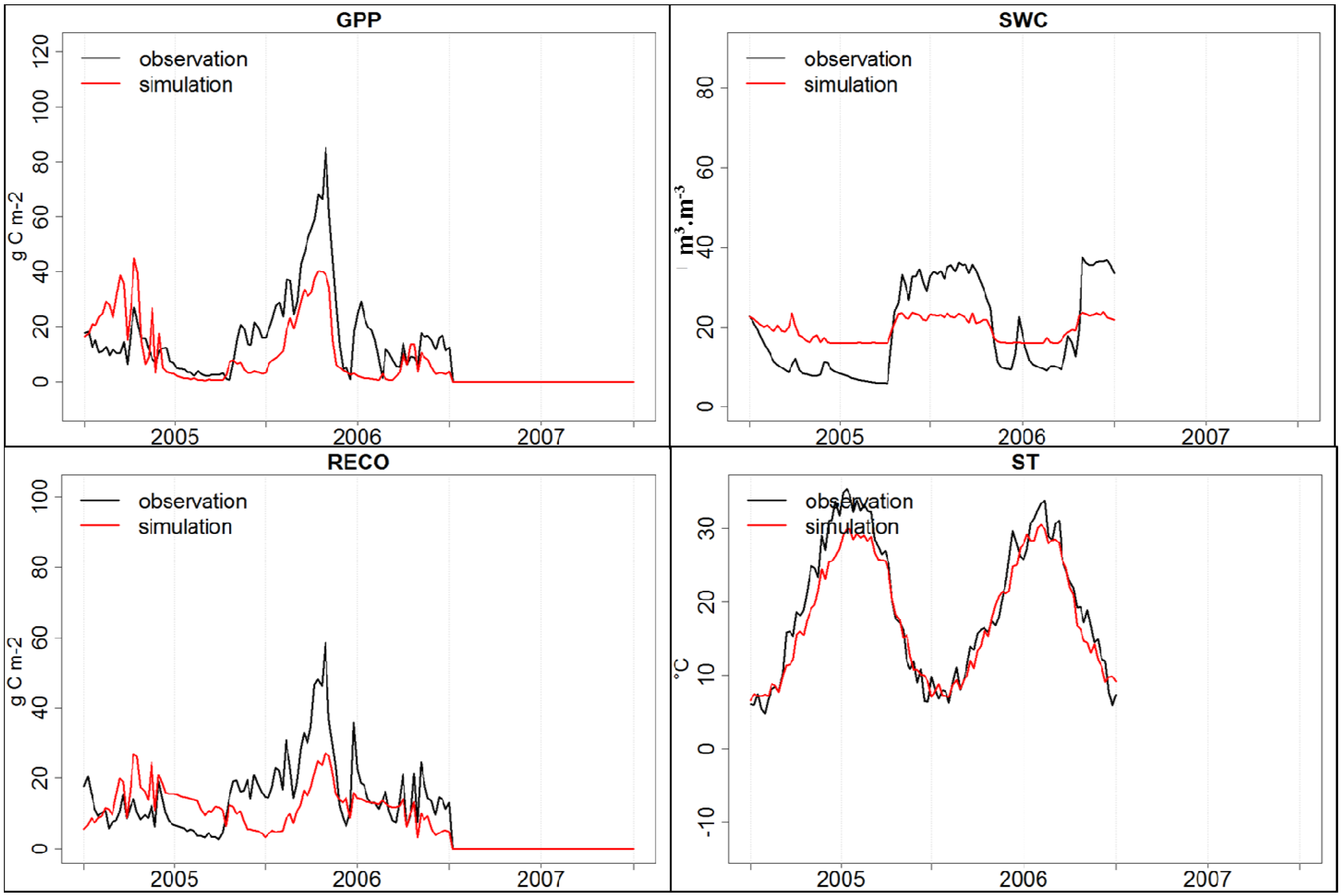


Fig. A5. The variability of simulated GPP, RECO, soil temperature (ST) and soil water content (SWC) against the observed data for Mitra (Portugal) weekly values.