Are more complex physiological models of forest ecosystems better choices for plot and regional predictions?

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ABSTRACT

Process-based forest ecosystem models vary from simple physiological, complex physiological, to hybrid empirical-physiological models. Previous studies indicate that complex models provide the best prediction at plot scale with a temporal extent of less than 10 years, however, it is largely untested as to whether complex models outperform the other two types of models at plot and regional scale in longer timeframe (i.e. decades). We compared model predictions of aboveground carbon by one representative model of each model type (PnET-II, ED2 and LINKAGES v2.2, respectively) with field data (19—77 years) at both scales in the Central Hardwood Forests of the United States. At plot scale, predictions by complex physiological model were the most concordant with field data, suggesting that physiological processes are more influential than forest composition and structure. Hybrid model provided the best predictions at regional scale, suggesting that forest composition and structure may be more influential than physiological processes.

1. Introduction

Ecologists are increasingly interested in carbon dynamics at large temporal (e.g., decadal) and spatial (e.g., regional) scales (e.g., Thurner et al., 2014; Fang et al., 2014; Medvigy and Moorcroft, 2012). Forest ecosystem models are one of the primary tools used to predict future carbon dynamics of forest ecosystems (Rigo et al., 2013; Brown and Schroeder, 1999; Vanderwel et al., 2013; Malhi et al., 2006). Early forest ecosystem models are largely empirical-based while later models are increasingly process-based (Seidl et al., 2011; Bugmann, 2001). Based on complexity of physiological processes, most process-based forest ecosystem models can be classified into three types: simple physiological, complex physiological, and hybrid empirical-physiological.

Simple physiological models simulate carbon dynamics of forest ecosystems based on simple relationships between photosynthesis and environmental and biological variables (e.g., foliar nitrogen concentration). They operate at plot to watershed scales and usually use a monthly time step. Simple physiological models are applied to large areas (e.g., region) by dividing the area into raster cells, downscaling environmental variables to each raster cell, simulating carbon dynamics in each cell, and assembling the results for the region. This type of models is typically parameterized for forest ecosystem types (e.g., temperate deciduous forest), rather than individual species or plant functional type. Biomass is usually petitioned into different organs (e.g. root, stem and leaf) (Aber and Federer, 1992). Thus, simple physiological models do not simulate population-level processes such as competition and succession (e.g., Aber and Federer, 1992; Thornton et al., 2002). Furthermore, due to their coarse time steps, the coupling between atmospheric and physiological processes is relatively weak. However, this type of models is relatively easy to parameterize and requires the least computation power and time. PnET-II is an example of a simple physiological model and was originally designed to simulate forest ecosystem processes in a northern temperate forest (Aber and Federer, 1992).

Complex physiological models simulate carbon dynamics of forest ecosystems with close coupling between atmospheric conditions and physiological processes. They involve more variables than simple physiological models and use finer temporal scales (e.g., hourly) (e.g., Wang and Jarvis, 1990; Luo et al., 2001; Williams et al., 1996; Hanson et al., 2005). Similar to simple physiological models, complex physiological models simulate carbon dynamic with a grid cell system where environmental variables are

downscaled to each cell and results from each cell can be assembled to represent a region. The models track plant functional types (e.g., early successional temperate deciduous tree) with forest structure information (e.g., tree density) (e.g., Grant, 2001; Moorcroft et al., 2001). Thus, complex physiological models can simulate simplified succession dynamics. Plant functional type-size cohorts are used to represent forest composition and structures. This type of model can typically simulate both C3 and C4 photosynthetic pathways. Complex physiological models are usually applied to broad regions with large grid cell sizes (e.g. 50 km), within which a small number of patches of land (typically <1 ha each) is simulated to represent the entire cell (Snell et al., 2014). They typically do not provide species-specific information, which may limit their value, especially when species-specific carbon dynamics are of interest. The Ecosystem Demography model version 2 (ED2) is a complex physiological model (Medvigy et al., 2009; Moorcroft et al., 2001).

Hybrid empirical-physiological models typically employ empirical age–size relationships to simulate aboveground woody biomass (AWB) dynamics for each individual plant instead of simulating carbon dynamics through physiological processes. Hybrid models may incorporate some mechanistic processes such as exchange of carbon with the atmosphere and soil (e.g., Friend et al., 1997, 1993; Seidl et al., 2005). Hybrid models typically operate at daily time steps and are designed to simulate plot scale (typically between 0.1 and 1 ha) carbon and soil nutrient dynamics. They track size and density by individual trees and mechanistically simulate succession and competition, and consequently the dynamics of forest composition and structure, which can be a strength for research on species-specific dynamics. The computation power and time needed by this type of model are between those of the simple and complex physiological models. LINKAGES v2.2 is a hybrid model that simulates dynamics of forest structure and composition at the spatial scale of a plot and temporal scale of decades (Wullschleger et al., 2003).

Comparing model predictions with field data can reveal levels of prediction uncertainty and identify strengths and weaknesses of different models (Reynolds et al., 2001; Xiong et al., 2014). Many comparisons between forest ecosystem model predictions and field data have been conducted to provide insight into the relationship between model prediction and model complexity (e.g., Hanson et al., 2004; Huber et al., 2012; Sterba and Monserud, 1997; Amthor et al., 2001; Bond-Lamberty et al., 2006; Wang et al., 2014). For example, Huber et al. (2012) compared predictions from three forest process-based models with different levels of complexity against a subset of National Forest Inventory data from Austria for 15 years and found that the more complex model provided better predictions of annual volume increments at a plot scale. Hanson et al. (2004) compared model predictions from 13 forest process-based models with field data for a temperate oak forest site and the complex physiological models using hourly time steps generated the best predictions of hourly, daily, and annual carbon and water budgets. These findings suggest that complex models may provide the best predictions at small temporal and spatial scales.

Complex physiological models require extensive climate data, detailed ecophysiological parameters, high computing power, and longer simulation time than the other two types of models (Huber et al., 2012). At regional scales, detailed, precise atmospheric and soil variables may not be available and effects of environmental heterogeneity are simplified through data imputation and aggregation (e.g., Falkowski et al., 2010; Cutler et al., 2007; Wilson et al., 2012; Liang et al., 2014). Modelers should weigh model performance against applicability (Buchman and Shifley, 1983; Huber et al., 2012); therefore, it is important to know whether complex physiological models are better than simpler models for predictions

at large temporal and spatial scales.

We compared predictions of forest carbon dynamics in terms of AWB by three forest process-based models with different complexity levels against decadal observations of field data at plot and regional scales under current climate. We chose one representative model from each of the three process-based models types: simple physiological model (PnET-II), complex physiological model (ED2), and hybrid empirical-physiological model (LINKAGES v2.2). In terms of physiological process, model complexity increases substantially from PnET-II to LINKAGES v2.2, and to ED2, however, in terms of forest composition and structure, model complexity increases from PnET-II to ED2, to LINKAGES v2.2 (Fig. 1). We hypothesized that at the plot scale, forest composition and structure may not be as influential as physiological processes on forest carbon dynamics because composition and structure are not likely to change significantly at small spatial scales. Therefore, complex or simple physiological models should perform adequately. We hypothesized that at the regional scale, forest composition and structure may be more influential than physiological processes and the hybrid empirical-physiological model should perform better than the physiological models. We applied each model to three forest sites in the Central Hardwood Region in the United States that have long-term, plot-scale observations: Sinkin Experimental Forest in Missouri (30 years of data), Vinton-Furnace Experimental Forest in Ohio (33 years of data), and Kaskaskia Experimental Forest in Illinois (77 years of data). We also carried out regional analysis of aggregated plots, based on the United States Forest Service Forest Inventory and Analysis (FIA) data, for each of the three ecological subsections that included one of the forest sites used for plot scale analysis: Current River Hills (21 years of data), Western Hocking Plateau (19 years of data), and Lesser Shawnee Hills (25 years of data). At this spatial scale, we tested whether simplified environmental heterogeneity could still lead to good match between mean model predictions and mean field data.

We addressed the following questions regarding prediction of forest AWB dynamics: 1) Can a complex process-based model outperform simple and hybrid empirical-physiological models in terms of mean and absolute bias at a decadal temporal scale and different spatial scales (plot and regional), given its detailed data requirements? 2) How do prediction biases change from plot to regional scales for the same model? Comparing the strength and weakness of these three types of models can help identify process-based model designs and formulations that are most suitable for specific types of applications at different spatial scales.

2. Methods

2.1. Description of models

2.1.1. Simple physiological model (PnET-II)

PnET-II (Aber et al., 1995) is a lumped-parameter model that simulates photosynthesis, evapotranspiration and net primary production of forest ecosystems and is an improved version of PnET (Aber and Federer, 1992). The design of PnET-II is based on two principles: (1) maximum potential net photosynthetic rate under light-saturated condition is a function of foliar nitrogen concentration, and (2) water use efficiency (mg C fixed per g H_2O transpired) is a function of vapor pressure deficit. Based on these two principles, a link between carbon dynamics and water transpiration has been established, and the computation load for water transpiration has been greatly reduced since it only depends on vapor pressure deficit. PnET-II estimates maximum potential net photosynthetic rate, which is under light saturation condition. And then, net photosynthetic rate is calculated, accounting for effects of light attenuation, temperature, water availability and vapor pressure