

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

ARTICLE INFO

Article history:

Received 27 February 2017

Received in revised form

6 June 2017

Accepted 8 August 2017

Keywords:

Climate change

Temperature stress

Drought

Elevated CO₂

Cloudiness

Soil water

Forest succession

Mechanistic landscape model

LANDIS-II

PnET-Succession

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 CO₂ 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.

Published by Elsevier Ltd.

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

* Corresponding author.

E-mail address: egustafson@fs.fed.us (E.J. Gustafson).

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, CO₂, 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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

they can each be seen as limiting factors. Further, we hypothesized that response to temperature would be related to optimal temperature for photosynthesis, response to both precipitation and soil available water capacity would be proportional to drought tolerance, and that response to available light would depend on shade tolerance. We also expected that some interactions among treatment factors might be significant and perhaps non-intuitive because of the myriad relationships between the driving factors and sub-processes within the model.

2. Materials and methods

2.1. Simulation model

LANDIS-II simulates broad-scale ($>10^5$ ha) forested landscape dynamics, including succession, seed dispersal, multiple natural disturbance types, forest management, and climate change effects over long (i.e. centuries) temporal scales (Scheller et al., 2007). Landscapes are represented as a grid of interacting cells with user-defined cell size. Individual cells are assumed to be internally homogeneous with respect to abiotic conditions and vegetation characteristics, and are spatially aggregated into ecological land types with homogeneous climate and soils. Forest composition at the cell level is represented as the woody biomass of age cohorts of individual tree species that interact via a suite of vital attributes (e.g., growth capacity, shade tolerance, drought tolerance, longevity) to produce nondeterministic successional pathways sensitive to disturbance type and severity (Mladenoff, 2004).

PnET-Succession (De Bruijn et al., 2014) is one of several available LANDIS-II succession extensions, and it mechanistically projects tree species cohort growth by simulating photosynthetic production at a monthly time step. In PnET-Succession, cohorts compete for water and light in each cell. Cohort size (biomass) determines the priority of access to light, while access to soil moisture depends on each species' relative ability to extract soil water at the water potential of the cell. Cohort leaf biomass is sorted into canopy layers based on woody biomass, which is a surrogate for height, and light attenuates through the resulting mixed-species canopy according to the extinction coefficients of the component species. Soil water is tracked at the grid-cell level using a bulk-hydrology "bucket" model where the water holding capacity of the soil represents the size of the "bucket," with precipitation providing the input, and losses result from foliage interception, evaporation, runoff and percolation out of the rooting zone, and uptake by vegetation (transpiration).

Foliar nitrogen (FolN) is the primary determinant of photosynthetic capacity in PnET-Succession. When water is not limiting, the amount of photosynthesis for a given cohort increases with light available to the cohort (dependent on canopy position and leaf area) and atmospheric CO₂ concentration, and decreases with age and departure from species-specific optimal temperature for photosynthesis. Photosynthesis occurs in the months when average temperature exceeds the species specific minimum, allowing phenology to respond to variation in temperature. As soil water availability decreases, photosynthesis also decreases. PnET-Succession accounts for reductions in biomass accumulation due to growth and maintenance respiration. The model uses a Q₁₀ relationship in which a 10 °C increase in temperature results in a ten-fold increase in respiration rate (Atkins, 1978); foliar respiration depends on temperature and moisture, and maintenance respiration depends on temperature and biomass. When respiration exceeds photosynthetic production (e.g., from water and/or temperature stress), non-structural carbon reserves become depleted and mortality occurs when reserves are below a user-specified minimum at the end of a calendar year. Cohort

establishment probabilities are proportional to computed growth rates below the canopy for each species. Monthly temperature, precipitation, radiation and CO₂ inputs allow growth and establishment rates to vary in response to both gradual change and extreme events.

This approach provides robust capabilities for simulating global change effects on forests at landscape scales. First, PnET-Succession is based on first principles in that it uses primarily fundamental, well-established physiological relationships, making it robust under novel combinations of environmental inputs such as changing climate and CO₂ concentration. Second, explicit modeling of how the drought-tolerance of species affects competition, growth, and establishment can affect successional outcomes (Berdanier and Clark, 2016). Third, species-specific photosynthetic output varies with temperature: (a) net photosynthetic rate (NetPsn) peaks at a user-specified optimal temperature and declines at high temperatures as conductance declines with increasing vapor pressure deficit and (b) growing season length for each species varies according to its minimum temperature for photosynthesis. Fourth, monthly photosynthetically active radiation (PAR) is a model input, and cohorts use this incoming light based on their shade tolerance and light reaching lower canopy layers is reduced based on the leaf area and canopy extinction coefficient of the cohorts making up the canopy. If available radiation varies because of changes in cloudiness, this could also affect light competition. Fifth, elevated temperatures increase surface evaporation and reduce water use efficiency, other factors remaining constant. Outcomes of these local-level processes are emergent properties of the mechanistic simulation of growth (photosynthesis), which comes from the interaction of environmental and physiological attributes rather than phenomenological effects based on growth (biomass) observed under past conditions.

Physiological stress results from inadequate ability to compete for water and/or light, interactions with other life history attributes (e.g., intrinsic photosynthetic capacity, water use efficiency, longevity) or CO₂ concentrations. PnET succession allocates carbon (photosynthates) to pools of foliage, aboveground wood, roots, and non-structural carbon (energy) reserves. The model attempts to maintain non-structural carbon (NSC) at a fixed fraction (NSCfrac) of physiologically active biomass (0.05 in our study), allocating the remainder to foliage, wood and roots to maintain user-specified pool fractions. Because the model tracks carbon reserves, growth reductions under stress can cause reserves to become depleted by non-foliar respiration, which can ultimately result in direct mortality (McDowell et al., 2013; Gustafson et al., 2015). Alternatively, the level of carbon reserves can feed into disturbance extensions that simulate complete or partial disturbance mortality of stressed cohorts.

2.2. Local-level experiment

A local-level experiment (spatial interactions need not be simulated) was conducted using a full-factorial design with four treatment factors (temperature, precipitation, cloudiness (PAR) and soil texture (available water capacity)) applied to assemblages of four species on a single cell. Response variables were chosen to represent various aspects of physiological response to the treatments. Annual net productivity (NetPsn) of each cohort over the course of the growing season was chosen as the indicator of photosynthetic response, integrating effects of temperature on photosynthesis, respiration and length of growing season, as well as seasonal precipitation variability. Furthermore, net photosynthesis is limited in the model by reduction factors linked to each of the treatment factors. Cohort woody biomass was evaluated because it integrates photosynthetic output, water use efficiency

and maintenance respiration. Mean monthly NSCfrac was evaluated because it represents non-structural carbon reserves of the cohort, which are believed to be an indicator of plant stress and inversely correlated with likelihood of mortality (Gustafson et al., 2015; McDowell et al., 2013). The mean age attained by all cohorts on a cell was used as a measure of crowding-induced mortality (competitive exclusion), with a mean age <140 indicating that at least one cohort died prior to the end of the simulation. Rather than choose a single simulation year to compute response variables, we used the mean value observed over the course of each simulation for biomass, net photosynthesis, and NSCfrac, assuming that these averages represent the relative vigor and competitive ability of each cohort in response to the treatments and its competitors throughout its lifetime. For cohorts that died, only the years prior to death were included to represent the state of the cohort prior to death.

Experimental parameter settings (Tables 1 and 2) were applied for 100 years to even-aged (40 years old) assemblages of four species competing on a single cell. CO₂ concentration was not manipulated as an experimental treatment, but CO₂ for all factorial combinations followed the IPCC RCP 6.0 emissions scenario, extended beyond 2100 by Meinshausen et al. (2011) as Extended Concentration Pathways (ECP) in which concentration levels off at 752 ppm in 2150. When life history traits differ among species in an assemblage, certain combinations of abiotic conditions will favor the growth of some species while hindering the growth of others. Furthermore, these traits may interact in different ways depending on the traits of competitors such that the specific combination of life history traits of the species in an assemblage has a large impact on the outcome of their competition. We therefore randomized the life history traits of the four hypothetical deciduous tree species in each replicate by selecting one of three possible values for each of four specific life history traits (Table 1). These life history traits were chosen because they determine growth capacity (FolN) or control the physiological response to the treatments. Each random assemblage was simulated for all combinations (N = 81) of the full factorial of treatments (Table 2) and the response variables for a single species formed a single observation, along with the treatment levels and the values of the four life history traits. We simulated 250 species assemblages, resulting in 81,000 cohort observations.

We used weather data from Oconto county (Wisconsin, USA) (see below) from the period 1949–2010 to create a realistic baseline weather time series, and modified monthly mean baseline temperature and precipitation values by the treatment amount to create treatment weather time series, concatenating copies of those time series to create treatment time series sufficiently long for each experiment. Each treatment factor had three levels (Table 2). The

Table 1
Levels of species life history traits used to randomly create species assemblages for simulation.

Life history trait	Low	Mid	High
FolN (% wt.) ^a	2.2	2.5	2.8
HalfSat (μmol/m ² /s) ^b	275	437.5	600
H3/H4 (MPa) ^c	−0.98/−1.37	−1.07/−1.47	−1.16/−1.57
PsnTOpt (°C) ^d	19	23	27

^a Foliar nitrogen; determines maximum photosynthetic capacity in PnET-Succession.

^b Light level when photosynthesis is half of its full sunlight rate; determines shade tolerance.

^c Drought tolerance parameters; H3 is the water potential below which photosynthesis begins to decline; H4 is the water potential below which photosynthesis stops.

^d Optimum temperature for photosynthesis.

Table 2
Levels of the experimental parameter settings effects relative to the baseline climate.

Treatment factor	Abbreviation	Low	Mid	High
Temperature (°C)	T	+0	+3	+6
Precipitation (%)	Pr	−40	+0	+40
PAR (Light) (%) ^a	P	−10	+0	+10
AWC (Soil) (mm) ^b	AWC	60.5	107.5	150.8

^a Photosynthetically Active Radiation (μmol/m²/s).

^b Maximum available water capacity, calculated as field capacity – wilting point.

range of levels of temperature and precipitation in the experiment were set relative to historical monthly averages and encompass the range predicted by GCMs for the upper Midwest (USA). The mean growing season temperature of the +0 temperature treatment was 16.5 °C with a mean of 23.1 during the warmest month, and under the +6 treatment the values were 22.5 and 29.1 respectively. Historic monthly mean PAR measurements were similarly modified according to the treatment levels, which were chosen to be consistent with observations of global brightening and dimming due to changes in cloudiness and pollution (Wild, 2009). Soil texture was included as a factor because soil texture may have a large effect on the availability of water for tree photosynthesis for a given level of precipitation (Gustafson et al., 2016). The levels of the soil factor created a gradient of available water capacity (AWC), defined as field capacity minus wilting point, using three standard soil texture classes (sand, sandy loam, loam) (Saxton and Rawls, 2004) (Table 2). By using a historical weather stream rather than a GCM projection as a baseline, we eliminated the confounding effect of changes in the temporal patterns of precipitation and temperature variation.

Each replicate random assemblage was simulated on a single 30 m cell, and in each assemblage, a single cohort of each of the four hypothetical species was established on an empty cell in 1970 and grown for 40 years using fixed monthly averages of temperature, precipitation and PAR and constant CO₂ (385 ppm). The treatments were applied beginning in 2010 and run for 100 years. Establishment of new cohorts was not simulated to avoid confounding the experiment. We used PnET-Succession v1.2 (De Bruijn et al., 2014; Gustafson et al., 2016). The complete set of PnET-Succession input parameters is provided in the online Supplement.

2.3. Analysis

Our primary objective was to assess the relative magnitude of impact of each of the main effects on the dynamics of species responses under different competitive environments. We used a least-squares means procedure to compute mean responses to individual experimental effects by holding all covariates to their mean level (Searle et al., 1980). Our expectation was that these effects might potentially interact to produce non-intuitive dynamics. We focused on the relative magnitude of effects and intentionally avoided making inferences about the significance of differences because our model generated different populations for each combination of inputs, and differences in response variables could always achieve statistical significance with enough replicates (White et al., 2014). Readers can draw their own conclusions about significance by comparing 99% confidence intervals among treatment means. Another objective was to verify that the model responds to the driving factors as expected according to the well-established principles incorporated into the model algorithms. We therefore plotted the response variables against the levels of the relevant main effects and against levels of selected life history traits.

2.4. Landscape-level experiment

The landscape-level experiment was similar to the local-level experiment, but featured a large number of real species assemblages (using empirically estimated life history traits for each species) found on a 104,471 ha landscape in Oconto County (Wisconsin, USA), mapped at 30 m resolution (Fig. 1). The experiment included the spatial processes of seed dispersal and a generic stand-replacing disturbance to allow shade-intolerant species to persist. The purpose was to evaluate how the treatments, real species assemblages and the spatial processes of dispersal and disturbance interact to determine species composition at landscape scale. To reduce the factorial size at the landscape scale, we excluded the PAR treatment because it had the least effect in the local-experiment for most response variables, using the PAR = +0 level. Topographic relief is minimal and climate is essentially homogeneous across the study area, so we used the climate inputs (temperature, precipitation, PAR) of the local experiment for all ecological land types. Variation in soil type was included in the land type map, which was produced by assigning all SSURGO (Soil Survey Staff, 2013) soil map polygons to the most similar of the three soil types used in the local experiment (Fig. 1). The initial forest conditions (species and age cohorts) were those used by Janowiak et al. (2014), created using the methods of Wilson et al. (2012). Species establishment probabilities were calculated

dynamically by the model on each cell at each time step, being proportional to growth rates below the canopy for each species.

Stand-replacing disturbance was simulated using the Base Harvest v3.0 extension (Gustafson et al., 2000). We arbitrarily defined a grid of 5.8 ha (8×8 cells) stands across the landscape grid, and 3.3% of the stands were selected for harvest each decade (300 year return interval). Only stands dominated by aspen or jack pine of at least 30 years of age were selected for disturbance, and all cohorts of all species were removed. The harvest and output extensions used a 10-year time step and three replicates of each factorial combination (temperature x precipitation) were simulated for 400 years to allow landscape effects to fully develop. We analyzed the response to the treatments as a function of drought-tolerance, optimal temperature for photosynthesis (PsnTOpt) and forest type (Table 3), using the average biomass on all landscape cells at the end of each decade as the response variable. Our specific hypotheses at the landscape level were: 1) productivity response to precipitation will be inversely proportional to drought-tolerance (H3/H4), 2) response to temperature will be proportional to PsnTOpt, and 3) treatments will alter the relative abundance of forest types (composition). With only a single landscape, we could not evaluate the generality of our results, but we evaluated whether our results were consistent with the hypotheses by examining plots of species class biomass through time by treatment.

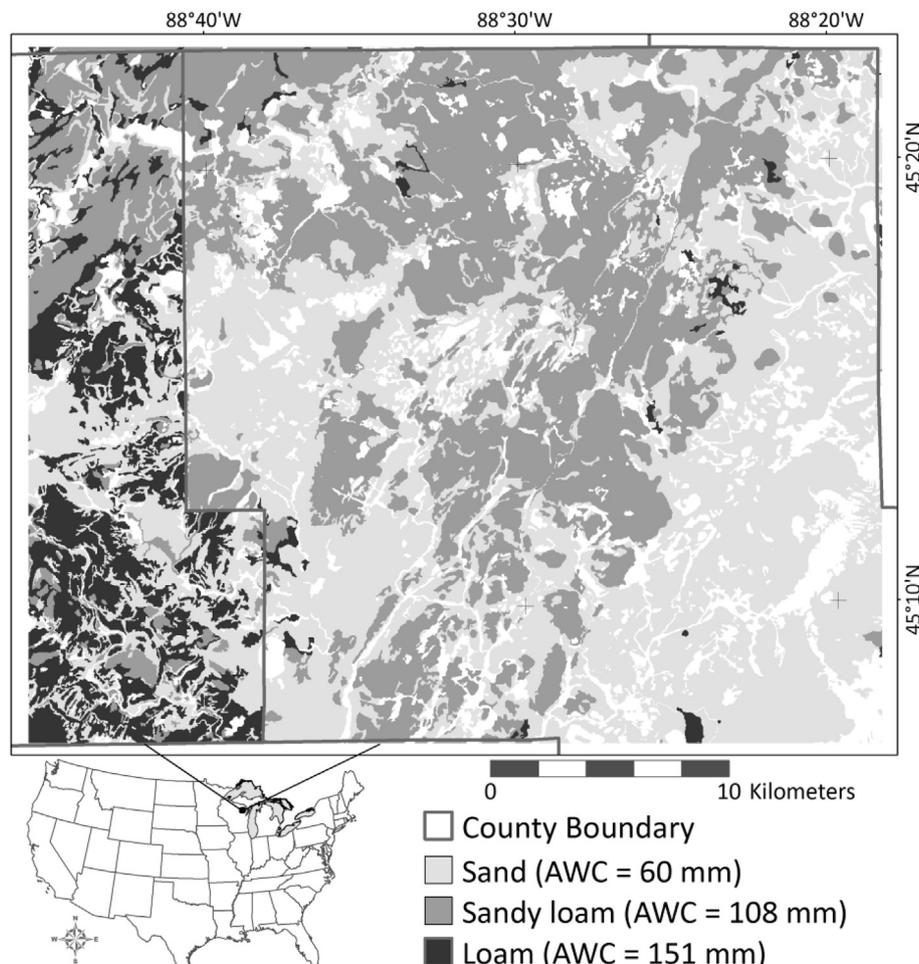


Fig. 1. Soil types used in the study area in Oconto county (Wisconsin, USA). Unshaded areas are non-forested and not included in the simulation.

Table 3
Species assigned to each forest type.

Forest type	Species
Aspen-birch	<i>Betula papyrifera</i> , <i>Populus balsamifera</i> , <i>P. grandidentata</i> , <i>P. tremuloides</i>
Pine-oak-hemlock	<i>Pinus strobus</i> , <i>P. resinosa</i> , <i>Quercus rubra</i> , <i>Tsuga canadensis</i>
Mixed oak	<i>Q. alba</i> , <i>Q. ellipsoidalis</i> , <i>Q. macrocarpa</i> , <i>Q. veletina</i>
Spruce-fir	<i>Picea glauca</i> , <i>Abies balsamea</i>
Mixed swamp conifer	<i>P. mariana</i> , <i>Thuja occidentalis</i>
Sugar maple-beech-basswood	<i>Acer saccharum</i> , <i>B. allegheniensis</i> , <i>Fagus grandifolia</i> , <i>Tilia americana</i>
Red maple	<i>A. rubrum</i>
Cherry-ash	<i>Prunus serotina</i> , <i>Fraxinus americana</i> , <i>F. pennsylvanica</i>

3. Results

3.1. Local experiment

At the local level, the effect of temperature on net photosynthesis was nonlinear such that NetPsn increased at the +3 °C level but declined at the +6 °C level, compared to the +0 °C level as shown in Fig. 2a. However, the production of wood biomass did not follow the behavior of NetPsn because maintenance respiration

costs increased with temperature, resulting in a consistent decline as temperature increased (Fig. 2b). Cohort energy reserves (NSCfrac) and cohort survival also decreased as temperature increased (Fig. 3) for similar reasons. The precipitation treatment had the greatest effect on most response variables, with increased precipitation resulting in greater NetPsn, wood biomass and energy reserves (Figs. 2 and 3). However, increased precipitation actually decreased mean cohort survival (Fig. 3b) within assemblages because less water stress initially allowed more productive species

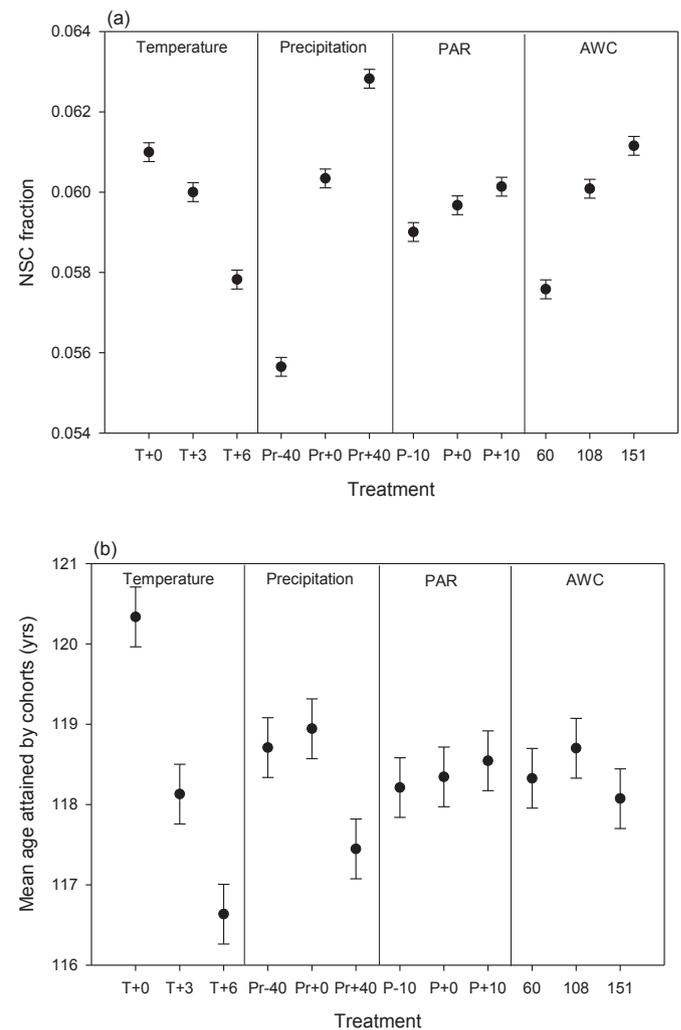
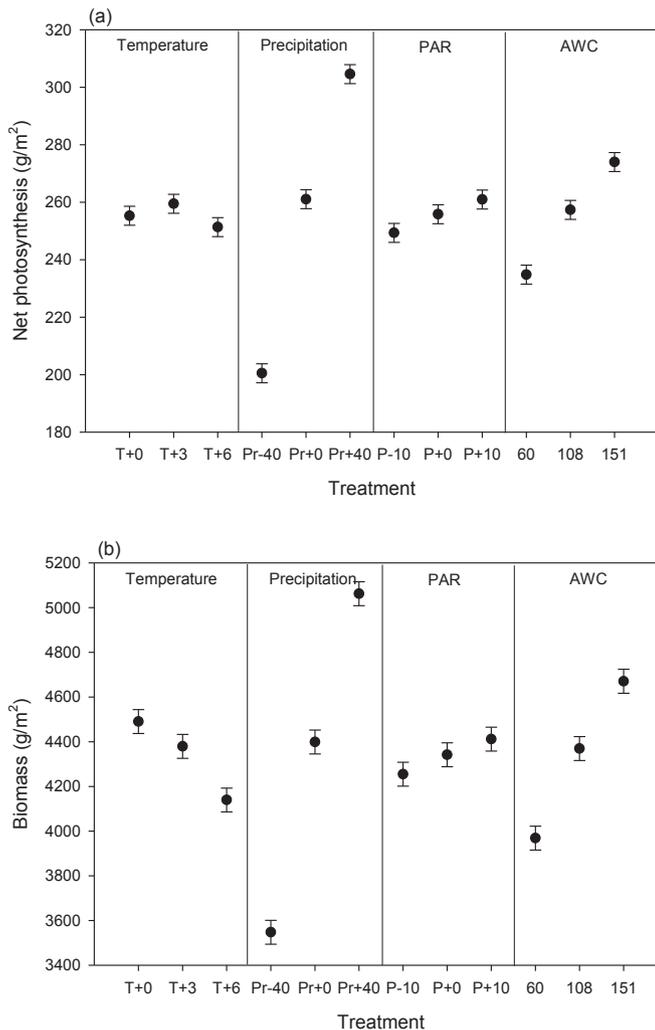


Fig. 2. Mean and 99% confidence intervals (whiskers) of (a) average annual net photosynthesis ($R^2 = 0.03$) and (b) woody biomass of living cohorts ($R^2 = 0.03$) over the 100 simulated years in response to the treatment levels, adjusted using least squares techniques. There was no evidence of important interactions. Treatment units and abbreviations as in Table 2.

Fig. 3. Mean and 99% confidence intervals (whiskers) of (a) cohort energy reserves ($R^2 = 0.04$) and (b) competitive exclusion $R^2 = 0.01$) of living cohorts in response to the treatment levels, adjusted using least squares techniques. There was no evidence of important interactions except perhaps between temperature and precipitation. Treatment units and abbreviations as in Table 2.

to put on biomass quickly and thus consume more water, resulting in quicker and greater water stress for all cohorts in later years. The greater water stress proved fatal to the less drought tolerant species, which in some cases were the more productive species. Although cohorts with greater biomass have priority access to water in the model, they also have higher maintenance respiration costs, which may quickly deplete their carbon reserves when chronic water stress occurs. Only the cohort survival variable accurately reflects cohort mortality because mortality tends to happen precipitously, and NetPsn and NSCfrac are depressed only briefly prior to cohort death. PAR was positively related to all response variables, but PAR had the least effect of all the treatments (Figs. 2 and 3). The effect of AWC was similar to that of precipitation for similar reasons, although the magnitude of the effect was less (Figs. 2 and 3). There was little apparent interaction between temperature and precipitation effects (Fig. 4) except for competitive exclusion, where cohort survival declined most when precipitation was least (Fig. 4c). Similarly, there was little apparent interaction between PAR and AWC effects (Fig. 5) except for competitive exclusion, where the effect of PAR was different for each level of AWC (Fig. 5c).

The interactions between the treatments and life history traits provided insights into the sometimes divergent behavior of the

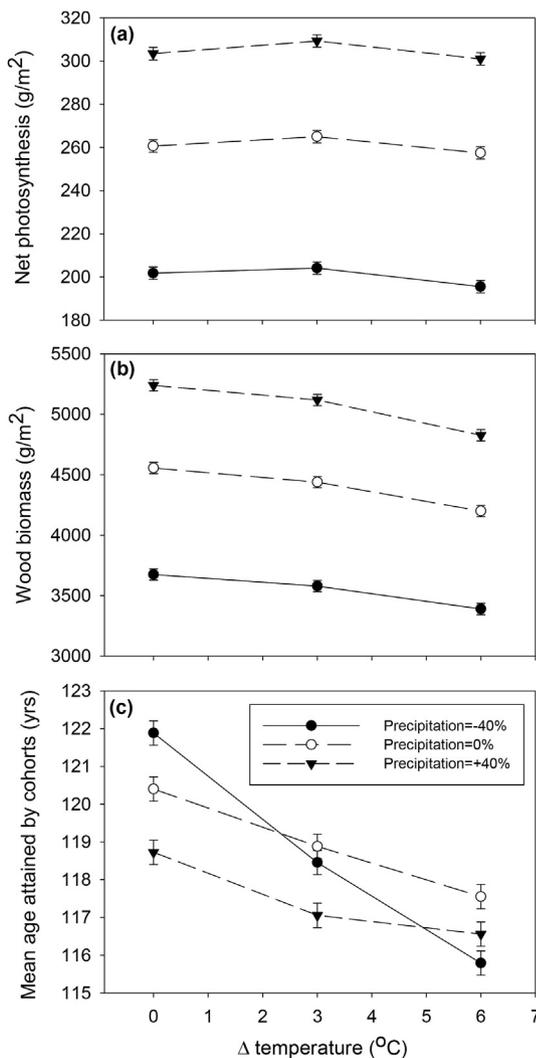


Fig. 4. Relative effect of the temperature and precipitation treatments at the local level. Error bars show one standard error of the adjusted means, and are often less than the width of symbols.

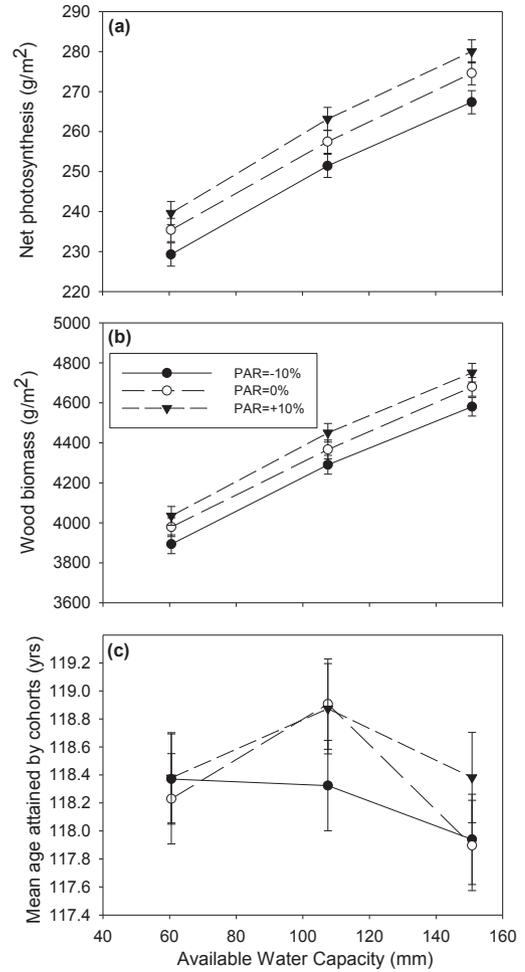


Fig. 5. Relative effect of the PAR and AWC treatments at the local level. Error bars show one standard error of the adjusted means, and are often less than the width of symbols.

response variables. Temperature and PsnTOpt interacted such that when optimum temperature was near the mean of the three temperature time series ($PsnTOpt = 23$), NetPsn was highest and temperature had little effect, but NetPsn declined with increasing temperature when PsnTOpt was low, and increased with temperature when PsnTOpt was high (Fig. 6a). Again, the production of wood biomass did not follow the behavior of NetPsn because maintenance respiration costs increased with temperature, resulting in a greater rate of decline in biomass as temperature increased (Fig. 6b). Energy reserves (NSCfrac) responded similarly for similar reasons, with the highest temperature markedly reducing energy reserves, especially for species with low PsnTOpt (Fig. 6c). Precipitation and drought-tolerance interacted such that increasing drought-tolerance (increasing H3/H4) decreased the effect of precipitation (Supplement Fig. 1). As drought-tolerance decreased, the effect on response variables was non-linear, reflecting the relation between water potential (pressure head) and the water-stress photosynthesis reduction factor in PnET-Succession. The response to light was driven almost entirely by shade-tolerance (HalfSat), with only energy reserves (NSCfrac) appreciably responsive to differences in PAR (Supplement Fig. 2). Although shade-intolerant cohorts grew well in the early years of the simulations, the results shown represent 100 years of growth, during which time the canopy closed and competition for light became acute.

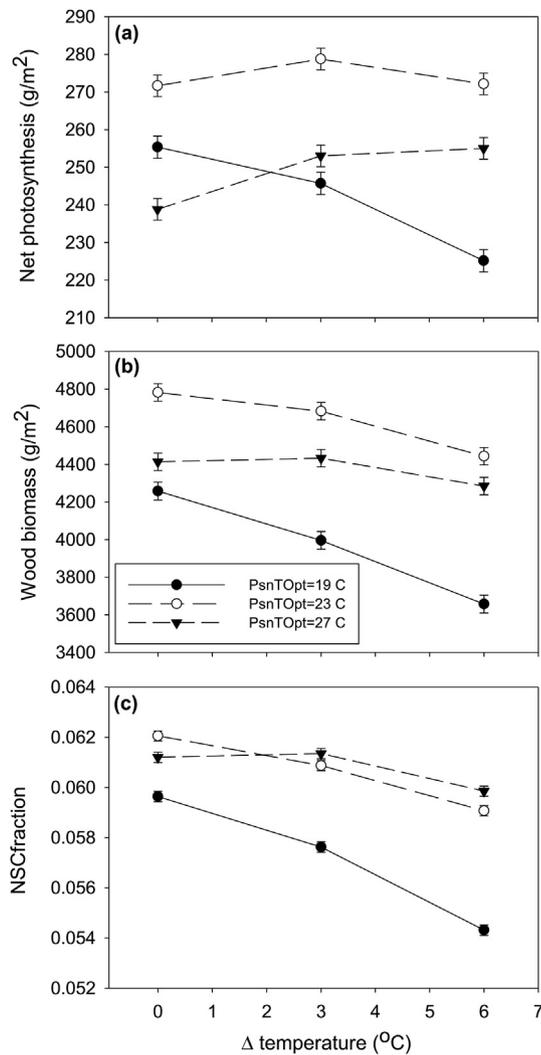


Fig. 6. Relative effect of temperature treatment levels and levels of the PsnTOpt life history trait at the cohort level. Error bars show one standard error of the adjusted means, and are often less than the width of symbols.

3.2. Landscape experiment

The effects of the treatments at the landscape scale were relatively subtle, and the short-term fluctuations through time were driven by the generic disturbance and cohort senescence. The precipitation treatment generally produced a greater increase of biomass as drought-tolerance declined, supporting the hypothesis that the biomass response to precipitation would be inversely proportional to drought-tolerance (Fig. 7). The effect of temperature on drought tolerance classes was weak except for the two least drought-tolerant classes, where the +6 temperature treatment increased biomass of the second least drought tolerant class ($H4 = -1.42$) at the expense of the least drought tolerant class ($H4 = -1.37$) under all precipitation treatments. The most drought-tolerance class ($H4 = -1.57$) declined to very low levels of biomass, likely because those species tend to be somewhat shade-intolerant. The temperature treatment produced effects on the biomass of PsnTOpt classes similar to those observed in the local-level experiment, weakly supporting our hypothesis that response to temperature would be proportional to optimal temperature for photosynthesis (Fig. 8). The class with PsnTOpt of 19–20 °C increased in biomass under the +3 °C treatment, but decreased

under the +6 °C treatment, similar to the local experiment results. The 21–22 °C class decreased in biomass with increasing temperature, the 23–24 °C was not clearly affected by temperature, and the 25–26 °C class increased with increasing temperature in the first 200 years, but by year 400 it was outperformed by the 23–24 °C class, presumably due to other factors such as age. Precipitation interacted with these effects slightly, especially at the highest temperature. Our hypothesis that treatments would alter forest composition at the landscape scale was not clearly supported. The rank order of forest type abundance did not change except for short periods of time, but the relative abundance of forest types was clearly affected by the treatments, particularly temperature (Fig. 9).

4. Discussion

One of the most compelling features of PnET-Succession is that its mechanistic simulation of growth and competition is based on well-established first principles, and that growth and competitive outcomes are emergent properties of the interactions of the processes simulated. The results of our study emerged from the interactions among photosynthetic capability (FolN), shade tolerance (HalfSat), drought-tolerance (H3/H4), optimal temperature (PsnTOpt) and soil texture (AWC) as a consequence of the experimental treatments. The model also accounts for the effects of temperature on respiration rate, water use efficiency (transpiration) and conductance, the effect of CO₂ concentration on conductance and the effect of leaf area and extinction coefficient on light competition. This is vital for studies of the response of forest ecosystems to environmental conditions that are outside of the domain under which they have been studied in the past (e.g., global changes) (Gustafson, 2013). For example, our finding that greatly elevated temperatures depress growth (Figs. 2–4) runs counter to conventional wisdom, which holds that the combination of elevated temperatures and longer growing seasons stimulates productivity. Our mechanistic model shows that this is true for modestly higher temperatures, but that multiple constraints (VPD, WUE, respiration costs) serve to greatly reduce net productivity at higher temperatures, even when PsnTOpt is high (Fig. 6). Such capabilities in a forest landscape model allow robust projections of the impacts of climate change at landscape scales by linking simulation of mechanistic competitive interactions with process-based disturbance modules, all driven by climate variables varying at a monthly time step.

4.1. Insights

In the local experiment, temperature ultimately had a variable effect (positive at +3 °C and negative at +6 °C) on NetPsn within and across cohorts, driven primarily by reduced stomatal conductance at elevated temperatures that was not offset by the increasing CO₂ concentrations of the ECP6 emissions scenario. Climate warming generally lengthens growing seasons, and is widely expected to increase forest productivity in temperate and boreal ecosystems based on a wide range of empirical data from the recent past (Boisvenue and Running, 2006; Cole et al., 2010). However, our results suggest that reduced stomatal conductance and elevated maintenance respiration in the middle of the growing season more than offset the longer season when climate warms to +6 °C, although the temperature at which productivity peaks depends on the species. In the model (and in real life), species that reach maximum photosynthetic capacity at lower temperatures where the constraints of conductance and respiration costs are minimal can out-grow species with higher optimal temperatures. The latter operate at suboptimal photosynthesis rates when the constraints of

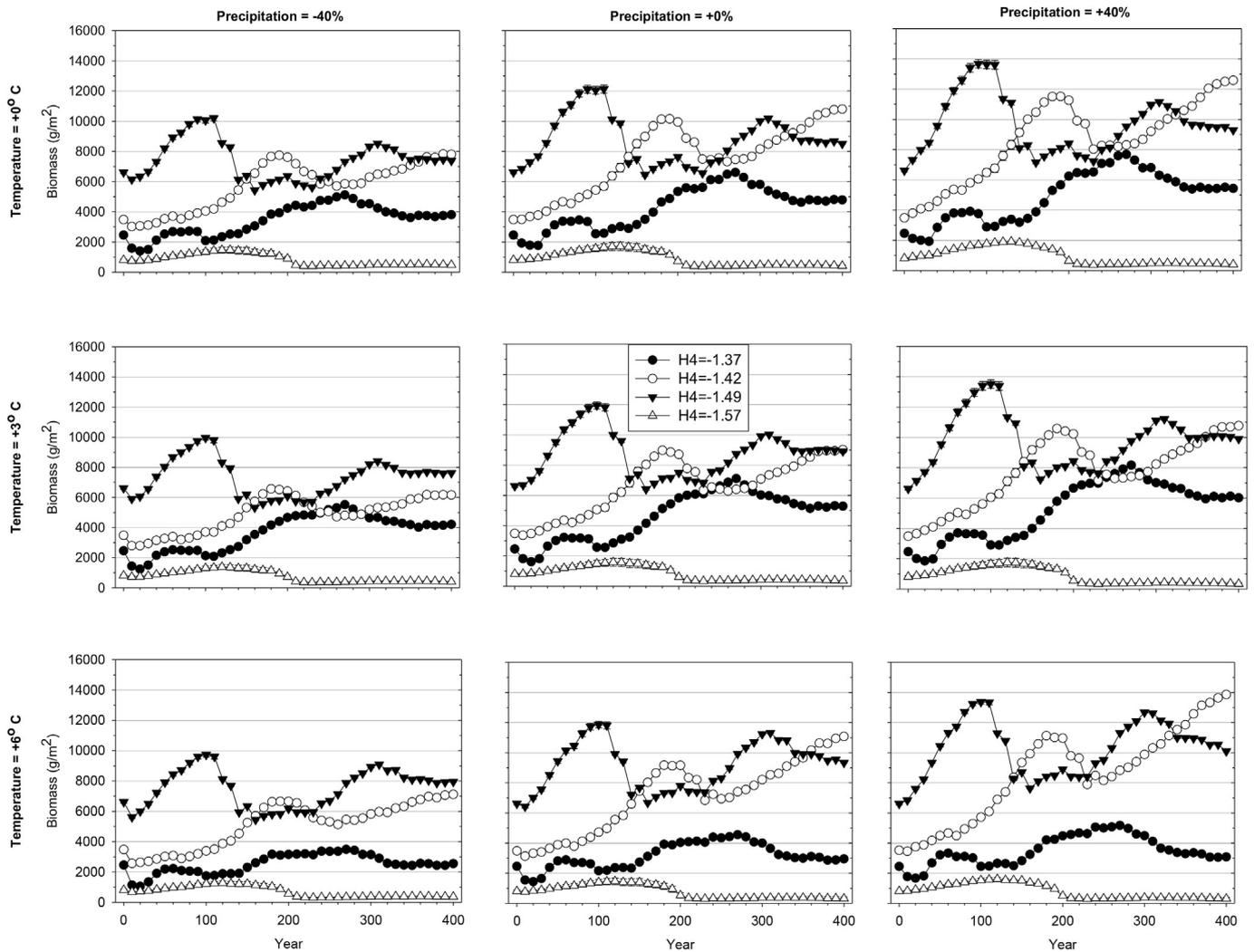


Fig. 7. Mean biomass of drought tolerance groups on all landscape cells. H3 and H4 were modified in tandem, and the H4 parameter specifies the soil water potential at which photosynthesis ceases. Each panel represents a treatment combination. Error bars show one standard deviation, and are often less than the width of symbols.

conductance and respiration are low, but face high respiration and transpiration costs when operating near their optimum temperature (Kubiske and Abrams, 1994; Rodríguez-Calcerrada et al., 2015). The net result is minimal to no gain in NetPsn at high temperatures even for species with higher optimal temperatures (Fig. 10). In non-random assemblages comprised only of species with optimal temperatures higher than current mean temperatures, elevated temperatures may have less of a negative effect than seen in our results, but the constraints of reduced conductance and increased respiration costs still apply. It is widely believed that elevated CO₂ will offset these constraints (Boisvenue and Running, 2006), but our results suggest that even a fairly high emissions scenario (752 ppm CO₂) may not be enough. In the landscape experiment, the +6°C temperature treatment negatively impacted many species, but only red maple (PsnTOpt = 26 °C, intermediate shade tolerance) was able to substantially increase biomass at the expense of species that were negatively affected (not shown).

Our results clearly show that water is the main limiting climatic factor for cohort growth, and its availability has a major impact on competitive outcomes. Both precipitation and AWC determine water availability; precipitation determines water inputs and AWC determines the size of the “bucket” that holds those inputs. We

found that each has about the same relative influence on growth (Figs. 2 and 3). In our model, cells with only young cohorts are not limited by water because their cumulative demand for water is low, but eventually the unconstrained growth associated with adequate water increases water demand (transpiration) such that water becomes limiting. As water potential drops, less drought-tolerant species have their photosynthetic output reduced while more drought-tolerant species (higher value of H3/H4) thrive (Kubiske and Abrams, 1994). As continued growth and leaf area production increases water consumption, or if water inputs are reduced (drought), the less drought-tolerant species will be completely unable to photosynthesize (water potential lower than H3/H4), while more drought-tolerant species may maintain a reduced level of photosynthesis sufficient to cover respiration costs (Noormets et al., 2008). This gives more drought-tolerant species a considerable competitive advantage, and if the water stress is chronic, less drought-tolerant species die because they are unable to replenish their carbon reserves (McDowell et al., 2013; Gustafson et al., 2016) or become vulnerable to mortality agents such as insects (Berdanier and Clark, 2016). (A link between PnET-Succession and LANDIS-II disturbance extensions (e.g., Biomass Insects) is currently in development.) In the landscape experiment, the –40% precipitation

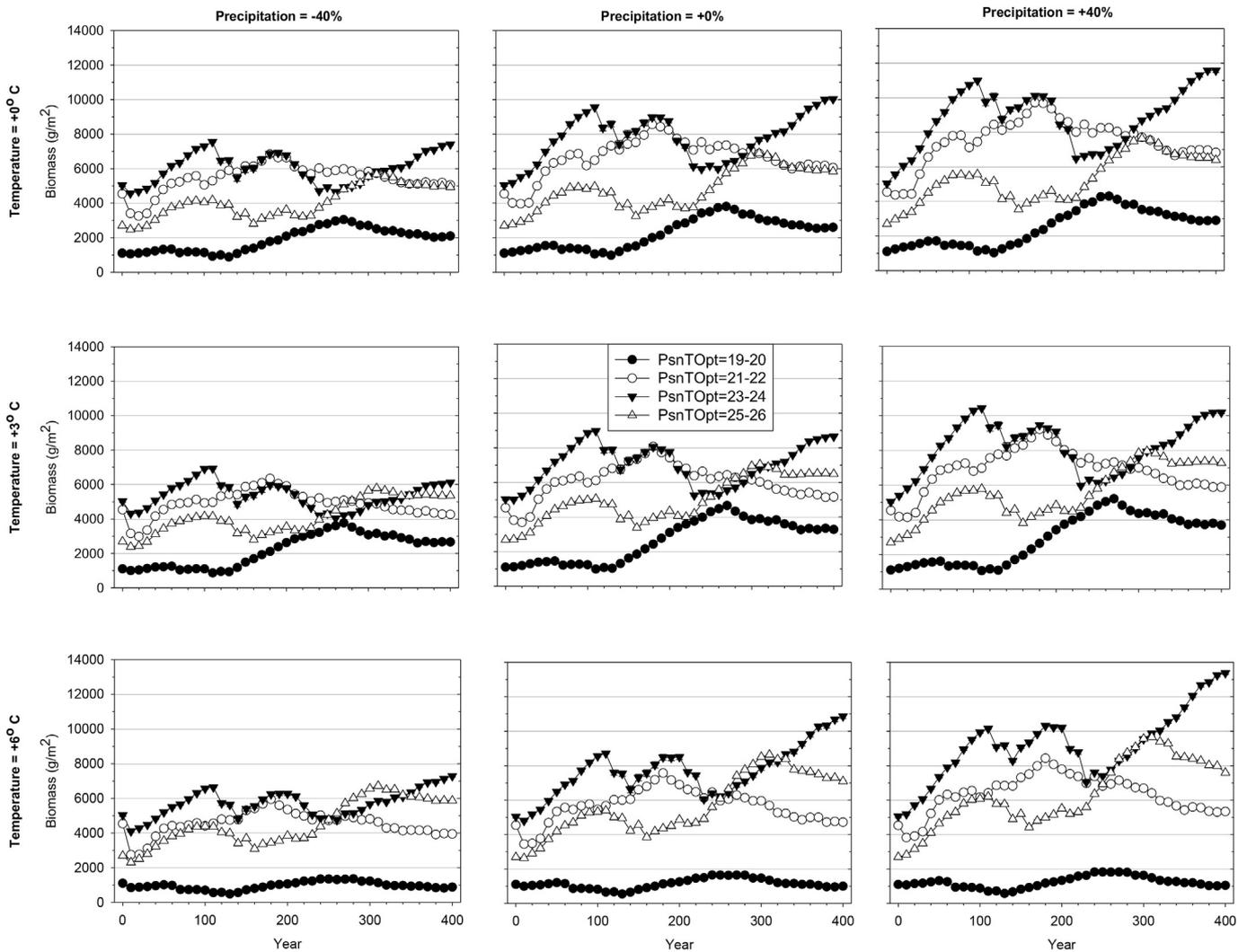


Fig. 8. Mean biomass of optimum temperature groups on all landscape cells. The PsnTOpt parameter specifies the temperature that is optimal for photosynthesis. Each panel represents a treatment combination. Error bars show one standard deviation, and are often less than the width of symbols.

treatment negatively impacted most species, but even the most drought-tolerant species were able to increase growth only slightly in response to negative impacts on their competitors (not shown).

Gustafson et al. (2016) showed that the mechanistic simulation of growth as the competition for light and water to support photosynthesis in PnET-Succession explained the empirical findings of Gustafson and Sturtevant (2013) that drought-induced mortality is better explained by drought duration than drought severity. Brief droughts allow cohorts to quickly replenish their carbon reserves when each drought ends, even when such droughts are frequent, while extensive droughts do not allow such replenishment, increasing the likelihood of mortality. In this study we showed that the model also simulates competitive interactions under chronic changes in precipitation that operate at temporal scales much longer than those of droughts, and that the cumulative effects of such chronic changes on competition can be important.

Not surprisingly, the effect of light (PAR) on growth is not as important as water (precipitation, AWC), but it is not trivial. Surface solar radiation (SSR) varies annually at a given site according to cloudiness, but it also varies globally at much longer time scales. SSR generally declined by 2–5% per decade between 1960 and 1990, and has been increasing at similar rates since then (Wild, 2009). These changes have been shown to not be externally

forced by the sun, but are driven by cloud abundance and atmospheric aerosol characteristics caused by anthropogenic emissions and volcanic activity (Farquhar and Roderick, 2003; Wild, 2009). Additionally, clouds diffuse light, which may actually increase photosynthetic efficiency because diffuse light penetrates deeper into the canopy than does direct sunlight (Gu et al., 2003). Our model does not simulate diffusion effects, modeling the extinction of direct radiation through each canopy layer (Aber and Federer, 1992). Nevertheless, it mechanistically simulates competition for light, and our finding that PAR effects are relatively modest compared to other factors suggests that adding model complexity to distinguish between direct and diffuse light may not be warranted.

Our results also provide perspective on results reported by others. For example, Duveneck et al. (2016) and Wang et al. (2016) reported a simulated increase in growth and biomass in northeastern US forests over the next century and attributed a significant positive effect to longer growing seasons resulting from climate warming. Myneni et al. (1997) related increased remotely-sensed NDVI at high northern latitudes to longer and warmer growing seasons ($<+4$ °C during the growing season), but their methods did not translate NDVI to biomass growth. Barber et al. (2000) used a 90-year tree-ring record of white spruce in Alaska to show that

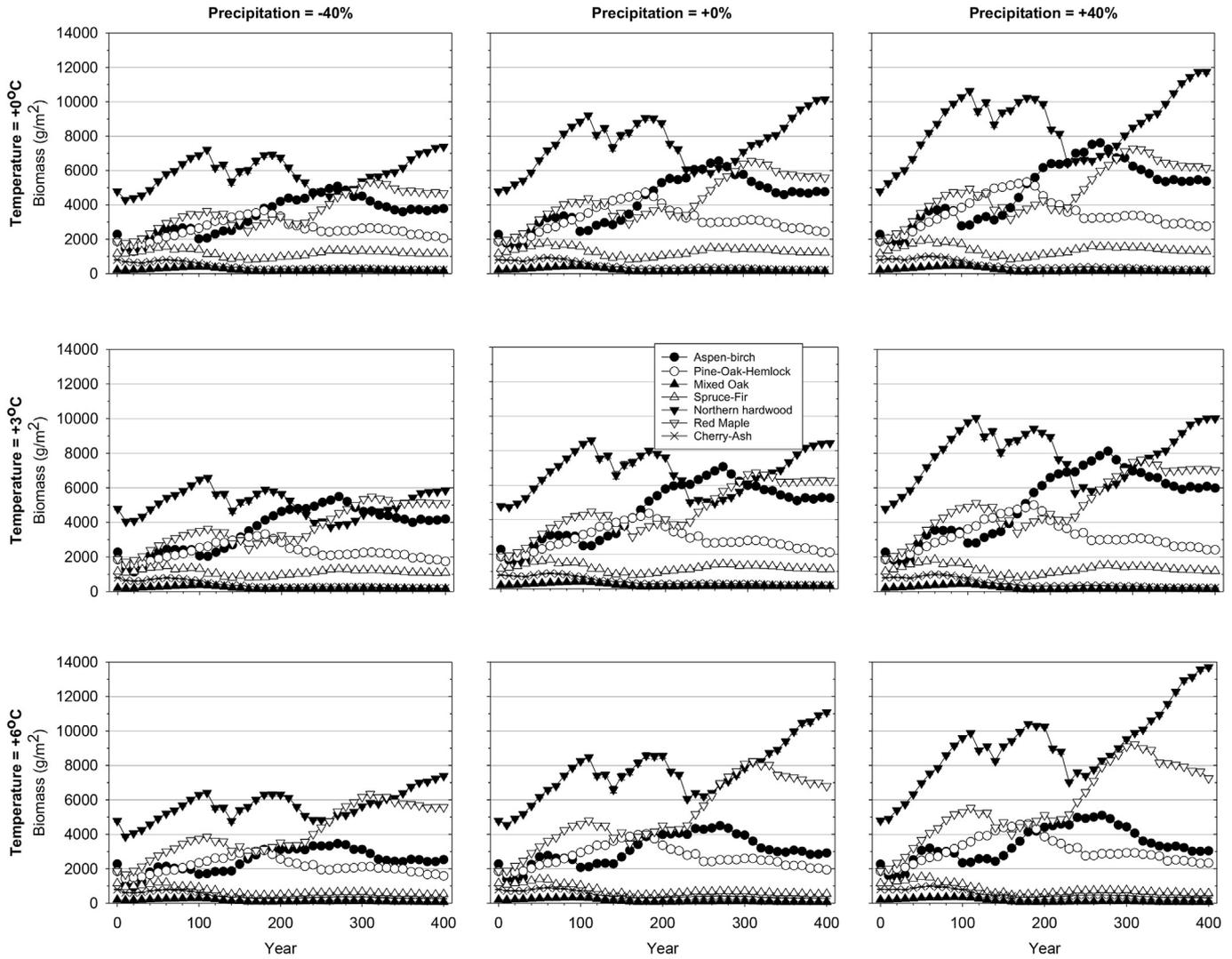


Fig. 9. Effect of the treatments on species composition. Values represent the mean biomass of species groups across all landscape cells. Each panel represents a treatment combination. Error bars show one standard deviation, and are often less than the width of symbols.

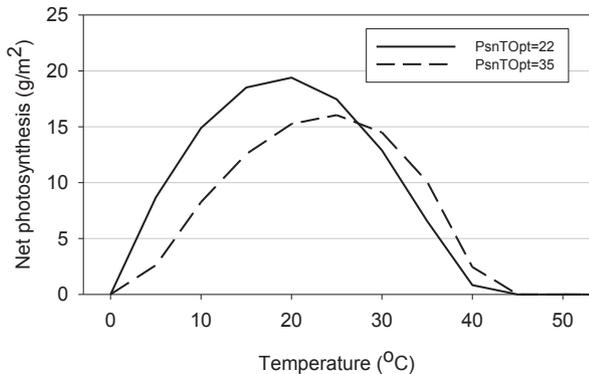


Fig. 10. Interaction in PnET-Succession of the species-specific parameter PsnTOpt and temperature on the rate of photosynthesis driven by elevated stomatal conductance and foliar respiration costs at higher temperatures.

growth has decreased with increasing temperature because of temperature-induced drought stress. Nemani et al. (2003) used climate data and productivity efficiency models to show that global climate changes (1982–1999) eased climatic constraints

(temperature, water and radiation) on plant growth globally, but those results do not reflect the more dramatic changes that have occurred in recent decades. Our results help interpret these published results, especially when a reader contemplates extrapolating them to growing season temperature increases of more than 3 °C.

4.2. Caveats

Our study used a simulation experiment to link climate drivers to tree competition outcomes. This resulted in some important differences from empirical experiments. 1) We decided that the best way to detect the signal of the main effects from the noise of differential competitive ability was to randomize the values of the parameters that control ability to compete for light, water and growing space. This resulted in some unrealistic combinations of species traits existing on a cell, but eliminating the correlation of life history traits enabled us to discover the interaction of traits and climate drivers. 2) We decoupled climate and CO₂ concentration to better observe climate effects. 3) Our precipitation treatment used historical temporal variation in precipitation, but in the future, drought events may become longer and more extreme, or precipitation events more intense but of shorter duration (IPCC, 2013).

Longer droughts were not simulated by our methods, so our results likely underestimate effects of the –40% precipitation treatment. 4) Our landscape experiment did not include disturbances other than those necessary to allow the shade-intolerant species to persist (aspen, birch, jack pine). Our finding that landscape change is subtle under climate change scenarios may not hold when disturbances that impact all species are included and when drought events become longer.

We also note that much of the dynamics in landscape-scale trajectories is not solely driven by the experimentally manipulated abiotic drivers. The major declines in biomass seen in Fig. 9 were likely caused by age-induced senescence (Pregitzer and Euskirchen, 2004; Drake et al., 2010) and death of multiple cohorts, which in turn released other cohorts. The local-level experiment had only young, even-aged assemblages without regeneration, while the landscape experiment had many uneven-aged, layered canopy cells that developed over 400 years, enabling ubiquitous desynchronization of cohort growth stages. Also, competitive ability was not determined solely by life history traits, because cohorts with greater biomass have an advantage in competition for light and water in the model. Furthermore, the disturbances simulated did not affect all species equally. Forest landscape dynamics are exceedingly complex because of the myriad biotic and abiotic factors that determine successional outcomes, illustrating the usefulness of the highly controlled local-level experiment to illuminate the interaction of specific abiotic drivers and life history traits.

Our study helps set expectations for the outcome of modeling studies that seek to project forest futures under climate and atmospheric changes. Elevated temperatures should not be expected to enhance productivity unless the temperature increase is modest, or unless precipitation also increases dramatically. Longer growing seasons and reduced stomatal conductance associated with increasing CO₂ concentrations may be not sufficient to offset the increased respiration caused by elevated temperatures. Competition for water was the major factor driving competitive outcomes and, therefore, forest succession. Carbon reserves (NSCfrac) were also reduced with elevated temperature, and although increased precipitation may mitigate this decline, increased precipitation may not be enough to reduce mortality rate under elevated temperatures (Fig. 4 c). Models used to make projections of landscape futures under climate change must have robust capabilities to simulate the impact of competition for water on forest dynamics, and linear effects of temperature should be avoided.

Acknowledgments

Funding was provided by the Northern Research Station of the USDA Forest Service and USDA National Institute of Food and Agriculture Grant #105321. Sue Lietz provided GIS assistance. We thank Nate Lichti, Matthew Duvencek, Yu Liang and three anonymous reviewers for critical reviews of the manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.envsoft.2017.08.001>.

References

Aber, J.D., Federer, C.A., 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92, 463–474.

Aber, J.D., Ollinger, S.V., Federer, C.A., et al., 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Clim. Res.* 5, 207–222.

Aber, J.D., Ollinger, S.V., Driscoll, C.T., 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecol. Model.* 101, 61–78.

Atkins, P.W., 1978. *Physical Chemistry*. Oxford University Press, Oxford UK, 1034 pp.

Barber, V.A., Juday, G.P., Finney, B.P., 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405, 668–673.

Berdanier, A.B., Clark, J.S., 2016. Multiyear drought-induced morbidity preceding tree death in southeastern U.S. forests. *Ecol. Appl.* 26, 17–23.

Boisvenue, C., Running, S.W., 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Glob. Change Biol.* 12, 862–882. <http://dx.doi.org/10.1111/j.1365-2486.2006.01134.x>.

Cole, C.T., Anderson, J.E., Lindroth, R.L., Waller, D.M., 2010. Rising concentrations of atmospheric CO₂ have increased growth of natural stands of quaking aspen (*Populus tremuloides*). *Glob. Change Biol.* 16, 2186–2197. <http://dx.doi.org/10.1111/j.1365-2486.2009.02103.x>.

Cuddington, K., Fortin, M.-J., Gerber, L.R., Hastings, A., Liebhold, A., O'Connor, M., Ray, C., 2013. Process-based models are required to manage ecological systems in a changing world. *Ecosphere* 4, 20. <http://dx.doi.org/10.1890/ES12-00178.1>.

Dale, V.H., Joyce, L.A., McNulty, S., et al., 2001. Climate change and forest disturbances. *BioScience* 51, 723–734.

De Bruijn, A., Gustafson, E.J., Sturtevant, B.R., Foster, J.R., Miranda, B.R., Lichti, N.L., Jacobs, D.F., 2014. Toward more robust projections of forest landscape dynamics under novel environmental conditions: embedding PnET within LANDIS-II. *Ecol. Model.* 287, 44–57.

Drake, J.E., Raetz, L.M., Davis, S.C., DeLucia, E.H., 2010. Hydraulic limitation not declining nitrogen availability causes age-related photosynthetic decline in loblolly pine (*Pinus taeda* L.). *Plant, Cell Environ.* 33, 1756–1766.

Duvencek, M., Thompson, J.R., De Bruijn, A., Gustafson, E., 2016. Recovery dynamics and climate change effects to future New England forests. *Landsc. Ecol.* <http://dx.doi.org/10.1007/s10980-016-0415-5> xx, x–y.

Farquhar, G.D., Roderick, M.L., 2003. Pinatubo, diffuse light, and the carbon cycle. *Science* 299, 1997–1998.

Gu, L., et al., 2003. Response of a deciduous forest to the Mount Pinatubo eruption: enhanced photosynthesis. *Science* 299, 2035–2038. <http://dx.doi.org/10.1126/science.1078366>.

Gustafson, E.J., 2013. When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. *Landsc. Ecol.* 28, 1429–1437.

Gustafson, E.J., Shifley, S.R., Mladenoff, D.J., He, H.S., Nimerfro, K.K., 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. *Can. J. For. Res.* 30, 32–43.

Gustafson, E.J., Shvidenko, A.Z., Sturtevant, B.R., Scheller, R.M., 2010. Predicting global change effects on forest biomass and composition in south-central Siberia. *Ecol. Appl.* 20, 700–715.

Gustafson, E.J., Sturtevant, B.R., 2013. Modeling forest mortality caused by drought stress: implications for climate change. *Ecosystems* 16, 60–74.

Gustafson, E.J., Keane, R.E., 2014. Predicting changes in forest composition and dynamics – landscape-scale process models. Online. <http://www.fs.usda.gov/ccrc/topics/process-models>.

Gustafson, E.J., De Bruijn, A.M.G., Kubiske, M.E., Pangle, R.E., Limousin, J.-M., McDowell, N., Sturtevant, B.R., Muss, J., Pockman, W.T., 2015. Integrating ecophysiology and forest landscape models to better project drought effects under climate change. *Glob. Change Biol.* 21, 843–856. <http://dx.doi.org/10.1111/gcb.12713>.

Gustafson, E.J., De Bruijn, A.M.G., Miranda, B.R., Sturtevant, B.R., 2016. Implications of mechanistic modeling of drought effects on growth and competition in forest landscape models. *Ecosphere* 7, e01253. <http://dx.doi.org/10.1002/ecs2.1253>.

He, H.S., 2008. Forest landscape models: definitions, characterization, and classification. *For. Ecol. Manag.* 254, 484–498.

IPCC, 2013. *Climate change 2013: the physical science basis*. In: Stocker, T.F., Qin, D., Plattner, G.-K., et al. (Eds.), Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY.

Janowiak, M.K., et al., 2014. Forest ecosystem Vulnerability Assessment and Synthesis for Northern Wisconsin and Western Upper Michigan: a Report from the Northwoods Climate Change Response Framework Project. Gen. Tech. Rep. NRS-136. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

Keane, R.E., Parsons, R., Hessburg, P., 2002. Estimating historical range and variation of landscape patch dynamics: limitations of the simulation approach. *Ecol. Model.* 151, 29–49.

Keane, R.E., Loehman, R.A., Holsinger, L.M., 2011. The FireBGCV2 Landscape Fire and Succession Model: a Research Simulation Platform for Exploring Fire and Vegetation Dynamics. Gen. Tech. Rep. RMRS-255. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO: USA.

Keane, R.E., Miller, C., Smithwick, E., McKenzie, D., Falk, D., Kellogg, L., 2015. Representing climate, disturbance, and vegetation interactions in landscape models. *Ecol. Model.* 309 (310), 33–47.

Kubiske, M.E., Abrams, M.D., 1994. Ecophysiological analysis of woody species in contrasting temperate communities during wet and dry years. *Oecologia* 98, 303–312.

Kurz, W.A., Beukema, S.J., Klenner, W., Greenough, J.A., Robinson, D.C.E., Sharpe, A.D., Webb, T.M., 2000. TELSA: the tool for exploratory landscape scenario analyses. *Comput. Electron. Agric.* 27, 227–242.

- Lischke, H., Zimmermann, N.E., Bolliger, J., Rickebusch, S., Löffler, T.J., 2006. TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecol. Model.* 199, 409–420.
- Loehman, R.A., Clark, J.A., Keane, R.E., 2011. Modeling effects of climate change and fire management on western white pine (*Pinus monticola*) in the northern rocky mountains, USA. *Forests* 2, 832–860.
- McDowell, N.G., Fisher, R.A., Xu, C., et al., 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel–experiment framework. *New Phytol.* 200, 304–321.
- Medlyn, B.E., Duursma, R.A., Zeppel, M.J.B., 2011. Forest productivity under climate change: a checklist for evaluating model studies. *Wiley Interdiscip. Rev. Clim. Change* 2, 332–355.
- Meinshausen, M., Smith, S., Calvin, K., et al., 2011. The RCP greenhouse gas concentrations and their extension from 1765 to 2500. *Clim. Change* 109, 213–241.
- Mladenoff, D.J., 2004. LANDIS and forest landscape models. *Ecol. Model.* 180, 7–19.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G., Nemani, R.R., 1997. Increased plant growth in the northern latitudes from 1981 to 1991. *Nature* 386, 698–702.
- Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B., Running, S.W., 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300, 1560–1563.
- Noormets, A., McNulty, S.G., DeForest, J.L., Sun, G., Li, Q., Chen, J., 2008. Drought during canopy development has lasting effects on annual carbon balance in a deciduous temperate forest. *New Phytol.* 179, 818–828.
- Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Glob. Change Biol.* 10, 2052–2077. <http://dx.doi.org/10.1111/j.1365-2486.2004.00866.x>.
- Rodríguez-Calcerrada, J., López, R., Salómon, R., Gordaliza, G.G., Valbuena-Carabaña, M., Oleksyn, J., Gil, L., 2015. Stem CO₂ efflux in six co-occurring tree species: underlying factors and ecological implications. *Plant, Cell Environ.* 38, 1104–1115.
- Running, S.W., Gower, S.T., 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiol.* 9, 147–160.
- Rupp, T.S., Starfield, A.M., Chapin, F.S., 2000. A frame-based spatially explicit model of subarctic vegetation response to climatic change: comparison with a point model. *Landsc. Ecol.* 15, 383–400.
- Sato, H., Itoh, A., Kohyama, T., 2007. SEIB–DGVM: a new Dynamic Global Vegetation Model using a spatially explicit individual-based approach. *Ecol. Model.* 200, 279–307.
- Saxton, K.E., Rawls, W.J., 2004. Soil water characteristic equations. Online database. <http://hrls.arsusda.gov/SPAW/SPAWDownload.html>.
- Schellhaas, M.J., van Esch, P.W., Groen, T.A., et al., 2004. CO2FIX V 3.1 - a Model for Quantifying Carbon Sequestration in Forest Ecosystems. ALTErrA Report no. 1068. ALTErrA, Wageningen, Netherlands.
- Scheller, R.M., Mladenoff, D.J., 2008. Simulated effects of climate change, fragmentation, and inter-specific competition on tree species migration in northern Wisconsin, USA. *Clim. Res.* 36, 191–202.
- Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., Mladenoff, D.J., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecol. Model.* 201, 409–419.
- Schumacher, S., Bugmann, H., Mladenoff, D.J., 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. *Ecol. Model.* 180, 175–194.
- Searle, S.R., Speed, F.M., Milliken, G.A., 1980. Populations marginal means in the linear model: an alternative to least squares means. *Am. Statistician* 34, 216–221.
- Seidl, R., Rammer, W., Scheller, R.M., Spies, T.A., 2012. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. *Ecol. Model.* 231, 87–100.
- Seidl, R., Vigl, F., Rossler, G., Neumann, M., Rammer, W., 2017. Assessing the resilience of Norway spruce forests through a model-based reanalysis of thinning trials. *For. Ecol. Manag.* 388, 3–12.
- Soil Survey Staff, 2013. Soil Survey Geographic (SSURGO) Database. Natural Resources Conservation Service, United States Department of Agriculture. Available online at: <http://sdmdataaccess.nrcs.usda.gov/>. Accessed [2/18/2015].
- Urban, M.C., Bocedi, G., Hendry, A.P., et al., 2016. Improving the forecast for biodiversity under climate change. *Science* 353 (6304). <http://dx.doi.org/10.1126/science.aad8466>.
- Wang, W.J., He, H.S., Thompson III, F.R., et al., 2016. Changes in forest biomass and tree species distribution under climate change in the Northeastern United States. *Landsc. Ecol.* <http://dx.doi.org/10.1007/s10980-016-0429-z>.
- White, J.W., Rassweiler, A., Samhuri, J.F., Stier, A.C., White, C., 2014. Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos* 123, 385–388.
- Wild, M., 2009. Global dimming and brightening: a review. *J. Geophys. Res.* 114, D00D16. <http://dx.doi.org/10.1029/2008JD011470>.
- Wilson, B.T., Lister, A.J., Riemann, R.L., 2012. A nearest-neighbor imputation approach to mapping tree species over large areas using forest inventory plots and moderate resolution raster data. *For. Ecol. Manag.* 271, 182–198.