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Forest structure in space and time: Biotic and abiotic determinants of canopy complexity and their effects on net primary productivity

Alex T. Fotis[a,*], Timothy H. Morin[b,c], Robert T. Fahey[d], Brady S. Hardiman[e], Gil Bohrer[b], Peter S. Curtis[a]

[a] Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 318 W. 12th Avenue, Columbus, OH 43210, USA
[b] Department of Civil, Environmental, and Geodetic Engineering, The Ohio State University, 2070 Neil Ave., Columbus, OH 43210 USA
[c] Department of Environmental Resources Engineering, 402 Baker Lab, 1 Forestry Drive, State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210 USA
[d] Department of Natural Resources and the Environment & Center for Environmental Science and Engineering, University of Connecticut, 1376 Storrs Road, Storrs, CT 06269 USA
[e] Department of Forestry and Natural Resources and Division of Environmental and Ecological Engineering, Purdue University, West Layafette, IN 47907, USA

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ABSTRACT

The structural dynamics of forest canopies involve complex interactions among the abiotic environment, stand structure, species composition and disturbance regimes. How the re-arrangement of tree canopies in space and time affects forest aboveground net primary productivity (*ANPP*) remains poorly understood, however. In this study, we analyzed a long-term dataset from a temperate deciduous forest in Northern Michigan, USA, to investigate two primary objectives: 1) what abiotic and biotic factors influence canopy complexity and its inter-annual variability, and 2) the direct and indirect effects that abiotic, biotic and canopy complexity variables have on *ANPP*. We hypothesized that inter-annual variability in canopy complexity would be lower in high complexity canopies and that temporal variability in complexity metrics would be inversely related to *ANPP*. We found that canopy complexity was highest in more taxonomically diverse stands with high variability in tree diameters and in stands dominated by *Populus tremuloides* and *Populus grandidentata.* Canopy complexity was lowest in stands dominated by *Quercus rubra* and *Pinus strobus*, which also had lower *ANPP*. Stands with a high stem density had lower inter-annual variation in canopy complexity, exhibited more height growth and an increase in canopy open space, which in turn enhanced *ANPP*. Our results provide novel empirical evidence linking temporal stability in canopy complexity to *ANPP*, and suggest that *variability* in canopy complexity over time, in addition to the overall mean canopy complexity, may be important when considering drivers of forest carbon uptake.

1. Introduction

Forest canopy structure influences a wide range of functional and ecological characteristics of forest ecosystems. For example, leaf clumping and canopy empty space increase light penetration to the forest floor leading to greater soil respiration and evaporation (Law et al., 2001). Variability in leaf arrangement influences within-canopy light environments (Fotis and Curtis, 2017; Iio et al., 2005), which alters the temperature and moisture content of the canopy air (Niinemets and Valladares, 2004) and affects the physiological and morphological properties of leaves (Catoni et al., 2015; Ellsworth and Reich, 1993). Gap fraction, canopy height, vertical leaf density profiles, and total leaf area affect the roughness length, which controls wind penetration into canopies and turbulence characteristics inside and above them, and thus affects the rate of gas diffusion into and out of the canopy (Bohrer et al., 2009; Maurer et al., 2013a).

Canopy organization also plays a pivotal role in structuring forest habitat characteristics. Deep canopy gaps allow light demanding, early successional species to establish in the understory (Oliver and Larson, 1996). Canopy gap fraction and size and leaf density affect the dispersal distance of seeds and therefore affect recruitment rates and spatial patterns (Bohrer et al., 2008; Maurer et al., 2013b). Canopy height affects bird nesting habitat (Hinsley et al., 2002) and is proposed as a driving mechanism for gliding locomotion in arboreal vertebrates (Dudley and DeVries, 1990). Dial et al. (2006) found that arthropod biomass and abundance was greatest in the most densely foliated areas

* Corresponding author.
E-mail addresses: fotis.2@osu.edu (A.T. Fotis), Morin.37@buckeyemail.osu.edu (T.H. Morin), robert.fahey@uconn.edu (R.T. Fahey), Hardimanb@purdue.edu (B.S. Hardiman), Bohrer.17@osu.edu (G. Bohrer), Curtis.7@osu.edu (P.S. Curtis).

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of the canopy with the lowest light and highest moisture content. Changes in canopy structure therefore have the potential to affect functional and ecological aspects of forests at multiple scales.

Forest canopy structure, or the arrangement of leaves, branches and empty space at a given time (Parker 1995), is primarily determined by stand characteristics such as community composition (Dial et al., 2004), species diversity (Jucker et al., 2015; Sapijanskas et al., 2014), and tree size distributions (Fahey et al., 2015; Pretzsch and Schütze, 2016). These stand characteristics, in turn, reflect the successional stage of the forest (Dial et al., 2011), the type, frequency, and severity of disturbance experienced (Fahey et al., 2015; Hardiman et al., 2013b), and local physiographic features such as topography, soil moisture and soil fertility (Pretzsch and Schütze, 2016; Whittaker, 1956; Zhang and Chen, 2015). Forests with high stem densities and tree size variability typically have more densely packed canopies (Jucker et al., 2015; Morin, 2015; Sapijanskas et al., 2014) and more variable leaf arrangements (Fahey et al., 2015). Densely packed canopies intercept more light and increase forest productivity (Morin 2015). Age related increases in structural complexity across a 200-yr chronosequence of deciduous forests in Michigan sustained aboveground net primary productivity (*ANPP*) into early-old growth stages (Hardiman et al., 2013a) and has been proposed as one mechanism maintaining higher than expected net ecosystem production (*NEP*) in century-old deciduous forests (Gough et al., 2016).

Changes in canopy structure determine, and are determined by, interactions among individual competing trees (Sorrensen-Cothern et al., 1993). The ability to colonize large gaps through lateral branch expansion or re-grow into smaller, internal spaces between adjacent tree crowns is related to tree size and shade-tolerance. Smaller individuals with higher shade-tolerance can expand laterally much quicker than larger, shade-intolerant trees (Hossain and Caspersen, 2012). Avoidance of neighbors among canopy individuals may be an indirect response to the shade cast by their crowns. Branch growth is reduced in the shade near neighbors and enhanced in high-light areas away from them (Kawamura, 2010, Kukk, 2015; Sorrensen-Cothern et al., 1993). Growth away from neighbors may also be due to the direct effects of twig breakage and dieback. This is caused by wind induced tree abrasion, which increases with tree height and slenderness (Hossain and Caspersen, 2012; Rudnicki et al., 2003) and varies among different species mixtures (Hajek et al., 2015).

There is a trade-off between resource investment and resource gain during canopy space exploration (Reiter et al., 2005). Exploration for light and avoidance of neighbors involves both construction and maintenance costs of branches and foliage. Resource acquisition is only beneficial at the whole-plant level when the resource gained (e.g., light to drive photosynthetic C gain) outweighs that invested (e.g., C allocated to new branch construction, Kawamura, 2010). Additionally, the more variable resources are within the canopy, the higher the risk to benefit ratio is of pursuing those resources (Kawamura, 2010; Reiter et al., 2005; Sorrensen-Cothern et al., 1993). A highly dynamic canopy, with variable resource availability in space and time, might lead to reduced *ANPP* due to the elevated construction and maintenance costs of active canopy exploration. This is consistent with simulations showing that NPP is lower in temperate forests which exhibited higher inter annual-variability in leaf area index (*LAI*) (Morin et al., 2011; Morin et al., 2014). Morin et al. (2011) concluded that the variability of forest characteristics, in addition to the mean, should be investigated as a potential driver of forest productivity. To our knowledge, the influence of inter-annual variability in canopy structure on forest productivity has not yet been empirically explored.

The two primary objectives in this study were to 1) examine how biotic and abiotic factors affect canopy complexity and its change over time in a northern deciduous forest, and 2) how the interplay between these two features and the biotic and abiotic factors affect *ANPP*. We hypothesize that canopy structural complexity is negatively related to the magnitude of its change over time (H1, Fig. 1a). That is, less complex canopies show *more* inter-annual variation in canopy structure. We previously found that less complex canopies at our site had greater light variability in the midcanopy (Fotis and Curtis, 2017). We suggest that this resource variability may lead to greater canopy exploration and high inter-annual variability in canopy structural metrics. We also hypothesize that high inter-annual variability in canopy complexity would have a negative effect on ANPP due to the higher construction and maintenance costs of active canopy exploration (H2, Fig. 1a).

2. Methods

2.1. Site description and physiography

Our study was conducted in a mixed northern hardwood forest at the University of Michigan Biological station (UMBS) in northern lower Michigan, USA (45°35.5′N, 84° 43′W). This forest plot has been part of the Ameriflux network since 1997 (Gough et al., 2013; Schmid et al., 2003). Meteorological and flux data from the site are available through Ameriflux site-ID US-UMB (Gough et al., 1999). The UMBS forest experienced widespread fire and intensive logging in the early 1900′s before entering protection, resulting in relatively homogenous forests that are approximately 100 years old. These forests are currently undergoing a transition from an early successional bigtooth aspen (*Populus grandidentata*) and paper birch (*Betula papyrifera*) assemblage, to one dominated by mid-successional red oak (*Quercus rubra*), red maple (*Acer rubra*), white pine (*Pinus strobus*) and late-successional American beech (*Fagus grandifolia*). The mean annual temperature is 6.8 °C and the mean annual precipitation is 805 mm (Matheny et al., 2014). Soils in this study are coarse-grained, mixed frigid Entic Haplorthods composed of 95% sand and 5% silt (Nave et al., 2011).

To investigate the influence of topo-edaphic variables on stand characteristics, canopy structure, and *ANPP*, we measured elevation (*Elv*), soil moisture (*SM*) and soil organic matter content (*OMC*) in all study plots (see Table 1). Elevation across UMBS was derived from an existing digital elevation model as part of the Michigan Statewide Authoritative Imagery and LiDAR program. Data had a horizontal accuracy of better than 1 m and a vertical accuracy of 0.029 m for non-vegetation returns. While aspect and slope are considered important drivers of carbon storage in temperate forests at landscape scales (900 ha; Fotis et al., 2017), we did not consider them to be an important influence on local abiotic conditions in this study due to the relatively flat surface in which the plots were distributed. Soil organic matter was calculated using the “loss-on-ignition” method (Kalra and Maynard, 1991). In 2016, five soil cores sampling the top 0–20 cm of soil were collected from each study plot. Samples were pressed through a 2 mm sieve, dried to constant mass and ignited at 500 °C for 24 h. Soil volumetric water content of the top 20 cm was measured at field capacity using a Time Domain Reflectometry probe. In June 2015, twelve random points in each plot were measured on two separate occasions after heavy rain events to ensure soil saturation.

2.2. Stand characteristics

To understand the drivers of canopy complexity and ANPP, we use multiple metrics, classified into three general classes of stand characteristics: (a) stand structural characteristics based on stem size and spatial patterns; (b) compositional characteristics describe species abundances; and (c) Canopy complexity metrics based on data describing the spatial distribution of canopy elements (leaf and branches) and collected with the portable canopy lidar (PCL).

2.2.1. Stand structure

In 1998, sixty 0.08 ha plots were established at 100 m intervals along 1 km transects radiating from the base of the US-UMB tower, and censused every 5 years. In 2010 and 2015, all live stems ≥ 10 cm