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MECHANISMS UNDERLYING PRODUCTION STABILITY IN TEMPERATE DECIDUOUS FORESTS

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

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Bachelor of Science. Fort Lewis College. December, 2016.

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VITA

Shea B. Wales was born on January 3, 1995 in Oakland, California. She is an American Citizen. She graduated from Bishop O'Dowd High School in Oakland, CA in 2009. In December 2016 she received a Bachelor of Science from Fort Lewis College, in Durango, CO. She majored in Environmental and Organismic Biology, and earned a minor in Environmental Policy. She anticipates receiving a Master of Science in Biology from Virginia Commonwealth University in May 2019.

ABSTRACT

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A persistent and reliable future terrestrial carbon (C) sink will depend on how stable forest production is under more variable climate conditions. We examined how age, forest structure, and disturbance history relate to the interannual variability of above-ground wood net primary production (NPPw). Our site in northern Michigan spans two experimental forest chronosequences and three late successional stands; the chronosequences have distinct disturbance histories, originating following either clear cut harvesting ("Cut Only") or clear cut harvesting and fire ("Cut and Burn"), and range from 21 to 108 years old. Annual NPPw was estimated using dendrochronology and site specific allometric equations. We used a portable canopy LiDAR (PCL) system to derive canopy rugosity, a measure of the variability and heterogeneity of vertical and horizontal leaf arrangement, to quantify plot level canopy complexity. Counter to our hypothesis, we found that NPPw stability was greatest in the most frequently disturbed, Cut and Burn stands and lowest in less recently disturbed, late successional forest communities. Opposing trends in chronosequence interannual variation of NPPw indicated that stand age and canopy complexity are not consistently related to production stability. Furthermore, sub-canopy leaf trait properties and breadth were not, as hypothesized, correlated with canopy complexity or NPPw stability. Our mixed findings suggest that multiple factors, including stand age and disturbance history, interact to influence NPPw stability, but also highlight an unexpected dichotomy in which disturbance legacies at our site negatively impact the long-term trajectory of annual forest NPPw, but enhance its interannual stability.

INTRODUCTION

The terrestrial carbon (C) sink is an important buffer against anthropogenic climate change. Fossil fuel combustion, land use changes and cement production are significant sources of atmospheric carbon dioxide (CO2), a potent greenhouse gas responsible for climate change (Canadell et al. 2007, Mohamed et al. 2004). Altering the chemical composition of the atmosphere has caused Earth's mean global temperature to rise at a rate unmatched in recorded geologic history (Williams and Dumroese 2013), and has already precipitated more frequent and severe weather (Johnstone et al. 2016, Seim et al. 2016, Kretchun et al. 2014). Current atmospheric CO2 concentrations are buffered by ocean and land carbon sinks, which combined, store nearly ½ of the anthropogenic CO2 emitted each year. Terrestrial vegetation is responsible for storing 30 % of this C (Bonan et al. 2008, Canadell et al. 2007), and although some uncertainty exists (Chen et al. 2012, Mohamed et al. 2004) in how much and where, northern hemisphere forests are estimated to sequester 10% of anthropogenic CO2 (Gough et al. 2008, Mohamed et al. 2004). Net primary production (NPP) is the amount of CO2 fixed by vegetation minus the amount of CO2 released during respiration. In simpler terms, NPP is the rate of C movement from the atmosphere into plant biomass. The question of what regulates year-to-year stability of forest NPP is a key fundamental knowledge gap relevant to Earth and ecosystem models, and to C management and policy.

A sustained future terrestrial carbon (C) sink will depend on how stable forest production is under an increasingly variable climate. What we know about the stability of the terrestrial C sink is largely informed by meteorological C flux (Musavi et al. 2017) and satellite (Mohamed et al. 2004) data that assesses inter-annual variation (IAV) of production on a global scale. These coarse scale analyses establish strong linkages between forest stand age, species diversity and production stability, but lack the mechanistic focus required to explain these relationships on a more regional or ecosystem scale.

The limited number of studies that do exist on the topic suggest production stability is variable across ecosystems and climatic conditions, and sensitive to disturbance. In tropical systems, where drought is rare, high IAV was correlated with variable precipitation (Mohamed et al. 2004). In temperate forests, IAV is most heavily influenced by photosynthetically active radiation (PAR; the wavelengths of light plants use to photosynthesize) and temperature (Gough et al. 2008, Mohamed et al. 2004), but overall NPP showed greater stability. Differences in IAV among ecosystems may arise when disturbance affects the suite of physiological and structural attributes available to maintain NPP under an array of conditions (Mohamed et al. 2004). It follows then, that systems more equipped to respond -- via a broad complement of physiological traits -- to a range of environmental stimuli, will display less sensitivity to climatic variability. A forest with a low IAV could signal greater physiological breadth, less sensitivity, and more sustained ecosystem structure and function over time (Musavi et al. 2017, Mohamed et al. 2004).

Structurally complex forests may host a broad suite of plant traits and translate to greater NPP stability. Forest complexity is shaped by climate, disturbance and shifts in species composition over time (Thom and Keeton 2019, Atkins et al. 2018). Forest age, which increases following a stand replacing disturbance, can stabilize production through improved soil conditions and fertility (Thom et al. 2019, Musavi 2017). Age is also associated with increased heterogeneity of canopy structure, which develops as succession occurs (Thom and Keeton 2019, Atkins et al. 2018, Fotis et al. 2017). This structural complexity leads to increased sub-canopy light penetration and triggers morphological and physiological adjustments that enhance light use efficiency in a variety of light conditions (Scheuermann et al. 2018, Musavi et al. 2017, Fotis et al. 2017, Niinemets et al. 2007). Thus, leaves in structurally complex forests may span a broader range of traits, affecting the magnitude and stability of production (Thom et al. 2019, Niinemets et al. 2010, Ishii and Asano et al. 2010, Niinemets et al. 2007).

We characterized interannual changes in wood NPP in two experimental forest chronosequences (spatially distinct, but related sites representing a range of forest ages) and three late successional forest stands. Specifically, we focused on how production stability relates to canopy complexity, and modifiers of forest structure, age and disturbance history. Our research examined (1) how IAV changes with age and disturbance history to evaluate if stands with greater canopy structural complexity have higher NPP stability. A second goal (2) was to evaluate whether a larger array of subcanopy leaf physiological and morphological trait expression is linked to greater canopy complexity and production stability.

METHODS

Study Site

Our site (45^{o}35'N 84^{o}43'W) is located in Northern Michigan at the University of Michigan Biological Station (UMBS). Short-lived, early successional Bigtooth Aspen (*Populus grandidentata*) and Paper Birch (*Betula papyrifera*) are in natural decline. Replacing them are primarily Red Oak (*Quercus rubra; QURU*) and Red Maple (*Acer rubrum; ACRU*), while later successional Sugar Maple (*Acer saccharum*), Eastern White Pine (*Pinus strobus; PIST*), Red Pine (*Pinus resinosa; PIRE*) and American Beech (*Fagus grandifolia; FAGR*) are gaining abundance (Stuart-Haëntjens, et al. 2015, Hardiman et al. 2011, Gough et al. 2010).

Pervasive logging in the late 1800s and early 1900s fundamentally changed the trajectory of Michigan's forests by fully rewinding ecosystem development and succession. Clear cut harvesting and subsequent burns abruptly converted multi-aged, structurally complex stands to much simpler, even-aged ones (Hardiman et al. 2011, Gough et al. 2007, Friedman and Reich 2005, Frelich and Reich 1995, Mitchell and Robson 1950). This land-use history makes our site regionally representative and provides us with an excellent position from which to examine the ecological consequences of disturbance and the implications of these widespread structural changes on carbon cycling rates and stability (Hardiman et al. 2011, Gough et al. 2007).

Clear-cut logging at and around UMBS occurred in 1911, and following subsequent forest re-growth, two experimental chronosequences were established (Table 1). A chronosequences is a series of spatially distinct stands that represent a range of forest ages. Each chronosequence includes four stands varying in age that were experimentally clear-cut harvested ("Cut Only") or clear-cut harvested and burned (“Cut and Burn”). Our site also includes three late successional forest communities located within 3 km of the two experimental chronosequences. Each stand contains two or three circular, 0.1 hectare (ha) plots (n = 29), with the exception of the 1998 stand, which allowed for only two rectangular 0.14 and 0.06 ha plots (Table 1*).

Long-term and study period climate assessment (Temperature and PAR)

Mean annual temperature, from 1897 to 2016, in Emmet County, MI was obtained from NOAA (National Centers for Environmental Information). Starting in 2016, eleven 10-year coefficients of variation (CV) in temperature were calculated. Mean annual air temperature and photosynthetically active radiation (PAR) data was obtained from the proximally located UMB AmeriFlux tower.

Net Primary Production of aboveground wood (NPP_w)

We estimated aboveground wood net primary production (NPPw) using dendrochronology. In 2017, the stems within each plot were censused for diameter at breast height (DBH; 1.37 m) and species (> 8 cm DBH). An increment borer was used to core a subset of censused stems (n = 318 total). In each plot, individuals were selected for coring based on species weighted basal area. The number of cores collected per plot ranged from nine to fourteen, depending on species composition and because a minimum of two individuals from each species were sampled.

We used an EPSON Expression 12000XL (Regent Instruments LA2400) scanner paired WinDENDRO (Regent Instruments, Québec, Canada) software to scan, digitize, and estimate the yearly growth (i.e., wood, xylem) increment (YGI) of each tree sampled from 2006 through 2016. YGIs were subtracted from the 2017 DBH to reconstruct ten annual DBH estimates for each tree. Yearly individual tree biomass (i.e., wood mass) was calculated using DBH and species -site or -region specific wood mass allometries:

$$Biomass = a(year\_DBH^{b})$$

The wood production of each cored tree was calculated as the year to year to changes in wood biomass, 2006 - 2016. Production was then scaled up from the individual to the stand by applying species-specific relative growth rates (RGRs) to the remaining population of trees and summing the total wood production of individual trees in a plot. To estimate relative growth rate (RGR), each individual tree production value was divided by the total wood biomass of the corresponding growth year.

When scaling up from directly cored individuals to the whole forest census, we assessed which factors influenced relative growth rate (RGR; dependent variable) using an ANCOVA and DBH, species and stand, as explanatory variables. Modeling indicated that species and stand, but not DBH, affected RGR. Yearly DBH and biomass were calculated for censused stems using the same method as previously stated. Species-, stand-, and year- specific RGRs and biomass were then multiplied to produce an estimate of NPPw (kg wood C mass) for each year. Individual tree NPPw, in each plot, was then summed and expressed on a carbon (C) per hectare (ha) scale, where 0.48 is the carbon fraction of dry wood.

$$NPP\ (kg\ wood\ C\ mass) * 0.48 / plot\ size$$

Lastly, we calculated the coefficient of variation (CV) of NPPw for each plot, to quantify the variability of NPPw over time.

Canopy Rugosity - Forest Structural Complexity

We quantified forest structural complexity using canopy rugosity. A measure of the variability and heterogeneity of vertical and horizontal leaf arrangement (Hardiman et al. 2013) that integrates leaf clumping, gaps and canopy height. Rugosity data was collected using a portable canopy LiDAR (PCL) system, which was worn by an operator while walking a pre-marked 40 meter transect passing through the center of each plot (n = 28; one DBF plot skipped). The data from each plot was then derived from a point cloud using the open R package, *forestr* (Atkins et al. 2017).

Leaf Level Physiological and Morphological traits

Our sampling of leaf physiological and morphological traits was designed to quantify subcanopy leaf trait means and variability within and between species. We focused our sampling efforts on three broadleaf (ACRU, QURU and FAGR) and two needleleaf (PIST and PIRE) species, common in all plots. Average plot leaf mass per area (LMA) was produced from three broad-leaf species, while fluorescence intensity (Fs) incorporated both broadleaf and needleleaf species.

Plots were sampled based on species presence, with up to eight individuals from each species selected. Trait measurements were taken on three leaves, chosen at random, from each individual (Total leaves measured: LMA n = 1542 and Fs n = 2541). Because of limited upper canopy access, we sampled only subcanopy leaves within 3 meters of the forest floor. Plot trait values were produced from a plot average.

Leaf mass per area (LMA), a morphological trait linked to light capture and primary production, was used to evaluate the form and structure of leaves. Leaf area was measured on fresh samples using a LI-3100C Area Meter (LI-COR Inc. Lincoln, NE, USA). Following drying at 55°C, leaves were weighed for mass.

We used Fluorescence intensity (Fs) as an instantaneous surrogate for leaf-level photosynthetic rate under ambient conditions. Fs measurements we taken on clear, windless days using an Opti-Sciences Y(II) Meter (Opti-Sciences Inc. Hudson, NH, USA).

Statistical analysis

Our results' statistical approach followed our objectives to examine how (Obj. 1) disturbance legacy, age and canopy rugosity are related to production stability (Obj. 2) and to determine if greater subcanopy trait variability is linked to greater NPPw stability.

We used an ANCOVA, with CV of NPPw as the dependent variable, age as the co-variate, and disturbance quantity as the explanatory variable (Once - Late succession; Twice - Cut Only; Thrice - Cut and Burn), to compare the production IAV of forest types with different disturbance histories.

Using a priori evidence for non-linear changes in mean NPP and canopy structure over time (Scheuermann et al. 2017, Pedro et al. 2017, Hardiman et al. 2013b), we ranked linear and curvilinear model fits. Given our limited sample size, linear, two parameter or inverse first-order models were selected based on adjusted R^2 values. Model selection and fitting procedure considered both model complexity (i.e., linear and non-linear fits) and individual and combined models. To address Obj. 1 and Obj. 2, we compared the variability of NPPw in the Cut and Burn and Cut Only chronosequences separately (Fig. 2A, 3, 4, Appendix I). When chronosequence slope estimates had overlapping 95% confidence intervals, we presented a single regression line (Fig 2B). Models were considered significant when $P < 0.05$, or moderately significant when $P < 0.1$. Statistical analysis was conducted in SigmaPlot 14.0. For clarity, our figures display a single stand value produced from plot means.

RESULTS

Climate trends and variability

Local air temperatures increased in the last century, with substantial interannual variability in air temperature and photosynthetically active radiation (PAR) during the last decade. A significant rise from 1897 to 2016 in mean annual air temperature, of 1.68 ^{o}C, was recorded for Emmet County, MI (Fig 1A; $P < 0.0001$, $R^2 = 0.25$). Interannual variability in air temperature, expressed as the 10-year coefficient of variation (CV), reached a maximum of >25 % in the 1920's and exceeded 15 % in the most recent decade (Fig 1B). From 2006 through 2016, our period of NPPw observation, we found that mean annual air temperature and photosynthetically active radiation (PAR) varied from year to year, as much as 4^{o}C (Fig 1C) and >100 μmol m^{-2} s^{-1} (Fig 1D). This degree of climate variability is large enough to drive year-to-year variation in C storage in nearby forests (Gough et al. 2008).

Production stability and disturbance history

NPPw stability was greatest in the most frequently disturbed forest chronosequence and lowest in late successional stands (Fig 2). The Cut Only stands had statistically similar mean CV of NPPw values compared to the other two forest types. The Cut and Burn CV of NPPw was significantly lower, by more than a quarter, than that of the late successional stands ($p < 0.05$).

Production stability and stand age

The Cut and Burn and Cut Only stands displayed opposing NPPw stability trends over time. Cut Only stands exhibited a significant curve-linear decline with age in the 10-yr CV of NPP_w, indicating greater NPPw stability in older stands. The CV of NPP_w declined over 7 decades by nearly half, but this trend was largely driven by a high interannual variation of 11 % in the young 32-yr-old stand (Fig 3A: p = < 0.0441, Adj $R^2 = 0.31$). In Cut and Burn stands, the trend was the opposite, with CV of NPP_w increasing from 5 % to 8 % over a ~60 year period of development (Fig 3A: $p = 0.0619$, Adj $R^2 = 0.31$). In our late successional forest communities, age does not result in greater production stability. Instead, these substantially older (DBF = 169, ENF and MIX = 134 yrs old) stands display comparable, if not slightly higher, interannual production variability (Fig 3A).

Canopy rugosity and stand age

Though changes with forest age in NPP_w stability differed between forest chronosequences, the successional trajectory of canopy structural complexity development was the same. The Cut and Burn and Cut Only stands exhibited a common significant increase in canopy rugosity (Fig 3B, p = < 0.0001, Adj R^2 = 0.77). Late successional forests mapped onto this rugosity-age trend, with canopies 1.5 - 2 times more complex than the oldest, most rugose chronosequence stands.

Production stability and canopy rugosity

Because canopy rugosity and stand age were strongly correlated, the relationships between NPP_w stability and canopy rugosity in the two chronosequences mirrored those between NPP_w stability and age (Fig 4). The CV of NPP_w within the Cut Only chronosequence showed a significant curve-linear decline as rugosity increased, dropping from about 11 % to 7 % across the experimental chronosequence rugosity range (Fig 4: p = 0.0345, Adj R^2 = 0.34). Canopy rugosity jumped from 3 m to almost 7 m between the two youngest Cut Only stands, and corresponded with abrupt decline in production variability. The interannual production variability of the Cut and Burn chronosequence increased significantly, by more than 2 % over the course of canopy development (Fig 4: P = 0.0487, Adj R^2 = 0.37).

Sub-canopy leaf morphological and physiological traits

Canopy rugosity, which was variably tied to NPPw stability, was not a consistent predictor of morphological or physiological trait means and variability. Our sampling approach was designed to capture the trait variability within and between species, so for reference we show plot means for each species (Fig 5A, B). The Cut Only chronosequence did not demonstrate any significant relationships between rugosity and mean LMA, CV of LMA or CV of Fs. Cut Only mean Fs did, however, increase significantly with rugosity (Fig 5D: p = 0.0007, Adj R^2 = 0.71). In the Cut and Burn chronosequence trait means and CVs displayed more significant associations with rugosity. As canopy rugosity increased in the Cut and Burn stands, the mean sub-canopy leaf mass per area (LMA) decreased significantly (Fig 5C: p = 0.0074, Adj R^2 = 0.62) and the variability of LMA increased marginally (Fig 5E: p = 0.0473, Adj R^2 = 0.05). Mean Fs in Cut and Burn stands was not related to rugosity, but the variability of Fs declined significantly with increasing rugosity (Fig 5F: p = 0.0097, Adj R^2 = 0.59). Results in and between chronosequences indicate that the variability of canopy arrangement does not match that of sub-canopy traits. Together, these highly mixed results illustrate that no clear pattern emerged linking NPPw stability to canopy complexity-constrained leaf trait characteristics.

DISCUSSION

Legacy of disturbance influences IAV

We found that the more severely disturbed Cut and Burn stands exhibited greater production stability than the least disturbed, late successional stands. This result was counter to our hypothesis that disturbance reduces NPP stability (Fig 2). Though several studies suggest disturbance may increase structural and functional heterogeneity and variability (Thom and Keeton 2019, Stuart-Haëntjens et al. 2015, Gough et al. 2013), our unanticipated result may be the secondary effect of a downward shift in production following repeated, severe disturbance (Gough et al. 2008). Prior work at our site demonstrated that repeated Cut and Burn disturbance resulted in reduced site fertility, leaf area index (LAI), and production for several decades (Gough et al. 2008, Scheuermann et al. 2018). Data from forested ecosystems are lacking, but a grassland study showed lower NPP was associated with less interannual variability and greater production stability (Craven 2018). Future work should focus on whether the inverse relationship between NPP magnitude and stability, observed in grasslands, applies to forested ecosystems and should identify the mechanisms that account for observed differences in functional stability among ecosystems following disturbance.

Role of forest Age and structural complexity on IAV

Our results indicate that neither forest age nor structural complexity were consistently linked to production stability. The chronosequences displayed divergent trends, exhibiting a loss of NPP stability in Cut and Burn stands and a gain in Cut Only (Fig 3A, 4) over both the age and canopy rugosity continuum. These opposing trends were primarily driven by differences in the youngest, least structurally complex chronosequence stands. Our finding of increasing stability in the Cut Only stands is consistent with work by Musavi et al. 2017, who found a strong positive relationship between stand age and production stability. They reasoned that as stands age, increasing site quality, species diversity and structural complexity promote more complementarity of resource use and enhance production stability (Musavi et al. 2017, Gough et al. 2007). However, the opposing relationship of the Cut and Burn stands indicates that advancing stand age and concurrent increases in structural complexity do not universally lead to improved NPP stability.

We hypothesized that canopy rugosity will follow similar mechanisms as species diversity, driving production stability through increased light absorption and use efficiency (Thom and Keeton 2019, Scheuermann et al. 2018, Fotis et al. 2017). A large body of work describes the stabilizing role of species diversity, which can broaden the range of environmental conditions within which an ecosystem can accrue biomass (Mandal et al 2018, Pollastrini et al. 2017, Loreau and Mazancourt 2013, Blüthgen and Klein 2011, Ishii et al. 2004, Bengtsson et al. 2000). A broader array of plant traits or functions, available when species richness is high, can promote NPP stability through the more complete acquisition and efficient resource use (Musavi 2017, Ishii et al. 2004, Bengtsson et al. 2000). Species richness at our site is not strongly correlated with age or structural complexity as is commonly assumed (Scheuermann et al. 2018, Musavi 2017, Hardiman et al. 2011), indicating that diversity is an unlikely driver of stability and that canopy rugosity can develop over time even without progressive increases in species richness (Fig 3B, Scheuermann et al. 2018). In older, more complex forest stands, greater subcanopy light transmission has been linked to more complete light absorption and higher NPP (Appendix I; Atkins et al. 2018, Fotis et al. 2017, Hardiman et al. 2011), but in the case of our results, not improved production stability (Fig 4).

Leaf level traits and canopy rugosity

We hypothesized that leaf trait complementarity would be greater in more structurally complex stands, thereby facilitating production stability. However, we observed no clear linkages, especially between the heterogeneity of canopy structural arrangement and the variability of sub-canopy leaf traits. The dominant light environment of the subcanopy appeared to shape leaf trait means and variability instead. A decline in the Cut and Burn mean leaf mass per area (LMA; Fig 5C), could have been caused by progressive shading of the sub-canopy over stand development (Fotis et al. 2017). Furthermore, the likelihood of self-shading is increased in tall, higher latitude forests, like ours, that experience lower solar angles (Smith et al. 1989). The shift towards a more shade-acclimated subcanopy could be beneficial in that shade-leaf phenotypes could increase LAI and light use efficiency (LUE) in low light conditions (Fotis et al. 2017, Hardiman et al. 2011, Ishii et al. 2004). This sun to shade leaf morphological transition may explain greater ambient leaf fluorescence (Fs) with increasing rugosity in the Cut Only chronosequence (Fig 5D; Fotis et al. 2017, Hardiman et al. 2011), but may not be meaningful within the context of production stability. Our results are too variable over our complexity gradient to extrapolate general or reliable conclusions from trends in the CV of LMA and Fs (Fig 5E, F). Instead, our data suggests that the sub-canopy may not be the best or only place to examine leaf-trait complementarity, and that there is a need for a deeper understanding of the relationships between light, canopy rugosity and production stability.

Conclusion

The reliability of our terrestrial carbon (C) sink will depend on how stable forest production is under an increasingly variable climate. Canopy rugosity, which exerts a strong influence over forest light distribution and absorption, failed to explain trends in interannual production variability as hypothesized. Instead, our results indicate that more frequently disturbed, Cut and Burn stands had higher production stability than less disturbed, late successional forest communities. The drivers of production stability, such as trait complementarity, structure, and disturbance, appear variable among forest ecosystems, despite prevailing theory and some high-profile papers (e.g., Musavi 2017). Future work should extend our assessment of forest morphological and physiological trait variability outside of the sub-canopy and more exhaustively address the effect of disturbance on production stability.

REFERENCES

Atkins, J., Fahey, R., Hardiman, B., & Gough, C. (2018). Forest Canopy Structural Complexity and Light Absorption Relationships at the Subcontinental Scale. Journal of Geophysical Research: Biogeosciences, 123(4), 1387-1405.

Atkins, J., Hardiman, B., Morin, T., Stovall, A., Zimmerman, N., & Gough, C. M. (2017). forestr: Calculates Forest and Canopy Structural Metrics. R Package Version 1.0. http://github.com/atkinsjeff/forestr

Bengtsson, Nilsson, Franc, & Menozzi. (2000). Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management, 132(1), 39-50.

Blüthgen, N. and Klein, A. (2011). Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. Basic and Applied Ecology. 12(4), 282-291.

Bonan, G. (2008). Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science (New York, N.Y.), 320(5882), 1444-9.

Canadell, Corinne Le Quéré, Michael R. Raupach, Christopher B. Field, Erik T. Buitenhuis, Philippe Ciais, . . . Gregg Marland. (2007). Contributions to accelerating atmospheric CO2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proceedings of the National Academy of Sciences, 104(47), 18866-18870.

Chen, J., Mo, G., Pisek, J., Liu, J., Deng, F., Ishizawa, M., & Chan, D. (2012). Effects of foliage clumping on the estimation of global terrestrial gross primary productivity. Global Biogeochemical Cycles, 26(1), GB1019.

Craven, D., Eisenhauer, N., Pearse, W., Hautier, Y., Isbell, F., Roscher, C., . . . Manning, P. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. Nature Ecology & Evolution, 2(10), 1579-1587.

Fotis, A., & Curtis, P. (2017). Effects of structural complexity on within-canopy light environments and leaf traits in a northern mixed deciduous forest. Tree Physiology, 37(10), 1426-1435.

Frelich, L., & Reich, P. (1995). Spatial Patterns and Succession in a Minnesota Southern-Boreal Forest. Ecological Monographs, 65(3), 325-346.

Friedman, S., & Reich, P. (2005). Regional legacies of logging: Departure from presettlement forest conditions in northern Minnesota. Ecological Applications, 15(2), 726-744.

Gough, C., Hardiman, B., Nave, L., Bohrer, G., Maurer, K., Vogel, C., . . . Curtis, P. (2013). Sustained carbon uptake and storage following moderate disturbance in a Great Lakes forest. Ecological Applications, 23(5), 1202-1215.

Gough, C., Vogel, C., Harrold, K., George, K., & Curtis, P. (2007). The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. Global Change Biology, 13(9), 1935-1949.

Gough, C., Vogel, C., Schmid, H., & Curtis, P. (2008). Controls on Annual Forest Carbon Storage: Lessons from the Past and Predictions for the Future. BioScience, 58(7), 609-622.

Gough, Vogel, Hardiman, & Curtis. (2010). Wood net primary production resilience in an unmanaged forest transitioning from early to middle succession. Forest Ecology and Management, 260(1), 36-41.

Hardiman, B., Bohrer, G., Gough, C., Vogel, C., & Curtis, P. (2011). The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology, 92(9), 1818-1827.

Ishii, H & Tanabe, S & Hiura, T. (2004). Exploring the Relationships Among Canopy Structure, Stand Productivity, and Biodiversity of Temperate Forest Ecosystems. Forest Science. 50(3). 342-355.

Ishii, H., & Asano, S. (2010). The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests. Ecological Research, 25(4), 715-722.

Johnstone, J., Allen, C., Franklin, J., Frelich, L., Harvey, B., Higuera, P., . . . Turner, M. (2016). Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment, 14(7), 369-378.

Kretchun, A., Scheller, R., Lucash, M., Clark, K., Hom J., Tuyl, S. (2014). Predicted effects of gypsy moth defoliation and climate change on forest carbon dynamics in the new jersey pine barrens. PLoS One. 9(8): e102531.

Loreau, M., & Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. Ecology Letters, 16(1), 106-115.

Mandal, S., Shurin, J., Efroymson, R., & Mathews, T. (2018). Functional divergence in nitrogen uptake rates explains diversity-productivity relationship in microalgal communities. Ecosphere, 9(5), E02228.

Mitchell, J., Lemay, Neil, & Wisconsin. (1952). Forest fires and forest-fire control in Wisconsin. Wisconsin State Conservation Commission in cooperation with U. S. Dept. of Agriculture, Forest Service.

Mohamed, Babiker, Chen, Ikeda, Ohta, & Kato. (2004). The role of climate variability in the inter-annual variation of terrestrial net primary production (NPP). Science of the Total Environment, 332(1), 123-137.

Niinemets, &. (2007). Photosynthesis and resource distribution through plant canopies. Plant, Cell & Environment, 30(9), 1052-1071.

Niinemets, &. (2010). A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecological Research, 25(4), 693-714.

Peng, & Apps. (1999). Modelling the response of net primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. Ecological Modelling, 122(3), 175-193.

Pollastrini, M., Nogales, A., Benavides, R., Bonal, D., Finer, L., Fotelli, M., . . . Bussotti, F. (2017). Tree diversity affects chlorophyll a fluorescence and other leaf traits of tree species in a boreal forest. Tree Physiology, 37(2), 199-208.

Scheuermann, C., Nave, M., Fahey, L., Nadelhoffer, E., & Gough, R. (2018). Effects of canopy structure and species diversity on primary production in upper Great Lakes forests. Oecologia, 188(2), 405-415.

Seim, A., Omurova, G., Azisov, E., Musuraliev, K., Aliev, K., Tulyaganov, T., . . . Linderholm, W. (2016). Climate Change Increases Drought Stress of Juniper Trees in the Mountains of Central Asia. PLoS ONE, 11(4), E0153888.

Smith, W., Knapp, A., & Reiners, W. (1989). Penumbral Effects on Sunlight Penetration in Plant Communities. Ecology, 70(6), 1603-1609.

Stuart-Haëntjens, E., Curtis, P., Fahey, R., Vogel, C., & Gough, C. (2015). Net primary production of a temperate deciduous forest exhibits a threshold response to increasing disturbance severity. Ecology, 96(9), 2478-2487.

Talie Musavi, Mirco Migliavacca, Markus Reichstein, Jens Kattge, Christian Wirth, T. Andrew Black, . . . Miguel D. Mahecha. (2017). Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity. Nature Ecology & Evolution, 1(2), 48.

Thom, D., Golivets, M., Edling, L., Meigs, G., Gourevitch, J., Sonter, L., . . . Keeton, W. (2019). The climate sensitivity of carbon, timber, and species richness co-varies with forest age in boreal-temperate North America. Global Change Biology, 15, 2019.

Thom, D., Keeton, W. (2019). Stand structure drives disparities in carbon storage in northern hardwood-conifer forests. Forest Ecology and Management, 442, 10-20.

White, Zak, & Barnes. (2004). Biomass accumulation and soil nitrogen availability in an 87-year-old *Populus grandidentata* chronosequence. Forest Ecology and Management, 191(1), 121-127.

Williams, M., & Dumroese, R. (2013). Preparing for Climate Change: Forestry and Assisted Migration. Journal of Forestry, 111(4), 287-297.

Table 1. Summary characteristics of 11 forest stands comprising two experimental chronosequences and three late successional stands.

Name	Disturbance History	Stand Initiation	Number of plots	Plot size (ha)	Forest Type
Cut and Burn	Twice cut, twice burned	1936	2	0.1	Deciduous Broadleaf (DBF)
		1954	2	0.1	
		1980	3	0.1	
		*1998	2	0.06, 0.14	
Cut Only	Twice cut, once burned	1911	3	0.1	Deciduous Broadleaf (DBF)
		1952	2	0.1	
		1972	3	0.1	
		1987	2	0.1	
DBF	Late Succession	1850	3	0.1	Deciduous Broadleaf (DBF)
ENF	Late Succession	1985	3	0.1	Evergreen Needle-Leaf (ENF)
MIX	Late Succession	1985	3	0.1	Deciduous Broadleaf and Evergreen Needle-Leaf (MIX)

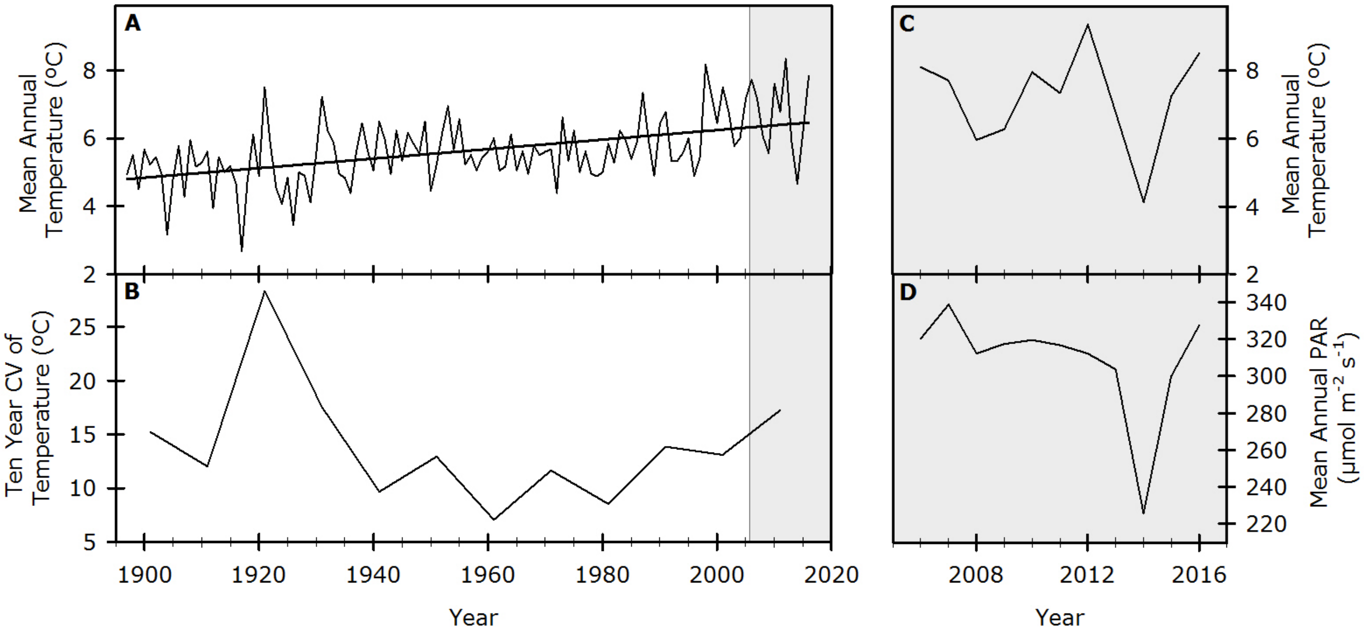


Figure 1. Emmet County, MI annual mean (**A**: $P < 0.0001$, $R^2 = 0.25$) and coefficients of variation (CV) in temperature (**B**, 10-year increments) from 1897 to 2016. Inset **C** and **D** highlight mean annual air temperature and photosynthetically active radiation (PAR) at our site from 2006 – 2016 (gray shading), the period during which we examined net primary production stability. Long-term (**A**, **B**) data obtained from NOAA (National Centers for Environmental Information) and short-term, 10-year (**C**, **D**) data obtained from the UMB AmeriFlux tower.

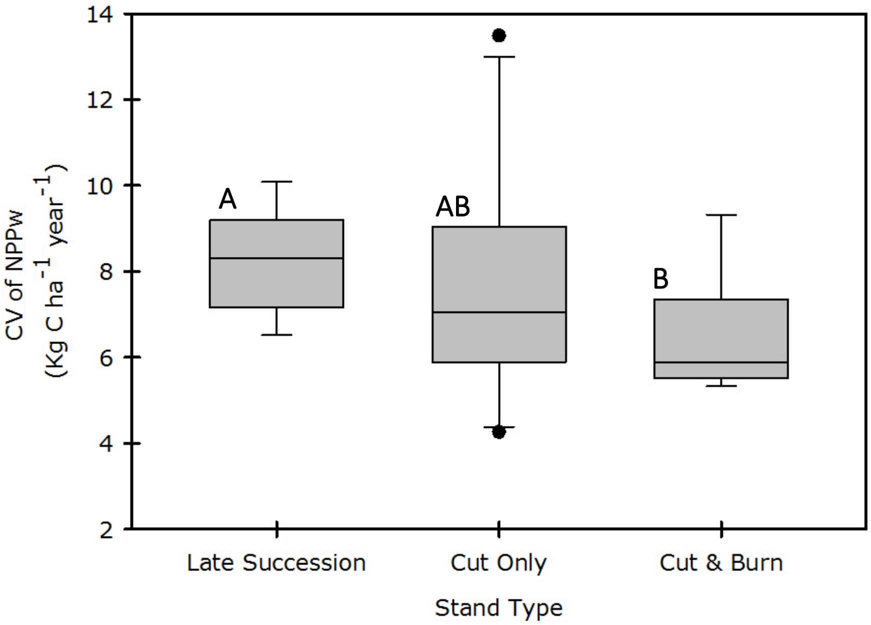


Figure 2. The mean coefficient of variation (CV) in wood net primary production (NPP_w) of stand types differing in disturbance history. Late successional stands, which have not been severely disturbed in over a century, had significantly different CV of NPP_w compared to Cut and Burn stands (alpha = 0.05). Cut Only stands were not significantly different from Late Succession or Cut and Burn stands.

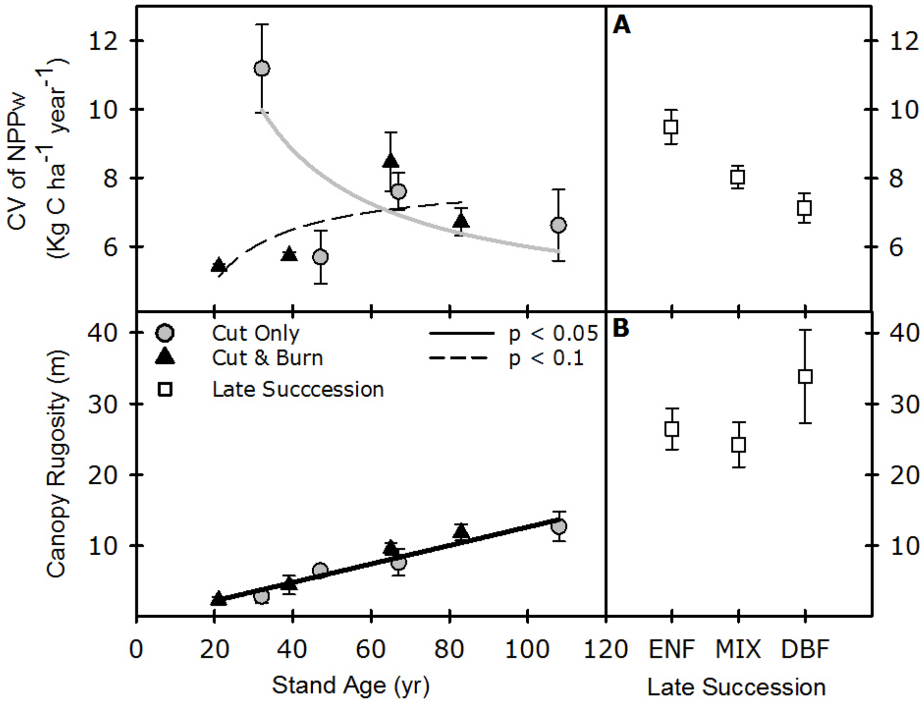


Figure 3. Forest stand age and late succession functional type in relation to stand coefficient of variation (CV) in annual wood net primary production (NPP_w, **A**) and canopy rugosity (**B**). CV of NPPw is significantly related to stand age in the "Cut Only" (**A:** p = < 0.0441, Adj R^2 = 0.31) chronosequence, but only moderately related in the "Cut and Burn" (**A:** p = 0.0619, Adj R^2 = 0.31) chronosequence. A common model, including "Cut Only" and "Cut and Burn" stands, described the relationship between canopy rugosity and stand age (**B**: p = < 0.0001, Adj R^2 = 0.77). Means ± 1 S.E.

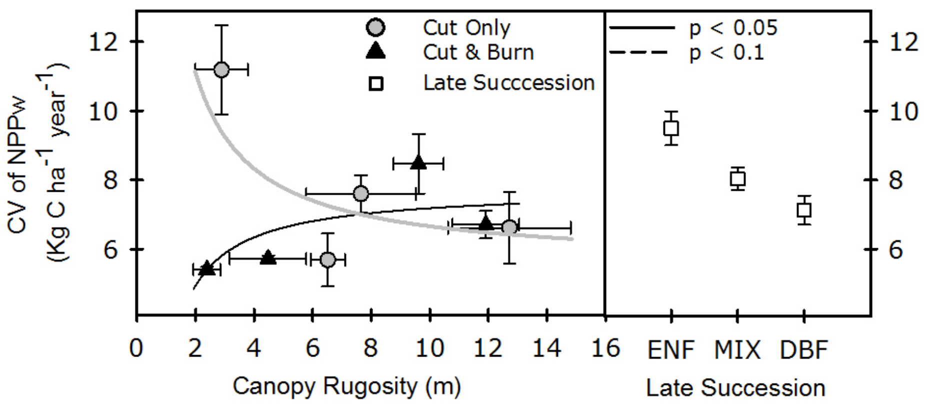


Figure 4. Stand coefficient of variation (CV) of interannual NPP_w relative to canopy rugosity for two chronosequences, and three late successional stands. The magnitude of NPP_w variability increased significantly with rugosity in the "Cut and Burn" ($P = 0.0487$, Adj $R^2 = 0.37$) chronosequence. In contrast, "Cut Only" ($p = 0.0345$, Adj $R^2 = 0.34$) stands demonstrate a significant relationship between more stable NPPw and higher canopy complexity. Means ± 1 S.E.

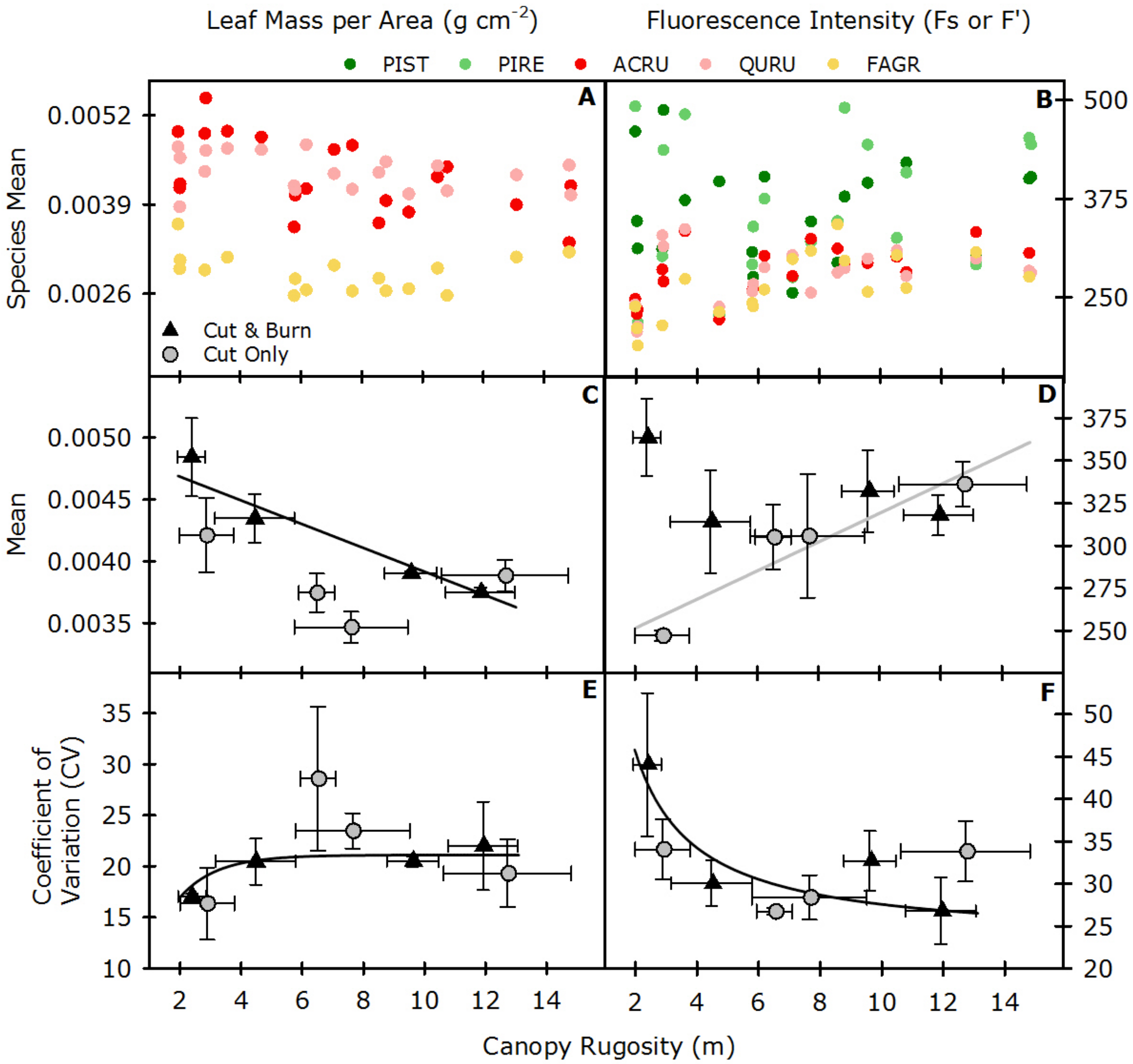
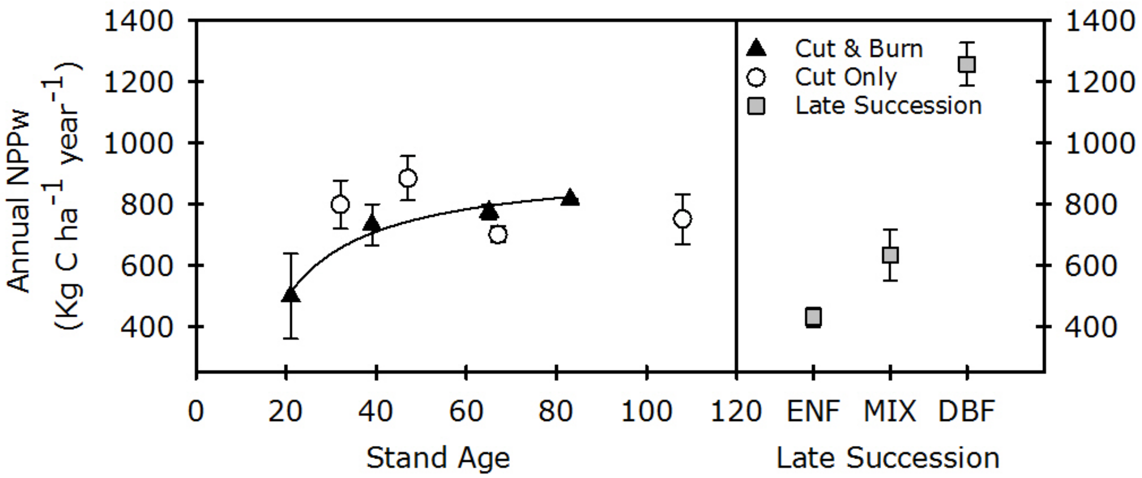


Figure 5. Subcanopy leaf trait means and variability across the continuum of canopy rugosity for both experimental chronosequences. Leaf mass per area and fluorescence intensity from subcanopy tree species are presented as plot means (**A**, **B**), stand means (**C**: p = 0.0074, Adj R^2 = 0.62, **D**: p = 0.0007, Adj R^2 = 0.71), and stand coefficients of variation (**E**: p = 0.0473, Adj R^2 = 0.05, **F**: p = 0.0097, Adj R^2 = 0.59). Means ± 1 S.E.



Appendix I. Annual NPP_w for two chronosequences and three late successional stands. Annual NPP_w for the “Cut & Burn” chronosequence is significantly related to stand age ($p = 0.011$, Adj $R^2 = 0.57$). Means ± 1 S.E.