



Virginia Commonwealth University
VCU Scholars Compass

Theses and Dissertations

Graduate School

2014

Forest Net Primary Production Resistance Across a Gradient of Moderate Disturbance

Ellen Goodrich-Stuart
Virginia Commonwealth University

Follow this and additional works at: <https://scholarscompass.vcu.edu/etd>



Part of the [Biology Commons](#)

© The Author

Downloaded from

<https://scholarscompass.vcu.edu/etd/627>

This Thesis is brought to you for free and open access by the Graduate School at VCU Scholars Compass. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of VCU Scholars Compass. For more information, please contact libcompass@vcu.edu.

© Ellen JoAnne Goodrich-Stuart May 2014

All Rights Reserved

**FOREST NET PRIMARY PRODUCTION RESISTANCE ACROSS A
GRADIENT OF MODERATE DISTURBANCE**

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

by

ELLEN GOODRICH-STUART
BACHELOR OF ARTS, UNIVERSITY OF RICHMOND, 2012
MASTER OF SCIENCE, VIRGINIA COMMONWEALTH UNIVERSITY, 2014

Advisor: CHRISTOPHER M GOUGH, PHD
ASSISTANT RESEARCH PROFESSOR, DEPARTMENT OF BIOLOGY

Virginia Commonwealth University
Richmond, Virginia
May, 2014

ACKNOWLEDGEMENTS

I would like to acknowledge several people who have been vital to my success. First and foremost, I would like to thank Dr. Christopher Gough, who has taken on many roles starting with that of the mentor, the friend, and the guidance counselor. Secondly, I would like to thank Cynthia Scheuermann, my trusted field technician, for spending endless hours in the field with me and helping me in the brainstorming and building of field equipment. Thank you to the Curtis Lab at Ohio State University for use of hemispherical imaging equipment. I would also like to thank my husband Rémy Haentjens and my family for their unwavering support and patience. I would also like to thank my committee members, Dr. Derek Johnson, Dr. Paul Bukaveckas, and Dr. Suzanne Robertson. Thank you to Dr. Christophe Vogel and others at the University of Michigan Biological Station for their assistance both in the lab and the field. Lastly, I would like to thank the US Department of Energy for their funding and support (Award No. DE-SC0006708).

TABLE OF CONTENTS

	Page
Acknowledgements.....	ii
Chapter	
1 Introduction	1
2 Materials and Methods	3
Study Site	3
Aboveground Wood Net Primary Production	5
Litter Trap Leaf Area Index	6
Hemispherical Imaging	6
Light Distribution	7
Production Efficiency	8
Leaf Physiological, Morphological, and Nitrogen Measurements	8
Statistical Analyses.....	9
3 Results.....	9
Production and Disturbance Severity	9

Canopy Structural and Environmental Responses to Increasing Disturbance	
Severity.....	10
Ecosystem Responses to Disturbance	10
Subcanopy Leaf Physiological, Nitrogen, Morphological Responses to Disturbance	
Severity.....	11
4 Discussion	12
References.....	16
Figures.....	23
Vita.....	33

Abstract

FOREST NET PRIMARY PRODUCTION RESISTANCE ACROSS A GRADIENT OF MODERATE DISTURBANCE

By Ellen JoAnne Goodrich-Stuart, B.A.

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

Virginia Commonwealth University, 2014

Major Advisor: Christopher M. Gough
Research Assistant Professor, Department of Biology

The global carbon (C) balance is vulnerable to disturbances that alter terrestrial C uptake and loss. Moderate disturbances that kill or defoliate only a subset of canopy trees such as insect defoliation, drought, and age-related senescence are increasing in extent and frequency; yet, little is known about the effect of moderate disturbance on forest production and the mechanisms sustaining or supporting the recovery of the C cycle across a range of moderate disturbance severities. We used a broad plot-scale gradient of upper canopy tree mortality within a large manipulation of forest disturbance to: 1) quantify how aboveground wood net primary production ($ANPP_w$) responds to a range of moderate disturbance severities and; 2) identify the primary mechanisms supporting $ANPP_w$ resistance or resilience following moderate disturbance. We found that $ANPP_w$ was highly resistant to moderate disturbance, with production levels sustained following the senescence of 9 to > 60 % of the upper canopy tree basal area. As upper canopy gap fraction increased with rising disturbance severity, greater light availability to the subcanopy enhanced leaf-level C uptake and the growth of this formerly light-limited canopy stratum, compensating for upper canopy production losses. As a result, whole-ecosystem production efficiency ($ANPP_w/LAI$) increased at high levels of disturbance severity and leaf area loss. These findings provide a mechanistic explanation for sustained $ANPP_w$ across the disturbance gradient, in which the physiological and growth enhancement of undisturbed vegetation was proportional to the level of disturbance severity. Our results have important

ecological and management implications, showing that moderate disturbances may minimally alter ecosystem functions such as C storage.

Keywords: disturbance; mortality; subcanopy; production-efficiency; light; carbon cycling; net primary production; northern Michigan, USA, forest; leaf-area index, LAI; canopy; resistance; resilience

Introduction

Forests store 1.1 ± 0.8 Pg carbon (C) annually in biomass, soils, and organic matter (Pan et al. 2011) and contain 60% of the Earth's terrestrial C stocks (McKinley et al. 2011). Yet, the future strength of this large terrestrial C sink is uncertain as disturbances that alter the C balance increase in extent and frequency across the globe (Amiro et al. 2010; Pan et al. 2011; Hicke et al. 2012; Gough et al. 2013). Stand-replacing disturbance events, such as high intensity fire or clear-cut harvest, generally cause ecosystems to become C sources for several years before regaining their C sink status (Kurz et al. 2008; Amiro et al. 2010; Bradford et al. 2013; Peckham et al. 2013). Considerably less is known about how forest C storage responds to moderate disturbance severities that kill only a fraction of canopy dominant trees. Moreover, our mechanistic understanding of how forest C storage recovers from disturbance is derived almost entirely from severe disturbance events, limiting our ability to forecast how C sink strength is and will be affected by a range of disturbance severities (Goetz et al. 2012).

Moderate disturbances that kill only a subset of trees – including insect outbreaks, windthrow, natural senescence, and partial harvests – have substantially different effects on forest structure than stand-replacing disturbances (Kneeshaw et al. 2011) and therefore can be expected to alter ecosystem functions, including C cycling, differently (Hardiman et al. 2013b). Studies that investigated net primary production (NPP) or net ecosystem production (NEP), two measures of ecosystem C storage, following single levels of moderate disturbance indicate differences among ecosystems in their capacity for resistance and resilience following moderate disturbance (Amiro et al. 2010; Hicke et al. 2012). Here, we use resistance to indicate stability in production following disturbance, and resilience to describe recovery following a temporary decrease in production (c.f. Gunderson 2000). While some studies of moderate disturbance have

found forest C storage responds with rapid resilience (Kasian et al. 2006; Amiro et al. 2010; Scheller et al. 2011), others have shown that forest production is entirely resistant to moderate disturbance (Granier et al. 2008; Amiro et al. 2010; Hicke et al. 2012; Gough et al. 2013). These studies provide valuable insight into the magnitude of functional change following a single level of disturbance, but fail to observe change across multiple levels of severity. Considerable uncertainty remains in how C storage responds to a range of disturbance severities and what mechanisms support resistance or resilience following disturbances that kill only a subset of trees (Birdsey et al. 2006).

The subcanopy plays a key mechanistic role in supporting the recovery of forest production following moderate disturbances that defoliate or kill a fraction of canopy dominant trees (Kaye et al. 2005; Le et al. 2007; Campbell et al. 2009; Saunders et al. 2012; Gough et al. 2013). As upper canopy trees senesce and gaps form, newly available light may stimulate the growth of previously light-limited vegetation (Nave et al. 2009, 2011; Edburg et al. 2011; Yang et al. 2011; Gough et al. 2013). Although a growth trade-off between upper canopy and subcanopy strata is a well-established mechanism supporting production recovery following moderate disturbance, forest ecosystems generally exhibit prolonged reductions in production following very high severity disturbance (Amiro et al. 2010; Hicke et al. 2012). These contrasting responses at different disturbance levels – one of rapid recovery and the other of sustained decline – suggest there is a disturbance threshold at which the subcanopy can no longer fully or rapidly offset production losses in the upper canopy.

We build on studies at the University of Michigan Biological Station (UMBS) centered on a large-scale experimental manipulation of moderate disturbance in which a third of the upper canopy trees were killed by stem girdling all mature aspen (*Populus*) and birch (*Betulacea*)

(Gough et al. 2013). Results from the experiment demonstrate that at the landscape scale NPP and NEP were resistant to moderate disturbance during the first five years following implementation of the experiment (Nave et al. 2011; Gough et al. 2013). Within the large manipulated 39 ha area, substantial variation in disturbance severity exists because of the heterogeneous distribution of girdled aspen and birch trees (Hardiman et al. 2013a). Here, we use a gradient of disturbance severity within the larger experiment to: 1) quantify how aboveground wood net primary production ($ANPP_w$) responds to a range of moderate disturbance severities and; 2) identify the primary mechanisms supporting resistance or resilience following moderate disturbance. Our plot-scale analysis spanning 9 to 69 % senesced tree basal area encompasses and substantially extends the landscape average of 39 %. Given prior results from our site showing high resistance to moderate disturbance at the landscape-scale (Gough et al. 2013) and low resilience following severe disturbance (Gough 2007), we postulated that $ANPP_w$ would respond non-linearly to increasing disturbance severity, remaining relatively stable as disturbance intensity increases before abruptly declining. We predicted that the subcanopy would play a critical role in supporting $ANPP_w$ resistance to moderate disturbance, but at higher disturbance levels upper canopy production losses would be too large to be fully offset by increased growth from undisturbed vegetation.

Materials and Methods

Study Site

We conducted our study at the University of Michigan Biological Station (UMBS) in northern Michigan, USA (45° 35N 84° 43W), with a mean annual temperature of 5.5° C and a mean annual precipitation of 817 mm (1942-2003) (Gough et al. 2013). The site is a century-old maturing aspen-dominated forest that developed following massive clear-cut harvesting and

wildfires in the early 20th century (Gough et al. 2007). Trees ≥ 8 cm diameter at breast height (D , 1.37 m) have a stem density of 700-800 ha⁻¹, a basal area of ~ 25 m² ha⁻¹, and the forest has a mean leaf area index (LAI) of 3.5. Bigtooth aspen (*Populus grandidentata*), trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*), all short-lived early successional species, once dominated the upper canopy and are now in decline (Gough et al. 2010). Red oak (*Quercus rubra*) and red maple (*Acer rubrum*) are gaining dominance in the upper canopy, with lesser representation of sugar maple (*Acer saccharum*), eastern white pine (*Pinus strobus*), and American beech (*Fagus grandifolia*). The subcanopy, the canopy stratum 1 to 5 m above the forest floor, is dominated mainly by red maple and red oak, and also includes American beech, sugar maple, *Amelanchier arboria* (service berry), *Acer pensylvanicum* (striped maple), *Pinus strobus* (white pine), *Pinus resinosa* (red pine), and *Ostrya virginiana* (American hophornbeam).

In May 2008, the Forest Accelerated Succession Experiment (FASET) was initiated to determine how and why ecological succession, disturbance, and climate change affect forest C fluxes and storage in a broadly distributed regionally representative forest ecosystem (see Nave et al. 2011). All early-successional aspen and birch trees (>6700) comprising 39 % of the pre-treatment basal area were stem girdled within a 39 ha area to test the primary hypothesis that net ecosystem production (NEP) will increase as the canopy becomes more biologically and structurally complex, and as nitrogen (N) is reallocated from early to later successional canopy dominants. Peak disturbance within the large treatment area occurred in 2010, when 97% of all girdled trees had senesced and leaf area index was 44 % lower than pre-disturbance values (Gough et al. 2013). This experimental disturbance is comparable in severity and extent to partial canopy defoliation caused by moderate wind, insect, and pathogen disturbances (Amiro et al. 2010).

Disturbance severity within the large manipulated area was quantified in each of 21, 0.8 ha permanent plots east of the base of a meteorological tower (Figure 1). Here, we define plot-level disturbance severity as the fraction of basal area (BA) ≥ 8 cm that senesced from stem girdling. We used pre-disturbance (2006) tree identification and diameter data to calculate the total BA of stem girdled aspen and birch. A large gradient of disturbance severity was represented across plots, spanning 9 to 69 % senesced basal area.

Our study design was intended to encompass and extend beyond the mean disturbance severity of the large manipulated area, while minimizing the effects of variables that could confound how and why production responds to increasing disturbance severity. To minimize the effects of site productivity and community composition, our examination of the mechanisms supporting ANPP_w resilience or resistance focused on a subset of 10 “intensive” measurement plots (filled circles in figures) with similar pre-disturbance upper canopy tree communities, and for which ANPP_w and LAI exhibited no statistical relationship with disturbance severity prior to peak disturbance (Appendix A). Within each plot, we randomly established along each cardinal axis from plot center non-overlapping 5 m radius subplots for measurements of light (fAPAR, fraction of absorbed photosynthetically active radiation), percent foliar nitrogen (N), maximum leaf net CO₂ assimilation, and canopy openness.

Aboveground Wood Net Primary Production

We quantified ANPP_w before and after peak disturbance severity. Aboveground woody biomass (M_a) was estimated annually from D measurements of all trees in each of the 21 treatment plots in 2006, 2010, and 2012. Every upper canopy tree (≥ 8 cm D) was identified and measured for D . Subcanopy saplings (trees < 8 cm D) were identified and their D recorded as < 2 cm, 2-3.9 cm, 4-

5.9 cm, and 6-7.9 cm. Site or region-specific allometric equations were used to relate D to M_a (Gough et al. 2008). Mean annual $ANPP_w$ of upper canopy and subcanopy strata was measured as the mean change in total aboveground wood mass between census years, providing a production value leading up to (2006-2010) and following peak disturbance (2010-2012) (Gough et al. 2013). We use $ANPP_w$ as our primary expression of C storage because it is quantified with high certainty and closely parallels more comprehensive, data-intensive measures of C uptake and storage (i.e., NEP, NPP) at our site (Gough et al. 2008).

Litter Trap Leaf Area Index

Leaf area index estimated from litter traps (LAI_t) was calculated in 2006 for 20 of the 21 plots and every year following experimental disturbance in 6 of the 10 intensive plots (Gough et al. 2010). Litterfall from three litter traps (0.264 m^2 each) within each measurement plot was collected weekly during peak leaf-fall and monthly otherwise, dried at 60°C , separated by species, and weighed. Leaf area index is the product of litterfall mass and specific leaf area (SLA) values (Gough et al. 2010).

Hemispherical Imaging

We used hemispherical images collected in intensive measurement plots during maximum LAI in 2013 to examine whether disturbance severity affected canopy structure. Images were taken under diffuse sky conditions in four subplot locations within each plot at 1 m and 5 m above the forest floor and at ground level using a leveled camera (Cannon A640 power shot, Cannon Inc., USA) with an 180° fisheye lens facing skyward and angled North (Frazer et al. 1999). For images above the forest floor, the camera was mounted on a custom-built vertical pole. For ground-level images, the camera was placed directly on the forest floor. We derived estimates of

LAI and canopy openness using Gap Light Analyzer (GLA Version 2.0) software (Simon Frazer University, Institute of Ecosystem Studies, Millbrook, NY, USA 1999) (Frazer et al. 1999) with the automatic optimal threshold algorithm applied (Nobis and Hunziker 2005).

We used hemispherical images to estimate LAI for all 10 intensive plots, since we did not have a complete LAI_t record of all sites over time, and to partition LAI of the upper canopy and subcanopy strata. We calibrated estimates of LAI from hemispherical images (LAI_h) against litter trap LAI (LAI_t) measurements by regressing the former against the latter and applying a linear correction. The two independently derived estimates of LAI were strongly correlated with an r^2 of 0.87 (and $p = 0.008$; $y = 2.6191x - 2.5146$).

Light distribution

We evaluated how light distribution within the canopy varied with disturbance severity by quantifying the subcanopy fraction of absorbed photosynthetically active radiation (fAPAR) in the 10 intensive measurement plots. A BF2 sunshine sensor (Delta-T Devices, Cambridge, UK) on the control meteorological flux tower continuously measured total and diffuse radiation above the canopy. Separate PAR sensors (SQ-110 Quantum Sensor, Apogee Instruments, Logan, Utah USA) were stationed at ground level and 5 m above the forest floor in four subplot locations within each plot and connected to a central datalogger (CR1000 Campbell Scientific, Inc., USA). To circumvent sunflecks, we quantified fAPAR for a minimum of 4 hours when light was >85% diffuse (e.g., Tobin and Reich 2009). To reduce the influence of solar angle, the 4-hour PAR time-series from each data sensor was averaged for both 5 m and ground level in each plot. Subcanopy fAPAR was then calculated as the light absorbed by vegetation between 5 m and

ground level. Because of poor diffuse conditions or sensor failure in 3 plots, we report results from 7 of 10 plots.

Production Efficiency

We evaluated production efficiency across the gradient of disturbance severity. Plot level production efficiency was estimated in our 10 intensive plots as the ratio of total aboveground net primary production ($ANPP_w$) to LAI_h (McCrary and Joleka 1998).

Leaf Physiological, Morphological, and Nitrogen Measurements

We examined whether subcanopy leaves adjusted their nutrient status, morphologies, and photosynthetic capacity in response to disturbance severity. We measured the light-saturated net CO_2 assimilation (A_{max}) of 2 to 4 fully developed subcanopy leaves in each of four subplots within the intensive measurement plots (for a total of 12-16 leaves per plot) using a LiCor-6400 Portable Photosynthesis System (LI-COR Inc., Lincoln, NE, USA). When available red oak and red maple were selected for sampling because of their relative dominance and broad distribution in the subcanopy irrespective of disturbance severity; however, American beech, the third most dominant subcanopy species, was selected when either red oak or red maple were not present. Following A_{max} measurements, we harvested leaves to obtain leaf mass per area (LMA) and leaf percent nitrogen (N). As a reference for the N status of sun-adapted leaves in the upper canopy, we collected 3 to 5 leaves from each of 4 to 5 dominant canopy trees using a shotgun in July, 2013. LMA was determined for each sampled leaf using a LI-COR LI-3100 area meter (LI-COR Inc., Lincoln, NE, USA) to measure leaf area and a scale to weigh leaf mass once dried. Processed leaves were dried at 60°C, ground in a Wiley mill, and leaf N concentration quantified using a Costech Analytical CHN analyzer (Costech International, Valencia, CA, USA).

Statistical Analyses

We used piece-wise regression analysis to determine how disturbance severity (i.e., the fraction of senesced basal area) related to absolute and relative changes in ANPP_w. Piece-wise regression was chosen because of our *a priori* understanding of high landscape scale resistance to disturbance and hypothesized non-linear threshold response of ANPP_w to increasing disturbance severity. We used linear regression analysis to examine how disturbance severity related to forest structural, functional, and environmental metrics, including canopy openness, LAI_h, A_{max}, LMA, and leaf percent N. Linear regression was used for these analyses because we had no *a priori* knowledge of how these response variables mathematically relate to disturbance severity. All statistical analyses used Sigmaplot 12.5 and R 3.1.0 statistical software. Relationships were considered significant when $p < 0.10$.

Results

Production and disturbance severity

Forest production was remarkably stable across the gradient of moderate disturbance, with ANPP_w declining significantly only at the highest levels of disturbance severity. Our piecewise regression analysis shows that ANPP_w did not change significantly when the fraction of basal area that senesced was between 9 and $\geq 60\%$. Though our sample size at the highest level of disturbance severity is small ($n = 3$ plots with $> 60\%$ senesced basal area), our analysis suggests that absolute and relative changes in ANPP_w were significant when the fraction of senesced basal area exceeded 66 % and 60 % within a plot ($p = 0.0014$, Figure 2a and 2b). These results suggest

a non-linear response to increasing disturbance severity, in which ANPP_w was resistant to rising moderate disturbance until a threshold was exceeded.

Canopy Structural and Environmental Responses to Increasing Disturbance Severity

Canopy structure varied substantially across the gradient of disturbance severity, affecting the light environment of the subcanopy. The LAI_h of the upper canopy (> 5 m vertical height) decreased significantly with increasing disturbance severity, indicating that plot scale leaf area has not fully recovered five years following the girdling treatment at the highest levels of disturbance ($p = 0.0348$, Figure 3a). Upper canopy openness, a measure of canopy gap size, increased by 1.5 times across the gradient of disturbance ($p = 0.0487$, Figure 3b), with subcanopy light availability increasing in parallel with gap formation ($p = 0.0645$, Figure 3c). Mean subcanopy fAPAR more than doubled from low to high disturbance severities. These results demonstrate that disturbance driven changes to upper canopy structure significantly increased the quantity of light absorbed by the subcanopy.

Ecosystem Responses to Disturbance

As disturbance severity increased, the subcanopy played an increasingly important role in maintaining plot level production. At low levels of disturbance, both the upper canopy and subcanopy sustained ANPP_w, with the relative contribution of the subcanopy increasing as disturbance severity increased. At the highest levels of disturbance severity, subcanopy production increased nearly 10 times ($p = 0.0002$, Appendix B) following peak disturbance and contributed 40 % to total ANPP_w ($p = 0.0014$, Figure 4a).

The emerging functional contribution of the subcanopy with increasing disturbance severity corresponded with improved production efficiency ($p = 0.10$, Figure 5). Production efficiency nearly doubled across the gradient of disturbance severity and was associated with a reduction in LAI_h at high levels of disturbance rather than by an increase in $ANPP_w$. This decline in LAI_h and concurrent stability of $ANPP_w$ suggest improvement in production efficiency was caused by improved leaf-level physiological functioning.

Subcanopy Leaf Physiological, Nitrogen, Morphological Responses to Disturbance Severity

Disturbance-driven increases in subcanopy growth and in production efficiency of the ecosystem coincided with leaf-level changes that are characteristic of sun-adapted leaves. For example, we observed almost a 2-fold increase in red oak foliar N concentrations across the disturbance-related gradient in canopy openness ($p = 0.0011$, Figure 6a). Red maple leaf percent N responded similarly across the same gradient, with a significant 30 % increase from low to high disturbance severity ($p = 0.0733$, Figure 6b). American beech foliar N concentrations were not significantly correlated with canopy openness ($p = 0.2534$, Figure 6c). Concomitant to the general trend of increasing foliar N in subcanopy vegetation was a significant increase in A_{max} with increasing canopy openness for all three dominant subcanopy species (Figure 6d-f). In red oak and red maple there was a 2-fold increase in maximum leaf-level net CO_2 assimilation, with red oak showing the greatest absolute increase in A_{max} with canopy openness. American beech increased its photosynthetic capacity significantly, but to a lesser extent. Subcanopy leaves also responded morphologically to increasing light availability as canopy gaps formed following disturbance. Red maple doubled its LMA across our gradient of canopy openness ($p = 0.036$, Figure 6g), a trend that suggests subcanopy red maple leaves became more morphologically similar to sun-adapted upper canopy leaves as disturbance severity increases. Red oak and American beech

LMAs were not correlated with canopy openness ($p = 0.1445$ and $p = 0.5987$, Figure 6h and 6i). Taken together, leaf N, photosynthesis, and morphology trends demonstrate that leaf-level adjustments were proportional to the level of disturbance severity and associated changes in the local light environment from upper canopy gap formation.

Discussion

We have shown that forest production can exhibit striking resistance to a range of moderate disturbance levels, with the subcanopy playing a key role in compensating for the mortality of dominant canopy trees. Our finding that production was fully sustained following the senescence of more than half of the upper canopy trees within a stand indicates a non-linear response to rising disturbance severity for this forest ecosystem, in which mechanisms are in place that entirely offset lost production up to some disturbance threshold. We found that as disturbance severity increased, an incremental improvement in subcanopy photosynthetic capacity and, consequently, subcanopy ANPP_w contributed to offsetting proportional declines in the upper canopy. We attribute this increase in subcanopy production to higher light availability and leaf nitrogen, which together likely drove increases in ecosystem-scale production efficiency at higher levels of disturbance. These results provide a mechanistic basis for functional resistance across a broad range of disturbance severities, showing that rates of compensatory growth were commensurate with disturbance severity.

Our study is among the first to demonstrate that C storage in wood biomass can exhibit complete resistance across a range of disturbance severities, suggesting an ecologically important non-linear response to rising disturbance intensity. Our finding that ANPP_w was resistant to moderate disturbance is supported by studies showing forests exhibited resistance (Gough et al.

2013; Granier et al. 2008) or rapid resilience (Amiro et al. 2010; Hicke et al. 2012) following a single level of moderate disturbance. Our assessment advances present understanding of how forests respond to a broad range of disturbance severities, demonstrating that production may remain relatively stable as disturbance intensity increases before declining, perhaps precipitously. A large decline in C storage at high disturbance severities is supported by studies conducted at our site and elsewhere showing a significant reduction in production following stand-replacing disturbance (Campbell et al. 2004; Kasian et al. 2006; Gough et al. 2007; Amiro et al. 2010). A non-linear response to increasing disturbance severity has important implications for ecosystem functioning, implying that some ecosystems may undergo substantial structural changes as a result of moderate disturbance without a commensurate functional change.

Sustained production following moderate disturbance at our site corresponded with canopy structural changes that improved production efficiency rather than with leaf area replacement. While production efficiency increased with disturbance severity, LAI_h did not fully recover at higher disturbance severities. Unlike severe stand-replacing disturbance, more moderate disturbances that kill only a subset of trees increase rather than decrease canopy complexity (Cole and Lorimer 2005), which may increase the efficient use of growth-limiting resources (Niinemets 2007; Portsmouth and Niinemets 2007; Campbell et al. 2009; Hardiman et al. 2011, 2013b). The heterogeneous distribution of senescent aspen and birch at our site has significantly increased canopy complexity following the girdling treatment by shifting the distribution of leaf area vertically throughout the canopy from the upper to the lower strata (Hardiman et al. 2013a). An increase in forest canopy complexity has been linked to higher rates of leaf photosynthesis as light becomes more evenly distributed throughout the canopy (Niinemets 2007; Kneeshaw et al. 2011).

At our site, subcanopy leaf physiology, morphology, and N status responses were proportional to disturbance severity and paralleled changes in gap fraction and light availability. With an increase in canopy gap fraction, light reallocation to the subcanopy incrementally caused leaves to become more light-adapted, with foliar N concentrations similar to those of upper canopy leaves (Appendix C). Additionally, all three dominant subcanopy species displayed significant increases in maximum leaf net CO₂ assimilation across the disturbance gradient. LMA displayed similar trends, though this morphological change was only significant in red maple. Other studies show similarly rapid leaf-level acclimation of nutrient status, physiology, and morphology to improved light availability (Naidu and DeLucia 1997; Frak et al. 2001; Portsmouth and Niinemets 2007; Rodriguez-Calcerrada et al. 2008; Gauthier and Jacobs 2009; Delagrange 2010), though lags of up to two years are reported (Jones and Thomas 2007).

Upper canopy and subcanopy vegetation responded rapidly to tree mortality, compensating for production losses from senescent trees. The relative contribution of upper canopy and subcanopy vegetation to production was dependent upon the severity of disturbance, with subcanopy trees contributing more to ANPP_w resistance as disturbance levels increased. A similar production trade-off between upper canopy and subcanopy vegetation has been observed following disturbances in other forest ecosystems (Sabo et al. 2008; Campbell et al. 2009). The subcanopy contribution to total ANPP_w at our site following peak disturbance was within the range reported for other sites. At higher levels of disturbance severity, the subcanopy generated ~ 40 % of total stand production, comparable to the upper limits for other forests (Sabo et al. 2008; Mission et al. 2007). Once basal area senescence exceeded 40 %, upper canopy trees were no longer a net contributor to ANPP_w resistance (Appendix B). Though the production of each

canopy stratum shifted with disturbance severity, their total was sufficient to sustain stable levels of production across a broad gradient until the highest level of disturbance severity examined.

Our findings have implications for forest C management as moderate disturbances increase in frequency and extent (Amiro et al. 2010; Hicke et al. 2012). Our results suggest that forest management strategies aimed at preventing moderate disturbances from pathogens, insects and wind, for example, may not be required to maintain C storage through biomass production. Additionally, more moderate disturbances may minimally alter C storage while increasing ecologically desirable physical complexity, an outcome that is in stark contrast to severe stand-replacing disturbances that severely reduce ecosystem complexity (Seymour et al. 2002; Hardiman et al. 2013a). Physical complexity introduced through moderate disturbance may instead sustain or enhance ecosystem services including animal biodiversity and nutrient retention (Thompson et al. 2011), a notion that forms the basis for emergent sustainable forest management approaches that balance partial timber harvests and ecological objectives.

We caution, however, that sustained forest production following moderate disturbance severity is not universal, with sensitivity to moderate disturbance varying considerably among ecosystems (Amiro et al. 2010). Though production and disturbance severity are non-linearly related at our site, considerable uncertainty remains regarding when and why forest production declines in response to increasing disturbance levels (Gough et al 2013). Additionally, the mechanisms supporting C storage resistance or resilience following disturbance are poorly characterized and may differ among forest ecosystems (but see Thiel and Perakis 2009; Hart et al. 2011). Elucidating the underlying mechanisms that support functional resilience or, at high disturbance severities, prolonged functional decline is critical to improving modeled forecasts of terrestrial C storage as disturbances increase globally (Williams et al. 2012).

REFERENCES

- Amiro BD, Barr AG, Barr JG, Black TA, Bracho R, Brown M, Chen J, Clark KL, Davis KJ, Desai AR, Dore S, Engel V, Fuentes JD, Goldstein AH, Goulden ML, Kolb TE, Lavigne MB, Law BE, Margolis HA, Martin T, McCaughey JH, Mission L, Montes-Helu M, Noormets A, Randerson JT, Starr G, and Xiao J. 2010. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *Journal of Geophysical Research-Biogeosciences* 115. doi:10.1029/2010JG001390
- Birdsey, R, Pregitzer, K, and Lucier, A. 2006. Forest carbon management in the United States: 1600-2100, *Journal of Environmental Quality*, 35, 1461-1469.
- Bradford, JB, Jensen, NR, Domke, GM, D'Amato, AW. 2013. Potential increases in natural disturbance rates could offset forest management impacts on ecosystem carbon stocks. *Forest Ecology and Management* 208: 178-187.
- Campbell, JL, Sun, OJ, and BE Law. 2004. Disturbance and net ecosystem production across three climatically distinct forest landscapes. *Global Biogeochemical Cycles*, 18, GB4017, doi:10.1029/2004GB002236.
- Campbell, J, Alberti G, Martin, J, Law, BE. 2009. Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada, *Forest Ecology and Management*, 257: 453–463.
- Cardinale, BJ, Matulich, KL, Hooper, DU, Bryes, JE, Duffy, E, Gamfeldt, L, Balvanera, P, O'Connor, MI, and Gonzalez, A. 2011. The functional role of producer diversity in ecosystems. *American Journal of Botany* 98(3): 572-592.
- Cole, WG and CG Lorimer. 2005. Probabilities of small-gap capture by sugar maple saplings based on height and crown growth data from felled trees. *Canadian Journal of Forest*

Research 35: 643–655

- Delagrange, S. 2010. Light- and seasonal-induced plasticity in leaf morphology, N partitioning and photosynthetic capacity of two temperate deciduous species. *Environmental and Experimental Botany*, 70(2011): 1-10.
- Frak, E, Roux, XL, Millard, P, Dreyer, E, Jaouen, G, Saint-Joanis, B and R Wendler. 2001. Changes in total leaf nitrogen and partitioning of leaf nitrogen drive photosynthetic acclimation to light in fully developed walnut leaves. *Plant Cell Environ.* 24:1279–1288.
- Frazer, GW, Canham, CD, and Lertzman, KP. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-color fisheye photographs, users manual and program documentation, version 2.0. Simon Fraser University and the Institute of Ecosystem Studies, Burnaby, British Columbia, Canada, and Millbrook, New York, USA.
- Gauthier, MM and Jacobs, DF. 2009. Short-Term Physiological Responses of Black Walnut (*Juglans nigra* L.) to Plantation Thinning. *Forest Science*, 55(3):221-229.
- Goetz, SJ, Bond-Lamberty, B, Law, BE, Hicke, JA, Huang, C, Houghton, RA, McNulty, S, O'Halloran, T, Harmon, M, Meddens, JH, Pfeifer, EM, Mildrexler, D, Kasishke, ES. 2012, Observations and assessments of forest carbon dynamics following disturbance in North America, *Journal of Geophysical Research*, 117, 1-17.
- Gough, CM, Vogel, CF, Harrold, KH, Georges, K, Curtis, PS. 200], The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest, *Global Change Biology*, 13, 1935-1949.
- Gough, C M, Vogel, CS, Schmid, HP, Su, HB, and Curtis, PS. 2008. Multi-year convergence of

- biometric and meteorological estimates of forest carbon storage, *Agricultural and Forest Meteorology*, 148, 158-170.
- Gough, CM, Vogel, CS, Hardiman, B, Curtis, PS. 2010, Wood net primary production resilience in an unmanaged forest transitioning from early to middle succession. *Forest Ecology and Management*, 260, 36-41.
- Gough, CM, Hardiman, BS, Nave, LE, Bohrer, G, Maurer, KD, Vogel, CS, Nadelhoffer, KJ, Curtis, PS. 2013. Sustained carbon uptake and storage following moderate disturbance in a Great Lakes forest. *Ecological Applications*, 23(5): 12012-1215.
- Granier, A, Breda, N, Longdoz, B, Gross, P and Ngao, J. 2008. Ten years of fluxes and stand growth in a young beech forest at Hesse, north-eastern France. *Annals of Forest Science* 65(7):13.
- Gunderson, LH. 2000. Ecological resilience - in theory and application. *Annual Review of Ecology and Systematics*, 31, 425-439.
- Hardiman, BS, Bohrer, G, Gough, CM, Vogel, CS, Curtis, PS. 2011. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest, *Ecology*, 92, 1818-1827.
- Hardiman, BS, Bohrer, G, Gough, CM, and Curtis, PS. 2013a. Canopy structural changes following widespread mortality of canopy dominant trees. *Forests*, 4: 537-552; doi:10.3390/f4030537
- Hardiman, BS, Gough, CM, Halperin, B. 2013b. Maintaining high rates of carbon storage in old forests: A mechanism linking canopy structure to forest function. *Forest Ecology and Management*, 298: 111-119.
- Hart, JL, Bhuta, AAR, Schneider, RM. 2011. Canopy Disturbance Patterns in Secondary

- Hardwood Stands on the Highland Rim of Alabama. *Castanea*, 76(1): 55-63. DOI: 10.2179/10-012.1
- Hicke, JA, Allen, CD, Desai, AR, Dietze, MC, Hall, DJ, Hogg, EH, Kashian, DM, Moore, D, Raffa, KF, Sturrock, RN, and Vogelmann, J. 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology* **18**:7-34.
- Jones, TA and Thomas, SC. 2007. Leaf-level acclimation to gap creation in mature *Acer saccharum* trees. *Tree Physiology*. 27: 281-290.
- Kashian, DM, Romme, WH, Tinker, DB, Turner, MG, and Ryan, MG. 2006. Carbon storage on landscapes with stand-replacing fires, *BioScience*, 56, 598–606.
- Kaye, JP, Hart, SC, Fule, PZ, Covington, WW, Moore, MM, and Kaye, MW. 2005. Initial carbon, nitrogen, and phosphorus fluxes following ponderosa pine restoration treatments. *Ecological Applications* 15:1581–1593.
- Kneeshaw, DD, Harvey, BD, Reyes, GP, Caron, MN, Barlow, S. 2011. Spruce budworm, windthrow and partial cutting: Do different partial disturbances produce different forest structures? *For. Ecol. Manag.* 262, 482–490.
- Kurz, WA, Stinson, G, Rampley, GJ, Dymond, CC, Neilson, ET. 2008. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proceedings of the National Academy of Sciences* 105, 1551–1555.
- McCrary RL, Jokela, EJ. 1998. Canopy dynamics, light interception, and radiation use efficiency of selected loblolly pine families. *For. Sci.*, 44: 64-72.
- McKinley, DC, Ryan, MG, Birdsey, RA, Giardina, CP, Harmon, ME, Heath, LS, Houghton, RA,

- Jackson, RB, Morrison, JF, Murray, BC, Pataki, DE, Skog, KE. 2011. A synthesis of current knowledge on forests and carbon storage in the United States. *Ecological Applications* 21, 1902–1924.
- Mission, L, Baldocchi, DD, Black, TA, Blankn, PD, Brunet, Y, Curiel Yuste, J, Dorsey, JR, Falk, M, Granier, A, Irvine, MR, Jarosz, N, Lamaud, E, Launiainen, D, Law, BE, Longdoz, B, Loustau, D, McKay, M, Paw, KT, Vesala, T, Vickers, D, Wilson, KB, Goldstein, AH. 2007. Partitioning forest fluxes with overstory and understory eddy-covariance measurements: A synthesis based on FLUXNET data. *Agricultural and Forest Meteorology*, 144: 14-32.
- Naidu, SL and DeLucia, EH. 1997. Acclimation of shade-developed leaves on saplings exposed to late-season canopy gaps. *Tree Physiol.* 17:367–376.
- Nave, LE, Vogel, CS, Gough, CM, Curtis, PS. 2009. Contribution of atmospheric nitrogen deposition to net primary productivity in a northern hardwood forest, *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 39, 1108-1118.
- Nave, LE, Gough, CM, Maurer, K, Bohrer, G, Le Moine, J, Munoz, AB, Nadelhoffer, KJ, Sparks, JP, Strahm, BD, Vogel, CS, Curtis, PS. 2011. Disturbance and the resilience of coupled carbon and nitrogen cycling in a north temperate forest. *Journal of Geophysical Research – Biogeosciences* 116, G04016.
- Niinemets, U. 2007. Photosynthesis and resource distribution through plant canopies. *Plant, Cell and Environment*, 30: 1052-1071.
- Nobis, M and Hunziker, U. 2005. Automatic thresholding for hemispherical canopy photographs based on edge detection. *Agricultural and Forest Meteorology*, 128: 243-250.
- Pan, Y, Birdsey, RA, Fang, J, Houghton, R, Kauppi, PE, Kurz, WA, Phillips, OL, Shvidenko, A,

- Lewis, SL, Canadell, JG, Ciais, P, Jackson, RB, Pacala, S, Mcuire, AD, Piao, S, Rautiainen, A, Sitch, S, Hayes, D. 2011. A Large and Persistent Carbon Sink in the World's Forest, *Science*, 333, 988-993.
- Peckham, SD, Gower, ST, Perry, CH, Wilson, BT, Stueve, KM. 2013. Modeling harvest and biomass removal effects on the forest carbon balance of the Midwest, USA. *Environmental Science & Policy* 25, 22–35.
- Portsmouth, A. and Niinemets, U. 2007. Structural and physiological plasticity in response to light and nutrients in five temperate deciduous woody species of contrasting shade tolerance. *Functional Ecology*, 21: 61-77.
- Rodriguez-Calcerrada, J, Reich, PB, Rosenqvist, E, Pardos, JA, Cano, FJ, and Aranda, I. 2008. Leaf physiological versus morphological acclimation to high-light exposure at different stages of foliar development in oak. *Tree Physiology*. 28: 761-771.
- Sabo, KE, Hart, SC, Sieg, CH, and Bailey, JD. 2008. Tradeoffs in overstory and understory aboveground net primary productivity in Southwestern ponderosa pine stands, *Forest Science*, 54, 408-416.
- Scheller, RM, Hua, D, Bolstad, PV, Birdsey, RA, Mladenoff, DJ. 2011. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake states Mesic forests. *Ecological Modelling* 222, 144–153
- Seymour, RS, White, AS, and deMaynadier, PG. 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management* 155:357-367.
- Thiel, AL, and SS Perakis. 2009. Nitrogen Dynamics across silvicultural canopy gaps in young forests of western Oregon. *Forest Ecology and Management*, 258: 273–287.

- Thompson, ID, Okabe, K, Tylianakis, JM, Kumar, P, Brockerhoff, EG, Schellhorn, NA, Parrotta, JA and Nasi, R. 2011. Forest Biodiversity and the Delivery of Ecosystem Goods and Services: Translating Science into Policy. *Bioscience* 61:972-981.
- Tobin, MF, and Reich, PB. 2009. Comparing indices of understory light availability between hemlock and hardwood forest patches. *Canadian Journal of Forest Research* 39:1949–1957.
- Williams, CA, Collatz, GJ, Masek, J, and Goward, SN. 2012. Carbon consequences of forest disturbance and recovery across the conterminous United States. *Global Biogeochemical Cycles* 26.
- Yang, YH, Luo, YQ and Finzi, AC. 2011. Carbon and nitrogen dynamics during forest stand development: a global synthesis. *New Phytologist* 190:977–989.

Figures

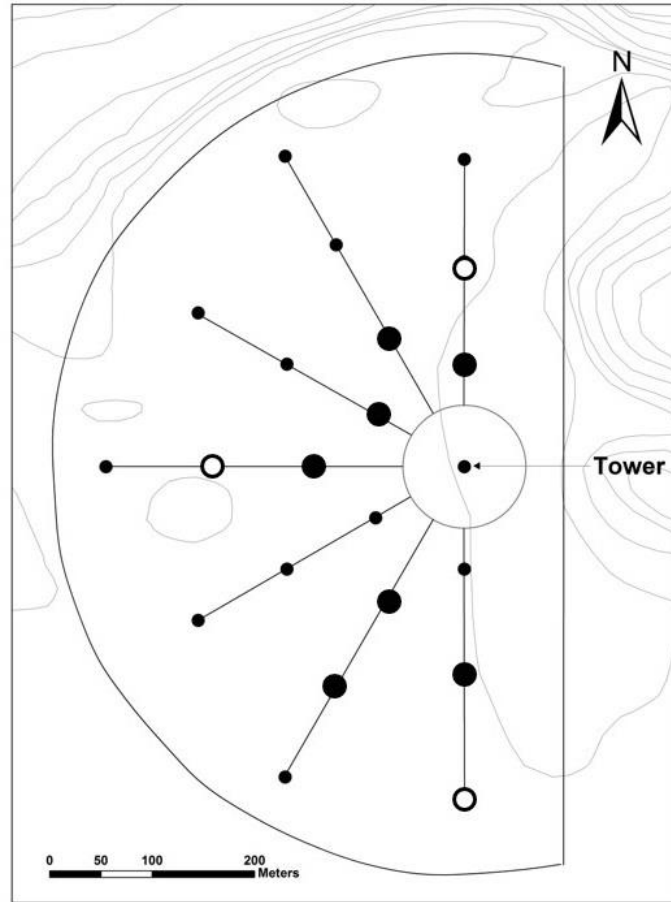


Figure 1: The study design of the Forest Accelerated Succession Experiment (FASSET) at the University of Michigan Biological Station. The semi-circle is the manipulated area, in which transects (lines) and 0.8 ha plots (circles) radiate from a 1.1 ha plot surrounding a meteorological tower. Wood ANPP_w and disturbance severity were quantified in all 21 plots, 0.8 ha plots. Large filled and open circles represent the 10 plots chosen for further measurements in this study. The large filled circles indicate the location of fAPAR analyses.

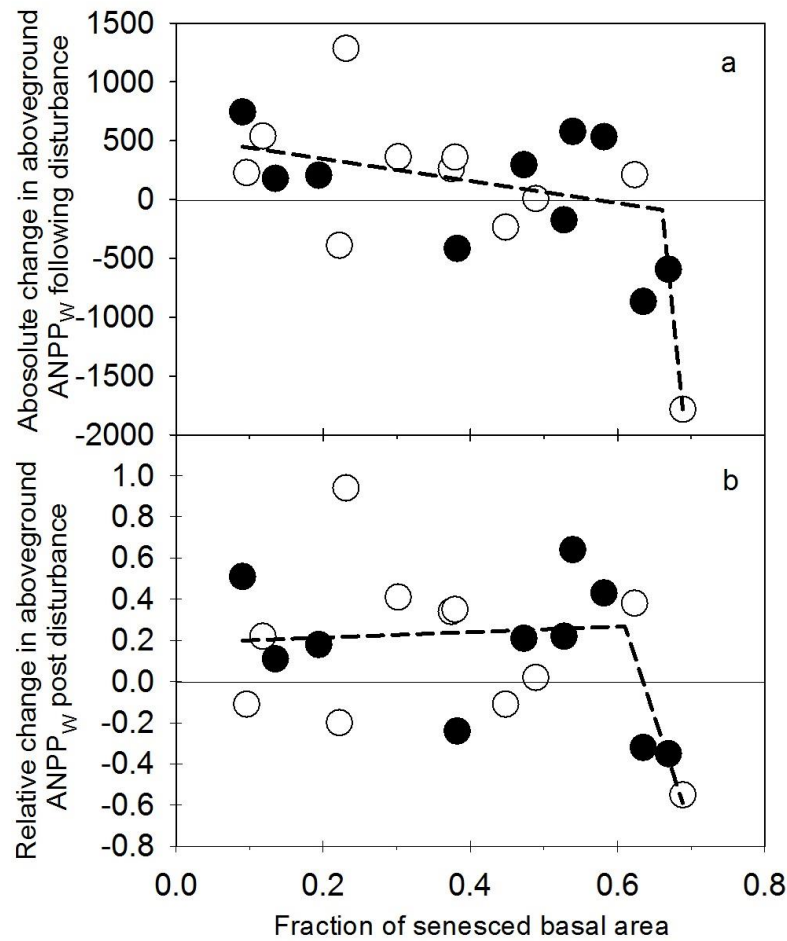


Figure 2. The absolute (a, $r^2 = 0.57$ and $p = 0.0012$) and relative (b, $r^2 = 0.48$, $p = 0.0014$) change in aboveground wood net primary production (ANPP_w) before (2006-2010) and after (2010-2012) peak disturbance in relation to the fraction of senesced tree basal area. Closed circles are the 10 chosen plots and open circles are the remaining 11 plots. The dashed line illustrates the resistance followed by the precipitous decline in production.

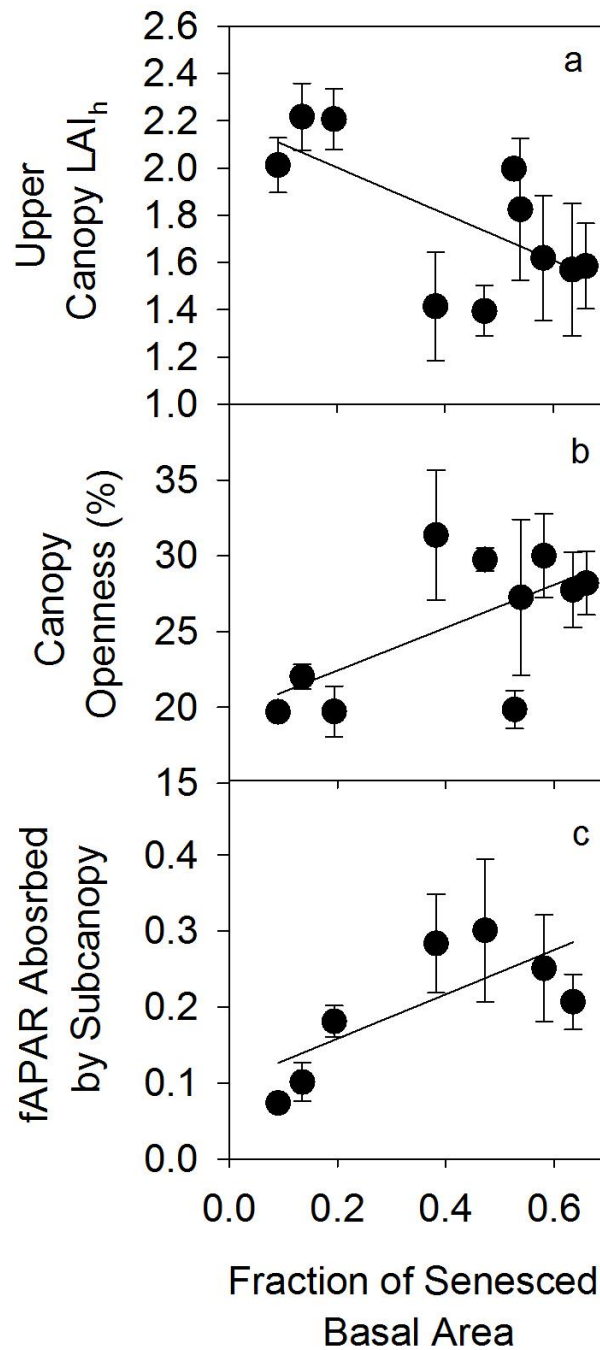


Figure 3. Mean (± 1 S.E.) upper canopy leaf area index (LAI_h) (a, $r^2 = 0.45$, $p = 0.0348$), upper canopy openness (b, $r^2 = 0.40$, $p = 0.0487$), and subcanopy fAPAR (fraction absorbed photosynthetically active radiation (c, $r^2 = 0.46$, $p = 0.0645$) in relation to disturbance severity the fraction of senesced basal area.

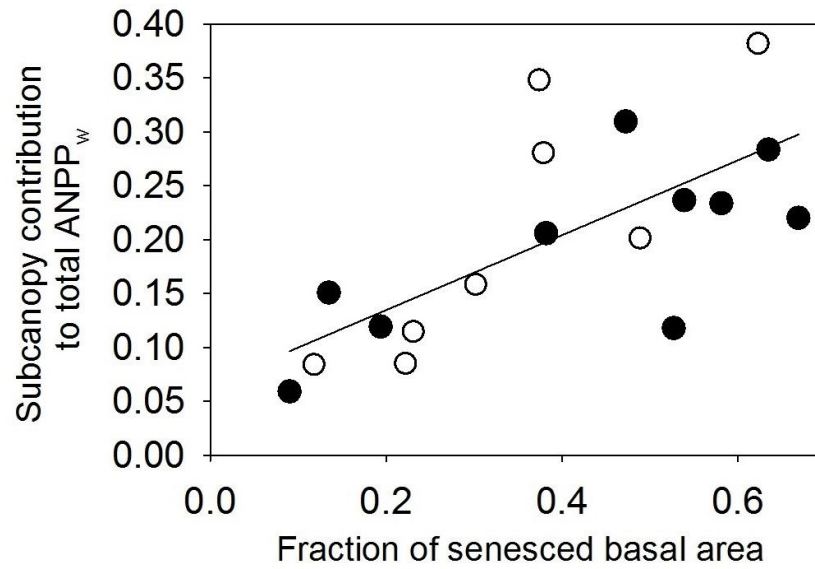


Figure 4. The relative contribution of subcanopy aboveground wood net primary production (ANPP_w) to total ANPP_w in relation to the fraction of senesced basal area ($r^2 = 0.48$ and $p = 0.0014$). All 21 plots are shown while the closed circles represent the subset of 10 measurement intensive plots.

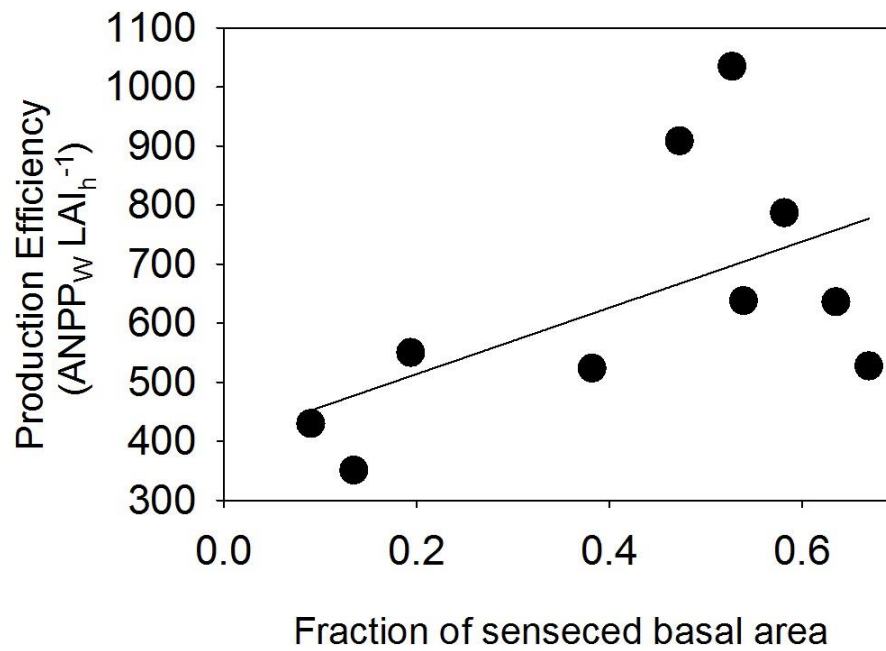


Figure 5. Production-efficiency following peak disturbance in relation to the fraction of senesced basal area ($r^2 = 0.3102$ and $p = 0.0944$). Production efficiency is defined at annual woody net primary production (ANPP_w) divided by leaf area index (LAI_h).

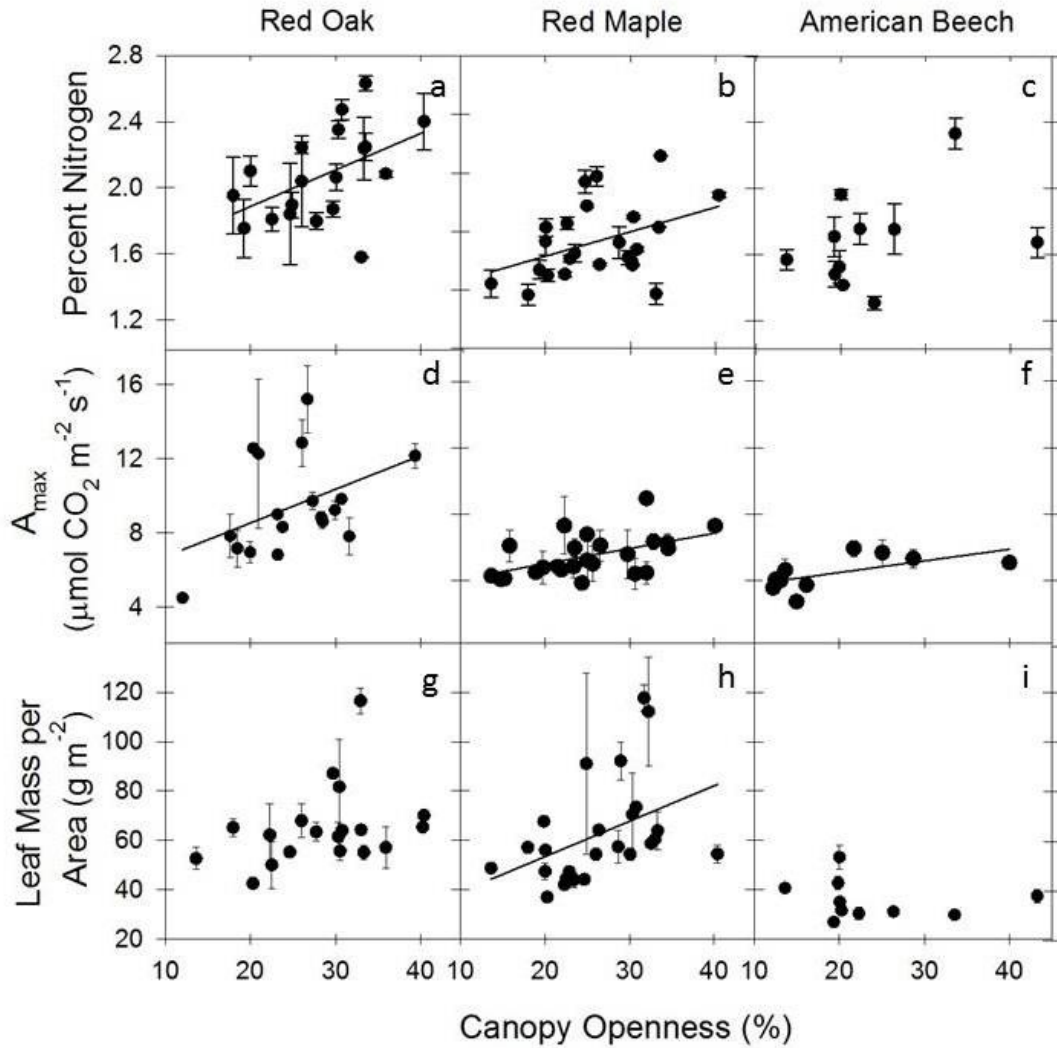
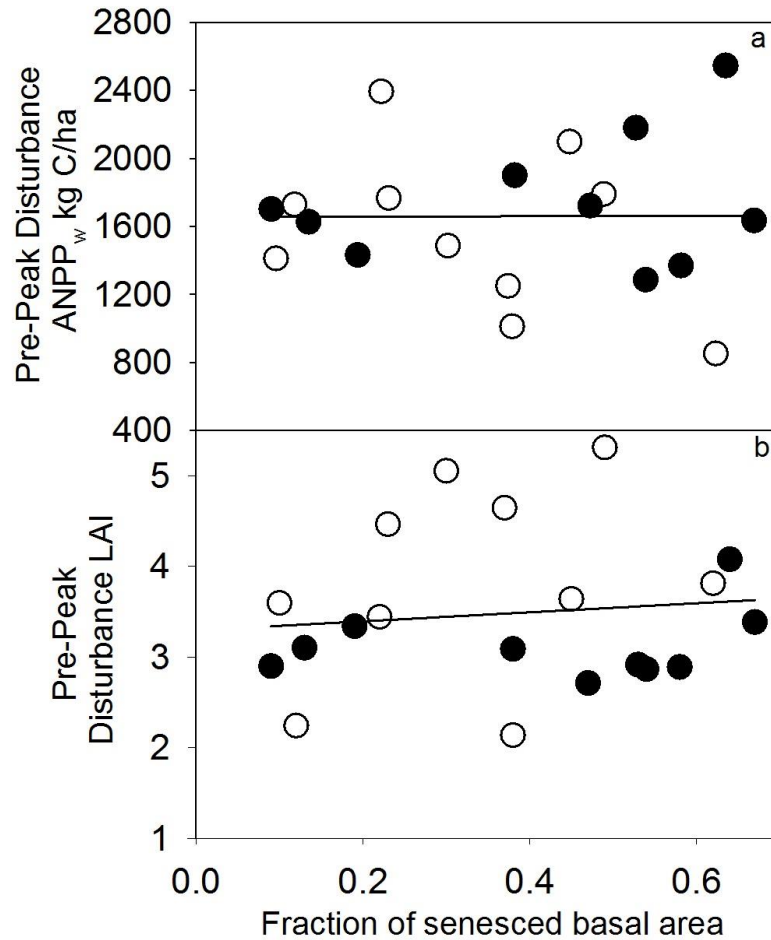
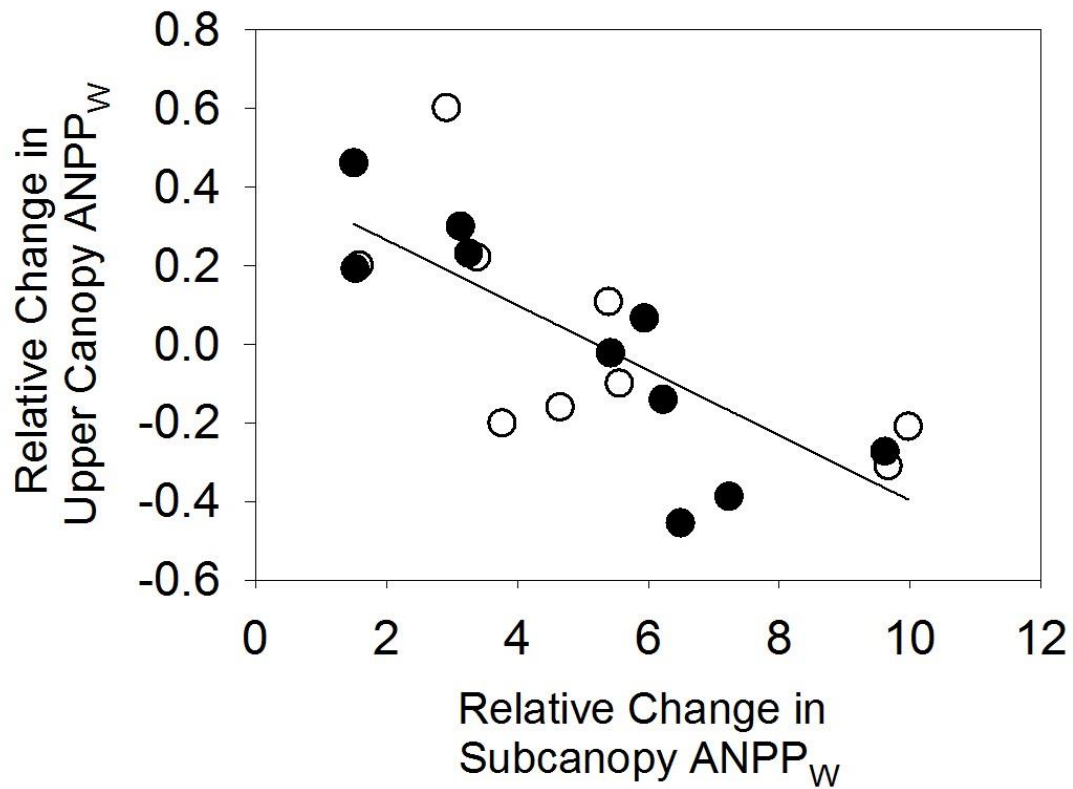


Figure 6. Leaf percent nitrogen (a-c), leaf maximum net CO₂ assimilation (A_{\max}) (d-f), and leaf mass area (g-i) (± 1 S.E.) characteristics in relation to local canopy openness. Measurements of 2-3 leaves were averaged in each 5m subplot rather than at whole plot scale. All regressions shown are significant when $p \leq 0.1$.

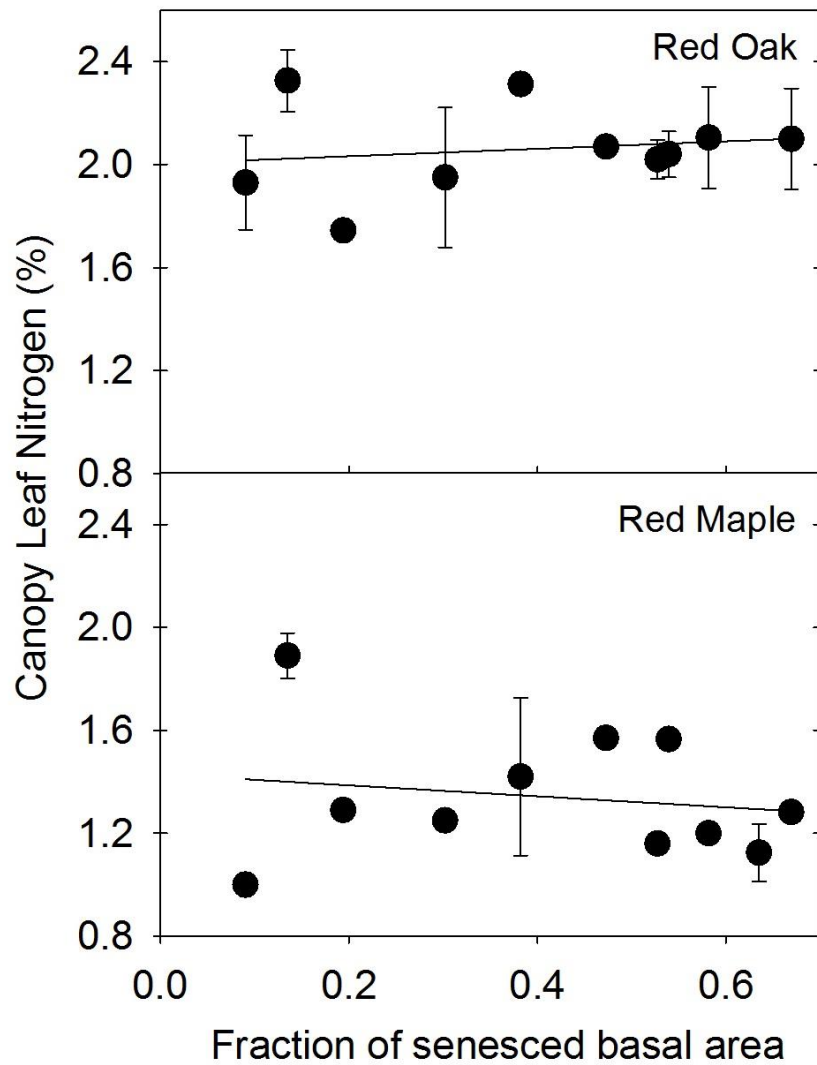
APPENDIX



Appendix A. Aboveground wood net primary production (ANPP_w) (a) and LAI before peak disturbance in 2010 (b). Plot ANPP_w and LAI were not significantly correlated with the fraction of senesced basal area prior to peak disturbance in all 21 plots (closed and open circles) and in the subset of 10 measurement intensive plots (closed circles) ($p > 0.9$ for all relationships), demonstrating that there was no pre-existing relationship between production and disturbance severity.



Appendix B. The relative change before and after peak disturbance in upper canopy ANPP_w in relation to the relative change in subcanopy ANPP_w (b , $r^2 = 0.5794$ and $p = 0.002$). The relative response of ANPP_w to disturbance by the subcanopy exceeded that of the upper canopy, with the subcanopy playing an increasingly important role in supporting resistance as disturbance severity increased.



Appendix C. The relationship between the fraction of senesced basal area and the percent nitrogen of upper canopy leaves (red oak, $p = 0.6421$ and red maple, $p = 0.6124$). Upper canopy leaf N did not differ across disturbance severities, an indication that upper canopy leaves, unlike those of the subcanopy, were already high in N and responded minimally to disturbance.

Appendix 1. Aboveground wood net primary production (ANPP_w) and litter trap leaf area index (LAI_t) for all plots prior to and following peak disturbance, the fraction of tree basal area girdled in each plots, and the 3 most dominant upper canopy tree species in each plot prior to disturbance. Plots and data in bold indicate the 10 plots selected for analysis of fAPAR, percent foliar N, photosynthetic capacity, and canopy openness. [Abbreviations for species here, e.g., Pogr – *Populus grandidentata*, Acru – *Acer rubrum*, Bepa – *Betula papyrifera*, Quru – *Quercus rubra*, Asca – *Acer saccharum*, Pist – *Pinus strobus*].

Plot	Pre-Peak Disturbance ANPP _w	Post-Peak Disturbance ANPP _w	Fraction of Basal Area Senesced	Pre-Peak Disturbance LAI _t	Post-Peak Disturbance LAI _h *	Community Composition based on pre-dist LAI
A1	1370	1905	0.58	2.89	2.53	Pogr, Acru, Bepa
A2	1286	1865	0.54	2.87	3.14	Quru, Pogr, Acru
A3	1250	1514	0.37	4.65	6.10	Asca, Pogr, Quru
B1	1723	2019	0.47	2.71	2.36	Pogr, Quru, Bepa
B2	1012	1373	0.38	2.14	N/A	Quru, Other, Bepa, Acru
B3	1767	3052	0.23	4.47	5.11	Bepa, Asca, Acru
C1	2546	1681	0.64	4.08	2.81	Acru, Pogr, Quru
C2	852	1063	0.64	3.81	N/A	Acru, Quru, Bepa
C3	1486	1851	0.30	5.06	3.07	Quru, Acru, Asca
D1	1901	1587	0.38	3.09	4.06	Quru, Pogr, Acru
D2	1634	1042	0.67	3.39	2.52	Pogr, Acru, Quru
D3	2099	1866	0.45	3.64	N/A	Quru, Acru, Pogr
E1	1790	1798	0.49	5.31	N/A	Acru, Pogr, Quru
E2	1412	1642	0.1	3.60	N/A	Quru, Acru, Pogr
E3	2395	2006	0.22	3.44	N/A	Quru, Pogr, Acru
F1	1627	1808	0.13	3.10	5.53	Quru, Pist, Acru
F2	1703	2449	0.09	2.90	6.19	Quru, Pist, Acru
F3	1730	2270	0.12	2.24	N/A	Quru, Acru, Pist
G1	3214	1431	0.69	N/A	N/A	N/A
G2	1432	1640	0.19	3.34	2.34	Quru, Pogr, Acru
G3	2180	2008	0.53	2.92	1.80	Pogr, Acru, Quru

*LAI_h where LAI_t was unavailable

Vita

Ellen JoAnne Goodrich-Stuart was born in Detroit, Michigan. She graduated from Mills E. Godwin High, Henrico, Virginia in 2008. Ellen received her Bachelor of Arts in Environmental Studies and German Studies with a concentration in Environmental Sciences from University of Richmond, Richmond, Virginia in 2012. She joined the Master of Science in Biology program at Virginia Commonwealth University, Richmond, Virginia in 2012.