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FOREST STAND STRUCTURE AND PRIMARY PRODUCTION IN RELATION TO ECOSYSTEM DEVELOPMENT, DISTURBANCE, AND CANOPY COMPOSITION

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University

by

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By: Cynthia M Scheuermann, B.S.

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Temperate forests are complex ecosystems that sequester carbon (C) in biomass. C storage is related to ecosystem-scale forest structure, changing over succession, disturbance, and with community composition. We quantified ecosystem biological and physical structure in two forest chronosequences varying in disturbance intensity, and three late successional functional types to examine how multiple structural expressions relate to ecosystem C cycling. We quantified C cycling as wood net primary production (NPP), ecosystem structure as Simpson's Index, and physical structure as leaf quantity (LAI) and arrangement (rugosity), examining how wood NPP-structure relates to light distribution and use-efficiency. Relationships between structural attributes of biodiversity, LAI, and rugosity differed. Development of rugosity was conserved regardless of disturbance and composition, suggesting optimization of vegetation arrangement over succession. LAI and rugosity showed significant positive productivity trends over succession, particularly within deciduous broadleaf forests, suggesting these measures of structure contain complementary, not redundant, information related to C cycling.

1. Introduction

Temperate forests are important components of the global carbon (C) cycle, collectively sequestering C in soils and biomass at a rate that approximates 9% of the annual C emissions from fossil fuel combustion (Pan et al. 2011). At the ecosystem-scale, forest physical and biological structure, and C cycling processes are dynamic, shifting with development and following disturbance (Pedro et al. 2015). The coupling of ecosystem structure and C cycling processes is central to ecological theory (Odum 1969, Gough et al. 2016), a prominent focus of empirical research (Reich 2012, Hardiman et al. 2011, Ishii et al. 2004), and represented in ecosystem simulation models (Antonarakis 2014). However, investigations of decade to century changes in coupled ecosystem structure-C cycling processes are rare because of challenges associated with empirically observing and interpreting ecological change over very long timescales. Moreover, investigations of ecosystem structure and C cycling over decades or more generally focus on structure or function, rather than the coupling the two, owing, in part, to each having roots in different ecological subdisciplines of community and ecosystem ecology, respectively. However, explicit mechanistic coupling of ecosystem structure-function over long timescales is essential to advancing fundamental understanding of long-term drivers of the C cycle and improving century-long C cycling simulations (Antonarakis 2014).

Net primary production (NPP) – the rate of C accrued in plant biomass over time – is correlated with several ecosystem structural features that change over decadal to century timescales and with disturbance, including physical complexity and leaf arrangement (Hardiman et al. 2013, Pretzsch 2014), biological diversity (Danescu et al. 2016; Pedro et al. 2015; Stoy et al. 2008), and leaf quantity (Reich 2012). Structural measures summarizing ecosystem-wide physical and biological complexity, and leaf quantity may serve as spatially integrative, non-

redundant proxies for processes dictating how limiting resources, such as light and nitrogen, are acquired, allocated, and used to drive canopy C fixation and NPP (Nadkarni et al. 2008; Ishii et al. 2004). For example, leaf area index (LAI), a measure of the quantity of photosynthetically active tissues, is globally correlated with NPP (Reich 2012). Tree species diversity, a putative surrogate of photosynthetic trait variation, has been positively related to NPP and canopy C fixation (Danescu et al. 2016, Stoy 2008). More recently, ecosystem physical complexity, characterized from the arrangement of canopy leaves, has been correlated with NPP, with leaf arrangement, but not quantity, indicating within-canopy resource distribution (Hardiman et al. 2013). More physically complex and heterogeneous canopies, with a broad array of crown architectures and heights, may more fully absorb and use light more efficiently to drive whole-canopy photosynthesis, leading to increased plant production at the ecosystem scale (Niinemets 2010). Plasticity in canopy physical structure over time and with disturbance, and among forest communities – in particular how vegetation is arranged in space – is not well-understood. Similar to theory motivating community "assembly rules" (Li and Waller 2016), a conserved trajectory of stand physical structural development, if observed, might suggest ecosystems arrange vegetation in space to optimize resource acquisition and use-efficiency to maximize canopy scale C assimilation.

Current understanding of canopy structural change during ecosystem development (Fig. 1) and following disturbance is concentrated on leaf quantity and biodiversity, rather than physical arrangement and heterogeneity. Following establishment, LAI and biological diversity generally progress in similar ways, initially increasing rapidly with forest age and reaching an asymptote and sometimes declining during middle successional stages as short-lived trees senescence from the canopy (Wang et al. 2014, Goulden et al. 2011). Disturbance severity and frequency affect

the successional speed and trajectory of LAI recovery and biological diversity, with higher levels and frequencies of disturbance altering LAI and community development trajectories for decades or more (Hardiman et al. 2013; Pedro et al. 2015; Pretzsch 2014). Similarly, physical complexity increases during early stages of ecosystem development as forests become multi-aged and, therefore, more heterogeneously structured; unlike biological complexity and LAI, physical complexity may increase into late successional stages as community composition no longer diversifies but small-scale dispersed disturbances continue to introduce physical complexity and heterogeneity (Hardiman et al. 2013, Gough et al. 2016).

Here, we examine how different ecosystem structural expressions summarizing vegetation quantity, arrangement, and diversity compare with one another and, we evaluate their mechanistic coupling with NPP across a range of successional stages, disturbance legacies, and late-successional communities. Our study uses as a model system spanning a broad structural gradient forests of the Upper Great Lakes region, particularly those that regrew following large-scale deforestation and burning in the late 19th to early 20th centuries (Gough et al. 2007) and less disturbed late-successional forests varying in dominant canopy functional type. We specifically take advantage of two well-documented chronosequences at the University of Michigan Biological Station (UMBS) with different disturbance legacies – clearcut harvesting with and without burning – initiated systematically to mimic regional disturbance events, in addition to late successional stands (Farmer 1958, Scheiner & Teeri 1981, White et al. 2004, Gough et al. 2007). Our analysis builds on prior work at our site and others coupling ecosystem structure with C cycling processes (Hardiman 2013, Gough 2010, 2007), expanding on this work by investigating how several different expressions of stand structure, hypothesized to capture unique functional information, develop and change across multiple axes of time, disturbance, and

community structure. Our work endeavors, as well, to serve as an example of how advancing

mechanistic understanding of decadal to century C cycling processes requires research that

integrates knowledge stemming from multiple ecological subdisciplines, including community

and ecosystem ecology, and plant physiology.

2. Materials and Methods

2.1. Study Site Description

Our study at the University of Michigan Biological Station (UMBS) in northern lower Michigan,

USA (45.56° N, -84.71° W) examined structure and C cycling in two forest chronosequences,

containing four stands each, with different disturbance histories, and three additional late

successional forest functional types (Liebman et al. *in review*). Our 11 total forest stands spanned

~200 years of ecological succession and were within 14 km of one another. The upper Great

Lakes region, including the stands in both chronosequences, experienced widespread clear-cut

and fire disturbance during the late 19th and early 20th centuries (Gough et al. 2007). Following

this region-wide disturbance, stands in a systematically clear-cut harvested forest

chronosequence (hereafter "*Cut Only*") were harvested in 1911, 1952, 1972, and 1987 (Farmer

1958). A more intensively disturbed chronosequence includes four stands experimentally clear-

cut harvested, with slash retained on site, and burned (hereafter "*Cut and Burn*") in 1936, 1954,

1980, and 1998 (Scheiner & Teeri 1981, White et al. 2004, Gough et al. 2007). Bigtooth Aspen

(*Populus grandidentata*) emerged as the dominant tree species following *Cut Only* and *Cut and

Burn* disturbances, consistent with regional patterns of increasing disturbance-related aspen

dominance a century ago. Three regionally representative late successional forest stands, the

eldest initiated prior to 1850, are potential successional 'end-member' climax communities. A mostly coniferous site (hereafter "ENF" for evergreen needleleaf) had an upper canopy dominated by Red Pine (*Pinus resinosa*) and a White Pine (*Pinus strobus*) understory. A mixed coniferous-deciduous site (hereafter "MIX" for mixed) includes Red Pine and White Pine canopy dominants with the additional presence of deciduous Bigtooth Aspen and subcanopy Northern Red Oak (*Quercus rubra)* and Red Maple (*Acer rubrum*). A primarily deciduous site (hereafter "DBF" for deciduous broadleaf) has a canopy of American Beech (*Fagus grandifolia*), Sugar Maple (*Acer saccharum*), Northern Red Oak (*Quercus rubra*), with lesser representation from Eastern Hemlock (*Tsuga canadensis*). Additional stand characteristics are described in detail in **Table 1**. The site has an average annual air temperature of 5.5°C and precipitation of 817 mm (Hardiman et al. 2013).

This sampling approach was designed to characterize multiple aspects of ecosystem-scale structure and function. Because our study includes experimental chronosequences initiated decades ago and late successional remnant forests, stand shapes and sizes are not uniform. Each stand contained two or three 0.1 ha plots, with one exception noted below, for a total of 29 sampling plots (Appendix 1), with plots treated as replicates for calculating stand means and error. Plots were circular with the exception of the *Cut and Burn* stand initiated in 1998 which, due to size constraints of the treatment area, consisted of two rectangular plots of 0.14 and 0.06 ha. Current soils and climate are relatively uniform among chronosequence stands and our chronosequences were systematically disturbed using the same experimental protocol (Appendix 1); however, limitations associated with space-for-time substitutions, including differences among stands in average atmospheric and climate conditions, necessitate caution when interpreting results (Davies and Gray 2015, Walker et al. 2010). Even so, our approach follows

that of several prior influential studies employing chronosequences to examine long-term C cycling processes (Peichl et al. 2006, Bond-Lamberty et al. 2004, Law et al. 2003).

2.2 Measures of canopy structure

Our ecosystem-scale characterization of canopy structure included three independently derived measures of structure previously shown to correlate with primary production, and known to change over the course of ecosystem development: leaf area index (Reich 2012), rugosity (Hardiman et al. 2013, 2011), and tree canopy diversity as Simpson's Index (Drake et al. 2011, Onaindia et al. 2004).

2.2.1 Leaf area index

We used hemispherical imaging to derive stand leaf area index (LAI), a commonly used measure of leaf (and therefore photosynthetic tissue) surface area and quantity per equivalent ground area. Three images were taken at 1.5m height in each plot: one in plot center and two additional randomly assigned locations. A north-facing, leveled Nikon D3200 outfitted with a 5.8mm 180° circular fisheye lens was used during times of uniform sky color (overcast sky, dawn, or dusk). Images were analyzed with Gap Light Analyzer (GLA) (Frazer et al. 1999) for effective LAI between zenith angles 0 to 60° to minimize error from nearby canopies outside plots. Automatic threshold levels for each image were determined using ImageJ (Schneider et al. 2012). Prior analysis at our site established strong correspondence ($r^2 = 0.87$) between independently derived hemispherical and litter-trap based LAI (Stuart-Haentjens et al. 2015).

2.2.2 Rugosity

We quantified stand physical structural complexity as rugosity, a measure of canopy structural heterogeneity derived from ground-based lidar (Hardiman et al. 2013, Hardiman et al. 2011). A Portable Canopy Lidar (PCL) system (Hardiman et al. 2011, Parker et al. 2004) generated a canopy hit-map along two 40 m transects, one running North to South and another East to West through each plot center. A modified lidar sampling protocol was followed for the 1998 origin *Cut and Burn* plots with shortened parallel transects (10m and 20m) running North to South. Though the effective sampling area was smaller than that of other stands, physical heterogeneity and canopy height were lower in this young stand, suggesting the sampling area was sufficient for capturing within-stand variation in complexity (Hardiman et al. 2013). Prior to analysis, lidar returns (i.e., hits) were allocated to 1m bins vertically (height within canopy) and horizontally (distance along transect) and raw hit data were processed to estimate stand rugosity using published MATLAB code (Hardiman et al. 2013). Rugosity expresses physical complexity as the variance in the horizontal and vertical distribution of vegetation:

(eqn. 1) $\quad\quad\quad R = \sigma(\sigma[VAI]_z)_x$

where rugosity (R) is the product of the standard deviations (σ) in horizontal (x) and vertical (z) vegetation area indexes (VAI) for each 1 x 1 m bin based on ratio of hits to sky returns.

2.2.3 Diversity Indices

To assess biological complexity, we calculated stand-scale Simpson's Index of Diversity from canopy tree data (DBH > 8cm) collected from plot surveys conducted in 2014. This complexity metric correlated with NPP at a nearby site (Gough et al. 2010) and others (Onaindia et al. 2004),

and describes both species richness and evenness where values closer to 1 indicate highest diversity (Morris et al. 2014).

2.3 fPAR Measurements

We quantified the fraction of photosynthetically active radiation absorbed by the canopy (fPAR) to determine whether light capture varied by age, disturbance history, and late successional functional forest type, and was related to forest structure and NPP. Instantaneous PAR was recorded in seven locations within each plot at 0m and 1m heights, using an AccuPAR LP-80 Ceptometer (Decagon Devices Inc., Pullman, Washington, USA). Coincident above-canopy PAR was inferred from nearby open-field measurements taken within 30 minutes of below-canopy PAR measurements, adjusted for solar angle and atmospheric conditions using the APOGEE Clear Sky Calculator parameterized with air temperature and relative humidity values measured from a nearby (within 10 km) meteorological tower, and unobstructed PAR. All measurements were taken between 10:30am and 2:30pm on clear days during late July to early August 2015. Mean fPAR was estimated as the ratio of concurrent below- and above-canopy PAR measurements.

2.5 Wood net primary production

To examine the forest primary production-structure relationships across age, disturbance type, and late successional forest functional type, we quantified stand annual wood NPP. In 2014, tree dendrometer bands were fitted within each plot to 10 to 20 % of trees with diameter at breast height (DBH) > 8 cm, including all dominant canopy species. DBH was recorded for each tree

with a dendrometer band in 2014 and 2015. Site-specific allometric equations were used to estimate wood mass from DBH, and to convert wood mass into kg C mass. NPPw was calculated as the kg C mass increment from 2014 to 2015 scaled to a hectare.

2.6 Light use efficiency

We quantified stand light use efficiency (LUE) to evaluate whether canopy structural measures affect how effectively absorbed light is used to drive primary production. LUE was calculated for each stand as the amount of net annual wood biomass production (as NPPw) divided by absorbed light (as fPAR). This method of calculation has been used previously at our site (Stuart-Haentjens et al. 2015) and is sensitive to changes in canopy structure (Hardiman 2013).

2.7 Statistical analysis

Our statistical approach examined whether canopy structural and primary production trajectories differed across disturbance history (via model fits over age) and across late successional forest functional type, and evaluated correspondence between canopy structural measures, fPAR and LUE, and primary production. Recognizing the non-linearity of canopy structural changes over time (Hardiman et al. 2013), we tested linear and curvilinear model fits; however, our model fitting procedure showed that a 3-parameter curvilinear model fitted to our small sample size (n = 4 plots/chronosequence) amounted to overfitting, with adjusted r^2 values consistently lower than that of the linear model. As a result, we present more conservative simple linear models. We first separately modeled changes over time in canopy structure and primary production for *Cut and Burn* and *Cut Only* chronosequences, statistically comparing slopes ($\alpha=0.05$) to test for

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different successional trajectories and combining plots from both chronosequences when slopes were not significantly different (p>0.05). Slopes were tested for significant difference from 0 at α=0.15. ANOVA with post-hoc LSD was used to compare the means of the three late successional functional types (ENF, MIX, DBF). Lastly, we conducted linear regression analyses incorporating all 11 plots to evaluate how generalizable relationships are between canopy structural measures, fPAR and LUE, and primary production across plots varying in age, disturbance history, and community composition.

3. Results

3.1 Canopy structural changes with age, disturbance, and canopy tree composition

Our results suggest that the successional development of canopy complexity in leaf arrangement, as expressed by rugosity, but not biological complexity or leaf quantity, was highly conserved regardless of pre-establishment disturbance history and late successional forest functional type. Over the course of ecosystem development, the physical complexity of the forest canopy, expressed as rugosity, followed a similar upward trajectory regardless of disturbance intensity (p=0.0001, adj. R^2=0.95; Fig. 2A), while leaf quantity as LAI and tree canopy diversity as Simpson's Index recovered more slowly following higher intensity disturbance prior to ecosystem establishment, with different model fits across chronosequence. Higher severity disturbance delayed the recovery of LAI and biodiversity. In the *Cut and Burn* chronosequence, LAI increased linearly (p=0.02, adj. R^2=0.93) and approached the higher values observed in the less intensively disturbed *Cut Only* plots several decades following stand initiation. This pattern of LAI over ecosystem development is in stark contrast to that observed in the *Cut Only*

chronosequence, which was stable across the age classes examined. Similarly, Simpson's Index of Diversity (SI) differed in recovery trajectories over time. SI was significantly lower in young *Cut and Burn* chronosequence plots relative to the *Cut Only* stands of similar age, suggesting a lag in the recovery of tree canopy diversity following more intense disturbance (Fig 2C).

Though the late successional functional types differed significantly in species diversity and LAI, all three stands converged on a strikingly similar stand-scale rugosity, suggesting conservation in the arrangement of vegetation across these three different late-successional ecosystems despite variation in dominant canopy species and leaf quantity. Canopy tree species diversity expressed as Simpsons' Index was significantly lower in the ENF late successional forest relative to both MIX and DBF, and LAI much higher in DBF (LAI=3.15) than in ENF (LAI=1.58) and MIX (LAI=1.77) forests (Fig 2B). Yet, the three stands had a similar mean stand rugosity value of ~26 m. Variances around this common stand-scale rugosity value were highest in the DBF forest, suggesting fine-scale (within-stand) variation in physical structure was greatest in the more species diverse, high LAI deciduous forest.

3.2 NPPw over successional development and correlation with canopy structure

Primary production changed with age similarly regardless of disturbance history; however, NPPw varied considerably among late successional forest functional types. Wood net primary production, NPPw, increased with stand age and followed a similar trajectory in older stands regardless of disturbance history even though model fits differed because of slightly offset stand age ranges represented in the two chronosquences (Fig. 3). *Cut Only* chronosequence NPPw increased linearly (p=0.06, adj. R^2=0.82; Fig. 3), with NPPw reaching a maximum of 1812 KgC

ha^{-1} yr^{-1} in the oldest century-old stand. *Cut and Burn* chronosequence stands followed a curvilinear rise to a maximum NPPw (p=0.1, adj. R^2=0.64; Fig. 3) approaching 1570 KgC ha^{-1} yr^{-1} in the oldest stand. In late successional stands, NPPw of DBF (2513 KgC ha^{-1} yr^{-1}) was significantly higher than that of MIX (763 KgC ha^{-1} yr^{-1}) and ENF (453 KgC ha^{-1} yr^{-1}) (Fig 3).

To examine whether canopy physical and biological structural attributes – shaped by disturbance history, succession, and tree species composition or functional type – are generalized predictors of NPPw, we modeled primary production for a number of stands as a function of rugosity, LAI, and Simpson's Index (Fig 4). Wood NPP was strongly correlated with LAI when all stands were included in a single linear model (p=0.001, adj. R^2=0.72; Fig 4B). Rugosity was a poor predictor of NPPw when all stands were included in the model, but was strongly correlated with NPPw when late successional ENF and MIX forests were excluded (p=0.0006, adj. R^2=0.81; Fig 4A). Simpson's Index of Diversity was a poor predictor of NPPw (Fig 4C).

3.3 Light capture and use-efficiency with age, disturbance, and composition (fig 5A-C)

Stand-scale light capture and light-use efficiencies varied depending on disturbance history and late successional functional type. Ground measurements of fPAR did not differ significantly with disturbance history or among late successional stands (Fig. 5A). However, at the 1m level above the herbaceous layer, successional trajectories of fPAR diverged, with the *Cut Only* stands following a positive linear trend with age (p=0.068, adj. R^2=0.80; Fig. 5B) and the more disturbed *Cut and Burn* stands exhibiting no significant trend with age. fPAR at 1m was significantly higher in the late successional DBF stand than in either MIX or ENF, with light

capture in the former approaching 97% of incoming PAR one meter above the forest floor (Fig. 5A-B).

Successional changes in stand light-use efficiency (LUE, as $NPPw/fPAR_0$) varied between the two chronosequences, though values in older forests were similar (Fig. 5C). Stand LUE varied from ~1500-1950 KgC ha^{-1} yr^{-1}, with the exception of very low LUE in the youngest, 16-yr-old *Cut and Burn* stand (890 KgC ha^{-1} yr^{-1}, Fig. 5C). LUE was markedly different across all three late successional forest functional types, with DBF (2568 KgC ha^{-1} yr^{-1}) far exceeding both the MIX (844 KgC ha^{-1} yr^{-1}) and ENF (496 KgC ha^{-1} yr^{-1}) stands (Fig. 5C).

3.4 Light resource availability and utility relative to canopy structural complexity as LAI and rugosity (fig 6A-D)

We combined all stands in a final analysis to explore whether fPAR and LUE link leaf arrangement and quantity with NPPw across the array of ecosystem structures shaped by successional stage, disturbance history, and community composition; we excluded canopy tree diversity from our analysis because it was not significantly correlated with NPPw. With increasing stand rugosity and LAI, light absorption as fPAR followed similar positive linear trends (Fig. 6; adj. R^2=0.32, p=0.039; adj. R^2=0.29, p=0.049). LUE increased linearly with LAI (adj. R^2=0.59, p=0.004; Fig. 6D), whereas rugosity was only significantly correlated with LUE (adj. R^2=0.74, p=0.002; Fig 6C) when MIX and ENF stands were excluded from the regression analysis.

4. Discussion

We have shown that our multiple measures of ecosystem biological and physical structure diverged during ecosystem development, in response to disturbance, and across late successional functional types, with implications for how light is captured, distributed and used to drive NPP. Ecosystem physical complexity, expressed as rugosity, exhibited a strikingly conserved successional trajectory, increasing with forest age and then plateauing to a common value in late successional stands, regardless of disturbance history and late successional canopy composition, suggesting a highly constrained trajectory in the assembly of stand-scale physical complexity. However, canopy leaf quantity, as LAI, and biological diversity, as Simpson's Index, varied substantially following stand establishment depending on prior disturbance history and late successional functional type. We found that differences among forest stands in wood NPP were mediated, in part, by physical structure- and leaf quantity-driven variation in light acquisition and use-efficiency. However, canopy physical complexity and, to a lesser extent, LAI were poor predictors of light-use efficiency in pine-dominated late-successional ecosystems, indicating that the ecosystem structural parameters we examined did not fully capture processes underlying NPP across functional types. Nonetheless, across structurally variable deciduous forest stands, leaf quantity and arrangement contained important complementary, and not fully redundant, mechanistic information tied to primary production.

The divergence of biological and physical structure following variable disturbance severities and among forest functional types is consistent with theoretical expectations and prior empirical observations, with the notable exception of decoupled physical and biological structure in late successional stands. In our study, leaf quantity and recovery of biological structure in the more severely disturbed *Cut and Burn* chronosequence lagged behind that of the less severely

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disturbed *Cut Only* chronosequence, while leaf arrangement or physical complexity changed uniformly over succession regardless of disturbance history. The former is consistent with studies showing disturbance history affects trajectories of community assembly and LAI (Frelich and Reich 1999, Nakashizuka 2001, Ruprecht et al. 2007, Zhang et al. 2009). At our site, greater fire-related losses of nitrogen in the *Cut and Burn* stand (White et al. 2004, Gough et al. 2007) likely stunted leaf production and plant community recovery without altering successional changes in leaf arrangement. Contrary to theory linking physical and biological structure (e.g., Ishii et al. 2003), late successional functional types converged on a similar mean stand rugosity, or physical complexity, despite having substantial differences in community composition and even though pine dominated stands had much lower LAI values. From a theoretical standpoint, the decoupling of the physical and biological structural complexity at our site is surprising because it suggests that the successional trajectory in ecosystem physical structure was independent of tree architectural variation presumably afforded by a greater variety of species, captured in Simpson's Index, and the quantity of plant canopy materials, in LAI, available to build physical complexity. While it would be expected for structural metrics and biodiversity to be closely coupled (Ishii et al. 2004), other studies find that metrics of physical structural diversity tend to outperform species diversity alone in impacting forest function as productivity (Danescu 2016).

A fixed successional trajectory of physical complexity, coupled within functional type to fPAR and LUE, suggests that leaf arrangement, irrespective of biological complexity, may have developed to optimize resource capture and use-efficiency to maximize productivity, a purpose which is mechanistically similar to the increased resource acquisition potential during community assembly. Though findings are mixed, several studies suggest plant communities,

including forests, assemble to maximize resource extraction in support of growth (Li and Waller 2016). However, numerous monospecific crop studies show that variation in physical complexity alone can drive substantial differences in light allocation and canopy physiology, LUE, and therefore production (Long et al. 2006, Shiratsuchi et al. 2006, Sarlikioti et al. 2011, Gitelson et al. 2015). Moreover, forest optimization modeling and theory suggest that physical structure, independent of biological diversity, affects LUE and canopy C fixation (Niinemets 2012, Retkute et al. 2015, Niinemets 2016). Our findings suggest that, with respect to C cycling processes, ecosystem assembly theoretical and empirical studies should consider how physical complexity, both alone and with biological complexity, affects resource use. However, that we did not observe a relationship between biological diversity and wood NPP does not dismiss community structure's role in constraining primary production, which may not have emerged as a significant predictor of wood NPP at our site because of the low range of biological complexity across stands (richness = 4 to 8). Moreover, functional diversity, rather than indexes of biological diversity such as Simpson's Index, may be superior indicators of C cycling processes as observed in studies of species richness and functional diversity in grassland systems (Tilman et al. 1997).

Similar to other studies (e.g., Reich 2012), leaf quantity, as LAI, was tightly coupled with wood NPP through its effects on light acquisition and use. Rugosity was an even stronger predictor of wood NPP than LAI across the DBF-only successional continuum, but the strength of this relationship did not persist when late successional MIX and ENF were included in the analysis. These findings are important because they indicate that leaf quantity and arrangement both contain relevant, but also not entirely comprehensive, functional information linking canopy structure with primary production. LAI is known to be tightly linked with productivity as a

representation of the ability of the forest to capture light (Reich 2012), but previous work at our site indicates that LAI may reach a saturation point before other attributes of physical structure, such as leaf arrangement (Hardiman et al. 2013). At odds with some, but not all, prior observations, biological structure, as SI, was not a significant predictor of NPP (Pedro et al. 2015, Liang et al. 2016). However, this study is over a gradient of ages at one boreal-temperate cusp site and does not consider regional trends in the biodiversity-NPP relationship necessarily.

These findings argue for a nuanced revision of prior theoretical, modeling, and observational work from multiple sub-disciplines in ecology showing that light capture and use-efficiency are key mechanisms linking ecosystem structure and C cycling function. Ecosystem and physiological ecologists have long-held LAI as a superior structural indicator of primary production (Asner et al. 2003, Reich 2012) while more recently theorizing and modeling the importance of physical arrangement to optimizing resource capture and efficiency (Parker et al. 2004, Hardiman et al. 2013). In a separate, but mechanistically similarly grounded, discussion among primarily community ecologists regarding the role of biological structure and resource use and acquisition, several studies established the connection between biological diversity (Pedro et al. 2015, Liang et al. 2016) or community composition (Tilman et al.1997) and C cycling processes at leaf to ecosystem scales. We suggest that these studies, rooted in different ecological subdisciplines, assume a similar mechanistic basis for structure-C cycling relationships: greater complexity yields higher growth-limiting resource acquisition. The conceptualizations of structure as LAI, community composition, biological diversity, or canopy structural arrangement are useful and not fully redundant in relation to C cycling function across a range of forest stands.

5. Conclusions

Multiple expressions of physical structure are important to predicting C cycling processes, and the way structure is conceptualized matters. Our findings suggest that physical complexity develops to optimize resource acquisition and use-efficiency, regardless of the quantity of building blocks (i.e., leaves) and variability in crown architecture (i.e., reflected in biodiversity). Leaf arrangement is a strong correlate of NPP within a functional type (DBF); LAI is moderately correlated with NPP across forest functional types; and biodiversity, at our site, was not a strong correlate. These differences indicate a need to elucidate the interactions between these multiple expressions of ecosystem structure related to NPP, especially across and within other forest functional types. Even using a functional type division across our late successional plots, we found these categories too broad. The difference between DBF and even MIX forests in our stands had different relationships of structure-function and therefore NPP trends. Measures of actual functional diversity as it relates to limited resource use would be more useful than measures such as Simpson's Index, which are often used as a proxy. Both leaf quantity and arrangement are functionally meaningful measurements of forest structure because they have relevance to some mechanism of light resource capture and use. However, leaf arrangement as rugosity works best in the functional type in which it was developed, and may not be as applicable to other forest types. There are multiple conceptualizations of structure-function relationships, originating in various subdiscipline-specific concepts for productivity, that relate physical structure broadly to productivity via increased resource use acquisition and efficiency in more heterogeneous or structurally complex systems. These different structure concepts are not totally redundant and contain information relevant to C cycling processes. Future work must explore the impacts on function as productivity when physical structural traits are decoupled.

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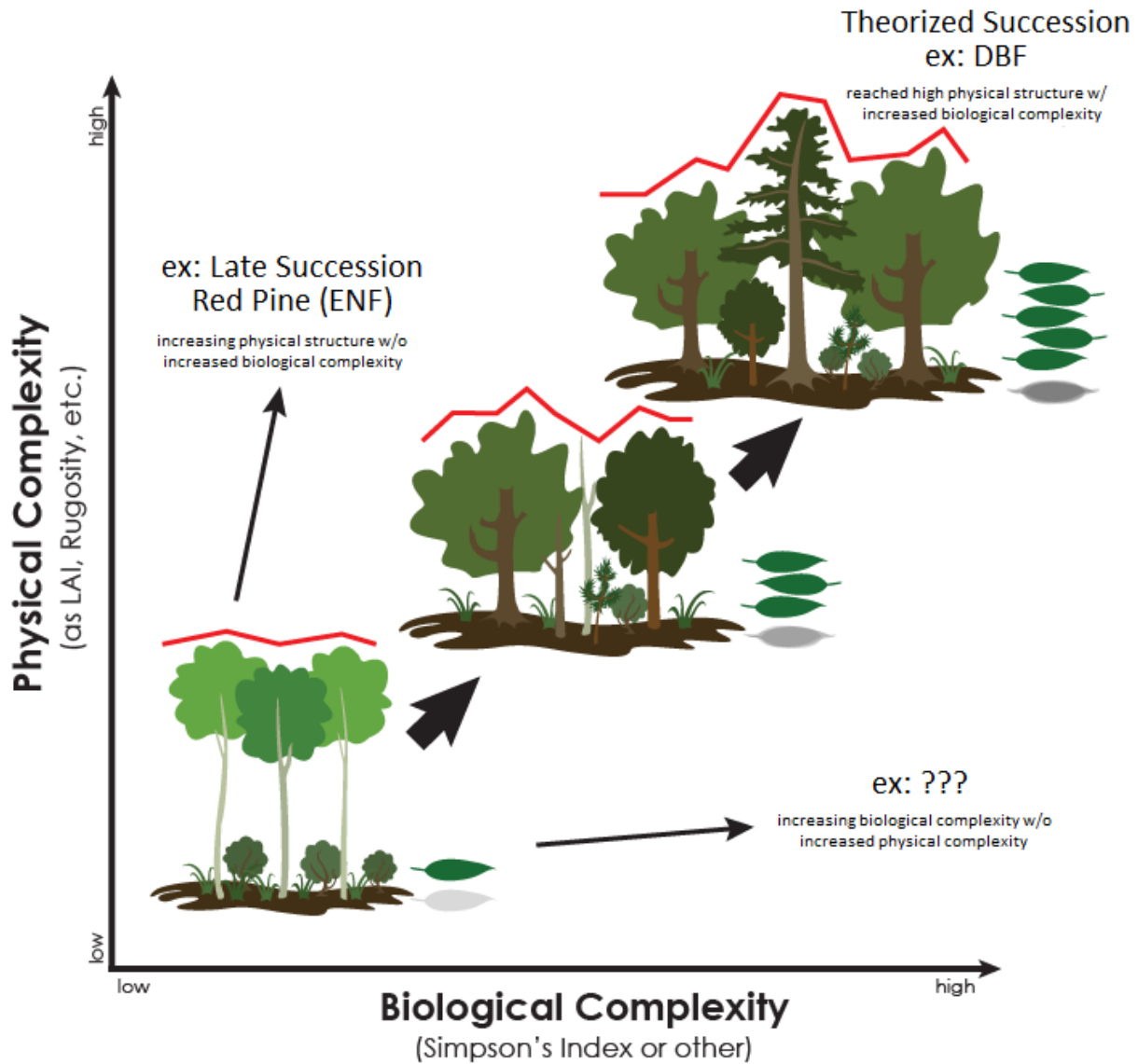
**Figure 1. Theoretical successional trajectories of biological and physical development in forests.** An example deciduous broadleaf forest is shown. Development of biological and physical complexity tends to, though may not always, be coupled over the course of succession, with disconnects potentially leading to different NPP or resource use abilities. Disturbance events may slow temporal progression towards complexity on either axis.
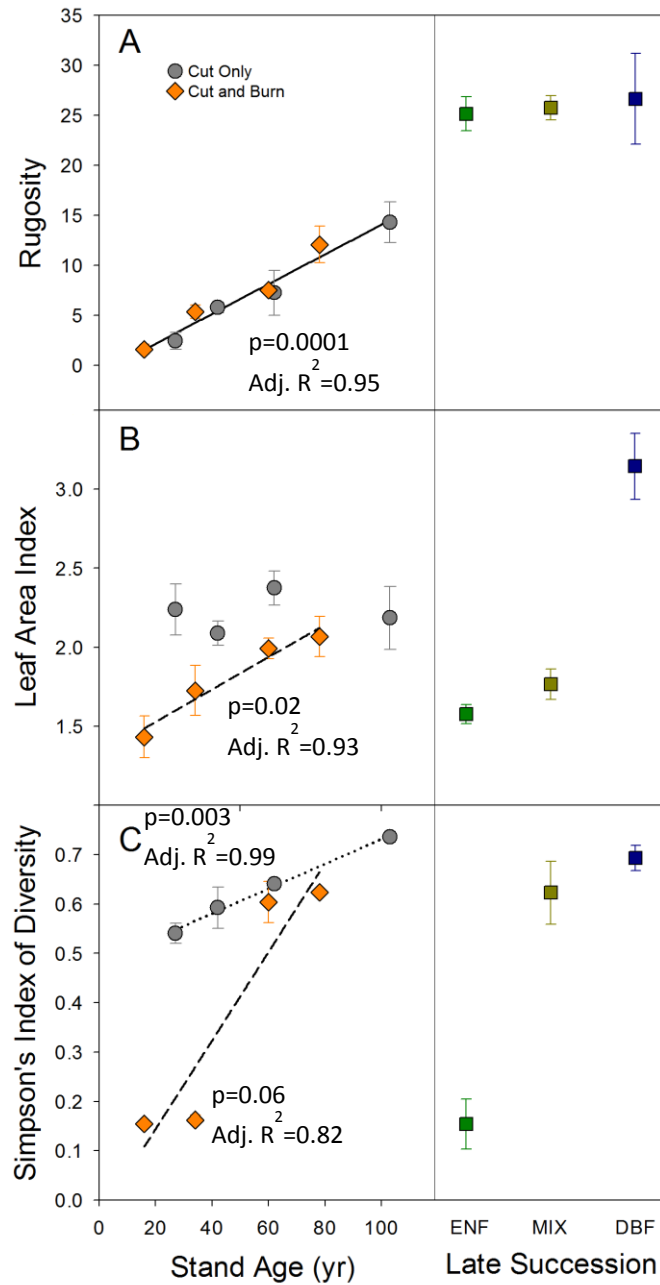
Figure 2. Rugosity (A), Leaf Area Index, and Simpson's Index of Diversity over ecosystem development and in late successional forest stands. The *Cut Only* (circles, dot line) chronosequence was clear-cut harvested prior to regrowth and the *Cut and Burn* (diamonds, dash line) chronosequence clear-cut harvested and burned. Solid line indicates plots combined in model. Means ± 95% CI.
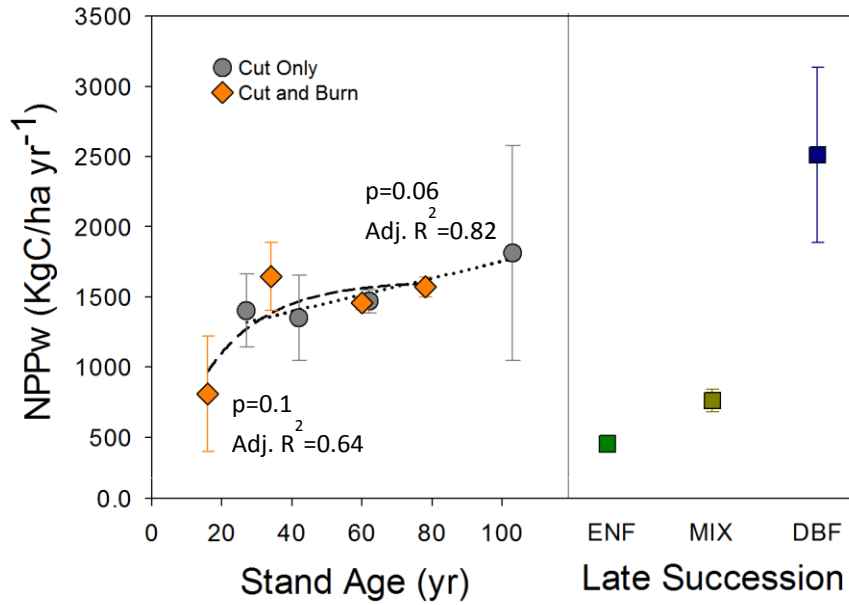
Figure 3. Annual Net Primary Production (NPPw) over successional age and late successional community composition. The *Cut Only* (circles, dot line) and *Cut and Burn* (diamonds, dash line) span early to mid-successional development. Late succession stands indicated with squares. Means ± 95% CI.
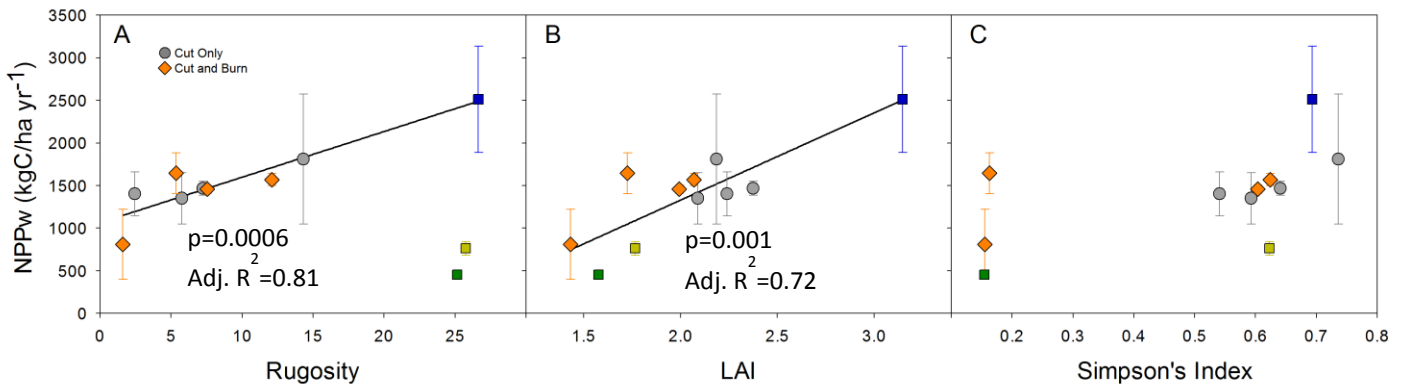
Figure 4. Physical and biological structure relative to NPPw in all stands. (A) Linear modelling of LAI-Rugosity relationship using all DBF plots, excluding pine-dominated ENF and MIX (B) Linear modeling of LAI-NPPw using all plots. Means ± 95% CI.
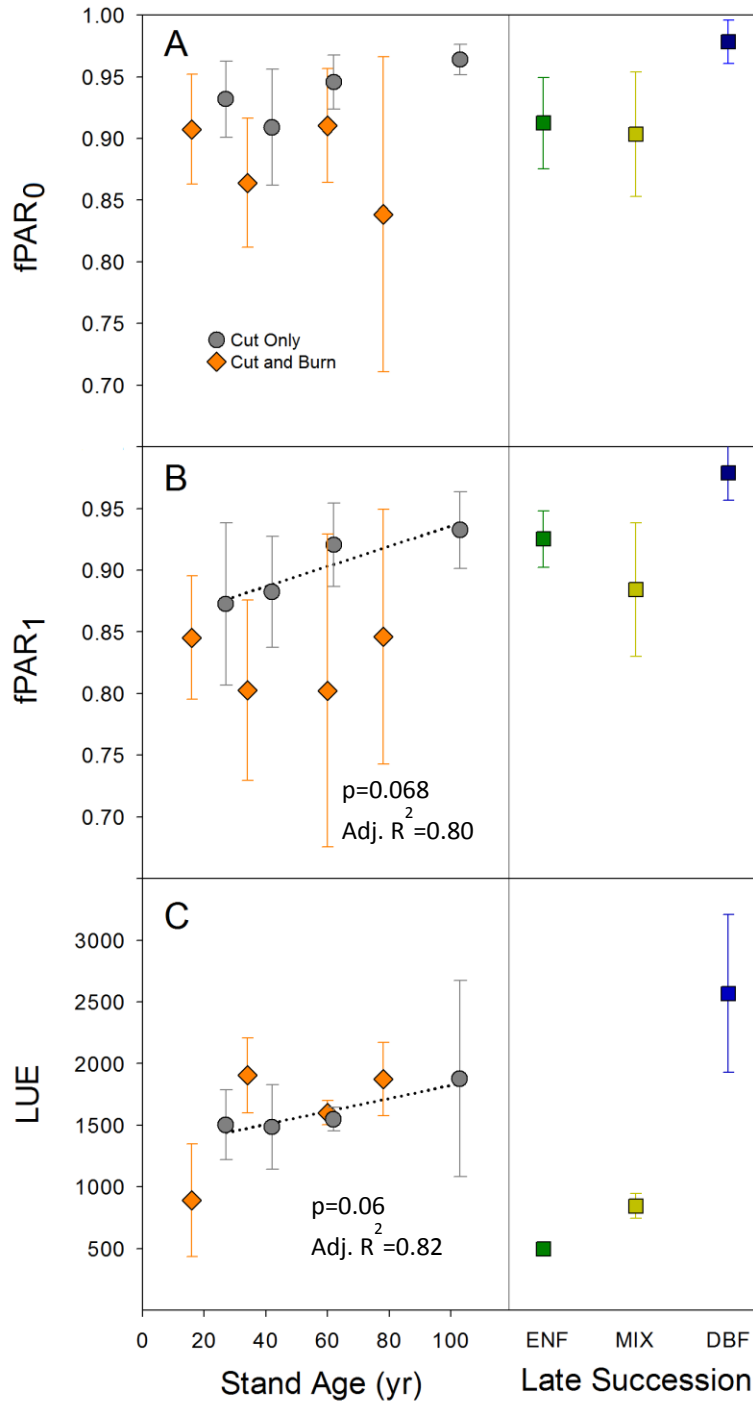
Figure 5. Light resource distribution and utilization over ecosystem development and successional community composition. Light resources expressed as full canopy fPAR from 0m measures ($fPAR_0$), canopy fPAR excluding herbaceous layer from 1m measures ($fPAR_1$), and light use efficiency (LUE). The *Cut Only* chronosequence (circles, dot line) and the *Cut and Burn* chronosequence differ in stand initiating disturbance intensity. Late succession stands vary in community composition. Means ± 95% CI.
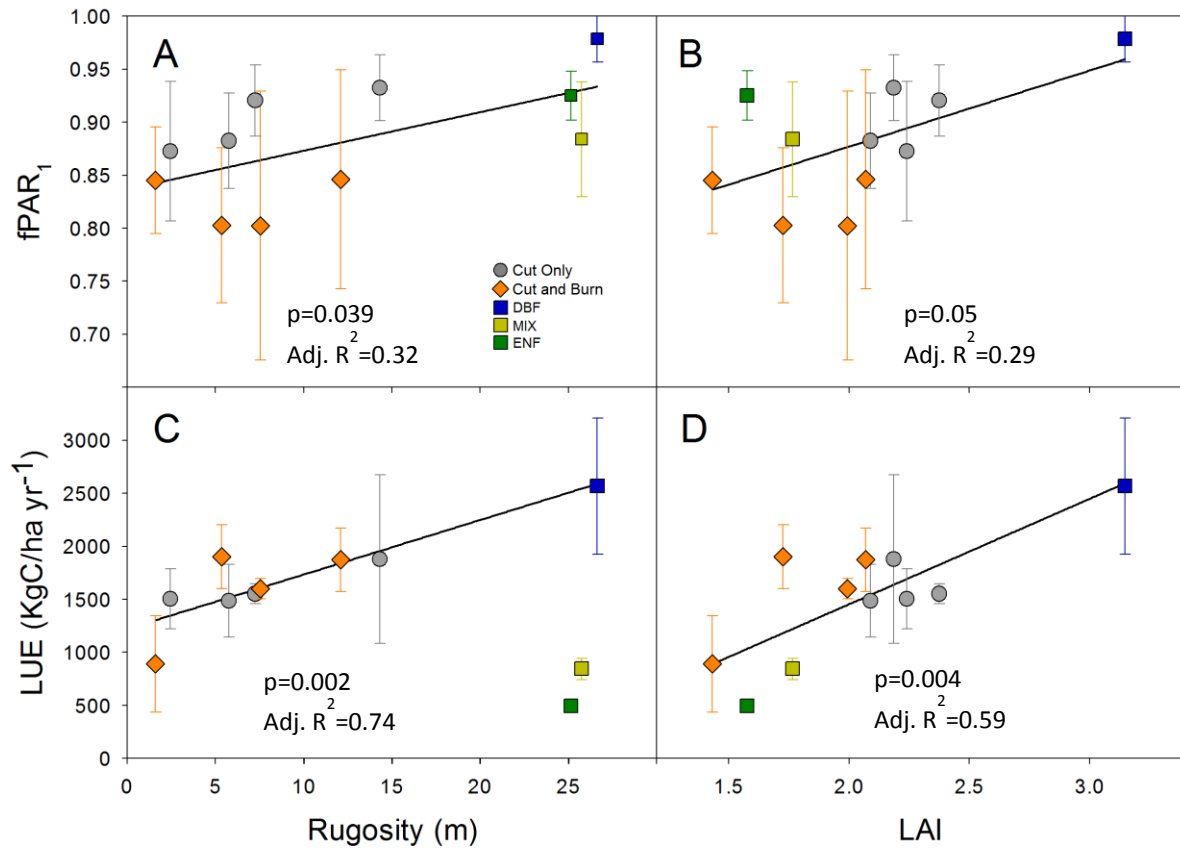
Figure 6. Light resource distribution and utilization efficiency as related to canopy structural measures rugosity and leaf area index (LAI). Light resources expressed as canopy fPAR excluding herbaceous layer (fPAR$_1$) and light use efficiency (LUE). (A-B, D) All stand types are combined in linear modelling. (C) Linear modelling of LAI-Rugosity relationship using all deciduous broadleaf plots, excluding pine-dominated ENF and MIX.

Table 1. Summary characteristics of 11 forest stands comprising two chronosequences and three late successional communities. Stand origin determined based on known establishment dates or tree cores. Dominant taxa in parenthesis indicate species of similar abundance but not dominant in crown position. POGR=*Populus grandidentata*, QURU= *Quercus rubra*, ACRU= *Acer rubrum*, PIST= *Pinus strobus*, PIRE= *Pinus resinosa*, BEPA= *Betula papyrifera*, FAGR= *Fagus grandifolia*, TSCA= *Tsuga canadensis*

Stand history		Landform		Soil	Forest cover (trees >8 cm DBH)		
Origin	Disturbance history	Parent material	Topography	Texture and classification	Stems ha^{-1}	Mean DBH	Dominant taxa
1998	*Cut and Burn*	outwash deposits	high-level plain	sandy Haplorthod	725	9.2	POGR (QURU)
1987	*Cut Only*	lake-modified outwash deposits	high-level plain	sandy Haplorthod	1523	10.6	POGR (QURU/ACRU)
1980	*Cut and Burn*	outwash deposits	high-level plain	sandy Haplorthod	1597	11.4	POGR (QURU/ACRU)
1972	*Cut Only*	outwash deposits	high-level plain	sandy Haplorthod	1960	12.5	POGR (QURU/ACRU)
1954	*Cut and Burn*	outwash deposits	high-level plain	sandy Haplorthod	1355	14.1	POGR, QURU (PIST)
1952	*Cut Only*	outwash deposits	high-level plain	sandy Haplorthod	1090	16.6	QURU (PIST/POGR)
1936	*Cut and Burn*	outwash deposits	high-level plain	sandy Haplorthod	1335	17.1	POGR (PIST, ACRU)
1911	*Cut Only*	lake-modified outwash deposits	high-level plain	sandy Haplorthod	793	21	POGR (QURU/PIST)
ENF/ 1885	Late successional community	lake-modified outwash deposits	low-level plain	sandy over gravelly Haplorthod	753	28.8	PIRE (PIST/BEPA)
MIX/ 1885	Late successional community	lake-modified outwash deposits	high-level plain	sandy Haplorthod	657	26.8	PIRE (POGR/PIST)
DBF/ 1850	Late successional community	lake-modified outwash deposits over till	gently sloping moraine	sandy over loamy Haplorthod	433	34	FAGR, TSCA, QURU, ACRU

Table 2. Model reporting. Details of best fit linear and curvilinear models (exponential rise to maximum). *Cut Only* and *Cut and Burn* models were combined if slope and intercept did not differ significantly. RUG= rugosity, LAI= leaf area index, SI= Simpson's Index, NPP= wood net primary production, fPAR= fraction photosynthetically active radiation utilized (top of canopy to 0m or 1m), LUE= light use efficiency.

model	plots	type	equation	p-value	Adj. r-sq.
RUG-age	*Cut and Burn*	linear	y= -0.6960+0.1562x	0.0196	0.9416
RUG-age	*Cut Only*	linear	y= 1.3525+0.1503x	0.0084	0.9749
RUG-age	*Combined*	linear	y= -0.8116+0.1489x	0.0001	0.9538
LAI-age	*Cut and Burn*	linear	y= 1.3219+0.0103x	0.0242	0.9283
LAI-age	*Cut Only*	linear	-	0.9510	-
SI-age	*Cut and Burn*	linear	y= 0.4805+0.0025x	0.0032	0.9903
SI-age	*Cut Only*	linear	y= -0.0353+0.009x	0.0635	0.8157
NPP-age	*Cut and Burn*	curvilinear	$y= 1614.1947(1-0.0574^x)$	0.10	0.64
NPP-age	*Cut Only*	linear	y= 1161.4184+5.9270x	0.06	0.82
NPP-RUG	*DBF Combined*	linear	y= 1064.4950+53.5813x	0.0006	0.8125
NPP-LAI	*All Combined*	linear	y= -719.7694+1025.0343x	0.001	0.7179
NPP-SI	*All Combined*	linear	y= 690.3086+1384.5898x	0.0733	0.2371
$fPAR_0$-age	*Cut and Burn*	linear	y= 0.912-0.0007x	0.4657	-0.0717
$fPAR_0$-age	*Cut Only*	linear	y= 0.9044+0.0006x	0.1910	0.4817

fPAR$_1$-age	*Cut and Burn*	linear	-	0.9909	-
fPAR$_1$-age	*Cut Only*	linear	y= 0.8541+0.0008x	0.0679	0.8033
LUE-age	*Cut and Burn*	curvilinear	-	0.1509	0.5815
LUE-age	*Cut Only*	linear	-	0.0606	0.8237
fPAR$_1$-RUG	*All Combined*	linear	y= 0.8369+0.0036x	0.0394	0.3242
fPAR$_1$-LAI	*All Combined*	linear	y= 0.7338+0.0717x	0.0498	0.2923
LUE-RUG	*DBF Combined*	linear	y= 1221.2819+51.4395x	0.0018	0.7391
LUE-LAI	*All Combined*	linear	y= -534.7807+995.0904x	0.0037	0.5853

Vita

      Cynthia M Scheuermann was born February 2, 1991 in Alexandria, Virginia. They graduated from West Potomac High School, Alexandria, Virginia in 2009. Following the completion of their Bachelor of Science in Biology from Virginia Commonwealth University, they continued on to join the VCU Forest Ecology lab group headed by Dr. Chris Gough as a field assistant, and then a graduate student. They have spent four summer research seasons at the University of Michigan Biological Station during this time and considers themself both a Virginian and a Michigander.