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Do rising temperatures always increase forest productivity? Interacting effects of temperature, precipitation, cloudiness and soil texture on tree species growth and competition

Eric J. Gustafson [a], [*], Brian R. Miranda [a], Arjan M.G. De Bruijn [a], [b], Brian R. Sturtevant [a], Mark E. Kubiske [a]

[a] Institute for Applied Ecosystem Studies, Northern Research Station, USDA Forest Service, 5985 Highway K, Rhinelander, WI 54501, USA
[b] Department of Forestry and Natural Resources, Purdue University, W. Lafayette, IN 47907, USA

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ABSTRACT

Forest landscape models (FLM) are increasingly used to project the effects of climate change on forested landscapes, yet most use phenomenological approaches with untested assumptions about future forest dynamics. We used a FLM that relies on first principles to mechanistically simulate growth (LANDIS-II with PnET-Succession) to systematically explore how landscapes composed of tree species with various life history traits respond to individual climate and abiotic drivers. Moderate temperature rise (+3 °C) concurrent with rising CO_2 concentration increased net photosynthesis of cohorts, but decreased biomass production because of increased maintenance respiration costs. However, an increase of 6 °C decreased both photosynthesis and biomass production, regardless of species optimal temperature. Increasing precipitation generally increased photosynthesis and biomass. Reduced cloudiness had a positive effect on photosynthesis and biomass, but much less than the other treatment factors. Our study informs expectations for the outcome of modeling studies that project forest futures under climate change.

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1. Introduction

Climate change is expected to alter temperature, precipitation and cloudiness throughout much of the world (IPCC, 2013), abruptly subjecting forests to abiotic conditions that are unprecedented since the last ice age. Forest managers often rely on models to predict how well potential management strategies will achieve objectives for ecosystem goods and services in the future. Most of these models rely heavily on a phenomenological approach, which uses the past to predict the future. However, given that global changes to climate and atmospheric composition will produce new conditions that have never been scientifically observed, phenomenological approaches are not reliable for the conditions of the future (Gustafson, 2013). Modifying such models to use more mechanistic approaches that rely on well-established ecophysiological mechanisms (first principles) and more directly link modeled system behavior to climate and atmospheric inputs will increase their robustness to the novel conditions of the future. In this study we use such a modified model to describe how distinct climate drivers interact with tree species life history traits to determine productivity and competitive ability. Our results can inform expectations for the outcome of modeling studies that seek to project forest futures under altered climatic and atmospheric conditions.

Managers have found forest landscape models (FLMs) useful for projecting future forest dynamics because they account for most of the factors that structure forested ecosystems at landscape spatial and temporal scales, particularly disturbances (He, 2008). Climate and atmospheric (i.e., global) changes are expected to impact forest dynamics and composition through direct (growth, establishment, competition and mortality) and indirect (altered climate-regulated natural disturbance regimes) effects. FLMs simulate these effects at

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[*] Corresponding author.
E-mail address: egustafson@fs.fed.us (E.J. Gustafson).

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a spatial scale intermediate between stand models (e.g., Forest-GCB, Running and Gower, 1991; PnET-CN, Aber et al., 1997), which simulate growth of individual trees and fluxes of materials within a forest stand and Dynamic Global Vegetation Models (DGVM, e.g., SEIB–DGVM; Sato et al., 2007), which mechanistically simulate growth and competition among vegetation types (e.g., biomes) at regional to global scales (Medlyn et al., 2011). Unlike both stand and DGVM models, FLMs are spatially explicit and simulate seed dispersal, competition, disturbance and succession of species (as opposed to trees or plant functional types) as distinct processes such that their interactions play out as emergent properties of the climate inputs (e.g., ALFRESCO (Rupp et al., 2000), Iland (Seidl et al., 2012), Landclim (Schumacher et al., 2004), LANDIS-II (Scheller et al., 2007), TreeMig (Lischke et al., 2006)). Because of these added spatial processes, FLMs generally simplify simulation of growth and competition compared to stand and DGVM models and are constructed using a mixture of mechanistic and phenomenological components. However, because phenomenological components are based on system behavior in the past (Schelhaas et al., 2004), they risk being not just imprecise, but biased, and in some cases, completely wrong (Cuddington et al., 2013; Gustafson, 2013; Keane et al., 2015; Urban et al., 2016).

Many disturbance processes in FLMs have explicit and empirically derived links to their climate drivers. However, the majority of FLMs have relatively weak links between key abiotic drivers (i.e., temperature, precipitation, CO_2, ozone) and species establishment, growth and competition (reviewed by Gustafson and Keane, 2014). Some FLMs simplistically simulate succession using probabilities of transition from one community type to another (e.g., LANDSUM (Keane et al., 2002), VDDT/TELSA (Kurz et al., 2000)), with probabilities modified to account for climate-induced changes. However, such modifications are usually somewhat *ad hoc*, and require assumptions about the complex interactions among the processes that determine succession. Other FLMs that model succession as a competitive process usually simplify the mechanisms of growth and competition by relying on average behavior within a time step (typically decadal), which consequently eliminates the impact of highly influential extreme events such as droughts or heat waves (e.g., Biomass Succession extension of LANDIS-II (Scheller et al., 2007)). These approaches have worked reasonably well to conduct controlled simulation experiments under historical climate conditions, but they are problematic when the models are used to project the impact of climate and atmospheric change on future forest dynamics because of the proliferation of uncertainty when future conditions fall outside the domain of most empirical studies (Dale et al., 2001 Gustafson, 2013; Keane et al., 2015).

To resolve this problem, more direct links between climate and atmospheric drivers and growth and competition are being added to FLMs, and these more mechanistically simulate growth and competition based on well-established first principles to make them more robust to unprecedented conditions. FireBGCv2 (Keane et al., 2011) mechanistically simulates all fundamental ecological processes at appropriate spatial and temporal scales and the model scales and integrates them to produce realistic landscape behavior. For example, growth (living and dead biomass) is estimated for representative forest stands by simulating photosynthesis of individual trees as they compete for light, water and nutrients with daily variation in temperature, precipitation and CO_2 concentration. These growth estimates are then imputed to all such stands on the landscape. Disturbances typically are simulated at broader scales, and respond to live and dead vegetation on landscape sites and to daily weather conditions. FireBGCv2 is strictly a research tool, but it provides robust capabilities to link climate change to forest landscape dynamics. iLand (Seidl et al., 2012) is very mechanistic, but because it simulates every tree on a landscape, the size of landscapes that can be simulated is limited. The LANDIS-II FLM (Scheller et al., 2007) can simulate large areas by stimulating growth as a competition for growing space among cohorts rather than individual trees. A more mechanistic approach within LANDIS-II was recently developed by De Bruijn et al. (2014) by embedding algorithms of the PnET-II stand-level ecophysiology model (Aber et al., 1995) in a LANDIS-II succession extension to mechanistically simulate tree species cohort growth on every landscape cell as a function of competitive interactions for light and water. Accordingly, photosynthetic rates (and therefore growth rates) vary monthly by species and cohorts as a function of precipitation and temperature (among other factors such as CO_2 concentration), which directly affect competition, and ultimately, successional outcomes. Thus, landscape dynamics emerge from the photosynthesis response of species to climate and atmospheric changes, (including extreme climatic events) according to life history traits such as shade and drought tolerance and optimum temperature for photosynthesis, coupled with spatial processes of dispersal and disturbance.

FLMs with relatively weak links to climate are being used to project future landscape dynamics under climate change (e.g., Scheller and Mladenoff (2008), Gustafson et al. (2010)). When such models are parameterized for novel future conditions for which empirical observations are not available, the input parameters are often based on assumptions about system behavior in that future, and such assumptions are rarely tested. There is therefore a critical need for a robust evaluation of the combined effects of changes in temperature, precipitation, cloudiness and CO_2 concentration to inform expectations of forest response to climate change to guide the development and interpretation of FLM studies of climate change. Mechanistic FLMs are difficult to test, primarily because of their reliance on a relatively large number of parameters and because appropriate evaluation data sets are rare. Gustafson et al. (2015) used PnET-Succession to predict the outcome of a precipitation manipulation experiment in a piñon-juniper ecosystem in New Mexico (USA), with considerable success. Loehman et al. (2011) used the mechanistic landscape model FireBGCv2 to simulate effects of altered temperatures (+2.1 and + 6.7 °C growing season temperature) and fire management on western white pines in Montana, USA, and found that higher temperatures increased abundance of western white pine because the resulting increase in fire more severely impacted its competitors. Seidl et al. (2017) used iLand to replicate the results of a controlled thinning trial of Norway spruce across an elevation (climate) gradient in Austria and found that the model reproduced the growth patterns measured in the experiment. Duveneck et al. (2016) used empirical data from 4118 forest inventory plots and monthly net ecosystem exchange at three New England flux tower sites to parameterize PnET-Succession to project the effects of climate change on New England forests. Nevertheless, these studies do not provide a comprehensive evaluation of the impact of individual climate drivers and their interaction.

In this study we used the mechanistic, first principles PnET-Succession model to produce such an evaluation. The objectives for our study were to 1) explore the interacting effects of temperature, precipitation, cloudiness and soil texture (available water capacity) on tree species growth and competition in a highly controlled simulation experiment at the local level, 2) determine how specific life history traits interact with climate and soils to affect growth and competition and 3) conduct a heuristic projection of the effect of global changes in climate and CO_2 concentration on forests as the changing drivers interact with spatial processes at the landscape scale in northern Wisconsin (USA). We hypothesized that response (growth and competitive ability) would be positively related to temperature, precipitation, light and soil texture because