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Senescent trees stabilize aboveground wood net primary production immediately after disturbance

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Contents

Vita

Maxim Simon Grigri was born on August 24th, 1991 in Philadelphia, PA as an American citizen. He graduated from Gateway Regional High School in Woodbury Heights, NJ in the spring of 2009. He earned his B.S. in Environmental Science at Ithaca College in Ithaca, NY. He worked in a variety of jobs in the environmental science discipline before returning to graduate school in the Fall of 2018.

Abstract

In the United States, forests sequester 17% of national carbon (C) emissions annually (UGCRP, 2018), however shifting forest disturbances threaten the stability of this essential C sink. Unlike the high severity, stand-replacing disturbances that were widespread a century ago, today's eastern temperate forests experience frequent low-to-moderate severity disturbances from invasive pests and pathogens with mixed effects on net primary production (NPP). Carbon cycling stability after disturbance has been reported, however, the mechanisms underlying immediate NPP stability or decline are not well understood. Through weekly measurements of production in a landscape scale experiment, we show that the sustained growth of senescent trees in the first year after disturbance stabilized aboveground wood net primary production (ANPPw) in an eastern temperate forest. We found no evidence for an immediate compensatory growth response from healthy trees that we hypothesized, but instead, aboveground accumulation of C and continued growth by senescent trees. Among disturbance severities (0, 45, 65, 85% gross leaf area loss) and two disturbance types concentrated in the lower and upper canopy, no difference in annual ANPPw relative to a control was observed. Further, we found early, but limited evidence that early successional plant functional types (PFT) contribute more to annual ANPPw than late successional PFTs at high severity disturbances (>65%). Our high-frequency ANPPw observations provide novel insights into the immediate response of a large C pool to disturbance, revealing initial mechanisms of stability useful as benchmarks for ecosystem models. We conclude that C cycling stability immediately following disturbance is largely dependent on the continued aboveground growth of senescent trees.

Keywords: Forest disturbance, Aboveground net primary production (ANPP), Ecosystem, Carbon cycle, Compensatory growth,

Introduction

North American temperate forests have sequestered carbon (C) for the last century (Bridsey et al., 2006; Williams et al., 2012), but the stability of this C sink is in question as disturbance regimes change (Pregitzer and Euskirchen, 2004; Seidle et al., 2017; Dale et al., 2001; Allen et al., 2010). While high severity, stand replacing disturbance like fire and the mountain pine beetle impact vast areas of dry western conifer forests (Hicke et al., 2013), most unmanaged temperate forests in the eastern half of the continent experience low to moderate severity disturbance (Sommerfeld et al., 2018; Flower & Gonzalez-Meler, 2015). Compared with stand-replacing disturbance, more moderate disturbances from host-specific pests and pathogens are characterized by a gradient of tree mortality and, because many of these invaders are novel, their effects on the C cycle are less understood (Kautz et al., 2018; Kautz, Meddens, Hall, & Arneth, 2017; Elkinton & Liebhold, 1990; Atkins et al., 2019). In particular, the impact on enduring C pools such as aboveground wood which accounts for ~ 40% of total stored forest C (Gough et al., 2008; Gough et al., 2009) make it important to characterize how wood net primary production (NPP) responds to disturbance.

While annual NPP responses are described for several forest ecosystems, much less is known about the short-term, highly dynamic changes that occur immediately following disturbance. In the longer-term, high severity disturbances reduce total ecosystem biomass and may temporarily transition forests from C sink to source (Hicke et al., 2012). For example, at our site, disturbances resulting in >60% tree mortality reduced productivity, but wood NPP was stable prior to this threshold (Stuart-Haentjens et al., 2015, Gough et al., 2013). Also over the longer-term, different disturbances have variable effects on canopy structure, with lasting effects on C cycling trajectories (Atkins et al., 2019; Amiro et al., 2010; Hicke et al., 2012). For example, gypsy moth defoliation reduced aboveground productivity for only a year, while emerald ash borer mortality resulted in a recovery period of more than five years (Hicke et al., 2012; Amiro et al., 2010; Cook et al., 2008). In contrast to studies focused on an annual time-step, no studies have examined high frequency NPP changes that immediately follow disturbance and which may be critical to shaping long-term trajectories of recovery (Atkins et al., *in prep*, Reyes & Neeshaw, 2008; Flower & Gonzalez-Meler, 2015). Identifying the initial processes that determine production stability or decline are essential to our understanding of forest C cycling response to disturbance.

A suite of complementary mechanisms may stabilize aboveground wood NPP ($ANPP_w$) immediately following disturbance, before canopy defoliation and associated changes in the light environment occur. While the sub-canopy responds to increased light availability in the long-term, observations of stable $ANPP_w$ at our site prior to defoliation suggest other mechanisms underlie initial stability (Stuart-Haentjens et al., 2015; Campbell et al., 2009; Gough et al., 2013). Prior to changes in light, phloem disruption causes a cascade of changes aboveground that may increase wood production above the injury. Photosynthesis continues in the canopy (Haber et al., *in prep*), but the flow of photosynthate to the roots is severed (Mei et al., 2014) resulting in an accumulation of starch and carbohydrates aboveground (Regier et al., 2009). This surplus of C may sustain or increase aboveground wood growth at the expense of belowground production (Regier et al., 2009; Mei et al., 2014; Winkler & Oberhuber, 2017).

Following senescence, the redistribution of growth limiting resources such as water and nutrients (Nave et al., 2011) may lead to the rapid compensatory growth by healthy trees (Flower et al., 2013). Moreover, the redistribution of resources among plant functional types (PFT) may vary depending on disturbance severity. Resource availability increases with disturbance severity (Stuart-Haentjens et al., 2015; Fahey et al., 2015), thus high severity events that liberate a lot of water and nutrients may favor fast-growing, early successional PFTs that are better adapted for resource acquisition. The initial timing and contribution of senescent and healthy trees to $ANPP_w$ following a phloem disrupting disturbance have not been described but filling this knowledge gap is important to identifying the mechanisms that support C cycling stability before deterioration of the canopy.

Using a landscape scale experiment, we characterized first-year daily and annual $ANPP_w$ responses to increasing disturbance severity and two disturbance types concentrated in different canopy strata. Our overarching goal was to identify the patterns and mechanisms underlying immediate, high-frequency aboveground wood production responses to disturbance. We focus on wood production because aboveground biomass makes up a substantial portion of forest C stocks, and a deterioration of this pool could impact long term forest C cycling. With an emphasis on first-year responses to disturbance, our objectives were to examine: daily and annual $ANPP_w$ among disturbance severity levels and disturbance types (Obj. 1); the contribution of healthy and senescent trees to total aboveground wood production (Obj. 2) and; early and late successional PFT contributions to annual $ANPP_w$ as disturbance severity increases (Obj. 3). We hypothesized that rapid compensatory growth by healthy trees would offset declines in senescent trees such that total annual $ANPP_w$ would remain stable at or below a 60% tree senescence threshold observed for our site (Stuart-Haentjens et al., 2015), while declining at higher severity. We predicted that as pioneer species, early successional PFTs would benefit most from high severity disturbance and contribute more to $ANPP_w$ above the 60% tree senescence threshold.

Methods

Site Description

My research took place at the University of Michigan Biological Station (UMBS) (45°35'N 84°43'W) in northern Michigan. Like many present-day hardwood forests in the upper Midwest, the 100-yr-old landscape of regrown forest is shifting from early successional aspen (*Populus*) and birch (*Betula*) to middle successional canopy species (Gough et al., 2007). Specifically, senescent bigtooth aspen (*Populus grandiosa*), paper birch (*Betula papyrifera*), and yellow birch (*Betula alleghaniensis*) are being replaced by red oak (*Quercus rubra*), red maple (*Acer rubrum*), and to a lesser extent, sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and white pine (*Pinus strobus*). The subcanopy is dominated by red maple and red oak while american beech, sugar maple, serviceberry (*Amelanchier*), white pine, red pine (*Pinus resinosa*), striped maple (*Acer pensylvanicum*), and balsam fir (*Abies balsamea*) are also present.

In May of 2019, the Forest Resilience Threshold Experiment (FoRTE) experimentally created a gradient of disturbance severity including 0%, 45%, 65%, or 85% gross leaf area loss induced by a stem-girdling treatment. Four replicates containing each disturbance severity level (including a control) were nested within separate forest types varying in species composition and site productivity (Figure 4). Within each whole-plot (0.5ha) two subplots (0.1ha) were established containing either: (1) a top-down, upper canopy disturbance in which trees were disturbed in order from largest diameter (D) to smallest D and (2) a bottom up, lower canopy disturbance that disturbs trees in order from smallest D to largest D.

Aboveground wood net primary production ($ANPP_w$)

We derived daily aboveground wood net primary production ($ANPP_w$) from repeated measurements of canopy (≥ 8cm DBH) and subcanopy (1-8cm DBH) stem diameters (D), as well as, seedling/sapling (< 1cm DBH) height (Gough et al., 2009). Beginning in Nov. 2018, 25% of canopy stems (~ 650 stems per severity) were surveyed for D using band dendrometers placed at breast height. Pre-disturbance D was recorded in April 2019 before Spring growth and weekly from May 2019 through August 2019, with final measurements in Nov. 2019. The distribution of dendrometer bands was proportional to the number of girdled and ungirdled trees within a subplot. To test for swelling above the girdle in senescent stems, a second band dendrometer was placed approximately 50 cm above the original band on a subsample of stems -- 5 senescent and 3 healthy per species -- spanning the most common canopy species present in the experiment. *Acer saccharum* and *Acer rubrum* exhibited significant differences of 59 % and 76 %, respectively, in the D of upper and lower bands ($P > 0.05$). The percent difference between upper and lower D locations was used to adjust D prior to calculating the species and D specific relative growth rates (RGR). RGRs were used to estimate D growth of the unsampled population, and we converted D growth to aboveground wood biomass accumulation with species and site specific allometries.

For smaller subcanopy stems with D <8cm, I repeatedly sampled D in 2x2 m vegetation plots from May 2019 to August 2019 using digital calipers. Where no subcanopy stems were present in the vegetation plot, the two closest subcanopy stems to vegetation plot center were selected. Subcanopy stem counts were conducted in one quarter (0.025 ha) of each subplot to estimate stem density. Mean D increment for each subplot was multiplied by the total stem count of a subplot to estimate growth of unsampled trees, and species and site specific allometries were used to calculate biomass increments.

In June 2019 and again in August 2019, all seedlings and saplings within one quarter of the 2x2 m vegetation plots were sampled for base D, previous growing season height (brown and woody), and present height (green and fleshy). Assuming conical shaped stems, stem volume was calculated using geometric calculations and site- and species-specific wood densities were applied to estimate wood biomass (Chave et al., 2009). Total (canopy + subcanopy + seedling/sapling) ANPP$_w$ is the sum of wood biomass from all canopy strata scaled to the hectare and converted to C mass by multiplying by a site specific carbon fraction of 0.48 (Gough, Vogel, Schmid, Su, & Curtis, 2008).

Statistical Analysis

We used a time series blocking split-plot analysis of variance (ANOVA) model to analyze differences in daily canopy ANPP$_w$ among disturbance severity and disturbance type treatments. In this model, disturbance severity (fully randomized within replicates) was the whole-plot and disturbance type (randomized within each whole-plot) was the split-plot. Because trees ≥8cm constituted 95% of ANPP$_w$ and measurements of subcanopy and seedlings/saplings were less frequent, we limited our analysis to canopy measurements. For comparisons of annual ANNP$_w$, a similar model, without time as a factor, was used to analyze differences among disturbance severities, disturbance types and plant functional types (PFT). Pairwise comparisons of ANPP$_w$ across time, disturbance severity, disturbance type, and PFT were performed using least squares differences (LSD) (α= 0.05). Standard error was estimated from the variation around mean ANPP$_w$ across replicates. Statistical analyses were performed in RStudio or SAS statistical software (SAS Institute, Cary NC, USA).

Results

Daily ANPP$_w$ among disturbance types and severities

Significant differences in daily ANPP$_w$ emerged among disturbance severities during the second half of the growing season, two months after disturbance occurred. Daily ANPP$_w$ reached a maximum of ~ 40 kg C ha-1 d-1 during mid-July in all disturbance severity levels, after which daily wood production was greater in the 65% and 85% disturbance severity treatments relative to the control (Figure 1A, $P < 0.0001$). In contrast, the location of disturbance in the lower (bottom-up) or upper (top-down) canopy strata had no effect on daily $ANPP_w$ (Figure 1B, $\alpha = 0.05$).

Annual $ANPP_w$ and contributions from senescent and healthy trees

The continued growth of senescent trees sustained annual $ANPP_w$ following disturbance (Figure 2A), despite occasional differences in daily aboveground wood production (Figure 1A, $P < 0.0001$). Mean annual $ANPP_w$ was 2246 kg C ha-1 yr-1 and did not differ significantly among disturbance severities or between disturbance types. The contribution from senescent trees to annual $ANPP_w$ was proportional to targeted experimental disturbance severity levels, accounting for 44%, 72%, and 82%, respectively (Figure 2A). Similarly, senescent trees in the bottom-up and top-down disturbances accounted for 53% and 80% of annual $ANPP_w$, respectively (Figure 2B, $\alpha = 0.05$).

Plant functional type (PFT) and stem size class contributions to annual $ANPP_w$

As disturbance severity increased, the contribution of the early successional plant functional types (PFT) to annual $ANPP_w$ increased. Early and late successional PFTs contributed similarly to annual $ANPP_w$ in the control, 45%, and 85%, but the early successional PFT accounted for significantly more aboveground wood production at the 65% disturbance severity level supplying 71% of annual $ANPP_w$ (Figure 3, $P < 0.012$). As with daily and annual $ANPP_w$, disturbance type did not affect PFT contributions to annual aboveground wood production (data not shown, $\alpha = 0.05$).

Among stem size classes, large (≥8 cm D) canopy trees were overwhelmingly the primary constituents of annual $ANPP_w$, regardless of disturbance severity and type. Large canopy trees contributed >95 % of total annual $ANPP_w$, with subcanopy (<8 cm D) and seedlings/saplings supplying the remainder of aboveground wood production (Supp. Figure A).

Discussion

Contrary to our hypothesis, annual $ANPP_w$ in the first year after disturbance was sustained by the growth of senescent rather than healthy trees, regardless of disturbance type or severity (Fig. 2A & 2B). Anticipating a rapid resource redistribution from senescent to healthy trees, we expected compensatory growth of healthy trees would offset declines in senescent tree productivity (Flower et al., 2013; Nave et al., 2011; Veblen et al., 1991; Lewis et al., 2015). For example, prior observations from our site revealed an increase in available nitrogen in the year after disturbance (Nave et al. 2011). However, we observed no decline in senescent tree growth along with parallel stability in leaf physiology and leaf area during the first growing season after disturbance (Haber et al., *in prep*, Atkins et al., *in prep*). A similar trend of continued growth was observed in an emerald ash borer impacted forest, where infested trees survived for 2-5 years following initial infestation (Knight et al., 2008; Flower et al., 2013). Moreover, other studies applying experimental girdling report continued aboveground wood growth and photosynthesis, along with high survival during the first year of disturbance (Fajstavr et al., 2017; Regier et al., 2010; Mei et al., 2014).

With stable leaf physiology and leaf area immediately after disturbance, higher late-season daily $ANPP_w$ in the middle and high severity (>65%) disturbance treatments suggests an accumulation of C above the disrupted phloem. When phloem is severed, the transport of new photosynthate to the roots is eliminated and, instead, retained aboveground (Winkler and Oberhuber, 2017). Our results are consistent with girdling experiments that show increased wood production and an accumulation of carbohydrates above the girdle (Winkler and Oberhuber, 2017; Fajstavr et al., 2017; Regier et al., 2010; Mei et al., 2014). For example, in girdled Norway spruce (*Picea abies*), an accumulation of carbohydrates above the girdle promoted radial stem growth (Winkler and Oberhuber, 2017). In contrast, cambial cell production below the girdle ceased immediately following disturbance in Scots pine (*Pinus sylvestris)* (Fajstavr et al., 2017), and the depletion of root carbohydrate pools was observed in ash (*Fraxinus mandshurica*) (Mei et al., 2014). It is understood that girdling increases aboveground C accumulation at the expense of belowground growth, but the specifics of C allocation to the stem or shoots is not well understood. Further, while sustained leaf physiological competency in senescent trees may have supported aboveground wood production immediately following disturbance, we expect a deterioration of the canopy in subsequent years will lead to declining wood productivity and eventual mortality.

Our findings provide limited support for the hypothesis that early successional plant functional types (PFT) contribute more to $ANPP_w$ than late successional PFTs at higher disturbance severities. At our site, the early successional PFT primarily consists of mature aspen (*Populus spp.*) that thrive following severe disturbance (Caspersen & Pacala, 2001). Stand replacing disturbances that result in an abrupt increase in available resources -- light, nitrogen (N), water -- favor fast-growing, early successional species that are adapted for opportunistic resource acquisition (Bormann & Likens, 1979; Curtis et al., 2000; Foster et al., 1997). While stable leaf area during the first year suggests light distribution was unchanged, disturbance rapidly increases nutrient availability at our site, particularly at higher disturbance severities (White et al., 2004, Nave et al. 2011). Apart from resource redistribution, an increase in early successional PFT contributions to $ANPP_w$ within rising disturbance severity may be driven by interactions between severity, stem size distribution, and growth. Relative to the disturbance in the lower canopy strata, we found a larger contribution to $ANPP_w$ by senescent trees in the upper canopy disturbance that targeted large D trees (Figure 2B) suggesting contributions to $ANPP_w$ increase with tree D (Flower et al., 2013; Bruhn et al., 2000) which is not independent of PFT at our site.

With little change in upper canopy leaf area, we found the subcanopy (D<8cm) was not significant to stabilizing aboveground wood production in the first growing season after disturbance. When defoliation-driven changes in the light environment are substantial, the subcanopy at our site is nearly half of aboveground production (Fahey et al., 2015; Stuart-Haentjens et al., 2015); conversely, the subcanopy contributes only ~5% to $ANPP_w$ (Fahey et al., 2015) in closed canopy forests at our site, which is consistent with our findings (Figure A). In the first year of disturbance, senescent trees retained their leaves, which likely corresponded with similarly nominal changes in the subcanopy light environment. Consistent with our observations of growth, subcanopy photosynthetic activity and leaf chemistry did not change in the first growing season following disturbance (Haber et al., *in prep*). Although the subcanopy contributed minimally to $ANPP_w$ in the first year of disturbance, we expect the contribution of this canopy strata to increase over time and in the higher disturbance severities as senescent tree crowns deteriorate (Stuart-Haentjens et al., 2015; Fahey et al., 2015).

Several caveats and limitations emerged when estimating ecosystem NPP from biometric measures of girdled trees. Despite adjusting our stem increments and $ANPP_w$ derivations to account for swelling above the girdle of senescent trees, the allometries used to estimate wood biomass were developed from the dimensions of healthy trees and may not apply perfectly to senescent trees. The disrupted flow of C from the shoots to the roots associated with phloem damage is apparent, but less is known about the initial aboveground distribution of structural C or wood growth. A healthy tree allocates most biomass to the stem, followed by branches and roots (Würth et al., 2005; Zheng et al., 2006; Poorter et al., 2012). As we observed, sustained or increased radial growth in the stem of girdled trees is common (Winkler and Oberhuber, 2017; Fajstavr et al., 2017). Similarly, concentrations of carbohydrates in the leaves of girdled trees have been shown to remain stable or increase slightly (Mei et., al 2014), suggesting aboveground C is not accumulating only in the stem, and is instead distributed similarly to a healthy tree. Without empirical evidence for aboveground growth distribution, however, further examination of allometric relationships of girdled trees is warranted to ensure accurate estimations of ecosystem productivity from biometric measures.

Conclusion

We conclude from our results that the mechanism supporting initial aboveground wood NPP following disturbance is continued growth of senescent trees. While stable NPP following moderate severity disturbance was previously observed at our site (Gough et al., 2013), we expected declines in ecosystem production to emerge in the first year past a 60% disturbance severity threshold (Stuart-Haentjens et al., 2015). Shifting within tree C allocation of senescent trees however, supported aboveground production stability regardless of disturbance type or severity. Reflected by significantly lower soil C efflux in disturbed forests at our site (Mathes et al., *in prep*), continued aboveground growth came at the cost of belowground productivity. Aboveground wood accounts for less than half of forest C storage (Gough et al., 2008), thus further investigation of above- and belowground C fluxes is needed to quantify total forest C uptake immediately after disturbance.

Our work is essential to understanding the short-term impacts of disturbance that may have long-term implications for the C cycling trajectory of northern temperate forests. While this study provides important insight to the mechanisms behind immediate production stability after disturbance, ongoing changes among live and eventual mortality among senescent trees of all canopy strata and PFTs warrant continued monitoring of disturbed forests at our site. Further, future work could help unravel the PFT and species-specific growth responses and investigate belowground resource redistribution with implications for ecosystem NPP stability.

References

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*(4), 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Amiro, B. D., Barr, A. G., Barr, J. G., Black, T. A., Bracho, R., Brown, M., Chen, J., Clark, K. L., Davis, K. J., Desai, A. R., Dore, S., Engel, V., Fuentes, J. D., Goldstein, A. H., Goulden, M. L., Kolb, T. E., Lavigne, M. B., Law, B. E., Margolis, H. A., … Xiao, J. (2010). Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *Journal of Geophysical Research: Biogeosciences*, *115*(G4). https://doi.org/10.1029/2010JG001390

Atkins, J. W., Bond-Lamberty, B., Fahey, R. T., Hardiman, B. S., Haber, L., Stuart-Haëntjens, E., LaRue, E., McNeil, B., Orwig, D. A., Stovall, A. E. S., Tallant, J., Walter, J. A., & Gough, C. M. (2019). *Multidimensional Structural Characterization is Required to Detect and Differentiate Among Moderate Disturbance Agents*. https://doi.org/10.20944/preprints201911.0082.v1

Atkins, J. W. (2020). [Canopy Structural Complexity in the First Year After Disturbance]. Unpublished raw data.

Birdsey, R., Pregitzer, K., & Lucier, A. (2006). Forest Carbon Management in the United States. *Journal of Environmental Quality*, *35*(4), 1461–1469. https://doi.org/10.2134/jeq2005.0162

Bormann, F. H., & Likens, G. E. (1979). Catastrophic Disturbance and the Steady State in Northern Hardwood Forests: A new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. *American Scientist*, *67*(6), 660–669. JSTOR.

Bruhn, D., Leverenz, J. W., & Saxe, H. (2000). Effects of tree size and temperature on relative growth rate and its components of Fagus sylvatica seedlings exposed to two partial pressures of atmospheric [CO2]. *New Phytologist*, *146*(3), 415–425. https://doi.org/10.1046/j.1469-8137.2000.00661.x

Campbell, J., Alberti, G., Martin, J., & Law, B. E. (2009). Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada. *Forest Ecology and Management*, *257*(2), 453–463. https://doi.org/10.1016/j.foreco.2008.09.021

Caspersen, J. P., & Pacala, S. W. (2001). Successional diversity and forest ecosystem function. *Ecological Research*, *16*(5), 895–903. https://doi.org/10.1046/j.1440-1703.2001.00455.x

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Curtis, P. S., Vogel, C. S., Wang, X., Pregitzer, K. S., Zak, D. R., Lussenhop, J., Kubiske, M., & Teeri, J. A. (2000). Gas Exchange, Leaf Nitrogen, and Growth Efficiency of Populus Tremuloides in a Co2-Enriched Atmosphere. *Ecological Applications*, *10*(1), 3–17. https://doi.org/10.1890/1051-0761(2000)010[0003:GELNAG]2.0.CO;2

Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., Simberloff, D., Swanson, F. J., Stocks, B. J., & Wotton, B. M. (2001). Climate Change and Forest DisturbancesClimate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience*, *51*(9), 723–734. https://doi.org/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2

Dietze, M. C., & Matthes, J. H. (2014). A general ecophysiological framework for modelling the impact of pests and pathogens on forest ecosystems. *Ecology Letters*, *17*(11), 1418–1426. https://doi.org/10.1111/ele.12345

Elkinton, J. S., & Liebhold, A. M. (1990). Population Dynamics of Gypsy Moth in North America. *Annual Review of Entomology*, *35*(1), 571–596. https://doi.org/10.1146/annurev.en.35.010190.003035

Fahey, R. T., Stuart-Haëntjens, E. J., Gough, C. M., De La Cruz, A., Stockton, E., Vogel, C. S., & Curtis, P. S. (2016). Evaluating forest subcanopy response to moderate severity disturbance and contribution to ecosystem-level productivity and resilience. *Forest Ecology and Management*, *376*, 135–147. https://doi.org/10.1016/j.foreco.2016.06.001

Fajstavr, M., Giagli, K., Vavrčík, H., Gryc, V., & Urban, J. (2017a). The effect of stem girdling on xylem and phloem formation in Scots pine. *Silva Fennica*, *51*(4). https://doi.org/10.14214/sf.1760

Fajstavr, M., Giagli, K., Vavrčík, H., Gryc, V., & Urban, J. (2017b). The effect of stem girdling on xylem and phloem formation in Scots pine. *Silva Fennica*, *51*(4). https://doi.org/10.14214/sf.1760

Flower, C. E., & Gonzalez-Meler, M. A. (2015). Responses of Temperate Forest Productivity to Insect and Pathogen Disturbances. *Annual Review of Plant Biology*, *66*(1), 547–569. https://doi.org/10.1146/annurev-arplant-043014-115540

Flower, C. E., Knight, K. S., & Gonzalez-Meler, M. A. (2013). Impacts of the emerald ash borer (Agrilus planipennis Fairmaire) induced ash (Fraxinus spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. *Biological Invasions*, *15*(4), 931–944. https://doi.org/10.1007/s10530-012-0341-7

Foster, D. R., Aber, J. D., Melillo, J. M., Bowden, R. D., & Bazzaz, F. A. (1997). Forest Response to Disturbance and Anthropogenic Stress. *BioScience*, *47*(7), 437–445. JSTOR. https://doi.org/10.2307/1313059

Gough, C. M., Flower, C. E., Vogel, C. S., Dragoni, D., & Curtis, P. S. (2009). Whole-ecosystem labile carbon production in a north temperate deciduous forest. *Agricultural and Forest Meteorology*, *149*(9), 1531–1540. https://doi.org/10.1016/j.agrformet.2009.04.006

Gough, C. M., Hardiman, B. S., Nave, L. E., Bohrer, G., Maurer, K. D., Vogel, C. S., Nadelhoffer, K. J., & Curtis, P. S. (2013). Sustained carbon uptake and storage following moderate disturbance in a Great Lakes forest. *Ecological Applications*, *23*(5), 1202–1215. https://doi.org/10.1890/12-1554.1

Gough, C. M., Vogel, C. S., Hardiman, B., & Curtis, P. S. (2010). Wood net primary production resilience in an unmanaged forest transitioning from early to middle succession. *Forest Ecology and Management*, *260*(1), 36–41. https://doi.org/10.1016/j.foreco.2010.03.027

Gough, C. M., Vogel, C. S., Schmid, H. P., & Curtis, P. S. (2008). Controls on Annual Forest Carbon Storage: Lessons from the Past and Predictions for the Future. *BioScience*, *58*(7), 609–622. https://doi.org/10.1641/B580708

Haber, L. (2020). [Leaf Physiological Response to Disturbance in the First Year After Disturbance]. Unpublished raw data.

Hicke, J. A., Meddens, A. J. H., Allen, C. D., & Kolden, C. A. (2013). Carbon stocks of trees killed by bark beetles and wildfire in the western United States. *Environmental Research Letters*, *8*(3), 035032. https://doi.org/10.1088/1748-9326/8/3/035032

Kautz, M., Anthoni, P., Meddens, A. J. H., Pugh, T. A. M., & Arneth, A. (2018). Simulating the recent impacts of multiple biotic disturbances on forest carbon cycling across the United States. *Global Change Biology*, *24*(5), 2079–2092. https://doi.org/10.1111/gcb.13974

Kautz, M., Meddens, A. J. H., Hall, R. J., & Arneth, A. (2017). Biotic disturbances in Northern Hemisphere forests – a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. *Global Ecology and Biogeography*, *26*(5), 533–552. https://doi.org/10.1111/geb.12558

Knight KS, Long RP, Rebbeck J, Smith A, Gandhi K, Herms DA (2008). How fast will trees die? A transition matrix model of ash decline in forest stands infested by emerald ash borer. In: Mastro V, Reardon R, Parra G (eds) Proceedings of the emerald ash borer research and technology development meeting; 2007 October 23–4; Pittsburgh. FHTET 2008–2007. Morgantown, WV: US Forest Service, Forest Health Technology Enterprise Team, pp 29–30

Lewis, K. J., Thompson, R. D., & Trummer, L. (2005). Growth response of spruce infected by Inonotus tomentosus in Alaska and interactions with spruce beetle. *Canadian Journal of Forest Research*, *35*(6), 1455–1463. https://doi.org/10.1139/x05-081

Mathes, K. (2020). *Thresholds of soil respiration stability across a disturbance severity gradient.* Unpublished mnuscript.

Mei, L., Xiong, Y., Gu, J., Wang, Z., & Guo, D. (2015). Whole-tree dynamics of non-structural carbohydrate and nitrogen pools across different seasons and in response to girdling in two temperate trees. *Oecologia*, *177*(2), 333–344. JSTOR.

Nave, L. E., Gough, C. M., Maurer, K. D., Bohrer, G., Hardiman, B. S., Moine, J. L., Munoz, A. B., Nadelhoffer, K. J., Sparks, J. P., Strahm, B. D., Vogel, C. S., & Curtis, P. S. (2011). Disturbance and the resilience of coupled carbon and nitrogen cycling in a north temperate forest. *Journal of Geophysical Research: Biogeosciences*, *116*(G4). https://doi.org/10.1029/2011JG001758

Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytologist*, *193*(1), 30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

Pregitzer, K. S., & Euskirchen, E. S. (2004). Carbon cycling and storage in world forests: Biome patterns related to forest age. *Global Change Biology*, *10*(12), 2052–2077. https://doi.org/10.1111/j.1365-2486.2004.00866.x

Regier, N., Streb, S., Zeeman, S. C., & Frey, B. (2010). Seasonal changes in starch and sugar content of poplar (Populus deltoides × nigra cv. Dorskamp) and the impact of stem girdling on carbohydrate allocation to roots. *Tree Physiology*, *30*(8), 979–987. https://doi.org/10.1093/treephys/tpq047

REYES, G. P., & KNEESHAW, D. (2008). Moderate-severity disturbance dynamics in Abies balsamea-Betula spp. forests: The relative importance of disturbance type and local stand and site characteristics on woody vegetation response. *Écoscience*, *15*(2), 241–249. JSTOR.

Rocha, A. V., & Goulden, M. L. (2008). Large interannual CO2 and energy exchange variability in a freshwater marsh under consistent environmental conditions. *Journal of Geophysical Research: Biogeosciences*, *113*(G4). https://doi.org/10.1029/2008JG000712

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, *7*(6), 395–402. https://doi.org/10.1038/nclimate3303

Sommerfeld, A., Senf, C., Buma, B., D’Amato, A. W., Després, T., Díaz-Hormazábal, I., Fraver, S., Frelich, L. E., Gutiérrez, Á. G., Hart, S. J., Harvey, B. J., He, H. S., Hlásny, T., Holz, A., Kitzberger, T., Kulakowski, D., Lindenmayer, D., Mori, A. S., Müller, J., … Seidl, R. (2018). Patterns and drivers of recent disturbances across the temperate forest biome. *Nature Communications*, *9*(1), 1–9. https://doi.org/10.1038/s41467-018-06788-9

Stuart-Haëntjens, E. J., Curtis, P. S., Fahey, R. T., Vogel, C. S., & Gough, C. M. (2015). Net primary production of a temperate deciduous forest exhibits a threshold response to increasing disturbance severity. *Ecology*, *96*(9), 2478–2487. https://doi.org/10.1890/14-1810.1

USGCRP, 2018: *Second State of the Carbon Cycle Report (SOCCR2): A Sustained Assessment Report*. [Cavallaro, N., G. Shrestha, R. Birdsey, M. A. Mayes, R. G. Najjar, S. C. Reed, P. Romero-Lankao, and Z. Zhu (eds.)]. U.S. Global Change Research Program, Washington, DC, USA, 878 pp.

Veblen, T. T., Hadley, K. S., Reid, M. S., & Rebertus, A. J. (1991). The Response of Subalpine Forests to Spruce Beetle Outbreak in Colorado. *Ecology*, *72*(1), 213–231. https://doi.org/10.2307/1938916

White, L. L., Zak, D. R., & Barnes, B. V. (2004). Biomass accumulation and soil nitrogen availability in an 87-year-old Populus grandidentata chronosequence. *Forest Ecology and Management*, *191*(1), 121–127. https://doi.org/10.1016/j.foreco.2003.11.010

Williams, C. A., Collatz, G. J., Masek, J., & Goward, S. N. (2012). Carbon consequences of forest disturbance and recovery across the conterminous United States: FOREST DISTURBANCE AND CARBON DYNAMICS. *Global Biogeochemical Cycles*, *26*(1), n/a-n/a. https://doi.org/10.1029/2010GB003947

Williams, C. A., Gu, H., MacLean, R., Masek, J. G., & Collatz, G. J. (2016). Disturbance and the carbon balance of US forests: A quantitative review of impacts from harvests, fires, insects, and droughts. *Global and Planetary Change*, *143*, 66–80. https://doi.org/10.1016/j.gloplacha.2016.06.002

Winkler, A., & Oberhuber, W. (2017). Cambial response of Norway spruce to modified carbon availability by phloem girdling. *Tree Physiology*, *37*(11), 1527–1535. https://doi.org/10.1093/treephys/tpx077

Würth, M. K. R., Peláez-Riedl, S., Wright, S. Joseph., & Körner, C. (2005). Non-Structural Carbohydrate Pools in a Tropical Forest. *Oecologia*, *143*(1), 11–24. JSTOR.

Zheng, Z., Feng, Z., Cao, M., Li, Z., & Zhang, J. (2006). Forest Structure and Biomass of a Tropical Seasonal Rain Forest in Xishuangbanna, Southwest China1. *Biotropica*, *38*(3), 318–327. https://doi.org/10.1111/j.1744-7429.2006.00148.x

Table 1 The pre-disturbance species composition, canopy and subcanopy stem density, and biomass of the four replicates. Each color-coded replicate is contained within a unique landscape that vary in species composition and site productivity (Figure 4A). Canopy and subcanopy standard error are in () next to mean stem density values. Species below 1% of total species composition were not included. Species codes are defined as: *Populus grandiose* (POGR), *Quercus rubra* (QURU), *Acer rubrum* (ACRU), *Acer saccharum* (ACSA), *Fagus grandifolia* (FAGR), *Pinus strobus* (PIST), *Pinus resinosa* (PIRE), and *Acer pensylvanicum* (ACPE).

	A	B	C	D
Canopy tree (>8cm D) composition	POGR (61%) ACSA (17%) ACRU (10%) FAGR (10%)	POGR (58%) ACRU (24%) QURU (9%) FAGR (4%)	QURU (43%) POGR (39%) PIST (6%) ACRU (6%)	QURU (72%) POGR (19%) PIST (4%) FAGR (1%)
Subcanopy tree (1-8cm D) composition	FAGR (49%) ACPE (42%) ACSA (4%) ACRU (3%) AMEL (2%)	FAGR (42%) ACRU (24%) ACPE (13%) AMEL (11%) QURU (9.5%)	PIST (40%) ACRU (19%) FAGR (19%) ACPE (18%) QURU (2%)	PIST (53%) ACRU (33%) FAGR (8%) QURU (4%) PIRE (2.4%)
Canopy stem density (stems ha^{-1}, >8cm D)	865 (32)	888 (46)	910 (55)	796 (81)
Subcanopy stem density (stems ha^{-1}, 1-8cm D)	2050 (356)	2630 (343)	1690 (331)	1045 (148)
Biomass (Kg C ha^{-1})	155,900 (19,000)^{a}	197,000 (13,900)^{ab}	229,900 (24,700)^{ab}	264,600 (15,800)^{c}

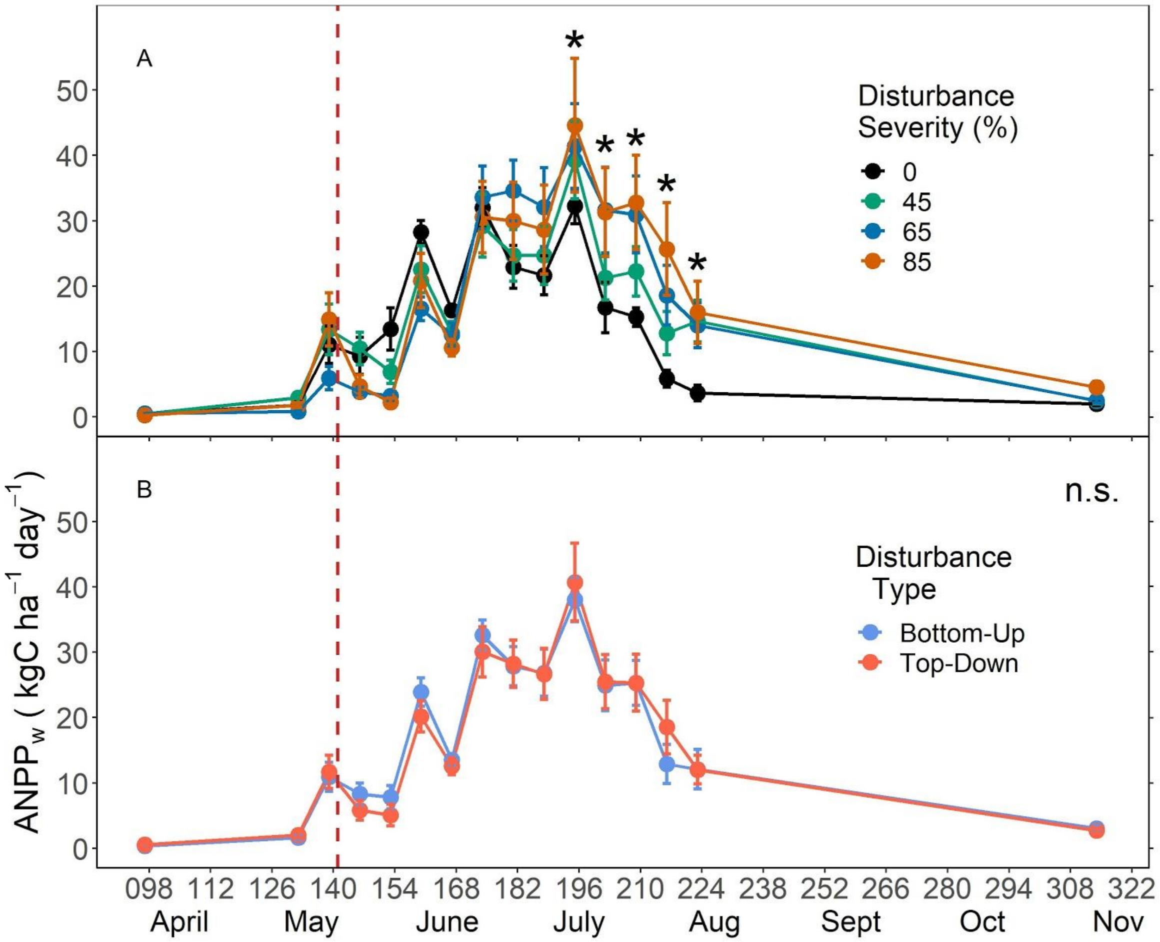

Figure 1. Daily ANPP$_w$ (+/- SE) by disturbance severity treatment (A) and disturbance type (B) in the first year after disturbance. The vertical dashed line represents the time of disturbance. Asterisks denote dates for which the 85% disturbance severity significantly ($P > 0.05$) differs from the control.

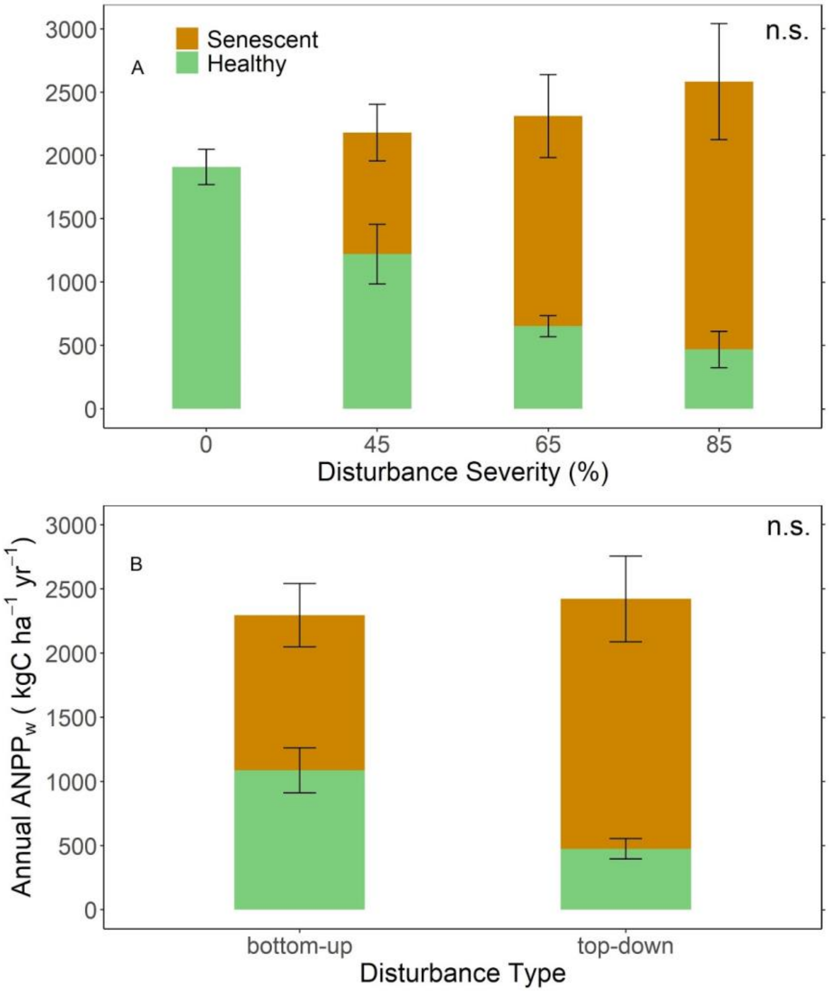

Figure 2. Contributions of senescent and healthy trees to total annual ANPP$_w$ (+/- SE) among disturbance severities (A) and types (B).

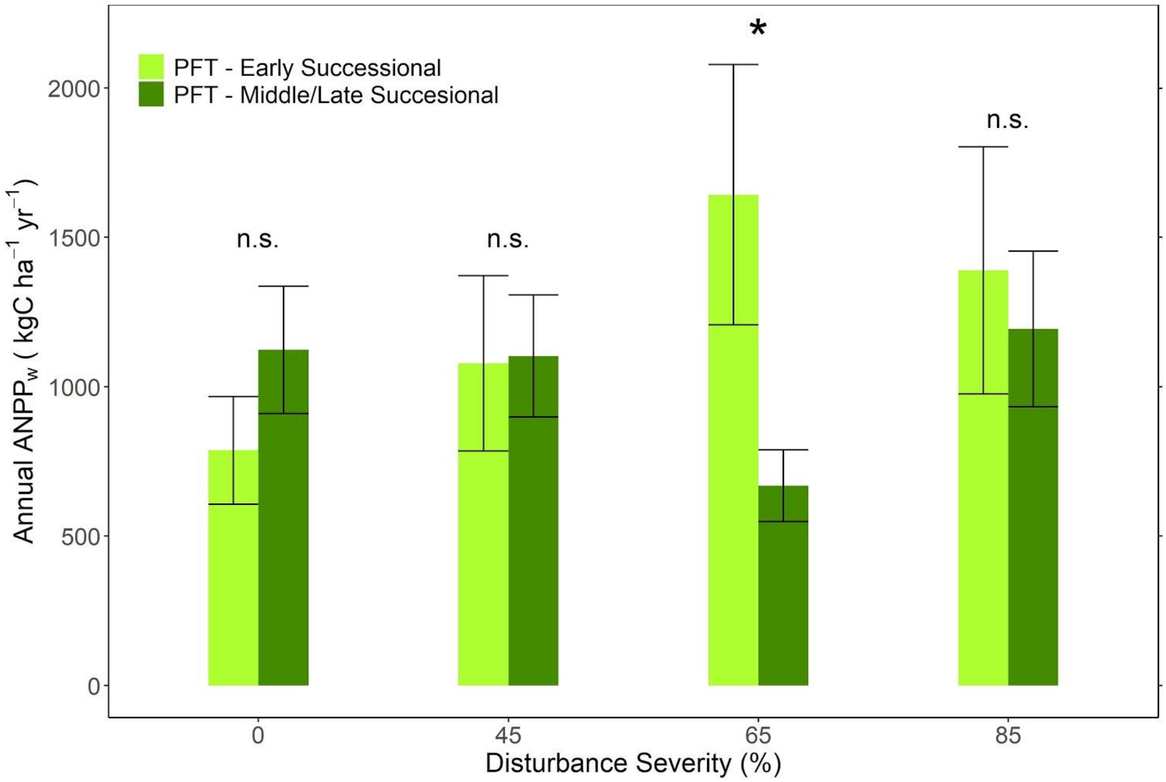

Figure 3. The contribution of early and late successional plant functional types (PFTs) to annual ANPP$_w$ (+/- SE) at each disturbance severity. Asterisks (*) denote significance ($P > 0.05$).

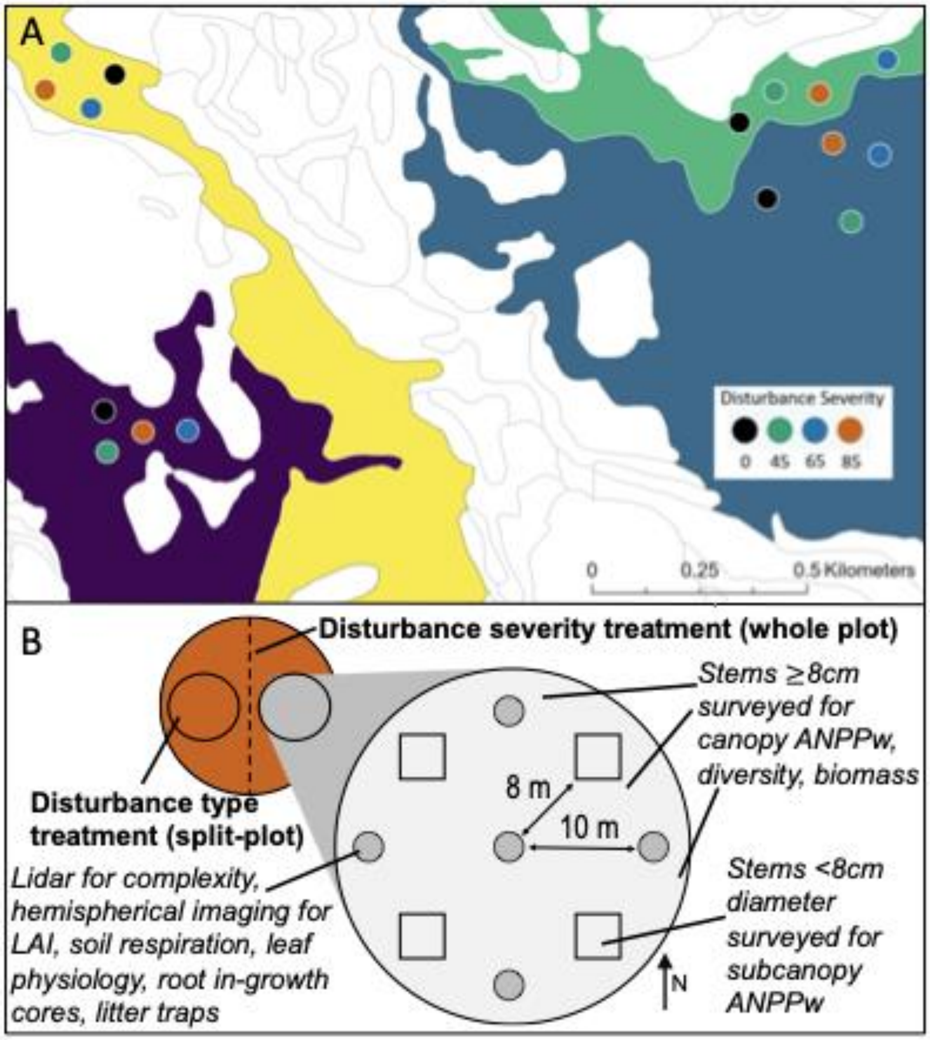

Figure 4 Replicate distribution (A) and split-plot experimental design (B) of the Forest Resilience Threshold Experiment (FoRTE). Replicates are distributed across unique soil and vegetation types common to the region. Distinct landscape types are distinguished by color (A) and match the colors designated to the replicates in Table 1. Each replicate contains four whole plots with the suite of disturbance severities (0, 45, 65, and 85% gross defoliation) (A) all of which are split by disturbance type (top-down or bottom-up) (B). 2x2 vegetation plots were used for subcanopy $ANPP_w$ sampling.

Appendices

Table A Blocking split-plot analysis of variance for the main effects of replicate, disturbance severity, time (week), and disturbance type on the daily $ANPP_w$. The week and disturbance type main effects and the interaction terms time(week)*disturbance severity and time(week)*disturbance type were tested against error terms with restrictions on randomization resulting from the split-plot experimental design. Restricted error terms are defined in (). The main effects replicate and disturbance severity were tested against the residual error.

Source	DF	Type I SS	MS	F ratio	*p* value
Replicate	3	3018.17262	1006.05754	15.55	<.0001
Disturbance Severity	3	1239.83753	413.27918	6.39	0.0004
Week	15	66281.10295	4418.74020	68.28	<.0001
Error *(rep*week)*	45	8930.40408	198.45342		
Disturbance Type	1	2.92377	2.92377	0.05	0.8319
Error *(rep*type)*	3	2773.86268	924.62089		
Week*Severity	45	8067.68524	179.28189	2.77	<.0001
Error *(rep*week*severity)*	144	22019.00111	152.90973		
Week*Type	15	598.90131	39.92675	0.62	0.8591
Error *(rep*week*type)*	45	2845.64444	63.23654		
Residual Error	192	12425.9053	64.7183		

Table B Blocking split-plot analysis of variance for the main effects of replicate, disturbance severity, plant functional type (PFT) and disturbance type on the annual $ANPP_w$. The main effects of PFT and disturbance type, as well as, the interaction terms of PFT*disturbance severity and PFT*disturbance type, were tested against error terms with restrictions on randomization resulting from the split-plot experimental design. Restricted error terms are defined in (). The main effects replicate and disturbance severity were tested against the residual error.

Source	DF	Type I SS	MS	F ratio	*p* value
Replicate	3	1540443.89	513481.30	1.91	0.1547
Disturbance Severity	3	938257.92	312752.64	1.16	0.3440
PFT	1	653425.42	653425.42	2.43	0.1320
Error (*replicate*PFT*)	3	7670539.30	2556846.43		
Disturbance Type	1	0.14	0.14	0.00	0.9994
Error (*replicate*type*)	3	1845505.78	615168.59		
PFT*Disturbance Severity	3	3751594.03	1250531.34	4.65	0.0106
Error (*replicate*PFT*severity*)	18	17217244.31	956513.57		
PFT*Disturbance Type	1	236936.14	236936.14	0.88	0.3571
Error (*replicate*PFT*type*)	3	1338193.84	446064.61		
Residual Error	24	6448355.10	268681.46		

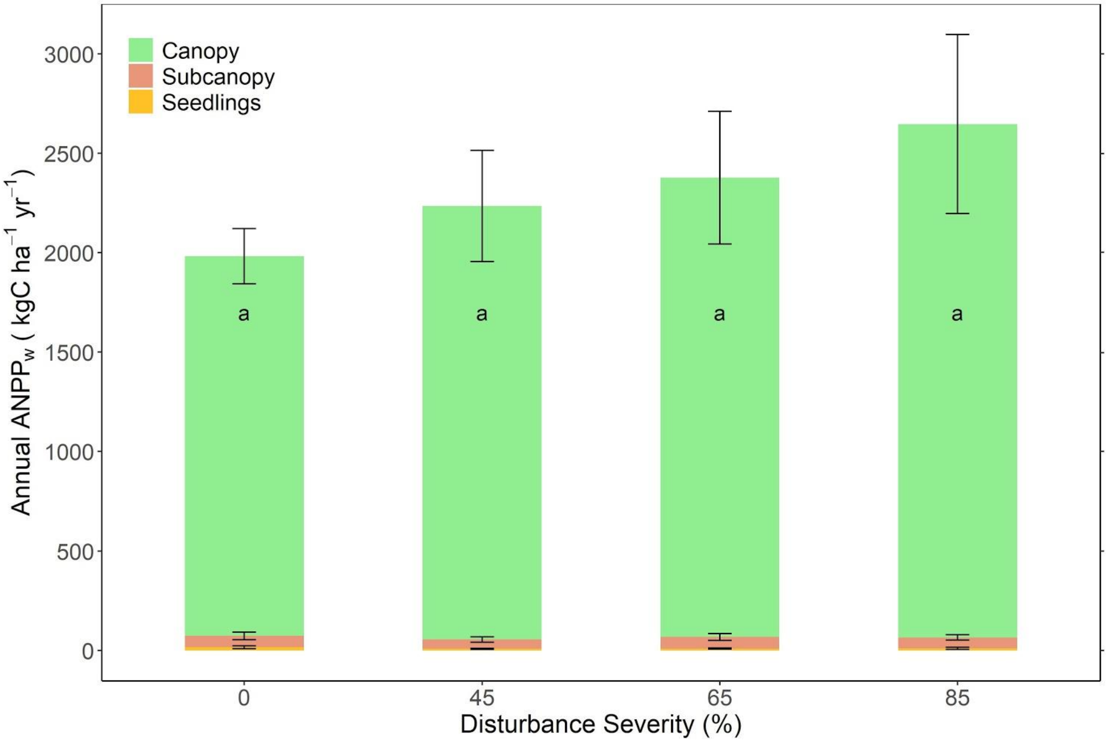

Figure A. A pairwise comparison of annual ANPPw (+/- SE) in the first year of disturbance. Letters (a) represent no significant ($P > 0.05$) difference in annual ANPPw among disturbance severities. Standard error is the variation around the mean annual ANPPw across subplots.