SHIFTS IN ARCTIC VEGETATION MAY FUEL FEEDBACKS TO CLIMATE CHANGE IN PEATLAND REGIONS

By

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A Thesis Submitted to The Honors College

In Partial Fulfillment of the Bachelors degree
With Honors in

Environmental Science

THE UNIVERSITY OF ARIZONA

MAY 2017

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Abstract

Changing sub-Arctic plant communities can be an important feedback to climate change, via shifts in quantity and quality of litter production. Litter inputs to soil have appreciable influence on soil organic matter and microbial dynamics and consequently may provide a feedback to climate change in the sub-Arctic. As permafrost peatlands thaw in response to climate change, the community composition of vegetation has been observed to shift from smaller and woodier shrubs to larger, more biodegradable sedges. We tested the hypothesis that carbon (C) stored in plant biomass increases across a permafrost thaw gradient by sampling both above- and below-ground biomass in a permafrost-underlain palsa, partially thawed bog, and fully thawed fen, all at Stordalen Mire in northern Sweden. Surprisingly, we found that total above- and below-ground biomass together do not significantly change from the intact to the fully-thawed habitats, despite previous research showing that net ecosystem productivity (NEP) appears to be higher in the fully thawed inundated fen. The lack of observed biomass increase despite the increase in NEP observed in other studies could be explained if the higher productivity sedges in fen sites have higher turnover, and transfer that productivity to SOM through high root exudation and/or litter deposition. We also observed a shift in plant community composition associated with loss of plant biodiversity across the gradient. These results suggest that plant community succession alters the quantity, type, and diversity of plant litter inputs to the soil. Such changes in litter quantity and type may be important drivers of decomposition rates and therefore the status of the ecosystem as a source versus sink for atmospheric C.

Introduction

Increasing Arctic temperature is causing permafrost thaw, which may significantly influence resident plant community structure, with potential feedbacks to climate from associated changes in productivity and litter inputs to soil. Previous work has found that warming-induced shifts in vegetation have crucial impacts on community composition and biodiversity in vegetation (Malmer et. al., 2005). In carbon-rich sub-arctic northern peatlands, where previously frozen soil destabilizes and reforms into wetland habitat, dominant vegetation shifts from smaller, woodier plants in permafrost-intact palsa regions to moss- or sedge-dominated bogs and fens (Malmer et. al., 2005). Previous studies found a heightened net ecosystem productivity (NEP) in the thaw impacted habitats in waterlogged peatlands (Bäckstrand et. al., 2010).

High-latitude soils in the Northern hemisphere are estimated to contain 1,400-1,800 petagrams (Pg) of historically immobile C, with approximately 277 Pg of this stock contained in peatlands within the permafrost zone (Tarnocai et. al., 2009). Recent warming in high-latitudes indicates that many non-forested biomes are currently a net carbon sink (Tape et al. 2006, Beck et al 2011), and that overall, the thawing of permafrost tends to be increasing these peatland carbon sinks, and balancing the local carbon budget (Payette et. al., 2004). Consequentially their CH_4 and carbon dioxide (CO_2) emissions due to concurrent shifts in resident plant community can create both inputs and a sink to the atmospheric system. Identifying and quantifying controls on future changes to CO_2 and CH_4 formation in response to shift in plant matter is crucial to distinguishing the status of the global carbon budget. We focus here on subarctic systems.

In Stordalen Mire in Abisko, Sweden, increasingly waterlogged habitats are associated with increased nutrient availability, increased productivity, and increased carbon dioxide (CO_2) uptake in the site's shifting plant communities (Malmer et. al., 2005). This increased productivity could partially offset the thaw-associated C release from biodegradation of soil C. However, these shifts in plant communities may also result in increased litter turnover and subsequent microbial decomposition at the end of the growing season creating both a carbon source the atmosphere. Plant turnover and inputs to soil are crucial controls on the status of the carbon balance in peatland ecosystems. We assessed plant community composition and biomass changes across a permafrost thaw gradient.

We hypothesized that as permafrost thaws, increases in productivity with thaw cause both belowground and aboveground biomass increase. Previous studies have observed a shift towards plants with longer roots that have an ability to obtain oxygen at lower depths with permafrost thaw (McConnell et. al., 2013). This adaptation in plants living in waterlogged areas helps them to survive anoxic conditions (McConnell et. al., 2013). The hypothesized increase in aboveground biomass with thaw will cause low-lying shrubs to become replaced by larger graminoids (Malmer et. al., 2005). Increases in biomass, whether above- or below-ground, would be consistent with the noted increase in NEP in these increasingly waterlogged habitats (Bäckstrand et. al., 2010).

We measured biomass in the early and peak-growing season (early June and late July) to test the hypothesis that total C stored in plant biomass increases across the thaw gradient. The amount of C stored in plant biomass that will be deposited as litter at the end of the season may be estimated by the amount of biomass measured at the site.-We further include a cross comparative analysis between parameter methodologies to determine which process is the best proxy for total litter turnover into the system. These procedures may become useful in the future to estimate shoot-to root ratios and serve as a proxy to biomass inputs after plant senescence.

Methods

Field site description: The research location, Stordalen Mire, is near Abisko Scientific Research Station in Abisko, Sweden, a century-old station with a long-term record of research in Arctic climate change and permafrost thaw (Åkerman and Johansson, 2008; Kokfelt et al., 2009). In carbon-rich sub-arctic northern peatlands, where previously frozen soil destabilizes and reforms into wetland habitat, dominant vegetation shifts from smaller, woodier plants in permafrost-intact palsa regions to moss- or sedge-dominated bogs and then fens along a permafrost thaw gradient (Malmer et. al., 2005).

Site and habitat selection: Quarter meter quadrats (0.25 cm x 0.25 cm) were placed in five replicate pairs at each of the three habitat types along the thaw gradient. Habitat types were determined by plant community composition and water level based on classifications by Malmer 2005. Palsa sites were determined by the presence of woody shrubs, primarily *E. nigrum* and *A. polifolia.* Bog sites were primarily identified by *Sphagnum sp.* and *E. vaginatum* growth and vicinity to still intact palsa regions. Fen sites were farther away and identified by the amount of sedges such as *E. angustifolium* and water level. Care was taken after random selection of sites to ensure that the paired plots in each habitat looked similar in community composition and biomass.

Plant percent cover and vascular green area measurement collection: Plant percent cover and vascular green area measurements (VGA) were taken for both plots at the beginning of the growing season and again before harvest. One plot from each pair was harvested early June 6-19th, and the other was late July 13-24th of 2015. Pictures were also taken before measurements at each time point.

Percent cover was estimated using visual guides. Two researchers were present to confirm approximations. The total plot percent cover could be more than 100% in the case that some plants would create canopy cover over other shorter lichens and mosses.

VGA is an index of green area of plants that can be estimated non-destructively (Wilson et. al., 2007). The green area of leaves on each species type were calculated as the product of leaf size and the number of leaves (Wilson et. al., 2007). The area of leaves was calculated by the application of species-specific formulae, with assumptions about the leaf shape (Wilson et. al., 2007). For species that did not strictly conform to the assumed geometric shapes, it was necessary to include correction coefficients (supplemental table 1). To determine these measures for each species, five representative leaves were selected and measured for each species, then the number of leaves were counted on each stem, and the number off-shooting stems per organism were counted. Stem area was calculated as follows:

$$Stem\ area = (2 * \pi * r) * h$$

Where r=radius and h=height

The total live area of each species was determined as the product of the leaf area and the number of leaves plus the product of the stem area and the number of stems. The green area of each species, i, is modelled by the equation:

$$GA_i = (L_A * L_N) + (S_A * S_n)$$

Where L_A is the average leaf area of the five chosen leaves that were picked on each plant, L_n is the average number of leaves per plant scaled to a quarter meter area, S_A is the average stem area of five randomly chosen plants scaled to a quarter meter area and S_N is the average number of stems on each plant multiplied by the number of plants that were counted within quarter meter area. Each of the five replicates were averaged.

Biomass above and below-ground harvest: In the palsa plots, the quarter meter quadrat was placed, and a bread knife was used to cut around the edges twice. A strategically selected spot that was found to be least destructive was cut from the middle, and a corner was cut from the larger chunk. This corner could then be levered up, and the sides were measured and cut to 15 cm in depth. Another quarter of the chunk was then cut in the same manner. The final half was then accessible enough to pull out. All clods were placed in a bucket and brought back to the research station for separation of plants from peat.

For bog plots, the quarter meter quadrat was first placed, and the bread knife was used to make cuts into the moss mat around the edges. The edges were separated from the surrounding environment by hand, and then the green *Sphagnum* was extracted by separating the still alive green shoots from the dead brown moss. The knife was used to cut further and extract any sedges such as *E. vaginatum* and *C. rostrata*. As sedges were extracted, special care was taken to ensure that as much as possible of the root was taken. Any uneven zones were felt for by hand, and a depth of about 20 centimeters was standardized. Any dead material was returned to the fresh hole. All clods were placed in a bucket and brought back to the research station for separation of plants from peat.

A similar routine was employed at the fen plots. The quadrat was placed in the desired area, and a bread knife was used to cut around the edges. Any *Sphagnum* that may have been present was removed. A serrated knife was used to dig out the deepest roots for any particularly large sedges, such as *E. angustifolium.* Depths were measured to around 20 centimeters and any dead material was returned to the fresh hole. All clods were placed in a bucket and brought back to the research station for separation of plants from peat.

Once in the research station, clods for each habitat were picked through with the goal of keeping roots intact for identification. Roots and above ground biomass were then separated into separate labeled bags and placed into a drying room for approximately a day. Each species was then weighed and returned to the room for another day before a second measurement was taken. This process was repeated until the weights of the bag stopped changing.

Results

Neither total standing biomass nor the aboveground portion of biomass varied detectably with habitat shifts early in the growing season (Fig. 1a). Bog and fen sites had relatively less below-ground biomass then they had aboveground. In contrast to the above-ground and total biomass values, the below-ground values were the only averages that were found to be statistically significantly different across habitats, with the palsa diverging significantly from both the bog and the fen sites based on a Tukey HSD test (Fig. 1, $p<0.05$).

At the peak of the growing season, total biomass was also not significantly different between habitat types based on a Tukey HSD test (Fig. 1b),).

Above-ground biomass values were notably similar across all three habitats with overlapping error bars. The below-ground biomasses were again found to be the only ones which varied significantly across habitat, with palsa and fen showing significantly more biomass than the bog (Fig. 1b, $p<0.05$).

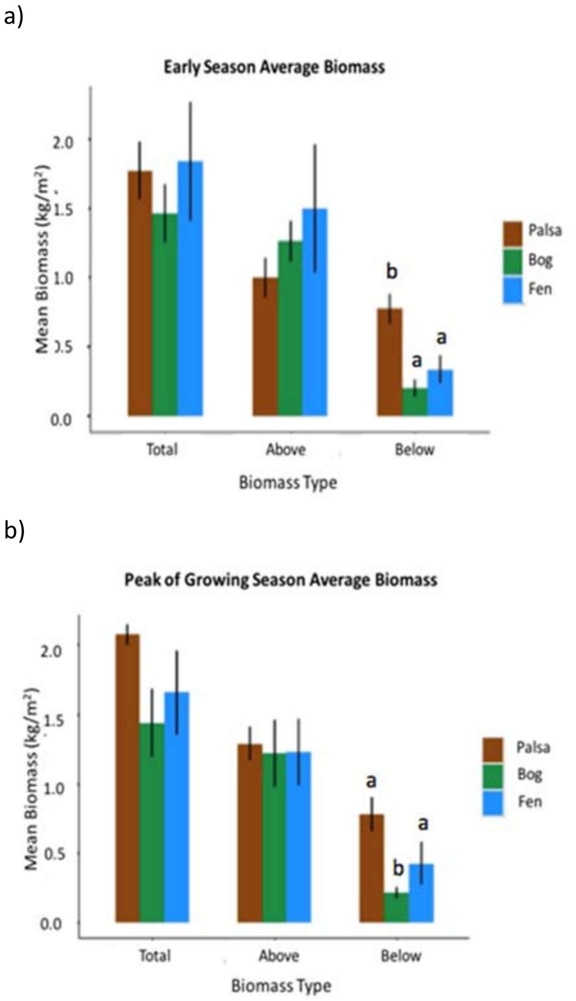


Figure 1: Standing mean stock of biomass (kg/m^2), across five replicates at each of the three key habitats that represent each stage of permafrost thaw succession, across the thaw gradient. Data is taken from above and below ground harvest during the first time point at the beginning of the growing season during the dates of June 6th-19th in a) and at approximately the peak of the growing season from July 13th-24th in b). Error bars are standard errors. Statistically significant differences were found using a Tukey HSD test ($p<0.05$) and are designated by letters.

Fen sites showed increases in biomass over the growing season as evidenced by their positive mean values, but also exhibited the widest spread amongst the replicates (Fig. 2). By contrast, the palsa and bog sites generally had lower negative means, with the smallest standard error bars between replicates in the bog sites. The mean totals in all the sites appeared to have most of their spread affected by above ground-biomass variability. The fen had the most variation with generally low or even negative growth values. The fen had both the highest mean total biomass increase and the highest mean above-ground biomass increase.

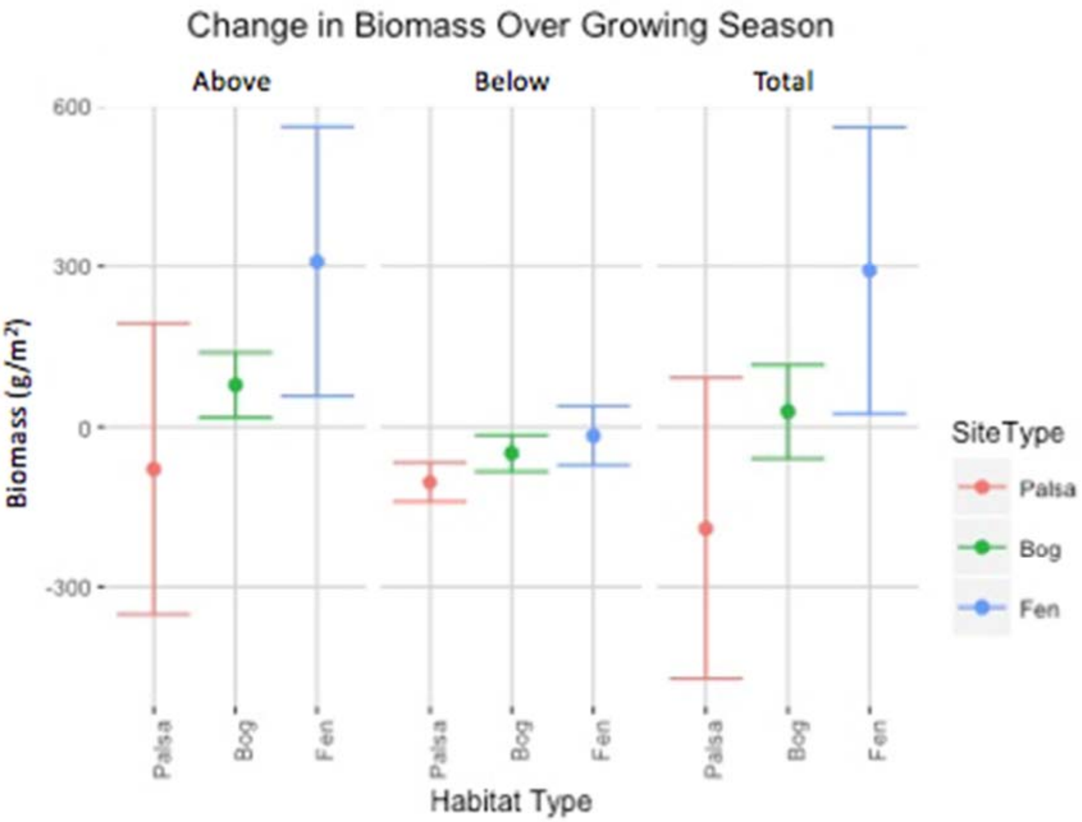


Figure 2: The difference between the early and the peak of the growing season biomass harvest data was found by subtracting each plot harvested at the peak of the growing season from its congruent paired plot taken in the early season. Each dot represents a mean of each of these five replicate values. Error bars represent standard error.

Plant diversity declined across the full gradient, based on the absolute abundance of plants in the early portion of the growing season, with the palsa having the most species (figure 3). The palsa site diversity in plants was inclusive of mainly small woody shrubs and small sedges. The largest absolute percent abundance in both the bog and the fen appeared to be *Sphagnum* moss. The bog appeared to have the highest biomass which was primarily comprised of Sphagnum moss with a few woody shrubs mixed in at negligible numbers. By contrast, the palsa did not appear to be dominated by any one species.

At the peak of the growing season, absolute abundance in vegetation at the palsa appeared to occur in similar but larger proportions to those in the early season. No one plant appeared to predominate. The bog was still dominated by *Sphagnum* moss but experienced a notable increase in the sedge *E. vaginatum.* The *Sphagnum* appeared to decrease dramatically between the early and the peak seasons at this site. The fen experienced a similar trend in *Sphagnum* moss but saw growth in the sedge species. Total overall biomass appeared to increase in all species at all sites, with the notable exception of *Sphagnum* moss. Dominant species appeared to shift in both the early and the peak of the growing season spatially across the thaw gradient from multiple equally dominant shrubs to a few dominant sedges in the fen (*C. rotundata* and *E. angustifolium*).

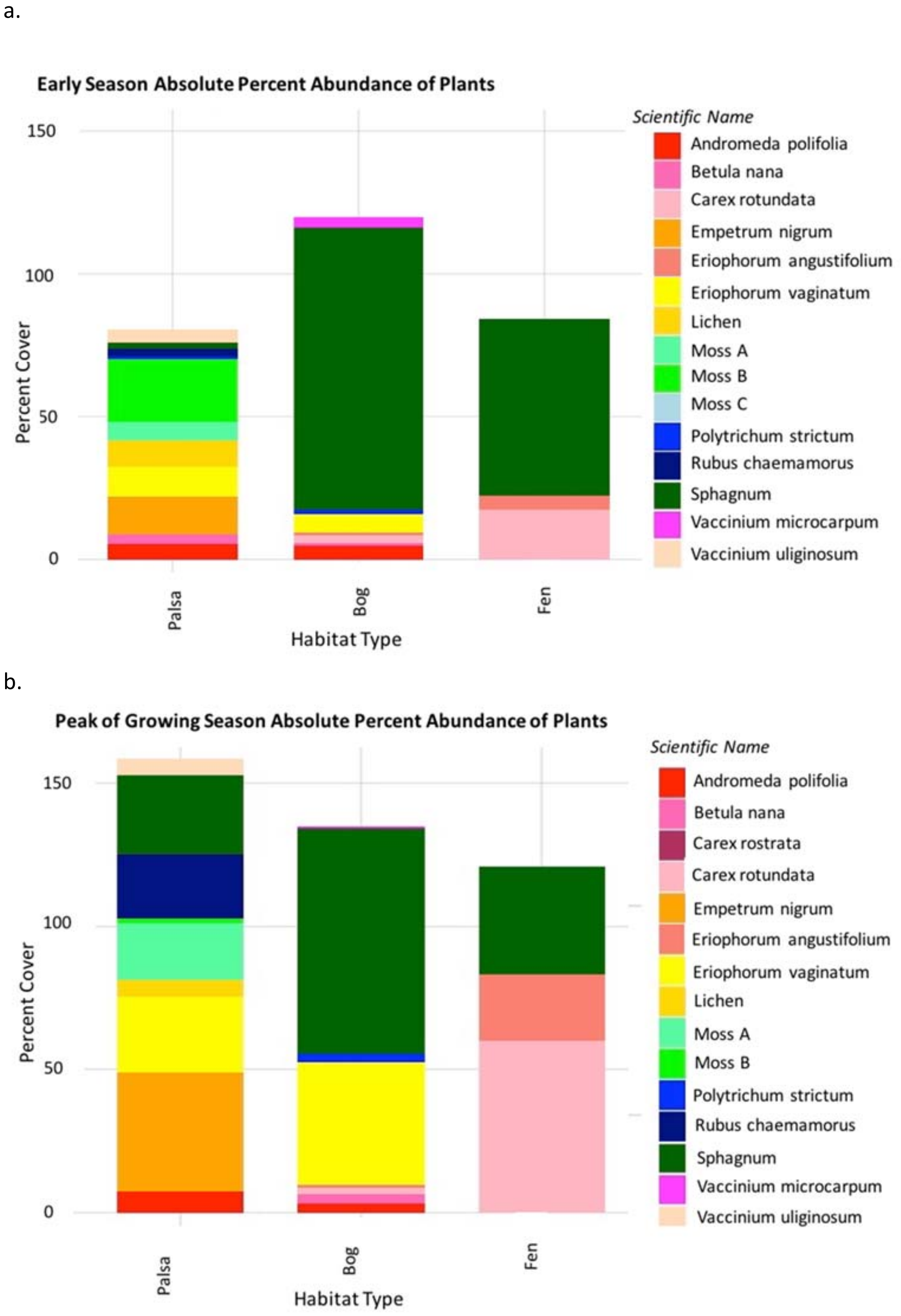


Figure 3: Stacked barplot comparison of absolute abundances (as percent cover) at each of the three key habitats that represent each stage in permafrost thaw succession. Values represent plant species averaged by each of the five replicate plots for each habitat type. Lichen and moss types were not identified in field, so unidentified moss species are designated by letters. *Sphagnum* moss was not differentiated.

Based on a scatterplot comparison of alternative methodologies to standard biomass harvest, percent cover appeared to better correlate with above ground biomass than VGA (supplemental figure 4, part a). The palsa (adjusted r-squared=0.6163, p=0.00435) and bog (adjusted r-squared=0.7585, p=0.0006382) sites appeared to have the lowest correlation coefficients. By contrast, the fen had the highest correlation (adjusted r-squared=0.8923, $p=2.389*10^{-5}$). All comparisons were found to be statistically significant ($p<0.05$).

VGA did not appear to correlate well with above ground biomass (Supplamental Fig. 4b). The palsa (adjusted r-squared=-0.01295, p=0.3744) and bog (adjusted r-squared=-0.00075, p=0.3481) were again found to have the smallest correlation coefficients. The fen was still the most highly correlated of the three habitat types (adjusted r-squared=0.1291, p=0.1651). All comparisons were not statistically significant ($p>0.05$).

Discussion

Surprisingly, we found that total above- and below-ground biomass together are not significantly different between the intact and the fully-thawed habitats, despite previous research showing that productivity appears to be higher in the fully water-logged fen. However, biodiversity significantly decreased from the intact to waterlogged sites. The lack of observed biomass increase despite the increase in NEP observed in other studies from this site could be explained if the C taken up by sedges in fen sites is deposited in SOM at increased rates either through root exudates or annual litter deposition. Since the shift in plant community composition is associated with the observed loss of plant biodiversity across the gradient, our results suggest that plant community succession alters the quantity, type, and diversity of plant litter inputs to the soil. Differences in litter quality have been previously linked to shifts in species and can therefore also impact decomposability (Dorrepaal et. al., 2005). We suggest that litter inputs to the soil are therefore increasing in both quantity and quality, resulting in a greater amount of bioavailable carbon input? to soil environments.

Sphagnum moss decreased between the early and late growing season in the bog and fen but increased in the palsa site. We suggest that increases in the water level in the bog and fen habitats due to a wet summer may have led to *Sphagnum* moss death.

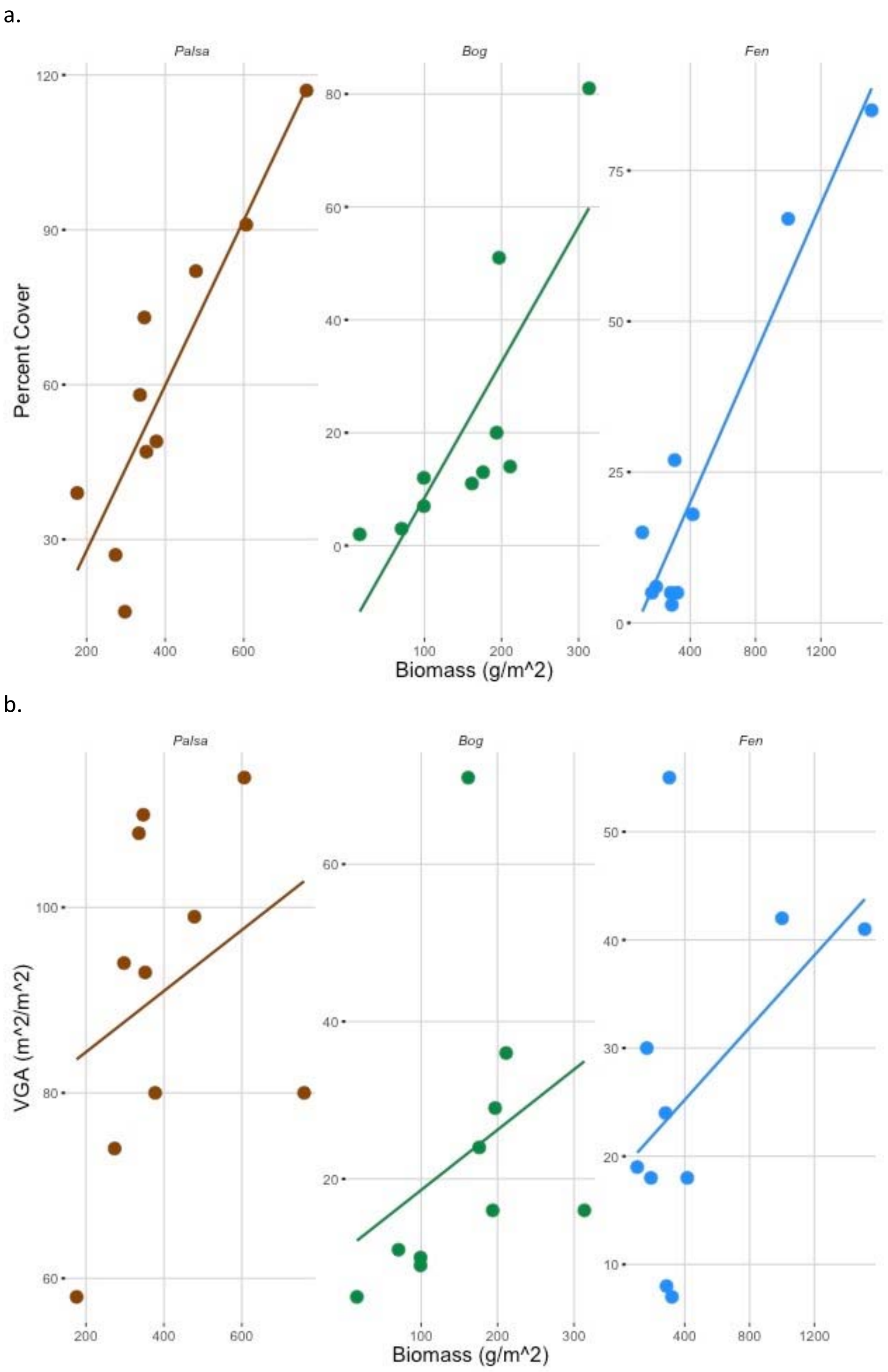
Comparisons in vascular green area and percent cover measurements to above ground biomass harvest values found percent cover to be correlated with above ground biomass. Surprisingly, VGA was not found to be correlated with above ground biomass, despite the original hypothesis and previous research (Wilson et. al., 2007). Our results suggest that percent cover may be a better methodology than VGA to predict above-ground biomass.

Our results do not support the original hypothesis that total C stored in plant biomass increases spatially across thaw succession gradients but rather supports a revised hypothesis that litter decomposition rates increase in sites impacted by thaw. We suggest that deposition of SOM in the form of litter into the soil is occurring at an increased rate. Our findings in seasonal biomass differences further support this idea because little to no change in biomass quantity over the growing season at the fully thawed fen sites suggests a heightened turnover of C to account for the increase in NEP observed in previous studies (Backstrand et. al., 2010). We found a significant decrease in plant biodiversity which can be expected to impact the diversity/type of plant litter inputs to the soil. Such changes in litter quantity and type may be important drivers of decomposition rates and future studies may find a subsequent impact the status of the ecosystem as a source versus sink for atmospheric carbon.

Appendix

Species	Leaf Shape	Correction Coefficient	Leaf Width (mm)	Leaf Length (mm)	Stem Width (mm)	Leafy Length (mm)
A. polifolia	EL		2		1	
B. nana	CL					
C. rotundata	HC		1			
E. angustifolium	RA	0.53				
E. nigrum	EL		1	3	1	20
E. vaginatum	HC		1			
R. chaemamorus	CL				2	
V. microcarpum	TR		1	2	1	
V. uliginosum	EL					
V. vitis-idaea	EL					

Supplemental Table 1 Species specific formulae for the calculation of both leaf and stem area. It became possible to include assumptions on stem widths and leaf dimensions after replication. CL=circle ($\pi*r^2$), EL= ellipse ($\pi*r_1*r_2$), HC= half cone ($r*L*\pi/2$), RA= rectangle ($W*L$), TR= triangle ($0.5*W*L$), where W=width, L=length and r=radius of leaf. Leafy length is included to denote the length from the tip of *E. nigrum* stems that included leaf offshoots. Leaves were counted within a 2 centimeter subsection of this length. *E. nigrum* stems were defined by visible 'heads' poking out of the overall mat. *C. rostrata* was not distinguished from *C. rotundata* in this portion of analysis. Moss and lichens were not included in this analysis.



Supplemental Figure 4: Scatterplot comparisons of alternative methodologies to biomass harvesting. Part a represents the percent cover values in comparison to above ground biomass and part b shows the VGA measurements in comparison to above ground biomass. Values for both the early and late seasons have been included. Each replicate plot for the two time points are included as an average of all parameter values. All values have been scaled up to a meter quadrat. The percent cover values were dimensionless, but were still scaled by a factor of four. Lines of best fit are included.

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