Forest Ecology and Management 397 (2017) 157–173

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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.

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).

http://dx.doi.org/10.1016/j.foreco.2017.04.040

and water balances, maintenance of nutrient retention and cycling, and mitigation of atmospheric CO_2 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; Luyssaert 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 Zumberge, 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-