



1 Arctic aquatic graminoid tundra responses to nutrient availability

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

29

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

31 1. INTRODUCTION

32 In the Arctic, plant growth is limited by several factors including low temperatures, short
33 growing-seasons (e.g. irradiance) and nutrients (Chapin et al., 1975; Shaver et al., 1998).
34 Although Arctic temperatures have increased dramatically over recent decades with parallel
35 increases in plant biomass, nutrients have been shown to be the main driver enhancing Arctic
36 tundra productivity compared to temperature in long-term experimental treatments (Boelman et
37 al., 2003; Johnson et al., 2000; Jónsdóttir et al., 2005; Shaver et al., 1998). Increased tundra
38 productivity has generally been explained by warming-mediated processes including increases in
39 nutrient availability through soil warming, heterotrophic decomposition, and nutrient release
40 from mineralization of organic matter and permafrost thaw (Keuper et al., 2012; Natali et al.,
41 2012; Pastick et al., 2019; Reyes and Lougheed, 2015). These factors highlight the complexity of
42 tundra plant growth and production under a warming and changing Arctic with implications for
43 carbon and energy budgets (McGuire et al., 2018; Oberbauer et al., 2007; Swann et al., 2010).



44 Unraveling the covarying climate and environmental controls influencing Arctic tundra
45 productivity is paramount for advancing our predictive understanding of the causes and
46 consequences of warming in tundra ecosystems and associated land-atmosphere feedbacks.
47 Nutrients play a key role influencing tundra plant production with complex effects on
48 ecosystem carbon balance. Early work by Chapin et al., (1975) and Shaver et al., (1998)
49 demonstrated that nutrients, particularly N and P, enhanced plant biomass and plant accumulated
50 nutrients in wet tundra communities. In contrast, temperature alone has shown no effect on
51 biomass production in long-term experimental treatments (Boelman et al., 2003; Johnson et al.,
52 2000; Jónsdóttir et al., 2005; Shaver et al., 1998). While nutrients drive productivity and
53 accumulation of new organic matter in the soil, nutrient enrichment can result in net carbon
54 losses by enhancing decomposition of old carbon stocks (Mack et al., 2004). These results
55 emphasize the importance of nutrient–carbon interactions in controlling ecosystem processes and
56 ecosystem C balance in arctic tundra.

57 Our study builds on previous experimental studies that examined nutrient impacts on wet
58 tundra (Beermann et al., 2015; Boelman et al., 2003; Lara et al., 2019; McLaren and Buckeridge,
59 2019; Shaver et al., 1998) by focusing on aquatic tundra, which are a relatively understudied
60 plant community in the Arctic. Aquatic emergent tundra plants are known to have the highest
61 productivity compared to terrestrial communities and contribute to a significant portion of
62 regional carbon sink and methane fluxes (Andresen et al., 2017; Joabsson and Christensen, 2001;
63 Lara et al., 2014). In recent decades, Arctic aquatic communities have increased in biomass and
64 cover (Andresen and Loughheed, 2015; Villarreal et al., 2012), likely attributed to an increase in
65 nutrient input leached from terrestrial systems through permafrost degradation and abrupt thaw
66 events into aquatic habitats (Reyes and Loughheed, 2015; Turetsky et al., 2020), but the impacts
67 of nutrients on Arctic aquatic plant communities have not been well documented in literature
68 (Andresen, 2014).

69 Nutrients have increased over the past 40 years in aquatic habitats (Loughheed et al., 2011)
70 with parallel biomass increases of aquatic graminoids (Andresen et al., 2017). This phenomenon
71 will likely become more pronounced as increasing temperatures in Arctic soils continue
72 enhancing nitrogen mineralization (Uhlířová et al., 2007; Weintraub and Schimel, 2003) as well
73 as permafrost degradation and nutrient leaching (Frey and McClelland, 2009; Keuper et al.,
74 2012; Reyes and Loughheed, 2015). With increased thaw and subsurface flow (Frampton et al.,
75 2013; Shiklomanov et al., 2013), these processes may provide substantial nutrient inputs to
76 freshwater ecosystems, however, there is increased need to assess the effects of these increased
77 nutrient inputs on aquatic tundra productivity.

78 Remote sensing has been used to detect and quantify plant productivity in Arctic systems
79 based on multispectral indices (Epstein et al., 2012; Pastick et al., 2019; Walker et al., 2012a).
80 Boelman et al., (2003) showed the applicability of the normalized vegetation index (NDVI) as a
81 tool to track spectral responses of wet sedge tundra to nutrients in fertilization and warming
82 experiments. Other studies employing digital repeat photography have successfully assessed
83 plant phenology, biomass and productivity by evaluating vegetation color with indices in the



84 visual spectral range (blue, green and red) (Andresen et al., 2018; Saitoh et al., 2012; Sonnentag
85 et al., 2012). Plant spectral responses to nutrient enrichment in aquatic communities are poorly
86 understood and its monitoring using remotely sense data would help monitor and quantify
87 potential carbon and energy feedbacks to the atmosphere at regional scales.

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

100 2. METHODS

101 2.1 Study Sites

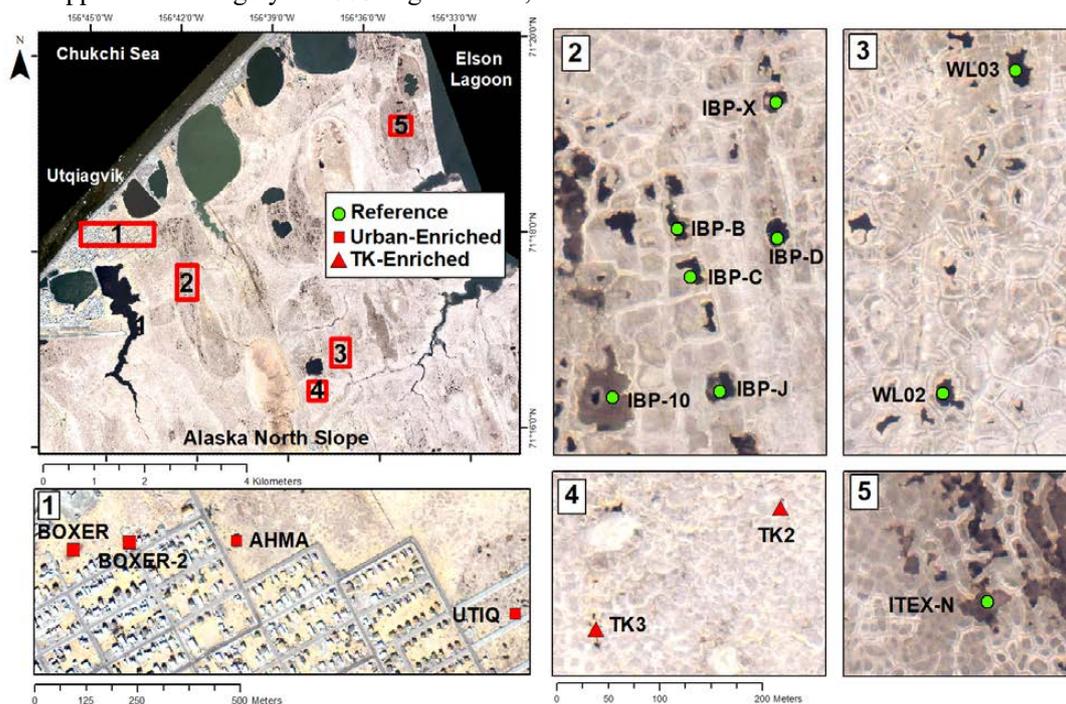
102 This study was conducted in the Barrow Peninsula, Alaska, (W156⁰, N70⁰) near the town
103 of Uqtiagvik (formerly known as Barrow). Physiographically, the area is located in the Arctic
104 Coastal Plain (ACP, ~60,000 km²) of northern Alaska, which stretches from the western coast
105 along the Chukchi Sea to the Beaufort coastal Canadian border. The ACP is dominated by thick
106 continuous permafrost with high ground-ice content for the Arctic peaty lowland of the
107 peninsula. A complex mosaic of ice-wedge patterned ground landforms developed over
108 millennial seasonal cycles of cracking, heaving, and thawing producing its characteristic pond-
109 and lake-dominated landscape (Andresen and Lougheed, 2015; Jorgenson and Shur, 2007).
110 These aquatic habitats are hosts for aquatic graminoid tundra that grows in shallow standing
111 water with a depth range 5-50cm. This study focuses on 2 species: *C. aquatilis* and *A. fulva*.
112 These graminoids are the dominant cover in aquatic habitats, generally growing in the edge
113 and/or inside tundra ponds (Andresen et al., 2017; Villarreal et al., 2012) and their distribution is
114 in low- and sub-Arctic. Although these species have growth forms in moist and dry tundra
115 (Shaver et al., 1979), this study focuses on their aquatic phenotypes.

116 A total of seventeen tundra ponds were sampled in early August 2013 along a nutrient
117 gradient with long-term sources of nutrients. Sites were grouped in four categories according
118 their geographic location and nutrient source as: (i) enriched urban, (ii) enriched thermokarst,
119 (iii) reference, and (iv) southern (Figure 1, 2, Appendix 1). Enriched urban ponds were located
120 within the town of Uqtiagvik, AK and their source of nutrients was mainly from village runoff.
121 Enriched thermokarst ponds were situated within the Barrow Environmental Observatory (BEO),



122 and their nutrient inputs originate from permafrost slumping into ponds. Reference sites were
123 located across the region in the historical International Biological Program (IBP) sites and in the
124 BEO; but these sites do not contain evidence of continuous permafrost slumping. Southern
125 latitude ponds were located 100 km south of Utqiagvik, near the town of Atqasuk, AK. We
126 sampled these ponds in order to expand the geographic footprint of the study and serve as
127 reference to Utqiagvik area. It is important to note that while *C. aquatilis* occurs in all ponds, *A.*
128 *fulva* does not occur in thermokarst ponds nor in IBP-C and WL02 ponds (Appendix 1).
129

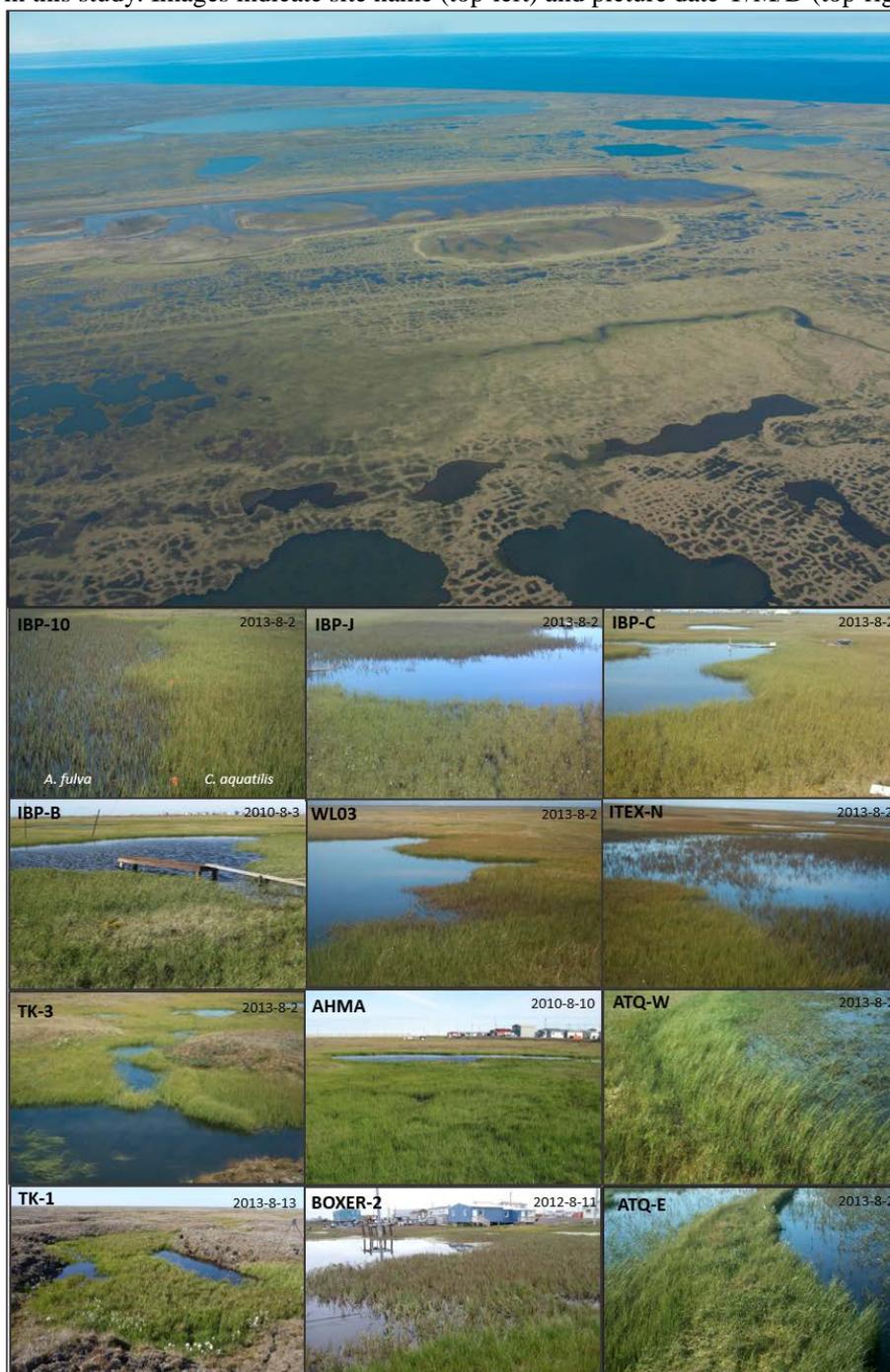
130 Figure 1. Map of Utqiagvik sites sampled in this study. For site details including southern sites
131 see Appendix 1. Imagery © 2008 DigitalGlobe, Inc.



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



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148 **2.2 Plant nutrients**

149 We collected live, green samples of *A. fulva* and *C. aquatilis* at peak growing season
150 (July 25–August 5, 2013). Each sample consisted of 10–15 plants collected from different water
151 depths and multiple haphazardly selected locations in pond habitats. The collected plants were
152 separated into leaves and roots, then rinsed with distilled water, oven-dried at 60 °C for 24 hrs
153 inside open paper envelopes, then shipped to Utah State University Analytical Labs (USUAL)
154 for immediate processing. Most macro- and micro-nutrients in leaves of each plant were
155 analyzed using an inductively-coupled plasma spectrometer (ICP-MS). Nitrogen was analyzed
156 by combustion analysis (HNO₃/H₂O₂ digestion, Leco Instrument).

157 **2.3 Ancillary data**

158 Concomitant with the collection of aquatic plants for nutrient analysis, we collected soil
159 and water samples, harvested aboveground plant biomass, measured spectral reflectance, and
160 monitored most sites using time-lapse photography (Andresen et al., 2018) (Figure 2). For each
161 site, sediment samples from the active root soil depth of 10–20cm for each species were collected
162 in triplicates within the site. Samples were then combined in a plastic bag and frozen until
163 analysis. In the lab, soil samples were air dried for 3 days after thaw, then analyzed for physical
164 and chemical factors including pH, electric conductance (EC), and macronutrients (P, K, and
165 Nitrate). Water chemistry was determined using standard methods as described in Lougheed *et al*
166 (2011). In contrast to sediment, which was sampled for each plant type, water samples from open
167 water mid-column were assumed to be representative of the whole pond, including both plant
168 species given the relatively well mixed environment.

169 Aboveground plant biomass was harvested within duplicate representative 50cm x 20cm
170 quadrats for each species at each site. In addition, reflectance measurements of canopy radiance
171 were collected at each site employing a single channel portable spectrometer (JAZ, Ocean
172 Optics) following the methods of Andresen *et al* (2018). Target radiance was cross-calibrated at
173 every pond site using a certified 99% reflective white spectralon calibration standard (WS-1,
174 Labsphere), which allowed for the estimation of the reflectance ratio between plot radiance and
175 the calibration standard radiance. Reflectance ratio measurements were acquired with a circular
176 footprint of ~1 m diameter at a nadir angle from terrain. We averaged NDVI measurements from
177 5 scans in each plot, and 4–6 plots per pond for comparison with leaf nutrients. Normalized
178 Difference Vegetation Index (NDVI) was estimated from reflectance ratio values in the red and
179 infrared wavelengths using the formula: $NDVI = (800\text{ nm} - 680\text{ nm}) / (800\text{ nm} + 680\text{ nm})$. NDVI
180 has become a standard proxy of plant productivity and biomass in the Arctic and has been used
181 to track plot (Andresen et al., 2018; Gamon et al., 2013; Soudani et al., 2012) to regional and
182 global seasonal and decade time-scale greening trends (Bhatt et al., 2010; Walker et al., 2012b;
183 Zeng and Jia, 2013). Parallel to reflectance NDVI measurements, we employed phenocams
184 (optical photography) at each site to calculate the “green excess” index (GEI) (Andresen et al.,
185 2018; Richardson et al., 2009) from peak season oblique images using the formula: $[2 * G - (R +$



186 B)] where G is the brightness value in the green, R is the brightness value in the red, and B is the
187 brightness value in the blue. For camera details and setup refer to Andresen *et al* (2018).

188 2.4 Statistical analysis

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

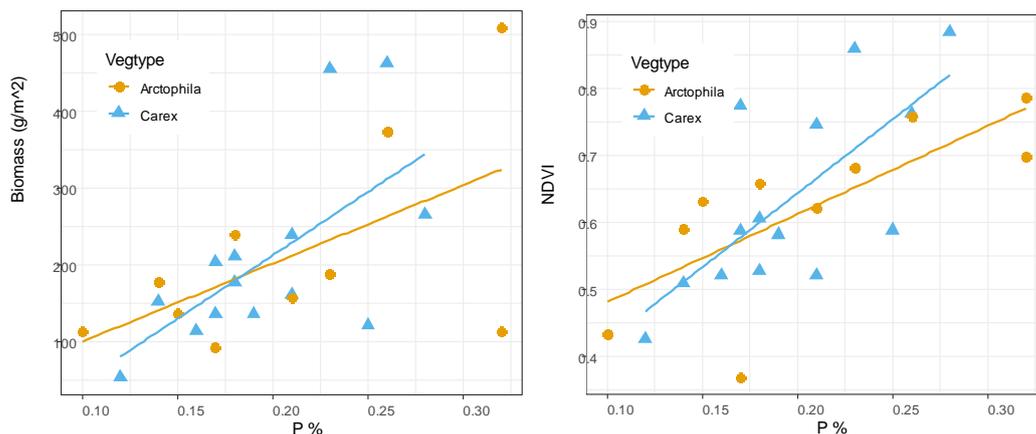
201 3. RESULTS

202 Examining the relationships between plant biomass and macronutrient (N, P) content of
203 the plant leaves and soil revealed that plant leaf phosphorus content was a primary determinant
204 of plant biomass, significantly explaining one-third of the variation in biomass for both species
205 (Figure 3). In addition, we found a positive linear relationship ($r = 0.7016$, $p < 0.01$) between leaf
206 phosphorus and NDVI (Figure 3). There were no significant relationships between plant biomass
207 and leaf nitrogen, nor between root nutrient content and soil nutrients. Among site types,
208 enriched sites (Urban and Thermokarst) have statistically higher soil, leaf and water nutrients
209 compared to reference sites ($p < 0.001$), no differences found for southern sites.

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

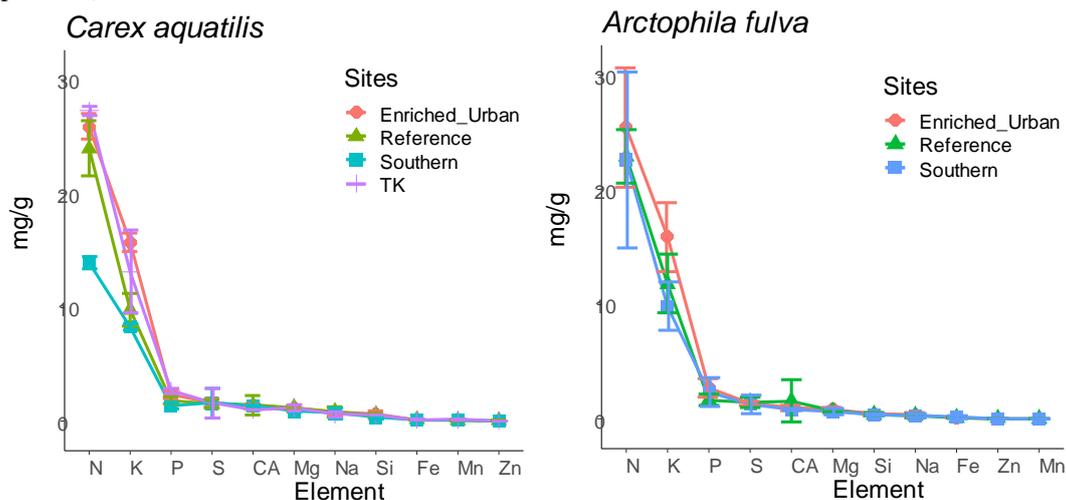
216 There were significant differences in green-up date and peak season Greenness Excess
217 Index (GEI) among species ($p < 0.01$, Table 1). *A. fulva* greened later (day 200 vs. 183) and had
218 lower GEI (9 vs. 33) as compared to *C. aquatilis*. These differences are associated to unique
219 phenotypic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

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223 Figure 3. Relationship between Phosphorus content (%) of leaves and dry weight aboveground
 224 biomass (left) and NDVI (right) for *Carex aquatilis* and *Arctophila fulva*. Biomass collected
 225 during peak growing season (first week of August). Each point represents site averages. *A. fulva*
 226 Biomass = $0.1401 + 0.0003228 * P\%$ ($R^2=0.32$, $p=0.06$). *C. aquatilis* Biomass = $0.1458 +$
 227 $0.0002451 * P\%$ ($R^2=0.40$, $p=0.01$). Both species Biomass = $0.1427 + 0.0002814 * P\%$ ($R^2=0.34$,
 228 $p=0.002$). *A. fulva* NDVI = $0.1401 + 0.0003228 * P\%$ ($R^2=0.55$, $p=0.01$). *C. aquatilis* NDVI =
 229 $0.04996 + 0.2305 * P\%$ ($R^2=0.47$, $p=0.004$). Both species NDVI = $0.01315 + 0.2984 * P\%$ ($R^2=0.47$,
 230 $p=0.002$).



231

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

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

Variable	<i>Arctophila fulva</i>		<i>Carex aquatilis</i>	
	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

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240 3.1 *Arctophila fulva*

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

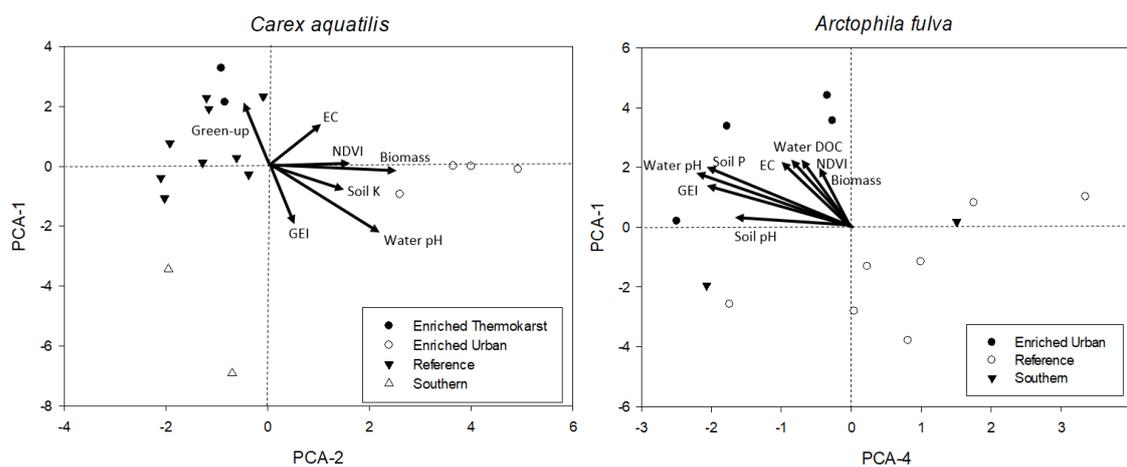
247 Site types for *A. fulva* were clearly separated along axes PCA-1 and PCA-4 (Figure 5).
 248 Enriched urban systems were located on the upper left quadrant, coinciding with higher
 249 concentrations of many leaf nutrients and environmental variables such as soil P, EC, water P,
 250 Si, DOC, plant biomass and higher green spectral indices (NDVI, GEI). Conversely, reference
 251 sites and those at southern latitude were located in the opposite quadrants of the plot with a wider
 252 distribution along PCA-4 and thus, wider variability in leaf nutrients and environmental
 253 conditions. Southern sites for *A. fulva* showed a similar distribution to reference sites (Figure 5).
 254



255 3.2 *Carex aquatilis*

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

261 The *C. aquatilis* PC plot of axes 1 and 2 also showed sites grouped by type (Figure 5).
262 We observed a good separation along PCA-2 of enriched urban ponds as compared to reference,
263 southern and enriched thermokarst. Similar to *A. fulva*, the enriched sites were found at the
264 positive end of an axis that was positively associated with water nutrients, alkalinity,
265 conductance, plant biomass, NDVI and soil K (Table 3). Environmental variables positively
266 associated with the vertical distribution of sites along axis 1 included soil EC, water nutrients
267 (TDP, SRP, NO₃), and negative correlations with water pH, alkalinity and *C. aquatilis* green-up
268 date (Table 2). We noticed grouping of enriched thermokarst and reference sites for *C. aquatilis*
269 in a portion of the plot associated with high electrical conductance and water TDP, SRP and
270 NO₃. Conversely to *A. fulva*, the southern sites were clustered away from other sites, in the lower
271 left quadrant, likely reflecting earlier green up, higher GEI, and lower soil and water nutrients.
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274 Figure 5. Plots of PCA site scores for *Arctophila fulva* (right) and *Carex aquatilis* (left) plant
275 nutrient data. Eigenvectors depict PCA axis correlations with environmental variables.
276 Eigenvectors are scaled for clarity.

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

<i>Carex aquatilis</i>						<i>Arctophila fulva</i>					
	Variance explained (%)	Axis <i>p</i> -value	Leaf Nutrient	<i>r</i>	<i>p</i> -value		Variance explained (%)	Axis <i>p</i> -value	Leaf Nutrient	<i>r</i>	<i>p</i> -value
PC axis 1	26	0.001	TN	0.84	0.000	PC axis 1	29	0.001	P	0.83	0.000
			Cu	0.72	0.001				Sr (log)	0.81	0.001
			Co (log)	0.66	0.019				K	0.80	0.001
			Na (log)	0.63	0.007				Al	0.76	0.003
			Mg	0.61	0.009				Mg	0.73	0.005
			Pb	0.58	0.016				B	0.71	0.007
			P	0.56	0.019				S	0.64	0.018
			Mo	0.54	0.024				Mn	0.63	0.021
			Zn	0.53	0.029				Ca (log)	0.53	0.061
			Al	-0.48	0.051				TN	0.50	0.079
			Ba (log)	-0.73	0.001				Pb	-0.54	0.057
			S	0.89	0.000				Fe (log)	-0.56	0.046
			K	0.85	0.000				Cr	0.86	0.000
			Sr (log)	0.74	0.001				As (log)	0.80	0.054
PC axis 2	24	0.001	Mn	0.65	0.004	PC axis 4	13	0.053	Zn	0.58	0.038
			Ba (log)	0.59	0.013				Ni	0.58	0.040
			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						

285

286 Table 3. PC axes correlations with environmental variables.

<i>Carex aquatilis</i>				<i>Arctophila fulva</i>					
	Environmental Variable	<i>r</i>	<i>p</i> -value		Environmental Variable	<i>r</i>	<i>p</i> -value		
PC axis 1	Green-up day	0.67	0.049	PC axis 1	Water Si	0.84	0.001		
	Water TDP (log)	0.56	0.020		Water SRP (log)	0.83	0.000		
	Water NO3 (log)	0.52	0.034		Water Sp. Conductance	0.80	0.003		
	EC (log)	0.47	0.069		Water TDP (log)	0.79	0.001		
	Water SRP (log)	0.44	0.076		Water Alkalinity	0.78	0.005		
	Water Alkalinity (log)	-0.61	0.020		NDVI	0.70	0.008		
	GEI	-0.62	0.078		Water DOC	0.69	0.019		
	Water pH	-0.70	0.004		Water TP (log)	0.67	0.012		
	PC axis 2	Water Sp. Conductance (log)	0.94		0.001	PC axis 4	EC (log)	0.66	0.027
		Water Alkalinity (log)	0.88		0.001		Soil P (log)	0.61	0.045
Biomass		0.84	0.001	Biomass (log)	0.59		0.034		
Water pH		0.73	0.002	Water pH	0.53		0.096		
Water Si (log)		0.58	0.018	Water pH	-0.68		0.021		
NDVI		0.56	0.071	GEI	-0.67		0.098		
Water SRP (log)		0.54	0.024	Soil P (log)	-0.67		0.025		
Water TDP (log)		0.53	0.029	Water Alkalinity	-0.62		0.044		
Soil K		0.50	0.050	Water Sp. Conductance	-0.59		0.057		
Water TP (log)		0.41	0.099	Soil pH	-0.53		0.075		



287 **4. DISCUSSION**

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

295 **4.1 Leaf nutrients**

296 The environmental gradient investigated in this study was highlighted by the principal
297 component analysis and allowed better understanding of the factors influencing leaf nutrients.
298 Our analysis shows how soil and water nutrients in ponds influence plant leaf nutrients and
299 aboveground biomass of aquatic tundra graminoids. The Arctic is typically nutrient limited in
300 inorganic forms of N and P in both soil (Beermann et al., 2015; Keuper et al., 2012; Mack et al.,
301 2004) and surface waters (Rautio et al., 2011). Arctic wet sedge in particular, has been noted to
302 be P limited given the highly organic soil which enhances recycling of N by mineralization of
303 soil organic matter (Beermann et al., 2015; Chapin et al., 1975). Primary productivity of
304 phytoplankton and periphyton in tundra ponds in the Utqiagvik area have been shown to be
305 largely NP co-limited (Lougheed et al., 2015). In line with other studies in moist and wet tundra,
306 aquatic *C. aquatilis* and *A. fulva* appear to be P limited (Beermann et al., 2015; Boelman et al.,
307 2003; Chapin et al., 1995; Mack et al., 2004) as observed by the significant relationship between
308 biomass and P leaf content (Figure 1). In fact, Lougheed et al (2015) suggested that macrophytes
309 may be outcompeting algae for available nitrogen, which may account for the N limitation of
310 algae but N sufficiency of plants. Soil nutrients were similar among cover types which may
311 explain the homogeneous leaf macronutrient concentrations among *C. aquatilis* and *A. fulva*.
312 However, we observed higher micronutrients and other non-essential minerals in *C. aquatilis*
313 compared to *A. fulva*. These disparities are likely attributed to differences in taxonomic groups
314 and thus, taxa-specific nutrient content (Chapin et al., 1975).

315 Compared to historical studies in the Utqiagvik area, we found that the major plant
316 macronutrients in *C. aquatilis* had increased since they were determined in 1970 by Chapin et al
317 (1975). N, P and Ca plant percentage content increased from 2.18 ± 0.09 to 2.4 ± 0.2 (10%
318 increase), 0.15 ± 0.02 to 0.18 ± 0.03 (20%), 0.08 ± 0.02 to 0.14 ± 0.08 (75%) respectively, for
319 samples collected in early August. However, K and Mg were lower compared to 1970. Increase
320 in leaf nutrients are concomitant with long-term observations of nutrient increases in tundra
321 ponds of nitrate, ammonia and soluble reactive phosphorus (Lougheed et al., 2011). Increased
322 plant nutrients may be a result of nutrient release from long-term increases of active layer depth
323 (Andresen and Lougheed, 2015), thawing permafrost (Keuper et al., 2012; Reyes and Lougheed,
324 2015) and nitrogen mineralization (Uhlířová et al., 2007; Weintraub and Schimel, 2003) leached
325 from terrestrial inputs. The remarkable increase in Ca observed between 1970 and 2013 is likely



326 associated to accumulation from high transpiration (Chapin, 1980) and suggests enhanced *C.*
327 *aquatilis* evapotranspiration rates compared to 50 years ago as a result of modern warmer
328 temperatures in both air and water (Andresen and Lougheed, 2015; Lougheed et al., 2011). It is
329 important to note that *C. aquatilis* has been shown to have phenotypical differences across
330 moisture gradients (Shaver et al. 1979). Thus, *C. aquatilis* sampled in wet meadows (Chapin et
331 al., 1975) might have different physiological characteristics, and therefore, different nutrient
332 tissue composition compared to *C. aquatilis* in aquatic habitats.

333 4.2 Nutrients, biomass, NDVI and GEI

334 NDVI of Arctic graminoid tundra has been noted to be a function of biomass caused by
335 increased nutrients (Andresen et al., 2018; Boelman et al., 2003, 2005; Epstein et al., 2012;
336 Reynolds et al., 2012). For example, Boelman et al. (2003) observed higher NDVI values in N
337 and P fertilized experimental treatments in wet sedge tundra communities compared to control
338 treatments. Also, Andresen et al (2018) noted higher NDVI and GEI greenness values
339 concomitant with higher biomass in enriched sites. Our study supports previous studies on the
340 importance of spectral measurements to be a function of environmental nutrient availability
341 through the enhancement of tundra biomass and leaf greenness at the plot level. In particular, this
342 study highlights phosphorus as the main nutrient augmenting aboveground biomass and plant
343 greenness in aquatic tundra. However, plot-scale spectral measurements such as NDVI and GEI
344 may differ from coarser remote sensing platforms given the spectral heterogeneity of the
345 radiance signal measured by the satellite sensor pixel (Guay et al., 2014) and caution should be
346 given to interpretations of NDVI with coarse imagery.

347 Increases in terrestrial productivity of the Arctic as inferred from coarse satellite NDVI
348 measurements have been directly attributed to increasing temperatures associated to sea ice
349 decline (Bhatt et al., 2010; Epstein et al., 2012). However, satellite based observations of tundra
350 change are complex (Myers-Smith et al., 2020) with differing trends of greening and browning
351 observed in recent decades (Pastick et al., 2019; Phoenix and Bjerke, 2016; Verbyla, 2008). At
352 the plot level, biological factors influencing spectral greenness signals include community
353 composition (Forbes et al., 2010) leaf area and phenology (Andresen et al., 2018; Post et al.,
354 2018). These factors are greatly influenced by nutrient environmental availability as shown in
355 this study and others (Andresen et al., 2018; Boelman et al., 2003). As permafrost degradation
356 and abrupt thaw events continue to increase in frequency (Andresen et al., 2020; Reyes and
357 Lougheed, 2015; Turetsky et al., 2020), it is imperative that we continue understanding plot-level
358 spectral signals and how they influence landscape-level satellite observations.

359 The wide range of environmental nutrient status and the broad spatial sampling
360 undertaken in this study provides a strong confidence on the use of spectral indices such as
361 NDVI to monitor environmental nutrient status at a regional scale. In particular, the strong
362 relationships between NDVI and phosphorous suggest that aquatic plant communities can be
363 used as hot-spots and/or hot moments indicators of nutrient availability and biochemical
364 landscape-scale processes. Hot-spots (disproportionately high reaction rates relative to the



365 surrounding landscape) and hot-moments (short periods of disproportionately high reaction rates
366 relative to longer time periods) are generally associated with rates and reactions of biochemical
367 processes (e.g. nutrient cycling, productivity) and often enhanced at the terrestrial-aquatic
368 interface where hydrological flow-paths mobilize substrates containing complimentary reactants
369 (e.g. nutrients) (McClain et al., 2003). Aquatic plant communities are situated at the terrestrial-
370 aquatic interface inside catch-points of small landscape drainages (e.g. ponds, low-center
371 polygons, ice wedge pits, etc) where biogeochemical changes such as mobilization processes
372 from permafrost degradation (hot-moment) and nutrient mineralization (hot-moment) can be
373 detected and mapped (hot-spot) with spatial detail over large areas.

374

375 5. Conclusion

376 This study highlights the influence and sensitivity of aquatic tundra plant communities to
377 environmental nutrient status. With projected increased warming and associated terrestrial
378 biogeochemical processes such as increased active layer depth and permafrost thaw, increased
379 nutrient availability and mineralization and enhanced ecosystem carbon dynamics, aquatic plants
380 will continue to be a hot-spot/hot-moment of change in structure and function as they sustain
381 encroachment of aquatic habitats that are increasing in nutrients with potential carbon and
382 surface energy feedbacks to climate. Characterizing mechanisms for detection and quantification
383 of biogeochemical responses to climate change employing remote sensing will continue to be
384 pivotal into understanding spatial and temporal evolution of the Arctic terrestrial and aquatic
385 systems and their interactions.

386

386 6. Appendix

387 Appendix 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/thermocarst	C	71.27496	-156.632653
TK3	Enriched/thermocarst	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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389
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401
402 **11. References**
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