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MODERATE SEVERITY DISTURBANCE HAS SIMILAR EFFECTS ON THE PRODUCTION OF THREE FORESTS NESTED WITHIN THE UPPER GREAT LAKES LANDSCAPE

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A thesis submitted to fulfill the requirements for the degree of Master of Science at Virginia Commonwealth University

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Acknowledgements

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Abstract

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Moderate severity disturbances, which only kill a subset of canopy trees (e.g., via insects, pathogens, and windthrow), are increasingly widespread, and can alter forest structure and production. Whether moderate severity disturbance similarly affects the net primary production (NPP) of different forest stands within inherently heterogeneous landscapes, however, is unknown. We experimentally disturbed three, 2-ha stands varying in forest structure and primary production, reducing stand basal area 38 to 66 % by stem girdling all mature early successional aspen (*Populus*) and birch (*Betula*). For nearly a decade, we examined how the forest stands restructured and recovered, and linked post-recovery physical and biological structure with light absorption and wood NPP. Disturbance significantly altered the structure of all stands and prompted a similar decade-long pattern of primary production decline and recovery. All stands exhibited an initial reduction in wood NPP, recovering to, or exceeded pre-disturbance levels within eight years. Following the recovery of wood NPP, more biologically diverse forest canopies with higher leaf area indexes captured more light, and, subsequently, had higher rates of wood NPP. We provide limited support that disturbance may enhance long-term primary production through its effects on canopy structural reorganization. We conclude that, while the forests examined responded similarly to disturbance, improved understanding of different forest ecosystems' response to disturbance remains critical to informing carbon management decisions across diverse landscape mosaics.

Introduction

As the world's largest terrestrial carbon (C) sink, forests collectively reduce atmospheric CO_2 and have the potential to lessen climate change by capturing an estimated 2.3±0.4 Pg C yr^{-1} through photosynthetic uptake and subsequent plant biomass accumulation (Pan et al. 2011). Forest net primary production (NPP), a measure of C accumulation in plant biomass, varies considerably across (Goodale et al. 2002; Pan et al. 2011; Pregitzer and Euskirchen, 2004) and within (Pan et al. 2011; Mckinley et al. 2011; Williams et al. 2012) forested landscapes, largely because of heterogeneously distributed disturbances, which occur along a continuum of severity (Gough et al. 2007; Hicke et al. 2012; Flower et al. 2015). While generalized patterns of NPP decline and recovery following severe, stand-replacing disturbance are well understood (Kashian et al. 2006; Gough et al. 2007; Amiro et al. 2010), less is known about how NPP is affected by moderate severity disturbances, such as extreme weather, insects, and pathogens, which kill a fraction of canopy trees. These moderate disturbances are increasing in frequency and extent globally (Dale et al. 2001; Amrio et al. 2010; Cohen et al. 2016), limiting forecasts of the global carbon budget (Pan et al. 2011; Goetz et al. 2012; Bond-Lamberty et al. 2015; Xiao et al. 2016).

Responses of NPP to disturbance may vary within large forest landscapes because of spatial variation in stand age, site conditions, physical structure, and community composition (Skovsgaard et al. 2009; Amiro et al. 2010; Reich, 2012; Peters et al. 2013; Hardiman et al. 2013a). Skovsgaard et al. (2009) demonstrated that site productivity can vary substantially among seemly homogenous stands, and that the variability in site conditions prior to disturbance can strongly influence how growth was affected by forest thinnings. Measures of physical canopy structural complexity have shown to correlate with gas exchange, light capture and use, and ultimately, productivity (Ishii et al. 2004; Parker et al. 2004; Hardiman et al. 2011; Reich,

2012), and may affect disturbance recovery dynamics (Gough et al. 2016). Recent findings from Upper Great lakes forests revealed that diversity (Gough et al. 2010; Scheuermann et al. in review), subcanopy growth (Stuart-Haëntjens et al. 2015; Fahey et al. 2016) and the distribution of leaves and stems (Hardiman et al. 2011; Hardiman et al. 2013b; Scheuermann et al. in review) drive primary production in forests experiencing tree mortality caused by succession and disturbance. Other sites have also found that plant community composition, including diversity, can be an important factor influencing NPP, with higher diversity driving rates of production resilience following disturbance (Reinikainen et al. 2014; Pedro et al. 2015; Metz et al. 2016; Danescu et al. 2016). It has recently been proposed that new growth stimulated by tree morality may lead to changes in physical and biological structure that enhance forest structural complexity and, in turn, productivity (Gough et al. 2016). Though some of these relationships have been investigated at the landscape scale, few studies have focused on how stands that vary in local site conditions, physical structure, and composition respond to moderate disturbance, yet this knowledge could reduce C forecasting and modeling uncertainty.

Here, we evaluated whether forest stands differing in pre-disturbance canopy composition and productivity respond similarly to moderate severity disturbance, and we examined relationships between wood NPP and canopy structure following disturbance recovery. Our work builds on findings from an experimental manipulation of an Upper Great Lakes forest landscape showing landscape-scale forest production was highly resistant to moderate severity disturbance (Nave et al. 2011; Gough et al. 2013; Stuart-Haëntjens et al. 2015). Our specific objectives were to: (Obj. 1) evaluate whether stands differing in pre-disturbance productivity and composition follow similar patterns of restructuring and wood NPP recovery following a moderate severity disturbance; (Obj. 2) Following restructuring and the recovery of wood NPP,

we aim to link several measures of ecosystem structure to resource capture and wood NPP across these stands.

Methods

Study Site and Experimental Design

We conducted our research at the University of Michigan Biological Station (UMBS) in northern lower Michigan, USA (45.56° N, -84.71° W). The region, comprised mainly of secondary mixed temperate forests, has a mean annual temperature of 5.5°C and a mean annual precipitation of 817 mm (Gough et al. 2013). Extensive clear-cutting and fire in the late 19th and early 20th centuries reset the ecological succession of forests, abruptly transitioning late successional white pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*) forests to forests dominated by early successional aspen (*Populus spp.*) and birch (*Betula papyrifera*). A century later, as early successional canopy species begin to senesce, red maple (*Acer rubrum*), red oak (*Quercus rubrum*), American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), ash (*Fraxinus spp.*) black cherry (*Prunus serotina*), white pine (*Pinus strobus*), serviceberry (*Amelanchier spp.*), and striped maple (*Acer pensylvanicum*) are emerging as dominant tree species (Gough et al. 2007; Fahey et al. 2016).

With advancing mortality of aspen and birch occurring region-wide, our study centers on an ecosystem-scale manipulation of moderate severity disturbance designed to evaluate changes in forest structure and C cycling dynamics following the mortality of early successional tree species. The Forest Accelerated Successional ExperimenT (FASET), in which all mature aspen and birch trees were stem girdled and retained onsite in 2008, was implemented in a single 33-ha landscape and is the focus of all prior studies (Nave et al. 2011; Gough et al. 2013; Hardiman et al. 2013a, Stuart-Haëntjens et al. 2015; Fahey et al. 2016). Our study focused on three separate

2-ha stands with total basal area reductions from aspen and birch mortality of 36 to 68% (Table 1), a degree of disturbance severity is similar that from insect pests and windthrow (Amrio et al. 2010; Hicke et al. 2012; Flower et al. 2013). The 2-ha treatment stands span a representative range of Upper Great Lakes deciduous forest stands, and are hereafter are referred to as HIGH, MED or LOW, referencing their variability in primary production, ecosystem structure, and micro-environment (Table 1). Measurements were conducted in one to three 0.08-ha sampling plots per stand depending on the year and measurement (Figure 1).

Core long-term measurements in the 2-ha treatment stands included wood net primary production (NPPw) and leaf area index (LAI), which began in 1997 and were repeated through multiple periods of disturbance and recovery. We defined the periods as follows: 1) *pre-disturbance*, the period prior to the 2008 experimental disturbance; 2) *disturbance*, the period during which statistically significant declines in LAI and NPPw were observed, relative to pre-disturbance; 3) *post-disturbance and recovery* (2011-2015), the period in which LAI and NPPw were recovering to pre-disturbance levels; and 4) *post-recovery* (2016), when all stands were no longer statistically significant from, or significantly exceeded, pre-disturbance LAI and NPPw values (Figure 2). Because our study includes a synthesis of long-term data collected prior to the disturbance experiment, the number and frequency of measurements varies across time. We considered plots within a stand the unit of replication and, while acknowledging the lack of consistent treatment replication, this 2-decade long dataset offers a valuable long-term perspective of forest structure and C cycling dynamics. Our approach is methodologically aligned with other long-term ecosystem manipulations and observational studies (e.g. C flux towers), where treatment replication is not practical (Gough et al. 2010; Davies and Grey, 2015).

Litter Trap Leaf Area Index

Leaf area index (LAI) was quantified beginning in 1997 from litter traps, serving as a primary measure of changes in forest canopy structure during all periods of disturbance and recovery. Litter trap distribution and sample size varied substantially over the 20-year collection period, with leaf litter collected annually from two or three litter traps (0.264 m^2) placed in one to three plots per stand. Specifically, from 1997-2001 and again in 2014-2015, litter was collected in one plot per stand, with each plot containing three litter traps. A felled tree in 2015 reduced the litter trap sample size by one in the HIGH stand. From 2006-2013 and in 2016, litter was collected in all nine sampling plots, with two or three litter traps per plot, and, with the exception of 2016, dried litter was pooled by stand prior to weighing (hence within-stand variation could not calculated). Litter, collected weekly in autumn and monthly otherwise, was dried at 60°C, separated by species, and weighed. Leaf area index is calculated as the product of litter fall dry mass and site-specific specific leaf area values (Gough et al. 2013).

Wood Net Primary Production, Wood Mass, and Stem Density

We quantified annual canopy and subcanopy aboveground wood net primary production (NPPw), the annual accumulation of aboveground woody growth, for nearly two decades to track how disturbance affects long-term forest production. The diameter at breast height (DBH) was recorded for all canopy trees (≥ 8 cm DBH) in 1997 (LOW and HIGH, n=1 plot per stand); 1998 (MED, n=1 plot); 2001 (All, n=1 plot per stand); 2006 (All, n=2 plots per stand); 2010 (All, n=3 plots per stand); 2015 (All, n=3 plots per stand); and 2016 (All, n=3 plots per stand). We tallied subcanopy stems (< 8 cm DBH) by species and diameter class (<2 cm, 2–3.9 cm, 4–5.9 cm, or 6–7.9 cm) in 1998 (All, n=1 plot per stand); 2001 (All, n=1 plots per stand); 2006 (All, n=2 plots per stand); 2010 (All, n=1 plot per stand) and 2016 (All, n=3 plots per stand). We surveyed the

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entire plot area in 1998, 2001, 2006, and 2010, and in five non-overlapping 5 m radius subplots

located in each plot (49% of the whole plot area) in 2016. We used an increment hammer to

collect outer xylem cores for a subset (≥20%) of surveyed subcanopy trees in the 4-5.9 and 6-7.9

cm DBH class in each plot during the summer of 2016. Annual stem growth increments were

measured to 0.001 mm using a Velmex stage micrometer (Bloomfield, NY), and a mean

increment growth time-series was constructed for each plot and DBH class. We estimated the

number of trees in each DBH class in a given year by interpolating plot-level changes in tree

stem density between census years, in which all trees were inventoried. We used the midpoint

DBH of each diameter class for wood mass estimates. Canopy and subcanopy NPPw were

derived at the plot-level from the annual increment growth of aboveground live wood, using site

and species-specific (canopy) or softwood/hardwood-specific (subcanopy) allometric equations

relating DBH to wood mass. Absolute wood mass was converted to carbon mass using a site-

specific conversion factor of 0.48 g of C g^{-1} of dry wood mass (Gough et al. 2013).

Post-Recovery Canopy Structure

We derived a suite of ecosystem structural parameters during 2016 to evaluate how post-

recovery structure relates to canopy light capture and wood NPP. We characterized canopy

structural complexity in 2016 from data collected by a ground-based Portable Canopy LiDAR

(PCL) that quantified the physical arrangement of leaves above 1m from the forest floor (Parker

et al. 2004; Hardiman et al. 2011; Hardiman et al. 2013a). The application of this approach, used

previously at our site, is detailed in Hardiman et al. 2011. Briefly, we collected PCL data along a

40 m transect passing through the center of each plot to create a 2D canopy hit-map. Raw

LiDAR data was processed using published MATLAB code. We report rugosity (the variance in

the horizontal and vertical vegetation hits) and top rugosity (the variability of outer canopy

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surface height)— canopy structural complexity measures shown to relate to primary production

at our site (Hardiman et al. 2011, 2013b; Fahey et al. 2015; Scheuermann et al. in review).

We derived tree diversity values for each plot using basal area and species count data

from a 2016 census, and compared these pre-disturbance values derived from 2001 or 2006

census data. We expressed tree diversity as Shannon's Diversity Index (H') for the subcanopy

(<8 cm DBH), canopy ($\geq$ 8 cm DBH) and combined (canopy and subcanopy). We chose H'

because it has recently been used at our site (Fahey et al. 2016), and is a very common metrics

that combines both the evenness and richness of a site into one measure (Hill, 1973; Gorelick,

2006), and does not favor dominant or rare species like Simpson's Diversity Index (Magurran,

1988; Liang et al. 2007).

We used hemispherical imaging to characterize vertical LAI (LAI_h) profiles in 2016.

Images were taken at the center of five non-overlapping subplots located within each sampling

plot under homogenously diffuse sky conditions at ground level, 2 m, 4 m, 6 m, 8 m, and 10 m

vertical heights using a telescoping pole, a camera leveled by a gimbal, and a 180° fisheye lens

facing skyward. We used ImageJ software (Schneider et al. 2012) to split images into red, green

and blue components, and to obtain threshold values by applying the *minimum* algorithm on the

blue component, which is optimal for canopies with large gaps (Prewitt and Mendelsohn, 1966;

Walter, 2009). Estimates of LAI_h were derived from processed images using Gap Light Analyzer

(V. 2.0) software (Frazer et al. 1999). The mean of the five subplot estimates were taken to

create one plot-level LAI_h value per height. We normalized 2 m LAI_h against litter trap LAI to

obtain realistic LAI_h values (R^2=0.63, p=0.01).

Post-Recovery Light Absorption

We quantified light intercepted by forest canopies from the fraction of photosynthetically

active radiation (fPAR) absorbed at the plot-scale, evaluating how post-recovery ecosystem structural measures relate to canopy light absorption and, in turn, primary production. Sixty PAR measurements at 1 m height were collected 1 m apart along the cardinal axes of each plot using an AccuPAR ceptometer (Decagon Devices Inc., Pullman, Washington, USA). Measurements were taken within two hours of solar noon on cloudless days during the summer of 2016. Above canopy PAR was measured continuously using a BF2 sunshine sensor (Delta-T Devices, Cambridge, UK) within 1 km of understory measurements.

Statistical Analyses

We used analysis of variance (ANOVA) to test for mean differences in LAI, NPPw, stem density, wood mass, Shannon's diversity index (H') and LAI_h between years, ecological periods, or heights and among stands, non-metric multidimensional scaling (NMS) to evaluate changes over time in canopy species composition, and regression analysis to evaluate relationships between post-recovery structure, primary production, and light capture. Full factorial two-way ANOVAs were used to evaluate significant changes over ecological periods and between stands for litter trap LAI and NPPw. Plot-scale disturbance (as percent basal area loss) was included as a covariate to LAI and NPPw ANOVAs to adjust for plot-level variability in disturbance severity, adjusting for the effects disturbance severity has on LAI and NPPw (Flower et al. 2015; Stuart-Haëntjens et al. 2015). We only used 2010 values to characterize the disturbance period for LAI because 2010 was the first year where LAI values significantly declined. Full factorial three-way ANOVAs were conducted to test for the main effects and interactions of disturbance, stand, and DBH class on stem density and wood mass distribution. Full factorial two-way ANOVAs were performed to test for the effect of stand and disturbance on H' for the subcanopy (<8 cm DBH), canopy (≥8 cm DBH) and combined layers, and to evaluate differences in LAI_h

across stands and by height. LSD Post-Hoc analysis was run to find where differences occur within ANOVAs. To characterize changes in canopy species composition, non-metric multidimensional scaling (NMS) ordination was performed using PC-ORD (V. 5.31) (McCune and Mefford, 2006) using the ''slow-and-thorough'' autopilot setting. Finally, we used regression analysis to examine how structural metrics related to NPPw, and fPAR in the 2016 post-recovery phase. Assumptions of normality and equal variances for all tests were checked. Wood mass, stem density, and litter trap LAI values were $\log_e$ transformed prior to analysis due to non-normality and heteroscedasticity. ANOVAs were performed using JMP pro (V. 12.2), and regression analyses were performed using Sigmaplot (V. 13) software. All relationships were considered significant when $p \leq 0.1$.

Results

Long-term leaf area index and wood net primary production response to disturbance

The three biologically distinct forest stands exhibited similar trends of decline and recovery in leaf area index (LAI) and wood net primary production (NPPw) following moderate severity disturbance. Though mean LAI and NPPw differed among stands (LAI: $p=0.04$; NPPw: $p=0.0004$) and ecological periods (LAI: $p=0.0009$; NPPw: $p=0.0001$), the lack of a statistical interaction between stand and ecological period for NPPw indicated that stands followed parallel patterns of primary production over time (Table 2; Figure 2). For example, during peak disturbance, NPPw was similarly reduced in all stands relative to pre-disturbance levels (HIGH: -49%, $p=0.05$; MED: -59%, $p=0.09$; LOW: -47%, $p=0.1$). In contrast, we observed a significant statistical interaction between stand and ecological period for LAI ($p=0.08$), with HIGH (-37%, $p=0.02$) and LOW (-31%, $p=0.002$), but not MED, declining during peak disturbance in 2010. All stands recovered to pre-disturbance LAI and NPPw levels by the 2011-2015 post-disturbance

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phase (p≥0.4), with the exception of LAI in the LOW stand (p=0.002), which did not recover until the 2016 post-recovery phase. Notably, in the 2016 post-recovery, NPPw and LAI significantly increased in the HIGH stand (+31%, p=0.08; +20%, p=0.09, respectively) compared to pre-disturbance levels.

Ecosystem structure before and after disturbance

Following disturbance, we observed a similar relative increase in total stem density, a common proliferation of smaller stems, and a comparable decline in the wood mass of large stems in all stands. The absence of a significant interaction between disturbance and stand for both stem density and wood mass indicates similar patterns of change in all stands following disturbance, regardless of differences among sites in canopy composition, extent of moderate severity disturbance, and pre-disturbance productivity levels (Table 3; Figure 3). In all stands, disturbance significantly increased mean total stem density (p=0.0003) by increasing subcanopy stems from 3520 to 4600 stems ha^{-1}, and decreased mean total wood mass (p<0.0001), as canopy wood mass declined on average in all stands from 75.0 to 42.8 Mg C ha^{-1} (p=0.02) (Table 3). In 2016, both stem density (p≤0.02) and wood mass (p≤0.002) significantly increased in the smaller 2-3.9 cm, 4-5.9 cm, and 6-7.9 cm DBH stem classes, causing subcanopy wood mass to more than double from 1.3 to 2.7 Mg C ha^{-1}. Although disturbance reduced the wood mass of large trees, mean stem density of canopy (> 8 cm DBH) trees was not significantly different in the post-recovery phase, suggesting rapid in-growth of subcanopy stems into the largest diameter class following disturbance.

Tree canopy compositional changes among stands following aspen and birch decline were more nuanced (Figure 4), but with red maple and red oak emerging as the two dominant canopy species accounting for 83±6% of post-disturbance basal area (BA) across the sampled

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landscape. Our NMS ordination preformed on canopy species composition yielded a significant 3D solution (stress=5.35, Monte Carlo test: p=0.04), with the substantial shift along Axis 1 indicating movement away from aspen dominance. The strong separation along Axis 2 and strong stand grouping both pre and post-disturbance highlights the site-specific compositional trajectories of each stand. The canopy of the HIGH stand was the most diverse in the post-recovery period (p=0.07), though > 80% of the basal area was red maple (60±17% BA) and sugar maple (22±15% BA). The MED stand, following disturbance, was dominated by red maple (62±3% BA), with substantial red oak (28±6% BA) and American beech (8±4% BA). The LOW stand was the only site comprised mostly of red oak (77±8% BA) after disturbance, with some red maple (19±7.6%), white pine, and American beech. Subcanopy species dominance was largely similar at each site with the exception of American beech, which significantly increased in MED and HIGH stands (p≤0.001) (Figure 5).

We observed declines following disturbance in canopy only and total (canopy and subcanopy) tree diversity, as Shannon's diversity index (H'), in the lower LOW and MED, but not HIGH, productivity forest stands (Table 4; Figure 6). We observed a significant (p=0.09) decrease in mean canopy tree diversity when all stands were included in analysis, owing to the ubiquitous decline of aspen and birch, while we saw no significant change in subcanopy diversity. Tree diversity in the least productive and structurally complex LOW stand was most vulnerable to moderate disturbance. All stands had statistically similar mean canopy and total H' prior to the disturbance, but in the post-recovery period, the LOW stand had significantly lower canopy and combined H' relative to MED and HIGH stands (p≤0.08). This trend was driven by significant declines in canopy (p=0.08) tree diversity in the LOW stand, while MED and HIGH stands maintained canopy H' after disturbance (Figure 6).

The post-recovery vertical distribution of leaf area differed among stands ($p<0.0001$) and with canopy height ($p<0.0001$) (Table 5). A significant interaction between stand and height ($p=0.027$) indicated significantly different patterns in the vertical distribution of LAI among stands. The HIGH stand had higher LAI than MED and LOW stands ($p\leq0.0003$) when all heights were included in analysis, while the MED stand tended to have higher LAI in the subcanopy (≤4 m), and the LOW stand tended to have higher LAI in the upper canopy (>6 m) based on slopes (Figure 7).

Post-recovery structure, NPPw, and light capture interactions

Following the recovery of wood NPP and LAI, we examined ecosystem structure-primary production relationships among plots, finding leaf area and tree diversity, but not physical complexity, were significantly correlated with primary production. We regressed biological diversity as H' total (subcanopy and canopy), the LiDAR based canopy structural complexity metrics describing leaf arrangement as rugosity and top rugosity, and leaf quantity as LAI against NPPw (Figure 8). Post-recovery NPPw increased linearly with LAI ($R^2=0.68$, $p=0.006$) and H' combined ($R^2=0.56$, $p=0.02$), but had no significant relationship with either physical canopy structural complexity metric.

Lastly, we evaluated whether canopy light absorption serves as a mechanistic linkage between structural attributes and production relationships, finding fPAR significantly coupled tree diversity and LAI with wood NPP. We first established a significant positive relationship between NPPw and fPAR ($R^2=0.38$, $p=0.077$) (Figure 8). Relationships between structural metrics and fPAR were similar to the relationships we observed with wood NPP, as light absorption increased alongside H' ($R^2=0.40$, $p=0.067$) and LAI (adj. $R^2=0.42$, $p=0.035$), but decreased with top rugosity ($R^2=0.52$, $p=0.029$) (Figure 9).

Discussion

We have shown that three forest stands, varying in pre-disturbance productivity and canopy composition, exhibited similar patterns of wood NPP decline and recovery following moderate severity disturbance. Similar to prior studies examining comparable levels of disturbance (Amiro et al. 2010; Hicke et al. 2012; Flowers et al. 2013), we observed an initial decline in production of 47 to 59%, with all stands recovering to pre-disturbance primary production values in less than a decade. Following the recovery of production and LAI in all stands, light absorption, and in turn, primary production were well predicted by leaf area index and tree diversity, forest structures shaped by both local site conditions and disturbance. Our observations show that the primary production response to moderate severity disturbance can be similar among structurally variable stands, and that a suite of conventional ecosystem structural features may be preserved as principal drivers of primary production across the landscape following disturbance.

Like prior studies of moderate severity disturbance, we attribute resilience across stands in primary production to a shared response of rapid compensatory growth of surviving canopy and subcanopy trees, facilitated by the reallocation of growth limiting resources away from senescent individuals to surviving vegetation. Our finding that resilience in primary production, which more than doubled on average when weighted by basal area, was partially supported by rapid growth of large canopy trees, , is supported by many prior studies (Romme et al. 1986; Brown et al. 2010; Pfeifer et al. 2011; Hicke et al. 2012). Disturbance also stimulated the release of subcanopy trees, leading to three times more subcanopy contribution to total wood NPP in periods following disturbance, which is consistent with prior studies at our site (Stuart-Haëntjens et al. 2015; Fahey et al. 2016) and elsewhere (Campbell et al. 2009; Brown et al. 2010; Edburg et

al. 2011). Moreover, we found that a greater density of larger subcanopy stems (4-7.9 cm DBH) was a significant predictor of the relative increase in production since peak disturbance (%) (R^2=0.75, p=0.025) and post-recovery light absorption and (Figure 10).

During the 2016 post-recovery period, we observed significantly greater primary production in the HIGH stand, indicating that moderate disturbance may trigger enhanced long-term primary production in some sites, though this single observation should be interpreted with caution. Moderate disturbances can increase canopy physical complexity (Cole and Lorimer 2005; Hart, 2016), which has been posited to increase primary production through more efficient light capture and use, particularly by subcanopy vegetation (Portsmuth and Niinemets 2007; Campbell et al. 2009; Hardiman et al. 2013b; Gough et al. 2016). However, we found limited evidence for physical complexity driving increased primary production at our site, observing no significant relationship between canopy complexity metrics, rugosity and top rugosity, and post-recovery production. Instead, the observed enhancement in the HIGH stand coincided with an increase in post-recovery leaf area, and a corresponding positive relationship between LAI and production (Figure 8). Even so, we acknowledge that our results are limited and could be a short-term effect resulting from rapid growth. We also cannot rule out the possibility that other sources of inter-annual variability in primary production supported increased plant growth in 2016, highlighting the need for, and value, of long-term production monitoring following disturbance.

Acknowledging that local site conditions and disturbance shape and reshape ecosystem structure (Skovsgaard et al. 2009; Reinikainen et al. 2014), we evaluated plot scale relationships between primary production and restructured canopies in the post-recovery phase, finding leaf area and tree canopy diversity were linked with wood NPP through their common effects on canopy light capture. LAI exhibited the strongest positive relationship with plot-level primary

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production, and is a well-known driver of productivity globally (Reichle 1981; Reich et al. 2012) and at our site (Hardiman et al. 2013b; Scheuermann et al. in review). Tree species diversity is also broadly linked to primary production (Zhang et al 2012; Liang et al. 2016), with diverse forest canopies at our site (Gough et al. 2010) and elsewhere (Kelty, 2006; Forrester et al. 2006) exhibiting higher productivity. Though the mechanisms underpinning diversity's affect on forest production remain an important topic of research, resource complementarity, in which different species utilize resources uniquely in space and time, has been implicated (Loreau, 1998; Chesson, 2000; Adler et al. 2007; Forrester, 2014). We found that more diverse plots had more leaf area (R^2=0.85; p=0.0004), and captured more light (Figure 8) suggesting resource complementarity among species likely supported the observed increase in light capture and production at our site. Following disturbance, we find that more productive canopies reorganized in a way that optimized the quantity of leaf area, likely through diversity-related complementarity effects.

Unlike leaf area and tree canopy diversity, LiDAR-based canopy structural complexity metrics were not correlated with wood NPP following disturbance. Our findings contrast with prior research showing decadal patterns of primary production in minimally disturbed forests is strongly correlated with canopy structural complexity measures (Hardiman et al. 2011, 2013b; Scheuermann et al. in review). However, our observations that canopy rugosity and top rugosity were not significantly related to primary production following disturbance are consistent with those from a nearby recently disturbed forest (Hardiman et al. 2013a), suggesting that disturbance may temporarily decouple NPP from canopy rugosity. The linkage between primary production and canopy structural complexity may lag behind leaf area because it takes more time for canopy branches to grow, explore and fully fill in upper canopy gaps created by the senesce

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of dominant trees than it does for the stand or plot to recover leaf area. Particularly in more disturbed sites (> 60% BA reduction), it has been found that mean canopy height and structural complexity were reduced even as LAI recovered, because taller canopies are needed to provide the physical space required for the development of more complex arrangements (unpublished data; Hardiman et al. 2013a). Our results agree with those findings, showing a strong negative relationship between disturbance severity (as % BA loss) and mean canopy height ($R^2 = 0.59$, p=0.016). The post-recovery vertical leaf profile also hints at this in the more disturbed MED and HIGH stands, showing a steep drop in leaf area above lower subcanopy strata (≤ 4 m) (Figure 7). Canopy complexity metrics, unlike LAI and tree canopy diversity, appear to recover and stabilize more slowly following disturbance, and are better indicators of productivity over decade to century in stands changing more slowly due to succession (Hardiman et al. 2013b; Scheuermann et al. in review). These contemporary complexity metrics have high potential, but we show there is value in measuring several structural features to serve as proxies for primary production, as the degree of usefulness of each metric may be dynamic over different timescales and due to different environmental pressures.

Conclusions

We conclude that pre-disturbance site conditions, including productivity and composition, may minimally drive general patterns of forest primary production resilience following moderate disturbance., Though limited, we present evidence showing our most productive site may be experiencing production enhancement eight years after the disturbance, stressing the need for more long-term C cycling measurements following disturbance. Conventional measures of forest structure, tree canopy diversity and leaf area were conserved as production indicators following LAI and NPP recovery, while more novel LiDAR-based

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measures of canopy structural complexity were not correlated with primary production. Key questions still remain pertaining to when and why different canopy structural metrics related to ecosystem production. Understanding how disturbances affect diverse forest assemblages within landscapes, and characterizing when different structural-production relationships are most useful as proxies of production remain critical moving forward as the C cycling science community more broadly seeks to improve forecast C storage forecasts in a world with increasing disturbance frequency and extent.

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Tables and Figures

Table 1: Pre-disturbance aboveground wood net primary production (NPPw; 1997/98-2001), biomass (2001/06), aspen and birch biomass (% of total), basal area (BA, 2001/06), aspen and birch BA (% of total), leaf area index (LAI [dimensionless], 2007), aspen and birch LAI (% of total), and soil volumetric water content (VWC, %, 2008) for each stand. Mean± S.E.

Stand	NPPw (Mg C ha^{-1} yr^{-1})	Canopy Wood Biomass		Canopy Basal Area		LAI		4-7.9 cm stem density (stems ha^{-1})	Soil VWC (%)
		Total (Mg C ha^{-1})	Aspen & Birch (%)	Total (m^2 ha^{-1})	Aspen & Birch (%)	Total	Aspen and Birch (%)		
HIGH	3.22	94.0±8.3	74.1±8.1	31.1±2.5	64.6±8.9	5.86	36.0	425±151	19.0±0.018
MED	2.14	79.3±15.4	75.4±2.7	27.4±4.1	68.4±3.5	4.58	38.5	454±174	12.5±0.022
LOW	1.76	76.6±10.6	33.2±9.0	25.1±3.8	36.1±9.7	3.37	29.5	71±4	10.4±0.025

Table 2: Full factorial two-way ANOVA results testing for the effects stand, ecological period (seen in Figure 2), and the stand*ecological period had on both LAI (Dimensionless) and NPP (Mg C ha^{-1} yr^{-1}). Significant differences are in bold.

Term	DF	Litter trap LAI			NPP		
		Sums of Squares	F-value	p-value	Sums of Squares	F-value	p-value
Stand	2	0.17	3.40	**0.0449**	7646786	14.63	**0.0004**
Ecological Period	3	0.51	6.86	**0.0009**	11348383	14.47	**0.0001**
Stand*Ecological Period	6	0.31	2.07	**0.0820**	1369897	0.87	0.5381
Disturbance (covariate)	1	0.02	0.79	0.3817	291892	1.12	0.3085

Table 3: Full factorial three-way ANOVA results for stem density (stems ha^{-1}) and biomass (Mg C ha^{-1}). We tested for the effect of our experimental disturbance, different stands, DBH classes, and all interaction terms. Analyses were preformed on log$_e$-transformed values. Significant differences are in bold.

Term	DF	Stem Density (stems ha^{-1})			Biomass (Mg C ha^{-1})		
		Sums of Squares	F value	P-value	Sums of Squares	F value	p-value
Disturbance	1	4.78	15.21	**0.0003**	6.02	20.72	**<0.0001**
Stand	2	11.93	18.98	**<0.0001**	21.62	37.23	**<0.0001**
DBH Class	4	90.67	72.11	**<0.0001**	377.91	325.35	**<0.0001**
Disturbance*Stand	2	0.54	0.87	0.4265	0.82	01.40	0.2539
Disturbance*DBH Class	4	4.24	3.37	**0.0153**	8.91	7.67	**<0.0001**
Stand*DBH Class	8	6.19	2.46	**0.0230**	11.37	4.90	**0.0001**
Disturbance*Stand*DBH Class	8	0.81	0.32	0.9540	0.78	0.33	0.9490

Table 4: Full factorial two-way ANOVA testing for differences between stands, and the effect that disturbance or disturbance*stand had on Shannon's Diversity Index (H') for the subcanopy, canopy and combined (subcanopy and canopy) strata. Significant differences are in bold.

Term	DF	H' Combined			H' Canopy			H' Subcanopy		
		Sums of Squares	F-value	p-value	Sums of Squares	F-value	p-value	Sums of Squares	F-value	p-value
Disturbance	1	0.11	2.26	0.1588	0.22	3.31	**0.0939**	0.01	0.16	0.6961
Stand	2	0.42	4.18	**0.0419**	0.26	1.94	0.1865	2.18	16.02	**0.0004**
Disturbance*Stand	2	0.08	0.87	0.4446	0.08	0.60	0.5668	0.02	0.14	0.8699

Table 5: Full factorial two-way ANOVA results of the effects of stand and height for vertical LAI$_h$ profiles. Height was analyzed as a continuous variable. Significant differences are in bold.

| Term	DF	LAI$_h$		
		Sums of Squares	F value	p-value
Stand	2	4.01	14.21	**<0.0001**
Height	1	7.96	55.34	**<0.0001**
Stand*Height	2	1.12	3.89	**0.0272**
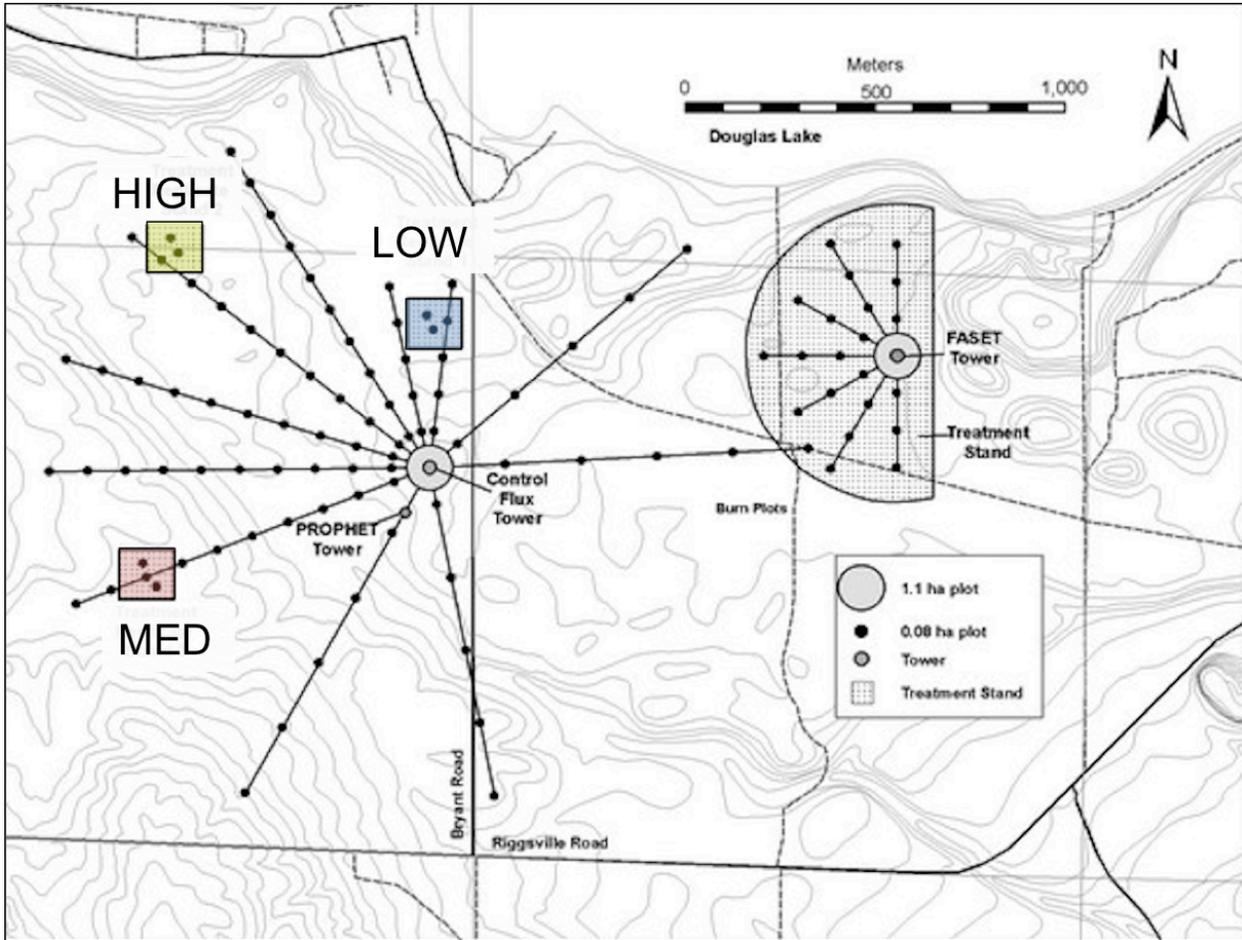
Figure 1: A topographic map illustrating the layout of the Forest Accelerated Successional Experiment at the University of Michigan Biological Station in northern Lower Michigan. Color-shaded areas represent the 2-ha treatment stands. The non-colored semicircular shaded area represents the 33-ha treatment area where prior studies have been focused. The names of treatment stands correspond with Table 1. Dots within shaded area represent the three-0.08 ha sampling plots nested within each stand.
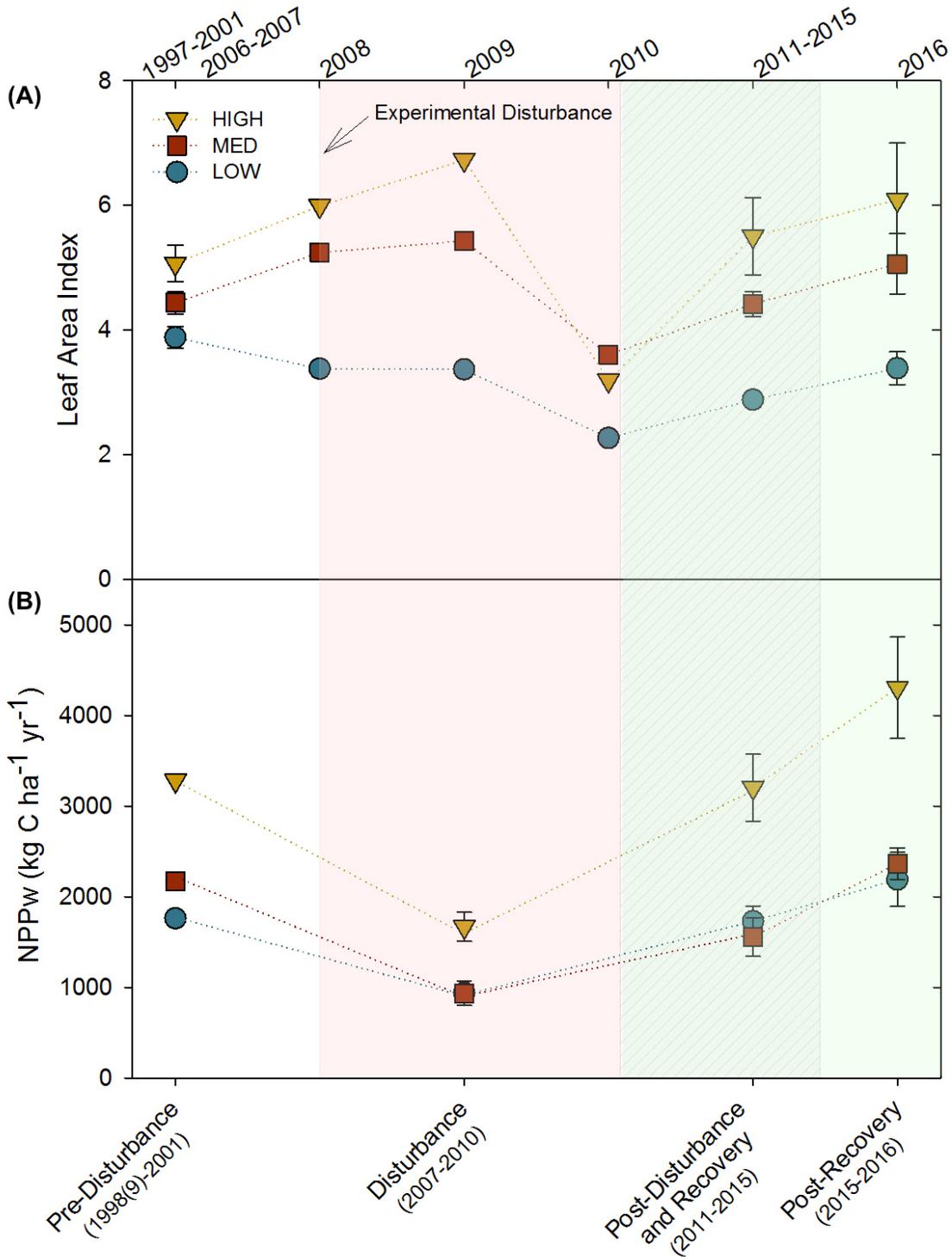
Figure 2: (A) Leaf area indices (LAI) and (B) wood net primary productivity (NPPw) for the three 2-ha treatment stands over time. Shaded areas correspond with ecological periods along the lower X-axis. When possible, values shown represent mean±SE.
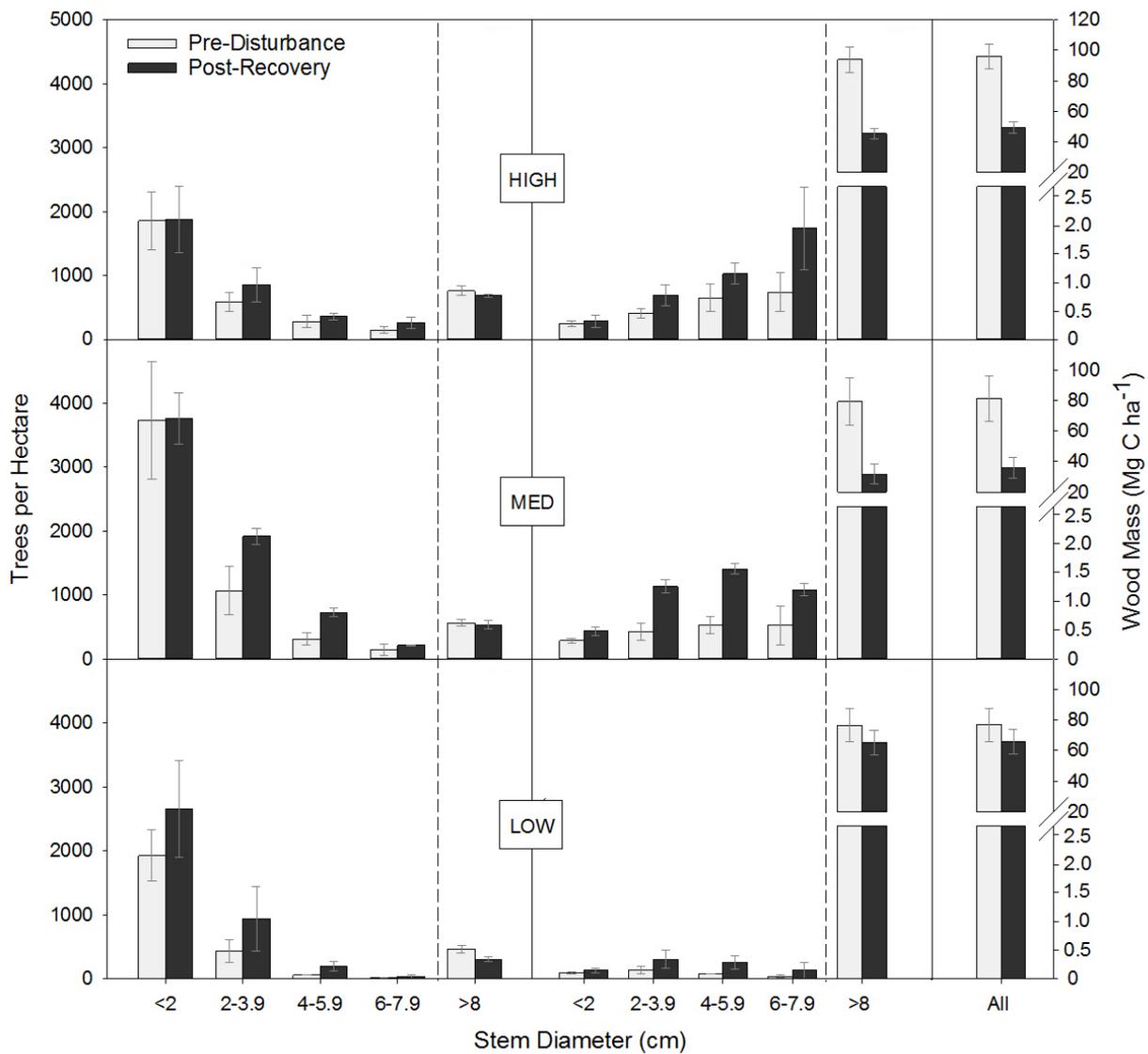
Figure 3: The density of tree stems per hectare (left) and the contribution to wood mass (right) (mean±SE) for each defined stem diameter class per treatment stand prior to the experimental disturbance (2001 or 2006) and following the recovery of leaf area index and wood net primary production (2016).
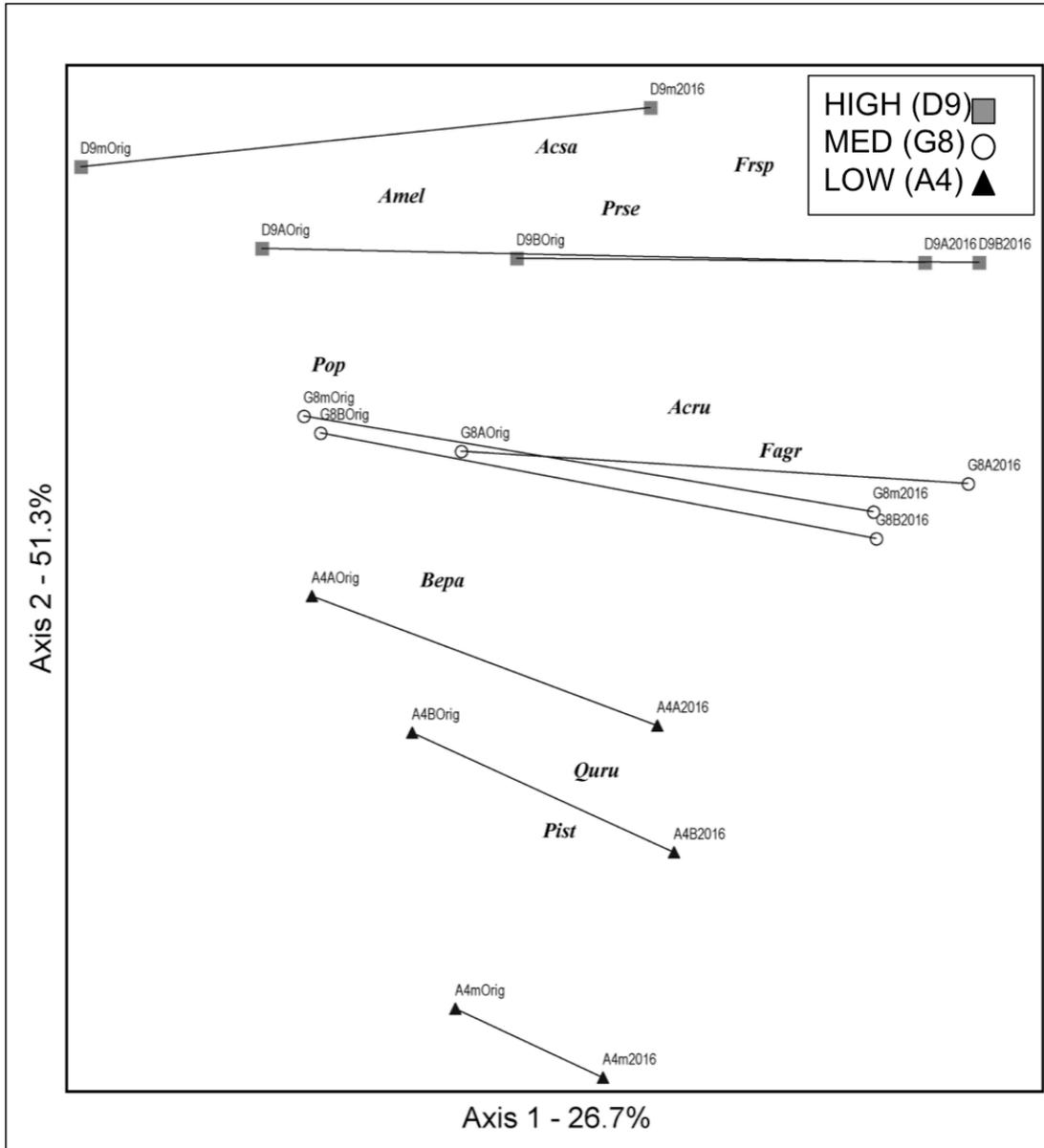
Figure 4: Non-metric multidimensional scaling (NMDS) ordination of canopy tree species community composition for the three treatment stands (three axes, stress=5.4%, Monte Carlo test: p=0.04). Species were weighted by basal area dominance. Names are coded using the first two letters of the genus and specific epithet of the species. A list of occurring species is outlined in the methods section.
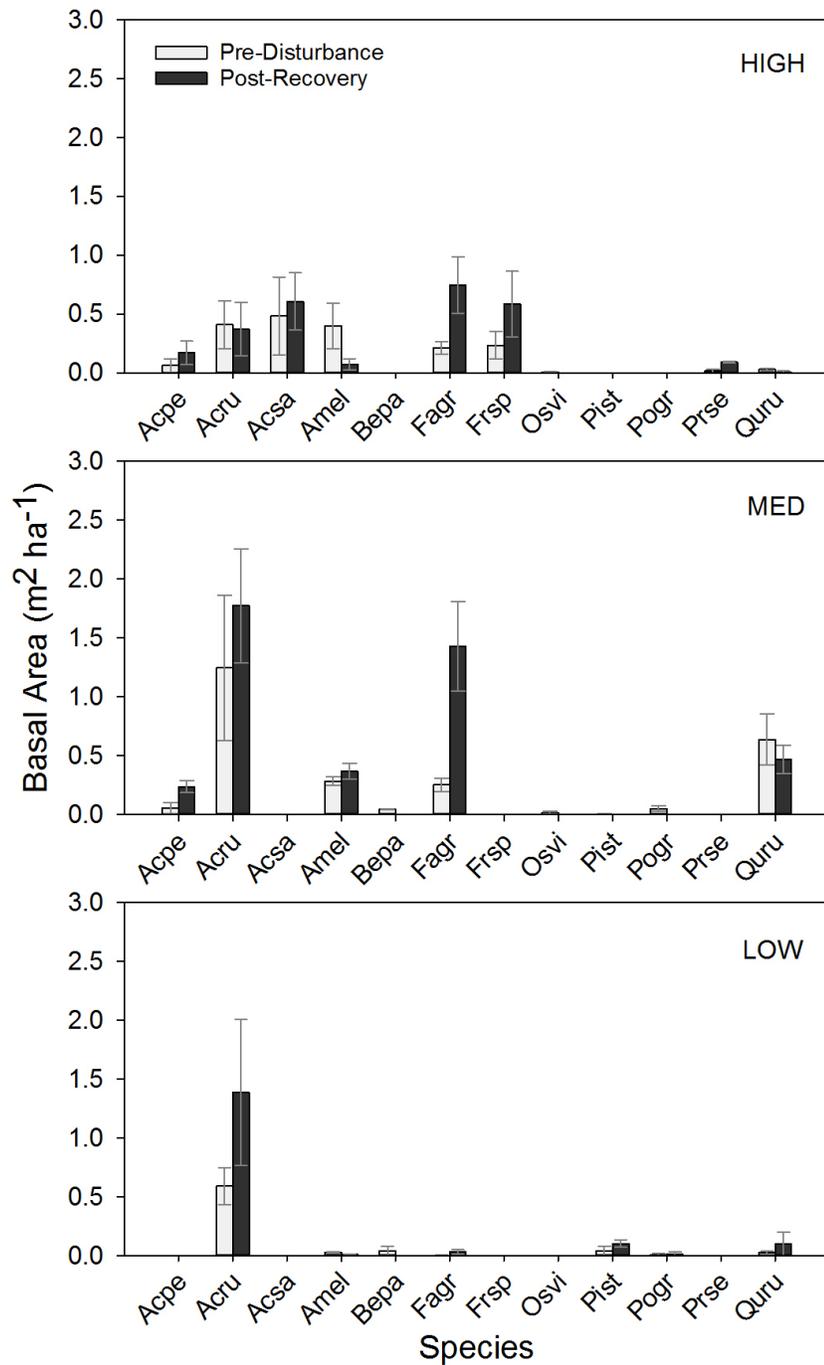
Figure 5: Mean basal area dominance (±SE) by species and per treatment stand prior to the experimental disturbance (2001 or 2006) and following the recovery of leaf area index and wood net primary production (2016). Names are coded using the first two letters of the genus and specific epithet of the species. A list of occurring species is outlined in the methods section.
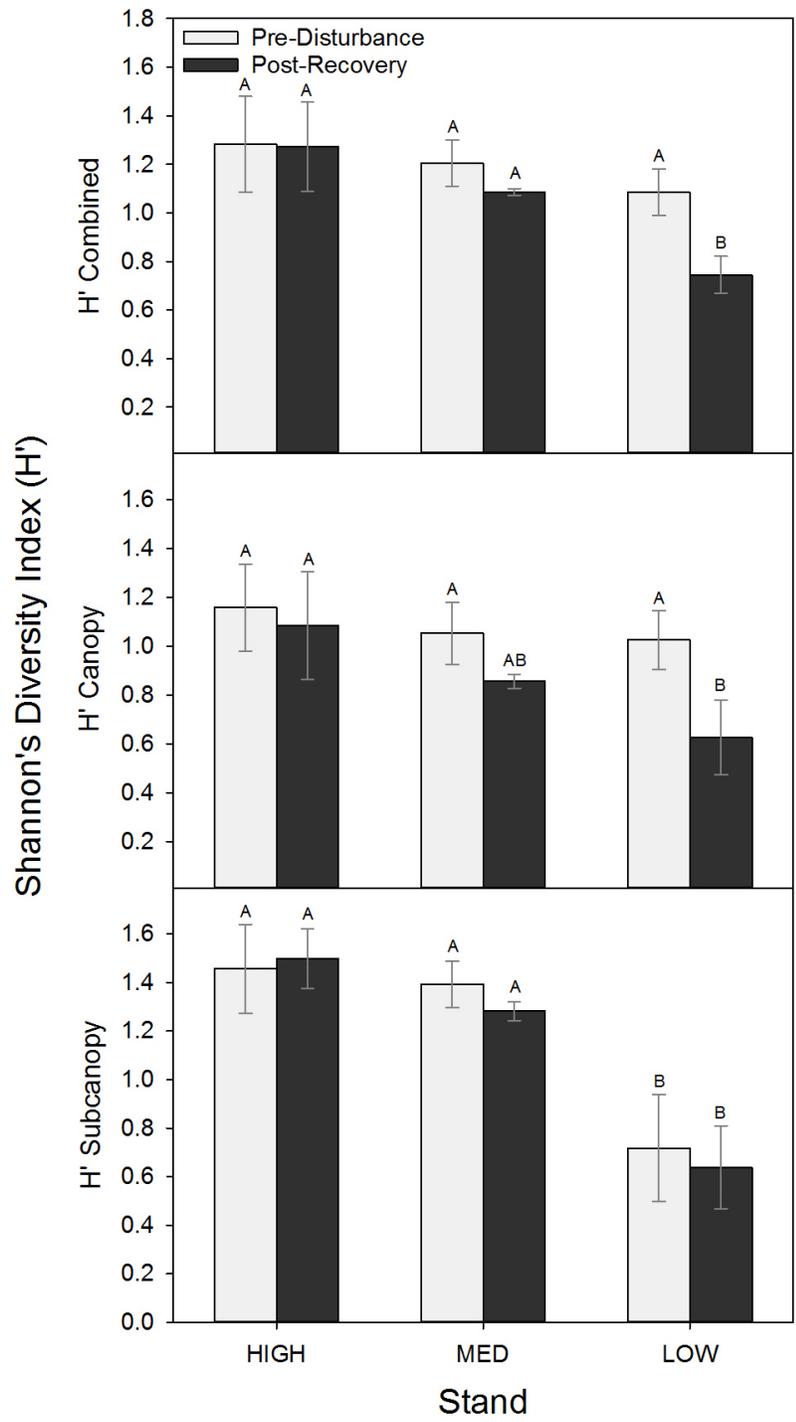
Figure 6: Pre-disturbance (2001 or 2006) and post leaf area index and wood net primary production recovery (2016) Shannon's diversity index (H') values (mean±SE) for each treatment stand.
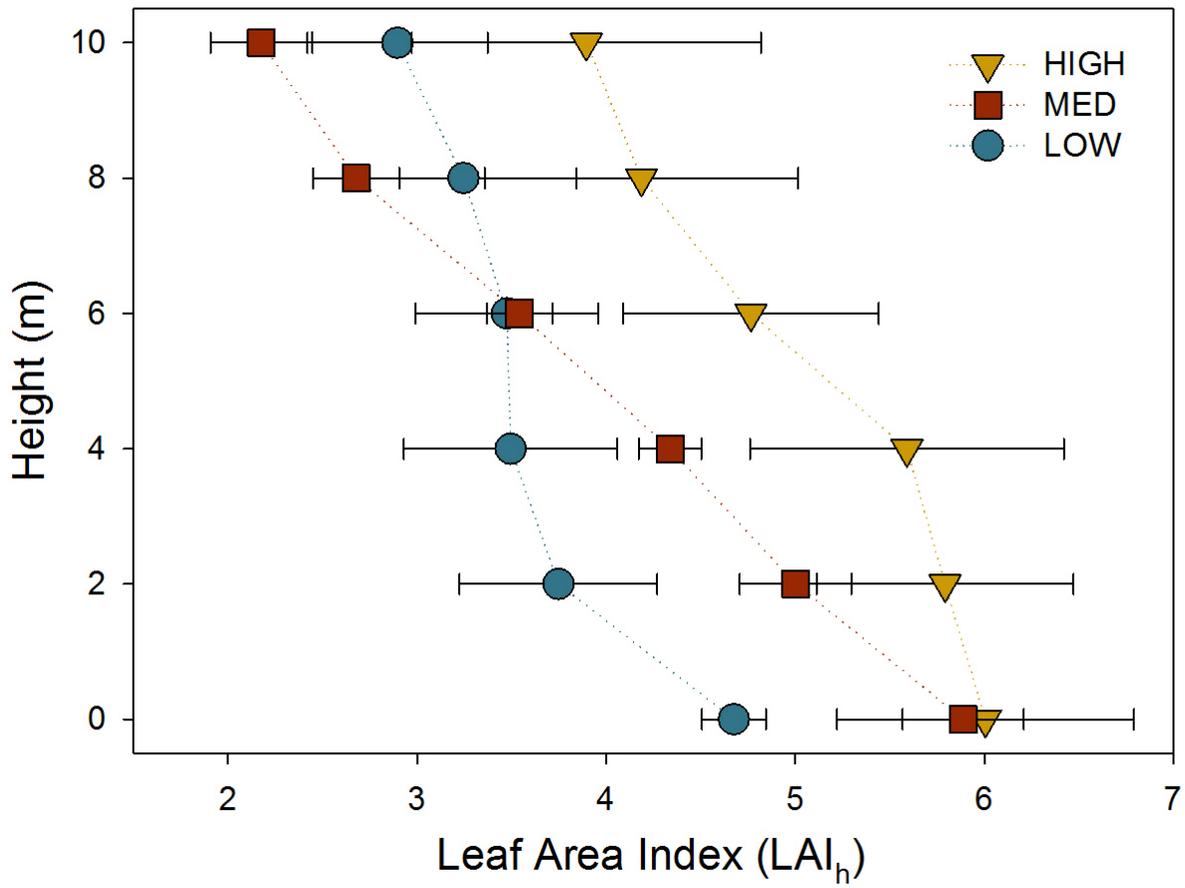
Figure 7: Mean post-recovery (2016) leaf area index derived from hemispherical imaging (LAI_h) for each stand taken from 2m vertical intervals.
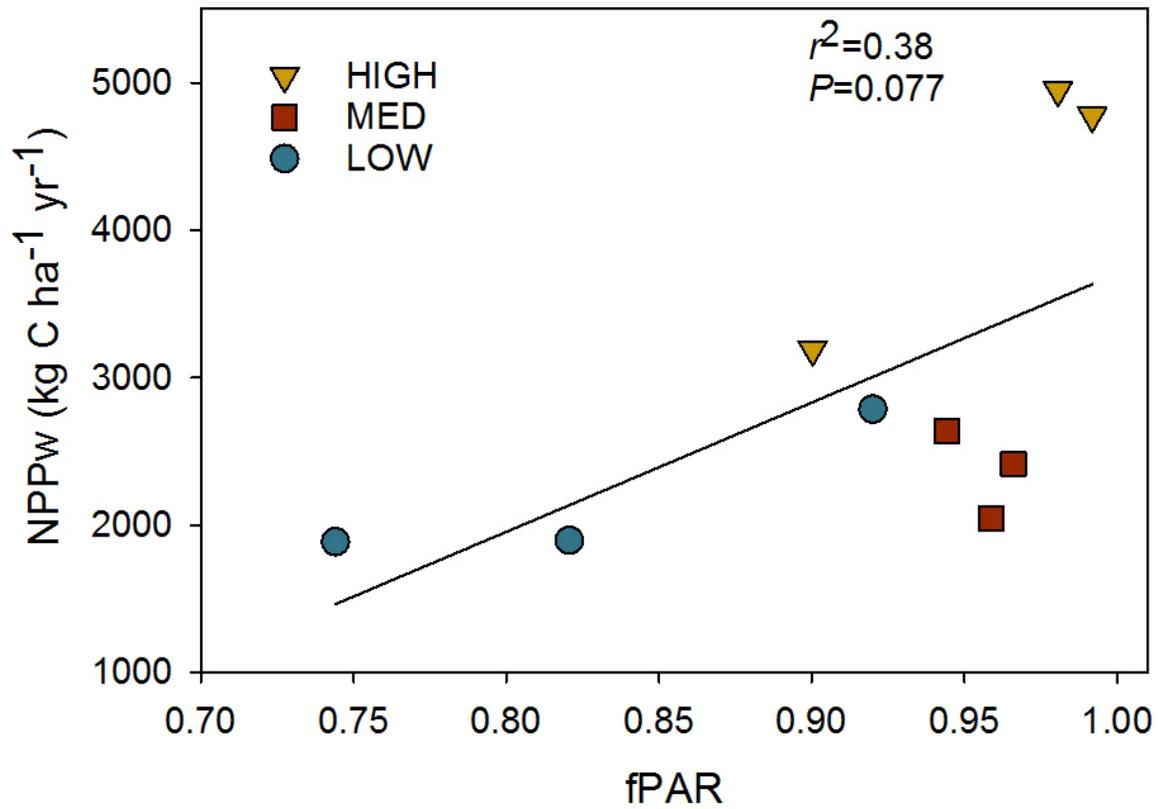
Figure 8: The post-recovery (2016) relationship between the fraction of photosynthetically absorbed radiation (fPAR) and wood net primary production (NPPw) (kg C ha^{-1}yr^{-1}).
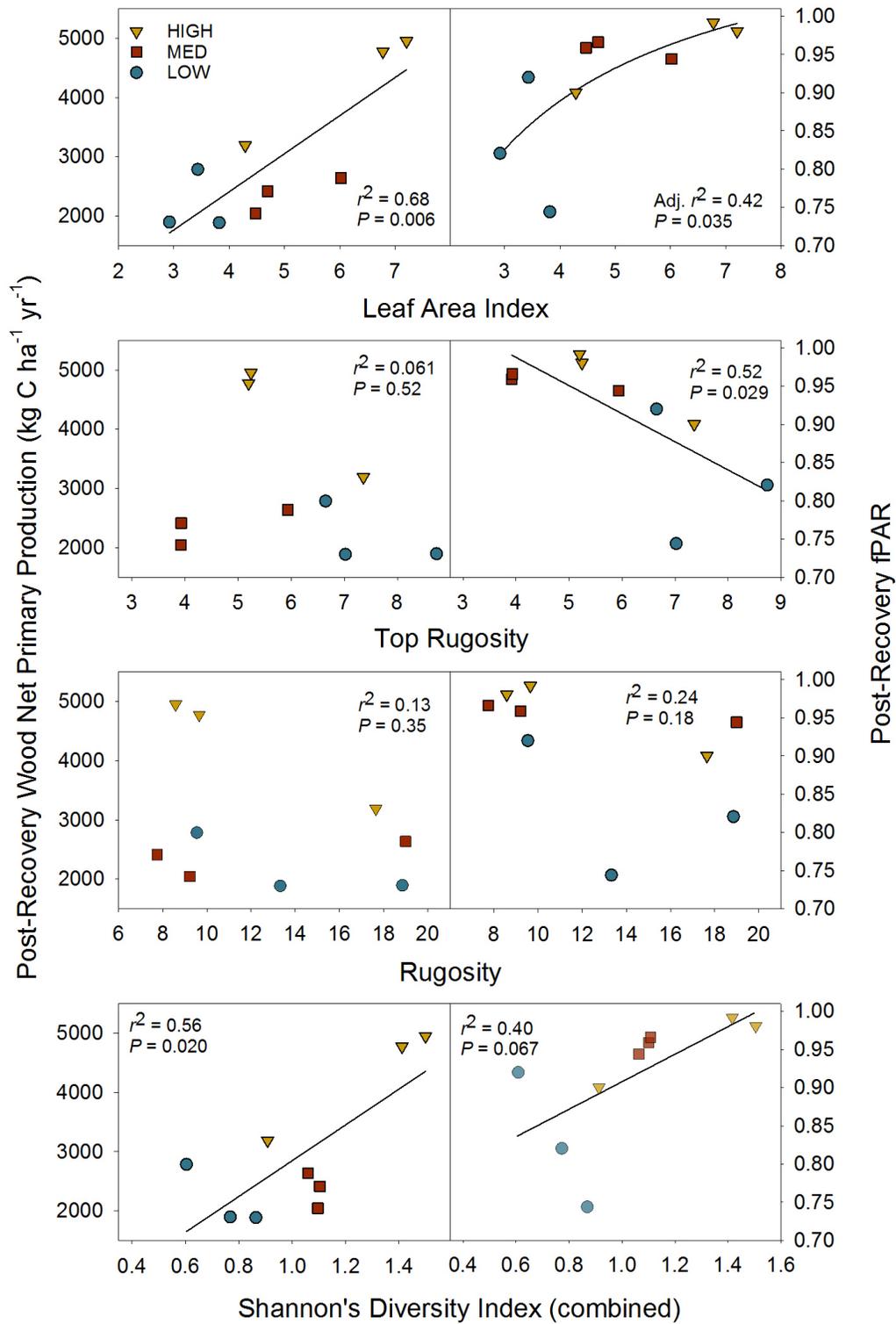
Figure 9: The post-recovery relationship different structural metrics have with wood net primary production (NPPw) and the fraction of photosynthetically available light (fPAR).
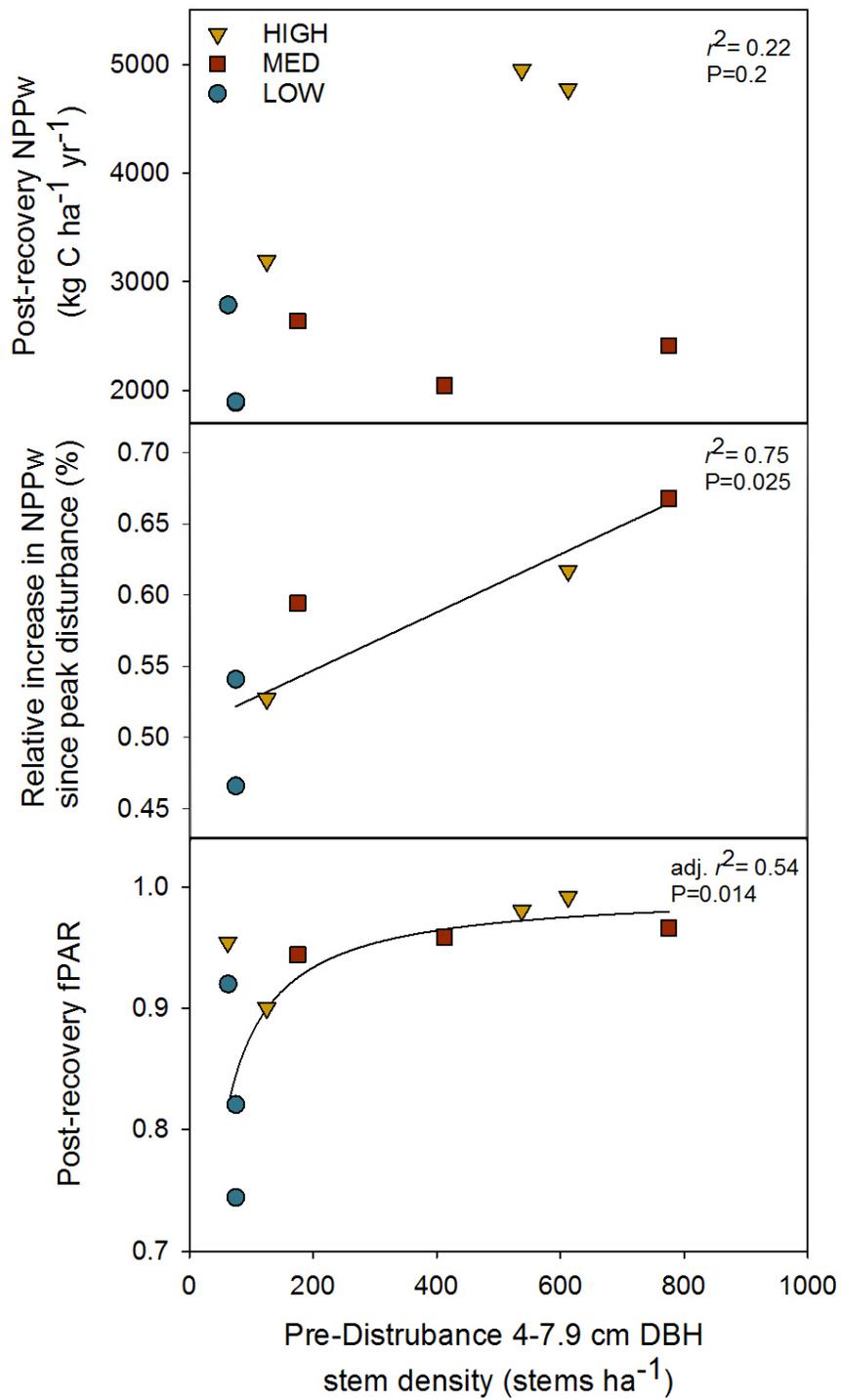
Figure 10: The density of larger subcanopy stems (4-7.9 cm DBH) prior to disturbance does not have a direct relationship with post-recovery (2016) wood net primary production (NPPw), but it does have a relationship with the relative increase in NPPw since peak disturbance (%), and the fraction of photosynthetically active radiation (fPAR) post-recovery.

Vita

Benjamin Tai Sagara was born on July 29th, 1992, in Greenville, South Carolina. He graduated from Mauldin High School, located in Mauldin, South Carolina in 2011. Ben then received a Bachelor of Science Degree in Biology with a minor in Environmental Studies from the College of Charleston in Charleston, South Carolina, graduating *magna cum laude* in May of 2015. He joined the Master of Science in Biology program at Virginia Commonwealth University, Richmond, Virginia in August of 2015.