

Scaling Aspen-FACE experimental results to century and landscape scales

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Abstract The Aspen-FACE experiment generated 11 years of empirical data on the effect of CO₂ enrichment and elevated ozone on the growth of field-grown trees (maple, birch and six aspen clones) in northern Wisconsin, but it is not known how these short-term plot-level responses might play out at the landscape scale over multiple decades where competition, succession and disturbances interact with tree-level responses. In this study we used a forest landscape model (LANDIS-II) to scale these site level results to broader temporal and spatial scales. These general principles emerged from the results. (1) The productivity of taxa under future conditions is the primary determinant of short-term taxon dominance. (2) Longer-term, longevity and shade tolerance may supersede productivity as the determinant of importance, depending on the disturbance regime. This result offers hope that, even in the face of atmospheric changes, managers may have some control over future forest composition and carbon sequestration through modification of disturbance regimes. (3) Changes in the abundance of taxa were mostly gradual and none of the taxa were extirpated from the landscape, even under treatments for which they were poorly adapted.

This suggests that as atmospheric conditions change, abrupt extirpations are expected to be rare. (4) Similarly, different taxa fared relatively well under different treatments. This suggests that maintaining species and genetic diversity is a prudent forest management strategy in the face of global change. (5) Accounting for spatial processes is important because seed dispersal and establishment may limit the ability of some species to colonize available habitat.

Keywords Aspen-FACE · Scaling · Global change · Ozone pollution · Forest composition · Carbon dynamics · Forest landscape modeling · LANDIS-II

Introduction

Atmospheric CO₂ concentration (denoted [CO₂]) has increased about 39 % since the beginning of the industrial revolution and it will increase further with continued fossil fuel burning (Siegenthaler et al. 2005). Fossil fuel use also releases nitrogen oxides (NO_x), which react in the troposphere with O₂ and volatile organic compounds, primarily CH₄, in the presence of sunlight to produce ozone (O₃). These gases affect plants in direct and opposite ways. Increased [CO₂] is known to increase plant productivity and in the last 50 years has stimulated growth of

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aspen forests in the upper Great Lakes region of the U.S. (Cole et al. 2010). The recent increase in $[\text{CO}_2]$ may also have altered composition of some terrestrial ecosystems (Bond and Midgley 2000; Kgope et al. 2010). Tropospheric O_3 is considered the most significant air pollutant negatively affecting forest productivity worldwide. Ozone is a potent oxidizer that disrupts cell function leading to decreased productivity, necrosis, and plant mortality (Karnosky et al. 2005). Although very high concentrations of tropospheric O_3 are episodic, the background concentration has steadily increased, and may have already decreased forest productivity by up to 13 % (Felzer et al. 2004).

The Aspen-FACE experiment generated 11 years of empirical data on the effect of elevated $[\text{CO}_2]$ and $[\text{O}_3]$ on the growth, health and mortality of native aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*) and sugar maple (*Acer saccharum*) in a field setting in northern Wisconsin, USA (Kubiske et al. 2007). The FACE treatments were CO_2 [350–380 ppm (control) and 550 ppm (elevated)] and O_3 [30–50 ppb (control) and 60–80 ppb (elevated)] concentrations and their combination, replicated three times. Three species (hereafter, taxa) combinations were planted within three subsets of each treatment ring: (1) maple and aspen clone-216, (2) birch and clone-216, and (3) six clones of aspen, two of which died out early in the experiment. The maple and birch seedlings came from open-pollinated seed sources in northern Wisconsin. Results showed that elevated $[\text{CO}_2]$ tends to enhance growth rates while elevated $[\text{O}_3]$ tends to inhibit growth, reduce vigor and resistance to insects and disease, and increases mortality. However, there were important differences in the response to $[\text{CO}_2]$ and $[\text{O}_3]$ levels among taxa. Some taxa were more O_3 -tolerant than others, and the response to enrichment was not uniform (Karnosky et al. 2005). Furthermore, various clones of aspen had divergent responses to the treatments, including one (clone-8) that fared better under elevated $[\text{O}_3]$ and worse under elevated $[\text{CO}_2]$ because its competitors had a greater response to those treatments (Kubiske et al. 2007; Moran and Kubiske 2013). These differences, primarily due to differences in antioxidant production and stomatal O_3 uptake, have potentially important consequences for forest dynamics in the future because changes in the relative growth and mortality rates of species may alter

competitive relationships and affect forest succession and equilibrium dynamics (Karnosky et al. 2005).

There has been some attempt to scale these results to the stand scale (e.g., Karnosky et al. 2005), but it is not known how these one-decade plot-level responses might play out at the landscape scale over multiple decades where competition, succession and disturbances interact with the tree-level responses. In this study we used a landscape disturbance and succession model (LANDIS-II) as a tool to scale these site level results to much broader spatial and temporal scales. Our objectives were to (1) develop a method to use LANDIS-II to scale site-level, experimental results to landscape scale, and (2) to conduct a virtual replication of the Aspen-FACE experiment at landscape spatial and temporal scales to investigate the effects of altered atmospheric composition on forest composition and succession dynamics. The results can be used to help managers understand how future atmospheric conditions might impact forest dynamics and the future abundance of species that have economic and ecological value.

Materials and methods

Overview

We scaled Aspen-FACE results to landscape scale using a two-stage approach. First, we temporally scaled the single-decade FACE results to multiple decades using a single-site version of the LANDIS-II succession algorithms (LANDIS-II-Site). This allowed us to study site-level temporal trends without the confounding effects of spatial processes such as contiguous disturbances and seed source neighborhoods. We then scaled FACE results both temporally and spatially using LANDIS-II. In both stages we used the models to conduct simple, replicated 2×2 factorial simulation experiments that were directly analogous to the Aspen-FACE experiment (Dickson et al. 2000), and to explore taxon combinations that did not occur in the experiment. The purpose of the first stage was to study the details of how taxon combinations interact competitively on a single site over time under the treatments and with a single disturbance at year 50 that removed all tree biomass. The purpose of the second stage was to identify how all the taxa interact competitively and spatially (via dispersal)

under the treatments and in the presence of regular disturbance.

Simulation models

LANDIS-II (Scheller et al. 2007) is a process-based forest landscape disturbance and succession model that simulates the forest generative processes of dispersal, establishment, growth and competition, and the forest degenerative processes of senescence and disturbances such as insects and timber harvesting at large spatial scales (>1,000 ha) and long temporal scales (centuries). We used the LANDIS-II Biomass Succession extension (Scheller and Mladenoff 2004), which simulates the processes of establishment, growth, competition and senescence as they affect the biomass of cohorts of species (taxa) on a collection of landscape sites (grid cells). The extension simulates the processes of species establishment (propagule arrival and the establishment of a viable cohort), competition for “growing space” and senescence, based on life history attributes of the species. Other processes that kill cohorts or remove some of their biomass can be simulated by independent disturbance extensions.

Cohort net growth in LANDIS-II is a function of the species and age of the cohort, abiotic environment (held constant in this study), and competition, and is estimated as gross growth minus competition-related mortality. Cohorts of all species present on a cell compete for available ‘growing space,’ which becomes more available as disturbance or senescence causes loss of biomass from competing cohorts. The biomass extension calculates the aboveground net primary productivity (ANPP) of each cohort as a function of the maximum biomass (MaxBiomass) the site can support such that, in the absence of competition from other cohorts, ANPP increases with cohort age using a growth function (curve) that is calibrated by MaxANPP (highest ANPP that a species can biologically attain), slowing asymptotically as total site biomass approaches MaxBiomass. In the absence of competition, maximum growth increment occurs at the midpoint between cohort establishment and maximum biomass. A second function removes some of the accumulated cohort biomass to represent competition-related mortality at a rate that also reaches its maximum at MaxBiomass. A third function removes cohort biomass as the cohort approaches the longevity of the species (senescence). More details on these functions may be found in

Scheller and Mladenoff (2004) and Scheller (2012). In this study, MaxANPP was derived from Aspen-FACE data as described below.

LANDIS-II-Site (v2.3, Miranda 2012) is a simple Microsoft Windows-based utility that implements the LANDIS-II cohort and biomass growth and senescence calculations for up to six species on a single site. LANDIS-II-Site (L2-Site) includes the ability to establish new cohorts (assuming universal seed availability) and to simulate loss of biomass by disturbance at a single user-specified time step.

Generating LANDIS-II parameters from Aspen FACE data

The key LANDIS-II parameter varied in our study was MaxANPP for each taxon under each treatment. Because the Aspen FACE experiment was harvested after only 11 growing seasons, there are no data on maximum ANPP under the treatments. Furthermore, no taxon was grown in monoculture in the experiment. Our approach to parameterize the models for the purposes of this study was to calculate percent change in total aboveground biomass over the life of the experiment relative to the control plots for each taxon under each treatment, and modify the MaxANPP estimates used in another LANDIS-II study in northern Wisconsin (Scheller and Mladenoff 2005) by those percentages. Previous LANDIS studies did not distinguish individual aspen clones, so we calculated the percent deviation of the cumulative biomass of each clone from the average of all clones under each treatment, and modified Scheller and Mladenoff’s (2005) MaxANPP estimate for aspen by those percentages for each clone under each treatment (Table 1). Modeled growth curves using these estimates were compared to Aspen-FACE growth trajectories, and they were calibrated so that the modeled curve was approximately parallel to empirical trajectories (Fig. 1) by modifying the growth shape parameter (Table 2) that controls how rapidly ANPP reaches MaxANPP. Given that growth is not modeled very mechanistically in the Biomass Succession extension, the agreement was surprisingly good. The modeled curve for maple was higher than empirical trajectories because maple was somewhat suppressed by co-dominant aspen (clone-216) in the Aspen-FACE experiment (Kubiske et al. 2007). Much of the difference between modeled and empirical curves

reflects the fact that no taxa were grown in monoculture in the Aspen-FACE experiment. The counterintuitive increase in MaxANPP of clone-8 under elevated $[O_3]$ (Table 1) resulted because clone-8 was less susceptible to O_3 damage than the other clones of aspen, and it was therefore “released” to grow better when its competitors were stunted by O_3 . Similarly, the decline of maple, clone-8 and clone-216 under elevated $[CO_2]$ was caused by suppression by superior competitors under that treatment. MaxBiomass parameters (Table 2) were taken from stand carbon density estimates for live trees at the 99th percentile of stand volume in the upper Midwest (Smith et al. 2006), and they were held constant among treatments.

The Aspen-FACE experiment demonstrated that $+ [CO_2]$ significantly increased leaf area index (LAI) whereas $+ [O_3]$ significantly decreased LAI (Karnosky et al. 2005). This affects how quickly shade develops under the treatments, which has important implications for the establishment of taxa, depending on their shade tolerance. The Biomass Succession extension does not explicitly model LAI, but assumes that shade is a function of the proportion of MaxBiomass that is present on the site (Scheller and Mladenoff 2004). Biomass Succession recognizes five shade classes, and a species cannot establish under a shade class that has a higher value than its shade tolerance class (Table 2). MaxANPP values determine how fast a taxon grows and advances through the series of shade classes, and the user specifies at what proportion of MaxBiomass the site advances to the next shade class. We defined these thresholds such that the time taken to advance (as determined by MaxANPP) to shade class 1 (too shady for aspen to establish) and shade class 2 (too shady for birch to establish) was consistent with the effects of the treatments on LAI as seen in Aspen-FACE. The

Table 1 MaxANPP (g/m^2) parameter values used as inputs to the LANDIS-II model for each of the four treatments

Taxon	Treatments			
	Control	+CO ₂	+O ₃	+CO ₂ + O ₃
Sugar maple	649	398	472	360
Paper birch	587	813	466	659
Aspen-clone-8	426	390	588	714
Aspen-clone-42	549	900	432	799
Aspen-clone-216	494	394	213	448
Aspen-clone-271	1,130	1,716	579	934

only treatment with a different set of thresholds (i.e., slightly longer time to develop shade) was $+ [O_3]$ because that treatment retarded canopy development.

Stage 1: single site simulations

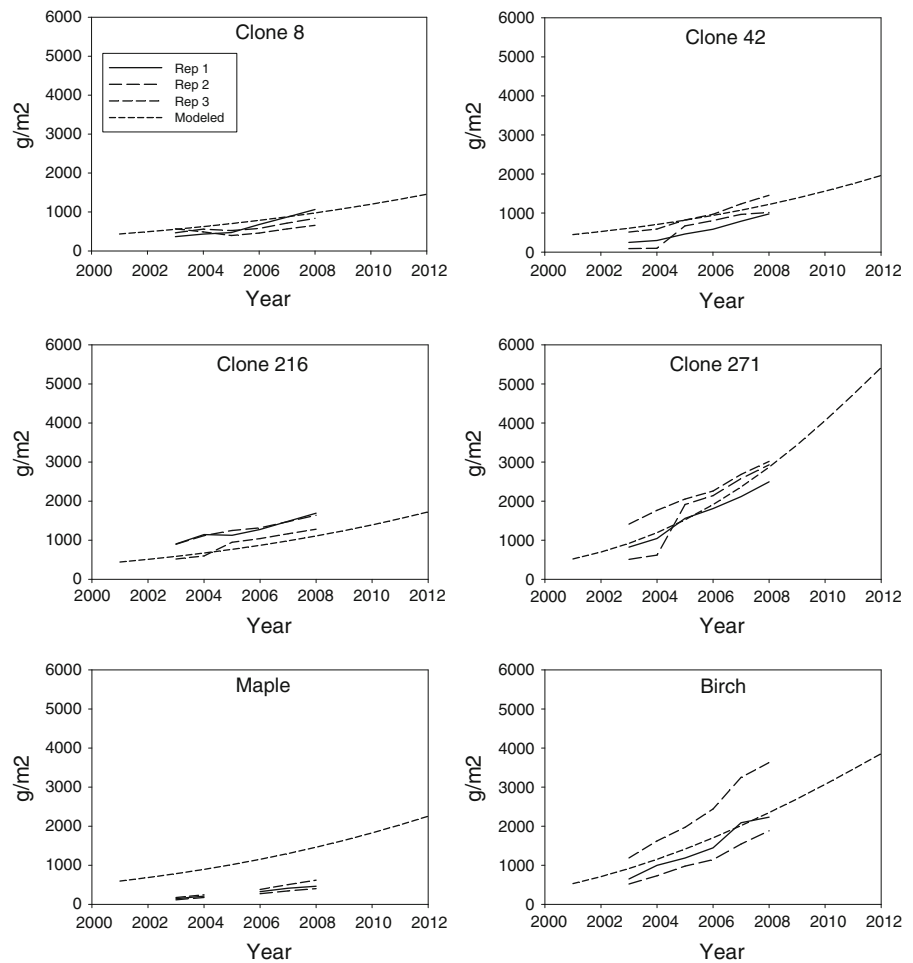
We conducted a complete set of factorial simulations for a single site using L2-Site, varying only MaxANPP (Table 1) and shade class thresholds to reflect the treatments as described above. Other parameters (Table 2) were derived from the literature (Burns and Honkala 1990) or for other LANDIS studies (Scheller and Mladenoff 2005). Because shade-tolerant maple would tend to gradually exclude all other taxa, we simulated a single stand-replacing disturbance at year 50 so that we could observe species dynamics before and after disturbance. Forty replicate simulations were conducted for approximately twice the longevity of aspen (180 years). We also conducted simulations with all six taxa co-occurring on a site to explore the dynamics of a species combination that did not occur in the Aspen-FACE experiment.

Stage 2: landscape simulations

We used version 6.0 (Scheller et al. 2007) of LANDIS-II to conduct the landscape simulations, using the same parameter values used in stage 1. We used neutral model landscapes (Gardner et al. 1987) to create the initial landscape patterns (see below) to allow us to model the spatial interaction of taxa while avoiding the confounding effects of varying soil properties, land use and disturbance legacies present on real landscapes. This approach allowed the landscape experiments to provide insight into the landscape effects of the treatments alone. We investigated the effects of two initial spatial dispersions of taxa: spatially random and multifractal (clumped). The random maps dispersed the Aspen-FACE taxon combinations randomly across the landscape. This configuration resulted in no cells being more than a few cells from all taxa, resulting in few dispersal barriers. The clumped maps created greater dispersal barriers to assess the interaction of a clumped spatial pattern and seed dispersal via a comparison with the 6-taxa results generated with L2-Site (above), in which seeds of all taxa were always present.

We generated replicate neutral model initial condition maps (256×256 cells, 5,898 ha) using QRULE

Fig. 1 Comparison of biomass measured in the Aspen-FACE experiment and modeled by L2-Site (control treatment)



(Gardner 2011), choosing the cell width (30 m) to be similar in size to an Aspen-FACE treatment ring. For spatially random maps each cell was randomly assigned to one of three equally likely taxon combinations that occurred in the Aspen-FACE experiment, and each taxon was represented by a single age cohort (1–10 year) as in the FACE experiment (Fig. 2a). To allow comparison with L2-Site results, we generated additional random maps with a 6-taxon combination. For multifractal maps we arbitrarily set the aggregation parameter (h) = 0.3 to produce a moderately aggregated spatial pattern of taxon combinations (Fig. 2b). Each cell was randomly assigned to one of three equally likely taxon combinations that were modifications of the Aspen-FACE combinations: (1) all six taxa; (2) birch, clone-8, clone-42; (3) maple, clone-216, clone-271. The 6-taxon combination was the focus of analysis, allowing comparison with the L2-Site

results. The other taxa combinations provided spatially distributed propagules to the 6-taxon stands after they were disturbed. None of these initial conditions maps represent a realistic spatial pattern of the taxa, but allowed all taxa to interact spatially (via dispersal) and compete, and any spatial pattern that developed was interpreted as an unconfounded, emergent property of the competitive dynamics under the experimental treatments, given the pattern of the initial conditions.

We modeled succession using the Biomass Succession v3 extension of LANDIS-II (hereafter L2-landscape) (Scheller and Mladenoff 2004), which simulates succession as described above for L2-Site. In addition, it simulates dispersal of propagules. In the absence of disturbance we would expect aspen and birch to disappear from a landscape because they are pioneer species. We therefore simulated a generic

Table 2 Selected LANDIS-II taxon parameter values used in the simulations

Taxon	Longevity (years)	Sexual maturity (years)	Shade tolerance ^a	Effective seed dispersal distance (m) ^b	Max. seed dispersal distance (m) ^c	Vegetative reproduction probability ^d	Max. sprouting age (years) ^e	P_{est}^f	Max. taxon biomass (Mg/ha) ^g	Growth shape parameter ^h
Sugar maple	250	40	5	100	200	0.5	90	0.32	207.0	0.8
Paper birch	120	20	2	200	5,000	0.8	100	0.80	153.0	0.6
Aspen clone-8	100	15	1	500	5,000	0.9	90	0.98	153.0	0.8
Aspen clone-42	100	15	1	500	5,000	0.9	90	0.98	153.0	0.8
Aspen-clone-216	100	15	1	500	5,000	0.9	90	0.98	153.0	0.8
Aspen-clone-271	100	15	1	500	5,000	0.9	90	0.98	153.0	0.8

^a Index of ability to establish under shade. Least shade tolerant = 1, most shade tolerant = 5

^b 95 % of propagules disperse within this distance

^c 100 % of propagules disperse within this distance

^d Probability of sprouting after disturbance mortality

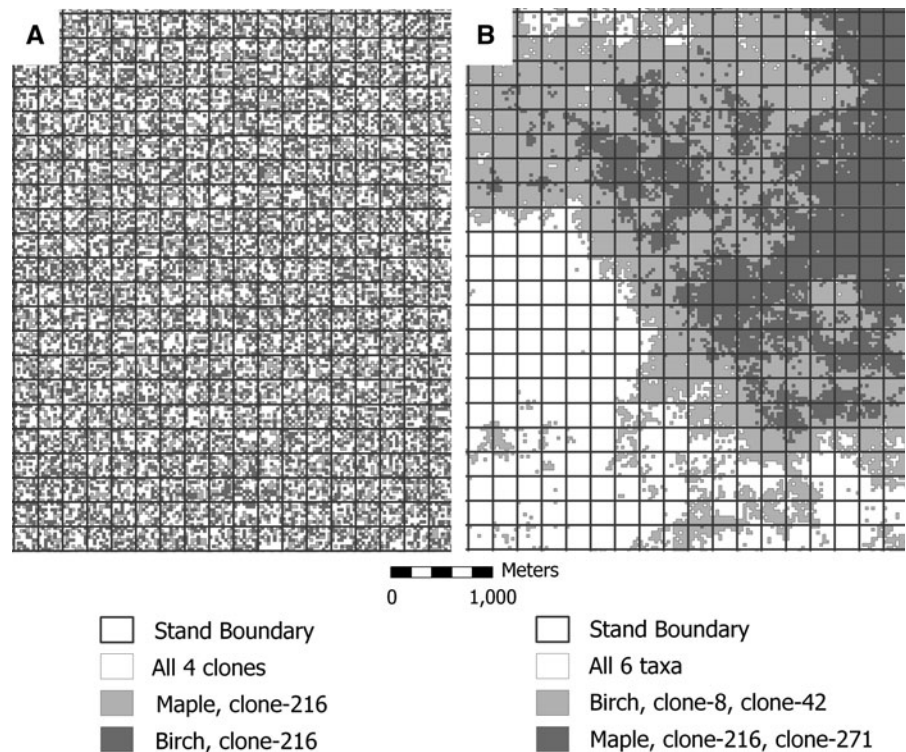
^e Maximum age that a taxon will reproduce vegetatively after disturbance

^f Probability of establishment; probability that the taxon will establish given propagules and sufficient light

^g Maximum biomass that a taxon can attain on a site

^h Parameter that controls that rate at which the ANPP of young cohorts reaches MaxANPP (Table 1). Lower values cause the curve to initially be steeper

Fig. 2 Example neutral model input maps showing the initial spatial distribution of taxa and the stand boundaries used to simulate disturbance by LANDIS-II. **a** Spatially random map. **b** Multifractal (spatially clumped) map. Approximately one-quarter of each map is shown



stand-replacing disturbance regime using the Biomass Harvest extension (Gustafson et al. 2000). We arbitrarily defined a grid of 5.76 ha (8×8 cells) polygons across the landscape grid, and simulated complete removal of all cohorts of all taxa within polygons according to the experiment. On the random landscapes the disturbance was designed to disperse a generic high-intensity disturbance across the landscape at each time step, and a randomly selected 12.5 % of the polygons were disturbed each decade (80 year return interval). On the clumped landscapes the disturbance mimicked that of the L2-Site experiments; all polygons dominated by the 6-taxa “type” were disturbed at year 50, while stands of the other two “types” were never disturbed, and propagules could disperse from those sites into the disturbed polygons. These disturbance regimes were not intended to mimic any real disturbance agent(s), but to introduce controlled disturbances to meet the experimental objectives. Stands were not selected for disturbance unless the youngest cohort age was at least 21 years; consequently no disturbance occurred until year 30. All extensions used a 10-year time step. Each treatment was simulated for 180 years, with three replicates of each treatment and initial condition map.

Analysis procedures

For the L2-Site simulations, we plotted live above-ground biomass over simulated time for various taxon combinations, using trends and variability (i.e., error bars) to evaluate how relative dominance was affected by the treatments and the interaction of competitors. To show average long-term treatment effects we created a bar chart of mean biomass (by taxa) across all 18 time steps. Biomass was very dynamic through time, and using the mean value integrated the response to the treatments over the entire time series. We also plotted taxon biomass, total biomass and ANPP through time to visually assess the temporal variability of system dynamics under the treatments. Based on observed dynamics, we chose the end of the simulation period (year 180) to conduct a full-factor ANOVA on response variables calculated from various maps output by L2-landscape. Variables included measures of forest composition (% of each taxon and % of each age class), spatial pattern (Aggregation Index, He et al. 2000) and productivity of each taxon (average cell total biomass and ANPP). The main fixed effects of $[\text{CO}_2]$ and $[\text{O}_3]$ were estimated using generalized linear mixed models via PROC GLIMMIX in SAS

v9.3 (SAS Institute Inc. 2011). We did not include interaction terms because they were shown to be insignificant in the Aspen-FACE experiment (Zak et al. 2011). Shapiro–Wilks test and visual examination of stem and leaf plots (UNIVARIATE procedure) were used to determine the distribution of each response variable. We used a normal distribution with an identity link function for all response variables. We evaluated the relative influence of main effects using LSMEANS and Tukey’s comparisons, showing four classes of P-values to help assess significance. Finally, for the clumped landscapes, we plotted live above-ground biomass over simulated time for the 6-taxon combination for comparison with the L2-Site results to assess the effect of dispersal barriers.

Results

Site simulation results

Temporal dynamics at the site scale were driven by relative productivity, establishment and shade tolerance. The variability (error bars) seen in the graphs was a consequence of stochastic establishment (i.e., vegetative reproduction probability) and probability of establishment (P_{est}) (Table 2). When a taxon failed to

establish after the disturbance in a model run, its normal growing space became occupied by co-occurring taxa. Initial conditions were identical for each treatment in all model runs. Because the model calculates initial biomass based on productivity, initial values in graphs should be thought of as year one values.

Analogous to the Aspen-FACE four-clone experimental unit, the relative biomass of the clones was directly proportional to the productivity of the clones under the treatments, and their biomass dynamics were synchronized because their longevities were identical (Fig. 3). The relatively higher productivity of clone-8 under the +O₃ treatment somewhat compensated for the reduction in productivity of other clones. The total biomass of all clones at year 120 (Fig. 3) was 14,794 and 13,119 g/m² under the control and +O₃ treatments, respectively. For the maple/clone-216 combination, maple eventually dominated because of its greater longevity and the shade-intolerance of aspen (Fig. 4). However, clone-216 was generally able to dominate after disturbance even when its productivity was less than maple because of its greater probability of re-sprouting (and establishment by seeding). Clone-216 was able to dominate before the disturbance only when the maximum productivity of maple was less than or approximately equal to that of clone-216. Birch was always dominant over clone-216 because it always had

Fig. 3 L2-Site result. Long-term effect of treatments on aboveground live biomass on a single site occupied by aspen clones. A disturbance at year 50 removed all living biomass. Error bars show one SD of 6 replicates

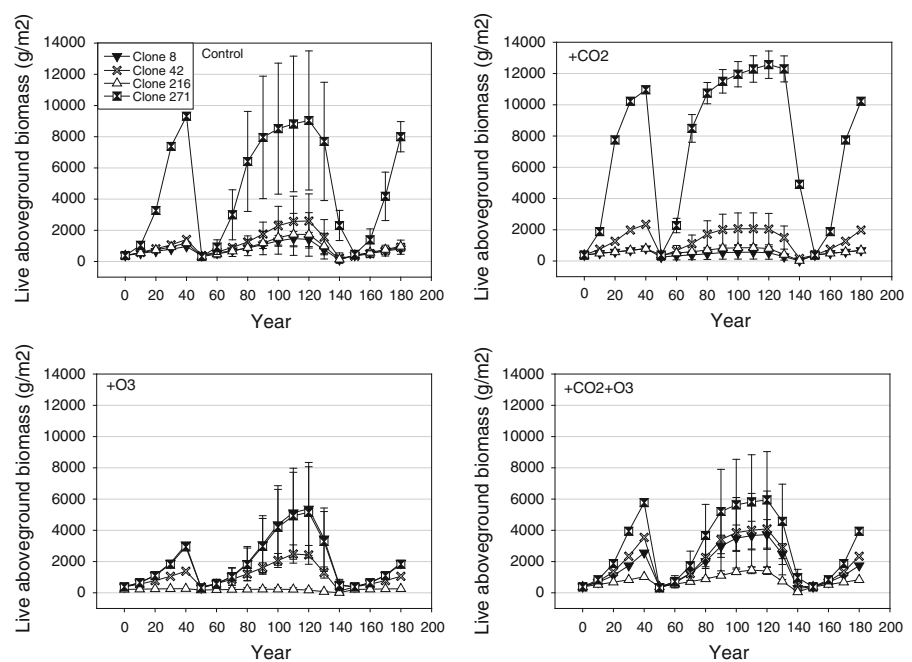
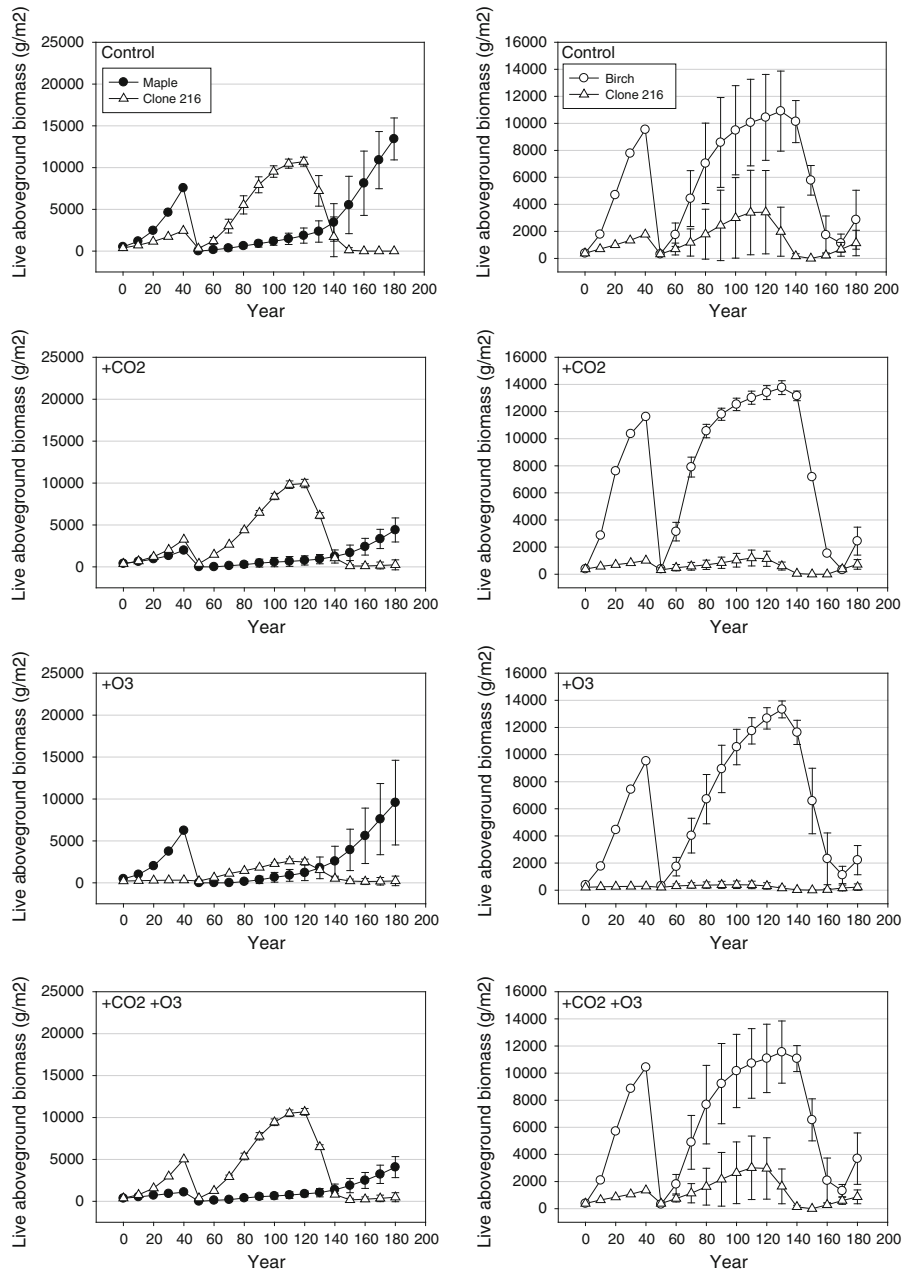


Fig. 4 L2-Site result. Long-term effect of treatments on aboveground live biomass on a single site occupied by maple and clone-216 (*left*) or birch and clone-216 (*right*). A disturbance at year 50 removed all living biomass. Error bars show one SD of 6 replicates



higher productivity and lived slightly longer (Fig. 4). The magnitude of the difference in biomass between the two species was about proportional to the difference in productivity (Table 1), and variability was less when the productivity difference was high.

When a taxon combination that did not occur in the Aspen-FACE experiment (all taxa) was simulated by L2-Site, the relative biomass of taxa generally sorted

by productivity, but over time the effects of longevity and shade tolerance began to appear (Fig. 5). Maple eventually began to assert dominance because of its longevity, although the slope of the rate at which maple overtook its competitors was determined by the productivity of maple relative to the other taxa under the treatments (Table 1). For example, under the +CO₂ and +CO₂ +O₃ treatments, maple dominance

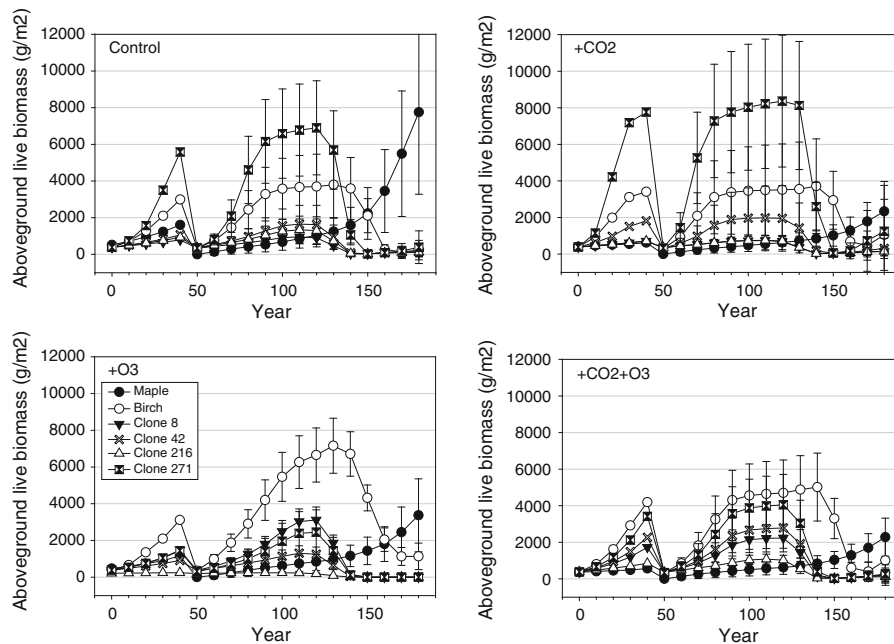


Fig. 5 L2-Site result. Long-term effect of treatments on aboveground live biomass on a single site occupied by all six taxa. A disturbance at year 50 removed all living biomass. Error bars show one SD of 40 replicates

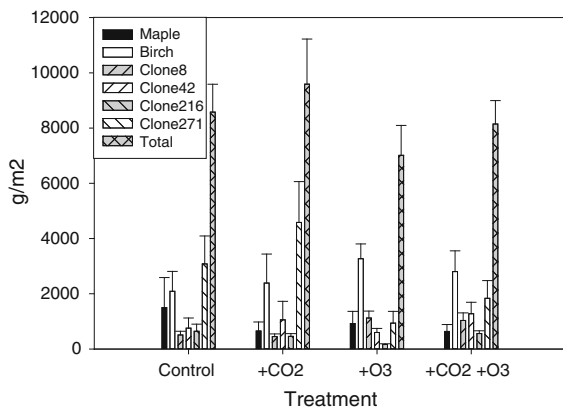


Fig. 6 L2-Site result. Mean biomass (over 180 years) of all taxa simulated together. Error bars show one SD of 40 replicates

was delayed until the other taxa died off (after year 250) and were unable to establish under the then well-developed maple canopy. In this simulation, the mean biomass of each taxon over 180 years was not always proportional to productivity (Fig. 6), illustrating that establishment, shade tolerance and longevity create dynamics that affect competitive interactions. These interactions also affect the total biomass (all taxa) produced on a site over 180 years (Fig. 6).

Landscape simulation results

Taxon biomass on random landscapes initialized with Aspen-FACE combinations was virtually identical to L2-Site results (Figs. 3, 4) because dispersal barriers were inconsequential. The total aboveground biomass on the landscape (Fig. 7a) initially increased rapidly because of the high ANPP of young cohorts, declined as disturbance and senescence of the pioneer species occurred, and then stabilized as species abundance approached equilibrium. Similar to the Aspen-FACE experiment, total biomass was always highest under the +CO₂ treatment and lowest under the +O₃ treatment, while the Control and +CO₂ +O₃ treatments were very similar. Mean ANPP showed a very similar temporal pattern (Fig. 7b).

GLIMMIX tests on random landscape simulations showed that both the CO₂ and O₃ treatments significantly affected the abundance of all taxa except clone-216 (Table 3). The treatments had a limited effect on age classes. Because only maple has a longevity that exceeds 140 years, the oldest age classes consisted only of maple. The abundance of maple was affected by both treatments, so it is surprising that the abundance of the oldest age classes was not. However, maple abundance was relatively

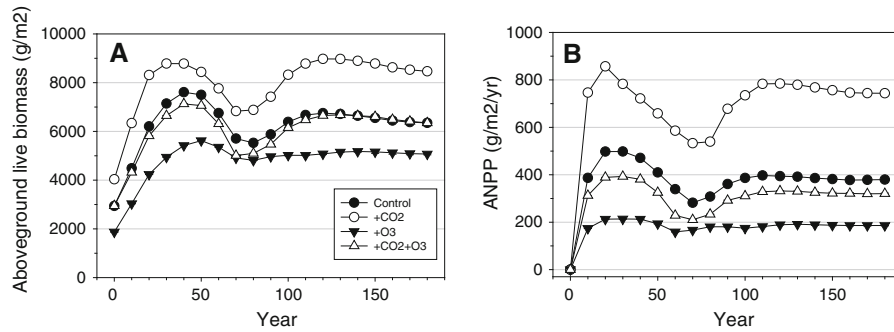


Fig. 7 L2-landscape result. Long-term effect of treatments (with regularly occurring stand-replacing disturbance) on total landscape biomass (a) and mean ANPP (b) through simulated

time on 5,898 ha neutral model random landscapes. Error bars show one SD of 3 replicates and are generally less than the width of the symbols

Table 3 GLIMMIX results from L2-landscape simulations on random maps for response variables at year 180

Response variable	CO ₂		O ₃	
	Ambient (mean, se)	Elevated (mean, se)	Ambient (mean, se)	Elevated (mean, se)
% Sugar maple	5.26 (0.70)**	2.06 (0.70)**	4.95 (0.70)*	2.7 (0.70)*
% Paper birch	51.64 (6.91)**	19.49 (6.91)**	18.57 (6.91)**	52.56 (6.91)**
% Aspen clone-8	5.96 (1.20)*	0.82 (1.20)*	0.06 (1.20)**	6.73 (1.20)**
% Aspen clone-42	3.24 (0.70)**	7.44 (0.70)**	6.90 (0.70)*	3.78 (0.70)*
% Aspen clone-216	0.79 (0.19)	0.68 (0.19)	0.78 (0.19)	0.69 (0.19)
% Aspen clone-271	33.11 (6.54)**	69.51 (6.54)**	68.75 (6.54)**	33.87 (6.54)**
All aspen combined (%)	43.10 (6.22)**	78.45 (6.22)**	76.48 (6.22)**	45.06 (6.22)**
% 1–40 year age class	60.92 (0.27)	61.37 (0.27)	61.38 (0.27)	60.91 (0.27)
% 41–100 year age class	32.03 (0.34)*	33.22 (0.34)*	33.18 (0.34)*	32.07 (0.34)*
% 101–140 year age class	5.55 (0.42)*	3.86 (0.42)*	3.83 (0.42)*	5.58 (0.42)*
% 141–180 year age class	0.68 (0.04)	0.72 (0.04)	0.74 (0.04)	0.66 (0.04)
% >180 year age class	0.82 (0.04)	0.83 (0.04)	0.87 (0.04)	0.90 (0.04)
Mean # cohorts	2.42 (0.15)*	1.81 (0.15)*	1.79 (0.15)*	2.44 (0.15)*
AI-taxon ^a	0.661 (0.030)	0.574 (0.030)	0.579 (0.030)	0.656 (0.030)
AI-age ^b	0.894 (0.003)*	0.883 (0.003)*	0.883 (0.003)*	0.894 (0.003)*
Total biomass (kg/m ²) ^c	5.71 (0.10)***	7.41 (0.10)***	7.41 (0.10)***	5.71 (0.10)***
ANPP (g/m ² /year) ^d	282.9 (27.1)***	532.2 (27.1)***	561.8 (27.1)***	253.3 (27.1)***

Columns contain least squares means for the levels of the fixed treatment effects. Significant differences between treatment levels are indicated by asterisks. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

- ^a Aggregation Index calculated from taxon maps
- ^b Aggregation Index calculated from age maps
- ^c Mean total biomass of map cells
- ^d Mean total aboveground net primary productivity of map cells

low because of the chronic disturbance, and the effect on age class would likely be significant with fewer disturbances. The treatments did affect the mean number of cohorts on cells, with +CO₂ reducing cohort richness and +O₃ increasing it, reflecting

competition and shade effects under each treatment. The treatments did not affect the aggregation of taxa on the landscape, but +CO₂ reduced the aggregation of age classes and +O₃ increased it. Elevated [CO₂] significantly increased total biomass and mean ANPP

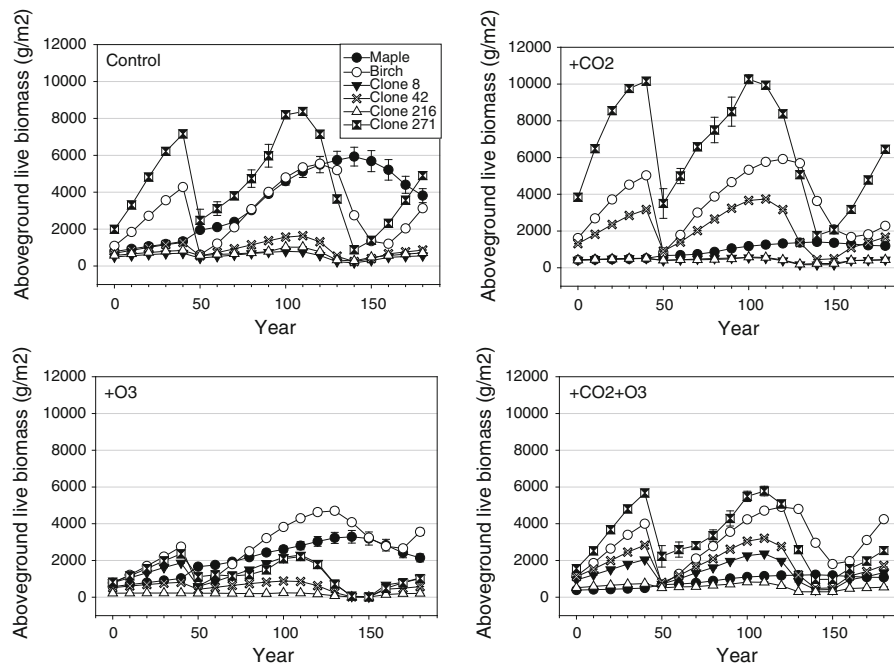


Fig. 8 L2-landscape result. Mean aboveground live biomass of the cells within all six-taxon stands ($N = 376$) simulated on clumped landscapes. Error bars show one SD of 3 replicates. This figure is directly comparable to Fig. 5

across the landscape, and $+O_3$ significantly reduced them.

On clumped landscapes the dynamics of taxa composition was different than on single sites (compare Fig. 8 to Fig. 5), primarily by reducing the access of shade-tolerant maple to much of the landscape because of limited dispersal ability. L2-Site assumes ubiquitous seed rain by all taxa, but the simulation of actual seed dispersal in LANDIS-II shows that this assumption does not hold on structured landscapes for species with low vagility. Clone-271 does well because it usually has the highest ANPP, and birch generally does well because of its longevity and a growth shape parameter that allows it to grow more aggressively than other taxa when a new site is being colonized.

Discussion

Our study scaled a high-profile site-level field experiment to landscape spatial and temporal scales. Because most upper Midwest tree species were not included in the experiment, we did not attempt to predict future forest landscape dynamics under elevated CO_2 and ozone, but rather produced a first-cut

exploration of the landscape implications of elevated CO_2 and ozone for these forests. Our goal was enlightenment rather than realism. The insights from this study can only be understood in light of the assumptions made, the model used, the input parameters used and the study design.

Assumptions

(1) The magnitude of treatment effects on productivity over the first 11 years of stand development was assumed to persist into the future. (2) Species life history attributes (e.g., shade tolerance, longevity, P_{est} , etc.) were assumed to be unaffected by the treatments. (3) The maximum biomass that a taxon can attain was also assumed to be unaffected by the treatments. Although it is likely that some of these assumptions may not hold under future atmospheric conditions, we had no empirical basis to estimate alternative assumptions, so we simply report them here, recognizing that our results are to some degree an artifact of these assumptions. However, the assumptions were held constant across treatments, so differences in responses can be attributed to the treatments, given the initial conditions and the assumptions.

Insights

Productivity is a key driver of the competitive interactions among taxa, being the primary determinant of short-term forest dynamics. However, over longer time frames (centuries), species longevity and shade tolerance can change forest composition in profound ways that are dependent on the disturbance regime. Dispersal ability also can enhance or limit the ability of species to colonize available sites, thereby impacting landscape-scale forest dynamics. Such dispersal effects will likely be exacerbated within fragmented landscapes, as indicated by our simulations on clumped landscapes.

Our results suggest that elevated $[\text{CO}_2]$ and $[\text{O}_3]$ may have some effects on forest composition and spatial patterns at landscape scale. Our results are certainly not definitive because most of the species found in Lakes States forests were not included in the simulations. However, it does appear that the abundance of specific aspen clones may be significantly affected as natural selection occurs under future atmospheric conditions. For example, clone-271 gains competitive advantage under elevated $[\text{CO}_2]$, and clone-8 under elevated $[\text{O}_3]$ (Table 3). Also, where birch and aspen co-occur, our results suggest that elevated $[\text{O}_3]$ will cause an increase in birch at the expense of aspen (Table 3). Clone-271 and birch both appear to have an advantage when both $[\text{CO}_2]$ and $[\text{O}_3]$ are elevated (Fig. 8). Each of these results is consistent with those from the short-term Aspen-FACE experiment (Kubiske et al. 2007, Moran and Kubiske 2013) and our study provides an important temporal and spatial scaling of that experiment.

Elevated $[\text{CO}_2]$ resulted in an increase in total biomass by year 180 of about 30 %, but elevated $[\text{O}_3]$ resulted in a similar decrease (Table 3). Elevated $[\text{CO}_2]$ approximately doubles productivity (ANPP) by year 180, but elevated $[\text{O}_3]$ decreases productivity by about half. Thus, any gains from the fertilization effect of CO_2 are more than offset by losses to elevated $[\text{O}_3]$. Our simulations account for the effects of altered growth rate on competition among taxa. We did expect to see differences in carbon sequestration and productivity because those are the primary treatment effects as input to the model, and those differences modified taxa composition over time in conjunction with differences in longevity and shade tolerance. At broad spatial and temporal scales in the presence of chronic

disturbance, it appears that elevated $[\text{CO}_2]$ produces a significant increase in standing biomass (Table 3; Fig. 7a), while elevated $[\text{O}_3]$ markedly reduces landscape biomass.

In our study, we treated tropospheric ozone as an elevated chronic disturbance, as opposed to occasional spikes in $[\text{O}_3]$ that sometimes reach forested areas. The $+\text{O}_3$ treatment of the Aspen-FACE experiment elevated background $[\text{O}_3]$ and spikes of much higher $[\text{O}_3]$ naturally impacted the site. LANDIS-II was unable to simulate O_3 spikes at the weekly time scale. Our modeling results suggest that delayed canopy closure due to elevated O_3 results in recruitment of more age classes. In the Aspen-FACE experiment, the thinner tree canopy in the elevated O_3 treatment was accompanied by greater herbaceous understory biomass (Bandeuff et al. 2006). LANDIS-II projected a similar effect by extending the stand recruitment phase of stand development.

Caveats

The Aspen-FACE experiment did not grow any taxon in monoculture, and some of the treatment effects on each taxon were confounded slightly by competitive effects. We therefore kept Aspen-FACE co-occurring taxa together in the simulations, although additional taxa were sometimes added. Our model parameters may be less robust when a taxon is modeled without a taxon with which it was associated in the experiment.

We modeled a simplified forest with just three species that were distributed on random and fractal landscapes. Real forests have more species with more complicated interspecific competition dynamics, and their spatial distribution may be even more structured. It is not well-established how other species will respond to elevated $[\text{CO}_2]$ and $[\text{O}_3]$ in the field. However, our results indicate the scale at which the effects may play out (centuries), and show that even the “losers” under a given treatment may persist indefinitely at some level on the landscape. With a random spatial distribution of taxa, dispersal was likely not a limiting factor for the establishment of new cohorts of any taxon. The patchiness of real landscapes is most likely to impact species with limited dispersal ability, unless they are ubiquitous.

A number of hypotheses have been proposed in the global change literature that could be over-riding factors for the results from our modeling study. Our

results depended primarily on elevated $[\text{CO}_2]$ and $[\text{O}_3]$ effects on productivity, and long-term responses to productivity have been questioned, particularly with respect to elevated $[\text{CO}_2]$. Luo et al. (2004) proposed that higher litter inputs and greater demand for N at the ecosystem level would eventually constrain the CO_2 fertilization effect. There is evidence for this phenomenon in some experiments (Norby et al. 2010) but not others including Aspen-FACE (Finzi et al. 2007; Drake et al. 2011; Zak et al. 2011). A second possibility is that elevated $[\text{CO}_2]$ may directly affect species' shade tolerance. While mechanistic support for this has been proposed (Sage 1990; Kubiske and Pregitzer 1996), there has been little experimental evidence supporting it (Herrick and Thomas 1999; Kubiske et al. 2002). In experiments, the largest effect on understory plants has been shown to be canopy development, with greater LAI in elevated $[\text{CO}_2]$, and lower LAI in elevated $[\text{O}_3]$, as discussed above. Lastly, species establishment in LANDIS-II is a function of site conditions, seed production and dispersal. In two separate experiments, seeds of *Pinus taeda* and *B. papyrifera* developed in elevated $[\text{CO}_2]$ had greater viability and concentrations of storage lipids compared to controls (Hussain et al. 2001; Darbah et al. 2008). The extent to which seed production, development, and viability among sympatric tree species might differ in response to increased $[\text{CO}_2]$ and $[\text{O}_3]$ is entirely unknown.

Our study did not incorporate other aspects of global change, such as land use or climate change. Land use change, specifically forest fragmentation, might affect the ability of species to disperse across the landscape. Elevated temperatures may lengthen growing seasons and affect growth rates differentially among species (Dragoni et al. 2011; Wu et al. 2011). Precipitation may also change (increase or decrease), which may also differentially affect species growth and mortality rates (Hogg et al. 2008). The incidence of drought stress is almost certain to increase because of increased evapotranspiration demand, which has the potential to dramatically shift forest composition (Frelich and Reich 2010). It is not known how these climate changes will interact with elevated $[\text{CO}_2]$ or $[\text{O}_3]$ to affect species competitive ability, but it is likely that some of those interactions will be significant (Wyckoff and Bowers 2010; Wu et al. 2011), particularly with drought stress. It is important to clarify that we did not explicitly model the

physiological processes of $[\text{CO}_2]$ enrichment or $[\text{O}_3]$ effects using (for example) PnET (Ollinger et al. 1997, Xu et al. 2012). Because LANDIS-II is a landscape model, it is appropriate to use the Aspen-FACE treatment effects on MaxANPP as an alternative to simulating and validating the treatment effects via physiological processes. Nonetheless, the latter is a useful avenue for future research.

Conclusions

Although this study represents just a first step in understanding forest dynamics at broad temporal and spatial scales under potential future atmospheric conditions, a few general principles can be formulated. (1) The productivity of species under future conditions is the primary determinant of short-term species importance. (2) Over a longer-term, longevity and shade tolerance may supersede productivity as the determinant of importance, depending on the disturbance regime. This result offers hope that, even in the face of atmospheric changes, managers may have some control over future forest composition and carbon sequestration through modification of disturbance regimes. (3) Changes in the abundance of taxa were mostly gradual and none of the taxa we studied was extirpated from the landscape, even under treatments for which they were clearly poorly adapted. This suggests that as atmospheric conditions change, surprise extirpations are expected to be rare. (4) Similarly, different taxa fared relatively well under different treatments. This suggests that maintaining species and genetic diversity is a prudent forest management strategy in the face of global change. (5) Accounting for spatial processes is important because seed dispersal and establishment may limit the ability of some species to colonize available habitat.

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