



Physiographic factors underlie rates of biomass production during succession in Great Lakes forest landscapes



Lucas E. Nave^{a,b,*}, Christopher M. Gough^c, Charles H. Perry^d, Kathryn L. Hofmeister^{a,e}, James M. Le Moine^{a,b}, Grant M. Domke^d, Christopher W. Swanston^f, Knute J. Nadelhoffer^{a,b}

^a University of Michigan, Biological Station, Pellston, MI 49769, United States

^b University of Michigan, Department of Ecology and Evolutionary Biology, Ann Arbor, MI 48109, United States

^c Virginia Commonwealth University, Department of Biology, Richmond, VA 23284, United States

^d USDA-Forest Service, Northern Research Station, St. Paul, MN 55108, United States

^e Cornell University, Department of Natural Resources, Ithaca, NY 14850, United States

^f USDA-Forest Service, Northern Research Station, Houghton, MI 49931, United States

ARTICLE INFO

Article history:

Received 2 March 2017

Received in revised form 24 April 2017

Accepted 27 April 2017

Available online 5 May 2017

Keywords:

Ecosystem classification

Landform

Soil texture

Soil moisture status

Natural drainage

ABSTRACT

Biomass production in living trees is the basis of numerous forest ecosystem functions and services. However, rates of and controls on biomass production vary widely across temperate forests, particularly over successional timescales of decades and centuries. Biomass production in temperate forests is most often interpreted within the context of biotic or top-down controls, such as species composition or disturbance. However, there is need to investigate how bottom-up physiographic factors, such as landform attributes, drainage, and soil properties mediate biomass production. In order to investigate patterns, controls, and potentials for biomass production across spatial levels ranging from individual ecosystems, to landscapes, to entire regions, we synthesized long-term forest inventory datasets from the United States Great Lakes region, placed them in the context of a hierarchical ecological unit classification, and tested the influence of physiographic factors on biomass production rates and temporal trajectories across ecological levels. Key findings include: 1) At nearly all ecological levels, physiographic controls (e.g., soil texture, drainage class, water table depth) on soil moisture status are significant predictors of variation in biomass production rates, with mesic sites accumulating biomass more rapidly than xeric sites, which, in turn accumulate biomass more rapidly than hydric sites. 2) Aboveground live biomass can apparently continue to accumulate through 2–3 centuries of succession, exceeding 300–400 Mg ha⁻¹ on mesic sites throughout the region. 3) Stand age distributions indicate that hydric sites are harvested least often, while the high production rates of mesic sites suggest they are most appropriate for frequent harvesting. 4) Median, 1st-quartile, and 3rd-quartile growth rates of individual ecosystems, landscapes, and ecoregional subsections and sections reveal ecological units in which forests may vary in their potential for increases or decreases in biomass production, e.g., due to management interventions, climate change, or disturbances. Specifically, some units have tightly constrained distributions, suggesting little capacity for change in production rates relative to observed medians, while other units have wide variation in biomass production rates, indicating the potential for relatively large increases or decreases in production. Altogether, the results of this analysis show that physiography exerts widespread, bottom-up controls on biomass production across the region of study, and can be used in spatially explicit frameworks to understand ecosystem functioning and inform scientific forest management.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Biomass production in living vegetation is a major determinant of ecosystem functioning. This process integrates hydrologic and biogeochemical cycles (e.g., carbon and nitrogen), and thus influences associated ecosystem services such as mediation of energy

* Corresponding author at: UMBS, 9133 Biological Rd., Pellston, MI 49769, United States.

E-mail address: lukenave@umich.edu (L.E. Nave).

and water balances, maintenance of nutrient retention and cycling, and mitigation of atmospheric CO₂ production and climate change (Bonan, 2008; Ellison et al., 2005; Nave et al., 2011). Through its interactions with other biotic components, biomass production is a foundation for biodiversity maintenance, community composition and structure, and trophic interactions in forest ecosystems (Clark et al., 2001; Facelli and Pickett, 1991; Hardiman et al., 2011). However, even as biomass production may be conceived of as strongly influencing ecosystem structure and functioning, it may be best viewed as interacting with other drivers, and itself responding to bottom-up, physical controls distributed non-randomly across Earth's surface (Barnes et al., 1982). These physical factors, falling under the discipline of physiography, include climate, landform, parent material, soil, and hydrologic regime. Some of these factors (e.g., macroclimate, landform and its topoclimatic influences) are essentially independent of the biota, while others (e.g., microclimate, soils) are subject to substantial biotic feedbacks. Taking this view of forest ecosystems, in which all components interact, biomass production is an integrative attribute that can be used as an index of whole-ecosystem functioning, and its variation over time and space tested to discern the role of physiographic factors in longer-term and larger-scale questions of interest to researchers and forest managers.

Patterns of long-term change in forest biomass, and the mechanisms underpinning these changes, have challenged researchers studying ecosystem succession for many decades (Brown and Parker, 1994; Möller et al., 1954; Ovington, 1962; Wardle et al., 2004; Whittaker and Woodwell, 1969). Although a predictive understanding of forest biomass production over successional timescales is a longstanding goal of ecosystem ecologists, and would advance scientific forest management, its development is hindered by differences of philosophy and methods. Specifically, researchers interested in forests as long-term C sinks have variously used different measures to place them within a C budgeting framework, including annual vegetation production rates (e.g., net primary production; Gower et al., 1996), annual ecosystem C sequestration rates (e.g., net ecosystem production; Gough et al., 2016), or C accumulation within ecosystem pools over long timescales (e.g., live biomass, “dead biomass”; Keeton et al., 2011). To be clear, each of these metrics is justifiable for different questions or timeframes of interest. However, methodological differences underlie inconsistencies among the studies that propose or affirm numerous different trajectories of biomass production (e.g., Lichstein et al., 2009; Luysaert et al., 2008; Siccama et al., 2007). Unfortunately, it is not clear what proportion of this variation between studies is due to real effects of underlying factors, such as forest type (Foster et al., 2014) or successional stage (Halpin and Lorimer, 2016), and what proportion is driven by methodological differences (e.g., in metrics or study designs). Altogether, these matters make it difficult to offer a consistent revision to the older paradigm, which holds that forest biomass production declines asymptotically to zero over successional timescales (Bormann and Likens, 1979; Kira and Shidei, 1967; Odum, 1969; Ryan et al., 1997). Regardless, it is clear that additional long-term studies of forest succession and biomass production offer opportunities to constrain patterns (and differences), attribute mechanisms, and increase predictability of biomass production over successional time. With this as the goal, living aboveground biomass is a sound metric because it is among the largest C pools, shows a generally consistent increase over successional timeframes, and is straightforward to measure (Pregitzer and Euskirchen, 2004). Furthermore, living aboveground biomass is typically the only ecosystem component that is directly manipulated by management, and is the material utilized for the wide range of forest products on which society depends. Overall, there is a need to place long-term studies of forest aboveground biomass production in a framework that can

explain both successional and spatial patterns in biomass production, and as a result provide predictive, place-based information useful to forest managers. In the present study, we synthesized long-term forest inventory datasets from a variety of sources, placed them in a hierarchical ecological unit classification framework, and examined relationships between biomass production and physiographic factors over multi-decadal to multi-century timescales. Through this approach, we addressed these specific questions: 1) How do rates of aboveground biomass production differ among the landforms and ecosystems comprising a single, well-studied landscape during the first century of stand development, and what physiographic factors control these differences? 2) What are the patterns and potentials of biomass production over 1–3 century timescales on this same landscape? 3) Do physiographic controls operating at the landscape level scale up through successively higher hierarchical ecological levels? 4) What is the range of variation in aboveground biomass production rates among units at larger ecological levels, and what might this variation suggest about the potential for increases or decreases in biomass production?

2. Methods

2.1. Study area

This research synthesizes data collected at two scales. Its foundation is a well-characterized landscape in northern Michigan in the United States (U.S.) with a place-based, highly detailed forest ecological unit classification system and long-term records of biomass production. This intensively studied landscape is situated within a broader ecoregion that spans the northern Great Lakes.

2.1.1. Landscape-level intensive area

This portion of the research was conducted at the University of Michigan Biological Station (UMBS), U.S. (45.56°, –84.72°), where the mean annual temperature is 5.5° and mean annual precipitation is 817 mm (including 294 cm snowfall). The UMBS is a ~4400 ha field station occupying a landscape formed by the deposition and modification of glacial parent materials at the end of Laurentian glaciation, between 14,000 and 11,000 years before present (Blewitt and Winters, 1995; Lapin and Barnes, 1995; Spurr and Zumbege, 1956). The core of this landscape is the till deposited directly by the wasting ice mass; till occupies the highest elevations (up to 276 m a.m.s.l. on UMBS property) and is present as ground, interlobate, and drumlinized moraines. However, moraines are exceeded in extent by outwash plains, which were deposited by meltwater flowing away from the margins of the wasting ice mass. These major landforms were re-worked during regional glacial re-advances 12,600–10,500 years ago and by glacially mediated lakes 4,300–3000 years before present, which left behind minor landforms such as dunes, beach ridges, ice- and lake-margin terraces. Relatively little geomorphic alteration has occurred on the landscape since that time, and the bedrock (Silurian limestone and Devonian shale) is buried beneath 100–200 m of glacial deposits. Glacial geomorphology exerts strong control over soil development and climate in the vicinity of UMBS. Moraine soils are mostly Lamellic and Alfic Haplorthods formed in heterogeneous mixtures of sandy to sandy clay loam till (USDA Subgroups), while outwash soils are predominantly Entic Haplorthods formed in coarser, well-sorted sands (with occasional gravel at locations more proximal to the wasting ice). Soils in the lowest (wettest) landscape positions are predominantly Endoaquods, Endoaquents, and Haplosaprists, respectively; Endoaquods formed in coarse-textured, low-lying outwash-lake plains with seasonally high water tables, Endoaquents are in similar parent materials and topographic positions but have semipermanent sat-

uration, and the Haplosaprists consist of 50–100 cm of permanently saturated, well-decomposed organic matter atop the underlying coarse-textured outwash-lake plain deposits. Northern Michigan's climate is continental, but modified in complex ways by the Laurentian Great Lakes (which increase precipitation and decrease temperature extremes), and by local topographic gradients (which influence precipitation patterns and increase temperature extremes). Low-lying outwash plains at UMBS experience occasional killing frosts during the growing season, and colder winter temperatures (extremes as low as -40°) than higher-elevation outwash plains and locations adjacent to inland lakes. Current vegetation at UMBS, which is almost completely forested, reflects the broader land use history of the upper Great Lakes region. Namely, clearcutting and uncontrolled wildfires between 1870 and 1923 replaced pre-exploitation forests of *Pinus resinosa* Aiton, *P. strobus* L., *Tsuga Canadensis* (L.) Carriere, and long-lived hardwoods (*Acer saccharum* Marshall, *Fagus grandifolia* Ehrh., *Quercus rubra* L.) with mixed deciduous-conifer forests dominated by early-successional taxa such as *Populus grandidentata* Michx. and *Betula papyrifera* Marshall on uplands, and *P. tremuloides* Michx., *Abies balsamea* L., *Thuja occidentalis* L., *Alnus incana* L., and *Salix* L. in wetlands. Across most of UMBS, mixtures of early-successional taxa dominate, though these have been giving way to longer lived hardwoods and conifers since the late 1980s (Gough et al., 2010; Jones et al., 1993). Isolated stands on UMBS property (4, totaling < 200 ha) contain considerably older dominant trees and avoided clearcutting, affording opportunities to study them as references for later successional stages. Two of these stands were lightly cut in the 1880–1890 timeframe (Appendix A: Forestry Plots BS40A, BS40E, BS40F), one was very lightly cut from the 1890s through the 1940s (Colonial Point), and the fourth has no residual stumps (common in logged areas) and apparently regenerated following a stand-replacing wildfire in 1890 (Forestry Plots BS42A, B, C).

2.1.2. Province 212: the Laurentian mixed forest

The USDA Forest Service developed a framework in 1993 to organize the U.S. land base into a hierarchical structure of ecological units for planning and management purposes (Cleland et al., 1997; McNab et al., 2007). The National land base is divided into domain, division, and province units; each province covers hundreds of thousands of square kilometers and is identified by a distinct climate type and dominant potential natural vegetation. Lower-level units (section, subsection, sub-subsection, landtype association, landtype, and landtype phase) are differentiated by increasingly localized information about geologic formations, surface deposits, landforms and soils. The framework represents an ongoing process, but the involvement of scientists spanning a range of disciplines ensures that its approximations and classifications of ecological units can serve as a rigorous, testable framework for research on forest ecology and management. In our study, intended to identify patterns of and controls on forest biomass production, we use physiographic and soils information from across province 212, the Laurentian Mixed Forest province, with the intent of assessing the repeatability of results across scales.

Province 212 spans ~261,000 km² across the northern portions of the Great Lakes region (Michigan, Wisconsin, and Minnesota). The province has a humid, continental climate with cold winters and warm summers, which fosters mixtures of warmer-temperate (e.g., *Acer* spp., *Quercus* spp., *Betula alleghaniensis* Britton, *Populus grandidentata*, *Pinus strobus*) and cold-tolerant boreal (e.g., *Picea* spp., *Abies* spp., *B. papyrifera*, *P. tremuloides*, *P. banksiana* Lamb.) tree taxa. The province has a generally consistent land use history throughout, having undergone clearcutting and uncontrolled wildfires from the late 1800s to early 1900s. Modern forest management began around the middle of the 20th century, and is widespread but not particularly intensive (Bates et al., 1993;

Gahagan et al., 2015; Gerlach et al., 2002; Palik et al., 2003; Stone, 2002). Typical treatments include clearcutting in early-successional deciduous or mixed cover types (40–80 year rotations), periodic selective harvesting in longer-lived deciduous cover types, and thinning – clearcutting cycles in plantation conifers. As with the UMBS landscape described in Section 2.1.1, all of province 212 was covered by ice during Laurentian glaciation, although its geological formations, surface deposits, and landforms vary widely. Roughly the south-eastern half of the province is underlain by Paleozoic sedimentary bedrock, which is buried beneath 0–500 m of coarse to fine, weakly acid to circumneutral glacial drift; the north-western half has Precambrian (predominantly igneous) bedrock and thinner deposits of more acidic glacial drift and fine-textured postglacial lake sediments. The climate is coldest and driest in the northwestern part; throughout the province, interior subsections have more extreme temperatures and lower precipitation than areas located adjacent to (particularly downwind; south or east) of the moderating influence of the Great Lakes (Albert, 1994). The most widespread USDA soil Orders are Spodosols, Alfisols, Inceptisols and Histosols. Spodosols and Alfisols are predominant on coarse and fine-textured glacial and glacio-lacustrine deposits, respectively, Inceptisols occur primarily where glacial deposits are thinner and a greater share of the parent materials are derived from locally weathered or transported bedrock, and Histosols occur in low, wet landscape positions where organic detritus accumulates in place atop underlying sediments or bedrock.

2.2. Datasets

To address our questions of interest, we synthesized datasets related to vegetation, ecosystem, and soil properties across a range of spatial levels. For the intensive, landscape-level portion of our analysis, we synthesized forest inventory, physiographic and soil datasets from UMBS data resources; for the extensive, province-level portion of our analysis, we compiled similar datasets developed during the ongoing National Forest Inventory (NFI), maintained by the USDA Forest Service, Forest Inventory and Analysis (FIA) National Program (O'Connell et al., 2016). We describe below the steps performed in raw data selection and compilation; descriptions of data manipulation and analysis follow under Section 2.3.

2.2.1. Stand-level forest inventory data

At the stand (site) level, we compiled forest inventory data from plots located on UMBS property (Table 1), some of which date back to the early decades of UMBS (established in 1909). Historical data on the plots, including their dates of establishment, census, stand initiation and disturbance are from a variety of sources, including theses and dissertations (e.g., Farmer, 1958; Kilburn, 1957), technical reports and books (e.g., Albert and Minc, 1987; Barnes, 2009; Bradley, 1947; Spurr, 1956), personal communications (R. Vande Kopple, UMBS Resident Biologist), and dendrochronological verification in the field by us and other UMBS researchers. Because the plots used for this analysis were established for many reasons over a long timeframe, they differ in size, measurement frequency, and sampling protocols. However, all plots provide forest inventory data from documented censuses in forest stands with well-known disturbance histories. Stand-level disturbance information and the citations and methods used for these determinations are specified in Appendix A. Collectively, we gleaned more than 60,000 measurements of identities (to species level) and sizes of individual, living trees and shrubs from plot inventories spanning 80 years. We used well-established allometric equations (Gough et al., 2008) to compute total aboveground biomass on a per-stem basis for each census. For each census, we summed individual stem biomass values to the plot scale, and scaled each plot to a unit hectare for statistical comparisons of aboveground biomass density (Mg ha⁻¹), or its rate of

Table 1
Descriptive information about the forest inventory plots used in landscape-level analyses at UMBS.

Plot set	Reference	Forest type ^a	Description/purpose of establishment; resampling interval	n plots	Size (ha)	First census	Latest census	Stand ages (yr)
AmeriFlux plots	Gough et al. (2008)	Mesic to xeric mixed D/C	Systematic plot network for a ~ 100 ha eddy-flux tower footprint; ~5 year cycle	75	0.08	2003	2015	80–92
Colonial point	Hardiman et al. (2013)	Mesic mixed D/C	Forest composition and biomass inventory of late-successional reference stand	3	0.08	2005	2014	172–181
50 Year plots	Roberts and Richardson (1985)	Xeric to hydric D, C, S	Ecological references for studying succession; 10–30 year cycle	6	0.04	1938	2008	19–111
Cooper plots	Cooper (1981)	Mesic to xeric D	Replicates of 50 Year Plots; 5–10 year cycle	3	0.04	1969	2014	58–103
Forestry plots	Spurr (1956)	Xeric to hydric D, C	Stemwood production monitoring in older stands; 10–30 year cycle	7	0.2–0.4	1934	2014	52–301
Burn plots	Gough et al. (2007)	Xeric mixed D/C	Succession following experimental cutting and burning; ~decadal cycle	4	0.04–0.1	1957	2014	3–78
Wells plot	Sakai et al. (1985)	Mesic D	Community ecology and demography; 5–10 year cycle	1	1.0	1974	2000	63–89
Good site aspen	Koerper and Richardson (1980)	Mesic D	Stemwood production assessment; single harvest with dendrochronology	1	0.15	1975		28–63
Honeysuckle swamp	Nave et al. (submitted for publication)	Hydric C	Forest inventory in support of first-order wetland soil survey	8	0.04	2015		135

^a Forest types are generalized by physiographic setting (xeric, mesic, hydric; see Section 2.3.1) and functional composition (Conifer, Deciduous, Shrub, see Section 2.1.1).

production ($\text{Mg ha}^{-1} \text{ yr}^{-1}$), depending on constraints imparted by data availability or the question of interest.

2.2.2. Physiographic and soil data for the UMBS landscape

For the landscape-level portion of the analysis, we tested whether physiographic and soil attributes explained variation in rates or spatial patterns of aboveground biomass production using tests described under Section 2.3. But first, in order to synthesize the physiographic and soil datasets, we utilized the UMBS landscape ecosystems survey and classification (Pearsall et al., 1995; Lapin and Barnes, 1995; Zogg and Barnes, 1995). This effort, which spanned two decades and the entire UMBS property, differentiated unique landscape ecosystem types on the basis of their location on discrete landforms (major and minor), as well as their differences in topoclimate, microclimate, soil characteristics, and vegetation composition. This multi-factor hierarchical classification nests the UMBS landscape within the National framework of ecological units described in Section 2.1.2 (Albert, 1994; Cleland et al., 1997; McNab et al., 2007). Conforming to the National hierarchy, the UMBS landscape approximates a landtype association (thousands to hundreds of hectares), with its major and minor landforms correlating to landtypes (hundreds of hectares), and its smallest units—the 125 unique landscape ecosystem types on the UMBS property—synonymous with landtype phases (tens of hectares). While such localized ecological unit classifications are not available in most areas, they have a history of development and application in Germany, Canada, China, and elsewhere in Michigan, and their integration within the larger National hierarchy allows for testing the broader relevance of local inferences (Barnes et al., 1982; 1992; Kashian et al., 2003; Pregitzer and Barnes, 1984; Rowe, 1972; Spies and Barnes, 1985; Host et al., 1988). Datasets and products from the UMBS landscape ecosystems project are curated in the UMBS Information Management System (<http://umbs.lsa.umich.edu/research/>), and include raw field data, vegetation and soil databases from the 268 plots installed within the various landscape ecosystem types, and classifications and maps of landforms and ecosystem types (Pearsall, 1995). One consideration of note to our interpretation of soils data pertains to what we call the “forest floor” in the present analysis. Because soil descriptions for the landscape ecosystems project spanned many years and investigators, few of whom were trained in pedology, and because non-native earthworms have been mixing the O and A horizons for decades (Crumsey et al., 2014), we elected to sum the thicknesses of these horizons into a soil layer termed the “forest floor.” This terminology departs from USDA soil classification and hinders the ability to place some of our results in a pedogenic context, but it recognizes the ongoing changes in soil morphology at UMBS and the difficulty of judging the thicknesses of the two horizons (which are often quite thin) separately in the field. Lastly, we note that the soil description and sampling activities of the landscape ecosystems project produced two types of data: field determinations of horizon thicknesses, texture classes, parent materials, water table depths, and natural drainage classes; lab measurements of pH (in water) and particle-size distribution (Bouyoucos, 1936). Both types of data are used in our analyses relating biomass production to soil properties.

2.2.3. Biomass, physiographic and soil data for the Laurentian Mixed Forest province

For this portion of our data synthesis, our intent was to aggregate data from higher ecological levels to test the broader relevance of landscape-level findings, and also to investigate variation in biomass production rates among spatial units at those higher ecological levels. Therefore, we acquired observations of forest biomass, soil, and physiographic properties from all of province 212 from the FIA Database (FIADB; <https://apps.fs.usda.gov/fia/datamart/>). We briefly describe here the approach

and organization of data collected in the NFI to document how we synthesized this dataset. The FIA program was initiated in the 1930s as a systematic program to quantify attributes of and change in forest land across the U.S. The core NFI sampling unit is the plot, of which there is one permanent plot on approximately every 2400 ha across the U.S., with each plot placed randomly within a systematic hexagonal grid (Bechtold and Patterson, 2005). Sampling of each plot is conducted on fixed area subplots that vary in size depending on the metric, with inventory of canopy-level trees (>12.7 cm dbh) being conducted on four 0.016 ha subplots. This design enables the larger plot to capture fine-scale spatial variation, and the proportion of the plot under each condition is recorded in the field. For example, if an NFI plot straddles two distinctly different conditions, such as a recent clearcut and a mature stand, or a wetland terrace and an adjacent steep slope, the proportion of each subplot within the two different conditions (clearcut vs. mature, level vs. steeply sloping) is recorded in the field, and the measurements (e.g., tree size and number, age) associated with each condition are associated with that condition in the FIADB. Thus, it is not the plot, but the condition, that is the unit of replication in our analysis. Soil measurements, on the other hand, are taken at the plot level since 2000, and only on a subset of the overall NFI plot network. To reduce the likelihood of boundary effects in our analysis, we only used soils collected in single-condition plots when assembling our biomass/soils dataset. One potential complication of our data interpretation in either dataset (biomass/physiography or biomass/soil) derives from the resampling that is a core feature of the NFI program, as all permanent NFI plots with at least one forest land condition are visited every 5–7 years and tree (e.g., diameter at breast height) and site-level (e.g., slope) attributes are re-measured. For our analysis, in order to eliminate non-independent, repeated measures at the same locations, we utilized only the most recent observation of each forest condition (biomass/physiography) or plot (biomass/soil). A second, equally critical consideration pertains to NFI protocols for assigning stand ages. Specifically, the stand age assigned to each forest condition in FIADB depends somewhat upon subjective judgments in the field, because measurement crews select and core several dominant or co-dominant trees representing each forest condition. The ages of the individual trees are then used to compute a weighted average for the stand, where the weights are the proportions of each tree species/size (assumed age) class. This approach has considerable potential for error and uncertainty, neither of which are readily assessed. For younger and/or more even-aged stands, errors and uncertainties are likely modest; however, older stands with greater structural or compositional complexity have the potential for considerable deviation from their estimated/computed stand ages. Naturally, this consideration places limits to inferences that can be drawn from NFI data, which are considered in greater detail in the Discussion. These caveats aside, the resulting datasets that we synthesized from NFI sources for this analysis span the entire province, and include 16,063 observations of unique forest conditions for the biomass/physiography dataset and 375 unique forest plots for the biomass/soils dataset. Additional information on field sampling procedures, laboratory soil analyses, and allometric biomass estimation and other database-level protocols are available as part of the NFI program (<http://www.fia.fs.fed.us>).

2.3. Data analysis

The subsections below describe our data manipulations (e.g., transformations), statistical tests and criteria, and data visualization techniques.

2.3.1. Plot- to landscape-level data analysis

In the first portion of our analysis, we utilized our master database of plot-level aboveground biomass stocks at UMBS in two dis-

tinct ways to address our questions of interest. First, to test for landscape patterns in and controls on biomass production in mid-successional stands (the time period for which data were most plentiful), we calculated a mean annualized rate of aboveground biomass production for each plot by dividing its aboveground biomass density by its stand age, for the census event closest to a base age of 75 years (range 63–80 years at the time of census). We then used this annualized rate of biomass production as the response parameter in categorical analyses to test whether groups defined by physiographic factors (e.g., landform, soil texture) or composition (dominant tree taxa) had different mean annualized biomass production rates during mid-succession. Second, to test rates of and assess potentials for aboveground biomass production over timeframes greater than a century, we included each plot-level aboveground biomass density observation as a sample of a forest ecosystem at a known age, and used multiple regression to test how aboveground biomass densities varied as a function of age and physiographic parameters. In the case of this regression analysis, while some of the observations are not independent because they represent resampling at the same locations, this approach circumvents some of the problems associated with chronosequence-based approaches to studying succession (Walker et al., 2010; Yanai et al., 2000). Furthermore, the availability of systematically sampled, independent NFI data allow for analyses that will indicate whether this pseudo-replication at the landscape level is producing erroneous inferences at broader scales. In all of our statistical analyses of aboveground biomass, whether in terms of biomass density (standing stock) or annualized rate of production, biomass response parameters were not normally distributed; square-root transformation normalized these parameters in order to meet this assumption of parametric analyses. For all analyses, we used SigmaPlot (SYSTAT Software, San Jose, CA USA), accepted test results as significant when $P < 0.05$, and discuss marginally significant results ($0.05 < P < 0.10$) as tendencies.

Our specific tests for significant effects of physiographic and soil parameters on biomass production were as follows. First, we assigned each forest inventory plot (all of which are georeferenced) to the appropriate ecological unit in the UMBS landscape ecosystems hierarchy (major landform, minor landform, landscape ecosystem type) in order to assess whether biomass production rates in mid-successional stands differed among groups at any of these levels, using t-tests or ANOVA with Fisher's LSD multiple comparisons. (Parenthetically, we note here that we also tested whether plot-to-plot variation in the dominant tree species was a significant predictor of variation in biomass production rates across plots; although composition was not of interest to the present physiographic analyses, it is of broader interest.) Second, we summarized and averaged essential physiographic and soil properties (parent material, natural drainage class, water table depth, soil horizon thicknesses, texture, and pH) for each landscape ecosystem type, in order to assess whether biomass production in the plots located within each landscape ecosystem type differed according to these properties (once again with ANOVA and Fisher's LSD). Third, to test whether longer-term patterns of biomass production differed according to physiographic setting, a hydrologically-defined categorization that we conceived to distinguish forests from outwash (xeric) landforms, moraine (mesic) landforms, and lake-marginal wetlands (the latter of which is not defined as a physiographic unit in the UMBS landscape ecosystems hierarchy, but includes ecosystems with a water table within 1 m of the surface), we used multiple linear regression with age and dummy variable coding (to assign each biomass value to one of the three physiographic settings) as the predictors.

2.3.2. Subsection- to province-level data analysis

In the province-level dataset for assessing variation among physiographic classes (PHYSCLCD, the NFI variable for differentiat-

Table 2

Annualized rates of aboveground biomass production and areas for the two most extensive major landforms present on the UMBS landscape.^a Biomass values are reported as means, with standard error and sample size (# of plots) in parentheses. Square-root transformed means differed significantly between the two groups (*t*-test, $P = 0.002$).

Major landform	Biomass production (Mg ha ⁻¹ yr ⁻¹)	Area (ha)
Outwash plain	1.83 (0.07, 71)	3382
Moraine	2.30 (0.15, 21)	904

^a Ice contact landforms (kettle-kame complexes) occupy the remaining 86 ha of the UMBS landscape, but forest inventory data are not available from these areas.

Table 3

Annualized rates of aboveground biomass production for minor landforms on the UMBS landscape.^a Biomass values are reported as means, with standard error and sample size (# of plots) in parentheses. Square-root transformed means differed significantly among groups (ANOVA, $P = 0.015$), but multiple comparisons are neither shown nor emphasized.

Minor landform	Biomass production (Mg ha ⁻¹ yr ⁻¹)
High-level outwash – ice marginal terrace	1.69 (0.20, 4)
High-level outwash – dune on lake plain	1.75 (NA, 1)
High-level outwash – lake plain	1.78 (0.12, 29)
High-level outwash plain	1.79 (0.08, 30)
Low-level outwash plain	1.82 (0.04, 2)
Interlobate moraine	2.30 (0.15, 21)
High-level outwash – ice-mediated, ponded depression	2.43 (0.34, 5)

^a Other minor landforms are present on the UMBS landscape, but forest inventory data are not available from these areas.

ing xeric, mesic, and hydric settings) and ecological units (section, subsection) in aboveground biomass, the response parameters (standing stock of aboveground biomass, annualized rate of aboveground biomass) were not normally distributed and could not be normalized by any transformations. Therefore, we used non-parametric tests (Kruskal-Wallis with Dunn's multiple comparisons) to test for significant differences among physiographic groups. To perform continuous analyses relating aboveground biomass to stand age and physiographic class, we used the square-root transformed aboveground biomass (which was the least non-normal) as the response variable in a multiple linear regression that included age and physiographic class (with 3 levels) coded into 2 dummy variables. This is the same approach as we

Table 4

Annualized rates of aboveground biomass production and areas for landscape ecosystems on the UMBS landscape.^a Biomass values are reported as means, with standard error and sample size (# of plots) in parentheses. Square-root transformed means differed significantly among groups (ANOVA, $P < 0.001$), but multiple comparisons are neither shown nor emphasized.

Ecosystem group	Type	Biomass production (Mg ha ⁻¹ yr ⁻¹)	Area (ha)	Natural drainage class ^b
High-level outwash - wetlands	53	0.44 (NA, 1)	74	PD
	55	1.24 (NA, 1)	143	PD
	83	1.35 (NA, 1)	40	SPD
High-level outwash - upland ice-marginal terraces	96	1.70 (0.28, 3)	42	ED
	99	1.65 (NA, 1)	10	ED
	74	1.75 (NA, 1)	136	ED
High-level outwash - upland, calcareous, non-banded subsoil	44	1.77 (0.29, 3)	246	ED
High-level outwash - upland, non-calcareous, non-banded subsoil	37	1.77 (0.08, 26)	210	ED
	36	1.87 (0.17, 4)	284	ED
	38	2.43 (NA, 1)	15	SED
High-level outwash - upland, calcareous, banded subsoil	47	1.98 (0.45, 4)	24	SED
	48	1.83 (0.34, 4)	15	WD
	42	1.44 (0.05, 4)	46	WD
High-level outwash - upland, noncalcareous, banded subsoil	39	1.94 (0.21, 10)	104	SED
	15	1.82 (0.04, 2)	126	MWD
	Deep, high-level outwash on moraine uplands	59	1.60 (0.09, 5)	163
60		2.64 (0.31, 2)	125	WD
82		2.70 (0.27, 4)	7	MWD
Thin, high-level outwash over till on moraine uplands	109	2.31 (0.20, 11)	166	SED
	113	3.20 (0.12, 3)	112	WD

^a Additional landscape ecosystems are present on the UMBS landscape, but forest inventory data are not available from these areas.

^b Poorly drained, somewhat poorly drained, moderately well drained, well drained, somewhat excessively drained, excessively drained.

used at the UMBS landscape level, however; in this test, all observations were truly independent, allowing for critical assessment of the results from the landscape-level test described in Section 2.3.1. To compare aboveground biomass production rates across ecological units (section and subsection), which in some cases differed in their median ages, we divided the aboveground biomass of each forest condition by its age, eliminated values $>6 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ($<1\%$ of the dataset) as outliers relative to the bulk of the data distribution, and compared groups using the same non-parametric categorical testing approach described above. Aboveground biomass values in the dataset used to test for significant effects of soil properties (litter layer and forest floor thickness, pH and texture class at 0–10 and 10–20 cm depths in the mineral soil) on biomass were also non-normal. Therefore, as with the biomass/physiography dataset, we used nonparametric tests for categorical analyses, and square root-transformed biomass values in continuous analyses (*i.e.*, regression). For these analyses, we used the annualized rate of aboveground biomass production as the response parameter to control directly for stand age across the relatively limited number of observations. Lastly, as with the UMBS landscape-level analyses, we tested whether forest composition was a significant predictor of variation in annualized rates of aboveground biomass production because it is of interest to many who study and apply forest biomass data. In this case, we used Kruskal-Wallis to test whether FIA category codes distinguishing broad forest type groups (*e.g.*, oak/pine, maple/beech/birch, spruce/fir) had significantly different median biomass production rates.

2.3.3. Geospatial data visualization

We downloaded province, Ecological section and subsection polygons from the USDA-Forest Service Geodata Clearinghouse, extracted province 212 and its associated sections and subsections, and visualized their median and 3rd quartile biomass production rates in ArcGIS 10.4.1 (ESRI, Redlands, CA USA).

3. Results

3.1. Landscape-level variation in biomass production rates during mid-succession

The UMBS landscape consists of ecological units that differ significantly in their rates of aboveground biomass production during

mid-succession. Separated into its coarsest spatial units, the major landforms, mean rates of aboveground biomass production differ significantly on outwash vs. moraine (Table 2). At a finer level, minor landforms differ significantly in their rates of aboveground biomass production (Table 3). At the lowest level of the hierarchy, landscape ecosystem types (Table 4) also differ significantly in their rates of aboveground biomass production. In contrast to the significant differences in biomass production rates between ecological units, biomass production rates during middle succession do not differ according to forest composition (data not shown; ANOVA, $P = 0.30$).

Underlying the landscape-level variation in biomass production rates are physiographic and soil properties related to hydrology and parent material texture, which exert significant control on rates of biomass production among the different landscape ecosystems. Where water tables are within 1 m of the soil surface, ecosystems have significantly lower rates of aboveground biomass production than do ecosystems lacking high water tables (t -test, $P = 0.01$, 1.33 vs. 1.97 Mg ha⁻¹ yr⁻¹). Natural drainage also acts as a constraint: soils with mesic drainage classes (MWD, WD) tend to support higher biomass production rates than xeric (SED, ED) and hydric classes (SPD, PD), although only the poorly drained class was statistically significantly different from the mesic and xeric classes (Table 5).

Ecosystems on the three major soil parent materials differ significantly in their rates of biomass production (Table 6), with the

Table 5

Annualized rates of aboveground biomass production for forests on UMBS landscape ecosystem types differing in their natural drainage classes. Biomass values are reported as means, with standard error and sample size (# of plots) in parentheses. Square-root transformed means differed significantly between groups (ANOVA, $P < 0.001$), with superscripts identifying significantly different groups.

Natural drainage class	Biomass production (Mg ha ⁻¹ yr ⁻¹)
Poorly drained (PD)	0.84 (0.40, 2) ^a
Somewhat poorly drained (SPD)	1.35 (NA, 1) ^{ab}
Moderately well drained (MWD)	2.41 (0.25, 6) ^b
Well drained (WD)	2.15 (0.22, 13) ^b
Somewhat excessively drained (SED)	2.03 (0.11, 33) ^b
Excessively drained (ED)	1.78 (0.07, 37) ^b

Table 6

Annualized rates of aboveground biomass production for forests on UMBS landscape ecosystem types differing in soil parent materials. Biomass values are reported as means, with standard error and sample size (# of plots) in parentheses. Square-root transformed means differed significantly between groups (ANOVA, $P < 0.001$), with superscripts identifying significantly different groups.

Soil parent material	Biomass production (Mg ha ⁻¹ yr ⁻¹)
Organic materials	0.84 (0.40, 2) ^a
Coarse-textured drift	1.80 (0.06, 49) ^b
Fine-textured drift	2.15 (0.11, 41) ^c

Table 7

Soil silt + clay percentage for the landscape ecosystems occupying the two most extensive major landforms at UMBS, as a function of depth. Values are medians, with 1st and 3rd quartiles and number of observations (distinct landscape ecosystem types) in parentheses. Asterisks denote significant differences between major landforms (Mann-Whitney U test).

Depth	Outwash plain	Moraine
10 cm ^{**}	8.4 (7.5–9.4, 11)	12.9 (10.6–13.7, 4)
20 cm [*]	8.2 (7.4–9.7, 11)	12.6 (10.3–14.0, 4)
150 cm	3.2 (1.8–22.1, 11)	12.8 (5.1–30.1, 4)

^{*} $P < 0.10$.

^{**} $P < 0.05$.

highest rates on fine-textured drift (soils including any materials finer than sand), intermediate rates on coarse-textured drift (sand and coarser), and the lowest rates on organic (wetland) soils.

Considering only the upland ecosystems, soils on moraine are finer-textured than soils on outwash plain landforms, although variability in parent material texture tends to increase in depth while the significance of differences declines concurrently (Table 7).

Ecosystems on the two major landforms tend to have marginally different forest floor thicknesses (t -test, $P = 0.077$, 8.3 cm for moraine vs. 4.9 cm for outwash), but eluvial and spodic horizon thicknesses do not differ, nor does soil pH at any depth. Across all ecosystems, soil texture, pH, and forest floor thicknesses are correlated with one another (Pearson correlation tests, all $P < 0.05$, $r > 0.50$), as well as with rates of aboveground biomass production. The strongest predictor of the rate of biomass production is forest floor thickness (linear regression); while soil texture and pH at 10 cm have lower correlation coefficients, they are also significant predictors of biomass production (Fig. 1).

3.2. Landscape-level variation in late-successional biomass patterns and potentials

At the landscape level, forest ecosystems on lake-marginal wetlands (water table within 1 m), outwash plain, and moraine landforms differ significantly in their long-term (>100 yr) rates of aboveground biomass production (Fig. 2, Table 8): forests on low-lying lake marginal wetlands have the lowest rates, forests on outwash plains are intermediate, and forests on moraines have the highest and most variable rates. Forest ecosystems on moraines have the greatest long-term potential for aboveground biomass production; the oldest stand (181 years) held 475 Mg ha⁻¹ when censused in 2014, which was nearly 40 Mg ha⁻¹ higher than its previous census 9 years prior. The oldest wetland forest on the landscape, aged at just over 300 years, is approaching 300 Mg ha⁻¹. The oldest forests on outwash plains are just over 120 years since initiation; these are intermediate between the mesic and hydric physiographic settings of moraine vs. lake-marginal wetland and held in the range of 250 Mg ha⁻¹ during their most recent censuses.

3.3. Forest biomass, its controls and potential production at broader ecological levels

The significant influence of physiographic setting (outwash, moraine, and lake-marginal wetland) noted at the UMBS landscape level as a significant constraint on aboveground biomass production does not extend to the subsection level. Specifically, forest conditions in the NFI database that fit into xeric, mesic and hydric physiographic classes do not differ in their aboveground biomass stocks, median ages, or rates of biomass production in the Presque Isle Lake and Till Plains subsection. However, the significance of physiographic setting re-emerges at the higher levels of the geographic hierarchy. Across the Northern Lacustrine-influenced Lower Michigan section (Fig. 3A) and across the entire Laurentian Mixed Forest province (Fig. 3B), physiographic classes accumulate biomass at significantly different rates (Table 8). At both levels, biomass production is significantly greater on mesic than xeric and hydric physiographic classes, although the slope coefficients for the physiographic class dummy variables indicate that the upland (xeric and mesic) classes are more similar to each other than either is to the hydric class. Forest composition is not a significant predictor of biomass production at the subsection level, but emerges at section and province levels ($P < 0.001$ for each). In particular, wetland forest types (*i.e.*, spruce/fir and elm/ash/cottonwood) differ from the most widespread upland forest types (*i.e.*,

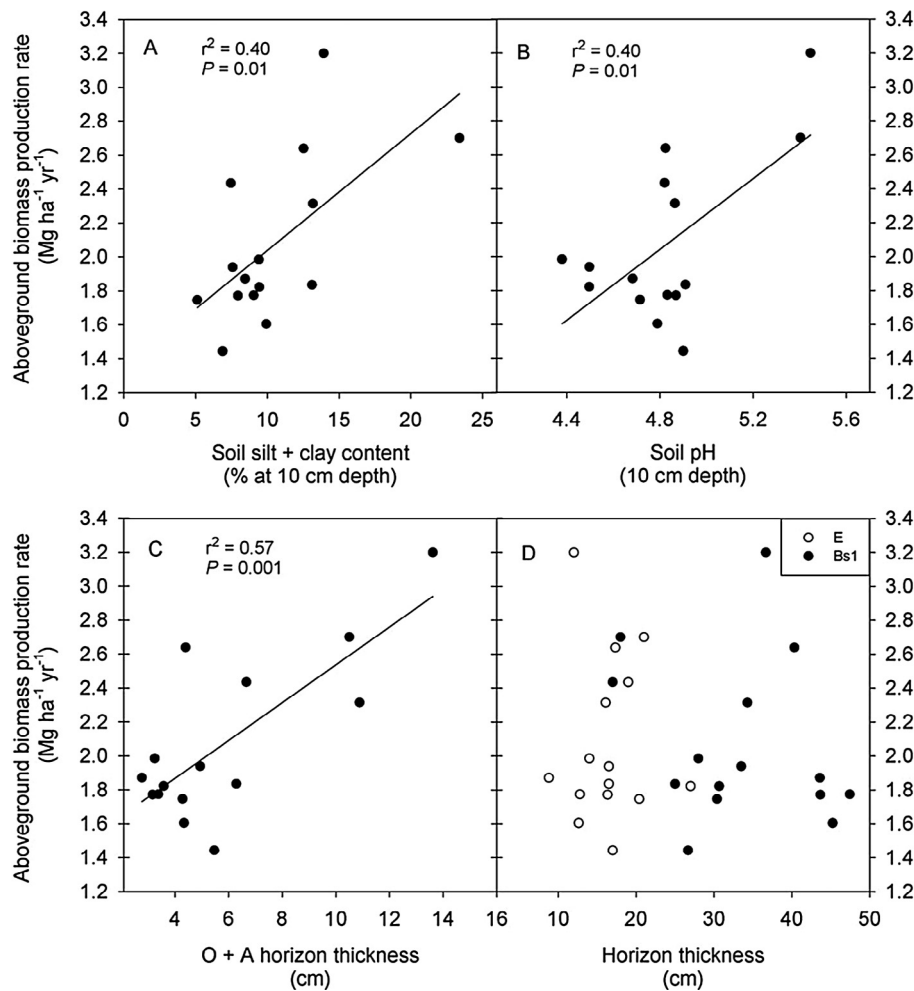


Fig. 1. Relationships between soil properties and the annualized rate of aboveground biomass production, for landscape ecosystems possessing both long-term forest inventory plots and soil pits. Each point represents the averaged biomass production rate of all plots, and all soil pits, within a landscape ecosystem type. Best-fit statistics correspond to linear regression models relating biomass production rates to soil parameters.

pine, oak/pine, aspen/birch, and maple/beech/birch), but the upland types do not differ from each other except for maple/beech birch vs. other upland types at the province level.

Across the province, median rates of annualized aboveground biomass production range from 0.68 to 1.50 Mg ha⁻¹ yr⁻¹ among sections, with the lowest rates in the interior northwestern portion of the province and the highest rates along the southern shorelines of the Great Lakes (Fig. 4). Subsection-level median rates of annualized aboveground biomass production range from 0.54 to 2.05 Mg ha⁻¹. As with section-level spatial patterns, rates are generally lowest in the northwest; however, the finer level of detail reveals significant within-section variability throughout much of the province (Fig. 5). Biomass production potential, indicated by 3rd-quartile rates of aboveground biomass production (Fig. 6), shows broadly similar relative spatial patterns between sections, although some sections have greater differences between their realized (median) and potential biomass production rates. At both levels of the hierarchy, percentage differences between the realized (median), potential high (3rd quartile, denoted as P+), and potential low (1st quartile, denoted as P-) biomass production rates are used to indicate a functional range in biomass production rates that could result from management or climate change (Table 9).

Soil parameters (forest floor thickness, mineral soil pH and texture at 0–10 and 10–20 cm) are for the most part not correlated

with each another at any level of the ecological hierarchy, and are generally poor predictors of annualized aboveground biomass production rates at subsection and section levels. Only across the entire province do statistical tests indicate significant effects of soil texture, with both depths showing significantly different rates of biomass production among groups (Table 10). Forests with surface soils of loamy or sandy textures have significantly higher rates of biomass production than forests on organic soils; forests with clayey and coarse sandy surface soils exhibit intermediate rates. Considering subsoil textures, forests with, loamy, clayey and sandy textures all have significantly higher biomass production rates than forests growing on subsoils with organic or coarse sandy textures.

4. Discussion

Physiographic factors that control soil moisture status influence biomass production rates at nearly all levels of the ecological unit hierarchy, from the ecosystem-level variation in drainage classes and water table depths at UMBS (Table 5, Fig. 2), to the differences in biomass production rates among xeric, mesic, and hydric physiographic classes at the section and province levels (Fig. 3). In contrast, soil texture is an important control on biomass production rates at landscape (Tables 6 and 7, Fig. 1) and province levels (Table 10), but not in the intermediate levels of the hierarchy. For-

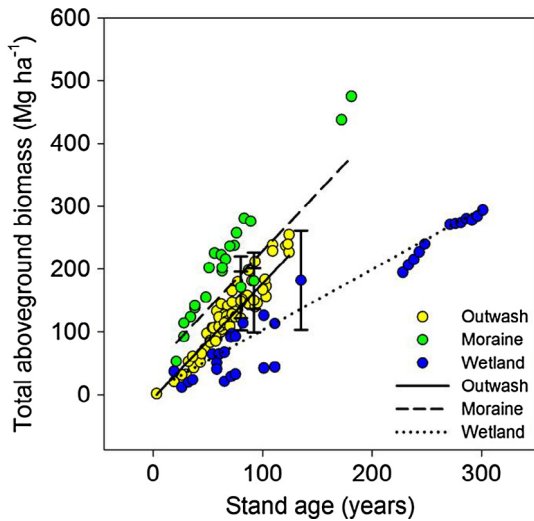


Fig. 2. Standing stocks of aboveground biomass as a function of stand age and physiographic setting, for permanent forest inventory plots on the UMBS landscape. Simple scatterplot points represent data obtained from periodic re-measurements of long-term plots in forests of known age in each physiographic setting (15 on outwash, 6 on moraine, 4 on wetland). Scatterplot points with error bars (standard deviations) are used to represent intensive, single-year campaigns to measure plots in even-aged stands in each physiographic setting (57 on outwash, 18 on moraine, 8 on wetland). Best-fit lines, derived from multiple linear regressions on age and physiographic setting, were fit using all scatterplot points (see Table 8 for regression statistics).

est composition, which only becomes important at the broadest (section and province) levels, provides yet another indication that controls on biomass production differ in their relative influence at different levels of spatial organization. In essence, these results are an affirmation of hierarchical ecological classification, which assigns different weights to climatic, biotic, geologic, and pedologic factors across its levels (Albert, 1994; McNab et al., 2007). Perhaps more important to the present analysis, the relationships between soil texture and biomass production at different spatial levels lead to different inferences: at the UMBS landscape level, it would appear that other considerations aside, increasingly fine-textured surface soils support ever-increasing rates of biomass production. The broader applicability of this reasoning is belied at the province level where, in contrast, the finest-textured surface soils do not

support the highest biomass. Specifically, at this broadest level, production rates on clay surface soils are not statistically distinguishable from either the most productive (loamy to sandy) or least productive (organic) soils. This interpretation of the influence of soil texture on biomass growth covers the full range of soil textures across the province and refines the longstanding, cross-site generalization that finer-textured soils support greater tree growth, net primary production, or C storage (Grigal and Ohmann, 1992; Hannah, 1969; Hannah and Zahner, 1970; Host et al., 1988; Koerper and Richardson, 1980; Reich et al., 1997; White and Wood, 1958; Van Eck and Whiteside, 1963). Specifically, by utilizing a set of NFI data, drawn systematically from across the region, this analysis places an upper bound on this reasoning and serves as a check for studies based on sites deliberately (non-randomly) selected according to forest composition. Nonetheless, some of these studies (e.g., Grigal and Ohmann, 1992; Reich et al., 1997) serve as outstanding examples of integration for their recognition of co-variance among physiographic and other ecosystem factors (e.g., soil, forest composition). In the present analysis, considering physiography and soil texture together establishes a generalizable inference that, from landscape to province levels, mesic moisture status and intermediate soil textures (mixtures of clay, silt and sand) support the highest biomass production rates, xeric moisture status and coarse-textured soils (sand, coarse sand, and gravel) have intermediate biomass production rates, and hydric moisture status support organic soil development and the lowest rates of biomass production (Fig. 1, Tables 6, 8, 10).

One fundamentally important constraint underlies the results of this analysis, and precludes it from being considered mechanistic in a reductive, state-factor sense. Physiographic, ecosystem, vegetation, and soil properties are not distributed on Earth in a factorial design, and thus do not act in isolation. Ecosystems are integrative, and therefore, biomass production rates are best viewed as co-varying with multiple, linked ecosystem properties. As an example, consider that organic soils, poor drainage, high water tables, and slow-growing conifers are all indicators of the same underlying physiography. Across province 212, this sort of ecosystem occurs as a repeating unit at low, cold, saturated landscape positions, even as the levels of its factors may vary. Soils range from fibric to sapric; saturation ranges from permanent to seasonal; arboreal vegetation may be dominated by acidophilic *Picea mariana* (Mill.) Britton, Sterns & Poggenb. or calciphilic *Thuja occidentalis* L. Nonetheless, in terms of their slow biomass production

Table 8

Statistics for multiple regression models relating the standing stock of aboveground biomass to stand age and physiographic conditions, from landscape (UMBS) to whole-province levels (NFI data). Parameters are presented for the regression model from each of four hierarchical levels; in each case the response variable is the square-root transformed aboveground biomass stock. The default model predicts biomass for forest conditions with xeric physiographic settings as a function of age; activation of either dummy variable (PHYS_1 or PHYS_2) adds a coefficient with a significantly different slope for either a hydric or mesic physiographic condition, respectively. Significant parameters are indicated in bold.

Level	Term	Coefficient	S.E.	t	P	r ²
Landscape (UMBS)	Constant	45.73	6.64	6.89	<0.001	0.53
	Age	1.18	0.07	16.43	<0.001	
	PHYS_1	-120.52	10.66	-11.31	<0.001	
	PHYS_2	50.80	7.16	7.09	<0.001	
Subsection (NFI)	Constant	3.98	0.90	4.41	<0.001	0.17
	Age	0.05	0.01	5.32	<0.001	
	PHYS_1	0.37	0.96	0.38	0.701	
	PHYS_2	1.00	0.80	1.24	0.218	
Section (NFI)	Constant	8.40	4.03	2.09	0.037	0.25
	Age	1.35	0.06	23.53	<0.001	
	PHYS_1	-32.04	5.25	-6.11	<0.001	
	PHYS_2	6.76	3.31	2.04	0.041	
Province (NFI)	Constant	1.63	0.04	39.89	<0.001	0.31
	Age	0.03	0.00	78.53	<0.001	
	PHYS_1	-1.07	0.04	-24.48	<0.001	
	PHYS_2	0.09	0.04	2.24	0.025	

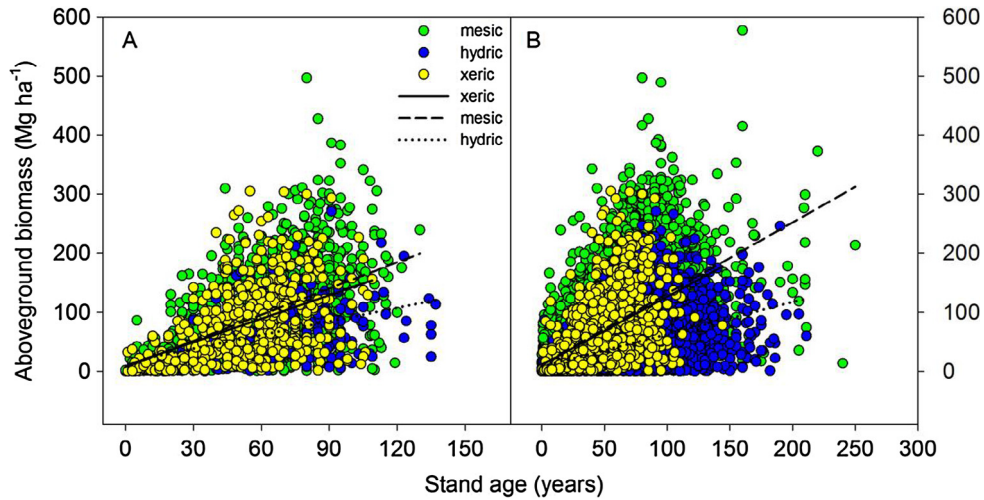


Fig. 3. Standing stocks of aboveground biomass as a function of stand age and physiographic class, for NFI observations from the Northern Lake-influenced Lower Michigan section (panel A) and all of the Laurentian Mixed Forest province (panel B). Each point represents an observation of a spatially unique forest condition since the year 2000, where stand age is known. Best-fit lines are derived from multiple linear regressions on age and physiographic class, and identify the significantly different rates of biomass production of the three physiographic classes (see Table 8 for regression statistics).

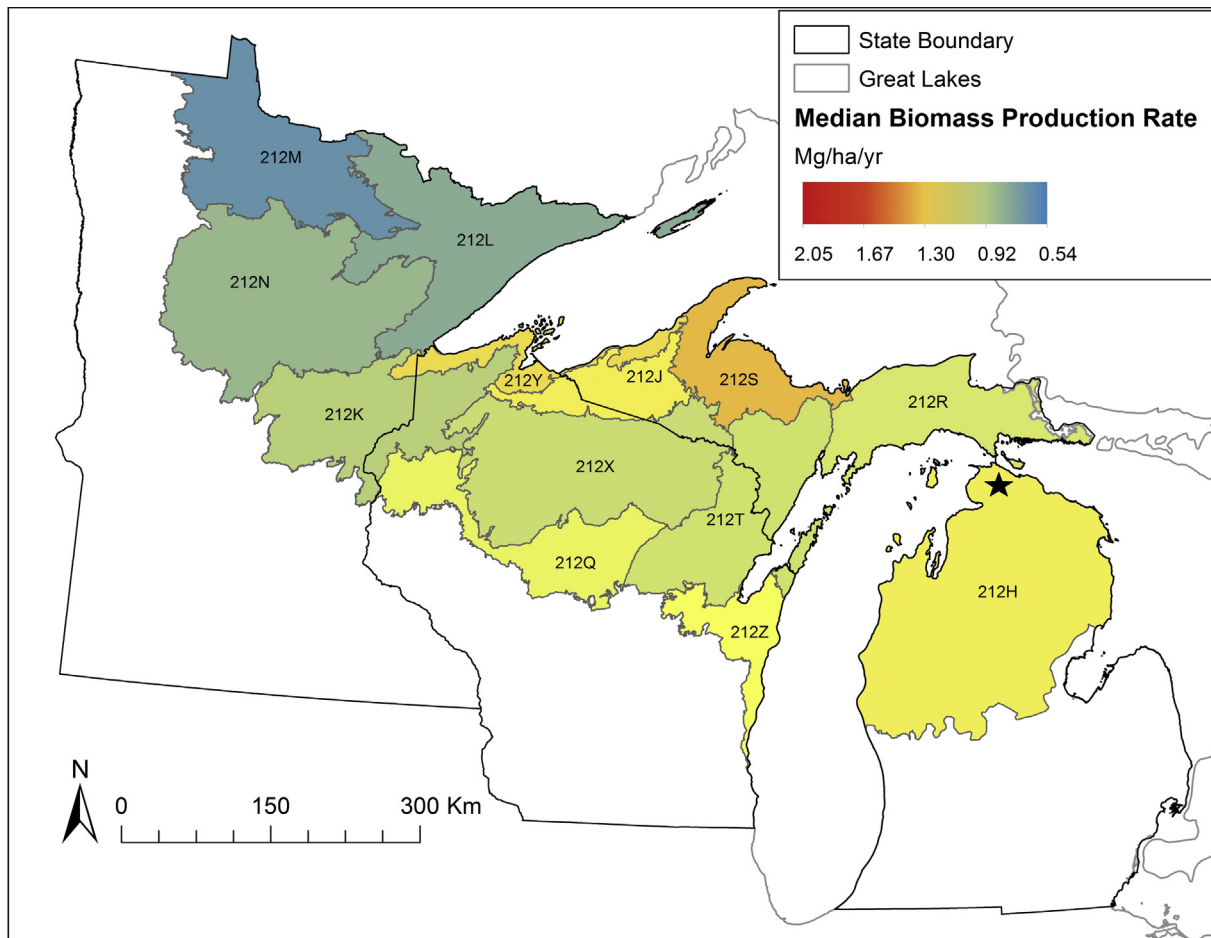


Fig. 4. Median rates of aboveground biomass production ($\text{Mg ha}^{-1} \text{yr}^{-1}$) for the 13 ecoregional sections within province 212 (the Laurentian Mixed Forest province). Map shows State and Great Lakes outlines, with a color ramp indicating higher rates of production in warmer colors and lower rates of production in cooler colors. Star denotes the location of UMBS, the intensively studied landscape in this analysis.

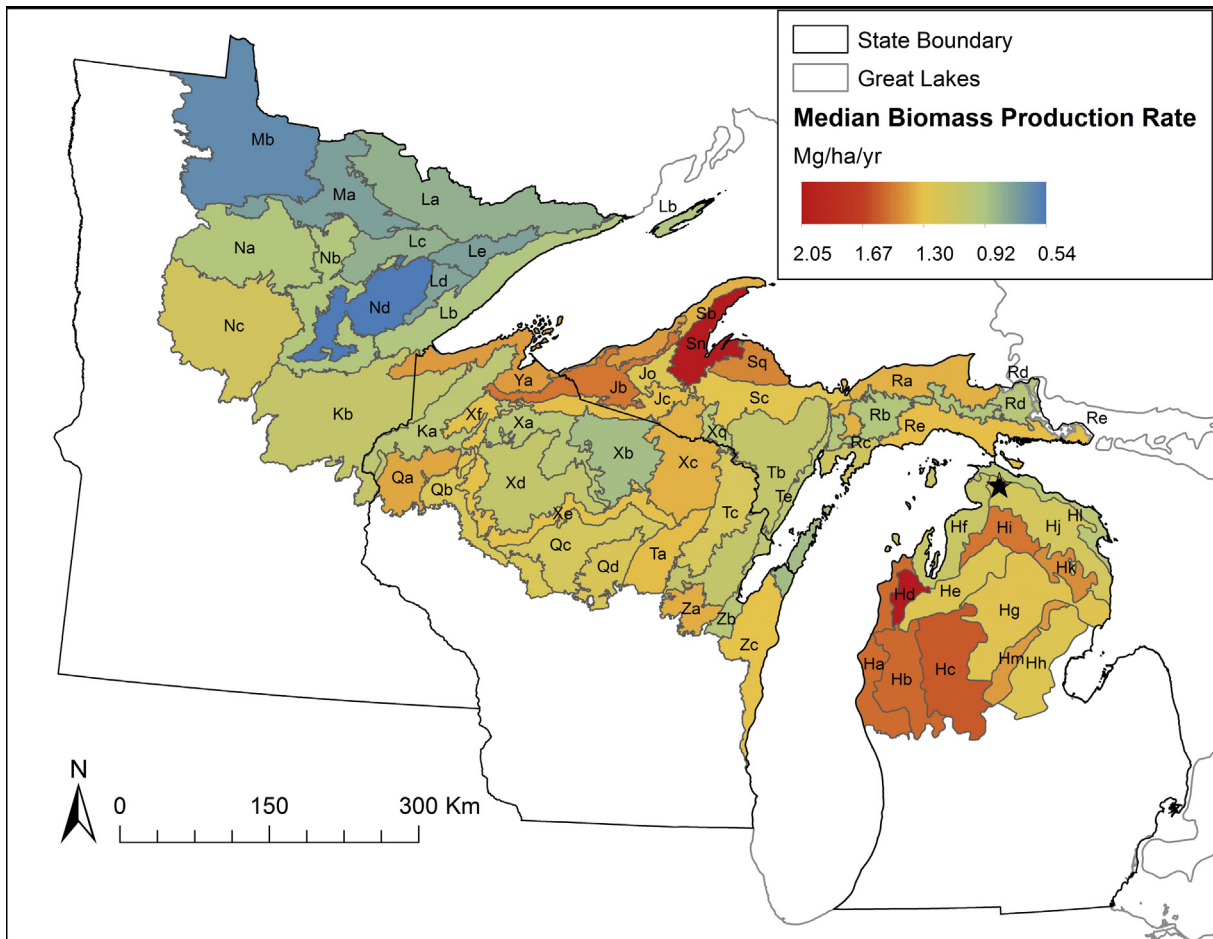


Fig. 5. Median rates of aboveground biomass production ($\text{Mg ha}^{-1} \text{yr}^{-1}$) for the 58 ecoregional subsections within province 212 (the Laurentian Mixed Forest province). Map shows State and Great Lakes outlines, with a color ramp indicating higher rates of production in warmer colors and lower rates of production in cooler colors. Star denotes the location of UMBS, the intensively studied landscape in this analysis.

rates, these ecosystems function similarly within their broader landscapes, regardless of where those landscapes are situated. Similarly, entire sections (e.g., 212M, 212L) have comparable biomass production relative to the broader province. The reality of this co-variance, and the significant difference in biomass production rates for wetland vs. upland forest types noted in Section 3.3 highlight the inability to take vegetation out of its physiographic context, or, in statistical terms, the confounded relationship between physiography and forest composition at broader levels. Confounded relationships (i.e., co-varying ecosystem factors) are of course not limited to physiography and forest composition; as described in Section 2.1.2 climate and soil texture also vary broadly across the province, and such co-variance may underlie the apparent trend we attribute to soil texture across the region.

Ecosystems are also integrative locally, i.e., in ways that do not scale across spatial levels. On the UMBS landscape, ecosystems with finer-textured soils are those which have greater amounts of soil parent materials derived from glacial till. Till at UMBS consists of finer, calcareous and feldspathic sediments that were deposited directly by the ice in some ecosystems, or intermixed with the sandy (siliceous) outwash during the final, local stages of glacial advance and retreat. Thus, the significantly higher silt + clay content of moraine soils at UMBS, and the positive correlations between silt + clay, pH, and forest floor thickness across soils, indicate autocorrelation between these factors, as well as with base cation and N availability (Jin et al., 2008; Nave et al., 2014; Zak et al., 1989). All of these factors support the higher biomass

production rates in mesic landforms and ecosystem types at UMBS (Tables 2–4). At the broader province level, fine-textured soil materials include a wider range of geologic parent materials; thus, at this scale, the positive influence of soil texture becomes decoupled from pH, which has no detectable effect on biomass production rates. Taking a longer view of the co-variance among soil factors and biomass production leads to farther-reaching conclusions about ecosystems; specifically, that individual factors are sometimes indicators of more complex underlying relationships, and that at larger spatial levels the specific factors that emerge as good statistical indicators may change. This demonstrates that while a hierarchical analysis such as we have done here may be useful and scalable, a better analysis is one that includes multiple sites (e.g., landscapes) nested within the larger, more encompassing units (e.g., the province). Such a design would potentially allow for, e.g., the disentanglement of physiography, climate, and forest composition as constraints on biomass production.

Our results from long-term plot data at UMBS and scattered NFI observations from late-successional forests across the province suggest that live aboveground biomass can increase in Great Lakes forests for centuries (Figs. 2 and 3). However, many investigators have inventoried the scattered examples of late-successional forests in the province, especially in Upper Michigan and northern Wisconsin (Crow, 1978; Fahey et al., 2015; Halpin and Lorimer, 2016; Mroz et al., 1985; Rutkowski and Stottlemeyer, 1993; Woods, 2016), and if there is an internally consistent pattern within any of these more detailed, site-specific analyses—much

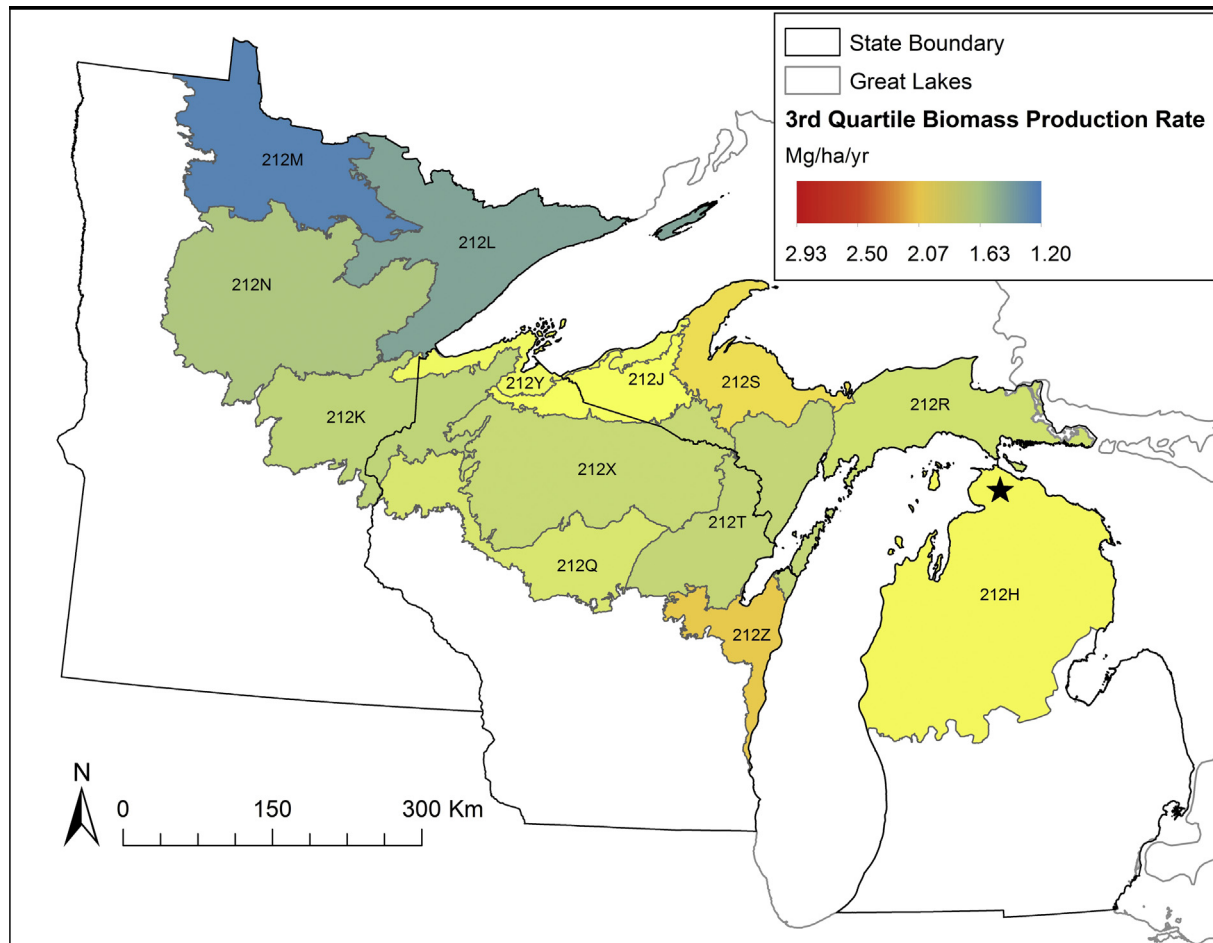


Fig. 6. Third-quartile rates of aboveground biomass production ($\text{Mg ha}^{-1} \text{yr}^{-1}$) for the 13 ecoregional sections within province 212 (the Laurentian Mixed Forest province). Map shows State and Great Lakes outlines, with a color ramp indicating higher rates of production in warmer colors and lower rates of production in cooler colors. Star denotes the location of UMBS, the intensively studied landscape in this analysis.

less, any pattern that can be generalized across them—it is that defining the age of old, uneven-aged forests is challenging (Lorimer and Halpin, 2014). In some cases, such as a clear cohort of a dominant species (e.g., 1830 fire-origin *Tsuga canadensis* in Woods, 2016), stand age is fairly straightforward, yet there is no consistent difference in biomass C stocks or their rate of accumulation as compared to other late-successional forests on the same landscape. This inconsistency suggests that local (landscape, ecosystem, or even finer-level) sources of variation may drive local exceptions to the generalized trend we suggest here. Nonetheless, compared to the upper limits on standing aboveground biomass (~ 280 to $>450 \text{ Mg C ha}^{-1}$) suggested by researchers working across province 212 (and adjacent northeastern U.S. provinces; Keeton et al., 2011), the NFI data synthesized for the present analysis suggest that there is the potential for continued C sequestration in live biomass across the province (Fig. 3). While it may be difficult to make the case for this potential in the oldest forests, given issues with defining and measuring their age, and the inconsistent trajectories reported in the literature, the age class distribution of forests across the province is insightful. Across all NFI observations, the median stand age is 60 years, with 1st and 3rd quartiles spanning an interval of 36–79 years. This range of ages reflects that management is widespread across the province, and indicates that, for a typical non-managed forest, continued C accumulation in live biomass is likely for many decades in the absence of disturbance. In the context of managed forests, significant differences in age distribution between physiographic classes suggest several interesting

trends and opportunities across the province. Wetlands are left uncut for longer (median age = 70, IQR = 51–90), reflecting slower growth rates, and perhaps difficulty of mechanized access according to best management practices or less valuable fiber. Xeric sites, which regrow biomass more slowly than mesic sites, may be harvested more often based on their younger age distribution (49, 29–65 vs. 60, 33–75). An additional possibility, not mutually exclusive, is that the current age distributions of xeric vs. mesic forests reflect the history of logging across the region. Specifically, forests on both physiographic classes may have been harvested concurrently, and the older age distribution of the mesic forests reflects that they became ready for harvesting again sooner than the xeric forests, which were harvested more recently. Regardless what underlies the significant differences between physiographic classes and their age distribution, it is the mesic physiographic classes that are best suited to forest biomass removals from both a production and a C sequestration perspective. Furthermore, given concerns that poorer sites may be more impacted by biomass removals than better sites, mesic sites may be less vulnerable to repeated biomass removals than xeric sites (Thiffault et al., 2011, 2014).

The ecological units of province 212 are a meaningful lens through which to view ecosystem function, and a sound basis for planning and management. The low rates of production in the interior northwestern-most sections of the province suggest interactions among a short growing season, low precipitation, and nutrient-poor geologic parent materials that result in forests that produce biomass slowly and are accordingly less well suited for

Table 9

Biomass production rates and potentials for relative increase or decrease by section (in bold) and subsection (both in $\text{Mg ha}^{-1} \text{yr}^{-1}$). Biomass production rate is the median for each unit. Potential decrease (P–) and increase (P+) for each unit is calculated as the percentage difference between the median and the 1st quartile or 3rd quartile, respectively, such that a small difference indicates a median rate with little possibility for either increase or decrease, and a large difference indicates the possibility for large increases or decreases, e.g., as a result of management or climate change.

Unit	Med.	P–	P+	Unit	Med.	P–	P+	Unit	Med.	P–	P+
212H	1.34	52	57	212M	0.68	58	86	212T	1.15	52	59
212Ha	1.53	68	61	212Ma	0.73	56	83	212Ta	1.31	54	56
212Hb	1.54	49	40	212Mb	0.62	56	100	212Tb	1.06	52	64
212Hc	1.59	56	52	212N	0.91	54	92	212Tc	1.17	47	62
212Hd	2.05	43	43	212Na	0.95	49	90	212Te	1.03	49	55
212He	1.22	51	72	212Nb	0.94	53	88	212Tf	0.88	47	73
212Hf	1.10	55	82	212Nc	1.15	52	75	212X	1.12	54	65
212Hg	1.25	56	54	212Nd	0.54	55	121	212Xa	1.00	53	74
212Hh	1.23	51	44	212Q	1.25	59	54	212Xb	0.89	52	84
212Hi	1.50	48	39	212Qa	1.37	55	48	212Xc	1.34	55	54
212Hj	1.16	49	60	212Qb	1.19	60	54	212Xd	1.06	53	66
212Hk	1.43	55	75	212Qc	1.16	63	53	212Xe	1.28	50	48
212Hl	1.01	60	78	212Qd	1.20	49	66	212Xf	1.28	58	83
212Hm	1.40	43	72	212R	1.17	53	63	212Xg	1.02	58	42
212J	1.35	51	53	212Ra	1.34	45	70	212Y	1.40	52	45
212Jb	1.50	47	56	212Rb	0.95	56	63	212Ya	1.40	52	45
212Jc	1.30	56	54	212Rc	1.14	64	60	212Z	1.29	44	73
212Jo	1.22	64	53	212Rd	0.97	35	65	212Za	1.35	59	72
212K	1.06	54	72	212Re	1.30	51	50	212Zb	0.99	41	133
212Ka	1.01	55	81	212S	1.50	46	44	212Zc	1.29	40	68
212Kb	1.07	53	69	212Sb	1.34	68	49				
212L	0.84	54	80	212Sc	1.26	48	57				
212La	0.82	54	71	212Sn	1.84	43	32				
212Lb	0.93	53	84	212Sq	1.46	27	39				
212Lc	0.82	57	95								
212Ld	0.75	57	71								
212Le	0.73	60	104								

Table 10

Annualized rates of aboveground biomass production for NFI plots with different soil textures at 0–10 and 10–20 cm depths. Biomass values are reported as means, with standard error and sample size (# of plots) in parentheses. Within each soil depth, square-root transformed means differed significantly between textures (ANOVA, $P < 0.001$), with superscripts identifying significant differences.

Texture class	0–10	10–20
Organic	0.98 (0.06, 49) ^a	0.94 (0.06, 47) ^a
Clayey	1.20 (0.06, 47) ^{ab}	1.28 (0.05, 66) ^b
Loamy	1.32 (0.03, 114) ^b	1.31 (0.04, 66) ^b
Sandy	1.27 (0.04, 83) ^b	1.32 (0.04, 98) ^b
Coarse sand	1.20 (0.15, 9) ^{ab}	1.05 (0.11, 15) ^a

short-rotation management (Fig. 4). On the other hand, higher rates of production in sections located immediately downwind of the prevailing (NW) winds across the Great Lakes section indicate their positive, moderating influence on climate, perhaps most notably growing season length (Albert, 1994). The same phenomenon is indicated at a finer spatial level, comparing the subsections adjacent to Lake Superior to those further inland (Fig. 5). At more localized levels, such as on the UMBS landscape, significant differences among minor landforms (Table 3) and among landscape ecosystem types (Table 4) hold the potential to inform planning and management. However, compared to the farther-reaching inferences of our overall analysis, these categorical differences among ecological units are less important than the underlying physiographic drivers of those differences, rendering case-by-case comparisons of mean biomass accumulation rates of minor landforms and landscape ecosystem types of less interest. Thus, in this analysis, we neither show nor emphasize the statistical comparisons between those ecological units, and report the results to inform future research and management at UMBS.

The ecological unit framework also affords an opportunity to explore variability in biomass production rates at section and subsection levels. Whether examined at section or subsection levels,

there appear to be at least two fundamentally different modes of variability in biomass production rates across the province (Table 9). Specifically, some ecological units (e.g., section 212S, subsection 212Sq) have relatively tightly constrained distributions about their medians, suggesting less capacity for change in biomass production. This contrasts with units that appear to hold the potential for large increases or decreases in biomass production rates, should management, climate change or other disturbances push forests in either direction from their current medians (e.g., 212M, 212Le). Assessments such as these are necessarily coarse, and perhaps best viewed as broad expectations that inform increasingly specific management strategies, approaches, and ultimately (at the site or project level) tactics. The identities of such strategies, approaches, and tactics are beyond the scope of this work, but likely target the proximal mechanisms that link physiography with biomass production, such as soil moisture status and nutrient availability, which can be influenced by management. As a case in point, the UMBS landscape reveals the limitation of the broad patterns revealed at the section and subsection levels, and highlights the power of having a landscape ecosystem classification that can inform management tactics at the individual project level. At UMBS, median biomass production rates on outwash plain, moraine, and wetland physiographic settings (1.68, 2.51, 0.98 $\text{Mg ha}^{-1} \text{yr}^{-1}$, respectively) are near to or greater than the 3rd quartile rates of the xeric, mesic, and hydric physiographic classes in the NFI dataset, whether computed at the subsection, section, or whole-province levels ($X = 1.99$, $M = 2.03$, $H = 0.99 \text{ Mg ha}^{-1} \text{yr}^{-1}$). This demonstrates that UMBS forests tend to be quite productive (i.e., not representative), and as a result the management tactics most appropriate for them would differ from the broad expectations set at higher ecological levels. In this case, the tactics employed on an individual project, which would probably occur within one or a few individual landscape ecosystems, are best constrained by the physiographic and soil factors known to control or co-vary with biomass production at the local level,

such as soil wetness and pH. In light of earlier discussion of the integration and autocorrelation of ecosystem factors, appropriate management tactics might manipulate water tables (e.g., through artificial drainage or flooding), soil water holding capacity or nutrient availability (e.g., organic or inorganic amendments).

Within this framework, we interpret variability in biomass production rates as an index of the potential for forests to increase or decrease their biomass production in response to factors such as management or climate change. However, this interpretation carries assumptions and caveats that are necessary to enumerate prior to discussion. First, we interpret the per cent differences between median, 3rd and 1st quartile biomass production rates in the regional NFI dataset as an index of biomass variability or stability in forests dominated by mature, established trees. In this sense, we are using an *a posteriori* index, based on spatial variation in biomass production rates in established forests, to make an inference about the future. These inferences may be misleading, particularly over longer timeframes, because we do not assess understory composition nor recruitment, and the magnitudes of future management and climate impacts are not predictable at sub-regional (e.g., subsection to site) levels. Therefore, our assumption is that the next several decades of the future will not be significantly different than the recent decades that have produced the biomass production rates we observe across forests now comprising the NFI dataset. Over longer time frames, major changes in forest composition due to climate change or human disturbances are likely across the region (Nowacki and Abrams, 2015; Scheller et al., 2011; Scheller and Mladenoff, 2005) which could cause more variability in biomass production rates than is presently associated with the influence of physiographic factors. In the context of these uncertainties, alternative approaches to constraining and predicting biomass C stocks and fluxes are quite helpful.

One of the best of examples of these complementary approaches is represented by Scheller and Mladenoff (2005), who used NFI data, hierarchical ecoregional units, landscape simulation (LANDIS-II) and general circulation models to predict trajectories of forest composition and aboveground biomass 200 years into the future over a 1.5 M ha area in northern Wisconsin. While some of the findings of that study validate results of our analysis, such as different trajectories of aboveground biomass among different ecological units, other findings highlight the limits to the scope of our analysis. For example, dispersal limitations of southern species, coupled with the loss of northern species, are expected to drive an overall decline in biomass stocks that is further exacerbated by disturbance and management activities (biomass removals). In light of the importance of disturbance to forest C sequestration, another large-scale assessment of interest to our analysis is one that used remote sensing, NFI data, and ecosystem modeling (InTEC) to partition changes in U.S. forest C stocks over the last 100 years to disturbance vs. non-disturbance factors (Zhang et al., 2012; Pan et al., 2011). That work generated a 250 m resolution map of U.S. forest age structure (mean age and variability in age), net ecosystem production (NEP) rates vs. age for different forest type groups, and indicated that disturbance has different impacts on C sequestration in different U.S. regions. In the “North” region, encompassing the northeastern quarter of the U.S., forest C sequestration during the past century has been predominantly driven by the recovery of biomass pools in forests aggrading after historic (19th- early 20th century) disturbances, although the rate of annual sequestration across the region has been declining since the 1980s as forestlands become older and global change factors (e.g., N deposition, climate variability) have become more important (Zhang et al., 2012).

As a final example of how complementary approaches can inform our analysis of physiographic constraints of biomass production, we consider how forest plots, eddy covariance networks and modeling can be integrated to examine controls on spatial and temporal variability in carbon fluxes over an 11,000 km² area in northern Wisconsin (Burrows et al., 2003; Desai et al., 2010; Fassnacht and Gower, 1997). In this region, which has heterogeneous physiography, ecosystem types, stand ages, and management regimes, C accumulation in woody biomass constitutes over half of aboveground net primary production (NPP), and varies twofold from forested wetland to upland aspen cover types (Burrows et al., 2003). While not mapped according to a multi-factor, hierarchical ecosystem classification framework, this landscape possesses contrasting landforms, and rates of woody biomass production are higher on moraine than outwash landforms (Fassnacht and Gower, 1997). Importantly, interannual variability in the whole-ecosystem C balance (net ecosystem exchange; NEE), as measured by the WLEF tall tower is driven most strongly by temporal dynamics in water table levels. Collectively, these results—which bear not on long-term trends, but on spatial and temporal variability in C fluxes and their controls—arrive at the same inferences as our analysis, which documents the fundamental importance of physiography and soil moisture to biomass C stocks and production throughout middle succession.

5. Conclusion

Ongoing biomass aggradation and measured accumulation of large biomass stocks in mature forests across the Laurentian Mixed Forest province has broader relevance to the role of north-temperate forest carbon storage in partially mitigating anthropogenic CO₂ emissions. Observations that 100–300 year old forests can continue to accumulate living biomass suggest that, on landscapes throughout the region, most forests (which are dominantly 40–80 years old) are capable of mitigating CO₂ emissions for decades into the future. At spatial levels from the individual ecosystem to the whole province, rates of biomass production are controlled, in part by physiographic and soil factors that influence moisture regimes and availability. This controlling influence of bottom-up factors on biomass production at multiple spatial levels provides an underlying mechanistic basis to inform research and management decisions developed within the same hierarchical, multi-factor ecological unit framework.

Acknowledgments

This analysis rests upon the labor of hundreds of researchers who have visited UMBS and collected data from long-term plots over the course of many decades, field crews that have sampled NFI plots throughout the Great Lakes region, and to acknowledge each individual is impossible. Recent and active researchers who have made particularly significant contributions to UMBS datasets and historical information are Dennis Albert, Art Cooper, Bob Fahey, Bob Farmer, Julia Fisher, Brady Hardiman, Joel Heinen, Claudia Jolls, Greg Koerper, Marc Lapin, Leah Minc, Douglas Pearsall, Bob Pillsbury, Curtis Richardson, Mark Roberts, Ann Sakai, John Syring, Laura Syring, Bob Vande Kopple, Nick Van Dyke, and Chris Vogel. We are grateful to the National Science Foundation (Award No. DEB-1353908) and the USDA-Forest Service, Northern Research Station (Agreements No. 13-CR112306-077 and 16-CR-112306-071) for the financial support to conduct this research. Lastly, we acknowledge two anonymous reviewers who provided constructive comments that improved this work.

Appendix A.

Disturbance history, age estimation methods and references for long-term plots at the University of Michigan Biological Station.

Plot set	References	Description of disturbance history and age estimation methods
AmeriFlux plots	Barnes (2009), Gough et al. (2008), Kilburn (1957, 1960a,b), Koenig (1960)	75 plots across a 100 ha flux tower footprint. Widespread, charred pine stumps indicate clearcutting and repeated fires ca.1880–1923 described in foundational UMBS literature (summarized in Barnes, 2009). 12 plots visited/30 trees cored by Gough in 2004 to compute site indices for dominant/codominant <i>P. grandidentata</i> . Mean origin year was 1923, except two plots burned in the 1950s (young ages and conspicuous fire lines); these excluded from this analysis
Colonial point	Albert and Minc (1987)	3 plots across a ~1 ha area in a ~100 ha forest tract that escaped the clearcutting and extensive fires that swept the region. Habitation and agricultural use by Native Americans from pre-European times up to the early 1900s reported in Albert and Minc (1987). Five dominant <i>T. canadensis</i> cored by Gough in 2011, oldest year of establishment was 1839. Highly uneven-aged structure for the larger 100 ha tract reported in Albert and Minc, including a 1763-origin <i>T. canadensis</i> <100 m from one of the 3 plots reported in this analysis
50 Year plots	Briggs et al. (1986), Roberts and Richardson (1985)	Clearcutting and repeated fires, ca. 1880–early 1900s. Increment cores taken in 1979 from an unspecified number of dominant <i>Populus</i> spp. in each of the 4 plots. Plot origin years were 1908/1909 (#2), 1919 (#3), 1921 (#4), 1919 (#5)
Cooper plots	Cooper (1981)	Clearcutting and repeated fires, 1880–early 1900s. Increment cores taken in each of the three plots by Cooper in 1978 from an unspecified number of dominant <i>P. grandidentata</i> . Origin years for the three plots were 1910/1911
Forestry plots	Bradley (1947), Spurr (1956)	For BS34 (1 plot), 30 trees cored and reported in unpublished 1950s UMBS papers. Data suggest two early cohorts, followed by ongoing recruitment: 6 trees dating to 1879, 5 dating to 1913–1916. Stand was probably logged 1879–1880 as with others located between Douglas and Burt Lakes. For BS42 (3 plots, fire-origin), 1919–1930 reconnaissance by Gates (1926), as reported in Bradley (1947) as “Aspen Set VII.” If this stand was logged, its stumps were completely consumed by fires. For BS40 (2 plots), 6 <i>P. resinosa</i> cored in 1953, with an average origin year of 1890. Charred stumps in the stand suggest logging and fires, with cutting in 1879–1880 based on location between Douglas and Burt Lakes. For BS40A (1 plot), 8 <i>T. canadensis</i> spanning a range of diameters cored in 1995 by R. Vande Kopple (UMBS Resident Biologist, 1979–2016); origin years ranged from 1712 to 1860. Stand may have been cut for pine in the 1879–1880 timeframe based on location adjacent to Burt Lake
Burn plots	Farmer (1958), Gates (1926), Gough et al. (2007)	Clearcutting and repeated fires, ca.1880–early 1900s. Plot installations (clearcut + burn treatments) and data collections are all within the record of research at UMBS. For this analysis, data are from 1936- and 1954- origin plots, measured in 1957, 1979, 1998, 2014
Wells plot	Benninghoff and Cramer (1963), Koenig (1960)	Clearcutting and repeated fires, ca.1880–early 1900s. Reported in Benninghoff and Cramer (1963) and Koenig (1960) as clearcut between 1871 and 1900, and last burned between 1918–1923. Cores taken on this 1 ha plot from an unspecified number of <i>P. grandidentata</i> by Wells in 1976 indicate origin years ranging from 1916 to 1926
Good site aspen	Richardson and Koerper (1981)	Clearcutting and repeated fires, ca.1880–early 1900s. Dendrochronological analysis of cross sections from 10 dominant <i>P. grandidentata</i> by Koerper and Richardson in 1975 showed a mean origin year of 1923 ± 2
Honeysuckle swamp	Kilburn (1957, 1960a,b), Barnes (2009)	Oral history accounts of early UMBS landuse reported in Kilburn (1957; 1960a,b) and verified therein with increment cores of regenerating pine. The area between Douglas and Burt Lakes was reportedly logged in 1879–1880. Plot sampling in 2015 revealed cut (but not burned) stumps in this semipermanently saturated wetland area, suggesting regeneration was following cutting (not fire)

References

- Albert, D.A., 1994. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. USDA Forest Service, General Technical Report NC-178. 250pp.
- Albert, D.A., Minc, L.D., 1987. The Natural Ecology and Cultural History of the Colonial Point Red Oak Stands. University of Michigan Biological Station, Technical Report, p. 80.
- Barnes, B.V., 2009. Vegetation history and change, 1840–2009, pp. 36–49, in: K.J. Nadelhoffer, A.J. Hogg, B.A. Hazlett (Eds.), The Changing Environment of Northern Michigan, University of Michigan Press, Ann Arbor, 214pp.
- Barnes, B.V., Pregitzer, K.S., Spies, T.A., Spooner, V.H., 1982. Ecological forest site classification. *J. Forest.* 80, 493–498.
- Barnes, B.V., Xu, Z., Zhao, S., 1992. Landscape ecosystems of the Korean pine-hardwood forests of the Changbai Mountain Preserve, northeast China. *Can. J. For. Res.* 22, 144–160.
- Bates, P.C., Blinn, C.R., Alm, A.A., 1993. Harvesting impacts on quaking aspen regeneration in northern Minnesota. *Can. J. Forest Res.-Revue Canadienne De Recherche Forestiere* 23, 2403–2412.
- Bechtold, W.A., Patterson, P.L. (Eds.), 2005. The Enhanced Forest Inventory and Analysis Program - National Sampling Design and Estimation Procedures. Gen. Tech. Rep. SRS-80. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, p. 85.
- Benninghoff, W.S., Cramer, K.J., 1963. Phytosociological analysis of aspen communities on three site classes for *Populus grandidentata* in western Cheboygan County, Michigan. *Vegetatio* 11, 253–264.
- Blewitt, W.L., Winters, H.A., 1995. The importance of glaciofluvial features within Michigan's Port Huron moraine. *Ann. Assoc. Am. Geogr.* 85, 306–319.
- Bonan, G.B., 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444–1449.
- Bormann, F.H., Likens, G.E., 1979. Catastrophic disturbance and the steady-state in northern hardwood forests. *Am. Sci.* 67, 660–669.
- Bouyoucos, G.J., 1936. Directions for making mechanical analyses of soils by the hydrometer method. *Soil Sci.* 42, 225–229.
- Bradley, H.L., 1947. The aspen association in the Douglas Lake area. University of Michigan Biological Station, 18pp (Unpublished paper).
- Briggs, G.M., Jurik, T.W., Gates, D.M., 1986. A comparison of rates of aboveground growth and carbon dioxide assimilation by aspen on sites of high and low quality. *Tree Physiol.* 2, 29–34.
- Brown, M.J., Parker, G.G., 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. *Can. J. For. Res.* 24, 1694–1703.
- Burrows, S.N., Gower, S.T., Norman, J.M., Diak, G., Mackay, D.S., Ahl, D.E., Clayton, M. K., 2003. Spatial variability of aboveground net primary production for a forested landscape in northern Wisconsin. *Can. J. For. Res.* 33, 2007–2018.
- Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., 2001. Measuring net primary production in forests: Concepts and field methods. *Ecol. Appl.* 11, 356–370.
- Cleland, D.T., Avers, P.E., McNab, W.H., Jensen, M.E., Bailey, R.G., King, T., Russell, W. E., 1997. National hierarchical framework of ecological units. In: Boyce, M.S., Haney, A. (Eds.), *Ecosystem Management: Applications for Sustainable Forest and Wildlife Resources*. Yale University Press, New Haven, CT, pp. 181–200.
- Cooper, A.W., 1981. Aboveground biomass accumulation and net primary production during the first 70 years of succession in *Populus grandidentata* stands on poor sites in northern lower Michigan. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), *Forest Succession: Concepts and Application*. Springer-Verlag, New York, pp. 339–360.
- Crow, T.R., 1978. Biomass and production in three contiguous forests in northern Wisconsin. *Ecology* 59, 265–273.
- Crumsey, J.M., Le Moine, J.M., Vogel, C.S., Nadelhoffer, K.J., 2014. Historical patterns of exotic earthworm distributions inform contemporary associations with soil physical and chemical factors across a northern temperate forest. *Soil Biol. Biochem.* 68, 503–514.
- Desai, A.R., Helliker, B.R., Moorcroft, P.R., Andrews, A.E., Berry, J.A., 2010. Climatic controls of interannual variability in regional carbon fluxes from top-down and bottom-up perspectives. *J. Geophys. Res.* 115, G02011.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhous, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3, 479–486.
- Facelli, J.M., Pickett, S.T.A., 1991. Plant litter - its dynamics and effects on plant community structure. *Bot. Rev.* 57, 1–32.
- Fahey, R.T., Fotis, A.T., Woods, K.D., 2015. Quantifying canopy complexity and effects on productivity and resilience in late-successional hemlock-hardwood forests. *Ecol. Appl.* 25, 834–847.
- Farmer, R.E., 1958. Some effects of prescribed burning following clear-cutting in poor site aspen. School of Forestry, University of Michigan, Ann Arbor. M.S. Thesis, 53pp.
- Fassnacht, K.S., Gower, S.T., 1997. Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. *Can. J. For. Res.* 27, 1058–1067.
- Foster, J.R., D'Amato, A.W., Bradford, J.B., 2014. Looking for age-related growth decline in natural forests: unexpected biomass patterns from tree rings and simulated mortality. *Oecologia* 175, 363–374.
- Gahagan, A., Giardina, C.P., King, J.S., Binkley, D., Pregitzer, K.S., Burton, A.J., 2015. Carbon fluxes, storage and harvest removals through 60 years of stand development in red pine plantations and mixed hardwood stands in Northern Michigan, USA. *Forest Ecol. Manage.* 337, 88–97.
- Gates, F.C., 1926. Plant succession about Douglas Lake, Cheboygan County, Michigan. *Bot. Gaz.* 82, 170–172.
- Gerlach, J.P., Gilmore, D.W., Puettmann, K.J., Zasada, J.C., 2002. Mixed-species forest ecosystems in the Great Lakes region: a bibliography. Staff Paper Series Number 155. Department of Forest Resources, Minnesota Agricultural Experiment Station. St. Paul, MN, 279pp.
- Gough, C.M., Curtis, P.S., Hardiman, B.S., Scheuermann, C.M., Bond-Lamberty, B., 2016. Disturbance, complexity and succession of net ecosystem production in North America's temperate deciduous forests. *Ecosphere* 6, e01375.
- Gough, C.M., Hardiman, B., Vogel, C.S., Nave, L., Curtis, P.S., 2010. Wood net primary production resilience in an unmanaged forest transitioning from early to middle succession. *For. Ecol. Manage.* 260, 36–41.
- Gough, C.M., Vogel, C.S., Harrold, K., George, K., Curtis, P.S., 2007. The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. *Glob. Change Biol.* 13, 1935–1949.
- Gough, C.M., Vogel, C.S., Schmid, H.P., Su, H.-B., Curtis, P.S., 2008. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. *Agric. For. Meteorol.* 148, 158–170.
- Gower, S.T., McMurtrie, R.E., Murty, D., 1996. Aboveground net primary production decline with stand age: Potential causes. *Trends Ecol. Evol.* 11, 378–382.
- Grigal, D.F., Ohmann, L.F., 1992. Carbon storage in upland forests of the Lake States. *Soil Sci. Soc. Am. J.* 56, 935–943.
- Halpin, C.R., Lorimer, C.G., 2016. Long-term trends in biomass and tree demography in northern hardwoods: an integrated field and simulation study. *Ecol. Monogr.* 86, 78–93.
- Hannah, P.R., 1969. Stemwood production related to soils in red pine plantations in Michigan. *Forest Sci.* 15, 320–326.
- Hannah, P.R., Zahner, R., 1970. Nonpedogenetic texture bands in outwash sands of Michigan: their origin, and influence on tree growth. *Soil Sci. Soc. Am. J.* 34, 134–136.
- Hardiman, B.S., Bohrer, G., Gough, C.M., Vogel, C.S., Curtis, P.S., 2011. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. *Ecology* 92, 1818–1827.
- Hardiman, B.S., Gough, C.M., Halperin, A., Hofmeister, K.L., Nave, L.E., Bohrer, G., Curtis, P.S., 2013. Maintaining high rates of carbon storage in old forests: A mechanism linking canopy structure to forest function. *For. Ecol. Manage.* 298, 111–119.
- Host, G.E., Pregitzer, K.S., Ramm, C.W., Lusch, D.P., Cleland, D.T., 1988. Variation in overstory biomass among glacial landforms and ecological land units in northwestern lower Michigan. *Can. J. Forest Res.-Revue Canadienne De Recherche Forestiere* 18, 659–668.
- Jin, L., Williams, E., Szramek, K., Walter, L., Hamilton, S., 2008. Silicate and carbonate mineral weathering in soil profiles developed on Pleistocene glacial drift (Michigan, USA): Mass balances based on soil water geochemistry. *Geochim. Cosmochim. Acta* 72, 1027–1042.
- Jones, E.A., Reed, D.D., Mroz, G.D., Liechty, H.O., Cattellino, P.J., 1993. Climate stress as a precursor to forest decline: paper birch in northern Michigan, 1985–1990. *Can. J. For. Res.* 23, 29–33.
- Kashian, D.M., Barnes, B.V., Walker, W.S., 2003. Ecological species groups of landform-level ecosystems dominated by jack pine in northern Lower Michigan, USA. *Plant Ecol.* 166, 75–91.
- Keeton, W.S., Whitman, A.A., McGee, G.C., Goodale, C.L., 2011. Late-successional biomass development in northern hardwood-conifer forests of the northeastern United States. *Forest Sci.* 57, 489–505.
- Kilburn, P.D., 1957. Historical development and structure of the aspen, jack pine, and oak vegetation type on sandy soils in northern lower Michigan. School of Forestry, University of Michigan, Ann Arbor. Dissertation, 267pp.
- Kilburn, P.D., 1960a. Effect of settlement on the vegetation of the University of Michigan Biological Station. *Michigan Acad. Sci., Arts Lett.* 45, 77–81.
- Kilburn, P.D., 1960b. Effects of logging and fire on the xerophytic forests in northern Michigan. *Bull. Torrey Bot. Club* 87, 402–405.
- Kira, T., Shidei, T., 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Jpn. J. Ecol.* 17, 70–87.
- Koenig, R.L., 1960. Variation in tree size and quality of naturally occurring bigtooth aspen clones in northern Lower Michigan. M.S. thesis, School of Natural Resources, University of Michigan, Ann Arbor.
- Koerper, G.J., Richardson, C.J., 1980. Biomass and net annual primary production regressions for *Populus grandidentata* on 3 sites in northern Lower Michigan. *Can. J. For. Res.* 10, 92–101.
- Lapin, M., Barnes, B.V., 1995. Using the landscape ecosystem approach to assess species and ecosystem diversity. *Conserv. Biol.* 9, 1148–1158.
- Lichstein, J.W., Wirth, C., Horn, H.S., Pacala, S.W., 2009. Biomass chronosequences of United States forests: Implications for carbon storage and forest management. In: Wirth, C., Gleixner, G., Heimann, M. (Eds.), *Old-Growth Forests: Function, Fate, and Value*. Springer, New York, pp. 301–341.
- Lorimer, C.G., Halpin, C.R., 2014. Classification and dynamics of developmental stages in late-successional temperate forests. *For. Ecol. Manage.* 334, 344–357.
- Luyssaert, S., Schulze, E.D., Börner, A., Knohl, A., Hessenmoller, D., Law, B.E., Ciais, P., Grace, J., 2008. Old-growth forests as global carbon sinks. *Nature* 455, 213–215.
- McNab, W.H., Cleland, D.T., Freeouf, J.A., Keys, J.E., Nowacki, G.J., Carpenter, C.A., 2007. Description of Ecological Subregions: Sections of the Conterminous United States. USDA, Forest Service, Washington, DC, p. 80.

- Möller, C.M., Müller, D., Nielsen, J., 1954. The dry matter production of European beech. *Det Forstlige Forsøgsvaesen i Danmark* 21, 327–335.
- Mroz, G.D., Gale, M.R., Jurgensen, M.F., Frederick, D.J., Clark, A., 1985. Composition, structure, and aboveground biomass of two old-growth northern hardwood stands in Upper Michigan. *Can. J. For. Res.* 15, 78–82.
- Nave, L.E., Drevnick, P.E., Heckman, K.A., Hofmeister, K.L., Veverica, T.J., Swanston, C. W. Soil hydrology, physical and chemical properties control carbon and mercury distribution in a postglacial lake-plain wetland. *Geoderma*. (submitted for publication).
- Nave, L.E., Gough, C.M., Maurer, K.D., Bohrer, G., Hardiman, B.S., Le Moine, J., Munoz, A.B., Nadelhoffer, K.J., Sparks, J.P., Strahm, B.D., Vogel, C.S., Curtis, P.S., 2011. Disturbance and the resilience of coupled carbon and nitrogen cycling in a north temperate forest. *J. Geophys. Res.-Biogeosci.* 116, G04016.
- Nave, L.E., Sparks, J.P., Le Moine, J., Hardiman, B.S., Nadelhoffer, K.J., Tallant, J.M., Vogel, C.S., Strahm, B.D., Curtis, P.S., 2014. Changes in soil nitrogen cycling in a northern temperate forest ecosystem during succession. *Biogeochemistry* 121, 471–488.
- Nowacki, G.J., Abrams, M.D., 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? *Glob. Change Biol.* 21, 314–334.
- Odum, E.P., 1969. Strategy of ecosystem development. *Science* 164, 262–270.
- O'Connell, B.M., Conkling, B.L., Wilson, A.M., Burrill, E.A., Turner, J.A., Pugh, S.A., Christensen, G., Ridley, T., Menlove, J., 2016. The forest inventory and analysis database: database description and user guide for phase 2 (version 6.1.1). USDA Forest Service. Available online at https://www.fia.fs.fed.us/library/database-documentation/current/ver611/FIADB_User_Guide_P2_6-1-1_final.pdf.
- Ovington, J.D., 1962. Quantitative ecology and the woodland ecosystem concept. *Adv. Ecol. Res.* 1, 103–192.
- Palik, B., Cease, K., Egeland, L., Blinn, C., 2003. Aspen regeneration in riparian management zones in northern Minnesota: Effects of residual overstory and harvest method. *Northern J. Appl. Forestry* 20, 79–84.
- Pan, Y., Chen, J.M., Birdsey, R.A., McCullough, K., He, L., Deng, F., 2011. Age structure and disturbance legacy of North American forests. *Biogeosciences* 8, 715–732.
- Pearsall, D.R., 1995. Landscape ecosystems of the university of Michigan biological station: ecosystem diversity and ground –cover diversity. School of Natural Resources and Environment, University of Michigan, Ann Arbor. Dissertation, 396pp, plus maps.
- Pearsall, D.R., Barnes, B.V., Zogg, G.R., Lapin, M., Ring, R.R., 1995. Landscape Ecosystems of the University of Michigan Biological Station. School of Natural Resources and Environment, University of Michigan, Ann Arbor, p. 66. Technical Report.
- Pregitzer, K.S., Barnes, B.V., 1984. Classification and comparison of the upland hardwood and conifer ecosystems of the Cyrus H. McCormick Experimental Forest, Upper Peninsula, Michigan. *Can. J. Forest Res.* 14, 362–375.
- 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.
- Reich, P.B., Grigal, D.F., Aber, J.D., Gower, S.T., 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78, 335–347.
- Richardson, C.J., Koerper, G.J., 1981. The influence of edaphic characteristics and clonal variation on quantity and quality of wood production in *Populus grandidentata* Michx. in the Great Lakes region of the U.S.A. *Der Forstlichen Bundesversuchsanstalt Wien* 142, pp. 271–292.
- Roberts, M.R., Richardson, C.J., 1985. Forty-one years of population change and community succession in aspen forests on four soil types, northern lower Michigan, U.S.A. *Can. J. Bot.* 63, 1641–1651.
- Rowe, J.S., 1972. Forest Regions of Canada. Fisheries and Environment Canada, Canadian Forest Service, p. 172. Technical Report.
- Rutkowski, D.R., Stottley, R., 1993. Composition, biomass and nutrient distribution in mature northern hardwood and boreal forest stands, Michigan. *Am. Midland Naturalist* 130, 13–30.
- Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: Pattern and process. In: Begon, M., Fitter, A.H. (Eds.), *Advances in Ecological Research*, vol. 27. Elsevier Academic Press, London, pp. 213–262.
- Sakai, A.K., Roberts, M.R., Jolls, C.L., 1985. Successional changes in a mature aspen forest in northern lower Michigan: 1974–1981. *Am. Midl. Nat.* 113, 271–282.
- Scheller, R.M., Hua, D., Bolstad, P.V., Birdsey, R.A., Mladenoff, D.J., 2011. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. *Ecol. Model.* 222, 144–153.
- Scheller, R.M., Mladenoff, D.J., 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. *Glob. Change Biol.* 11, 307–321.
- Siccama, T.G., Fahey, T.J., Johnson, C.E., Sherry, T.W., Denny, E.G., Girdler, E.B., Likens, G.E., Schwarz, P.A., 2007. Population and biomass dynamics of trees in a northern hardwood forest at Hubbard Brook. *Can. J. For. Res.* 37, 737–749.
- Spies, T.A., Barnes, B.V., 1985. A multi-factor ecological classification of the northern hardwood and conifer ecosystems of Sylvania Recreation Area, Upper Peninsula, Michigan. *Can. J. For. Res.* 15, 949–960.
- Spurr, S.H., 1956. Forestry Sourcebook, 1956. University of Michigan Biological Station, Technical Report, p. 46.
- Spurr, S.H., Zumbege, J.H., 1956. Late Pleistocene features of Cheboygan and Emmet Counties, Michigan. *Am. J. Sci.* 254, 96–109.
- Stone, D.M., 2002. Logging options to minimize soil disturbance in the northern Lake States. *Northern J. Appl. Forestry* 19, 115–121.
- Thiffault, E., Barrette, J., Pare, D., Titus, B.D., Keys, K., Morris, D.M., Hope, G., 2014. Developing and validating indicators of site suitability for forest harvesting residue removal. *Ecol. Indicators* 43, 1–18.
- Thiffault, E., Hannam, K.D., Pare, D., Titus, B.D., Hazlett, P.W., Maynard, D.G., Brais, S., 2011. Effects of forest biomass harvesting on soil productivity in boreal and temperate forests - a review. *Environ. Rev.* 19, 278–309.
- Van Eck, W.A., Whiteside, E.P., 1963. Site evaluation studies in red pine plantations in Michigan. *Soil Sci. Soc. Am. Proc.* 27, 174–177.
- Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. *J. Ecol.* 98, 725–736.
- Wardle, D.A., Walker, L.R., Bardgett, R.D., 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305, 509–513.
- Wells, J.R., 1978. Tree populations of a mature aspen forest in Cheboygan County, Michigan. *The Michigan Botanist* 17, 73–79.
- White, D.P., Wood, R.S., 1958. Growth variations in a red pine plantation influenced by a deep-lying fine soil layer. *Soil Sci. Soc. Am. J.* 22, 174–177.
- Whittaker, R.H., Woodwell, G.M., 1969. Structure, production, and diversity of the oak-pine forest at Brookhaven, New York. *J. Ecol.* 57, 155–174.
- Woods, K.D., 2016. Multi-decade biomass dynamics in an old-growth hemlock-northern hardwood forest, Michigan, USA. *Peer J.* 2. <http://dx.doi.org/10.7717/peerj.598>. 2:e598.
- Yanai, R.D., Arthur, M.A., Siccama, T.G., Federer, C.A., 2000. Challenges of measuring forest floor organic matter dynamics: repeated measures from a chronosequence. *For. Ecol. Manage.* 138, 273–283.
- Zak, D.R., Host, G.E., Pregitzer, K.S., 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern Lower Michigan. *Can. J. For. Res.* 19, 1521–1526.
- Zhang, F., Chen, J.M., Pan, Y., Birdsey, R.A., Shen, S., Ju, W., He, L., 2012. Attributing carbon changes in conterminous U.S. forests to disturbance and non-disturbance factors from 1901 to 2010. *J. Geophys. Res.* 117, G02021.
- Zogg, G.P., Barnes, B.V., 1995. Ecological Classification and Analysis of Wetland Ecosystems, Northern Lower Michigan, USA. *Can. J. Forest Res.-Revue Canadienne De Recherche Forestiere* 25, 1865–1875.