FINAL REPORT, 2011-2014. FORECASTING CARBON STORAGE AS EASTERN FORESTS AGE: JOINING EXPERIMENTAL AND MODELING APPROACHES AT THE UMBS AMERIFLUX SITE.

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Abstract

At the University of Michigan Biological Station (UMBS) AmeriFlux sites (US-UMB and US-UMd), long-term C cycling measurements and a novel ecosystem-scale experiment are revealing physical, biological, and ecological mechanisms driving long-term trajectories of C cycling, providing new data for improving modeling forecasts of C storage in eastern forests. Our findings provide support for previously untested hypotheses that stand-level structural and biological properties constrain long-term trajectories of C storage, and that remotely sensed canopy structural parameters can substantially improve model forecasts of forest C storage. Through the Forest Accelerated Succession ExperimenT (FASET), we are directly testing the hypothesis that forest C storage will increase due to increasing structural and biological complexity of the emerging tree communities. Support from this project, 2011-2014, enabled us to incorporate novel physical and ecological mechanisms into ecological, meteorological, and hydrological models to improve forecasts of future forest C storage in response to disturbance, succession, and current and long-term climate variation.

Our core objectives at the outset of this project were to:

1. Identify the physical, biological, and ecological mechanisms by which disturbance and succession interact with climate to govern landscape-level variability in C fluxes and storage.
2. Integrate newly identified mechanisms as components in the canopy-atmosphere -interaction module within the Ecosystem Demography (ED2) model.
3. Use continuous data from US-UMB to evaluate the short- and intermediate-term forecasts from ED2 of carbon budgets throughout the successional shift, and study the sensitivity of these effects to inter-annual weather variability.
4. Using ED2, provide long-term regional projections of forest C storage over an array of forecasted climate conditions and forest communities, representing different disturbance regimes.
5. Leverage this novel, large-scale experiment to build and maintain a multi-disciplinary climate change research platform encompassing biogeochemistry, atmospheric chemistry and hydrology.

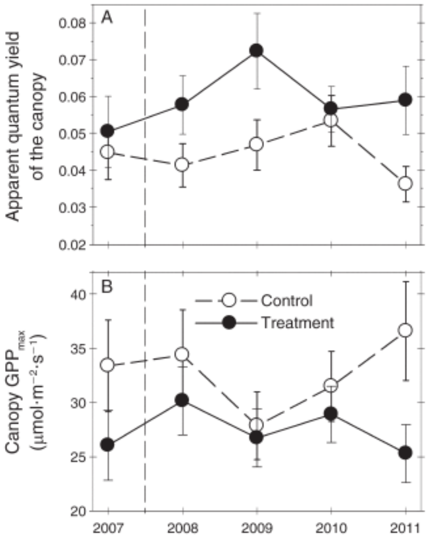
Our report is composed of three sections: 1) Research activities and highlights, 2) Research products and publications, and 3) Student degrees supported.

1. Research activities and highlights

In this section we describe highlights from key publications appearing during the reporting period. This is not an exhaustive list, but serves to document our success in achieving our core objectives and where we have extended those objectives. This section is divided into three parts: A) Carbon and nitrogen cycle dynamics, B) Soil – tree – atmosphere hydraulic coupling, and C) Modeling.

A. Carbon and nitrogen cycle dynamics

We found striking C cycling resilience following moderate disturbance to the forest (Gough et al. 2013, Fig. 1). Canopy quantum yield, a measure of light-use efficiency, and maintenance of light absorption maintained net ecosystem production (NEP) and aboveground wood net primary production (NPP) when leaf area index (LAI) of the treatment forest temporarily declined by nearly half its maximum value. In the year following the foliar biomass (or LAI) minimum, redistribution of nitrogen (N) in the treatment forest from senescent early successional aspen and birch to non-girdled later successional species facilitated the recovery of total LAI to pre-disturbance levels. Sustained canopy physiological competency following disturbance coincided with a downward shift in maximum canopy height, indicating that compensatory photosynthetic C uptake by undisturbed, later successional subdominant and subcanopy vegetation supported C uptake resistance to disturbance. These findings have implications for ecosystem management and modeling, demonstrating that forests may tolerate considerable leaf area losses without diminishing rates of C uptake.



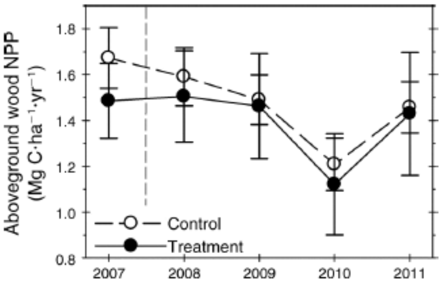


Figure 1. Apparent quantum yield of the canopy, canopy maximum gross primary production GPP$_{max}$, and aboveground wood net primary production (NPP) at control (US-UMB) and Treatment (FASET, US-UMd) sites. Dashed line indicates timing of the disturbance treatment (Gough et al., 2013).

To test the hypothesis that age-related increases in canopy structural complexity improve resource-use efficiency and to evaluate canopy structural influences on forest C storage over successional timescales, we measured the fraction of photosynthetically active radiation absorbed by the canopy (fAPAR), foliar N$_{mass}$, and aboveground net primary production (ANPP) in a chronosequence of 39 stands spanning >160 years of forest development. We found that increasing canopy complexity over the course of forest development mediates greater resource-use efficiency in these forests (Figure 2, Hardiman et al. 2013). Forest stands with more structurally complex canopies had higher light and nitrogen use efficiencies (LUE & NUE) and higher ANPP. Rugosity had a bigger influence on ANPP across all stands than did LAI, demonstrating the greater long-term influence of leaf area arrangement, rather than quantity within the canopy on forest C storage. We conclude that canopy structural complexity may facilitate greater resource use efficiency (RUE) in aging forests and so increase ANPP compared to structurally simpler canopies in young forests, thus maintaining significant C storage potential in aging forests. We suggest that forest managers should incorporate canopy structural complexity as a robust proxy of stand C storage potential in forests differing widely in age and disturbance history.

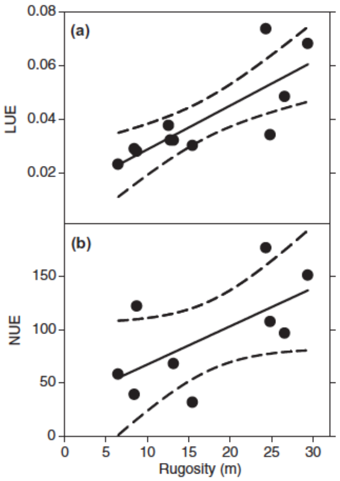


Figure 2. Relationships between Light Use Efficiency (LUE, a), Nitrogen Use Efficiency (NUE, b), and canopy rugosity. R^2=0.6 and 0.32 for LUE and NUE, respectively. Areas bounded by dotted lines are 95% confidence intervals (Hardiman et al. 2013).

We used a plot-scale gradient of tree mortality within the large disturbance manipulation to examine the relationship between disturbance severity and forest production. Specifically, we quantified how aboveground wood net primary production ($ANPP_w$) responds to a range of disturbance severities and identified mechanisms supporting $ANPP_w$ resistance or resilience following moderate disturbance. In Stuart-Haëntjens (2015) we found that $ANPP_w$ declined non-linearly with rising disturbance severity, remaining stable until > 60 % of the total tree basal area senesced (Fig. 3). As upper canopy openness increased from disturbance, greater light availability to the subcanopy enhanced the leaf-level photosynthesis and growth of this formerly light-limited canopy stratum, compensating for upper canopy production losses and a reduction in LAI. As a result, whole-ecosystem production efficiency ($ANPP_w$/LAI) increased with rising disturbance severity, except in plots beyond the disturbance threshold. These findings provide a mechanistic explanation for a non-linear relationship between $ANPP_w$ and disturbance severity, in which the physiological and growth enhancement of undisturbed vegetation is proportional to the level of disturbance until a threshold is exceeded. These results also have important ecological and management implications, demonstrating that in some ecosystems forest production and disturbance are non-linearly related.

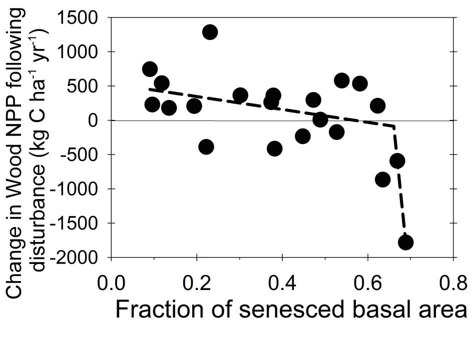


Figure 3. Changes in wood NPP across a gradient of disturbance severity, characterized as the fraction of senesced basal area within a 0.1 ha plot (Stuart-Haëntjens et al., 2015).

Nitrogen (N) transformations in forest soils are fundamentally important to plant and microbial N nutrition and the N balance of forest ecosystems, but changes in the patterns and rates of N transformations during forest succession are poorly understood. In order to better understand how soil N cycling changes during ecosystem succession, we analyzed four years of soil N cycling measurements in a 90-year-old secondary forest undergoing dieback of early-successional, dominant canopy trees (Nave et al. 2014). We expected that tree mortality would decrease root biomass, leading to increased soil NH_4^+ availability, and that these changes would prompt fundamental shifts in the N cycle such as the initiation of significant nitrification and increased cycling of oxidized N compounds in gas phase and soil solution. As expected, indices of soil NH_4^+ and NO_3^- availability increased with successional stage (defined as the proportion of dead trees), and were negatively correlated with the amount of fine root biomass (Fig. 4). However, the standing amount of fine root biomass was not affected by tree mortality; increased soil NH_4^+ and NO_3^- availability therefore more likely resulted from successional increases in N-mineralization than decreases in root N uptake. Nitrification (as indicated by NO efflux as a proxy) increased due to elevated substrate (NH_4^+) availability, and the soil solution NO_3^- concentration increased as a result. Soil N_2O efflux was not affected by succession, nor was it related to other N cycling parameters. Collectively, these results indicate that recent successional advancement has accelerated soil N cycling and shifted the N economy of this ecosystem towards greater importance of NO_3^-.

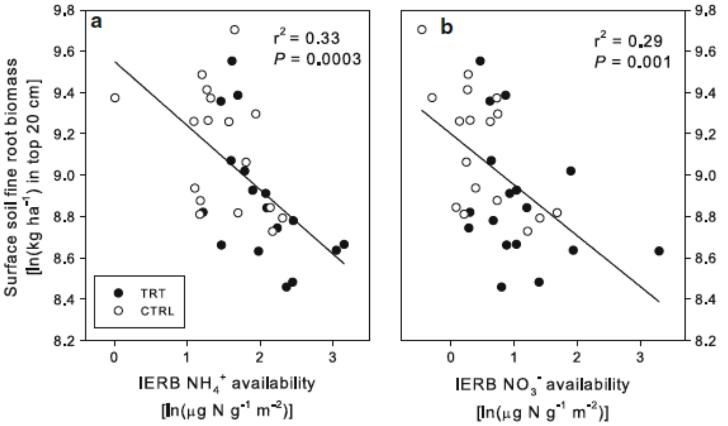


Figure 4. Relationships between the amount of fine root biomass in surface soil and the availability of NH_4^+ (panel a) and NO_3^- (panel b) as measured by ion exchange resin bags (IERBs) for n=8 plots each in the control and treatment forests. Points represent ln-transformed plot-level annual mean values across 4 years; best-fit statistics correspond to simple linear regression models fit to the data (Nave et al. 2014).

B. Soil – tree – atmosphere hydraulic coupling

Forested ecosystems may experience intermediate disturbances that involve changes of crown-scale canopy characteristics. When such changes occur, soil moisture under disturbed canopy may become either drier or wetter, depending on the interplay between small-scale hydrological processes, tree-scale vegetation function, and meteorological forcing. We conducted half-hourly, three-meter deep measurements of soil moisture at four plots at UMBS. Two of the plots (one aspen- and the other oak-dominated) are located near the US-UMB tower; this forest area represents an undisturbed control site. Two other plots are located near the US-UMd flux tower. The data collected at the four plots provide observational evidence of changes in hydrological dynamics that were induced by species-specific crown-scale disturbances of the canopy structure (He et al. 2013). Figure 5 shows that the soil water storage under the girdled aspen was persistently higher, as compared to the undisturbed plots over the observational period of 2009–2011. These results suggest that the larger water storage resulted from increased net precipitation and reduced transpiration during growing seasons following the girdling operation. These processes “outcompeted” the presumably enhanced interception and transpiration by understory plants as well as increased soil evaporation. Additionally, surface soil layer at the disturbed plot exhibited highest temporal variability among all monitored plots. The moisture profiles at the four plots were different, with the disturbed plot exhibiting relatively wetter shallow soil layers. Furthermore, water loss at the disturbed plot was concentrated in shallower soil layers, signifying a shift of uptake and/or change of dominant processes.

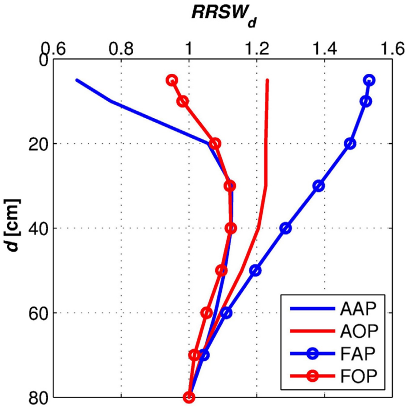


Figure 5. Mean growing season (2010-2011) Root-zone Relative Soil Wetness factor (RRSWd), measured in the deep soil-moisture pits at depths, d, 0–80 cm throughout the root zone at the four plots - Control (US-UMB) site aspen plot (AAP); Control site oak plot (AOP); US-UMd (FASET) experimental site aspen plot (FAP); and experimental site oak plot (AOP) (He et al. 2013).

Thomsen et al. (2013) reported analyses of the dynamics of leaf water potential in two broad-leaf deciduous tree species under a range of air vapor pressure deficits and soil conditions. During nights when the soil is dry, the diffuse-porous, isohydric and shallow-rooted *Acer rubrum* does not recharge its xylem and leaf water storage to the same capacity that is observed during nights when the soil is moist. The ring-porous, deep-rooted *Quercus rubra* displays a more anisohydric behavior and appears to be capable of recharging to capacity at night-time even when soil moisture at the top 1 m is near wilting point, probably by accessing deeper soil layers than *A. rubrum*. Compared to *A. rubrum*, *Q. rubra* displays only a minimal level of down-regulation of stomatal conductance, which leads to a reduction of leaf water potential during times when vapor pressure deficit is high and soil moisture is limiting (Fig 6). We determine that the two species, despite typically being categorized by ecosystem models under the same plant functional type – mid-successional, temperate broadleaf – display different hydraulic strategies. These differences may lead to large differences between the species in water relations, transpiration and productivity under different precipitation and humidity regimes.

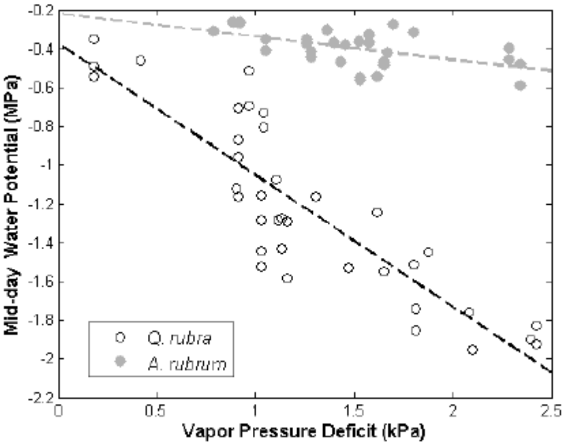


Figure 6. Relationship between mid-day leaf water potentials of *Q. rubra* and *A. rubrum* and sub-canopy vapor pressure deficit. *A. rubrum* shows very mild response to VPD while *Q. rubra's* response slope to VPD is significantly steeper, indicating that this species is exhibiting an anisohydric response while *A. rubrum* is more isohydric and closes stomata when water storage levels in the stem are low (Thomsen et al. 2013).

Intermediate disturbances shape forest structure and composition, which may in turn alter carbon, nitrogen, and water cycling. Matheny et al. (2014) used data from FASET/US-UMd to simulate an accelerated age-related senescence associated with natural succession. Using 3 years of eddy covariance and sap flux measurements in the US-UMd treatment plot and US-UMB control plot, we analyzed disturbance-induced changes to plot level and species-specific transpiration and stomatal conductance. We found transpiration to be ~15% lower in disturbed plots than in un-manipulated control plots. However, species-specific responses to changes in microclimate varied. While red oak and white pine showed increases in stomatal conductance during post disturbance (62.5 and 132.2%, respectively), red maple reduced stomatal conductance by 36.8%. We used the hysteresis between sap flux and vapor pressure deficit to quantify diurnal hydraulic stress incurred by each species in both plots (Fig. 7). Red oak, a ring porous anisohydric species, demonstrated the largest mean relative hysteresis, while red maple, bigtooth aspen, and paper birch, all diffuse porous species, had the lowest relative hysteresis. We employed the Penman-Monteith model for LE to demonstrate that these species-specific responses to disturbance are not well captured using current modeling strategies and that accounting for changes to leaf area index and plot microclimate are insufficient to fully describe the effects of disturbance on transpiration.

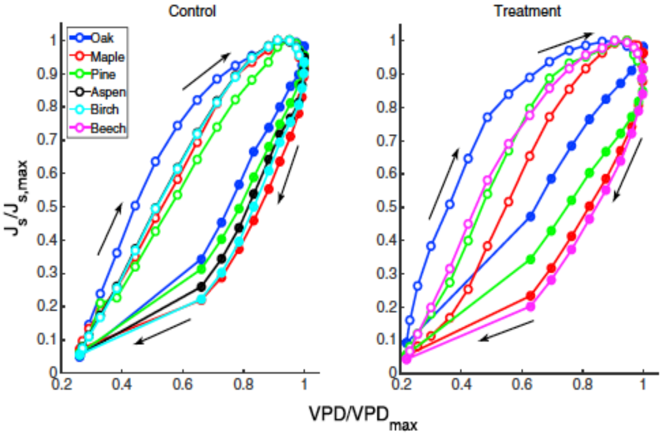


Figure 7. Relative hysteresis between sap flux and VPD during daylight hours over all size classifications for each species. Both Js and VPD have been normalized by their respective daily maxima. Open symbols represent pre-noon hours, closed symbols are afternoon. Arrows indicate the direction of the hysteresis. There were larger differences between the extent of hysteresis in different species in the disturbed treatment plot. These differences were consistent with the trees hydraulic strategy (Matheny et al. 2014).

C. Modeling

Over forested canopies, the physical structure of vegetation interacts with wind by exerting drag on the flow, thus generating turbulent mixing that is necessary for scalar transport. Mauer et al. (2013) used 11 years of above canopy wind speed measurements from spatially and temporally heterogeneous forest environments to disentangle the effects of different features of changing canopy structure on the surface roughness parameters: displacement height (d), roughness length (z_0), and the aerodynamic canopy height (h_a). We found a significant increasing long-term trend of dormant-season (leaf-off) h_a, which closely resembles the rate of biometrically derived vertical stem growth over years (Fig. 8). We showed that the values of d and z_0 trade-off with higher d and shorter z_0 when leaf area is high in the growing season. Using airborne lidar measurements and a footprint model for flux-source location detection, we showed that these d and z_0 trade-offs also correspond with the spatial differences between taller and shorter subplot patches. We show that incorporating seasonal-scale temporal heterogeneity of d and z_0 into surface-flux and ecosystem models will improve their accuracy. However, incorporating simple empirical modifications to surface-structure roughness parameters due to inter-annual variation in canopy height and leaf area did not lead to improved modeling of frictional velocity within this study. Further investigation of structure–roughness relationships is needed to incorporate these aspects. Finally, this study proposes a meteorological-based method for estimating vertical stem growth in undisturbed forest environments by tracking h_a over time.

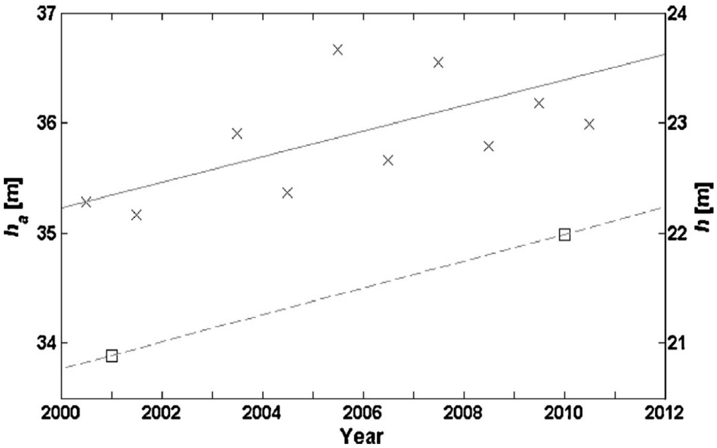


Figure 8. Long-term trend of dormant season, site-level aerodynamic-effective height, h_a, at the control site (crosses, left y-axis). A significant trend of 11.7 cm/yr was determined using linear regression ($r^2 = 0.48$, $P = 0.01$) (solid gray line). Observed tree-stem height, h (squares, right y-axis), at the control site showed a nearly identical trend of 12.2 cm/yr mean growth rate (dashed gray line) (Mauer et al. 2013).

There currently are numerous data sources available for estimating the timing of recurrent plant phenology transitions. Garrity et al. (2011) compared measurements from several phenology data sources to understand the relationship between phenology metrics derived from these data sources and the timing of seasonal transitions in net ecosystem exchange (NEE) (Fig. 9). We identified the timing of start, peak, end and the duration of the carbon uptake season, as well as the timing of the transitions from sink to source and source to sink using 11 years of NEE data from UMBS. Using fitted logistic functions we identified proxy metrics for phenological transitions from the time series of Albedo, fraction of absorbed photosynthetically active radiation (fPAR), Plant Area Index (PAI), and MODIS normalized difference vegetation index (NDVI), enhanced vegetation index (EVI), and leaf area index (LAI) products of various spatial representations. We found that no single source of phenological data was able to accurately describe annual patterns of flux phenology. However, for each transition in NEE (e.g., start of season, transition to net sink), the metrics from one or more data sources were significantly ($p < 0.05$) correlated with the timing of these recurring events. A marginally significant trend toward a longer NEE carbon uptake period over 11 years was not detected by any of the metrics, primarily because none of the metrics were available for the full duration of the NEE data, and NEE did not show significant and consistent trends during the sub-sets of the time when proxy data were available. The results of our study highlight the relative strengths and weaknesses of each phenology data source for directly estimating seasonal transitions and interannual trends in carbon flux phenology of a deciduous forest.

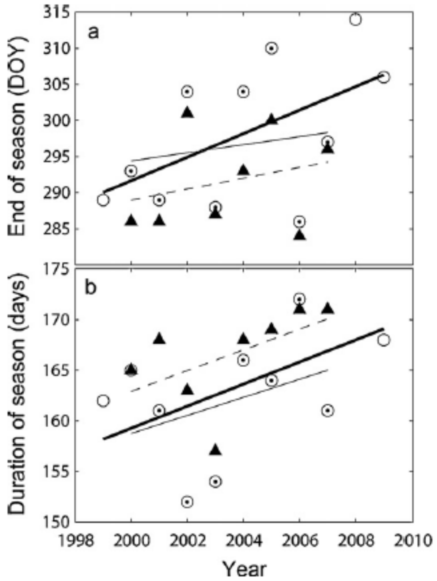


Figure 9. Interannual trends of (a) end of season (EOS) and (b) duration of season (DOS). In both cases, the LAI-2000 data source was significantly correlated with the annual variability in the timing of each of these carbon flux phenology features. Open circles represent 11 years of NEE-derived EOS (panel a) and DOS (panel b). The solid black line is the least squares fit to these observations. The triangles represent the metrics derived from LAI-2000 measurements, available for 8 of the 11 years. The dotted circles represent NEE-derived transitions for the same years as LAI-2000 measurements were available. The dashed and the solid gray lines mark the linear regression for LAI-2000 and the NEE-derived DOS (respectively) during the same years that LAI-2000 observations were available (Garrity et al. 2011).

Frasson et al (in review) used the Ecosystem Demography version 2 (ED2) model to test the hypotheses that in temperate mixed-deciduous forests: (1) disturbances that affect only a subset of species impact the carbon cycle differently from disturbances that are not species-specific. In particular, disturbances that target early successional tree species will lead to higher carbon uptake by the post-recovery, mid- and late-successional community, and (2) increasing disturbance intensity leads to more pronounced short-term decreases in carbon uptake. To test these hypotheses, we employed a series of virtual experiments conducted using ED2 to evaluate the sensitivity of a temperate mixed-deciduous forest to different levels and types of disturbance (Fig 10). Our simulation scenarios included a control (undisturbed) case, a homogeneous disturbance case where we removed 30% of all trees regardless of their functional type (i.e., early or later successional deciduous as well as conifers), and three cases of increasing disturbance intensity where 70%, 85%, and 100% of only early-successional deciduous trees were removed. Our results indicate that homogeneous, non-plant functional type-specific disturbances led to longer recovery times and to a smaller increase in long-term carbon sequestration compared to complete removal of early-successional deciduous trees only (11% versus 25% increases respectively). When disturbances targeted only early-successional trees, the short-term impact on net ecosystem CO_2 exchange and its post-disturbance recovery time were relatively insensitive to varying disturbance intensities. However, the long-term carbon dynamics were sensitive to disturbance intensity, with greater early-successional tree mortality leading to increased carbon uptake over time.

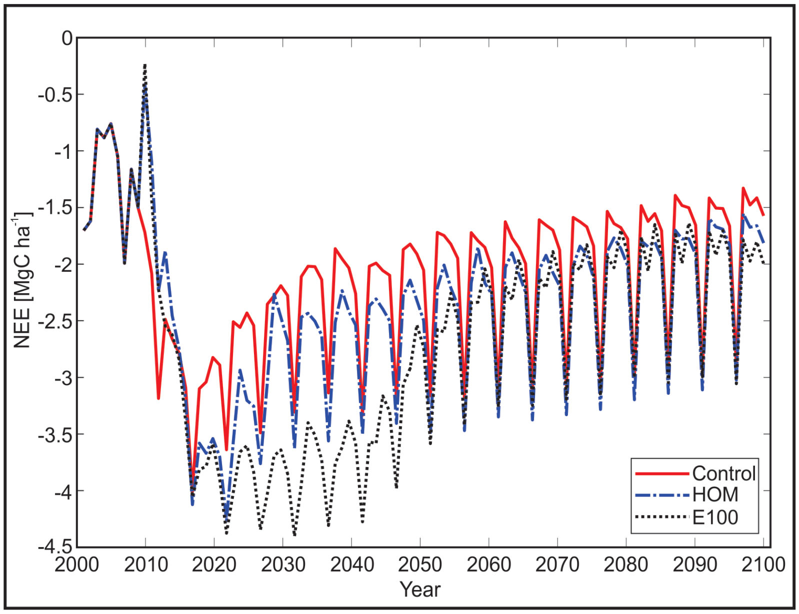


Figure 10. Time series of modeled, monthly, plot-level *NEE* in the full 100 years of ED2 simulations, for cases of no disturbance (solid red line), homogeneous disturbance (HOM, dash-dot blue line) that affects all species at an equal proportion (30% of LAI) and the E100 disturbance, (100% removal of early-successional deciduous PFT, dashed black line, accounting for 30% of total plot LAI). The 5-year cycles in NEE visible in this figure are a result of recycling 5 years of meteorological forcing throughout the simulation (Frasson et al. in review).

Bond-Lamberty et al. (2015) tested whether three forest ecosystem models—Biome-BGC, a classic big-leaf model, and the ZELIG and ED gap-oriented models—could reproduce the resilience to moderate disturbance observed in FASET. Each model was parameterized, spun up, and disturbed following similar protocols, and run for 5 years post-disturbance. The models replicated observed declines in aboveground biomass well. Biome-BGC captured the timing and rebound of observed leaf area index (LAI), while ZELIG and ED correctly estimated the magnitude of LAI decline (Fig. 11). None of the models fully captured the observed post-disturbance C fluxes, in particular gross or net primary production (NPP). Biome-BGC NPP was correctly resilient, but for the wrong reasons, and could not match the absolute observational values. ZELIG and ED, in contrast, exhibited large, unobserved drops in NPP and net ecosystem production. The biological mechanisms proposed to explain the observed rapid resilience of the C cycle are typically not incorporated by these or other models. It is thus an open question whether most ecosystem models will correctly simulate the gradual and less extensive tree mortality characteristic of moderate disturbances.

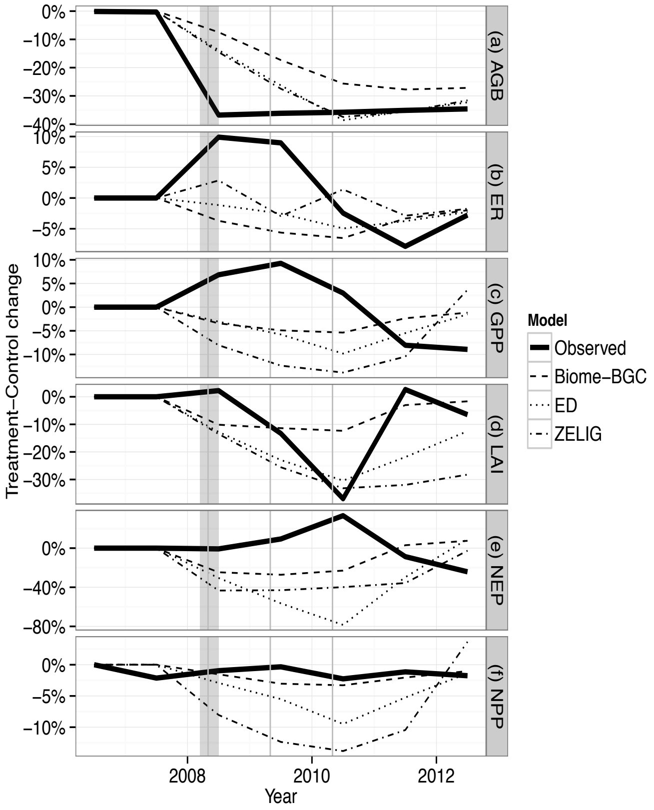


Figure 11. Model performance in replicating observations from FASET (US-UMd). Panels include (a) aboveground biomass (AGB), (b) ecosystem respiration (ER), (c) gross primary production (GPP), (d) leaf area index (LAI), (e) net ecosystem production (NEP), and (f) net primary production (NPP). Vertical shaded area shows time of FASET's girdling (Bond-Lamberty et al. 2015).

2. Research products and publications

As an AmeriFlux Management Program Core Site we post NEE, ancillary meteorological data and comprehensive biological data (BADM) from our tower cluster (the UMBS AmeriFlux control site, US-UMB, and the FASET disturbance site, US-UMd) to the Fluxnet data site at CDIAC. This posting is current through 2015. Our project web site, listing many meta-data and biometric data, is at http://flux.org.ohio-state.edu/.

Our site facilitates numerous synergist activities with other investigators and the funding of new proposals. As evidence of the level and quality of the research products resulting from this project we have 53 peer-reviewed publications during the 2011-2014 reporting period, 24 from site-level work and 29 from collaborative engagements within Fluxnet. These are listed below (site-level*; **PI/co-PI bold**, student/post-doc#).

Barr AG, Richardson AD, Hollinger DY, Papale D, Arain MA, Black TA, **Bohrer G**, Dragoni D, Fischer ML, Gu L, Law BE, Margolis HA, McCaughey JH, Munger JW, Oechel W, Schaeffer K. 2013. Use of change-point detection for friction-velocity threshold evaluation in eddy-covariance studies. *Agricultural & Forest Meteorology* 171:31-45.

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Fu, D., B. Chen, H. Zhang, J. Wang, T. A. Black, B. D. Amiro, **G. Bohrer,** P. Bolstad, R. Coulter, A. F. Rahman, A. Dunn, J. H. McCaughey, T. Meyers, and S. Verma. 2014. Estimating landscape net ecosystem exchange at high spatial-temporal resolution based on Landsat data, an improved upscaling model framework, and eddy covariance flux measurements. *Remote Sensing of Environment* 141:90-104.

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3. Student degrees supported

There have been 11 PhD students, 5 MS students, and 2 post-doctoral researchers supported in whole or in part by this project during the reporting period. They are:

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As an NSF supported Research Experience for Undergraduates (REU) site and with other sources of funding, a large number of undergraduate researchers have worked at our site during the reporting period. See http://flux.org.ohio-state.edu/ for names and institutional affiliations.