Arctic aquatic graminoid tundra responses to nutrient availability

Andresen CG[1,2] and Lougheed VL[2].
[1]Geography Department, University of Wisconsin Madison, Madison, WI, USA.
[2]Biological Sciences Department, University of Texas at El Paso, El Paso TX, USA.

Correspondence email: candresen@wisc.edu

Abstract: Unraveling the environmental controls influencing Arctic tundra productivity is paramount for advancing our predictive understanding of the causes and consequences of warming in tundra ecosystems and associated land-atmosphere feedbacks. This study focuses on aquatic emergent tundra plants, which dominate productivity and methane fluxes in the Arctic coastal plain of Alaska. In particular, we assessed how environmental nutrient availability influences production of biomass and greenness in the dominant aquatic tundra species: *Arctophila fulva and Carex aquatilis*. We sampled a total of 17 sites distributed across the Barrow Peninsula and Atqasuk, Alaska following a nutrient gradient that ranged from sites with thermokarst slumping or urban runoff to sites with relatively low nutrient inputs. Employing a multivariate analysis, we explained the relationship of soil and water nutrients to plant leaf macro- and micro-nutrients. Specifically, we identified soil phosphorus as the main limiting nutrient factor given that it was the principal driver of aboveground biomass (R^2=0.34, p=0.002) and Normalize Difference Vegetation Index (NDVI) (R^2=0.47, p=0.002) in both species. Plot-level spectral NDVI was a good predictor of leaf P content for both species. We found long-term increases in N, P and Ca in *C. aquatilis* based on historical leaf nutrient data from 1970s of our study area. This study highlights the importance of nutrient pools and mobilization between terrestrial-aquatic systems and their potential influence on productivity and land-atmosphere carbon balance. In addition, aquatic plant NDVI spectral responses to nutrients can serve as landscape hot-spot and hot-moment indicator of landscape biogeochemical heterogeneity associated with permafrost degradation, nutrient leaching and availability.

Keywords: NDVI, permafrost thaw, thermokarst, biomass, productivity, hot-spot, hot-moment

1. INTRODUCTION

In the Arctic, plant growth is limited by several factors including low temperatures, short growing-seasons (e.g. irradiance) and nutrient availability (Chapin *et al* 1975, Shaver *et al* 1998). Although Arctic temperatures have increased dramatically over recent decades with parallel increases in plant biomass, nutrients have been shown to be the main driver enhancing Arctic tundra productivity compared to temperature in long-term experimental treatments (Shaver *et al* 1998, Boelman *et al* 2003, Jónsdóttir *et al* 2005, Johnson *et al* 2000) and in long-term field observations (López-Blanco *et al* 2020). Increased tundra productivity has generally been explained by warming-mediated processes including increases in nutrient availability through soil warming, heterotrophic decomposition, and nutrient release from mineralization of organic matter and permafrost thaw (Reyes and Lougheed 2015, Natali *et al* 2012, Keuper *et al* 2012, Pastick *et al* 2019). In addition, abrupt thaw and recent lake drainage events enhanced during warm Summers has also contributed to increased productivity through the availability of fertile soils (Turetsky *et al* 2020, Loiko *et al* 2020, Nitze *et al* 2020, Jones *et al* 2012). These factors highlight the complexity of tundra plant growth and production under a warming and changing Arctic with implications for carbon budgets (Oberbauer *et al* 2007, McGuire *et al* 2018). Unraveling the covarying climate and environmental controls influencing Arctic tundra productivity is paramount for advancing our predictive understanding of the causes and consequences of warming in tundra ecosystems and associated land-atmosphere feedbacks.

Nutrients play a key role influencing tundra plant production with complex effects on ecosystem carbon balance. Early work by Chapin et al., (1975) and Shaver et al., (1998) demonstrated that nutrients, particularly N and P, enhanced plant biomass and aboveground plant nutrients in wet tundra communities. In contrast, temperature alone has shown no effect on biomass production in long-term experimental treatments (Shaver *et al* 1998, Boelman *et al* 2003, Jónsdóttir *et al* 2005, Johnson *et al* 2000). While nutrients drive productivity and accumulation of new organic matter in the soil, nutrient enrichment can result in net carbon losses by enhancing decomposition of old carbon stocks (Mack *et al* 2004). These results emphasize the importance of nutrient–carbon interactions in controlling ecosystem processes and ecosystem C balance in arctic tundra.

Our study builds on previous experimental studies that examined nutrient impacts on wet tundra (Shaver *et al* 1998, Boelman *et al* 2003, McLaren and Buckeridge 2019, Beermann *et al* 2015, Lara *et al* 2019) by focusing on aquatic tundra, which are a relatively understudied plant community in the Arctic. Aquatic emergent tundra plants are known to have the highest productivity compared to terrestrial communities and contribute to a significant portion of regional carbon sink and methane fluxes (Lara *et al* 2014, Joabsson and Christensen 2001, Andresen *et al* 2017). In recent decades, Arctic aquatic communities have increased in biomass and cover (Villarreal *et al* 2012, Andresen and Lougheed 2015), likely attributed to an increase in nutrient input leached from terrestrial systems through permafrost degradation and abrupt thaw events into aquatic habitats (Turetsky *et al* 2020, Reyes and Lougheed 2015), but the impacts of nutrients on Arctic aquatic plant communities have not been well documented in literature (Andresen 2014).

Nutrients have increased over the past 40 years in aquatic habitats (Lougheed *et al* 2011) with parallel biomass increases of aquatic graminoids (Andresen *et al* 2017). This phenomenon will likely become more pronounced as increasing temperatures in Arctic soils continue enhancing nitrogen mineralization (Uhlířová *et al* 2007, Weintraub and Schimel 2003) as well as permafrost degradation and nutrient leaching (Keuper *et al* 2012, Reyes and Lougheed 2015, Frey and McClelland 2009, Fouché *et al* 2020). With increased thaw and subsurface flow (Frampton *et al* 2013, Shiklomanov *et al* 2013), these processes may provide substantial nutrient inputs to freshwater ecosystems, however, there is increased need to assess the effects of these increased nutrient inputs on aquatic tundra productivity.

Remote sensing has been used to detect and quantify plant productivity in Arctic systems based on multispectral indices (Pastick *et al* 2019, Epstein *et al* 2012, Walker *et al* 2012b). Boelman et al., (2003) showed the applicability of the normalized vegetation index (NDVI) as a tool to track spectral responses of wet sedge tundra to nutrients in fertilization and warming experiments. Other studies employing digital repeat photography have successfully assessed plant phenology, biomass and productivity by evaluating vegetation color with indices in the visual spectral range (i.e. blue, green and red) (Saitoh *et al* 2012, Sonnentag *et al* 2012, Andresen *et al* 2018). Plant spectral responses to nutrient enrichment in aquatic communities are poorly understood and its monitoring using remotely sense data would help monitor and quantify potential carbon and energy feedbacks to the atmosphere at regional scales.

With current and projected warming and nutrient loading into Arctic aquatic systems, it is important to understand nutrient impacts on aquatic emergent vegetation, and how these changes can be detected and modeled using remote sensing methods. In this study, we sampled tundra pond sites that followed a nutrient gradient that range from sites with thermokarst slumping or urban runoff to sites with relatively low nutrient inputs. We aim to characterize nutrient limitation of aquatic emergent tundra vegetation and spectral responses of this vegetation to nutrient inputs. We focus on the influence of soil and water nutrients on plant biomass and greenness of *Carex aquatilis* and *Arctophila. fulva*, the dominant aquatic emergent vascular plants in the Arctic coastal plain (Villarreal *et al* 2012, Andresen *et al* 2018) to answer the questions of: (i) how is aquatic tundra responding to nutrient availability? (ii) How environmental nutrient status influence leaf nutrients in aquatic tundra? (iii) What are the spectral responses (NDVI) of aquatic tundra to nutrient availability?

2. METHODS

2.1 Study Sites

This study was conducted in the Barrow Peninsula, Alaska, (W156^0, N70^0) near the town of Uqtiaġvik (formerly known as Barrow). Physiographically, the area is located in the Arctic Coastal Plain (ACP, ~60,000 km^2) of northern Alaska, which stretches from the western coast along the Chukchi Sea to the Beaufort coastal Canadian border. The ACP is dominated by thick continuous permafrost with high ground-ice content for the Arctic peaty lowland of the peninsula (Hinkel *et al* 2003). Soil organic horizon varies across the landscape due to the age of the landform (i.e. drained thaw lake basin) and cryoturbation of the soil. Nonetheless, sites are located in old and ancient drained thaw lake basins where the surface organic thickness ranges between 15 and 35cm from surface (Hinkel *et al* 2003). A complex mosaic of ice-wedge patterned ground landforms developed over millennial seasonal cycles of cracking, heaving, and thawing producing its characteristic pond- and lake-dominated landscape (Andresen and Lougheed 2015, Jorgenson and Shur 2007). These aquatic habitats of the ACP are hosts for aquatic graminoid tundra that grows in shallow standing water with a depth range 5-50cm. This study focuses on 2 species: *C. aquatilis* and *A. fulva.* These graminoids are the dominant cover in aquatic habitats, generally grow as monotypic stands on the edge and/or inside tundra ponds (Villarreal *et al* 2012, Andresen *et al* 2017) and their distribution is in low- and sub-Arctic.

Although these species have growth forms in moist and dry tundra (Shaver *et al* 1979), this study focuses on their aquatic phenotypes.

A total of seventeen tundra ponds were sampled in early August (4th-9th) 2013 along a nutrient gradient with long-term sources of nutrients. Sites were grouped in four categories according their geographic location and nutrient source as: (i) enriched urban, (ii) enriched thermokarst, (iii) reference, and (iv) southern (Figure 1, 2, Appendix 1). Enriched urban ponds were located within the town of Utqiaġvik, AK and their source of nutrients was mainly from village runoff. Enriched thermokarst ponds were situated within the Barrow Environmental Observatory (BEO), and their nutrient inputs originate from permafrost slumping into ponds. Reference sites were located across the region in the historical International Biological Program (IBP) sites and in the BEO; but these sites do not contain evidence of continuous permafrost slumping. Southern latitude ponds were located 100 km south of Utqiaġvik, near the town of Atqasuk, AK. We sampled these ponds in order to expand the geographic footprint of the study and serve as reference to Utqiaġvik area. It is important to note that while *C. aquatilis* occurs in all ponds, *A. fulva* does not occur in thermokarst ponds nor in IBP-C and WL02 ponds (Appendix 1).

Figure 1. Map of Utqiaġvik sites sampled in this study. For site details including southern sites see Appendix 1. *Imagery © [2012] DigitalGlobe, Inc.*

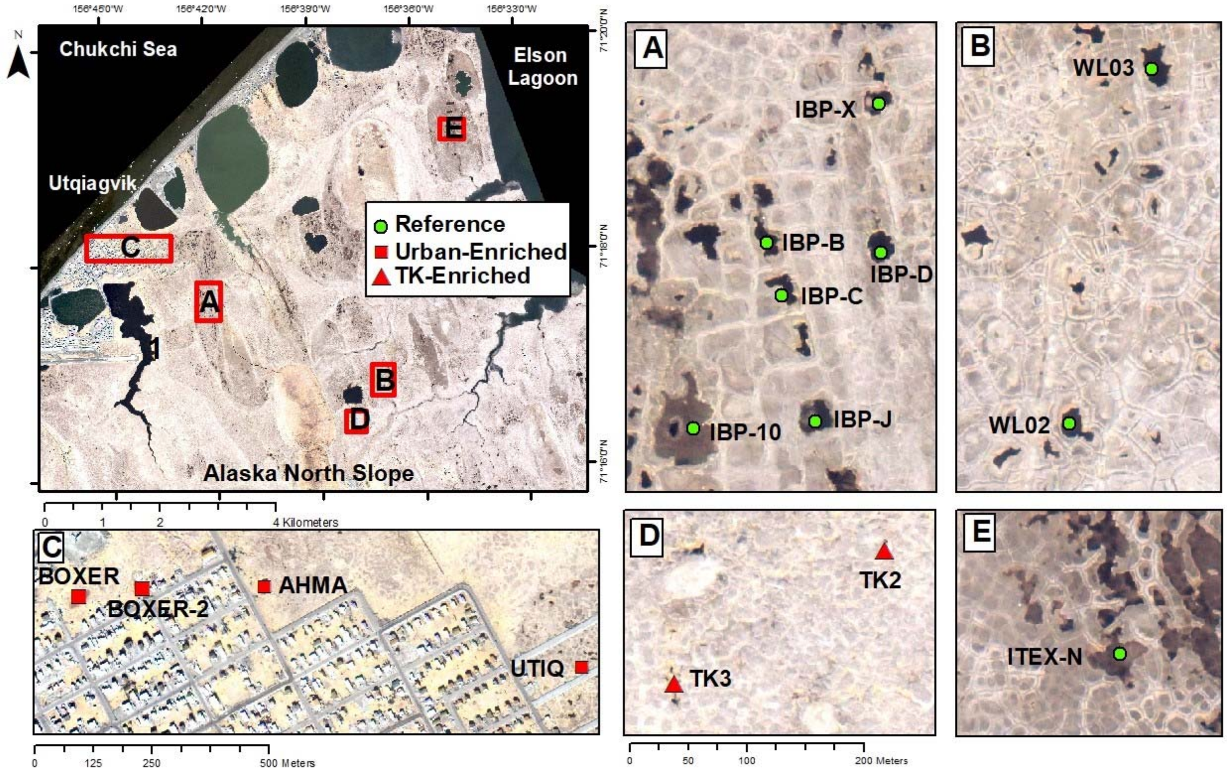
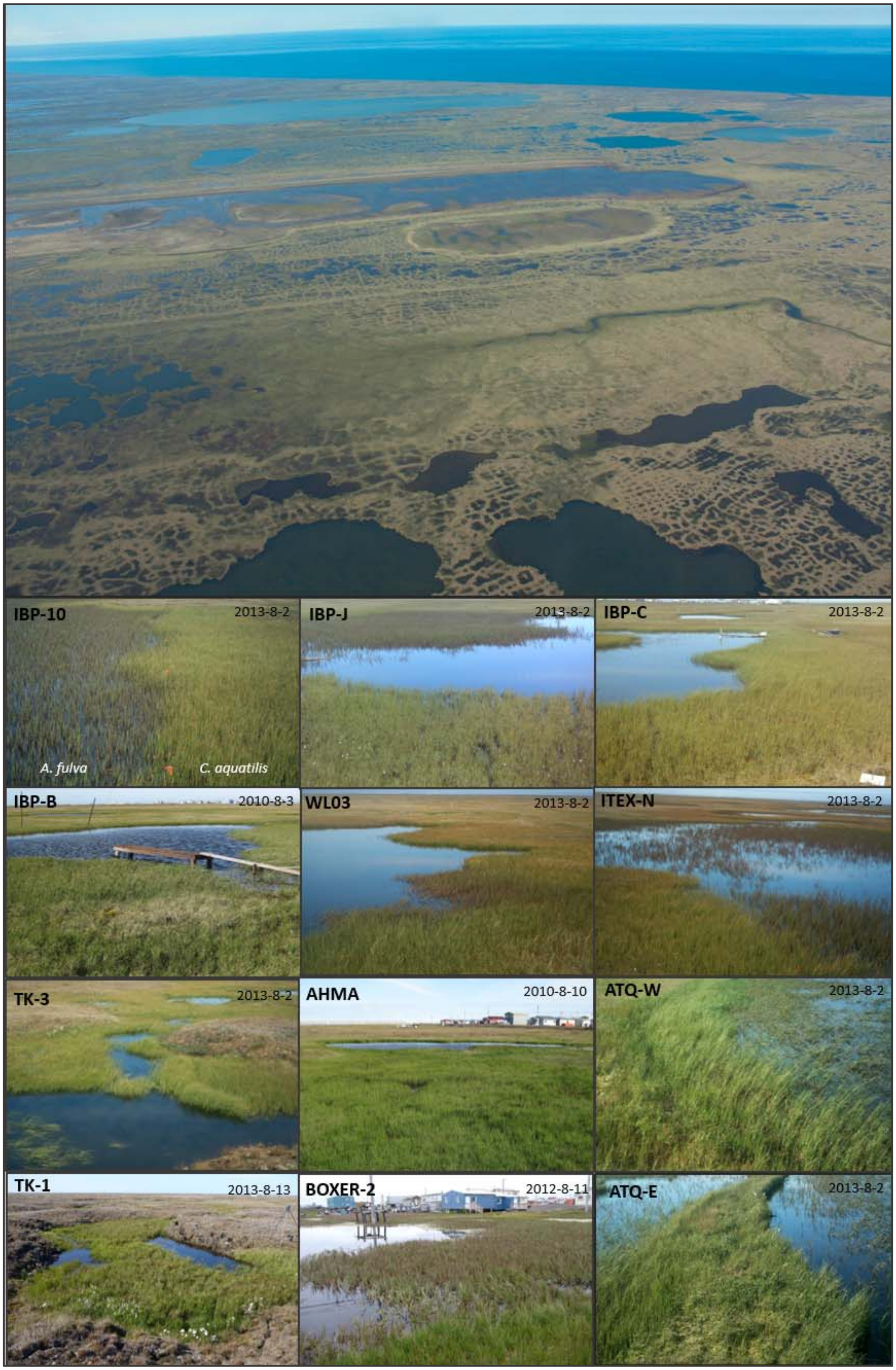


Figure 2. Aerial view the Arctic coastal plain near Utqiaġvik, AK, and examples of sites sampled in this study. Images indicate site name (top-left) and picture date Y/M/D (top-right). Photos by C. Andresen.


IBP-10
2013-8-2
A. fulva
C. aquatilis
IBP-J
2013-8-2
IBP-C
2013-8-2
IBP-B
2010-8-3
WL03
2013-8-2
ITEX-N
2013-8-2
TK-3
2013-8-2
AHMA
2010-8-10
ATQ-W
2013-8-2
TK-1
2013-8-13
BOXER-2
2012-8-11
ATQ-E
2013-8-2

2.2 Plant nutrients

We collected live, green samples of *A. fulva* and *C. aquatilis* at peak growing season (July 25-August 5, 2013). Each sample consisted of 10-15 plants collected from different water depths and multiple randomly selected locations in pond habitats within monotypic stands of each species. The collected plants were separated into leaves and roots, then rinsed with distilled water, oven-dried at 60˚C for 24 hrs inside open paper envelopes, then shipped to Utah State University Analytical Labs (USUAL) for immediate processing. Most macro- and micro-nutrients in leaves of each plant were analyzed using an inductively-coupled plasma spectrometer (ICP-MS). Total nitrogen was analyzed by combustion analysis (HNO_3/H_2O_2 digestion, Leco Instrument).

2.3 Ancillary data

Concomitant with the collection of aquatic plants for nutrient analysis, we collected soil and water samples, harvested aboveground plant biomass, measured spectral reflectance, and monitored most sites using time-lapse photography (Andresen *et al* 2018) (Figure 2). For each site, sediment samples from the active root soil depth of 10-20cm for each species were collected in triplicates within the site. Samples where then combined in a plastic bag and frozen until analysis. Soil at this depth range (10-20cm) was a combination of mineral and organic horizon and varied among sites and within each site. Thus, the combination of 3 soil samples in each site aided to minimize soil heterogeneity discrepancies and give an overall picture of soil conditions at each site. In the lab, soil samples were air dried for 3 days after thaw, then analyzed for physical and chemical factors including pH, electric conductance (EC), and macronutrients (For logistical reasons, only P, K, and Nitrate were analyze). Water chemistry followed standard methods (American Public Health Association 1998) where nitrate-nitrogen was quantified by cadmium reduction; ammonia using phenate method; total phosphorus by ascorbic acid method with persulfate digestion; soluble reactive phosphorus by the ascorbic acid method; and, silica using the heteropoly blue method. In contrast to sediment, which was sampled for each plant type, water samples from open water mid-column were assumed to be representative of the whole pond, including both plant species given the relatively well mixed environment.

Aboveground plant biomass was harvested within duplicate representative 50cm x 20cm quadrats for each species at each site. In addition, reflectance measurements of canopy radiance were collected at each site employing a single channel portable spectrometer (JAZ, Ocean Optics). Following Andresen et al (2018), reflectance measurements were collected during sunny conditions between 12 and 4 pm for maximum solar elevation angles (29^0-33^0, ~2pm is highest https://www.esrl.noaa.gov/) and to best match satellite observations. The person doing the collection was standing in the opposite direction of the solar azimuth angle to avoid any effects of shading by the instrument or person. All plots for both aquatic species were inundated at time of sampling (including soil, plant and spectral samples) with a water depth (±SD) of 25.2 ± 4.6 for *A. fulva* and 10.3 ± 3.22 cm for *C. aquatilis*. Solar specular reflection of water on aquatic emergent plant spectral measurements was insignificant given that solar elevation angles are relatively low in the Arctic (~33^0, peak season) and solar specular reflection was outside of the ~1 m spectral footprint of the measured plot. The reflectance ratio was estimated between plot radiance at nadir and the calibration standard radiance. White calibration standard (38 mm wide) was positioned 30 mm at nadir below the field spectrometer optic fiber (field of view of 25°) at each calibration, then capped closed to minimize degradation. NDVI measurements from 5 scans were averaged in each plot, and 4–6 plots per pond for comparison with leaf nutrients. Normalized Difference Vegetation Index (NDVI) was estimated from reflectance ratio values using the formula: NDVI = (800 nm− 680 nm) / (800 nm+ 680 nm). NDVI is a standard proxy of plant productivity and biomass in the Arctic and has been used to track plot (Soudani *et al* 2012, Gamon *et al* 2013, Andresen *et al* 2018) to regional and global seasonal and decade time-scale productivity trends (Bhatt *et al* 2010, Walker *et al* 2012a, Zeng and Jia 2013).

Parallel to reflectance NDVI measurements, we employed phenocams (optical photography) at each site to calculate the "green excess" index (GEI) (Richardson *et al* 2009, Andresen *et al* 2018) from peak-season oblique images using the formula: [2*G - (R + B)] where G is the brightness value in the green, R is the brightness value in the red, and B is the brightness value in the blue. Oblique-angle GEI collected from cameras in this study is strongly associated to nadir-angle NDVI for both *A. fulva* and *C. aquatilis* (Andresen *et al* 2018). For additional camera details and setup refer to Andresen *et al* (2018).

2.4 Statistical analysis

We employed principal components analysis (PCA) to generate linear combinations of the plant leaf nutrient data to describe the primary gradients in plant nutrient enrichment among the sites. PCA assumes linear relationships among variables, which was confirmed with scatterplots prior to analysis. Plant nutrient data was standardized to zero mean and unit variance and $\log_{10}$ transformed where applicable to obtain a normal distribution. PCA axes were then associated to environmental data (i.e. soil and water nutrients, plant biomass, NDVI, GEI) using a Pearson correlation. Variables were log-transformed as required to meet the assumptions of normality. All statistical analyses were performed in SAS JMP software v4.0. Significance of the PC axes was confirmed in PC-ORD. Differences in environmental and biological characteristics among areas within ponds dominated by *C. aquatilis* and *A. fulva* were assessed using a paired t-test, with areas compared within each sampled pond. Green-up dates by phenocams were determined using a regression tree analysis as described in Andresen *et al* (2018).

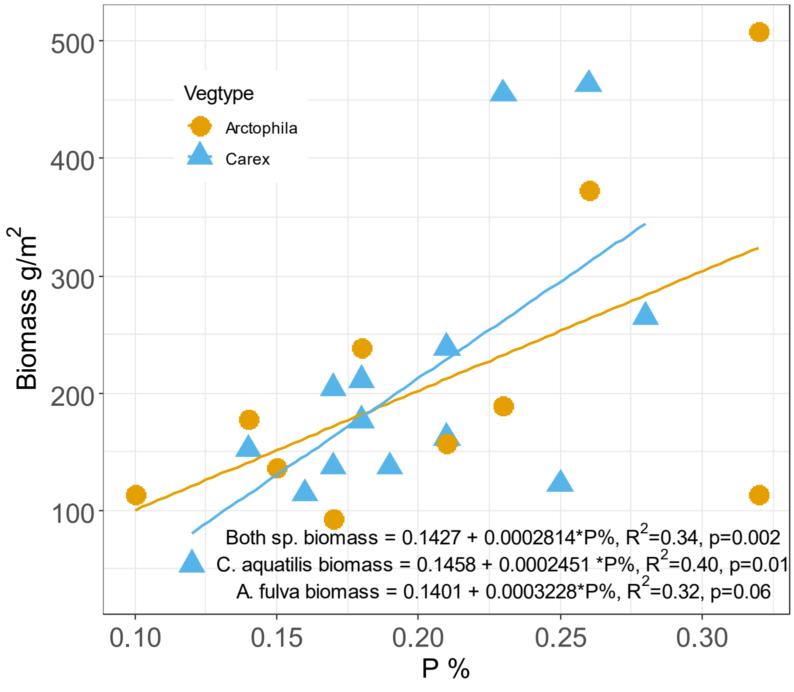
3. RESULTS

Examining the relationships between plant biomass and macronutrient (N, P) content of the plant leaves and soil revealed that plant leaf phosphorus content was the primary determinant of aquatic plant biomass, significantly explaining 40% of the variation in biomass of *C. aquatilis* (p=0.01) and 32% of the biomass variation of *A. fulva* (marginally significant at p=0.6). Combining both aquatic species, leaf P significantly explains 34% of aboveground biomass variability with p=0.002 (Figure 3).

In addition, we found a positive linear relationship ($R^2 = 0.48$, $p<0.01$) between leaf phosphorus and NDVI (Figure 3). There were no significant relationships between plant biomass and leaf nitrogen. Among site types, enriched sites (Urban and Thermokarst) have statistically higher soil, leaf and water nutrients compared to reference sites ($p<0.001$), no differences found for southern sites.

There were no significant differences in leaf and soil macro-nutrients among plant species in a given pond from reference sites (paired t-test, $p>0.05$) (Table 1). However, leaf micronutrients among plant species differed. We found significantly higher amounts of leaf Al, B, Ba, Mn, Na, Ni, Si and Zn in *C. aquatilis* compared to *A. fulva* ($p<0.05$ level). The most abundant leaf element in both plant species was N, followed in decreasing order by K, P, S and Mg and these ratios were consistent across the nutrient gradient sites (Figure 4).

There were significant differences in green-up date and peak season Greenness Excess Index (GEI) among species ($p<0.01$, Table 1). *A. fulva* greened later (day 200 vs. 183) and had lower GEI (9 vs. 33) as compared to *C. aquatilis*. These differences are associated to unique phenotypic properties between species in the visual spectral range (Andresen *et al* 2018). There was no corresponding difference in NDVI or biomass among species ($p>0.05$).



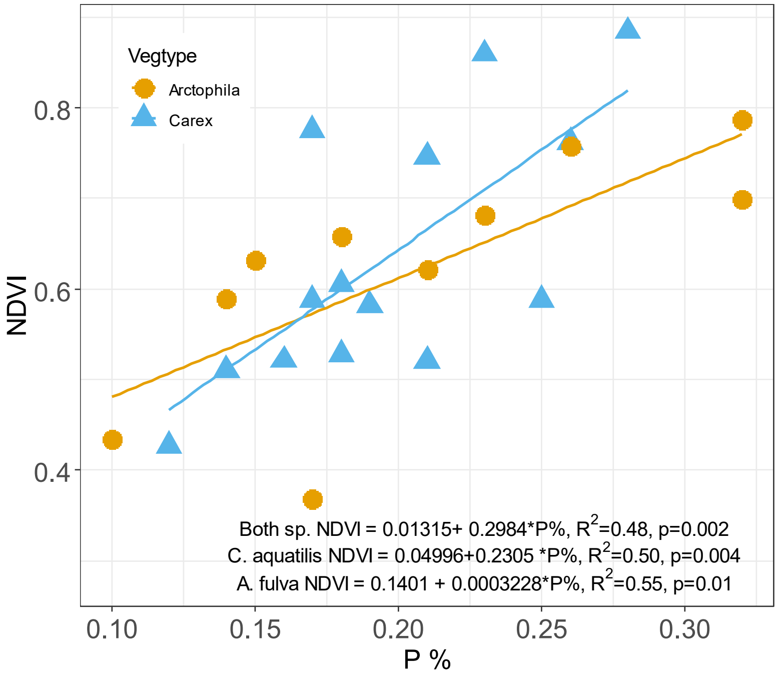


Figure 3. Relationship between Phosphorus content (%) of leaves and dry weight aboveground biomass (left) and NDVI (right) for *Carex aquatilis* and *Arctophila fulva*. Biomass collected during peak growing season (first week of August). Each point represents site averages.

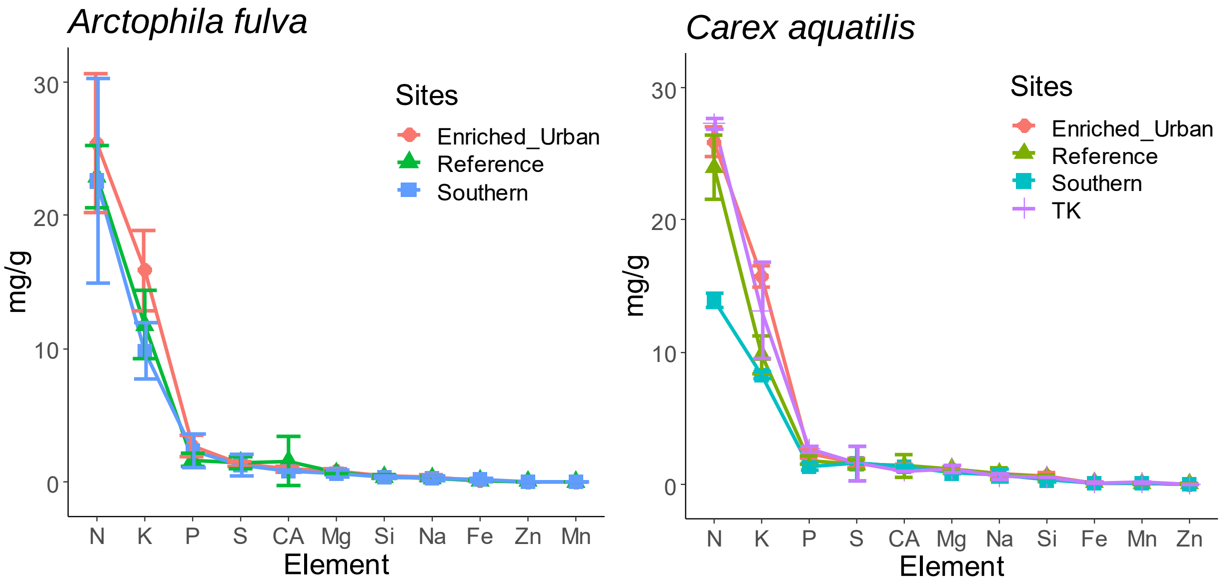


Figure 4. Descending order of element concentration in aboveground tissue among plant species. Error bars represent one standard deviation from mean.

Table 1. Range of environmental variables by vegetation type from 17 ponds in Utqiaġvik and Atqasuk, Alaska. (*) represents significantly different among species at $p<0.01$. Range represents min and max.

	Arctophila fulva		*Carex aquatilis*	
Variable	Mean	Range	Mean	Range
Soil pH	5.23	4.7-6.3	5.14	4.7-6.3
Soil EC (dS/m)	0.86	0.26-2.75	0.589	0.12-2.67
Soil P, available (mg/kg)	4.78	2.1-10.5	5.625	2-21.3
Soil K, available (mg/kg)	42.82	19-80	44.188	11-109
Soil Nitrate-N (mg/kg)	1.87	0.01-7.6	1.2	0.01-3.8
*Greening day (DOY)	198	198-199	182	175-191
*GEI	8.57	0-18	33.44	29-37
NDVI	0.65	0.485-0.759	0.646	0.459-0.860
Biomass (g/m^2)	222.23	124-532	197.4	109-365
Leaf TN (%)	2.36	1.71-3.06	2.36	1.35-2.76
Leaf P (%)	0.2	0.1-0.32	0.2	0.012-0.28
Root TN (%)	1.1	0.67-1.45	0.96	0.69-1.2
Root P (%)	0.15	0.06-0.56	0.13	0.07-0.26

3.1 *Arctophila fulva*

For *A. fulva*, the first four PC axes explained 72% of the variation in plant leaf nutrients. However, only axis 1 and 4 were significant ($p<0.05$). Axis 1 explained 29% of the variation and was positively correlated with the plant macronutrients N, P, K, Ca, Mg, S as well as other elements such as Al, B, Ba, Mn, S, Zn, and negatively correlated with Ni, Pb and Fe. On the other hand, PC axis 4 explained 13% of the variation and was positively correlated with As, Ca, Cr, Ni, Si, Zn. (Table 2, Figure 5).

Site types for *A. fulva* were clearly separated along axes PCA-1 and PCA-4 (Figure 5). Enriched urban systems were located on the upper left quadrant, coinciding with higher concentrations of many leaf nutrients and environmental variables such as soil P, EC, water P, Si, DOC, plant biomass and higher green spectral indices (NDVI, GEI). Conversely, reference sites and those at southern latitude were located in the opposite quadrants of the plot with a wider distribution along PCA-4 and thus, wider variability in leaf nutrients and environmental conditions. Southern sites for *A. fulva* showed a similar distribution to reference sites (Figure 5).

3.2 *Carex aquatilis*

C. aquatilis PC axis 1 and 2 explained 50% of the variation in the plant nutrient data. PC axis 1 (26%) showed positive relationships with important macronutrients N, P, and Mg and other elements such as Al, Ba, Co, Cu, Fe, Mo, Pb, Zn. PC axis 2 explained 24% of the variation in leave nutrients and was positively associated with Al, Ba, K, Mn, P, S, Sr, and negatively associated with Ni, Mo, Se, Zn (Table 2).

The *C. aquatilis* PC plot of axes 1 and 2 also showed sites grouped by type (Figure 5). We observed a good separation along PCA-2 of enriched urban ponds as compared to reference, southern and enriched thermokarst. Similar to *A. fulva*, the enriched sites were found at the positive end of an axis that was positively associated with water nutrients, alkalinity, conductance, plant biomass, NDVI and soil K (Table 3). Environmental variables positively associated with the vertical distribution of sites along axis 1 included soil EC, water nutrients (TDP, SRP, NO_3), and negative correlations with water pH, alkalinity and *C. aquatilis* green-up date (Table 2). We noticed grouping of enriched thermokarst and reference sites for *C. aquatilis* in a portion of the plot associated with high electrical conductance and water TDP, SRP and NO_3. Conversely to *A. fulva*, the southern sites were clustered away from other sites, in the lower left quadrant, likely reflecting earlier green up, higher GEI, and lower soil and water nutrients.

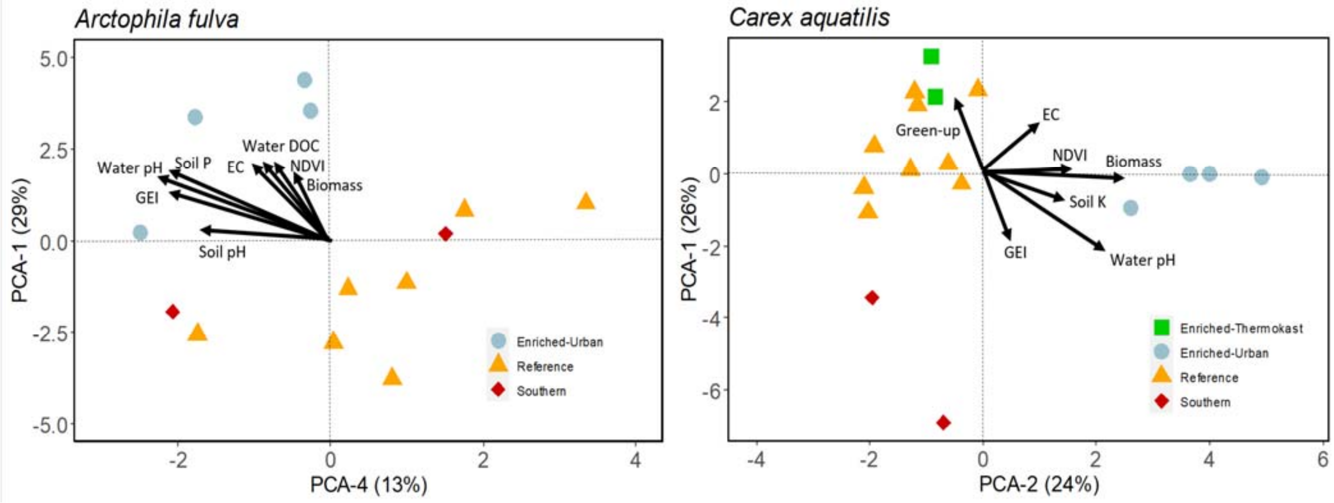


Figure 5. Plots of PCA site scores for *Arctophila fulva* (left) and *Carex aquatilis* (right) plant nutrient data. Eigenvectors depict PCA axis correlations with environmental variables. Eigenvectors are scaled for clarity.

Table 2. Correlation coefficients between PC axes and leaf nutrients for *Carex aquatilis* (right) and *Arctophila fulva* (left).

Arctophila fulva

	Variance explained (%)	Axis *p-value*	Leaf Nutrient	*r*	*p*-value
PC axis 1	29	0.001	P	0.83	0
			Sr (log)	0.81	0.001
			K	0.8	0.001
			Al	0.76	0.003
			Mg	0.73	0.005
			B	0.71	0.007
			S	0.64	0.018
			Mn	0.63	0.021
			Ca (log)	0.53	0.061
			TN	0.5	0.079
			Pb	-0.54	0.057
			Fe (log)	-0.56	0.046
PC axis 4	13	0.053	Cr	0.86	0
			As (log)	0.8	0.054
			Zn	0.58	0.038
			Ni	0.58	0.04

Carex aquatilis

	Variance explained (%)	Axis *p-value*	Leaf Nutrient	*r*	*p*-value
PC axis 1	26	0.001	TN	0.84	0.000
			Cu	0.72	0.001
			Co (log)	0.66	0.019
			Na (log)	0.63	0.007
			Mg	0.61	0.009
			Pb	0.58	0.016
			P	0.56	0.019
			Mo	0.54	0.024
			Zn	0.53	0.029
			Al	-0.48	0.051
			Ba (log)	-0.73	0.001
PC axis 2	24	0.001	S	0.89	0.000
			K	0.85	0.000
			Sr (log)	0.74	0.001
			Mn	0.65	0.004
			Ba (log)	0.59	0.013
			P	0.56	0.020
			Se (log)	-0.48	0.052
			Ni	-0.62	0.008
			Mo	-0.63	0.007
			Zn	-0.66	0.004
			Ni (log)	-0.85	0.000

Table 3. PC axes correlations with environmental variables.

Arctophila fulva

	Environmental Variable	*r*	*p*-value
PC axis 1	Water Si	0.84	0.001
	Water SRP (log)	0.83	0
	Water Sp. Conductance	0.8	0.003
	Water TDP (log)	0.79	0.001
	Water Alkalinity	0.78	0.005
	NDVI	0.7	0.008
	Water DOC	0.69	0.019
	Water TP (log)	0.67	0.012
	EC (log)	0.66	0.027
	Soil P (log)	0.61	0.045
	Biomass (log)	0.59	0.034
	Water pH	0.53	0.096
PC axis 4	Water pH	-0.68	0.021
	GEI	-0.67	0.098
	Soil P (log)	-0.67	0.025
	Water Alkalinity	-0.62	0.044
	Water Sp. Conductance	-0.59	0.057
	Soil pH	-0.53	0.075

Carex aquatilis

	Environmental Variable	*r*	*p*-value
PC axis 1	Green-up day	0.67	0.049
	Water TDP (log)	0.56	0.020
	Water NO3 (log)	0.52	0.034
	EC (log)	0.47	0.069
	Water SRP (log)	0.44	0.076
	Water Alkalinity (log)	-0.61	0.020
	GEI	-0.62	0.078
	Water pH	-0.70	0.004
PC axis 2	Water Sp. Conductance (log)	0.94	0.001
	Water Alkalinity (log)	0.88	0.001
	Biomass	0.84	0.001
	Water pH	0.73	0.002
	Water Si (log)	0.58	0.018
	NDVI	0.56	0.071
	Water SRP (log)	0.54	0.024
	Water TDP (log)	0.53	0.029
	Soil K	0.50	0.050
	Water TP (log)	0.41	0.099

4. DISCUSSION

We explored the effects of plant nutrient enrichment in the dominant aquatic tundra species of the Arctic Coastal Plain: *A. fulva* and *C. aquatilis*. Our study is unique as it focuses on aquatic emergent plants and is based on natural responses to non-experimental, long-term nutrient enrichment compared to previous studies of fertilization treatment experiments. Plant leaf nutrients were a function of soil and water nutrients in Arctic tundra ponds. Phosphorus was the main driver of biomass in aquatic plants and plant greenness measured by NDVI in both plant species.

4.1 Leaf nutrients

The environmental gradient investigated in this study was highlighted by the principal component analysis and allowed better understanding of the factors influencing leaf nutrients. Our analysis shows how soil and water nutrients in ponds influence plant leaf nutrients and aboveground biomass of aquatic tundra graminoids. The Arctic is typically nutrient limited in inorganic forms of N and P in both soil (Mack *et al* 2004, Keuper *et al* 2012, Beermann *et al* 2015) and surface waters (Rautio *et al* 2011). Similar to aquatic growth forms, moist and wet tundra *C. aquatilis* and *A. fulva* appear to be P limited (Chapin *et al* 1995, Mack *et al* 2004, Boelman *et al* 2003, Beermann *et al* 2015) given the highly organic soil which enhances recycling of N by mineralization of soil organic matter (Beermann *et al* 2015, Chapin *et al* 1975). On the aquatic side, primary productivity of phytoplankton and periphyton in tundra ponds in the Utqiagvik area (including some of our study sites) have been shown to be largely NP co-limited (Lougheed *et al* 2015). In fact, Lougheed et al (2015) suggested that macrophytes may be outcompeting algae for available nitrogen, which may account for the N limitation of algae but N sufficiency of plants. Soil nutrients were similar among cover types which may explain the homogeneous leaf macronutrient concentrations among *C. aquatilis* and *A. fulva*. However, we observed higher micronutrients and other non-essential minerals in *C. aquatilis* compared to *A. fulva*. These disparities are likely attributed to differences in taxonomic groups and thus, taxa-specific nutrient content (Chapin *et al* 1975).

We designed the sample collection to give an overall representation of plant-soil relationships for detection using remote sensing. The plant leaf samples and soil samples were not taken within the exact location, but rather, plants were collected in different areas of the monotypic stands trying to have a diverse representation of the species within each pond. Similarly, soils were collected in 3 different locations within the same area and mixed together for processing. However, given the high heterogeneity in soil properties on polygonal tundra due to cryoturbation, the relationships between soil and leaf nutrients are likely weakened and may explain the low strength of the relationships of Figure 3.

Compared to historical studies in the Utqiaġvik area, we found that the major plant macronutrients in *C. aquatilis* had increased since they were determined in 1970 by Chapin et al (1975). N, P and Ca plant percentage content increased from 2.18±0.09 to 2.4±0.2 (10%

increase), 0.15±0.02 to 0.18±0.03 (20%), 0.08±0.02 to 0.14±0.08 (75%) respectively, for samples collected in early August. However, K and Mg were lower compared to 1970. Increase in leaf nutrients are concomitant with long-term observations of nutrient increases in tundra ponds of nitrate, ammonia and soluble reactive phosphorus (Lougheed *et al* 2011). Increased plant nutrients may be a result of nutrient release from long-term increases of active layer depth (Andresen and Lougheed 2015), thawing permafrost (Reyes and Lougheed 2015, Keuper *et al* 2012) and nitrogen mineralization (Uhlířová *et al* 2007, Weintraub and Schimel 2003) leached from terrestrial inputs. The remarkable increase in Ca observed by Chapin *et al* (1975) between 1970 and 2013 is likely associated to accumulation from high transpiration (Chapin 1980) and suggests enhanced *C. aquatilis* evapotranspiration rates compared to 50 years ago as a result of modern warmer temperatures in both air and water (Lougheed *et al* 2011, Andresen and Lougheed 2015). It is important to note that *C. aquatilis* has been shown to have phenotypical differences across moisture gradients (Shaver et al. 1979). Thus, *C. aquatilis* sampled in wet meadows (Chapin *et al* 1975) might have different physiological characteristics, and therefore, different nutrient tissue composition compared to *C. aquatilis* in aquatic habitats.

This study focused on peak season to reflect peak biomass (Andresen *et al* 2017) and greenness (Andresen *et al* 2018) of aquatic graminoid tundra with different environmental nutrient status. In addition, peak season is the preferred timing for assessing long-term Arctic greenness trends from satellite platforms (Walker *et al* 2012b, Bhatt *et al* 2010). Nutrients are known to affect seasonal phenology of aquatic graminoids by promoting earlier green-up date as well as higher season greenness (Andresen *et al* 2018). However, the relationship between environmental nutrient status and seasonal plant nutrient dynamics is unclear in tundra graminoids and should be further investigated.

There are other important seasonal considerations that are worth noting. Concentrations of leaf nutrients have been shown to vary through the growing season in tundra vegetation communities. In graminoids, N and P peak within 10 days of snowmelt and gradually decrease to half of their concentration over the course of the growing season Chapin 75. On the other hand, water and soil nutrients may increase over the season in ponds as active layer thaws and soil biogeochemical processes activate (e.g. N mineralization) resulting in increased nutrient leaching from terrestrial to aquatic systems. Evaporation and evapotranspiration likely help increase nutrient concentrations in small ponds. As climate change continues to stretch the growing season, we need to further understand seasonal dynamics of plant nutrients and its implications on productivity and land-atmosphere carbon exchange.

4.2 Nutrients, biomass, NDVI and GEI

NDVI of Arctic graminoid tundra has been noted to be a function of biomass caused by increased nutrients (Boelman *et al* 2003, 2005, Epstein *et al* 2012, Raynolds *et al* 2012, Andresen *et al* 2018). For example, Boelman et al. (2003) observed higher NDVI values in N and P fertilized experimental treatments in wet sedge tundra communities compared to control treatments. Also, Andresen et al (2018) noted higher NDVI and GEI greenness values concomitant with higher biomass in enriched sites. Our study supports previous studies on the importance of spectral measurements to be a function of environmental nutrient availability through the enhancement of tundra biomass and leaf greenness at the plot level (Andresen *et al* 2018, Boelman *et al* 2005). In particular, this study highlights phosphorus as the main nutrient augmenting aboveground biomass and plant greenness in aquatic tundra. Aquatic tundra graminoids studied here showed higher biomass in nutrient rich sites which translated to higher plot-level greenness (e.g. NDVI, GEI). We suspect that the combination of nutrient-induced factors such as (i) increased plant density thorough increased foliage and leaf area as well as (ii) plant vitality from chlorophyll production and other pigments enhanced NDVI and GEI spectral signatures. It is important to consider that plot-scale spectral measurements such as NDVI and GEI may differ from coarser remote sensing platforms given the spectral heterogeneity of the radiance signal measured by the satellite sensor pixel (Guay *et al* 2014) and caution should be given to interpretations of NDVI with coarse imagery.

Increases in terrestrial productivity of the Arctic as inferred from coarse satellite NDVI measurements have been directly attributed to increasing temperatures associated to sea ice decline (Bhatt *et al* 2010, Epstein *et al* 2012). However, satellite based observations of tundra change are complex (Myers-Smith *et al* 2020) with differing trends of greening and browning observed in recent decades (Pastick *et al* 2019, Verbyla 2008, Phoenix and Bjerke 2016). At the plot level, biological factors influencing spectral greenness signals include community composition (Forbes *et al* 2010) leaf area and phenology (Andresen *et al* 2018, Post *et al* 2018). These factors are greatly influenced by nutrient environmental availability as shown in this study and others (Boelman *et al* 2003, Andresen *et al* 2018). As permafrost degradation and abrupt thaw events continue to increase in frequency (Turetsky *et al* 2020, Reyes and Lougheed 2015, Andresen *et al* 2020), it is imperative that we continue understanding plot-level spectral signals and how they influence landscape-level satellite observations.

The wide range of environmental nutrient status and the broad spatial sampling undertaken in this study provides a strong confidence on the use of spectral indices such as NDVI to monitor environmental nutrient status at a regional scale. In particular, the strong relationships between NDVI and phosphorous suggest that aquatic plant communities can be used as hot-spots and/or hot moments indicators of nutrient availability and biochemical landscape-scale processes. Hot-spots (disproportionately high reaction rates relative to the surrounding landscape) and hot-moments (short periods of disproportionately high reaction rates relative to longer time periods) are generally associated with rates and reactions of biochemical processes (e.g. nutrient cycling, productivity) and often enhanced at the terrestrial-aquatic interface where hydrological flow-paths mobilize substrates containing complimentary reactants (e.g. nutrients) (McClain *et al* 2003). Aquatic plant communities are situated at the terrestrial-aquatic interface inside catch-points of small landscape drainages (e.g. ponds, low-center polygons, ice wedge pits, etc) where biogeochemical changes such as mobilization processes from permafrost degradation (hot-moment) and nutrient mineralization (hot-moment) can be detected and mapped (hot-spot) with spatial detail over large areas.

5. Conclusion

This study highlights the influence and sensitivity of aquatic graminoid tundra community to environmental nutrient status. In particular, we addressed that (i) aquatic graminoids were responding to higher soil and water nutrient availability through increased biomass and greenness, (ii) phosphorus was the principal limiting nutrient driving aquatic graminoid plant biomass as well as (iii) positively enhancing plot-level NDVI spectral signatures. With projected increased warming and associated terrestrial biegeochemical processes such as increased active layer depth and permafrost thaw, increased nutrient availability and mineralization and enhanced ecosystem carbon dynamics, aquatic plants will continue to be a hot-spot/hot-moment of change in structure and function as they sustain encroachment of aquatic habitats that are increasing in nutrients with potential carbon and surface energy feedbacks to climate. Characterizing mechanisms for detection and quantification of biogeochemical responses to climate change employing remote sensing will continue to be pivotal into understanding spatial and temporal evolution of the Arctic terrestrial and aquatic systems and their interactions.

6. Appendix

Apendix 1. Study sites and plant types. Plants species included *C. aquatilis* (C) and *A. fulva* (A).

Site	Site type	Plant species	Latitude	Longitude
AHMA	Enriched/urban	A,C	71.303809	-156.741201
ATQ-E	Southern	A,C	70.447892	-157.362756
ATQ-W	Southern	A,C	70.457525	-157.401083
BOXER	Enriched/urban	A,C	71.303617	-156.752594
BOXER-2	Enriched/urban	A,C	71.304114	-156.748877
IBP-10	Reference	A,C	71.2935	-156.70433
IBP-B	Reference	A,C	71.294924	-156.702552
IBP-C	Reference	C	71.2946	-156.70210
IBP-D	Reference	A,C	71.294851	-156.700166
IBP-J	Reference	A,C	71.293626	-156.70144
IBP-X	Reference	A,C	71.295801	-156.699817
ITEX-N	Reference	A,C	71.318141	-156.58322
TK1	Enriched/thermokarst	C	71.27496	-156.632653
TK3	Enriched/thermokarst	C	71.273975	-156.636431
UTIQ	Enriched/urban	A,C	71.302004	-156.722267
WL02	Reference	C	71.2797	-156.61891
WL03	Reference	A,C	71.2823	-156.61625

7. **Data Availability:** Arctic data center https://arcticdata.io/

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9. **Authors Contributions:** CGA and VLL collected and processed the data and wrote the manuscript.

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