Title: The response of boreal peatland community composition and NDVI to hydrologic change, warming and elevated carbon dioxide

Running head: Peatland NDVI response to climate change

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Abstract

Widespread changes in arctic and boreal Normalized Difference Vegetation Index (NDVI) values captured by satellite platforms indicate that northern ecosystems are experiencing rapid ecological change in response to climate warming. Increasing temperatures and altered hydrology are driving shifts in ecosystem biophysical properties that, observed by satellites, manifest as long-term changes in regional NDVI. In an effort to examine the underlying ecological drivers of these changes, we used field-scale remote sensing of NDVI to track peatland vegetation in experiments that manipulated hydrology, temperature, and carbon dioxide (CO$_2$) levels. In addition to NDVI, we measured percent cover by species and leaf area index (LAI). We monitored two peatland types broadly representative of the boreal region. One site was a rich fen located near Fairbanks, Alaska at the Alaska Peatland Experiment (APEX), and the second site was a nutrient-poor bog located in Northern Minnesota within the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment. We found that NDVI decreased with long-term reductions in soil moisture at the APEX site, coincident with a decrease in photosynthetic leaf area and the relative abundance of sedges. We observed increasing NDVI with elevated temperature at the SPRUCE site, associated with an increase in the relative abundance of shrubs and a decrease in forb cover. Warming treatments at the SPRUCE site also led to increases in the LAI of the shrub-layer. We found no strong effects of elevated CO$_2$ on community composition. Our findings support recent studies suggesting that changes in NDVI observed from satellite platforms may be the result of changes in community composition and ecosystem structure in response to climate warming.

Introduction

An increase in vegetation greenness, as measured via the Normalized Difference Vegetation Index (NDVI), has been observed across the northern hemisphere in recent decades. A number of studies have linked this change to climate warming. Substantial evidence suggests that shorter, less severe winters are resulting in warmer spring temperatures and extended growing seasons leading to changes in peak values and timing of NDVI (Myneni et al. 1997, Tucker et al. 2001, Delbart et al. 2008, Karlsen et al. 2009). Northern regions are also experiencing an increase in mean annual precipitation in both winter and summer seasons that may contribute to the changes observed in NDVI (Hinzman et al. 2005, Post et al. 2009, Walsh et al. 2011, Bintanja & Seltan 2014). The shift in greenness has been particularly

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pronounced in the high arctic, and has been linked with an increase in shrub cover (Goetz 2005, Tape et al. 2006, Beck and Goetz 2011, Myers-Smith et al. 2011, Myers-Smith 2015). Remote sensing studies of the boreal region have yielded mixed results compared to those in the arctic. Although previously consistent with arctic greening, trends in the boreal region reversed in the late twentieth century showing a decrease in NDVI (“browning”), likely resulting from moisture limitation (Myneni et al. 1997, Beck & Goetz 2011, Piao et al. 2011, Buermann et al. 2014, Verbyla 2015, Park et al. 2016, Pheonix & Bjerke 2016). These findings highlight the complex spatiotemporal relationships among climate, vegetation change, and NDVI at regional scales.

Although there is strong indication that NDVI is changing across the boreal region, there is limited research describing what may be driving the observed trends. Given the low spatial resolution of many satellite products, combined with a limited number of field studies that manipulate global change drivers, it is unclear whether shifts in NDVI are the result of impacts on vegetation biophysical parameters (e.g., leaf area index (LAI)), vegetation community composition, or other processes. The studies that have used NDVI as a monitoring technique in peatlands have found relationships with water table position (Meingast et al. 2014), standing biomass and rates of ecosystem production (Hope et al. 1991, Boelman et al. 2003, Boelman et al. 2005, La Puma et al. 2007) and vegetation cover, particularly of shrubs (Hope et al. 1991, Riedel et al. 2004, Walker et al. 2003, Meingast et al. 2014). In this research, we sought to provide context to observed trends in NDVI through analysis of field-scale experiments that manipulate various global change drivers of peatland vegetation.

Peatlands are widely distributed across the circumpolar north. They account for approximately nineteen percent of soil area in the northern permafrost region (Tarnocai et al. 2009). Because of their large carbon stores (Gorham et al. 1991, Bridgham et al. 2006, Yu et al. 2010), peatlands are crucial to regulating the global climate system (Chapin et al. 2000). Furthermore, peatland ecosystems are particularly vulnerable to climate change because of the combined risk they face from rising temperatures and changing hydrologic conditions. Experimental manipulation of peatland hydrology has demonstrated that decreasing moisture availability results in peatlands becoming a source of CO₂ due to lower gross primary productivity (GPP) relative to ecosystem respiration (ER) rates in rich and poor fens, (Strack et al. 2009, Chivers et al. 2009, Olefeldt et al. 2017, Radu & Duval 2018) and bogs (Weltzin et al. 2000, 2001). Changes in hydrology also affect peat temperature (cf. Waddington et al. 2014). While increases in temperature have generally been shown to stimulate microbial activity and increase ER in peat (Moore & Dalva 1993, Silvola et al. 1996), assessments of interactive effects among temperature, soil moisture, and vegetation production are difficult in field settings (Johnson et al. 2013), and likely change over time (Chivers et al. 2009, Olefeldt et al. 2017). Yet, there are few long-term manipulation studies assessing
the role of multiple climate drivers on bog and fen biophysical properties simultaneously (Weltzin et al. 2000, Weltzin et al. 2003, Dieleman et al. 2015). Further understanding of the relationship between multiple global change drivers (e.g., warming, altered hydrology, and elevated CO₂), peatland ecosystem structure (i.e. LAI, community composition), and NDVI will elucidate recent trends in satellite observations across large areas of the boreal region.

Temperature and hydrology are strong controls on peatland community composition, which contributes to the carbon sequestration and storage potential of peatlands (Weltzin et al. 2000, Ward et al. 2009, Breeuwer et al. 2009, Dieleman et al. 2015, Goud et al. 2017, Olefeldt et al. 2017, Radu & Duval 2018). However, exactly how changes in climate affect vegetation community composition and function are likely to be different in bogs and fens, owing to differences in water residence time and nutrient status. For example, studies have shown that drying in nutrient-rich fen peatlands leads to an increase in shrub cover, a decrease in graminoid cover, and a decrease in annual GPP (Churchill et al. 2014). In nutrient-poor bog and poor fen systems, drying can also lead to increases in shrub cover and decreases in graminoid and moss cover (Weltzin et al. 2000, Weltzin et al. 2003, Breeuwer et al. 2009, Potvin et al. 2015, Radu & Duval 2018). However, effects of drying on productivity are mixed. Some studies have indicated that drying decreases GPP, while others have indicated that a shift from graminoid to shrub dominance could be associated with an increase in GPP, potentially offsetting increases in plant and soil respiration (Weltzin et al. 2000, Radu & Duval 2018).

Several studies have found a significant effect of increasing temperature on peatland community composition and GPP. However, previous research has yielded a range of results depending on peatland hydrological connectivity and nutrient status. For example, studies have indicated that warming in hydrologically-connected fen peatlands leads to shifts in dominance from non-vascular *Sphagnum* mosses to vascular plants such as graminoids (Weltzin et al. 2003, Dieleman et al. 2015). However, in nutrient-poor bog peatlands that lack connectivity with groundwater, warming also could lead to drying, potentially favoring shrub cover over graminoids (Weltzin et al. 2000, Weltzin et al. 2003). Although shrub cover is correlated with GPP, it is less clear how the potential increase in aboveground productivity will affect overall rates of ecosystem carbon exchange (Weltzin et al. 2000). These studies indicate that peatland aboveground productivity is determined by a series complex and poorly-resolved interactions among plant species, temperature, and hydrology.

While there is a developing literature on the effects of changing temperature and soil moisture on peatland ecosystem function, far fewer studies have investigated the effects of elevated CO₂ in peatlands. Peatland mesocosm experiments have yielded conflicting results that underscore the complexity of ecological responses to elevated CO₂. Some studies have shown that elevated CO₂ increases the productivity of

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peatland vascular plants, in particular graminoids (Grluke et al. 1989, Dieleman et al. 2015). Others have indicated no changes in vascular plant growth resulting from CO₂ fertilization alone, but have documented that the combined effects of nitrogen and CO₂ enrichment led to increases in the growth of both graminoids and shrubs (Berendse et al. 2001, Heijmans et al. 2001). These studies found no significant effect of elevated CO₂ on non-vascular productivity (Berendse et al. 2001, Dieleman et al. 2015). Ombrotrophic bog peatlands are by definition nutrient poor and typically dominated by Sphagnum mosses. This could indicate a relatively small effect of elevated CO₂ on the productivity of bogs as compared to fens. These studies suggest that bogs and fens might exhibit different responses to elevated CO₂ levels due to the unique responses of vascular versus non-vascular plant functional types.

The objective of this research was to examine the effects of a variety of global change drivers on peatland community composition and NDVI. We leveraged two different peatland ecosystem manipulation experiments, one located in a nutrient-rich fen and one in a nutrient-poor bog to test the effects of altered hydrology, increased temperature, and elevated CO₂, on plant community composition, LAI and NDVI. The Alaska Peatland Experiment (APEX) at the Bonanza Creek Long Term Ecological Research Station, manipulates water table in a nutrient-rich fen. The Spruce and Peatland Responses Under Changing Environments (SPRUCE) project at the Marcell Experimental Forest, Minnesota, USA manipulates temperature and CO₂ in a nutrient-poor bog. We predicted that drought would decrease NDVI at the rich fen site, coincident with a decrease in graminoid cover and an associated decrease in total leaf area. We predicted that warming and CO₂ fertilization would increase NDVI in the bog study system, coincident with a decrease in sedge cover and an increase in shrub cover, driving an overall increase in leaf area. Specifically, we predicted an increase in shrub cover with increasing temperature and elevated CO₂, and a decrease in graminoid cover coincident with drying. We hypothesized that NDVI would be highly sensitive to changes in vegetation composition, and in particular the abundance of woody shrubs. We measured the direct effects of changing climate drivers on biophysical and compositional properties of peatland vegetation, in order to further remote sensing applications in the area of global change ecology.

Materials and methods

Site Description

This study was conducted at two large-scale experiments representative of two types of common northern boreal peatlands- bogs and fens. Here we examined the effects of altered hydrology in a fen ecosystem, which naturally have fluctuating water tables, while the effects of altered temperature and atmospheric CO₂ were examined in a bog ecosystem lacking groundwater connectivity. The first site was at the
Alaska Peatland Experiment (APEX) at the Bonanza Creek Long Term Ecological Research Station, located forty kilometers west of Fairbanks, Alaska (64.82°N, 147.87°W). The experiment is located in a sedge-and-shrub-dominated rich fen on the floodplain of the Tanana River (See Table 2 for species list). APEX was initiated in 2005 to assess the long-term effects of altered hydrology on peatland ecology and biogeochemistry (Turetsky et al. 2008, Kane et al. 2010, Olefeldt et al. 2017). APEX consists of three water table manipulation plots, a raised, lowered, and control treatment, each 120 m² in size. The lowered treatment plot is drained by a trench (~40 cm wide, ~1 m deep) into the peat, which ranges in depth from 1-1.5 m. Water from the trench is then pumped into the raised water table treatment to keep it consistently flooded near the peat surface. The hydrology in the control plot is not manipulated, and its water table typically falls somewhere between the raised and lowered treatment plots. Target separation among water table treatments is approximately 20 cm during the growing season; however there has been considerable inter- and intra-annual variability in water table position over the last decade, consistent with variable hydrology in fen ecosystems (Olefeldt et al. 2017).

The second study site was at the Spruce and Peatland Responses Under Changing Environments (SPRUCE) project located at the Marcell Experimental Forest in northern Minnesota, USA (47.30°N, 93.29°W). The SPRUCE experiment was designed following a regression-based model in which ecological change could be measured in response to a broad range of increasing temperature treatments (Hanson et al. 2017). SPRUCE treatments were initiated in 2014 to explore the effects of increased above- and belowground temperatures and elevated CO₂ on ecological and biogeochemical processes at the southern edge of the boreal biome (Tfaily et al. 2014). The experiment is located within an ombrotrophic bog dominated by Sphagnum mosses, black spruce (Picea mariana) and tamarack (Larix laricina), with an understory of ericaceous shrubs, graminoids, and forbs. The experimental design consists of ten enclosed treatment plots with five temperature treatments (0, 2.25, 4.5, 6.75, and 9 °C) with and without elevated CO₂ (~900 ppm). The above- and belowground temperature treatments are implemented by maintaining a fixed differential from actual temperatures in the two reference plots. The plots consist of octagonal enclosures that are 12.8 m in diameter (114.8 m² in area), 8 m tall, with a belowground corral that penetrates through the peat to glacial material below, which averages 2.5 m deep across the site. The enclosures are maintained at a series of increasing temperatures by forced air and deep peat heating across a range of possible climate change scenarios (Hanson et al. 2017).

Vegetation Cover Sampling and Measurement of LAI

To determine the effects of experimental manipulation on community composition, surveys of species presence were conducted at both experiments. Slightly different sampling strategies were followed at each
site, according to the protocols associated with each experiment (Table 1). At APEX, species cover was recorded using a Point Bar Vegetation Survey method (Bonanza Creek LTER; Jonasson 1988). At the lowered and raised treatments, four replicate plots were sampled, and in the control treatment five replicates were sampled. Two transects were established perpendicular to each other across each of the 4-5 replicate 1x1 m vegetation plots. A laser pointer was inserted into ten evenly-spaced holes in a meter-long metal frame positioned at one meter above soil surface for each of the two transects, for a total of 20 points sampled per 1x1 m vegetation plot. In total, 80 or 100 points were sampled across the water table treatments. At each interception of the laser, species and height above the ground were recorded from the canopy to the surface of the peat. All live biomass was identified to species, and dead biomass was marked as “litter,” indicating that it was part of the thatch forming at the surface of the peat. Species were then categorized into plant functional type (Table 2), and percent cover of each plant functional type (PFT) was calculated for each plot based on the number of hits of each PFT relative to the entire sample.

Leaf area index (LAI) at APEX was calculated as the number of layers of photosynthetic vegetation between the canopy and the soil surface. The fractional cover of photosynthetic vegetation to non-photosynthetic vegetation (PV/NPV) was also calculated in each plot by taking the ratio between measured green leaf area and litter cover. Along with LAI, fractional cover of green leaf area to bare soil or litter has been shown to relate to NDVI due to the absorption of infrared light by non-photosynthetic biomass and exposed earth (Carlson & Ripley 1997). Thus, both LAI and the PV/NPV ratio were examined as potential drivers of NDVI.

Vegetation composition at SPRUCE was sampled at peak growing season in the twelve chambers spanning the full range of temperature and CO₂ treatments, plus the unchambered references. In each chamber, three plots 2 m² in size were sampled using a gridded frame of 1 x 2 m that was set onto fixed-PVC pipes installed at each plot corner to facilitate repeated data collection over the same area. Each frame was divided into 50 – 20 x 20 cm cells. Presence and absence of all species were recorded for each cell of the grid. Species were categorized into PFT’s for analysis according to the SPRUCE protocol (Table 2). We determined frequency of each PFT (as a surrogate for percent cover) as the number of cells where at PFT is present divided by the total number of cells sampled.

LAI was measured at SPRUCE using an LI-COR LAI 2200 (Lincoln, NE) instrument that estimated leaf area per unit ground area as the amount of incoming light available below a canopy (Gower & Norman 1991). LAI measurements were taken in late June of 2017, at peak growing season. Measurements were done near mid-day on a cloud free day. The reference sensor was positioned on a tripod in an open meadow with no nearby tree cover. Sensors were matched at the beginning of the field campaign. Light
diffusing lenses were used on both sensors to create uniform light conditions. Measurements were taken at two central sampling locations in each of the three vegetation community plots in each chamber. At each sampling location, two scans were taken each at 1 meter above the shrub canopy, and beneath the shrub canopy at the surface of the peat. The measurements taken above the shrubs represented the LAI of the tree canopy, which were then subtracted from the LAI values for the shrub layer to examine the effect of treatment on the shrub layer.

**NDVI Time Series Data Collection**

Both sites were instrumented with Decagon Inc. (Pullman, WA) NDVI sensors (Gamon et al. 2015) at the beginning of the 2016 growing season. They consisted of two sensors that measured irradiance at 630 and 800 nm, one upward looking to measure incoming light, the other downward looking to measure reflected light. The hemispherical (incoming) sensor is cosine corrected to account for sun angle. The downward pointing sensor has a field of view of 36°, and each sensor was installed at a height of 150 cm above the peat surface at both sites, which results in an instantaneous field of view of approximately 53 cm in diameter. Data were stored on Em50G data loggers with measurements collected every ten minutes throughout the growing season. NDVI was automatically calculated as the normalized ratio of a visible and a near-infrared band.

\[
NDVI = \frac{810 \text{ nm} - 650 \text{ nm}}{810 \text{ nm} + 650 \text{ nm}}
\]

During processing of the APEX field data, only NDVI values between 11:00 AM and 2:00 PM were included in the analysis, or approximately two hours on each side of solar noon (Gamon et al. 2015). At
SPRUCE, only values between 11:00 AM and 1:00 PM were included in the analysis. We used a slightly narrower window at SPRUCE given the differences in day length between the two sites. In addition, a threshold of 0.5 was applied at both sites to exclude NDVI measurements that may have occurred during very overcast days. The exclusion of observations taken when the sun was not directly overhead at both was done to minimize the potential for shading. At APEX, this was less of an issue since the site is open, hence the larger window of usable data, whereas SPRUCE has an intermittent canopy of spruce and tamarack trees, as well as a greater amount of instrumentation and interference by the chamber walls. For both sites, a daily average NDVI value was calculated for each measurement location.

**Plot-level measurement of NDVI**

To make a direct comparison of the relationship between community composition and NDVI, we also collected one-time plot-level measurements of NDVI using hand-held spectroadiometers above all of the vegetation plots at both study sites. At APEX we used an Analytical Spectral Devices FieldSpec Pro (Boulder, CO). Incoming solar reflectance was measured relative to a white Spectralon reference panel that reflected 100 percent of incoming radiation. Measurements were recorded under clear sky conditions, and white reference scans were performed between spectral data collection at each water table treatment plot, or approximately every five minutes. Scans were performed at one-meter above ground surface at nadir with a 25 degree foreoptic, resulting in a ground field-of-view (FOV) that was 47 cm in diameter:

\[
GFOV = 2 \frac{\text{height} \ast \tan(25^\circ)}{2}
\]

Data were collected during peak growing season, on June 29, 2016. Scans were performed within a one hour window on each side of solar noon, which occurred at approximately 12:30 pm. Reflectance was calculated “on the fly” by the instrument against a white reference scan that was performed immediately prior to data collection using a Spectralon panel (North Sutton, NH). White reference scans were performed between plots, or approximately every minute. Three scans were recorded above each vegetation plot and then averaged. NDVI was calculated using the same bands as the Decagon sensors (see Equation 1).

Sampling at SPRUCE was done using a PP Systems UniSpec-DC (Amesbury, MA) spectroradiometer. The fiber optic cable on the Unispec was fitted with a FOV restrictor that limited the FOV to approximately 15°. The instrument foreoptic was leveled at 1 m above the ground capturing an area of approximately 35 cm in diameter, or 0.1 m². Three scans were performed above each vegetation plot and...
averaged. White references scans were performed between each treatment. Reflectance was calculated for
the average of the three scans following the methods of Harris et al. (2014) and Wang et al. (2016).

\[
\frac{R_{\text{target}}}{I_{\text{downwelling}}} \div \frac{R_{\text{panel}}}{I_{\text{downwelling}}}
\]

(3)

In this equation, \(R_{\text{target}}\) is the light reflected from the vegetation canopy, \(R_{\text{panel}}\) refers to the reflectance of
the white reference panel, and \(I_{\text{downwelling}}\) refers to the upward-pointing sensor measuring the incoming
solar radiation. Data were collected in late season on September 22, 2016 under clear sky conditions
beginning at 1:00 pm. Data from the Decagon NDVI time series indicated that the growing season was
just past peak greenness at this time (Figure 2), and showed strong separation among treatments. NDVI
was calculated for each plot following Equation 1. We also performed a spectral resampling method to
the ASD and Unispec data to account for differences in the spectral resolution and spectral response
among instruments used in data collection (Supplemental Materials 1.1). Finally, we compared the NDVI
values collected using the hand-held spectral sensors with the NDVI values captured on the same day by
the Decagon sensors to determine whether there was agreement among instrument types. We found a high
level of agreement between NDVI values captured across platforms (see Figure S1).

Data Analysis

Vegetation cover data were analyzed for differences in PFT cover among the treatments at each site. Data
were analyzed using a multi-variate non-metric multidimensional scaling ordination using a Bray-Curtis
dissimilarity index to assess community-level differences among treatments. Permutation tests were used
in both cases to determine whether statistically significant differences existed in composition among
treatments, and to determine the strength of the relationship between NDVI and community composition.
Stress plots were used to diagnose the goodness of fit of the model. An alpha level of 0.05 was used to
determine whether treatment was a statistically significant predictor of variation within the community
ordination. The same method was used to determine whether plot-level NDVI values were significantly
correlated with variation in community composition. R-Vegan was used for all multi-variate analyses
(Oksanen et al. 2016).

We tested the effects of treatments on LAI and the ratio of photosynthetic to non-photosynthetic cover at
APEX using a one-way ANOVA with an alpha level of 0.05, with a Bonferroni post-hoc comparison of

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means to examine differences among treatments. LAI for SPRUCE was analyzed using a linear regression model with temperature as a continuous variable and CO$_2$ level included as a factor (Hanson et al. 2017).

Responses of NDVI to treatment at both sites were analyzed using ANOVA with date as a random effect. At SPRUCE, a two-factor ANOVA was used, with temperature included as a continuous variable and CO$_2$ level as a categorical variable. At APEX, a one-way ANOVA was used, with water table treatment included as a categorical variable. We also fit the processed daily time series data with seasonal curves to determine how treatment affected the timing of green-up, senescence, and peak NDVI. We fit the models using Gaussian parameters following the methods outlined in Chivers et al. (2009) and Wilson et al. (2007) for modeling seasonal vegetation dynamics in peatlands. Our model assumed that seasonal development of NDVI was unimodal and normally distributed. In our model:

$$\text{Daily NDVI}_i = 1e^{-0.5 \left( \frac{JD - \text{NDVI}_{\text{max}}}{b} \right)^2}$$

(4)

Where Daily NDVI$_i$ is daily NDVI in treatment $i$, NDVI$_{\text{max}}$ is the maximum NDVI value for the season, JD is the Julian day, and $b$ describes the shape of the Gaussian curve, estimated as one standard deviation on each side of NDVI$_{\text{max}}$.

**Results**

1) *Response of NDVI to hydrologic change, warming and elevated CO$_2$*

Model results show a highly significant effect of long-term hydrologic change at APEX on NDVI (ANOVA, $F_{3,156}=7.54$, $P < 0.001$). Values were significantly higher in the control and raised plots as compared to the lowered plot, which had lower NDVI values throughout the entire growing season (Figure 1). The lowered plot also peaked at a lower value compared to the control and raised treatments (Table 4). NDVI was highest in the control plot during the early part of the growing season, and showed greater peak values than either of the other treatments (Table 4). However, in the second half of the growing season, the raised plot had the greatest NDVI, which peaked at a somewhat later date (Figure 1, Table 4).

NDVI at SPRUCE showed a clear positive response to warming (Figure 2), but a mixed response to CO$_2$ level (Figure 3). Statistical analysis indicated a significant temperature effect and an effect of the interaction between temperature and CO$_2$ level, but a non-significant effect for CO$_2$ on its own (Table 3).
The chamber with the highest NDVI throughout the growing season was the +9°C treatment with elevated CO₂ (Figure 2, Table 4).

Overall, NDVI at both sites responded strongly to treatment, and at both sites the effect was evident early in the spring and was persistent throughout the entire growing season. Warming appeared to extend the growing season and drought appeared to result in a decreasing trend in NDVI. Both sites exhibited strong seasonal trends in NDVI, but had very different seasonal curves. At APEX, NDVI was already at above 0.5 when the sensors were installed, but by late August vegetation senescence resulted in a rapid drop off in NDVI, whereas at SPRUCE NDVI remained high (i.e., above 0.8) into late fall. These site differences may be attributed both to differences in experimental design and plant community type, as well as the differences in growing season length in Minnesota versus Alaska (Table 2).

2) Vegetation cover and LAI in response to hydrologic change, warming and elevated CO₂ and relationship to NDVI

We found differences in community composition by treatment at APEX. We found a higher average percent cover of graminoids in the raised and control plots (30% and 24% respectively), as compared with the lowered plot (21%). We also found a 5-10% greater cover of shrubs, equisetum, and mosses in the control plot over either of the other two plots. The lowered plot had a 10-20% greater litter cover than the raised or control plots. Results from the community ordination indicate a stress of 0.08 for two dimensions, and the permutation test indicated that water table treatment was significantly correlated with variation in community composition ($R^2 = 0.41$, $p = 0.025$). NDVI was also correlated with variation in community composition ($R^2 = 0.50$, $p = 0.040$). The percent cover of forbs and shrubs accounted for the largest sources of variation in the NMDS. The raised water-table treatment was associated with greater cover of forbs as compared to the control (Figure 4-A). The control was associated with the greatest cover of shrubs and mosses compared to other treatments. Both were the raised and control plots were associated with higher NDVI compared to the lowered plot, which was associated with greater litter cover relative to either of the other treatments. We did not observe any differences in community composition among replicate plots within water-table treatments indicating a homogenous canopy within each treatment.

We did not find significant differences in LAI among treatments at APEX (Figure 4-B). However, in our analysis of fractional cover we found that the ratio of photosynthetic to non-photosynthetic leaf area was significantly higher in the raised and control plots than the lowered plot ($F_{2, 10} = 6.72$, $P = 0.014$). The overall percent cover of litter was marginally greater in the lowered water table plot relative to either the
control or raised plots ($F_{2, 10} = 4.16, p = 0.049$). We attribute the lack of significant difference in LAI among treatments to the generally low LAI found at APEX (typically less than 2).

Results from the community composition sampling at SPRUCE indicated that the warmest treatments had approximately 10% greater shrub cover on average than the control plots, which had an 8% greater cover of forbs. The NMDS results of the community data at SPRUCE indicated that the temperature treatment was a strong correlate with community composition (stress, 0.33; permutation test $R^2 = 0.33, P = 0.004$).

Warmed plots were associated with greater shrub cover whereas ambient plots were associated with a greater cover of forbs (Figure 5-A). LAI at SPRUCE showed a clear positive effect of warming (Figure 5-B; $R^2 = 0.68, F_{3, 34} = 23.8, P < 0.001$, RMSE = 0.93). NDVI was positively associated with temperature treatment (Figure 5-A panel; $R^2 = 0.26, p = 0.037$), and thus by proxy shrub cover and LAI. We found no strong effects of elevated CO$_2$ on community composition. We also did not observe any differences in community cover among plots within temperature treatment.

Altogether, the results indicate that temperature (SPRUCE) and water table position (APEX) are strong controls on functional group composition and overall leaf area across different peatland ecosystems.

These results also demonstrate that variation in community composition induced by warming and altered hydrology has significant effects on NDVI.

**Discussion**

We observed significant effects of experimental manipulation on community composition, LAI, and NDVI associated with warming and hydrologic change. We discerned strong differentiation in composition at both sites, largely resulting from differences in the relative percent cover of shrubs, and changes in overall vascular leaf area. Changes in composition and LAI resulted in a strong effect on NDVI at both sites, indicating that the productivity and stature of vegetation in peatland ecosystems responded strongly to simulated climate change. These results are consistent with previous studies that have found positive relationships between NDVI and peatland ecosystem productivity (Boelman *et al.* 2003, Boelman *et al.* 2005). The effects of treatment on NDVI manifested as changes in peak NDVI values and in the timing of senescence in the manipulated ecosystems. These results highlight the role that shifting vegetation communities will play in determining ecosystem productivity in response to climate change in boreal peatlands.

**Response of NDVI to long-term hydrologic change**

We observed strong responses in both community composition and NDVI to long-term hydrologic change. The response of NDVI observed at the APEX site is consistent with prior research that found an
overall decrease in GPP with long-term drought (Churchill et al. 2013, Olefeldt et al. 2017). We found that the fraction of photosynthetic to non-photosynthetic leaf area was significantly higher in the raised and control water-table treatments as compared to the lowered water-table treatment. This indicates that, even if overall LAI showed only a non-significant trend towards being lower in the lowered water-table plot, the greater relative cover of litter to photosynthetic leaf area is likely driving this trend in NDVI.

Many studies have found that the relative cover of photosynthetic biomass is related to NDVI due to differences in the reflectance properties of living versus dead vegetation in both the visible and infrared regions of the electromagnetic spectrum (Gamon et al. 1995, Walker et al. 2003). In the case of APEX, differences in NDVI can most likely be attributed to differences in fractional cover, as well as decrease in graminoid cover in the lowered plot (Churchill et al. 2013). We also saw greater cover of shrubs, forbs, and mosses in the control plot, which were correlated with NDVI in our community ordination. Overall, low photosynthetic cover contributed to low NDVI values in the lowered plot, while higher leaf area, and a greater cover of a variety of PFTs contributed to higher NDVI values in the control plot.

We saw differences in NDVI even though the summer of 2016 was extremely rainy in central Alaska, and so achieving separation of water tables proved to be impossible late in the growing season (See Figure S2). Adding to this complexity, the peat surface has actually been subsiding at the lowered plot relative to the control and raised plots over time (Olefeldt et al. 2017), meaning that height of the water table above peat surface is actually greater over the lowered plot than that of the other treatments during flooded conditions (Figure S2). It is possible that this unequal pattern of flooding led to further decreases in NDVI as high water differentially occluded the signal from the vegetation (Figure 1). However, since NDVI had already peaked and begun to decrease in the lowered and control plots well before the major flooding occurred, the results from APEX should be interpreted primarily as the result of long-term hydrologic changes rather than the result of seasonal differences in water table position.

Unlike in the lowered water-table plot, we did not find strong differences in PFT cover between the control and raised water-table treatments. Therefore, the differences observed in NDVI between the control and raised water-table plots are more difficult to explain, particularly the seasonal dynamic in which NDVI in the raised plot peaked nearly a month later than the control plot (Figure 1). Given the results of our analysis of community composition, variation in NDVI may reflect differences in phenology resulting from subtle variation in species cover. For example, the control plot has a greater cover of one sedge species, Carex utriculata, whereas the raised plot has greater number of different sedge species, as well as a higher cover of mosses and forbs. Because sedges have been shown to begin senescing earlier than herbs or ericaceous shrubs, the differing NDVI seasonal curves could be attributed to the phenology of these plant functional groups (Leppälä et al. 2008). An additional unexplored
attribute of GPP that was not addressed through this study was the possibility of algal production during periods of inundation (Wyatt et al. 2012, DeColibus et al. 2017). Given the flooding that occurred in 2016, particularly later in the growing season, it is possible that algal growth masked some changes in vascular plant NDVI late in the growing season when water tables were high (Figure S2). The high water table also changes the relative stature of the vegetation, increasing the importance of open water reflectance and associated effects of chlorophyll-producing microorganisms. Further research on this topic could be particularly relevant in employing remote sensing data to track vegetation changes resulting from inundation or drainage across the northern region (Osterkamp & Romanovsky 1999, Riordan et al. 2006).

Response of NDVI to warming and elevated CO₂

We observed a particularly strong effect of warming on all aspects of vegetation community composition and biophysical properties measured at SPRUCE. Results indicate a strong positive effect of warming on NDVI, consistent with prior research findings (Boelman et al. 2003). This was particularly pronounced for the +9º C treatment, which had greater NDVI throughout the growing season. The +4.5º C treatment had similar NDVI values to the control treatments in the early and middle part of the growing season, but appeared higher than the control plots in the fall. An extension in growing season length with warming is to be expected, and these results are consistent with previous studies that have examined changing phenology across the northern hemisphere (Peñuelas & Filella 2001, Menzel et al. 2006). Shrub layer LAI also showed a strong positive linear response to warming. Warming is the probable driver of changes in LAI and increases in NDVI. Because the results of our NMDS analysis indicate a shift in the relative abundance of forbs and shrubs associated with warming, it is likely that the increase in both LAI and NDVI are resulting from an increased abundance of shrubs with warming. Because LAI is highly correlated with GPP, this result, along with our NDVI data point to an overall increase in aboveground GPP of this vegetation layer, coincident with an increase in shrub cover.

These results support several of the central hypotheses of the SPRUCE experiment. The original SPRUCE hypotheses predicted that annual net primary production (NPP) would not increase with warming overall, but that GPP would increase in some species and decrease in others (Hanson et al. 2009). Shifts in GPP will be due primarily to the effects of warming on peat soil moisture content and water table position which will favor vascular plants over mosses (Weltzin et al. 2003). An increase in the GPP of vascular plants and a decrease in the productivity of Sphagnum and other bryophytes resulting from interactions between temperature, soil moisture content, and nutrient availability are also predicted. Although our findings suggest an increase in GPP, NDVI is unsuited to examine belowground responses
to warming. Pairing NDVI measurements with ecosystem CO$_2$ flux measurements would help to further elucidate the relationship between apparent increases in productivity and potential changes in the rate of ecosystem respiration.

Our results also support the hypothesis of the SPRUCE project postulating that elevated CO$_2$ will have a greater effect on GPP at higher temperatures (Hanson et al. 2009). Elevated CO$_2$ levels did not have a clear effect on NDVI in the ambient or +4.5$^\circ$C treatments, but appeared to have an interactive effect at +9$^\circ$C, as supported by our model result indicating a significant interaction between CO$_2$ and warming (Table 2). Our results are also supported by research that suggests that the positive effects of elevated CO$_2$ on photosynthesis increases with warming (Long 1991, Luo 2008). As is the case with warming alone, this result may also be due to interactions between changing species composition and increases in leaf area and biomass in existing species. Research on the effects of carbon enrichment on Sphagnum has yielded contradictory findings; some studies have indicated that moss growth increases in response to elevated CO$_2$, and others have shown no effect (Berendse et al. 2001, Heijmans et al. 2001). However, a number of studies have shown that the productivity of vascular plants, particularly graminoids, increases in response to elevated CO$_2$ (Owensby et al. 2011, Norby et al. 2002, Nowak et al. 2004, Morgan et al. 2011). Although we cannot say definitively to which plant functional types the apparent effects of elevated CO$_2$ in the +9$^\circ$C treatment may be attributed, we would expect the positive effects of CO$_2$ enrichment to primarily affect vascular plant functional types. Because peatlands are characterized by a variety of vascular and non-vascular plants depending on their nutrient availability, we predict that future response of peatland vegetation to elevated CO$_2$ will be highly species-specific and dependent on nutrient status of the peatland (e.g. bog versus fen).

Relationship of NDVI to ecosystem GPP

Research has shown that NDVI correlates with aboveground NPP (Boelman et al. 2003), GPP (La Puma et al. 2007), and leaf area index (Carlson & Ripley 1997, Walker et al. 2003) and can therefore be thought of as combining multiple ecological responses to experimental manipulation into one measurement. Since NDVI responds to a variety of plant and community-level processes, it is difficult to identify the locus of the treatment effect, whether changes in species composition, leaf area, or leaf-level processes. In the case of APEX, differences in NDVI were due to the long-term effects of a decade worth of hydrologic manipulation on community composition and photosynthetic biomass. As discussed above, in high water years such as 2016 algal production could also have contributed photosynthetic capacity to the NDVI signal, because algal production is influenced by water table history at this site (Wyatt et al. 2012, DeColibus et al. 2017). At SPRUCE, warming affected the species composition and leaf area of the
vegetation community, which in turn had a strong effect on NDVI. Further measurement of leaf and ecosystem-level gas exchange and biomass measurements would strengthen our understanding of how unique peatland taxa are responding to global change.

Despite the demonstrated relationship between NDVI and GPP, recent literature on NDVI in moss-dominated systems has revealed limitations that should be considered when extrapolating these results to satellite observations of arctic and boreal change (May et al. 2018). Studies have shown that the unique moisture-holding capacity of non-vascular plants leads to poor relationships between GPP and NDVI due to the potential for large changes in spectral reflectance characteristics following the desiccation or re-wetting of moss communities (Bubier et al. 1997, May et al. 2018). Further, it has been shown that light-use efficiency, which forms the basis for the NDVI-GPP relationship, varies significantly in response to warming and drying in non-vascular plants as compared with vascular species (Huemmrich et al. 2010, Kross et al. 2016). At APEX, which is dominated by tall graminoid species, mosses accounted for less than ten percent of total cover on average in 2016. However, SPRUCE has significant moss cover, which has been negatively affected by the warming treatments. Although an examination of the role of moss decline on NDVI at SPRUCE was outside of the purview of this research, future remote sensing of peatlands should certainly take the role of non-vascular responses to climate change into account. Some studies have suggested that alternative indices that are more sensitive to foliar moisture content may aid in evaluating the response of moss-dominated communities to warming and hydrologic change (Van Gaalen et al. 2007, Harris et al. 2008, Meingast et al. 2014).

Implications for northern boreal and arctic ecosystems

Widespread shifts in NDVI have been observed across the circumpolar region over the past three decades. Arctic greening has been well documented through both field and remote sensing studies (Tape et al. 2006, Myers-Smith et al. 2011, Myers-Smith 2015, Ackerman et al. 2017). However, studies of the boreal have been less consistent: some have documented greening, while others have indicated a browning trend (Myneni et al. 1997, Piao et al. 2011, Park et al. 2016, Pheonix & Bjerke 2016). Through this research, we studied the effects of a range of global change drivers on the biophysical properties and NDVI of two types of common northern boreal peatlands. These results point to changes in aboveground leaf area and changes in community composition, and shrub cover in particular, as potential drivers of satellite observed trends in boreal NDVI. We found a positive response of NDVI to warming, coincident with the increase in shrub cover, and a negative response of NDVI to long-term drought. We show here that state factors such as temperature and hydrology are drivers of plant community composition and NDVI.

Previous studies have shown the effects of climate drivers on NDVI, but their relationship to community

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composition and structure has previously not been well resolved. Further research is needed to investigate
the interactive effects of warming and hydrologic change across different types of peatland ecosystems,
and to relate the findings of this research to satellite datasets to understand further how warming and
changes in hydrology are affecting ecological function across arctic and boreal regions.

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reviewers who helped to improve this manuscript prior to publication. The authors claim no conflicts of
interest.

Figure Captions

Figure 1: NDVI response to long-term water table manipulation at APEX. Weekly values are pictured for
clarity. Daily NDVI values are fitted with a seasonal curve derived using a non-linear least-squares
regression model. Error bars represent standard deviation of the mean.

Figure 2: SPRUCE NDVI in response to warming at SPRUCE. Weekly values are pictured for clarity.
Daily NDVI values are fitted with a seasonal curve derived using a non-linear least-squares regression
model. Error bars represent standard deviation of the mean.

Figure 3: Effects of CO2 on NDVI at SPRUCE experiment. Top: +0 degree Celsius, middle: +4.5 degree
Celsius, bottom: +9 degree Celsius temperature treatments.

Figure 4: NMDS and LAI results for APEX 2016 community composition. A) APEX community results
with treatment indicated by shape and NDVI mapped on to denote relationship to variation within
community composition. B) LAI in response to water table manipulation at APEX in which water table
555 treatment is analyzed as a factor.

Figure 5: SPRUCE NMDS and LAI results. A) Community response to experimental manipulation of
temperature and CO2, with NDVI relationship to community composition. B) LAI response to warming
and elevated CO2 at SPRUCE. The SPRUCE experiment is a regression-based design in which
temperature is analyzed as a continuous variable. Temperature is indicted by symbol. CO2 did not
emerge as a significant vector, and so is not included in the graph. NDVI and temperatures are mapped
on as correlated vectors to demonstrate the relationship between composition and temperature and
NDVI. Note: n values differ among treatments at SPRUCE due to the greater number of control chambers
relative to heated chambers.

Figure S1: Relationship between Degacon NDVI sensors and NDVI calculated using handheld
spectroradiometers.

Figure S2: Seasonal water table position measured at APEX field site.

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Table 1: Description of two study sites, data types, and differing data collection methods between sites.

<table>
<thead>
<tr>
<th></th>
<th>APEX</th>
<th>SPRUCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peatland type</td>
<td>Rich fen</td>
<td>Ombrotrophic bog</td>
</tr>
<tr>
<td>Location</td>
<td>Alaska, USA</td>
<td>Minnesota, USA</td>
</tr>
<tr>
<td>Experimental design</td>
<td>Water table manipulation with</td>
<td>Regression-based factorial</td>
</tr>
<tr>
<td></td>
<td>120 m² control, lowered and</td>
<td>between increasing temperature</td>
</tr>
<tr>
<td></td>
<td>raised treatments</td>
<td>and CO₂ level</td>
</tr>
<tr>
<td>Vegetation sampling</td>
<td>Point bar laser survey method</td>
<td>2 m² sampling frame method</td>
</tr>
<tr>
<td>LAI</td>
<td>Point bar laser survey method</td>
<td>LICOR LAI 2200</td>
</tr>
<tr>
<td>Spectral reflectance</td>
<td>ASD Fieldspec Pro</td>
<td>Unispec DC</td>
</tr>
<tr>
<td>Decagon NDVI sensors</td>
<td>One each located in the control,</td>
<td>Two each located in the +0, +4.5</td>
</tr>
<tr>
<td></td>
<td>lowered and raised WT treatments</td>
<td>and +9 degree C chambers, one</td>
</tr>
<tr>
<td></td>
<td>(3 total)</td>
<td>each in an ambient and elevated</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CO₂ chamber (6 total)</td>
</tr>
</tbody>
</table>
Table 1: List of species present at both peatland sites, and plant functional groupings used in analysis.

<table>
<thead>
<tr>
<th>Plant Functional Type</th>
<th>Species</th>
<th>Plant Functional Type</th>
<th>Species</th>
</tr>
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<tbody>
<tr>
<td>Forb</td>
<td>Drosera rotundifolia</td>
<td>Equisetum</td>
<td>Equisetum fluviatile</td>
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<tr>
<td>Forb</td>
<td>Maianthemum trifolium</td>
<td>Forb</td>
<td>Galium trifidum</td>
</tr>
<tr>
<td>Graminoid</td>
<td>Carex magellanica</td>
<td>Forb</td>
<td>Potamogeton gramineus</td>
</tr>
<tr>
<td>Graminoid</td>
<td>Carex oligosperma</td>
<td>Graminoid</td>
<td>Calamagrostis canadensis</td>
</tr>
<tr>
<td>Graminoid</td>
<td>Carex trisperma</td>
<td>Graminoid</td>
<td>Carex loliacea</td>
</tr>
<tr>
<td>Graminoid</td>
<td>Eriophorum vaginatum</td>
<td>Graminoid</td>
<td>Carex utriculata</td>
</tr>
<tr>
<td>Graminoid</td>
<td>Eriophorum virginicum</td>
<td>Moss</td>
<td>Sphagnum spp.</td>
</tr>
<tr>
<td>Shrub</td>
<td>Andromeda polifolia</td>
<td>Shrub</td>
<td>Potentilla palustris</td>
</tr>
<tr>
<td>Shrub</td>
<td>Chamaedaphne calyculata</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub</td>
<td>Kalmia polifolia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub</td>
<td>Rhododendron groenlandicum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub</td>
<td>Vaccinium angustifolium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub</td>
<td>Vaccinium oxyccocos</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 1: SPRUCE model of NDVI in response to experimental manipulation of temperature and elevated CO$_2$. Temperature was a continuous variable, and CO$_2$ was a factor (NDVI ~ temp * CO$_2$ + Error(Date)).

<table>
<thead>
<tr>
<th>SPRUCE</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>temp</td>
<td>2</td>
<td>1.033</td>
<td>0.517</td>
<td>179.850</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>CO$_2$</td>
<td>1</td>
<td>0.001</td>
<td>0.001</td>
<td>0.02</td>
<td>0.655</td>
</tr>
<tr>
<td>temp:CO$_2$</td>
<td>1</td>
<td>0.003</td>
<td>0.046</td>
<td>16.116</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Residuals</td>
<td>841</td>
<td>2.415</td>
<td>0.003</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 1: Model coefficients generated using non-linear least squares regression analysis. Models were fit by transforming date into Julian day values and then using peak NDVI values and standard deviation on either side of the peak to fit Gaussian curves to seasonal trends in NDVI. NDVI_{Max} refers to peak NDVI (i.e. k in a Gaussian distribution), NDVI_{Max JD} refers to the date of NDVI_{Max}, b denotes the shape of the curve (i.e. σ in a Gaussian distribution), n denotes the number of days of observations used to fit the model. RSS is the model residual sum of squares, and RMSE is the model root mean square error.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Model Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>APEX</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>0.841</td>
</tr>
<tr>
<td>Lowered</td>
<td>0.709</td>
</tr>
<tr>
<td>Raised</td>
<td>0.780</td>
</tr>
<tr>
<td>SPRUCE +0</td>
<td>0.798</td>
</tr>
<tr>
<td>+4.5</td>
<td>0.804</td>
</tr>
<tr>
<td>+9</td>
<td>0.846</td>
</tr>
<tr>
<td>+0 Ambient</td>
<td>0.811</td>
</tr>
<tr>
<td>+0 Elevated</td>
<td>0.791</td>
</tr>
<tr>
<td>+4.5 Ambient</td>
<td>0.818</td>
</tr>
<tr>
<td>+4.5 Elevated</td>
<td>0.791</td>
</tr>
<tr>
<td>+9 Ambient</td>
<td>0.837</td>
</tr>
<tr>
<td>+9 Elevated</td>
<td>0.855</td>
</tr>
</tbody>
</table>

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