Agricultural and Forest Meteorology 252 (2018) 155–166

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Merging a mechanistic enzymatic model of soil heterotrophic respiration into an ecosystem model in two AmeriFlux sites of northeastern USA

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ARTICLE INFO

Keywords:
Soil respiration
Soil carbon
Climate change
Q_{10}
DAMM
FöBAAR

ABSTRACT

Heterotrophic respiration (Rh), microbial processing of soil organic matter to carbon dioxide (CO_2), is a major, yet highly uncertain, carbon (C) flux from terrestrial systems to the atmosphere. Temperature sensitivity of Rh is often represented with a simple Q_{10} function in ecosystem models and earth system models (ESMs), sometimes accompanied by an empirical soil moisture modifier. More explicit representation of the effects of soil moisture, substrate supply, and their interactions with temperature has been proposed as a way to disentangle the confounding factors of apparent temperature sensitivity of Rh and improve the performance of ecosystem models and ESMs. The objective of this work was to insert into an ecosystem model a more mechanistic, but still parsimonious, model of environmental factors controlling Rh and evaluate the model performance in terms of soil and ecosystem respiration. The Dual Arrhenius and Michaelis-Menten (DAMM) model simulates Rh using Michaelis-Menten, Arrhenius, and diffusion functions. Soil moisture affects Rh and its apparent temperature sensitivity in DAMM by regulating the diffusion of oxygen, soluble C substrates, and extracellular enzymes to the enzymatic reaction site. Here, we merged the DAMM soil flux model with a parsimonious ecosystem flux model, FöBAAR (Forest Biomass, Assimilation, Allocation and Respiration). We used high-frequency soil flux data from automated soil chambers and landscape-scale ecosystem fluxes from eddy covariance towers at two AmeriFlux sites (Harvard Forest, MA and Howland Forest, ME) in the northeastern USA to estimate parameters, validate the merged model, and to quantify the uncertainties in a multiple constraints approach. The optimized DAMM-FöBAAR model better captured the seasonal and inter-annual dynamics of soil respiration (Soil R) compared to the FöBAAR-only model for the Harvard Forest, where higher frequency and duration of drying events significantly regulate substrate supply to heterotrophs. However, DAMM-FöBAAR showed improvement over FöBAAR-only at the boreal transition Howland Forest only in unusually dry years. The frequency of synoptic-scale dry periods is lower at Howland, resulting in only brief water limitation of Rh in some years. At both sites, the declining trend of soil R during drying events was captured by the DAMM-FöBAAR model; however, model performance was also contingent on site conditions, climate, and the temporal scale of interest. While the DAMM functions require a few more parameters than a simple Q_{10} function, we have demonstrated that they can be included in an ecosystem model and reduce the model-data mismatch. Moreover, the mechanistic structure of the soil moisture effects using DAMM functions should be more generalizable than the wide variety of empirical functions that are commonly used, and these DAMM functions could be readily incorporated into other ecosystem models and ESMs.

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https://doi.org/10.1016/j.agrformet.2018.01.026
Received 25 May 2017; Received in revised form 25 December 2017; Accepted 18 January 2018

1. Introduction

Soil heterotrophic respiration (Rh) is an important component of the global carbon (C) budget; releasing ~51–57 Pg C year $^{-1}$ (Bond-Lamberty and Thomson, 2010; Hashimoto et al., 2015), which is ~5–6 times greater than anthropogenic emissions (Le Quéré et al., 2014). Temperature sensitivity of Rh in most biogeochemical models is often represented with Q_{10} following Van't Hoff and Lehfeldt (1899) and Arrhenius (1889). Representation of empirically derived soil moisture functions in some models further complicates the matter. Empirical fits of precipitation and soil moisture effects on Rh generally rely on a variety of site-specific non-linear (polynomial and parabolic) functions (Linn and Doran, 1984; Schlentner and Cleve, 1985; Raich and Potter, 1995; Davidson et al., 2000; Savage and Davidson, 2001; Hanson et al., 2003; Reichstein et al., 2003). By failing to address the underlying biophysical processes mediated by soil moisture (and temperature); these empirical functions often have limited applicability to other study sites (Davidson et al., 2006a).

Soil moisture variation confounds the temperature response of Rh by affecting the diffusion of soluble-C substrates at low moisture and diffusion of oxygen (O_2) at high moisture contents (Skopp et al., 1990; Davidson et al., 1998, 2006a). When evapotranspiration exceeds precipitation under drying events, the reduced soil water film thickness limits diffusivity of C substrates and extracellular enzymes to active sites of enzymatic reaction and dampens Rh (Firestone and Davidson, 1989; Borken et al., 2006; Savage and Davidson, 2001; Cisneros-Dozal et al., 2006). On the other hand, when precipitation follows a drying event, a transient increase of Rh is often observed (Birch, 1958; Savage et al., 2009).

The Rh pulse after rewetting of dry soil is known to be sustained by resumption of microbial activity under favorable biophysical conditions (Moyano et al., 2013). Easily metabolized substrates (e.g. osmolytes or intracellular contents of dead microbial cells, photo-degradation products, and root exudates) accumulate during the drying event (Schimel et al., 2007; Manzoni et al., 2012). Increased accessibility (or greater mobility) of these substrates through hydraulically connected water-filled pore space (Lawrence et al., 2009) likely stimulate Rh after a wet-up event. These responses are often rapid, although they vary in intensity and duration, depending on the duration of the drying event, and the magnitude and timing of the pulse events that accompany substrate supply to heterotrophs (Borken et al., 2003; Borken and Matzner, 2009; Savage et al., 2009).

Substrate supply at the ecosystem-scale can also co-vary with temperature. For example, diffusion of both soluble-C substrates and gases (O_2) increases with temperature and thereby can increase the apparent temperature sensitivity of soil organic matter (SOM) decomposition (Moldrup et al., 2000; Gu et al., 2004; Davidson et al., 2006a; Moyano et al., 2013). Furthermore, seasonality of photosynthesis and belowground C allocation can influence the substrate supply to heterotrophs and soil respiration (soil R) (Craine et al., 1999; Högberg et al., 2001; Davidson and Holbrook, 2009; Reichstein et al., 2003; Wan and Luo, 2003; Curiel Yuste et al., 2004).

Together, moisture and substrate availability can obscure the temperature response of Rh and may significantly influence the seasonal and interannual variability of ecosystem C balance (Borken et al., 2006; Cisneros-Dozal et al., 2006; Davidson et al., 2006b,c). Hence, use of a more mechanistic module of Rh in ecosystem models and ESMs is warranted to address important environmental controls that modulate the apparent temperature sensitivity of Rh across different systems and among seasons within a system (Davidson and Janssens, 2006; von Lützow and Kögel-Knabner, 2009; Wieder et al., 2015; Luo et al., 2016).

Our main objective was to assess the impact of substrate supply and soil moisture on temporal dynamics of Rh, by coupling a biophysical soil enzyme kinetics model into a parsimonious ecosystem model at two

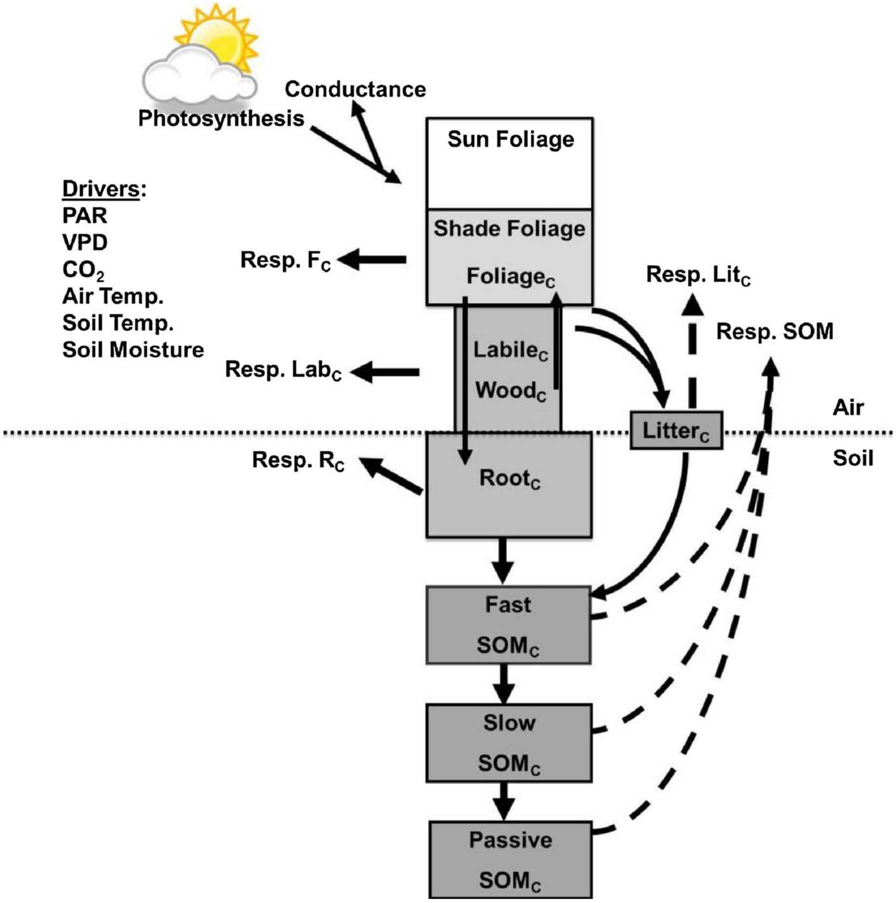

Fig. 1. Integrating DAMM (Dual Arrhenius and Michaelis-Menten, Davidson et al., 2012) soil flux model into FöBAAR (Forest Biomass, Assimilation, Allocation and Respiration, Keenan et al., 2012) ecosystem flux model. Dashed arrows represent CO_2 fluxes from litter and three SOM Pools (fast, passive, and slow pools), where we replaced FöBAAR's algorithms for Rh (Eq. (1)) with those of DAMM (Eq. (3)).

forest sites in the northeastern USA. To do so, we used the DAMM (Dual Arrhenius and Michaelis-Menten, Davidson et al., 2012, 2014) enzyme kinetics model of soil respiration and a forest C cycle model, FöBAAR (Forest Biomass, Assimilation, Allocation and Respiration, Keenan et al., 2012) (Fig. 1) within a model-data fusion framework, using a multiple constraints Markov-chain Monte Carlo algorithm (Raupach et al., 2005; Williams et al., 2009). The DAMM and FöBAAR models have overlapping and complementary domains. FöBAAR simulates canopy processes at high temporal resolution and C storage in vegetation and soils at a range of short to long time scales. It allocates C to belowground structures, but fast response soil processes depend on the classic Q_{10} response functions. In contrast, DAMM mechanistically represents fast responses of soil enzymatic processes, but it depends on assumptions or inputs from other models regarding soil C turnover and belowground plant allocation of C.

We have integrated subsurface soil process measurements with surface chamber fluxes and landscape-scale tower fluxes, leveraging ongoing eddy covariance and chamber measurements and allowing the scaling-up of process-based models and soil-flux measurements to the ecosystem scale in two AmeriFlux sites of northeastern USA (Howland Forest, ME and Harvard Forest, MA). These two sites allowed us to compare and contrast the value of the added mechanistic representation of Rh in each case and to examine how the same model structure performs when parameterized to different sites. Model-data fusion analyses have been conducted at both Harvard Forest (Keenan et al., 2012, 2013) and Howland Forest (Richardson et al., 2010; Carbone et al., 2016) using the FöBAAR model (or, its predecessor: data assimilation linked ecosystem carbon model, DALEC), demonstrating how different data streams (i.e. multiple constraints) contribute different types of information (i.e. about processes operating at different temporal scales) to the optimization, thereby reducing uncertainties. Both, DAMM and FöBAAR share a common philosophy that model structures should begin parsimoniously, and that complexity (including the number of parameters that must be estimated) should be added only when data are available to support it and when increased predictive utility can be demonstrated (Keenan et al., 2013).

Here we present a parsimonious but more mechanistic module for Rh that is readily incorporated into a broader ecosystem model. By doing so, we intend to demonstrate how other ecosystem models and ESMs could also adopt this approach. Our analysis is focused on the following questions: (1) Does the integration of a robust but still parsimonious model of Rh that explicitly simulates direct and indirect effects of temperature, moisture, and substrate supply into an ecosystem model improve the overall model performance?; (2) Can the merged model capture observed seasonal and interannual dynamics of respiration?; and (3) How sensitive is the merged model and its simulation of annual C budget components to variation in soil moisture, and does that sensitivity vary by season?

2. Materials and methods

2.1. Site descriptions

We have focused on two AmeriFlux sites in New England region of northeastern USA: Howland Forest near Howland, Maine, USA (45°12 N, 68°44 W), and Harvard Forest near Petersham, Massachusetts, USA (42°32 N, 72°11 W). The Howland Forest research site is a mature temperate-boreal transitional evergreen forest with hummock-hollow microtopography (i.e. a flat to gently rolling terrain with a maximum elevation change of lower than 68m within 10 km). This site is owned by the Northeast Wilderness Trust, which has dedicated the site to conservation and scientific research. The dominant tree species are red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.), with associated mixed hardwoods. This stand was selectively logged (not clear-cut) early in the 1900's, but has been minimally disturbed since that time. The soils have never been cultivated and are classified as Skerry fine sandy loam, Aquic Haplorthods. Mean annual temperature is + 5.5 °C, and mean annual precipitation is 1000 mm. See Fernandez et al. (1993) and Hollinger et al. (1999, 2004) for more information.

The Harvard Forest is a mixed deciduous hardwood forest, approximately 80 years old, with a hilly topography (elevation 340 m, http://harvardforest.fas.harvard.edu/gis-maps) and is owned and managed by Harvard University. Stands in this forest consist primarily of red oak (*Quercus rubra*) and red maple (*Acer rubrum*). Soils are classified as Canton fine sandy loam, Typic Distrochrepts. Mean annual temperature is + 8.5 °C and mean annual precipitation is 1026 mm. See Compton and Boone (2000) and Savage and Davidson (2001) for more information.

2.2. Data

2.2.1. Tower-based fluxes

Tower-based eddy covariance measurements of surface-atmosphere exchanges of CO_2, water, and energy fluxes have been made since 1996 and 1992 in Howland Forest (half-hourly interval) (Hollinger et al., 1999, 2004) and Harvard Forest (hourly interval) (Wofsy et al., 1993; Barford et al., 2001; Urbanski et al., 2007), respectively. Uncertainty estimates for NEE were adopted from Hollinger and Richardson (2005), where uncertainties were shown to follow a double-exponential distribution. Quality controlled hourly eddy-covariance observations (not gap-filled) of NEE and LE (http://ameriflux.lbl.gov/) were used to optimize the ecosystem model. Note that half-hourly measurements were averaged to hourly interval for Howland Forest tower data for a fair comparison of model performance between both sites.

2.2.2. Soil Respiration (Soil R) Measurements

The same chamber-based system (Savage and Davidson, 2003) was used for both Harvard and Howland Forests. Automated flux measurement systems have been operational near the main eddy covariance tower at the Howland Forest since 2004. Three sets of automated soil respiration (soil R) data are available from near the Environment Measurement Site tower at the Harvard Forest for 2003, 2010, and 2012–14. Manual flux measurements were available from both sites since 1996 with approximately six to eight replicates.

While high frequency automated chamber measurements were conducted during the snow-free growing season, manual flux estimates were obtained on a weekly to monthly interval for the entire year as conditions permitted. Both manual and automated measurements were comparable, but, they provide a trade-off for capturing the temporal vs spatial heterogeneity. Quality control was conducted using a series of protocols following Savage et al. (2008). Uncertainties for soil R measurements were characterized with the standard deviation of the flux where measurement errors increase linearly with the magnitude of the flux (Savage et al., 2009). See Savage and Davidson (2001, 2003) and Savage et al. (2009) for further details. More information on Soil R measurements is in the supplementary information (section, S1).

2.2.3. Root trenching for heterotrophic respiration (Rh)

We used classical root trenching experiment during 2013–15 at the Howland Forest (Carbone et al., 2016) and during 2013–14 at the Harvard Forest (Savage et al., 2013) to partition soil R into its autotrophic (Ra) and heterotrophic (Rh) components where the trench plot fluxes provide data for Rh and the difference between trenched and untrenched (control) plot provide constraints for root respiration (i.e. Ra). At Howland Forest, triplicate trenches were dug, each with 1 automated chamber in it, by excavating soils from 1 m depth covering an area of 3 m × 3 m. At Harvard Forest, one trench was dug to 50 cm depth, with 4 automated chambers in it, covering an area of 5 m × 5 m. The trench was then lined with a plastic wrap to prevent root growth back into the plots, and the soil layers were carefully backfilled. We had three untrenched plots at Howland Forest and four untrenched plots at

Harvard Forest. The CO_2 fluxes measured in the trenched plots were used to constrain Rh in the DAMM model.

2.2.4. Meteorological observations

Along with all soil R measurements, a soil temperature probe (Type-T thermocouple) and a soil moisture probe (Campbell Scientific CS616 water content reflectometer probes) were installed in each plot that recorded measurements half-hourly to hourly at 10 cm depth and stored the data on a Campbell Scientific CR10X. We used soil temperature and moisture measurements from the trenched plots for the DAMM model optimization. For validation of the model, we used soil moisture and temperature data from control chamber plots. Hourly gap-filled meteorological variables that drive the ecosystem model (incident photosynthetically active radiation (PAR), air temperature above the canopy, soil temperature at 10 cm depth, vapor pressure deficit (VPD), and atmospheric CO_2 concentration) were also obtained from site PIs. See supplementary information (section, S2) for explanation of filling missing data.

2.2.5. Ancillary data

Measurements of leaf area index (LAI), litterfall, woody biomass, observer-based estimates of bud-burst and leaf senescence, and soil organic C content were used as biometric constraints in the model. Biometric measurements were taken from Harvard Forest data repository (http://harvardforest.fas.harvard.edu/harvard-forest-data-archive) and Richardson et al. (2010) along with a few recent measurements from Howland Forest (personal communication, Holly Hughes and John Lee). Soil C pool turnover rates were constrained following Gaudinski et al. (2000) for Harvard Forest and Carbone et al. (2016) for Howland Forest. Uncertainties for ancillary data were represented as the standard deviation of all the available measurements.

2.3. Modeling approach

The FöBAAR model runs at a hourly time step, and is characterized by about 35 parameters and 7 C pools (wood, foliage, roots, litter, and three SOM pools), each with its own turnover rate varying in time from days to decades (Keenan et al., 2012). Both evergreen and deciduous plant trait versions of FöBAAR have been developed; the latter features an additional 6 parameters that control the phenology of canopy development and senescence. The model structure reflects a compromise between the competing objectives of minimizing complexity (so that the model is tractable, and only a limited number of observational data are required as constraints) and including sufficient detail to represent the major C cycling processes (canopy photosynthesis, allocation and growth, litterfall, decomposition, and autotrophic and heterotrophic respiration), and their relationships to climatic drivers.

FöBAAR calculates photosynthesis from two canopy fractions (sun and shade; Sinclair et al., 1976, Wang and Leuning, 1998) using a Farquhar/Ball-Berry approach (Farquhar et al., 1980; Ball et al., 1987; Baldocchi, 1994), and then allocates C to autotrophic respiration, Ra (growth and maintenance components), growth (leaves, wood, and roots), and storage (nonstructural C). SOM dynamics are modeled using a three-pool approach, with separate fast, slow, and passive pools (Jenkinson et al., 1987; Parton et al., 1987). Litter and root C are progressively transferred to the fast pool, then to the slow pool, and finally to the passive pool; soil R is the aggregate of root respiration (Ra) plus heterotrophic respiration (Rh) from the litter, fast, slow, and passive SOM pools. Water fluxes are coupled to photosynthesis through stomatal conductance, and feed back to soil water content through a simple bucket model. Key drivers for the FöBAAR model include air temperature, soil temperature, solar radiation, vapor pressure deficit, precipitation, and atmospheric CO_2 concentration. When constrained with field measurements, the model has been used to simulate forest C cycling on both fast (e.g. hours to days) and slow (decade +) time scales (Keenan et al., 2012, 2013). In the FöBAAR model, Rh of litter and three SOM pools are based on a simple temperature function like Q_{10}:

$$\mathrm{Rh_i} = \mathrm{Rh_{0,i}} \times \mathrm{C_i} \times \mathrm{f(T)} \times \Delta \mathrm{t} \tag{1}$$

$$\mathrm{f(T)} = 0.5 \times \exp.\ (\beta_i \times \mathrm{T}) \tag{2}$$

Where, Rh_0 (i.e. base rate) and β_i are parameters that vary among pools, C_i (i represent litter, fast, slow, and passive SOM pool, respectively). T is either air temperature (for litter pool) or soil temperature (for SOM pools) and t stands for time. We have replaced these equations with DAMM functions by introducing a reverse Michaelis-Menten (M-M) equation (Eq. (3)), where bulk enzyme (EnzPool) in soil is diffused to substrate through the water film and the amount of enzyme diffused (i.e. active enzyme concentration for reaction, $[Enz_{av}]$) depends on the thickness of soil water film (Eq. (5)). Thus, we employed a water limitation factor on top of the temperature limitation for Rh as follows:

$$\mathrm{Rh_i} = \mathrm{Vmax_i} \times \mathrm{C_i} \times ([\mathrm{Enz_{av}}]/(\mathrm{Km_{Enz}} + [\mathrm{Enz_{av}}])) \times ([\mathrm{O_2}]/(\mathrm{Km_{O2}} + [\mathrm{O_2}])) \tag{3}$$

$$\mathrm{Vmax_i} = \alpha_i \times \exp.\ (-\mathrm{Ea}/(\mathrm{R} \times \text{soil temperature})) \tag{4}$$

$$[\mathrm{Enz_{av}}] = \mathrm{EnzPool} \times \text{Diffusivity coefficient in liquid media} \times (\text{soil moisture, v v}^{-1})^3 \tag{5}$$

$$[\mathrm{O_2}] = \mathrm{O_2} \times \text{Diffusivity coefficient in air} \times (\text{air-filled porosity})^{4/3} \tag{6}$$

The DAMM model simulates soil enzymatic processes using these M-M, Arrhenius, and diffusion equations to account for both temperature and substrate supply controls of Rh. It is a parsimonious simplification that is somewhat analogous to early "big leaf" canopy process models (Sellers et al., 1997), in that it simulates soil reactions as a "big microsite" in the soil. Consistent with the "big microsite" approach articulated for the DAMM model structure (Davidson et al., 2014), we assume that the majority of extracellular enzymes can be represented by similar kinetic parameters, such as Ea and Km. Obviously, this is not universally true (Tang, 2015; Tang and Riley, 2013), just as all leaves simulated in "big leaf" models do not behave identically (Baldocchi and Meyers, 1998), but representing soil microbial metabolism at a "big microsite" permits model parsimony, and we test here its effectiveness.

The backbone of the DAMM model for aerobic soil R of a soluble C substrate is a simple M-M equation with two substrates, soluble organic C and O_2 (Eq. (3)). The Vmax (maximum velocity of a reaction) and Km (Michaelis-Menten half-saturation constant) are then linked to Arrhenius functions, which builds temperature sensitivity into the model (Eq. (4)). Diffusion equations simulate supply of the soluble C substrates and extracellular enzymes through water films (approximated by the cube of the volumetric water content, see Eq. (5) and Papendick and Campbell et al., 1981) and O_2 through air-filled pore spaces (as a power function of air-filled pore space, see Eq. (6) and Davidson and Trumbore, 1995). Thus, it adds soil moisture and air-filled porosity as controllers of process rates in addition to temperature and substrate supply. By combining M-M and Arrhenius kinetics, DAMM mechanistically demonstrates that the temperature dependency inherent in the Arrhenius function for predicting Vmax is not always an important controller of Rh when substrate concentrations (soluble C or O_2) are near their respective Km's. Key drivers for the DAMM model include soil temperature and soil moisture.

The effects of soluble-C substrate limitations at the enzyme reaction site were explicitly represented in Davidson et al. (2012) using a soil moisture-based diffusion equation combined with a forward M-M equation. The authors noted that extracellular enzymes also diffuse through soil water films to substrates, that enzyme diffusion has a similar effect as substrate diffusion, and that both are implicitly represented in the model by the same diffusion function. Moreover, we have no a priori knowledge nor any direct constraining measurements of microsite concentrations of either substrates or enzymes, so there is no strong theoretical basis in this circumstance for choosing between forward or reverse M-M kinetics. However, the reverse M-M equation

Table 1
Overall performance of DAMM-FöBAAR vs FöBAAR model.

	Optimization				Validation			
	FöBAAR		DAMM-FöBAAR		FöBAAR		DAMM-FöBAAR	
	Cost Func.[a]	R^2	Cost Func.[a]	R^2	Cost Func.[a]	R2	Cost Func.[a]	R^2
	Harvard multiyear (2013–2014) optimization				Harvard multiyear (1996-2010) validation			
Soil R	5.333	0.85	3.420	0.86	12.31	0.66	7.04	0.77-
Rh	6.325	0.81	4.560	0.83	–	–	–	–
	Howland multiyear (2013-2015) optimization				Howland multiyear (2000–2012) validation			
Soil R	5.418	0.55	3.060	0.57	5.48	0.64	5.36	0.66
Rh	6.385	0.59	4.011	0.62	–	–	–	–
					Harvard individual year validation for Soil R			
2003	–	–	–	–	1.89	0.73	1.36	0.83
2010	–	–	–	–	16.92	0.39	3.28	0.64
2012	–	–	–	–	4.12	0.74	3.17	0.81
	Howland individual year optimization for Soil R				Howland individual year validation for Soil R			
2002	2.48	0.74	0.86	0.91	3.63	0.65	1.62	0.80
2010	3.53	0.51	2.65	0.62	4.07	0.33	3.11	0.38

Cost functions for long-term validation (2000–2012) in Howland Forest is calculated from automated dataset, but cost functions for manual fluxes are also similar. All goodness of fit statistics (R^2) values are significant at 5% ($\alpha = 0.05$) level of significance.

[a] Cost function is calculated as the average uncertainty-weighted model-data mismatch as follows: $\frac{\sum(\text{data}_{t=i} - \text{model}_{t=i}) / \text{data uncertainty}_{t=i})^2}{\text{Number of data points}}$.

(Eq. (3)) and explicit simulation of diffusion of extracellular enzymes to substrates provides an advantage of maintaining a more parsimonious model structure, because it avoids the need to simulate and parameterize functions for four separate soluble-C substrate pools that correspond to the litter and three SOM pools of FöBAAR. In this case, diffusion of substrates is implicitly represented by this function as well, but we apply enzyme concentrations at the reaction site to the reverse M-M equation. The heterotrophic CO_2 production rates calculated by the modified DAMM structure are added to aboveground and belowground autotrophic processes simulated by FöBAAR, which provide estimates of total soil R, total ecosystem respiration, and net ecosystem exchange of C.

Prior distributions for all parameters in the combined DAMM-FöBAAR model are assumed to be uniform (non-informative or vague prior, in a Bayesian context). Prior values for FöBAAR model parameters that represent canopy processes and autotrophic components of soil R were directly obtained from Keenan et al. (2012). We had little *a priori* knowledge for the parameters related to the maximum velocity, Vmax of Rh in the DAMM module. Thus, prior ranges of pre-exponent or base rate (α_i) for litter and three SOM pools and activation energy (Ea) were obtained by providing a reasonable bound to the best fit model parameters from Davidson et al. (2012). Our prior range for half-saturation constant of the enzyme (Km_{Enz}) and enzyme pool (EnzPool) brackets the estimates from Schimel and Weintraub (2003). A broad prior range was assumed for half-saturation constant of O_2 (Km_{O2}) where the upper bound was set to atmospheric concentration of O_2 (21%, v v^{-1}).

Estimates of bulk density and particle density, parameters that determine total porosity, needed for the DAMM model were available in Fernandez et al. (1993), Davidson and Trumbore (1995), and Davidson et al. (2006a); we used these measurements made for the 0–10 cm soil depth for this modeling work. Following Davidson et al. (2012), we also set the diffusivity coefficient of soluble C substrate through water film and O_2 through air-filled pore space assuming two boundary conditions. In saturated soil, all soluble C substrates are available at the reaction site and under the perfectly dry condition; O_2 concentration in soil is identical to air-fraction. In the combined DAMM-FöBAAR model, α_i is a unitless (Log_{10}) quantity, which is multiplied with C_i (g C m^{-2}) at each time step (i.e. hour) such that the model calculates Rh_i for litter and three SOM pools in the unit of g C m^{-2} hr^{-1} (see Eq. (3), note that units for rest of the parameters on the RHS will cancel out).

We treated the initial size of all model pools as optimized parameters. A chi-square test of acceptance or rejection was used to determine which parameter sets were consistent with the observational data at 90% confidence (Press et al., 1993), which has also benchmarked by Fox et al. (2009). Our data uncertainty characterization follows that of Richardson et al. (2010) where data streams with greater confidence are accorded more weight in the cost function, thus, we have assigned an uncertainty-weighted RMSE multiplier of 5 for hourly NEE (Carbone et al., 2016).

For Howland Forest we ran the evergreen version of the model (Carbone et al., 2016) and for Harvard Forest we ran the deciduous version (Keenan et al., 2012) of the model. We optimized the model using the period when we had Rh constraints for the DAMM module from the trenching experiments along with the total soil R measurements (from control plots) using automated chambers and eddy-covariance measurements from tower (2013–2015 for Howland Forest and 2013–2014 for Harvard Forest). Model validations were conducted for decadal-scale soil R data as far back in as we have soil moisture measurements within the tower footprint. Thus, we compared the performance of DAMM-FöBAAR vs FöBAAR model for 2000–2012 in the case of Howland Forest (both automated and manual soil flux) and 1996–2010 (manual soil flux) for Harvard Forest. These decadal-scale datasets allowed us to evaluate if the DAMM-FöBAAR model can reproduce the observed inter-annual variability in soil R better than the FöBAAR-only version. We further assessed the sensitivity of the DAMM module for annual soil R budget by altering soil moisture content by 0.5× and 2× times and soil temperature by +5 °C and −5 °C, respectively.

3. Results and discussion

3.1. Overall agreement between data and model

3.1.1. Model calibration

DAMM-FöBAAR model calibration yielded lower cost functions for the control plots (soil R) and the trenched plots (Rh) than the FöBAAR model when optimized with 2013–15 dataset from Howland Forest (Table 1). Peak soil R fluxes were generally a little higher in the FöBAAR model than in the DAMM- FöBAAR model. For this reason, the FöBAAR model tended to better capture the unusually high fluxes (both soil R and Rh) in 2014 than the DAMM-FöBAAR model, but at the expense of a poor performance for a low flux year like 2015 (Fig. 2a,c).

DAMM-FöBAAR model calibration also yielded lower cost functions

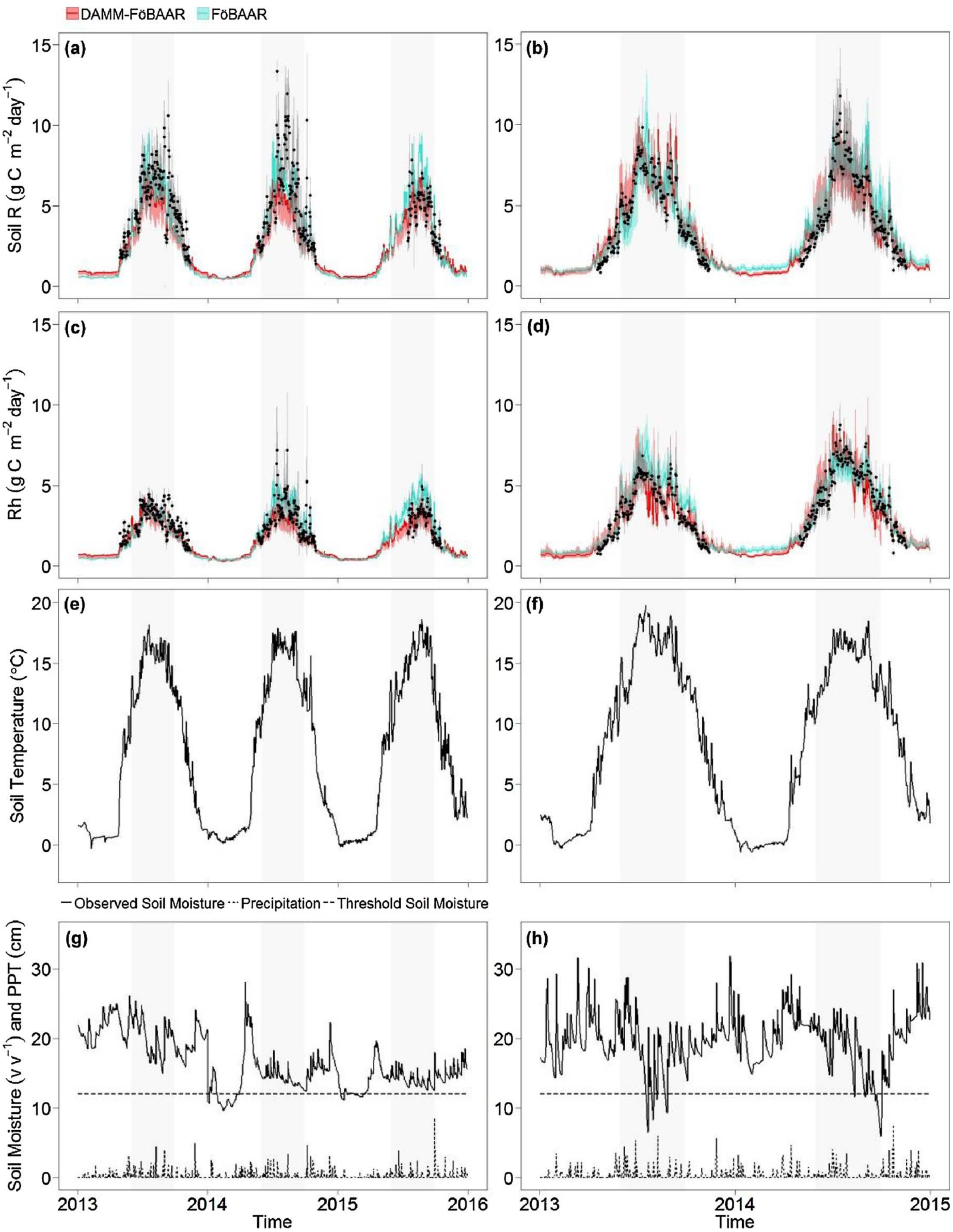

Fig. 2. Model performance during optimization in Howland Forest (a,c,e,g) and Harvard Forest (b,d,f,h) for soil R (a,b) and Rh (c,d). Model outputs represent daily integrated values. Red and turquoise lines in top two panels (a–d) represent output of DAMM-FöBAAR and FöBAAR model, respectively. Red and turquoise shading represent 90% CI based on a chi-square test of acceptance or rejection for DAMM-FöBAAR and FöBAAR, respectively. Black circles are measured fluxes and dark grey whiskers are uncertainty of the measured fluxes. Light grey shadings at the back represent summer months (June 1– September 30) for all years. Third panels (e,f) represent daily average soil temperature (°C). Daily integrated precipitation (cm, dotted), and daily average soil moisture (%, volumetric, solid) are represented in the bottom panels (g,h). The horizontal dashed line in bottom panels (g,h) represents the threshold soil moisture below which soil R is generally sensitive in these sandy soils (see text). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

than the FöBAAR model when optimized with 2013–14 dataset from Harvard Forest (Table 1). There was a general tendency for the DAMM-FöBAAR model to follow the soil moisture dynamics in the summer, which also coincides with a declining trend of Rh (and soil R) followed by an increasing trend, particularly evident in late summer (August) of 2013 (Fig. 2b,d). The FöBAAR model at Harvard Forest typically followed the seasonal trend of soil temperature, but did not capture the drying down or wet-up events.

Although R^2 values were only slightly improved in the DAMM-FöBAAR vs the FöBAAR model for both forests during optimization, R^2

values were generally higher for Harvard Forest than at Howland Forest (Table 1). Relatively lower R^2 values at Howland Forest compared to Harvard Forest can be attributed to sources of unknown variation not accounted for (e.g. microsite variation between chambers due to hummock-hollow microtopography in Howland Forest) in either model. Additionally, the larger range of soil moisture in the Harvard Forest than the Howland Forest may have captured larger variation by having stronger effects of soil moisture at the Harvard Forest, an emergent property of the Rh module in the DAMM-FöBAAR model. DAMM-FöBAAR model in Harvard Forest also yielded lower cost functions during optimization for nighttime NEE, but not in Howland Forest (Table S1). In general, DAMM parameters were well-constrained, i.e. the spreads of the accepted parameters were less than one-half the width of the prior ranges, given uniform prior distributions. See Supplementary information (section, S4) for discussion on the uncertainty of DAMM parameters.

3.1.2. Model validation using long-term dataset

Performance of the calibrated DAMM-FöBAAR model from Howland Forest was marginally improved as compared to the FöBAAR-only version when validated with decadal scale soil R dataset (both automated and manual fluxes; Table 1). In contrast, at the Harvard Forest, the performance of the DAMM-FöBAAR model was markedly improved compared to the FöBAAR-only version for the decadal scale validation, as evident by the data-model mismatch and goodness of fit statistics (Table 1). Further, residuals (i.e. observed-simulated Soil R) were considerably negative at lower soil moisture and higher temperature ranges for both sites for the FöBAAR-only model. Consequently, residuals for the FöBAAR model were statistically significantly correlated with soil moisture (positive) and soil temperature (negative), whereas there was no significant correlation of residuals for the DAMM-FöBAAR model (see Fig. S4 for more information).

Previously, Savage and Davidson (2001) observed a better fit of a coupled temperature-moisture regression model in the Harvard Forest compared to the Howland Forest, where a temperature-only model generally captured the dynamics of soil R from multiple years. Similarly, better performance of the DAMM-FöBAAR model in the long-term run using the Harvard Forest dataset is likely due to its hilly topography that frequently induces drying of soil moisture below an empirical threshold value of 12% ($v\ v^{-1}$) in summer, which previous work has shown to simultaneously decrease soil R rates at these sites (Savage and Davidson, 2001). In contrast, the generally flat, hummock-hollow micro-topography and the nearness of the water table to the soil surface at the Howland Forest may buffer the system from severe drying in most years (Hollinger et al., 1999). Within this context, the number of instances when ≥ 14 consecutive days with < 1 mm precipitation in the summer (June 1 to September 30) in last 20 years (1996–2015) was more than three times more common in the Harvard Forest (14 instances) than in the Howland Forest (4 instances). Although these two sites are located within the northeastern USA New England region, different site properties in these two forests explain why the moisture-induced substrate supply effect in the DAMM-FöBAAR model was more subtle at Howland Forest than at Harvard Forest for a longer time scale.

On a decadal scale (2000–2012), the time series of simulated soil R for DAMM-FöBAAR and FöBAAR diverged (see Fig. 3a insets) whenever volumetric soil moisture dropped below 12% for a brief period (e.g., 2001, 2002, 2007, and 2010; Fig. 3c), but was almost similar for most other times. Soil R dynamics were markedly altered due to drying-wetting cycle only in two (2002, 2010) out of these four drying events. Drying of soil in 2001 was too brief to induce severe water stress for Rh. On the other hand, the 2007 drying event occurred in early autumn which did not dampen the soil R rate much due to an accompanied trend of decreasing soil temperature. Overall, the seasonal trend of soil temperature dominantly controlled soil R fluxes in Howland Forest which outweighs the moisture-induced substrate limitation effect of DAMM-FöBAAR model on a decadal time scale.

Soil moisture at Harvard Forest was very dynamic where soil moisture dropped below an apparent threshold value (12%, $v\ v^{-1}$) in response to summer drying events in eight out of fifteen years of validation period (Fig. 4c). There was a general tendency for the FöBAAR model to over-estimate the peak soil R rates in dry summers (e.g. 1997, 1999, and 2001) and underestimate peak soil R in wet summers (2003, 2004, and 2008) (see Fig. 4a insets). The DAMM-FöBAAR model, on the other hand, more accurately simulated these dynamics by modulating the substrate/enzyme diffusion through water film. During dry summers, DAMM-FöBAAR model lowered peak soil R by limiting soluble C substrates at the reaction site and during wet summers, DAMM-FöBAAR model triggered peak R by increasing diffusion of soluble C substrate at the reaction site. The effects of soil moisture variation during synoptic drying events within individual dry years for both Howland Forest and Harvard Forest are explored further in the supplementary information (section S3).

Annual estimates of soil R based on linear interpolation between manual sampling points shown in Fig. 3 and 4, following Davidson et al. (1998) and Savage et al. (2008), are higher than annual sums from either simulation model (Fig. 5). This disagreement could be due to either overestimation of fluxes caused by interpolation or underestimated simulation fluxes during wetting events as discussed in the supplementary information (Section, S3). More importantly for this analysis, the combined DAMM-FöBAAR model produces a similar range between max and min and a similar standard deviation among years as the interpolated observations, whereas FöBAAR-alone simulated much smaller inter-annual variation (Fig. 5), which appears to be largely due to interannual variation of drying events and associated substrate supply effects on Rh.

As was the case for calibration, decadal-scale validation using the DAMM-FöBAAR model also better captured ecosystem respiration (i.e. night-time NEE) for the Harvard Forest run as compared to the FöBAAR model (cost function: 5.832 vs 7.195 in DAMM-FöBAAR vs FöBAAR model, respectively), but not in the Howland Forest run. Previous studies at Harvard Forest by Barford et al. (2001) and Urbanski et al. (2007) also indicated that ecosystem respiration was sensitive to soil moisture during late summer in dry years that corresponds to a relatively low rate of net ecosystem exchange of C. Lower ecosystem respiration during the dry season is a common observation in other ecosystems as well (Saleska et al., 2003; Xu et al., 2004). As soil R is a significant component (40–80%) of the ecosystem respiration in our study sites (Wofsy et al., 1993; Goulden et al., 1996; Phillips et al., 2010; Davidson et al., 2006b), a better representation of soil fluxes may translate into a better characterization of ecosystem C balance, and thus, net ecosystem exchange of CO_2 at the biosphere-atmosphere interface. Given that both models were optimized using identical datasets, but DAMM-FöBAAR outperformed FöBAAR in reproducing long-term dynamics of soil and ecosystem respiration, it indicates that improved functional forms of relationships between important processes and drivers can improve overall model performance by reducing the structural error of the model (Keenan et al., 2011).

3.1.3. Moisture effects across different ecosystems

In our temperate and boreal transition forests, substrate/enzyme diffusion effects can be secondary to the seasonal effect of temperature but more pronounced during drying and wetting events. Thus, the combined DAMM-FöBAAR model should afford more confidence in quantifying soil R dynamics in other ecosystems where episodic and stochastic nature of precipitation events primarily drives seasonal cycle of soil R (e.g. semi-arid, arid, and Mediterranean-type climate). To improve simulation of wet-up events, Oikawa et al. (2014) applied the DAMM model in a hot arid agricultural environment after adding a third substrate pool that represented a proxy of transient labile-C pool, which accumulated C substrate during the dry period and was released upon rewetting of soil. Freeze-thaw cycle may also exert substrate limitation on aerobic soil R by strongly limiting diffusion of soluble C

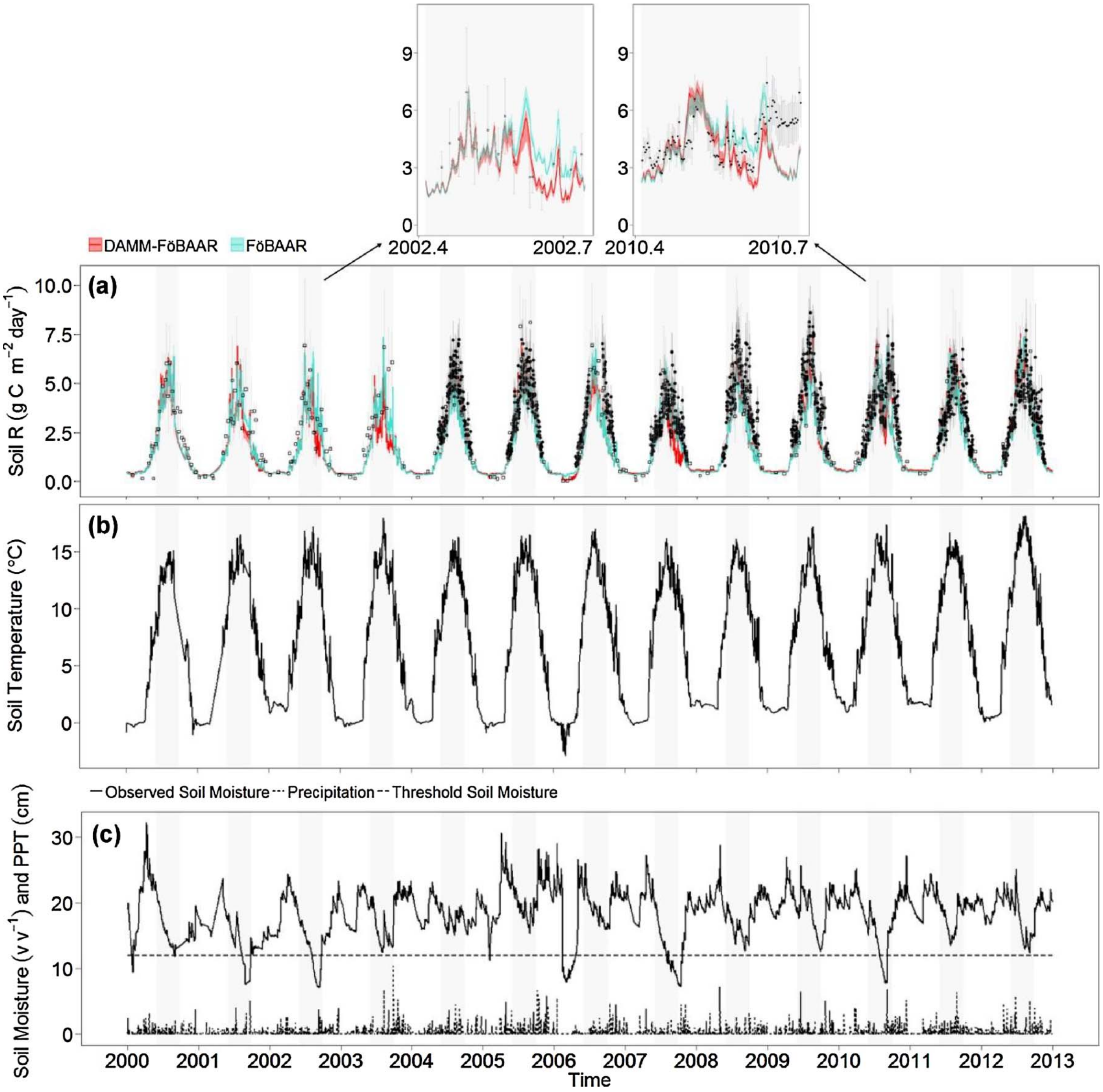

Fig. 3. Model validation in Howland Forest using long-term dataset (2000–2012). Model outputs represent daily integrated values. Red and turquoise lines in the top panel (a) represent output of DAMM-FöBAAR and FöBAAR model, respectively. Red and turquoise shading represent 90% CI based on a chi-square test of acceptance or rejection for DAMM-FöBAAR and FöBAAR, respectively. Closed circles (automated) and open squares (manual) are measured fluxes. Dark grey whiskers are uncertainty of the measured fluxes. Light grey shadings at the back represent summer months (June 1–September 30) for all years. Inset graphs represent soil R for two dry summers. Middle panel (b) represents daily average soil temperature (°C). Daily integrated precipitation (cm, dotted), and daily average soil moisture (%, volumetric, solid) are represented in the bottom panel (c). The horizontal dashed line in bottom panel (c) represents the threshold soil moisture below which soil R is generally sensitive in these systems in these sandy soils (see text). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

and O_2 across a narrow temperature range where soil water alters between ice and liquid water in soil pore space. Tucker, (2014) modified the DAMM model to account for these structural and functional changes in the soil during freeze-thaw events and was able to simulate large swings in substrate/enzyme diffusion in liquid water near 0 °C, thus explaining otherwise unrealistically large Q_{10} of soil R often reported at temperatures spanning seasonally frozen soil conditions.

It is important to note that intrinsic temperature sensitivity (e.g. the activation energy: “Ea” in Eq. (4)) remains constant but becomes less important in DAMM when moisture limits substrate/enzyme supply at the reaction site. In contrast, optimization of the FöBAAR model for dry years (e.g., 2002 and 2010 in Howland Forest) resulted in lowering the Q_{10} of litter and fast SOM pools, thus explicitly changing intrinsic temperature sensitivity represented by the model structure (Fig. S5, i–j). Alternatively, drying effects on Rh can be compensated by lowering the base respiration rate (or increasing the turnover time) of litter or soil C pool in a Q_{10}-styled model. This implies that an optimized model with an inadequate structure for belowground processes, like that in FöBAAR, may be able to provide the right answer but for the wrong reason. Because the M-M equations in the DAMM-FöBAAR model down-regulate the soil temperature effect on Rh from being fully observed under substrate/enzyme-limited conditions, the intrinsic activation energy does not need to change. We believe that this mechanistic linkage between Arrhenius and M-M kinetics makes the DAMM-FöBAAR model more generalizable than model structures with a variety of empirically derived soil moisture modifier(s) on Q_{10}s.

3.2. Sensitivity analysis

We demonstrated how temperature sensitivity of annual soil R interacts with substrate/enzyme diffusion using the DAMM-FöBAAR model by modifying the soil temperature regime by +5 °C and −5 °C. It is important to emphasize that once the model is optimized, the activation energy (Ea) of Rh was kept constant so that we can distinguish

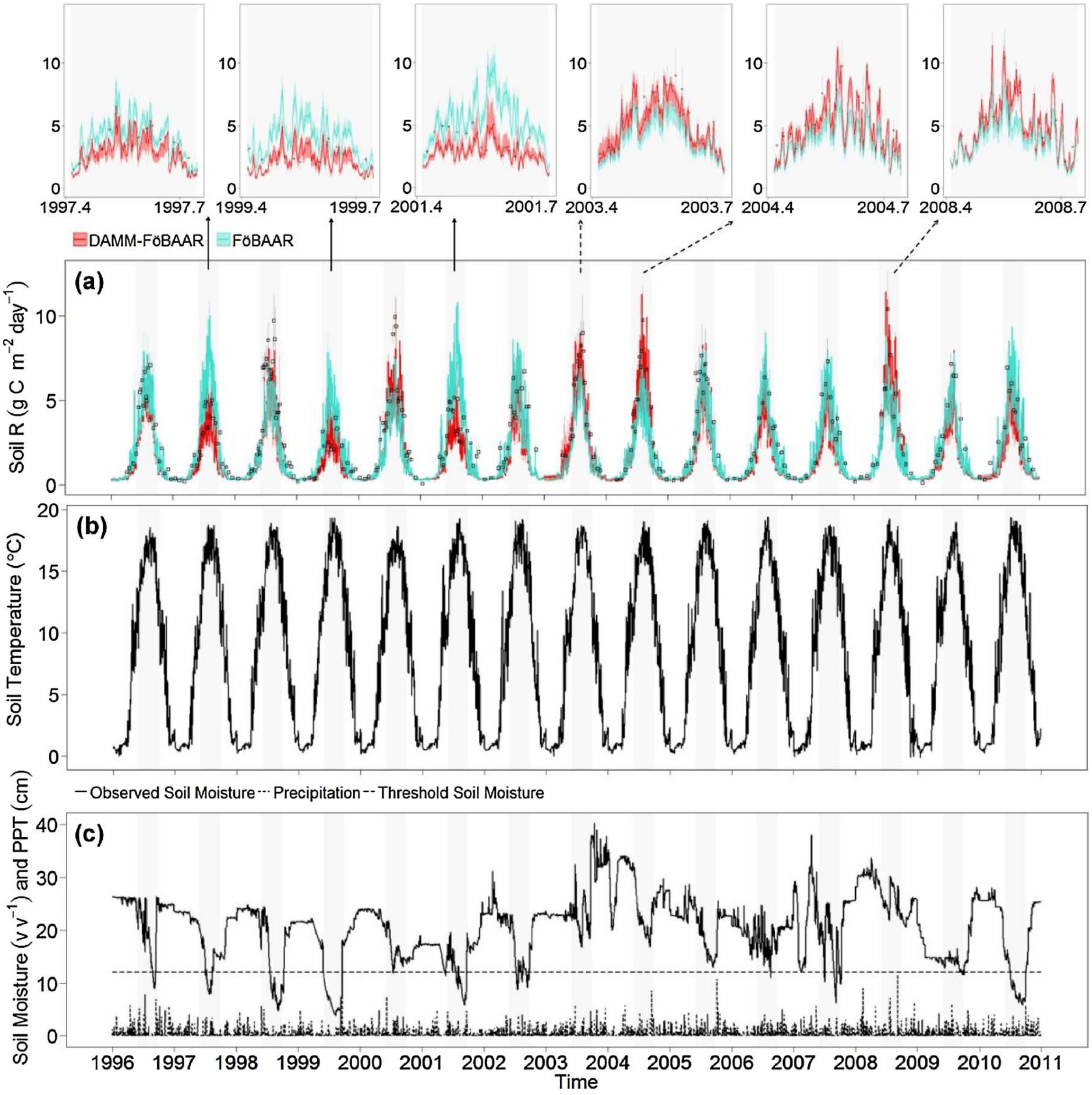

Fig. 4. Model validation in Harvard Forest using long-term manual dataset (1996–2010). Model outputs represent daily integrated values Red and turquoise lines in the top panel (a) represent output of DAMM-FöBAAR and FöBAAR model, respectively. Red and turquoise shading represent 90% CI based on a chi-square test of acceptance or rejection for DAMM-FöBAAR and FöBAAR, respectively. Open squares are measured fluxes (manual) and dark grey whiskers are uncertainty of the measured fluxes. Light grey shadings at the back represent summer months (June 1– September 30) for all years. Inset graphs represent soil R for dry (solid arrow) and wet (dashed arrow) summers, respectively. Middle panel (b) represents daily average soil temperature (°C). Daily integrated precipitation (cm, dotted), and daily average soil moisture ((%, volumetric, solid) are represented in the bottom panel (c). The horizontal black line in bottom panel (c) represents the threshold soil moisture below which soil R is generally sensitive in these systems in these sandy soils (see text). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

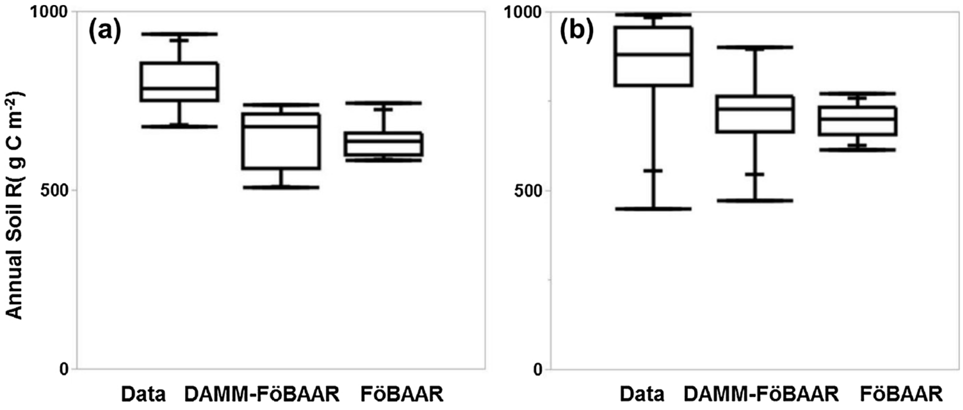

Fig. 5. Inter-annual variation in annual soil R for (a) Howland Forest and (b) Harvard Forest. Boxes represent annual soil R of observed data, DAMM-FöBAAR, and FöBAAR model, respectively.

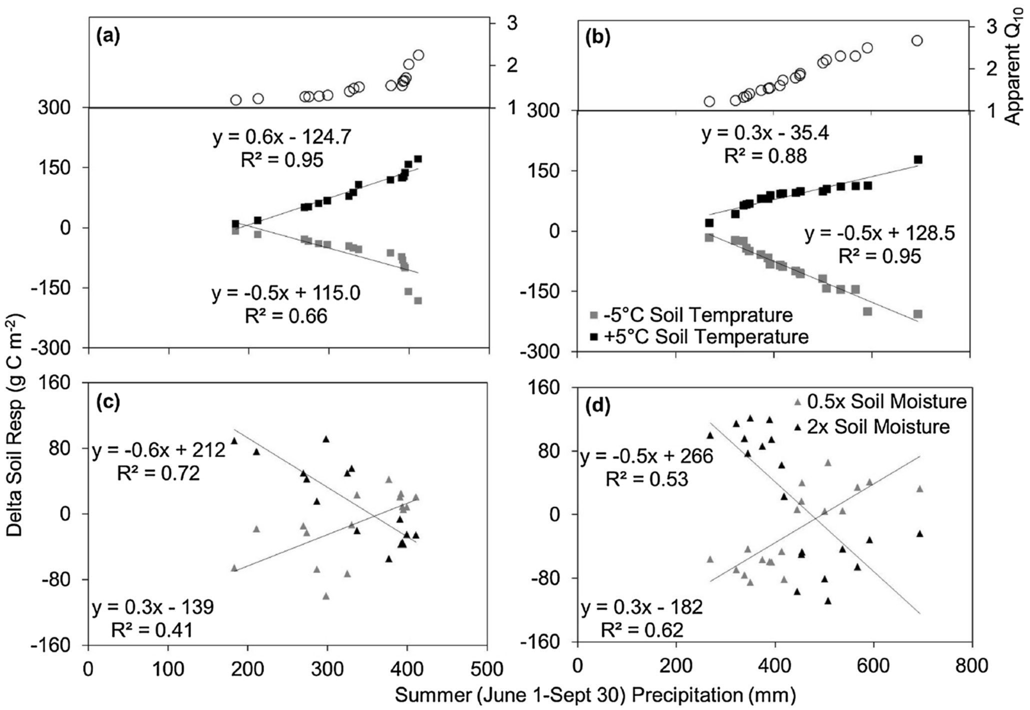

Fig. 6. Sensitivity analysis for (a, c) Howland Forest and (b, d) Harvard Forest using and +5 °C −5 °C of observed soil temperature (a, b) and 0.5× and 2× of observed soil moisture (c, d) for all data points using the DAMM-FöBAAR model. Apparent Q_{10} values are calculated using the ratio of annual soil R between +5 °C and −5 °C of observed soil temperature in both Howland and Harvard Forest. Change in annual Soil R fluxes are plotted on primary Y-axis and apparent Q_{10} values are plotted on secondary Y-axis (in a, b) against observed precipitation in summer months (June 1-Sept 30) for all years.

between intrinsic (i.e. due to inherent kinetic properties) and measured (or ‘apparent’) temperature sensitivity of annual soil R as modulated by substrate/enzyme variability at different soil moisture regimes. An increase or decrease of soil temperature by 5 °C had less of an effect on Rh in dry years than in wet years (Fig. 6a–b), because the diffusion of soluble substrates/enzymes through disconnected water-filled pore space primarily limits enzymatic reaction rates in dry years. In contrast, when soluble substrate/enzyme availability at the reaction site was high during wet years, significant increases and decreases of annual soil R were observed at higher and lower temperatures, respectively. We then calculated the apparent Q_{10} of annual soil R by taking the ratios of simulated annual soil R at +5 °C and −5 °C for all years.

Apparent Q_{10} of annual soil R was only slightly greater than one in dry years when substrate (soluble C) and enzyme availability was limited, indicating very little apparent temperature sensitivity under those conditions. The apparent Q_{10} was > 2 in wet years when substrate (soluble C) and enzyme availability was significantly enhanced (Fig. 6a–b), suggesting that the intrinsic temperature sensitivity ($Ea = 70$; equivalent to a Q_{10} of about 2.8 in this temperature range) was nearly fully expressed. This sensitivity analysis offers a mechanistic explanation of why apparent Q_{10} of Soil R often deviates from the intrinsic temperature sensitivity due to other environmental constraints that dictate substrate/enzyme availability.

Varying soil moisture by 0.5× and 2× of the observed values further sheds light on the importance of representing dual substrates (i.e. soluble-C/enzyme and O_2) using double M-M equations (see Eq. (3)) for aerobic respiration in the DAMM model (Fig. 6c,d). For instance, there was a general trend to decrease soil R with decreasing soil moisture (0.5× of original) for dry years and increasing soil R for wet years. Conversely, an increase of soil moisture (2× of original) tended to increase soil R in dry years and decrease soil R for wet years. Soluble-C substrate generally limits soil R in a dry summer, thus, lowering soil moisture further limits the diffusion of soluble-C substrates/enzymes to the reaction site. An increase in soil moisture, on the other hand, relieves the constraints of diffusion through water films and increases soil R. In a wet summer, however, solute diffusion may not be limiting, as the soil water content may be sufficiently close to field capacity so that solute diffusion is not strongly limited by soil water content. Instead, a further increase in soil moisture would reduce soil R in wet summers by limiting O_2 diffusion into the soil when soil moisture exceeds field capacity and the pore spaces become mostly water-filled. A decrease in soil moisture for a wet summer may not dry out the soil enough to limit significantly soluble-C diffusion but could favor more diffusion of O_2 through the soil air phase and ultimately increase aerobic respiration. Thus, these patterns are consistent with our general understanding that the peak soil R is observed at intermediate water contents (Linn and Doran, 1984; Skopp et al., 1990). In this sensitivity analysis, the 2× simulation resulted in some extended periods with soil moisture remaining above field capacity, which is unrealistic, so the sensitivity to high soil moisture contents may be overestimated.

3.3. *Scope for future improvements of the DAMM-FöBAAR model*

In the present version of DAMM-FöBAAR, the bulk soil enzyme concentration remains constant, but its concentration at the reaction site varies due to diffusional limitations related to soil moisture. Recently, Abramoff et al. (2017) incorporated the DAMM model in a microbial physiology-based soil organic matter decomposition model, MCNiP (Microbial Carbon and Nitrogen Phyisology), in which enzyme production and turnover vary temporally through linkages between carbon and nitrogen cycling processes and assumptions of carbon use efficiency (CUE). The DAMM-MCNiP model reproduced frequently observed seasonal hysteresis in the temperature-respiration relation. Incorporation of similar MCNiP algorithms into DAMM-FöBAAR or other ecosystem models and ESMs may provide further improvements, although it adds more parameters and reduces parsimony. Because it simulates both variation in enzyme production and diffusional constraints of substrate supply, DAMM-MCNiP was also able to apply equilibrium chemistry approximation (ECA) kinetics, which may be superior to using forward or reverse M-M approaches when enzyme and substrate concentrations can be simulated or measured independently (Tang, 2015; Tang and Riley, 2013). Similarly, incorporating microbial CUE could be valuable, as it largely dictates the uncertainty in long-term soil C stocks (Sihi et al., 2017), but also requires additional parameterizations that remain challenging due to variation in its fundamental definitions and measurement techniques.

4. Summary and conclusions

Soil moisture and substrate supply interact with temperature effects on respiratory processes.

Empirically fitted Rh models with soil temperature and moisture from a given study (or site) often fail to capture the full range of spatial and temporal variation in soil R as these models mask the mechanistic effect of substrate/enzyme supply on the enzymatic reaction rates. We added a mechanistic representation of Rh within an ecosystem model by combining the DAMM soil flux model with the FöBAAR model with relatively little additional model complexity. Our combined DAMM-FöBAAR model improved predictive capacity at one site (Harvard Forest) in most years and at another site in two dry years (Howland Forest).

Additionally, high frequency soil chamber measurements allowed us to evaluate how the peaks and drops in soil R followed the trajectories of soil moisture on seasonal and synoptic time scales at both sites. This indicated that substrate/enzyme supply as affected by diffusion through soil water films can be equally or more important during drying events than the intrinsic temperature sensitivity on a synoptic time scale. Sensitivity analyses by varying soil thermal and moisture regimes further demonstrated that the combined model can explain much of the observed variability in apparent temperature sensitivity of soil R often reported from different studies across various ecosystems.

Our findings show that the mechanistic representation of Rh in the combined DAMM-FöBAAR model appears to be robust across years and for two different forests, despite their differing frequency of drying events. Finally, the parsimonious structure of the DAMM module may allow its application to a wider range of sites and could be implemented into ecosystem and ESMs that focus on terrestrial-biosphere C exchange.

Acknowledgments

The project was supported by USDA grant # 2014-67003-22073. The trenching experiment at the Harvard Forest was supported by US Department of Energy, Office of Science, Terrestrial Ecosystem Science program awardDE-SC0006741. Research at Harvard Forest is supported by the National Science Foundation’s LTER program (DEB-1237491). Howland Forest is supported by the Office of Science (BER), US Department of Energy, and the USDA Forest Service's Northern Research Station. TFK was supported by the Director, Office of Science, Office of Biological and Environmental Research of the US Department of Energy under Contract DE-AC02-05CH11231 as part of the RGCM BGC-Climate Feedbacks SFA. The authors would like to acknowledge William Munger for providing the code for soil moisture bucket model. FORTRAN codes used for this modeling exercise and soil R data (and associated metadata) from Howland Forest are made available in the GitHub repository (https://github.com/trevorkeenan/FoBAAR-DAMM). Howland Field Crew (Holly Hughes and John Lee) assisted in ancillary measurements at the Howland Forest. Biometric data for the Harvard site is archived in the Harvard Forest Data Repository (http://harvardforest.fas.harvard.edu/harvard-forest-data-archive). Tower-based eddy-covariance data, as well as soil respiration data (both control and trench plots) used for this study, can be obtained from the AmeriFlux website (http://ameriflux.lbl.gov/). Soil R data (and associated metadata) from Harvard Forest are freely available in the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu:8080/exist/apps/datasets/showData.html?id=hf006, ID: HF006). The computations in this paper were run on the Odyssey cluster supported by the FAS Division of Science, Research Computing Group at Harvard University. We thank the guest editor and two anonymous reviewers for their careful insights which immensely helped to improve the quality of the article.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.01.026.

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