Mechanism sustaining high rates of carbon storage in mature forests of northern Michigan

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Introduction

As atmospheric carbon dioxide levels rise, it becomes increasingly important to understand the role of forests as carbon sinks. Disturbance events that alter the structure of forest ecosystems play a large role in determining the strength of a forest as either a source or a sink for carbon dioxide (Pan et al. 2011). Moderate disturbances that only partially defoliate the canopy have very different effects on forest carbon storage than severe stand-replacing disturbances (Nave et al. 2011). For example, the mixed deciduous forests of northern Michigan are currently undergoing moderate disturbance due to a decline in bigtooth aspen (*Populus grandidentata)* and white birch (*Betula papyrifera)* stands (Gough et al. 2010). Following clear-cut logging and wildfires in the early 20th century, aspen and birch became the dominant species. However, due to their relatively short life span, these species are now senescing. The Forest Accelerated Succession Experiment (FASET) at the University of Michigan Biological Station simulated this age-related senescence through the girdling of >6,700 aspen and birch in 2008. Prior research in FASET found that despite a 44% decrease in leaf area by 2010, net ecosystem production, a primary component of total ecosystem C storage, has been resistant (Gough et al., in preparation).

Though carbon storage resistance to moderate disturbance has been documented, the ecological mechanisms supporting this resistance are largely unknown. Though NPP generally increases with a decrease in tree density, dominant woody plants are usually better at utilizing resources than subdominant plants. This indicates that there is a threshold of subdominant canopy contribution to dominant canopy removal that sustains NPP during disturbance (Sabo et al. 2008). Gaining a better understanding of these community and ecosystem processes that support carbon storage resistance to moderate disturbance may help improve ecosystem models, and guide forest management practices.

Building on pre-disturbance (2006) and peak disturbance (2010) data collected from the FASET site, the objective of this study was to link canopy disturbance severity with changes in community composition and ecosystem functions, such as carbon and nitrogen cycling. Over a gradient of moderate disturbance severities, I determined the relative contributions of dominant and subdominant species to wood net primary production (NPP) resistance to partial canopy defoliation. Additionally, I examined how resource reallocation of nitrogen mediates the relative contributions of subdominant and subdominant species to wood NPP. I hypothesized that in areas of greater disturbance severity, the ratio of dominant to subdominant NPP contributions would be lower. This is because larger canopy gaps may allow for greater subdominant response as light and nitrogen are more readily reallocated to the understory.

Materials & methods

Study site

I conducted my work in 20 plots that span across a well-characterized disturbance severity gradient nested within the FASET forest. In 2008, >6700 early-successional aspen and birch trees in FASET were girdled to emulate the natural age-related senescence of these species. Disturbance severity in each plot was previously quantified during peak leaf area losses in 2010 by Gough et al. (in preparation) as gap fraction and clumping indexes.

Canopy subdominant net primary production estimates by species

I used recovery phase subdominant stem biomass measurements that build on pre-disturbance (2006) and peak-disturbance (2010) stem biomass data to quantify subdominant community and NPP shifts in response to moderate disturbance. In each plot, I identified and sorted all stems ≥ 1.37 m height (DBH) into diameter classes of 0-2 cm, 2-4 cm, 4-6 cm and 6-8 cm. Wood biomass estimates for each species were estimated from species-specific allometric equations relating DBH to wood biomass (Gough et al. 2008). Understory wood NPP was calculated as the biomass increment between years.

Canopy dominant net primary production estimates by species

Pre-disturbance and peak disturbance dominant biomass data has been previously collected via band dendrometers. I determined recovery phase dominant bole biomass by identifying and re-measuring the diameter at breast height (DBH) of all trees with a diameter ≥ 8 cm. Canopy dominant wood NPP was calculated as the

wood biomass increment between measurement years using species-specific

allometrics relating DBH to wood biomass (Gough et al. 2008).

Vertical nitrogen distribution

Leaf collection and analysis for nitrogen concentration at subdominant canopy level

and dominant canopy level indicate whether nitrogen is reallocated primarily to the

dominant or subdominant species. In each plot, samples were collected from the 3

most dominant species at 2 heights within the canopy. Leaves of each species were

pooled within each sample and analyzed for percent nitrogen.

Statistical analyses

Regression analyses were used to determine the relationship between shifts in

canopy dominant and subdominant contributions to NPP with increasing

disturbance severity. Several different indices of disturbance severity were used in

this analysis, including leaf area index loss, basal area of aspen and birch girdled,

and gap fraction of the canopy.

Results

Both dominant and subdominant NPP increased post-peak disturbance from 2010-2012.
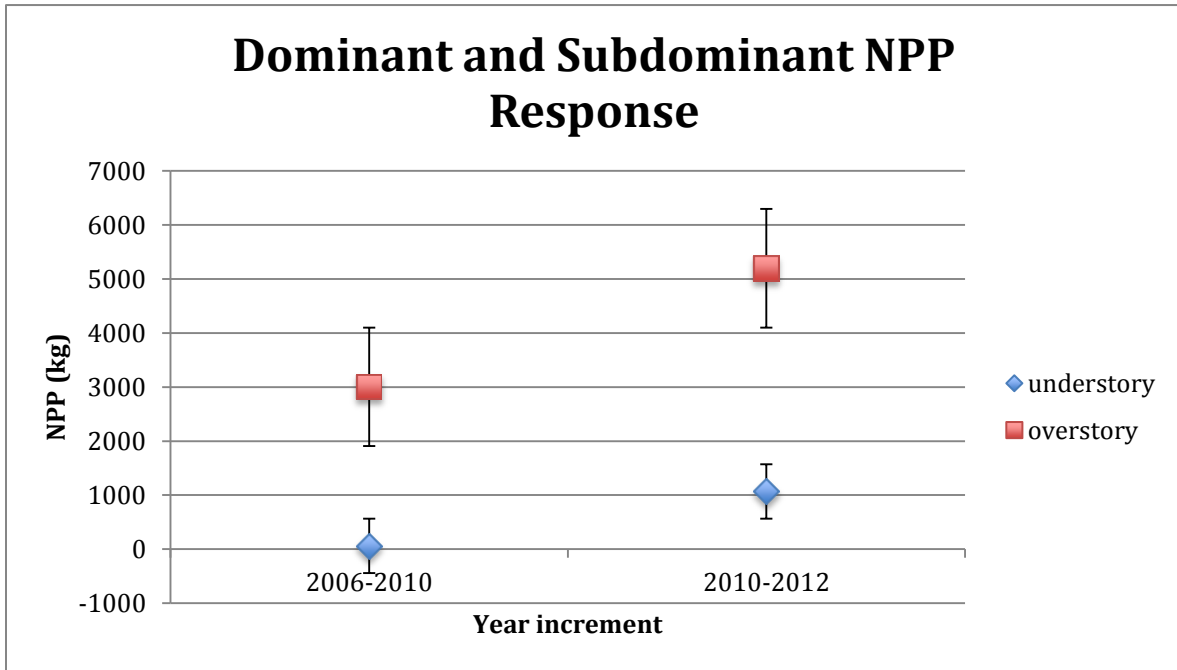

Dominant and Subdominant NPP Response

Figure 1: Dominant and subdominant NPP response to disturbance. The time period from 2006-2010 represents pre-peak disturbance NPP and the time period from 2010-2012 represents the post-peak disturbance recovery NPP.

There was no discernible significant relationship between disturbance severity and subdominant response (Figure 2).

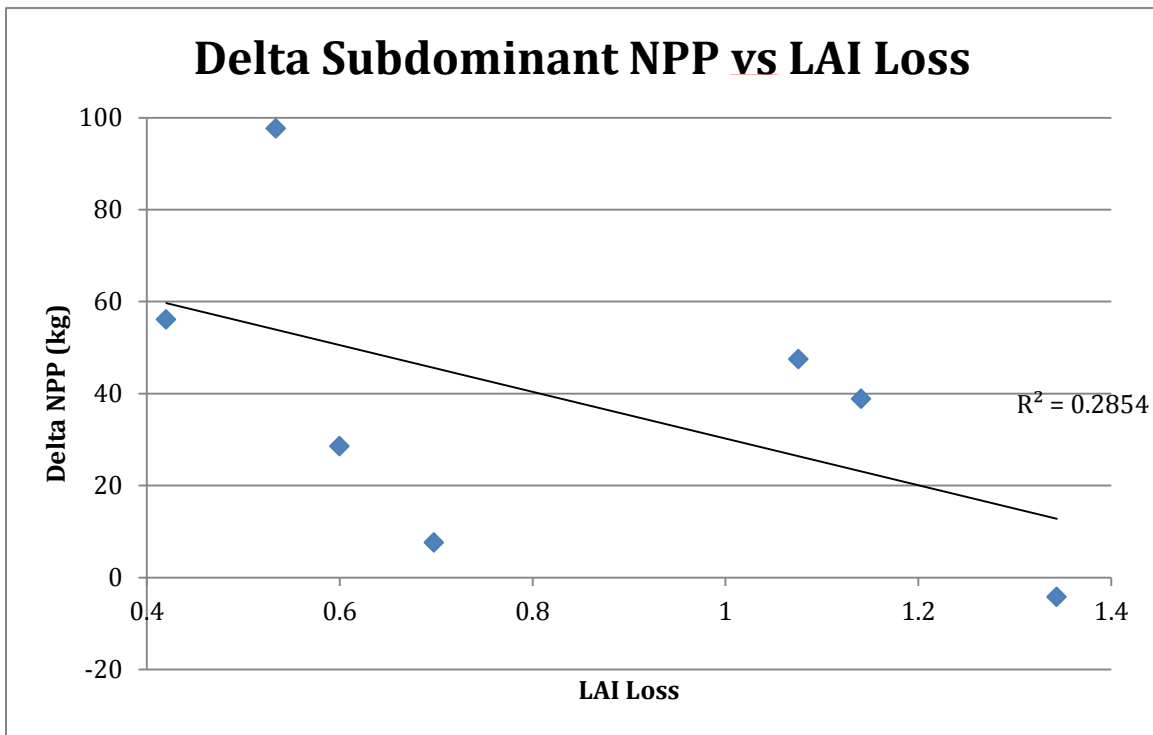## Delta Subdominant NPP vs LAI Loss

$R^2 = 0.2854$

Figure 2: The change in NPP from 2006-2012 to 2010-2012 over a range of disturbance severities (quantified by LAI loss from aspen and birch).

As shown in Figure 3, nitrogen was reallocated to both the subdominant and dominant canopy layers, with slightly more being allocated to the subdominant

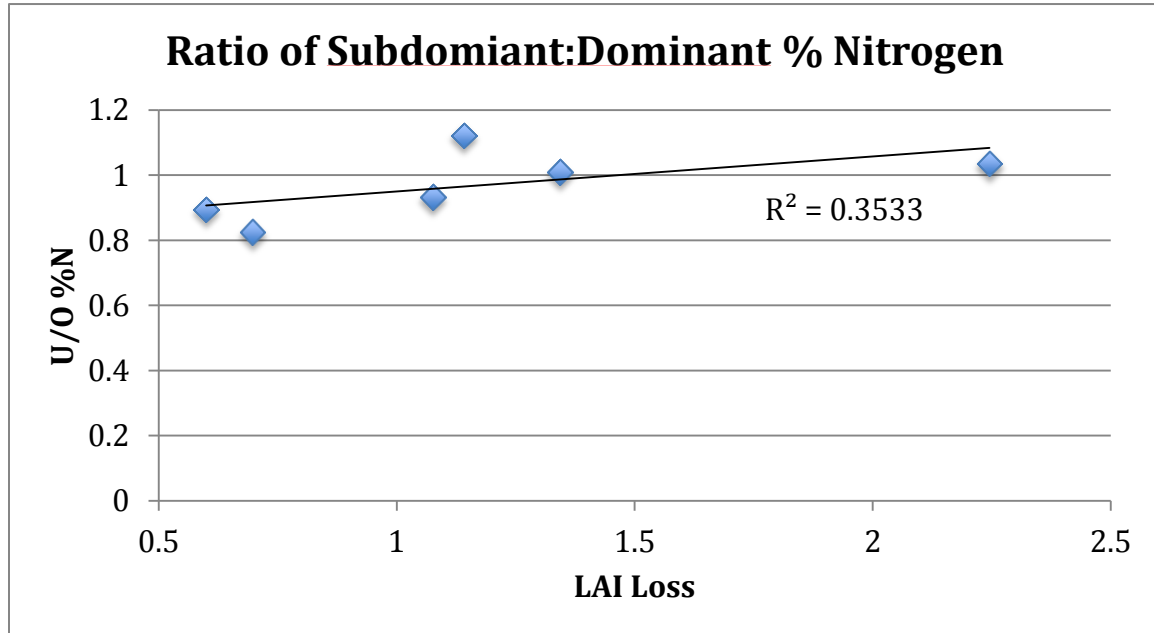canopy layer in proportion to the dominant canopy layer.

Figure 3: The ratio of subdominant to dominant percent nitrogen over a range of disturbance severities (LAI loss).

Discussion

As predicted, both dominant and subdominant NPP increased from 2010-2012. This is likely due to the new resources that became available as the aspen and birch senesced following girdling. Contrary to our hypothesis, no relationship between disturbance severity and understory response was found. It is possible that there was a variable response from the subdominant layer, but that this response was obscured by underlying differences in productivity and structural complexity between plots. Areas of greater disturbance severity were originally more aspen and birch dominated, and this may reflect lower inherent productivity in these plots. This productivity difference could have obscured variation in response related to

disturbance intensity, because the plots with low disturbance (low initial aspen-birch dominance) may have the highest potential productivity. The possibility of an obscured subdominant response is supported by the finding that slightly more nitrogen was reallocated to the subdominant canopy layer in relation to the canopy layer. If the subdominant canopy layer receives more nitrogen as disturbance severity increases, it would be expected to also have a greater NPP as disturbance severity increases.

Further studies could try to correct for the inherent differences in productivity between plots to see if this subdominant response is actually occurring. Future work could also address variation in response across gradients in species composition (both dominant and subdominant). It also may be useful to look at differing species responses to disturbance to see which species contributes the most to NPP resistance.

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