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The Pasture Simulation model – evaluation of plant acclimatory effects on grassland systems in France

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Abstract: The temperature responses of plant photosynthesis and respiration observed on single-plant species can be assumed to occur at the scale of a grassland ecosystem (which is a dynamic and competitive associations of plants). Based on the model for a single, fully expanded leaf as derived from experimental evidence and to gain insights into acclimatory and modulatory effects of growth temperature, we have: 1) improved a complex soil-vegetation-management model of grasslands, PaSim (Pasture Simulation model), and 2) evaluated it on multi-year datasets of plant biomass and C-water-energy fluxes in managed grassland systems. Illustrative results are presented for the French grassland site of Laqueuille, by comparing two grazing management treatments: high animal stocking rate and high nitrogen fertilisation (intensive) and low animal stocking rate with no fertilization (extensive). Model performances (reflected by mean square error, index of agreement and correlation coefficient) showed that accounting for plant acclimatory effects may help improving water and respiratory fluxes. However the pattern of results is generally complex (e.g. differences between management options), and a substantiation of results is required by assessing model performances on a range of sites and contrasting conditions (as listed in the paper).

Keywords: Grassland; Modelling; Plant acclimation

1. INTRODUCTION

The process-based Pasture Simulation model (PaSim, <https://www1.clermont.inra.fr/urep/modeles/pasim.htm>) was originally developed by Riedo et al. (1998) to simulate biogeochemical cycles in managed grasslands (clover-ryegrass swards). PaSim includes both grazing and cutting management options and provide a mechanistic view of the grassland ecosystem. It has been widely tested and applied to a large range of environmental conditions. For instance, it has been evaluated under conditions of water stress (e.g. Ben Touhami et al., 2015) and employed in climate change impact studies (Graux et al., 2013; Vital et al., 2013), in support of climate change mitigation (Graux et al., 2012) and vulnerability assessments (Lardy et al., 2014, 2015), and in the analysis of carbon and water cycles (Ma et al., 2015; Sándor et al., 2016). The model was recently improved in how it simulates plant photosynthesis and respiration so as to account for acclimatory and modulatory effects of growth temperature (Villalobos et al., 2015). An enhanced version of PaSim (MMS) was then evaluated in a comparative fashion against the original version (EMS) on multiple outputs under a variety of conditions in France, while a comprehensive analysis of the detailed temperature responses of photosynthesis and respiration lies outside the scope of the present study.

2. ACCLIMATION TO TEMPERATURE OF PHOTOSYNTHESIS AND RESPIRATION IN GRASSLANDS

We refer here to the Farquhar scheme of the photosynthetic device of plants as represented in PaSim (after Farquhar and von Caemmerer, 1982), where the maximum photosynthetic rate is calculated from the maximum rate at 20 °C, modulated by functions of plant nitrogen and carbon, a function of the CO₂-temperature interaction (in turn depending on the RuBisCO activity and the light-saturated photosynthesis), and a temperature factor. In the original form, the latter does not account for acclimation of plant physiological processes to varying growth temperatures as optimum temperature is set to a constant value all over the whole simulation. This approach was improved based on experimental evidence suggesting that optimum temperature can be estimated at any day via a linear regression on the average growth temperature calculated over a range of x previous days (taking $x=20$ days as a reference). The modulation of maximum photosynthesis was achieved as a function of the air temperature with an exponential sine function, where a common pattern is a bell-shape curve sustaining a plateau of maximum activity (after Malo, 2002). In the case of plant respiration, thermal acclimation was obtained by representing the linear decrease of maximum respiration with increasing growth temperature. Reference parameter values for the thermal acclimation responses were obtained from a series of independent experiments (Zaka et al., 2016).

3. GRASSLAND DATASETS

Table 1 summarizes the full set of grassland sites, years of available data and simulated outputs of this study. Grassland system 1 refers to a grassland manipulation experiment as from the French project VALIDATE (<http://presse.inra.fr/en/Resourcess/Press-releases/projet-Validate>). Grassland systems 2 and 3 refer to data provided by a long-term observational system, belonging to the SOERE-ACBB (Long-term Environmental Research Observation and Experimentation facility for Agro-ecosystems, Biogeochemical Cycles and Biodiversity) platform (<http://www.soere-acbb.com>), whose aim is to analyse the response of permanent grasslands to modifications of management practices. Full

model evaluation is ongoing. Section 4 anticipates some results for the site of Laqueuille.

Table 1. Locations, years of available data and evaluated variables.

Grassland system / Location	Years of available data	Evaluated variables	Notes
1 - Saint Genès-Champanelle (45° 43' N, 03° 01' E, 880 m a.s.l.)	2009-2012	Harvested biomass, soil temperature at 0.1 m, soil water content at 0.3 m, nitrogen fraction in harvested biomass	Management: - Cut+: 4-6 cuts per year - Cut-: 2-4 cuts per year Manipulation: - C: precipitations for a reference period (1969-1999) and ambient air temperature - WD: simulated future climatic conditions for the period 2040-2060 (A1B, IPCC, 2007) - CX: precipitation reduction and heat-wave in C - WXD: precipitation reduction and heat-wave in WD
2 – Theix (45° 43' N, 03° 01' E, 880 m a.s.l.)	2005-2013	Harvested biomass, nitrogen fraction in harvested biomass	(Zwicke et al., 2013) Three cuts per year with different soil properties and botanical composition between block 1 and block 2 (http://www.soere-acbb.com/caracteristiques-2)
3 – Laqueuille (45° 38' N, 02° 44' E, 1040 m a.s.l.)	2002-2011	Gross primary production, net ecosystem exchange, ecosystem respiration, soil temperature at 0.1 m, soil water content 0.1 m	Intensive (1.6 animal ha ⁻¹ yr ⁻¹ and 210 kg N ha ⁻¹ yr ⁻¹) and extensive (1.6 animal ha ⁻¹ yr ⁻¹ without N fertilization) management options (http://www.soere-acbb.com/caracteristiques-2)

4. EVALUATION AT LAQUEUILLE (FRANCE): ILLUSTRATIVE RESULTS

For illustrative purpose, we present the evaluation of PaSim at Laqueuille, for which detailed data of carbon and water fluxes are available for a grassland submitted to two grazing and fertilization regimes (intensive and extensive, Table 1). Figure 1 shows the range of weather conditions investigated, in terms of aridity (De Martonne, 1942) and heat waves frequency (Confalonieri et al., 2010).

Model calibration was carried out for a set of influential parameters, which were modified within their plausible ranges (with generation of 1000 sets of values by using the random Latin hypercube method) to ensure realistic representation of a variety of outputs in each treatment by comparing the model predictions with observational data (full data set). The agreement between simulations and observations was evaluated by the inspection of time series graphs (fluctuations of the output variables over time), and numerically, through three performance metrics of model evaluation: mean square error (best, $0 \leq \text{MSE} < +\infty$, worst), index of agreement (worst, $0 \leq d \leq 1$, best) and correlation coefficient (worst, $-1 \leq r \leq 1$, best).

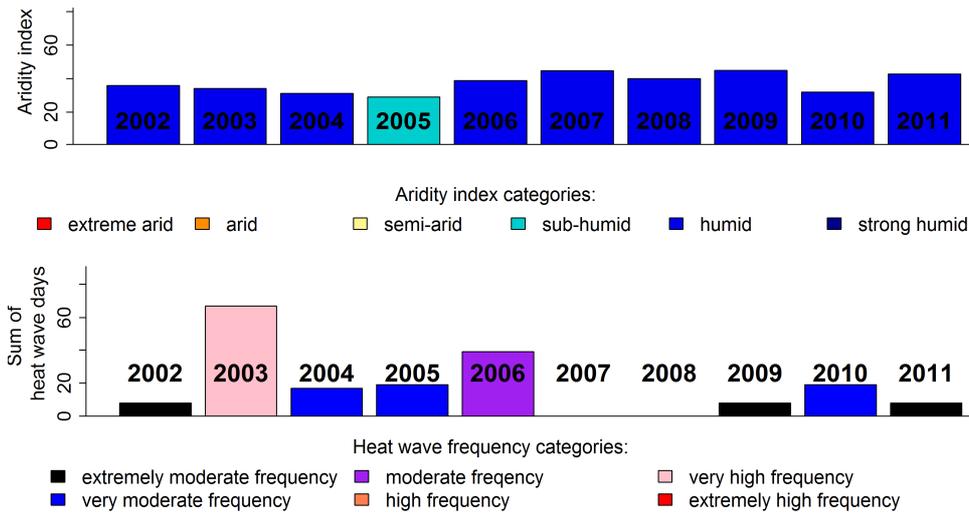


Figure 1. De Martonne aridity index (top) and heat wave days frequency (bottom) for different years at Laqueuille. The possibility to discriminate between thermo-pluviometric conditions associated with aridity (b) gradients is given by the range published by Diodato and Ceccarelli (2004): $b < 5$: extreme aridity; $5 \leq b < 14$: aridity; $15 \leq b < 19$: semi-aridity; $20 \leq b < 29$: sub-humidity; $30 \leq b < 59$: humidity; $b > 59$: strong humidity. The range limits of heat waves (hw) frequency are given by the number of the hw days as follows: $hw \leq 14$: extremely moderate frequency; $14 < hw \leq 28$: very moderate frequency; $28 < hw \leq 42$: moderate frequency; $42 < hw \leq 56$: high frequency; $56 < hw \leq 70$: very high frequency; $hw > 70$: extremely high frequency.

For illustrative purposes, the evaluation of actual evapotranspiration, gross primary production and ecosystem respiration is shown. Using weekly-aggregated data (after Ma et al., 2015 and Sándor et al., 2016), the performance of both EMS and MMS shows a quite complex pattern of results (Table 2). If simulated evapotranspiration was slightly improved with MMS on both managements (e.g. MSE from 37.54 to 36.32 and from 19.07 to 17.86 [g C m⁻² week⁻¹]² for intensive and extensive treatment, respectively), some improvements on gross primary productivity were only obtained with extensive management (e.g. MSE from 146.03 to 142.34 [g C m⁻² week⁻¹]²). The most considerable improvements were obtained with ecosystem respiration, where MSE lowered with both management options.

Table 2. Model performances based on different metrics calculated on weekly-aggregated values of actual evapotranspiration, gross primary productivity and ecosystem respiration at Laqueuille with two management options. EMS: existing modelling solution; MMS: modified modelling solution.

Actual evapotranspiration (mm week ⁻¹)				
Metrics	Management			
	Intensive		Extensive	
Observed mean	13.10		10.78	
	EMS	MMS	EMS	MMS
Simulated mean	8.81	9.04	8.58	8.87
Mean square error	37.54	36.32	19.07	17.86
Index of agreement	0.61	0.62	0.64	0.64
Correlation coefficient	0.85	0.85	0.88	0.88
Gross primary production (g C m ⁻² week ⁻¹)				
Metrics	Management			
	Intensive		Extensive	
Observed mean	35.55		29.01	
	EMS	MMS	EMS	MMS
Simulated mean	30.24	30.20	27.61	27.55
Mean square error	108.74	126.23	146.03	142.34
Index of agreement	0.63	0.64	0.58	0.61
Correlation coefficient	0.94	0.92	0.88	0.88

Ecosystem respiration (g C m ⁻² week ⁻¹)				
Metrics	Management			
	Intensive		Extensive	
Observed mean	29.32		22.96	
Simulated mean	EMS	MMS	EMS	MMS
Mean square error	23.87	24.21	23.58	19.97
Index of agreement	133.86	126.41	152.74	97.09
Correlation coefficient	0.56	0.57	0.52	0.61
	0.90	0.90	0.87	0.86

Figure 2 shows that using EMS may lead to distinct over-estimation of ecosystem respiration with extensive management (with peaks in the presence of frequent heat waves, i.e. years 2003 and 2006), while MMS approaches better observations.

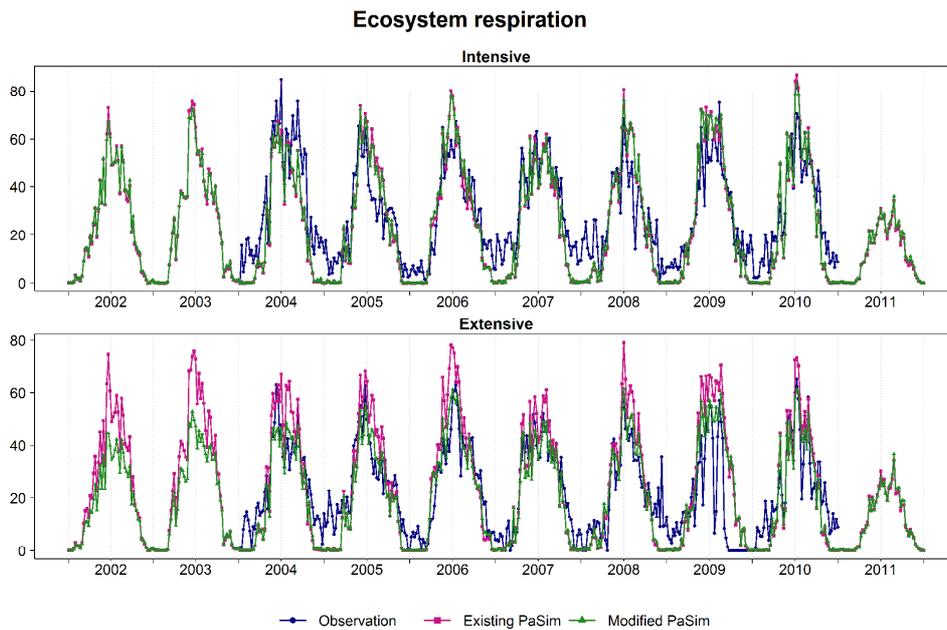


Figure 2. Simulated weekly-aggregated ecosystem respiration with both existing (EMS) and modified (MMS) PaSim against the observed data at Laqueuille with two management options.

5. CONCLUSION AND PERSPECTIVES

This study confirms the difficulty of estimating carbon and water fluxes from grassland systems, as already emerged from other studies (e.g. Ma et al., 2015; Sándor et al., 2016), and work is certainly still required to achieve satisfactory estimates. The new equations included in PaSim – accounting for plant acclimatory effects - improved model performances under certain circumstances in an upland grazed system of Central France. Where improvements were not obtained, overall simulations were not substantially different from those obtained with existing PaSim. For instance, the error in the estimate of gross primary productivity was only reduced with extensive management. Whether a smaller error amount was obtained with the estimates of ecosystem respiration, the response to plant acclimatory effects was more evident with extensive management. Such different performances under alternative management options need more in-depth studies. The most notable improvement in models estimates of ecosystem respiration obtained with MMS is important because it adds to model capabilities to estimate carbon balances.

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