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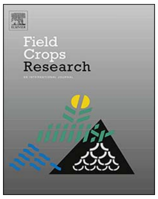

Plant acclimation to temperature: Developments in the Pasture Simulation model

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ABSTRACT

A modelling approach for the thermal acclimation of plant photosynthesis and respiration is presented that accounts for changes in the maximum carbon (C) assimilation with changing growth temperature. It is motivated by one key observation, i.e. the optimum temperature for plant processes increases with increasing growth temperature, and two corollary expectations: (i) this determines a modification of the response curve of C assimilation, and (ii) plant C release (respiration) is also affected by changing growth temperature. Simple relations are proposed to model these phenomena, consistent with the Farquhar model of photosynthesis. The incorporation of temperature acclimation of plant photosynthesis and respiration into the Farquhar-based scheme of the Pasture Simulation model (PaSim; EMS: existing modelling solution, MMS: modified modelling solution) is proposed as a way to reduce the uncertainty in estimations of harvested or standing above ground biomass and C fluxes from grassland systems in Central France. Here we show that, across a flux tower grassland site spanning two alternative grazing regimes (Laqueuille, 45° 38′ N, 02° 44′ E, 1040 m a.s.l.), acclimation parameterizations improve model ability to reproduce observed ecosystem respiration (especially with extensive grazing, where root mean square error [*RMSE*] lowered from 15.20 to 11.59 g C m^{-2} $week^{-1}$). An assessment at two grassland systems (Saint-Genès-Champanelle and Theix, 45° 43′ N, 03° 01′ E, 880 m a.s.l.) with alternative cutting regimes and climate conditions also showed some improvements in biomass estimates (e.g. with frequent cutting and experimental extreme summer event *RMSE* changed from 0.86 to 0.40 t DM ha^{-1}). The consequences of acclimation for simulated grassland outputs depend on the conditions evaluated which requires further studies. However, our results suggest that grassland modelling omitting plant temperature acclimation is likely to overestimate C emissions, thus biasing projections of future C storage and estimates of policy-making indicators.

1. Introduction

The effects of temperature on plant photosynthesis and respiration are major factors determining plant growth and its response to environmental changes (e.g. Dewar et al., 1999; Sage and Kubien, 2007). Climatic factors (alone or in combination) can limit grassland production and can affect biogeochemical cycles and carbon (C) budgets in different ways (He et al., 2016; Zhu et al., 2016). Climate extremes, in particular, may affect directly and indirectly grassland systems by altering physiology and behaviour of plants, with impacts on the productivity as well as the seasonality and quality of pasture production (e.g. Fay et al., 2008; Jentsch et al., 2009; Sippel et al., 2016).

Simulation modelling has an important role to play in understanding and quantifying the relationships, or trade-offs, between management and the production and environmental outputs from grassland systems but robust simulation models are needed for diagnosing and prognosing the impacts of environmental factors on the grassland production systems (Snow et al., 2014). Agricultural systems that include grazing ruminants, in particular, are characterised by a number of features (biologically diverse vegetation, economic returns derived from animals, etc.) that are not present in arable cropping systems and which present challenges to the experimentation, understanding and simulation modelling of these systems. Over the last decades, grassland models have been developed and used for a variety of purposes, including the analysis of complex interactions in grasslands (e.g. Rickert et al., 2000; Graux et al., 2011), and can provide insight into the ecosystem processes if model inputs are properly chosen and ecologically meaningful (Ben Touhami et al., 2013; Senapati et al., 2016; Pulina et al., 2017). We focus our study on the Pasture Simulation model (PaSim), which provides a mechanistic view of the processes and multiple interactions occurring in grassland systems (after Riedo et al., 1998). Here, in order to improve the simulation of grassland

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performances, we have modified the way how plant photosynthesis and respiration are simulated by PaSim so as to account for acclimatory and modulatory effects of growth temperature. A model for thermal acclimation of plants should be capable of characterizing the basic interactions of a collection of biochemical and physiological responses to temperature changes, in which the plant's response to a sustained change is manifested as alterations in the short-term response functions of physiological processes. Moreover, once calibrated, the model should explain the dependence on plant acclimation of production and environmental outputs. It is in this perspective that we addressed the thermal acclimation capacity of PaSim, where the photosynthetic process is based on Farquhar et al. (1980). The latter relies on the dependency of photosynthesis on the maximum rate of carboxylation of ribulose bisphosphate carboxylase (V_{Cmax}) and the maximum rate of photosynthetic electron transport ($J_{\max}$) (Wullschleger, 1993), which in turn depend on the response of assimilation rate (A) to sub-stomatal carbon dioxide (CO_2) concentration (C_i). Early studies of the ability of plants to acclimate to low temperatures indicated differences in photosynthetic capacities with contrasting growth regimes correlating with differences in V_{Cmax} activities while, at high temperatures, the improved photosynthetic performance of acclimated plants appear to be due to a combination of decreased respiration rates and temperature dependence of respiration, and an apparent increased thermal stability of photosynthetic CO_2 exchange (e.g. Pearcy, 1977; Armond et al., 1978; Berry and Björkman, 1980).

The entry point of this study is the photosynthetic acclimation notion as from Berry and Björkman (1980), i.e.: “environmentally induced changes in photosynthetic characteristics that result in an improved performance under the new growth regime”. It is known that the thermal acclimation of photosynthesis is associated with modifications to several photosynthetic variables, which include shifts in the thermal optimum of photosynthesis toward a new growth temperature and a relative homeostasis of the maximum photosynthetic rate across a range of growth temperatures (Way and Yamori, 2014). As growth temperature also affects leaf traits and the amount of nitrogen (N) per unit area, which are tightly related to maximum photosynthetic capacity, growth responses may be adaptive and contribute to the thermal acclimation of photosynthesis (Onoda et al., 2004; Sage and Kubien, 2007).

Extension of acclimation processes to the whole grassland ecosystem was assumed straightforward and followed the set of equations of PaSim, where temperature affects directly shoot/root growth and soil mineralisation and, indirectly, N uptake and N fluxes to the leaves. Using PaSim as a reference to simulate grassland systems, the purpose of this paper is to show that the temperature responses of plant photosynthesis and respiration observed on recent laboratory studies of the effects on single-plant species (based on experiences by Louarn et al. (2015) and Zaka et al. (2016, 2017) can be assumed to occur at the scale of a grassland ecosystem (with mixture of species under field conditions). Since grassland ecosystems are dynamic and competitive associations of plants, the performance of plant species observed under controlled conditions is only the first step in developing a model of the response of a grassland ecosystem. Salient processes were thus summarized and brought into a framework that enabled modification of the grassland system model. Expressed mathematically, the fundamental concepts of thermal acclimation were implemented into the PaSim code to illustrate that the system model has the elements needed to reproduce experimentally established system performances. Integrating a model of plant acclimation to temperature (in which photosynthesis and respiration are governed by acclimation to the growth temperature) to a complex soil-vegetation-management model can provide useful insights into plant acclimation. We thus extended the model PaSim to include growth temperature effects in a simplified way and use it to simulate multi-year datasets of plant biomass and C fluxes in managed grassland systems in Central France. The paper reports on comparisons between PaSim outputs and experimental data, assessing in a comparative fashion the existing (without acclimation) and modified (with acclimation) modelling solutions. The sensitivity of both solutions to alternative climate scenarios is also illustrated and discussed. We are less concerned with the detailed temperature responses of photosynthesis and respiration, a comprehensive analysis of which lies outside the scope of the present study.

2. Materials and methods

2.1. PaSim description and applications

PaSim is a deterministic, biogeochemical grassland-plot model incorporating climate data, soil properties, vegetation characteristics, livestock and management, and operating at a point in space on a subhourly time step. The model is suited to assess the effect of management practices, in terms of fertilization, grazing intensity and duration, and cutting frequency. The model calculates water, C and N pool dynamics as well as their fluxes. Photosynthetic-assimilated C is allocated at each time step to four pools (roots, leaves, stems/sheaths and ears). For each organ, the biosynthesis pathway implies a transition on four age classes from newly produced tissue until senescence. Animal milk production, enteric methane emissions and returns, and ecosystem respiration are C outflow fluxes. Accumulated above ground biomass, if not mown or grazed, enters a litter reservoirs. The litter is evenly distributed into the whole soil profile, segregated into its structural and substrate components. The soil organic matter also differentiates between active, slow and passive pools with different decomposition rates according to first-order kinetics. N inputs to the soil include atmospheric deposition, biological fixation by legumes and fertilizer addition. Losses of N occur via pathways that include nitrate leaching, ammonia volatilization, and gaseous emissions through microbial conversion of ammonium and nitrate (such as nitrification and denitrification). In the ground process scheme, the soil profile is divided into six layers, and soil temperature and moisture are simulated as a function of soil physical properties and plant water use in each layer of soil.

Including both grazing and cutting management options, PaSim is able to simulate a variety of grassland ecosystems and has been used to represent biogeochemical cycles and grassland production (Soussana et al., 2007; Vuichard et al., 2007; Graux et al., 2012; Ma et al., 2015) and in impact studies (e.g. Graux et al., 2013; Vital et al., 2013). PaSim is also being used for model comparison studies (e.g. as part of the MACSUR – Modelling European Agriculture with Climate Change for food Security, Sándor et al., 2016Sándor et al., 2016, Sándor et al., 2017Sándor et al., 2017). Some model weaknesses have been highlighted (e.g. overestimation of C losses under drought conditions) when simulating detailed multi-year datasets in a range of conditions (Ben Touhami and Bellocchi, 2015; Ma et al., 2015; Sándor et al., 2016).

In this study, the set of plant photosynthesis and respiration equations have been modified to include the effects of thermal acclimation.

2.2. Model of thermal acclimation of photosynthesis and respiration

The main point we wish to communicate can be conveyed most directly using the model for a single, fully expanded leaf discussed by Zaka et al. (2016) and shown in Fig. 1. This model is intended as a theoretical tool for gaining insights into one particular aspect of plant acclimation to temperature - the effect of growth temperature on photosynthesis and respiration – which may provide a framework for comprehensive models.

We refer here to the Farquhar scheme of the photosynthetic device of plants as represented in PaSim (Eq. (1); Riedo et al., 1998), where the maximum photosynthetic rate ($P_{\max}$) of the canopy is calculated from the maximum rate at 20 °C ($P_{\max,20}$), modulated by functions of plant N (P_{mN}) and C (P_{mC}), a function of the CO_2-temperature interaction (P_{mCO2T}, in turn depending on the Rubisco activity and the light-saturated photosynthesis, after Farquhar and von Caemmerer (1982), and a