Arctic aquatic graminoid tundra responses to nutrient availability

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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

44 soils (Turetsky *et al* 2020, Loiko *et al* 2020, Nitze *et al* 2020, Jones *et al* 2012). These factors
45 highlight the complexity of tundra plant growth and production under a warming and changing
46 Arctic with implications for carbon budgets (Oberbauer *et al* 2007, McGuire *et al* 2018).
47 Unraveling the covarying climate and environmental controls influencing Arctic tundra
48 productivity is paramount for advancing our predictive understanding of the causes and
49 consequences of warming in tundra ecosystems and associated land-atmosphere feedbacks.
50   Nutrients play a key role influencing tundra plant production with complex effects on
51 ecosystem carbon balance. Early work by Chapin et al., (1975) and Shaver et al., (1998)
52 demonstrated that nutrients, particularly N and P, enhanced plant biomass and aboveground plant
53 nutrients in wet tundra communities. In contrast, temperature alone has shown no effect on
54 biomass production in long-term experimental treatments (Shaver *et al* 1998, Boelman *et al*
55 2003, Jónsdóttir *et al* 2005, Johnson *et al* 2000). While nutrients drive productivity and
56 accumulation of new organic matter in the soil, nutrient enrichment can result in net carbon
57 losses by enhancing decomposition of old carbon stocks (Mack *et al* 2004). These results
58 emphasize the importance of nutrient–carbon interactions in controlling ecosystem processes and
59 ecosystem C balance in arctic tundra.
60   Our study builds on previous experimental studies that examined nutrient impacts on wet
61 tundra (Shaver *et al* 1998, Boelman *et al* 2003, McLaren and Buckeridge 2019, Beermann *et al*
62 2015, Lara *et al* 2019) by focusing on aquatic tundra, which are a relatively understudied plant
63 community in the Arctic. Aquatic emergent tundra plants are known to have the highest
64 productivity compared to terrestrial communities and contribute to a significant portion of
65 regional carbon sink and methane fluxes (Lara *et al* 2014, Joabsson and Christensen 2001,
66 Andresen *et al* 2017). In recent decades, Arctic aquatic communities have increased in biomass
67 and cover (Villarreal *et al* 2012, Andresen and Lougheed 2015), likely attributed to an increase
68 in nutrient input leached from terrestrial systems through permafrost degradation and abrupt
69 thaw events into aquatic habitats (Turetsky *et al* 2020, Reyes and Lougheed 2015), but the
70 impacts of nutrients on Arctic aquatic plant communities have not been well documented in
71 literature (Andresen 2014).
72   Nutrients have increased over the past 40 years in aquatic habitats (Lougheed *et al* 2011)
73 with parallel biomass increases of aquatic graminoids (Andresen *et al* 2017). This phenomenon
74 will likely become more pronounced as increasing temperatures in Arctic soils continue
75 enhancing nitrogen mineralization (Uhlířová *et al* 2007, Weintraub and Schimel 2003) as well as
76 permafrost degradation and nutrient leaching (Keuper *et al* 2012, Reyes and Lougheed 2015,
77 Frey and McClelland 2009, Fouché *et al* 2020). With increased thaw and subsurface flow
78 (Frampton *et al* 2013, Shiklomanov *et al* 2013), these processes may provide substantial nutrient
79 inputs to freshwater ecosystems, however, there is increased need to assess the effects of these
80 increased nutrient inputs on aquatic tundra productivity.
81   Remote sensing has been used to detect and quantify plant productivity in Arctic systems
82 based on multispectral indices (Pastick *et al* 2019, Epstein *et al* 2012, Walker *et al* 2012b).
83 Boelman et al., (2003) showed the applicability of the normalized vegetation index (NDVI) as a

84 tool to track spectral responses of wet sedge tundra to nutrients in fertilization and warming
85 experiments. Other studies employing digital repeat photography have successfully assessed
86 plant phenology, biomass and productivity by evaluating vegetation color with indices in the
87 visual spectral range (i.e. blue, green and red) (Saitoh *et al* 2012, Sonnentag *et al* 2012, Andresen
88 *et al* 2018). Plant spectral responses to nutrient enrichment in aquatic communities are poorly
89 understood and its monitoring using remotely sense data would help monitor and quantify
90 potential carbon and energy feedbacks to the atmosphere at regional scales.
91   With current and projected warming and nutrient loading into Arctic aquatic systems, it is
92 important to understand nutrient impacts on aquatic emergent vegetation, and how these changes
93 can be detected and modeled using remote sensing methods. In this study, we sampled tundra
94 pond sites that followed a nutrient gradient that range from sites with thermokarst slumping or
95 urban runoff to sites with relatively low nutrient inputs. We aim to characterize nutrient
96 limitation of aquatic emergent tundra vegetation and spectral responses of this vegetation to
97 nutrient inputs. We focus on the influence of soil and water nutrients on plant biomass and
98 greenness of *Carex aquatilis* and *Arctophila. fulva*, the dominant aquatic emergent vascular
99 plants in the Arctic coastal plain (Villarreal *et al* 2012, Andresen *et al* 2018) to answer the
100 questions of: (i) how is aquatic tundra responding to nutrient availability? (ii) How
101 environmental nutrient status influence leaf nutrients in aquatic tundra? (iii) What are the
102 spectral responses (NDVI) of aquatic tundra to nutrient availability?

103 **2. METHODS**

104   **2.1   Study Sites**

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

121 Although these species have growth forms in moist and dry tundra (Shaver *et al* 1979), this study
122 focuses on their aquatic phenotypes.
123   A total of seventeen tundra ponds were sampled in early August (4th-9th) 2013 along a
124 nutrient gradient with long-term sources of nutrients. Sites were grouped in four categories
125 according their geographic location and nutrient source as: (i) enriched urban, (ii) enriched
126 thermokarst, (iii) reference, and (iv) southern (Figure 1, 2, Appendix 1). Enriched urban ponds
127 were located within the town of Utqiaġvik, AK and their source of nutrients was mainly from
128 village runoff. Enriched thermokarst ponds were situated within the Barrow Environmental
129 Observatory (BEO), and their nutrient inputs originate from permafrost slumping into ponds.
130 Reference sites were located across the region in the historical International Biological Program
131 (IBP) sites and in the BEO; but these sites do not contain evidence of continuous permafrost
132 slumping. Southern latitude ponds were located 100 km south of Utqiaġvik, near the town of
133 Atqasuk, AK. We sampled these ponds in order to expand the geographic footprint of the study
134 and serve as reference to Utqiaġvik area. It is important to note that while *C. aquatilis* occurs in
135 all ponds, *A. fulva* does not occur in thermokarst ponds nor in IBP-C and WL02 ponds
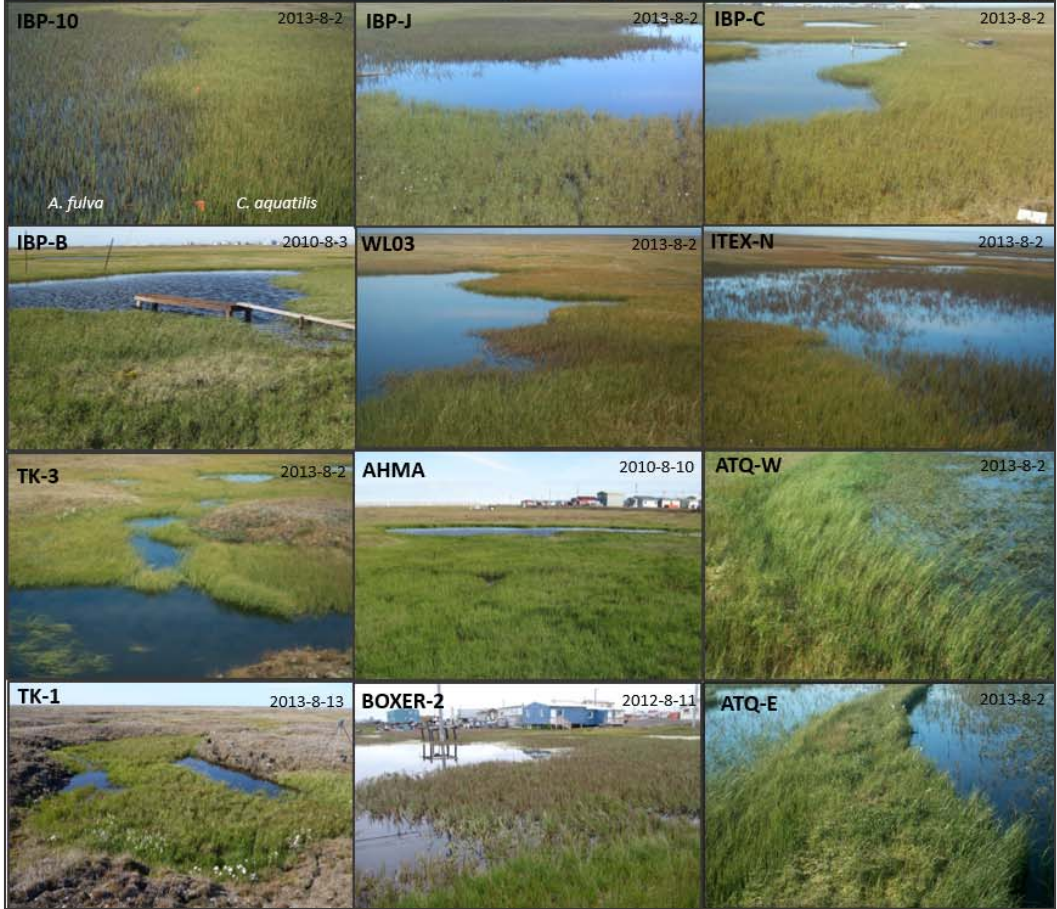136 (Appendix 1).
137
138 Figure 1. Map of Utqiaġvik sites sampled in this study. For site details including southern sites
139 see Appendix 1. *Imagery © [2012] DigitalGlobe, Inc.*
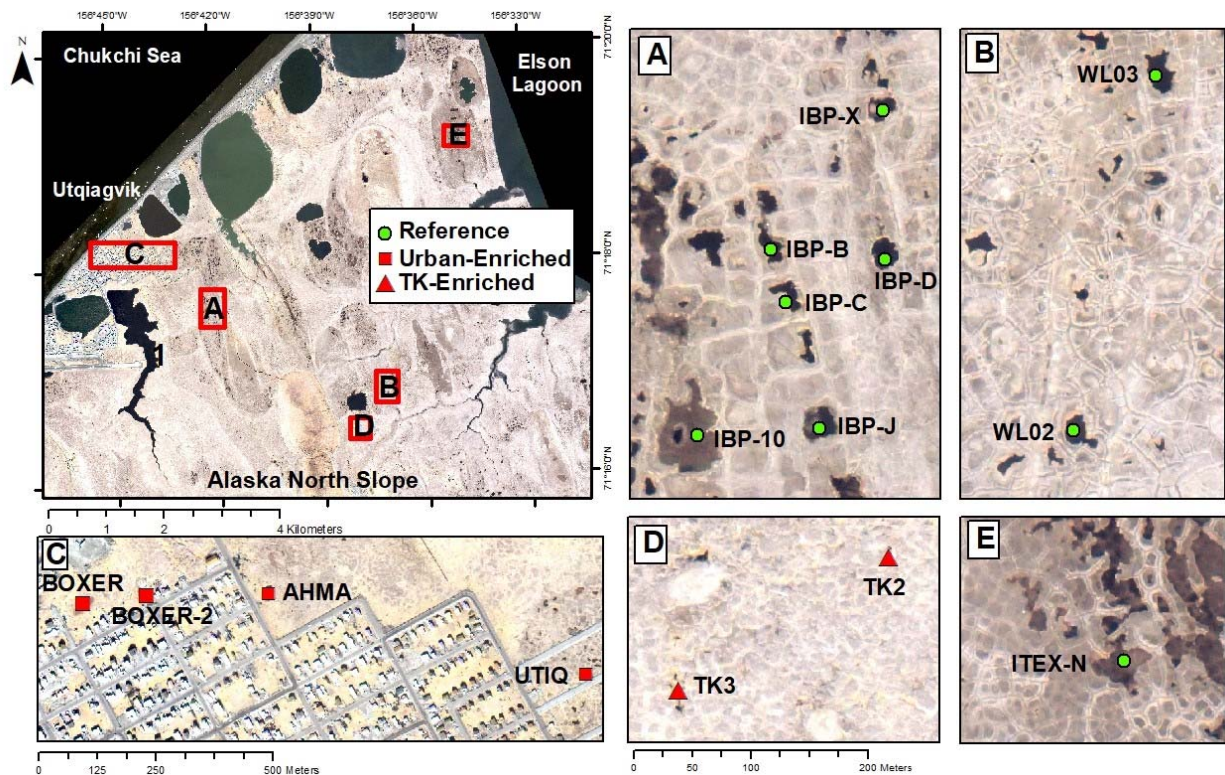
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153 Figure 2. Aerial view the Arctic coastal plain near Utqiaġvik, AK, and examples of sites sampled
154 in this study. Images indicate site name (top-left) and picture date Y/M/D (top-right). Photos by
155 C. Andresen.

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

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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

196 relatively low in the Arctic (~33^0, peak season) and solar specular reflection was outside of the
197 ~1 m spectral footprint of the measured plot. The reflectance ratio was estimated between plot
198 radiance at nadir and the calibration standard radiance. White calibration standard (38 mm wide)
199 was positioned 30 mm at nadir below the field spectrometer optic fiber (field of view of 25°) at
200 each calibration, then capped closed to minimize degradation. NDVI measurements from 5 scans
201 were averaged in each plot, and 4–6 plots per pond for comparison with leaf nutrients.
202 Normalized Difference Vegetation Index (NDVI) was estimated from reflectance ratio values
203 using the formula: NDVI = (800 nm− 680 nm) / (800 nm+ 680 nm). NDVI is a standard proxy of
204 plant productivity and biomass in the Arctic and has been used to track plot (Soudani *et al* 2012,
205 Gamon *et al* 2013, Andresen *et al* 2018) to regional and global seasonal and decade time-scale
206 productivity trends (Bhatt *et al* 2010, Walker *et al* 2012a, Zeng and Jia 2013).
207 Parallel to reflectance NDVI measurements, we employed phenocams (optical
208 photography) at each site to calculate the "green excess" index (GEI) (Richardson *et al* 2009,
209 Andresen *et al* 2018) from peak-season oblique images using the formula: [2*G - (R + B)] where
210 G is the brightness value in the green, R is the brightness value in the red, and B is the brightness
211 value in the blue. Oblique-angle GEI collected from cameras in this study is strongly associated
212 to nadir-angle NDVI for both *A. fulva* and *C. aquatilis* (Andresen *et al* 2018). For additional
213 camera details and setup refer to Andresen *et al* (2018).

214 **2.4 Statistical analysis**

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

227 **3. RESULTS**

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

234   In addition, we found a positive linear relationship ($R^2 = 0.48$, $p<0.01$) between leaf
235 phosphorus and NDVI (Figure 3). There were no significant relationships between plant biomass
236 and leaf nitrogen. Among site types, enriched sites (Urban and Thermokarst) have statistically
237 higher soil, leaf and water nutrients compared to reference sites ($p<0.001$), no differences found
238 for southern sites.
239   There were no significant differences in leaf and soil macro-nutrients among plant
240 species in a given pond from reference sites (paired t-test, $p>0.05$) (Table 1). However, leaf
241 micronutrients among plant species differed. We found significantly higher amounts of leaf Al,
242 B, Ba, Mn, Na, Ni, Si and Zn in *C. aquatilis* compared to *A. fulva* ($p<0.05$ level). The most
243 abundant leaf element in both plant species was N, followed in decreasing order by K, P, S and
244 Mg and these ratios were consistent across the nutrient gradient sites (Figure 4).
245   There were significant differences in green-up date and peak season Greenness Excess
246 Index (GEI) among species ($p<0.01$, Table 1). *A. fulva* greened later (day 200 vs. 183) and had
247 lower GEI (9 vs. 33) as compared to *C. aquatilis*. These differences are associated to unique
248 phenotypic properties between species in the visual spectral range (Andresen *et al* 2018). There
249 was no corresponding difference in NDVI or biomass among species ($p>0.05$).
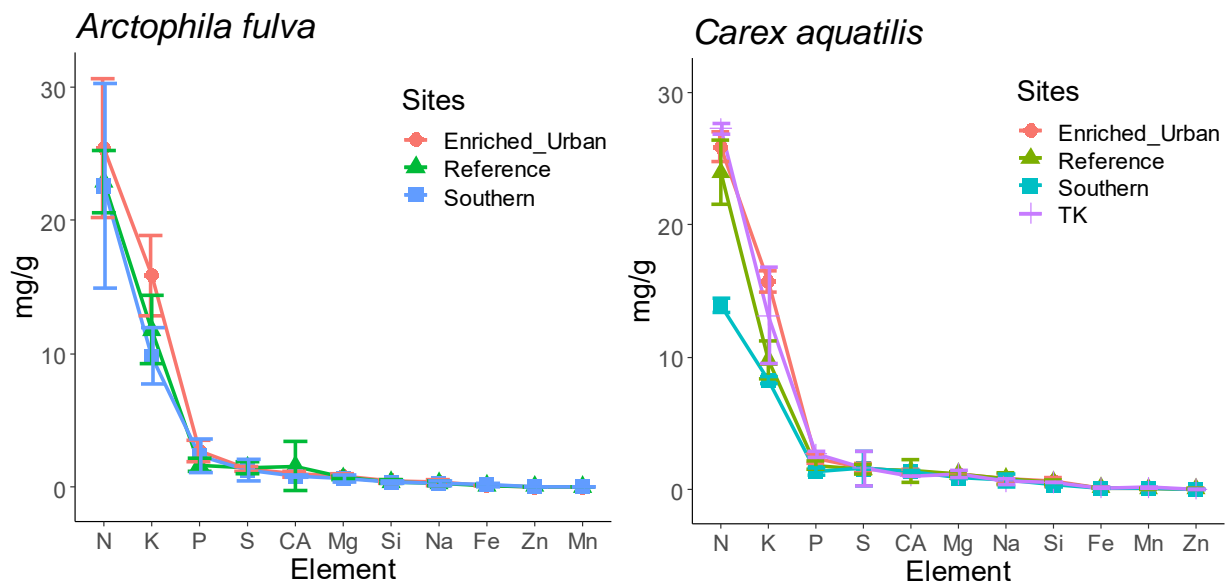250
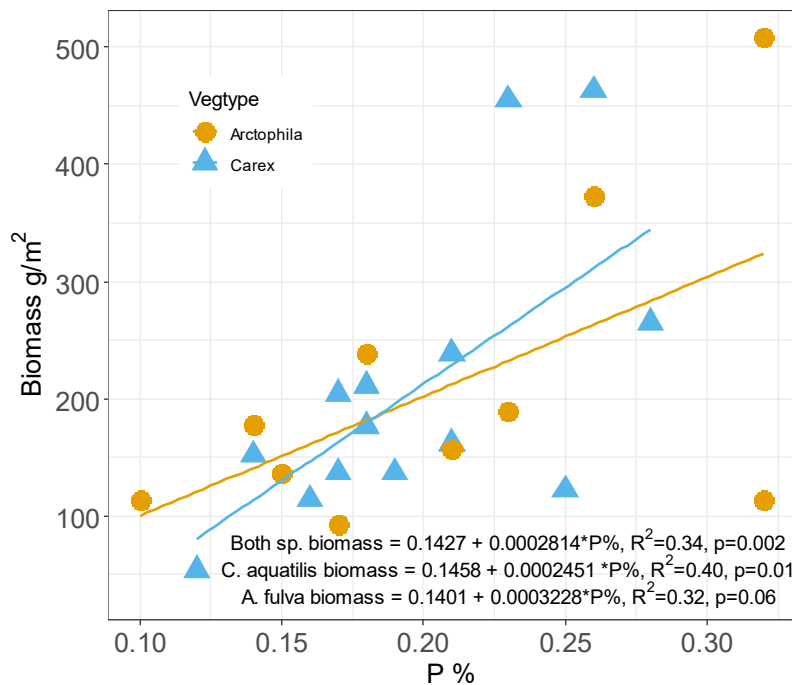
251
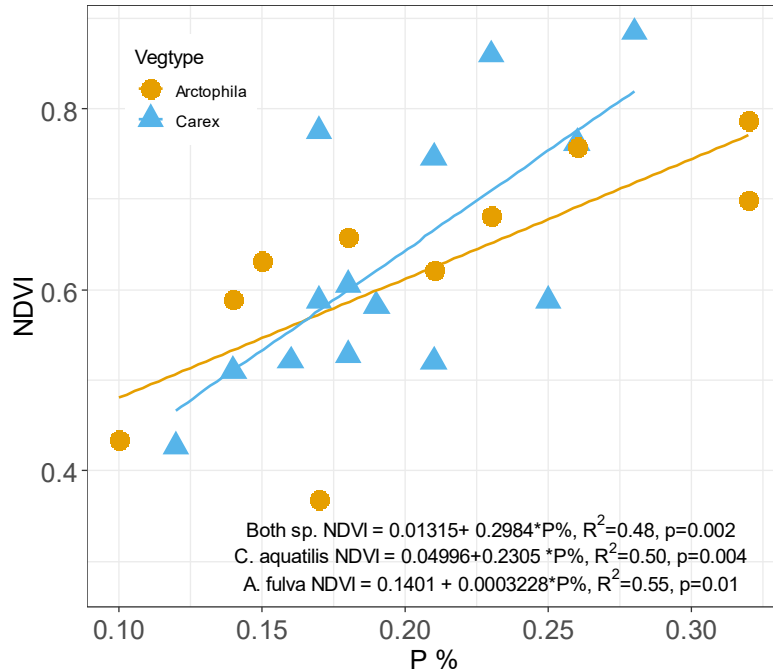
252
253 Figure 3. Relationship between Phosphorus content (%) of leaves and dry weight aboveground
254 biomass (left) and NDVI (right) for *Carex aquatilis* and *Arctophila fulva*. Biomass collected
255 during peak growing season (first week of August). Each point represents site averages.
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258 Figure 4. Descending order of element concentration in aboveground tissue among plant species.
259 Error bars represent one standard deviation from mean.
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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.
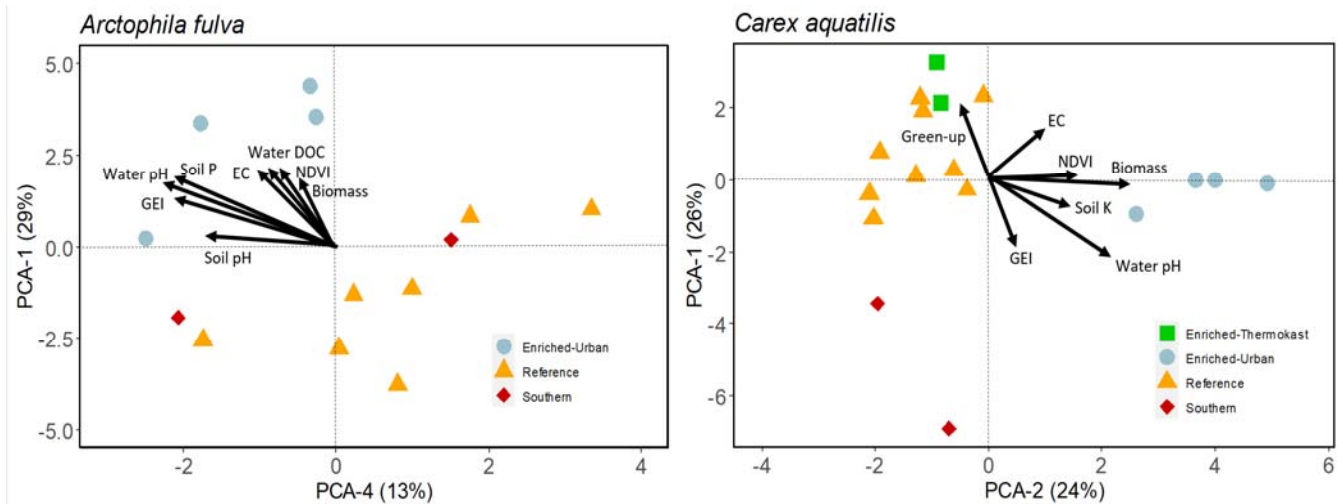
Figure 5. Plots of PCA site scores for *Arctophila fulva* (left) and *Carex aquatilis* (right) plant nutrient data. Eigenvectors depict PCA axis correlations with environmental variables. Eigenvectors are scaled for clarity.

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

	Arctophila fulva						*Carex aquatilis*				
	Variance explained (%)	Axis *p-value*	Leaf Nutrient	*r*	*p*-value		Variance explained (%)	Axis *p-value*	Leaf Nutrient	*r*	*p*-value
PC axis 1	29	0.001	P	0.83	0	PC axis 1	26	0.001	TN	0.84	0.000
			Sr (log)	0.81	0.001				Cu	0.72	0.001
			K	0.8	0.001				Co (log)	0.66	0.019
			Al	0.76	0.003				Na (log)	0.63	0.007
			Mg	0.73	0.005				Mg	0.61	0.009
			B	0.71	0.007				Pb	0.58	0.016
			S	0.64	0.018				P	0.56	0.019
			Mn	0.63	0.021				Mo	0.54	0.024
			Ca (log)	0.53	0.061				Zn	0.53	0.029
			TN	0.5	0.079				Al	-0.48	0.051
			Pb	-0.54	0.057				Ba (log)	-0.73	0.001
			Fe (log)	-0.56	0.046	PC axis 2	24	0.001	S	0.89	0.000
PC axis 4	13	0.053	Cr	0.86	0				K	0.85	0.000
			As (log)	0.8	0.054				Sr (log)	0.74	0.001
			Zn	0.58	0.038				Mn	0.65	0.004
			Ni	0.58	0.04				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

311

312 Table 3. PC axes correlations with environmental variables.

	Arctophila fulva					*Carex aquatilis*		
	Environmental Variable	*r*	*p*-value			Environmental Variable	*r*	*p*-value
PC axis 1	Water Si	0.84	0.001		PC axis 1	Green-up day	0.67	0.049
	Water SRP (log)	0.83	0			Water TDP (log)	0.56	0.020
	Water Sp. Conductance	0.8	0.003			Water NO3 (log)	0.52	0.034
	Water TDP (log)	0.79	0.001			EC (log)	0.47	0.069
	Water Alkalinity	0.78	0.005			Water SRP (log)	0.44	0.076
	NDVI	0.7	0.008			Water Alkalinity (log)	-0.61	0.020
	Water DOC	0.69	0.019			GEI	-0.62	0.078
	Water TP (log)	0.67	0.012			Water pH	-0.70	0.004
	EC (log)	0.66	0.027		PC axis 2	Water Sp. Conductance (log)	0.94	0.001
	Soil P (log)	0.61	0.045			Water Alkalinity (log)	0.88	0.001
	Biomass (log)	0.59	0.034			Biomass	0.84	0.001
	Water pH	0.53	0.096			Water pH	0.73	0.002
PC axis 4	Water pH	-0.68	0.021			Water Si (log)	0.58	0.018
	GEI	-0.67	0.098			NDVI	0.56	0.071
	Soil P (log)	-0.67	0.025			Water SRP (log)	0.54	0.024
	Water Alkalinity	-0.62	0.044			Water TDP (log)	0.53	0.029
	Water Sp. Conductance	-0.59	0.057			Soil K	0.50	0.050
	Soil pH	-0.53	0.075			Water TP (log)	0.41	0.099

313   **4. DISCUSSION**

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

321   **4.1   Leaf nutrients**

322   The environmental gradient investigated in this study was highlighted by the principal
323   component analysis and allowed better understanding of the factors influencing leaf nutrients.
324   Our analysis shows how soil and water nutrients in ponds influence plant leaf nutrients and
325   aboveground biomass of aquatic tundra graminoids. The Arctic is typically nutrient limited in
326   inorganic forms of N and P in both soil (Mack *et al* 2004, Keuper *et al* 2012, Beermann *et al*
327   2015) and surface waters (Rautio *et al* 2011). Similar to aquatic growth forms, moist and wet
328   tundra *C. aquatilis* and *A. fulva* appear to be P limited (Chapin *et al* 1995, Mack *et al* 2004,
329   Boelman *et al* 2003, Beermann *et al* 2015) given the highly organic soil which enhances
330   recycling of N by mineralization of soil organic matter (Beermann *et al* 2015, Chapin *et al*
331   1975). On the aquatic side, primary productivity of phytoplankton and periphyton in tundra
332   ponds in the Utqiagvik area (including some of our study sites) have been shown to be largely
333   NP co-limited (Lougheed *et al* 2015). In fact, Lougheed et al (2015) suggested that macrophytes
334   may be outcompeting algae for available nitrogen, which may account for the N limitation of
335   algae but N sufficiency of plants. Soil nutrients were similar among cover types which may
336   explain the homogeneous leaf macronutrient concentrations among *C. aquatilis* and *A. fulva*.
337   However, we observed higher micronutrients and other non-essential minerals in *C. aquatilis*
338   compared to *A. fulva*. These disparities are likely attributed to differences in taxonomic groups
339   and thus, taxa-specific nutrient content (Chapin *et al* 1975).

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

348

349   Compared to historical studies in the Utqiaġvik area, we found that the major plant
350   macronutrients in *C. aquatilis* had increased since they were determined in 1970 by Chapin et al
351   (1975). N, P and Ca plant percentage content increased from 2.18±0.09 to 2.4±0.2 (10%

14

352 increase), 0.15±0.02 to 0.18±0.03 (20%), 0.08±0.02 to 0.14±0.08 (75%) respectively, for
353 samples collected in early August. However, K and Mg were lower compared to 1970. Increase
354 in leaf nutrients are concomitant with long-term observations of nutrient increases in tundra
355 ponds of nitrate, ammonia and soluble reactive phosphorus (Lougheed *et al* 2011). Increased
356 plant nutrients may be a result of nutrient release from long-term increases of active layer depth
357 (Andresen and Lougheed 2015), thawing permafrost (Reyes and Lougheed 2015, Keuper *et al*
358 2012) and nitrogen mineralization (Uhlířová *et al* 2007, Weintraub and Schimel 2003) leached
359 from terrestrial inputs. The remarkable increase in Ca observed by Chapin *et al* (1975) between
360 1970 and 2013 is likely associated to accumulation from high transpiration (Chapin 1980) and
361 suggests enhanced *C. aquatilis* evapotranspiration rates compared to 50 years ago as a result of
362 modern warmer temperatures in both air and water (Lougheed *et al* 2011, Andresen and
363 Lougheed 2015). It is important to note that *C. aquatilis* has been shown to have phenotypical
364 differences across moisture gradients (Shaver et al. 1979). Thus, *C. aquatilis* sampled in wet
365 meadows (Chapin *et al* 1975) might have different physiological characteristics, and therefore,
366 different nutrient tissue composition compared to *C. aquatilis* in aquatic habitats.
367 This study focused on peak season to reflect peak biomass (Andresen *et al* 2017) and
368 greenness (Andresen *et al* 2018) of aquatic graminoid tundra with different environmental
369 nutrient status. In addition, peak season is the preferred timing for assessing long-term Arctic
370 greenness trends from satellite platforms (Walker *et al* 2012b, Bhatt *et al* 2010). Nutrients are
371 known to affect seasonal phenology of aquatic graminoids by promoting earlier green-up date as
372 well as higher season greenness (Andresen *et al* 2018). However, the relationship between
373 environmental nutrient status and seasonal plant nutrient dynamics is unclear in tundra
374 graminoids and should be further investigated.
375 There are other important seasonal considerations that are worth noting. Concentrations
376 of leaf nutrients have been shown to vary through the growing season in tundra vegetation
377 communities. In graminoids, N and P peak within 10 days of snowmelt and gradually decrease to
378 half of their concentration over the course of the growing season Chapin 75. On the other hand,
379 water and soil nutrients may increase over the season in ponds as active layer thaws and soil
380 biogeochemical processes activate (e.g. N mineralization) resulting in increased nutrient leaching
381 from terrestrial to aquatic systems. Evaporation and evapotranspiration likely help increase
382 nutrient concentrations in small ponds. As climate change continues to stretch the growing
383 season, we need to further understand seasonal dynamics of plant nutrients and its implications
384 on productivity and land-atmosphere carbon exchange.
385

386   **4.2   Nutrients, biomass, NDVI and GEI**
387 NDVI of Arctic graminoid tundra has been noted to be a function of biomass caused by
388 increased nutrients (Boelman *et al* 2003, 2005, Epstein *et al* 2012, Raynolds *et al* 2012,
389 Andresen *et al* 2018). For example, Boelman et al. (2003) observed higher NDVI values in N
390 and P fertilized experimental treatments in wet sedge tundra communities compared to control

391   treatments. Also, Andresen et al (2018) noted higher NDVI and GEI greenness values
392   concomitant with higher biomass in enriched sites. Our study supports previous studies on the
393   importance of spectral measurements to be a function of environmental nutrient availability
394   through the enhancement of tundra biomass and leaf greenness at the plot level (Andresen *et al*
395   2018, Boelman *et al* 2005). In particular, this study highlights phosphorus as the main nutrient
396   augmenting aboveground biomass and plant greenness in aquatic tundra. Aquatic tundra
397   graminoids studied here showed higher biomass in nutrient rich sites which translated to higher
398   plot-level greenness (e.g. NDVI, GEI). We suspect that the combination of nutrient-induced
399   factors such as (i) increased plant density thorough increased foliage and leaf area as well as (ii)
400   plant vitality from chlorophyll production and other pigments enhanced NDVI and GEI spectral
401   signatures. It is important to consider that plot-scale spectral measurements such as NDVI and
402   GEI may differ from coarser remote sensing platforms given the spectral heterogeneity of the
403   radiance signal measured by the satellite sensor pixel (Guay *et al* 2014) and caution should be
404   given to interpretations of NDVI with coarse imagery.
405   Increases in terrestrial productivity of the Arctic as inferred from coarse satellite NDVI
406   measurements have been directly attributed to increasing temperatures associated to sea ice
407   decline (Bhatt *et al* 2010, Epstein *et al* 2012). However, satellite based observations of tundra
408   change are complex (Myers-Smith *et al* 2020) with differing trends of greening and browning
409   observed in recent decades (Pastick *et al* 2019, Verbyla 2008, Phoenix and Bjerke 2016). At the
410   plot level, biological factors influencing spectral greenness signals include community
411   composition (Forbes *et al* 2010) leaf area and phenology (Andresen *et al* 2018, Post *et al* 2018).
412   These factors are greatly influenced by nutrient environmental availability as shown in this study
413   and others (Boelman *et al* 2003, Andresen *et al* 2018). As permafrost degradation and abrupt
414   thaw events continue to increase in frequency (Turetsky *et al* 2020, Reyes and Lougheed 2015,
415   Andresen *et al* 2020), it is imperative that we continue understanding plot-level spectral signals
416   and how they influence landscape-level satellite observations.
417   The wide range of environmental nutrient status and the broad spatial sampling
418   undertaken in this study provides a strong confidence on the use of spectral indices such as
419   NDVI to monitor environmental nutrient status at a regional scale. In particular, the strong
420   relationships between NDVI and phosphorous suggest that aquatic plant communities can be
421   used as hot-spots and/or hot moments indicators of nutrient availability and biochemical
422   landscape-scale processes. Hot-spots (disproportionately high reaction rates relative to the
423   surrounding landscape) and hot-moments (short periods of disproportionately high reaction rates
424   relative to longer time periods) are generally associated with rates and reactions of biochemical
425   processes (e.g. nutrient cycling, productivity) and often enhanced at the terrestrial-aquatic
426   interface where hydrological flow-paths mobilize substrates containing complimentary reactants
427   (e.g. nutrients) (McClain *et al* 2003). Aquatic plant communities are situated at the terrestrial-
428   aquatic interface inside catch-points of small landscape drainages (e.g. ponds, low-center
429   polygons, ice wedge pits, etc) where biogeochemical changes such as mobilization processes

430 from permafrost degradation (hot-moment) and nutrient mineralization (hot-moment) can be
431 detected and mapped (hot-spot) with spatial detail over large areas.
432
5. Conclusion

434   This study highlights the influence and sensitivity of aquatic graminoid tundra community to
435 environmental nutrient status. In particular, we addressed that (i) aquatic graminoids were
436 responding to higher soil and water nutrient availability through increased biomass and
437 greenness, (ii) phosphorus was the principal limiting nutrient driving aquatic graminoid plant
438 biomass as well as (iii) positively enhancing plot-level NDVI spectral signatures. With projected
439 increased warming and associated terrestrial biegeochemical processes such as increased active
440 layer depth and permafrost thaw, increased nutrient availability and mineralization and enhanced
441 ecosystem carbon dynamics, aquatic plants will continue to be a hot-spot/hot-moment of change
442 in structure and function as they sustain encroachment of aquatic habitats that are increasing in
443 nutrients with potential carbon and surface energy feedbacks to climate. Characterizing
444 mechanisms for detection and quantification of biogeochemical responses to climate change
445 employing remote sensing will continue to be pivotal into understanding spatial and temporal
446 evolution of the Arctic terrestrial and aquatic systems and their interactions.
447
6. Appendix

449 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

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