

ARTICLE

Snow and vegetation seasonality influence seasonal trends of leaf nitrogen and biomass in Arctic tundra

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Abstract

Climate change, including both increasing temperatures and changing snow regimes, is progressing rapidly in the Arctic, leading to changes in plant phenology and in the seasonal patterns of plant properties, such as tissue nitrogen (N) content and community aboveground biomass. However, significant knowledge gaps remain over how these seasonal patterns vary among Arctic plant functional groups (i.e., shrubs, grasses, and forbs) and across large geographical areas. We used three years of in situ field vegetation sampling from an 80,000-km² area in Arctic Alaska, remotely sensed vegetation data (daily normalized difference vegetation index [NDVI]), and modeled output of snow-free date to determine and model the seasonal trends and primary controls on leaf percent nitrogen and biomass (in grams per square meter) among Arctic vegetation functional groups. We determined relative vegetation phenology stage at a 500-m spatial scale resolution, defined as the number of days between the date of the seasonal maximum NDVI and the vegetation field sampling date, and relative snow phenology stage (90-m spatial scale) was determined as the number of days between the date of snow-free ground and the sampling date. Models including relative phenology stage were particularly important for explaining seasonal variability of %N in shrubs, graminoids, and forbs. Similarly, vegetation and snow phenology stages were also important for modeling seasonal biomass of shrubs and graminoids; however, for all functional groups, the models explained only a small amount of seasonal variability in biomass. Relative phenology stage was a stronger predictor of %N and biomass than geographic position, indicating that localized controls on phenology, acting at spatial scales of 500 m and smaller, are critical to understanding %N and biomass.

KEYWORDS

Arctic, biomass, carbon, functional group, leaf nitrogen, NDVI, nitrogen, phenology, plant functional group, snow phenology, vegetation phenology

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INTRODUCTION

Climate changes, especially winter warming and spatially variable changes to winter snow amounts and timing, are occurring rapidly in the Arctic (Landrum & Holland, 2020; Serreze et al., 2009). These changes are advancing vegetation phenology (Myers-Smith et al., 2019; Park et al., 2016), increasing vegetation biomass and growth (Buchwal et al., 2020; Jenkins et al., 2020), and altering the seasonal dynamics of plant leaf nitrogen (N) concentration and biomass, that is, carbon (C) content (Box et al., 2019; Zhao et al., 2015). Quantifying the relationship between changing phenology and leaf N and biomass at fine to coarse geographic scales, and among different vegetation functional groups, is critical to predicting their response to local climate conditions. Such changes have important implications for local and regional carbon cycling and nutritional traits of forage for Arctic herbivores.

Plant N content is an important control on the productivity of Arctic plants, as demonstrated both by the stimulation of Arctic plant growth following N addition (Chapin et al., 1995; Chapin & Shaver, 1996; Koller et al., 2016), and by the tight correlation of total canopy N and leaf area throughout the Arctic (Williams & Rastetter, 1999). Leaf %N controls photosynthetic rates of vegetation because %N varies with the content of ribulose-1,5-bisphosphate carboxylase-oxygenase (RUBISCO), an N-dense protein involved in photosynthesis (Evans, 1989). The strong link between canopy N and leaf area indicates that N availability is a primary constraint on carbon assimilation rates, explaining up to 80% of the variation of gross primary production in Arctic plant communities across different plant species compositions (Shaver et al., 2007; Street et al., 2012). As such, understanding the spatial and temporal dynamics of leaf N in different vegetation functional groups of the Arctic is critical to understanding and anticipating future C exchange in these regions.

Seasonal patterns of leaf N and biomass in Arctic ecosystems differ by vegetation functional group (Chapin et al., 1980). Many deciduous shrub species exhibit a trend of declining leaf %N throughout the season (Lenart et al., 2002; Welker et al., 2005). Graminoid species have a similar trend with %N beginning to decline shortly after leaf emergence (Richert et al., 2021; Sедinger & Raveling, 1986). In contrast, evergreen dwarf shrub species maintain low %N throughout the summer (Arndal et al., 2009; Richert et al., 2021; Welker et al., 2005). Mosses exhibit a slight decline in %N throughout the growing season, although the patterns of nutrient movement within the plant vary greatly among species (Chapin et al., 1980). Lichen and forb %N remain largely

consistent throughout the growing season (Chapin et al., 1980; Lenart et al., 2002).

Vegetation functional groups also differ in the response of %N and biomass to local climate conditions, as demonstrated in numerous snow and temperature manipulation experiments throughout the Arctic. Greater snow accumulation increases leaf %N in deciduous shrubs (Richert et al., 2021; Sullivan & Welker, 2005), and the increase is sustained throughout the summer season (Leffler & Welker, 2013). Graminoids and dwarf shrubs also exhibit higher %N in response to deeper snow, although the response is less pronounced than that of deciduous shrubs (Blok et al., 2015; Richert et al., 2021). Increased snow and temperature together also increase leaf %N in deciduous shrubs, but warming alone decreases %N (Leffler et al., 2022; Weih & Karlsson, 2001; Zamin et al., 2017). Warming alone also decreases leaf %N in evergreen shrubs (Hansen et al., 2006; Michelsen et al., 1996).

Several studies suggest that the observed differences in leaf %N following warming or increased snow accumulation may be a result of climate-driven changes in plant phenology in the early growing season (Leffler et al., 2022; Richert et al., 2021). Plant phenology may also play a role in determining differences in %N among functional groups due to the distinct seasonal patterns of %N. Therefore, predicting spatial and temporal variation in vegetation leaf N and biomass, and their response to local climate conditions, requires understanding the relationship with local controls on phenology and the spatial scale over which these responses vary. However, currently, this understanding is limited by the relative lack of studies sampling Arctic vegetation %N throughout the growing season, particularly among multiple functional groups and across broad geographical areas, and the absence of work relating ground-based observations of leaf %N and biomass to phenology over large geographic regions. In response to these limitations, our work explicitly pursues the following objectives:

1. Determine seasonal trends in leaf %N and biomass among Arctic vegetation functional groups by sampling a broad geographical region ($>80,000 \text{ km}^2$) in Arctic Alaska.
2. Establish and compare the primary predictors of seasonal trends in leaf %N and biomass among Arctic vegetation functional groups.
3. Model the seasonal variation in field measurements of %N and biomass of distinct Arctic vegetation functional groups from relative vegetation and snow phenology stages and other environmental variables.

Our results are critical to aid in projecting spatial and temporal vegetation response to climate change.

MATERIALS AND METHODS

Study area

This work took place in central Arctic Alaska, between the crest of the Brooks Range to the south and the Beaufort Sea to the north (Figure 1). The region is characterized by a polar climate and is underlain by permafrost. The southern-most portion of this region is in the Brooks Range at an elevation of ~1000 m and is characterized by sparse and dwarf shrub vegetation, including *Eriophorum angustifolium*, *Salix pulchra*, *Dryas* spp., *Betula nana*, *Rhododendron lapponicum*, and *Vaccinium uliginosum*. In the Brooks Range foothills, the elevation is ~650 m, and the vegetation consists primarily of tussock shrub tundra, including *E. vaginatum*, *B. nana*, *S. pulchra*, *V. vitis-idaea*, and *V. uliginosum*. Farther north, the surface elevation drops to ~100 m, and the vegetation is tussock tundra, including *E. vaginatum*, *B. nana*, *S. pulchra*, *V. vitis-idaea*, and *V. uliginosum*. On the coastal plain adjacent to the Beaufort Sea, the elevation drops to ~15 m, and

the landscape is characterized by wet sedge vegetation, including *Carex aquatilis* and *E. angustifolium*.

The study took place over three years: 2017–2019; these three years differed in precipitation and temperature. Annual precipitation was 388, 525, and 445 mm in 2017, 2018, and 2019, respectively, measured at Toolik Field Station (68.62° N, 148.59° W) in the southern portion of the study region (EDC, 2022). Mean annual temperature at the same location (air temperature at 3 m) was −6.8, −7.1, and −5.8°C in 2017, 2018, and 2019, respectively (EDC, 2022). The summer temperature, in particular, was lower in 2018 than in 2017 or 2019 (June mean temperature was 4.9°C in 2018, and 8.0 and 8.2°C in 2017 and 2019, respectively) (EDC, 2022).

Field vegetation sampling

We sampled 71 points, each consisting of three 1-m² plots within a 25-m² area, at three times during the growing

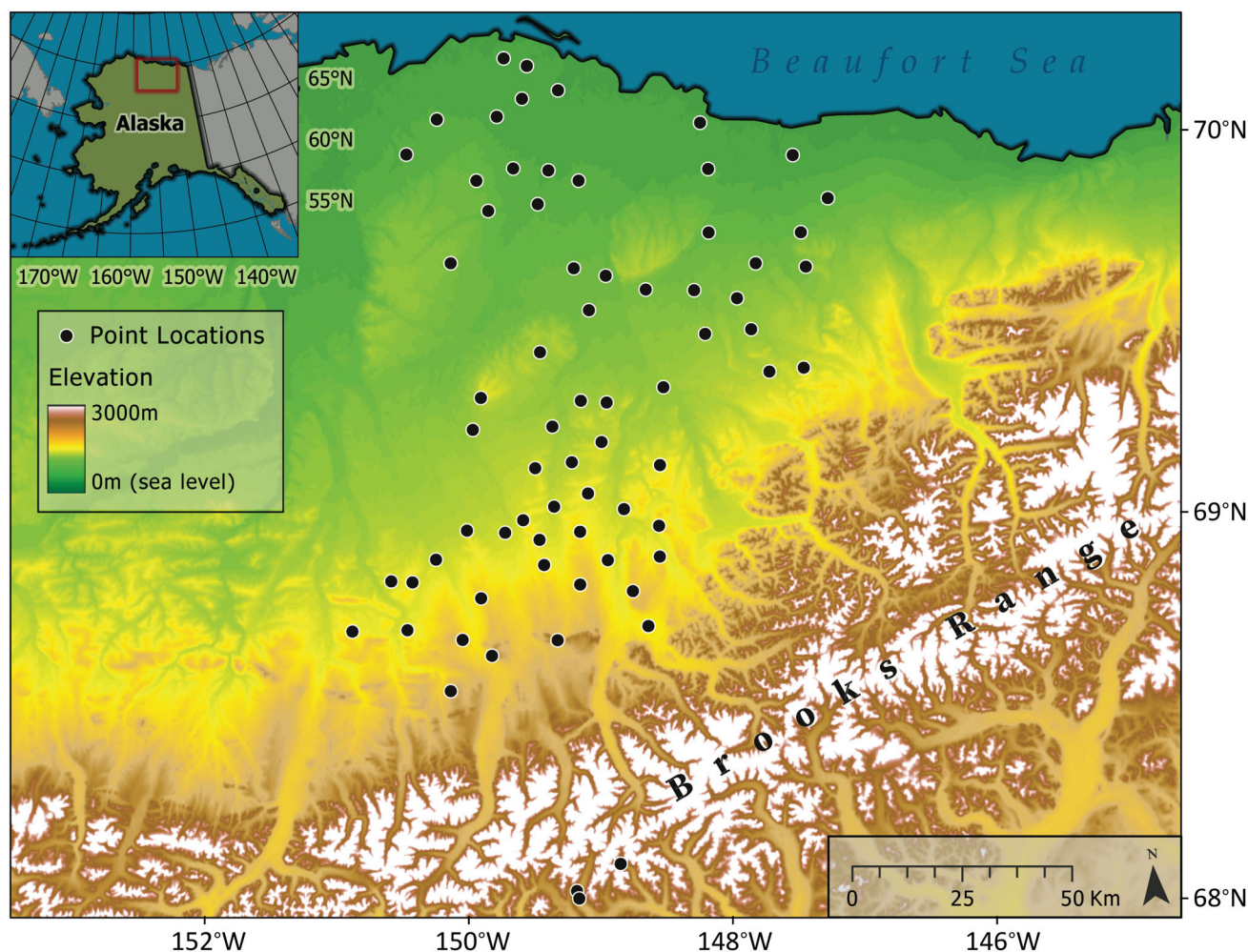


FIGURE 1 Map of the study region. Black dots indicate the location of the study points within Arctic Alaska. Colored shading represents elevation in meters above sea level.

season for three years (2017–2019). Approximately one-third of these points were sampled each year, for a total of 183 location–date combinations over our 80,000-km² study area. The sample periods were approximately 10–20 June, 14–23 July, and 16–27 September, designed to target the early, peak, and late growing seasons. To determine total biomass at each point at each sampling date, the three 1-m² plots were demarcated using a PVC frame with one plot located 5 m north of the point, one plot located 5 m southeast of the point, and one plot located 5 m southwest of the point. Within each plot, biomass of *Salix* and *Betula* species was determined by harvesting all biomass of these species above the ground surface within a box defined by “virtual planes” extending vertically from the plot edges. Biomass of all other species was determined by harvesting all plant material from three 0.2 × 0.2-m quadrats, also demarcated by PVC frames, located in a randomly chosen three of the four corners of the 1-m² frame, using the same technique. Mosses were sampled to a depth of 3 cm below moss surface. Samples were stored in clean paper bags for transport back to the lab for drying and sorting.

Community biomass and leaf N analyses

Vegetation samples were sorted to species. Green vegetation was separated from senesced vegetation, and leaves were separated from stems in all deciduous shrub samples. Following sorting, samples were dried in a 60°C oven for 48 h and weighed to the nearest 0.001 g to obtain biomass. Live biomass was summed by species and by plot. Final vegetation biomass data are reported by functional group (shrubs, dwarf shrubs, graminoid, forb, lichen, and bryophyte) and expressed in grams per square meter (Kelsey & Welker, 2022). Common species included in shrubs include *Salix* ssp., and *Betula nana*. All species in the shrub functional group are deciduous. Common species included in dwarf shrubs include *Andromeda polifolia*, *Arctostaphylos alpina*, *Cassiope tetragona*, *Dryas integrifolia*, *Empetrum nigrum*, *Rhododendron lapponicum*, *Rubus chamaemorus*, *Vaccinium uliginosum*, and *Vaccinium vitis-idaea*. The species of the dwarf shrub functional group are predominately evergreen.

Percent N was determined on the same tissue used for biomass measurement (only leaves for deciduous shrub species and green vegetation for graminoids). Following the recording of dry mass, vegetation was ground and homogenized to 1-mm particle size using a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA). A 2-g subsample was placed into a 2-mL micro-centrifuge tube with four 2.3-mm chrome steel beads and further ground for 2 min to a fine powder in a ball mill

(model 607, Mini-Beadbeater-16, Biospec Products, Bartlesville, OK, USA). The sample was further dried in the tube for 24 h in an oven at 100°C and stored in a desiccator. A microbalance was used to weigh 3.0–3.5 mg of sample into 5 × 9 mm tin capsules. Tissue %N was determined using a CHNSO elemental analyzer (model ECS 4010, Costech Analytical Technologies, Valencia, CA, USA) located at the University of Alaska-Anchorage (Kelsey & Welker, 2022).

Relative phenology stage and environmental data

Satellite measurements of normalized difference vegetation index (NDVI) (Rouse et al., 1973; Tucker, 1979) were obtained from the MODIS nadir BRDF-Adjusted Reflectance data product (MCD34A4 Collection 6). Daily NDVI values were obtained for the years of our study (2017–2019) at a spatial resolution of 500 m (Che et al., 2017) for each sampling location and date combination. Our analyses also used a metric of relative vegetation phenology stage, representing the number of days between the date of peak NDVI and our sample collection date. Peak of season (POS) for 2017–2019 was determined by creating a time series of daily NDVI for each pixel of the study region. A Savitzky–Golay filter (Savitzky & Golay, 1964) was used to remove noise from the time series. POS was determined as the date of the maximum seasonal NDVI value of the smoothed time series in each year. Our relative vegetation phenology stage metric was determined as the POS date minus the sampling date; a negative number indicates a sample collected before the peak, and a positive number indicates a sample collected after the peak. Relative vegetation phenological stage was determined individually for each vegetation sample at 500-m resolution.

Our analyses also used a metric of relative snow phenology stage, representing the number of days between when the ground became free of snow and the date of sampling. The snow-free date was determined for each pixel in our study region for the three years of our study at 90-m spatial resolution from outputs of snow depth produced by a suite of snow-distribution and snow-evolution modeling tools (SnowModel; Liston & Elder, 2006a) coupled with a meteorological model (MicroMet; Liston & Elder, 2006b). Descriptions of these SnowModel-simulation configurations and their validation with field snow observations are presented by Pedersen et al. (2021). The metric of relative snow phenology stage was determined for each of our vegetation sample date–location combinations by subtracting the snow-free day of year from the sampling day of year; a negative number indicates a sample collected before the

snow-free date, a positive number indicates a sample collected after all snow had melted. Relative snow phenological stage was determined individually for each sample-date combination at 500-m resolution.

Statistical analyses

We used linear mixed models to determine and compare the primary drivers of biomass and leaf %N and to characterize the seasonal trends in biomass and leaf %N among functional groups. We modeled the variation in biomass and leaf %N through the growing season as a function of relative vegetation and snow phenology stage, NDVI, as well as proximity to the Beaufort Sea, which is a seasonally ice-covered water body that affects the local climate on land. We used an all-subsets modeling approach that included NDVI, relative vegetation and snow phenology stages and their quadric terms, and distance to the coast (determined with ArcGIS spatial software) as fixed effects. Sample point was included as a random effect to account for repeated sampling throughout the seasons. To meet linearity assumptions, leaf %N and biomass values were transformed using natural logarithm or square root transformations when necessary. We used Akaike information criteria for small sample sizes (AIC_c ; Burnham & Anderson, 2002) to determine and compare the primary drivers of biomass and leaf N within each vegetation functional group. To understand the proportion of variation explained by these models, we calculated the marginal R^2 for all top models. We also determined model-averaged parameter estimates for all models with $\Delta AIC_c < 2$ to allow us to make formal inferences on the entire set of top models (Burnham & Anderson, 2002). All models were analyzed using the nlme package (Pinheiro et al., 2022) in the program R version 4.0.2 (R Core Team, 2021). Model-averaged parameter estimates and marginal R^2 values were calculated using the MuMIn package (Bartoń, 2014).

RESULTS

Seasonal mean %N varied among functional groups (Table 1). Forbs, shrub leaves, and graminoid live tissue had the highest mean %N (1.66 ± 0.77 , 1.4 ± 0.91 , and 1.18 ± 0.56 , respectively; mean \pm SD). The mean %N for dwarf shrubs, lichen, and bryophyte was lower (0.94 ± 0.35 , 0.76 ± 0.69 , and 0.84 ± 0.20 , respectively). Biomass also varied among functional groups, with bryophytes having the highest ($207.0 \pm 187.74 \text{ g m}^{-2}$) and forbs having the lowest ($4.86 \pm 10.81 \text{ g m}^{-2}$; Table 1). Shrub and graminoid biomass, here only the live leaves of each, were

TABLE 1 Differences in seasonal mean tissue N concentrations and biomass among functional groups.

Functional group	%N		Biomass (g m^{-2})	
	Mean	SD	Mean	SD
Shrub ^a	1.40	0.91	17.33	42.88
Graminoid ^a	1.18	0.56	72.85	85.55
Dwarf shrub	0.94	0.35	27.67	32.90
Forb	1.66	0.77	4.86	10.81
Lichen	0.76	0.69	15.05	25.05
Bryophyte	0.84	0.20	207.00	187.74

^aShrub and graminoid tissues analyzed included only live leaves.

$17.33 \pm 42.88 \text{ g m}^{-2}$ and $72.85 \pm 85.55 \text{ g m}^{-2}$, respectively. The median value for relative vegetation phenology stage was -15 (indicating 15 days before peak greenness; range: -71 to 67), the median NDVI value on the dates of vegetation sampling was 0.55 (range: 0 – 0.75), the median value for relative snow phenology stage was 51 (range: -3 to 129), and the median distance to coast was 120.2 km (range: 4.0 – 255.1 km).

Seasonal patterns in leaf %N and biomass varied among vegetation functional groups. The most pronounced differences among functional groups were observed in the seasonal trends of leaf %N. Shrub leaf %N was highest at the very beginning of the season and decreased thereafter (Figure 2). In contrast, graminoid leaf %N peaked around the middle of the growing season, coincident with maximum NDVI (i.e., when the relative vegetation phenology stage metric = 0). Lichen and dwarf shrub leaf %N remained relatively low throughout the growing season with little seasonal variation. Both forb and bryophyte leaf %N peak in the middle of the growing season, similar to the pattern observed in graminoids (Figure 2).

Seasonal patterns in biomass also varied among functional groups but differed from seasonal patterns of leaf %N. Shrubs and graminoids both displayed trends of biomass peaking coincident with the maximum seasonal NDVI, and this trend was more pronounced in graminoids than in shrubs (Figure 3). Dwarf shrub, forb, and lichen biomass remained constant throughout the growing season, whereas bryophyte biomass increased consistently throughout the growing season (Figure 3).

We developed models of leaf %N and biomass throughout the growing season for each vegetation functional group based on relative vegetation phenology stage, relative snow phenology stage, NDVI, and distance to coast. Relative vegetation or snow phenology stage, either its linear or quadratic term, appeared in the top models of leaf %N of every functional group except dwarf shrubs (Table 2). Relative snow phenology stage was

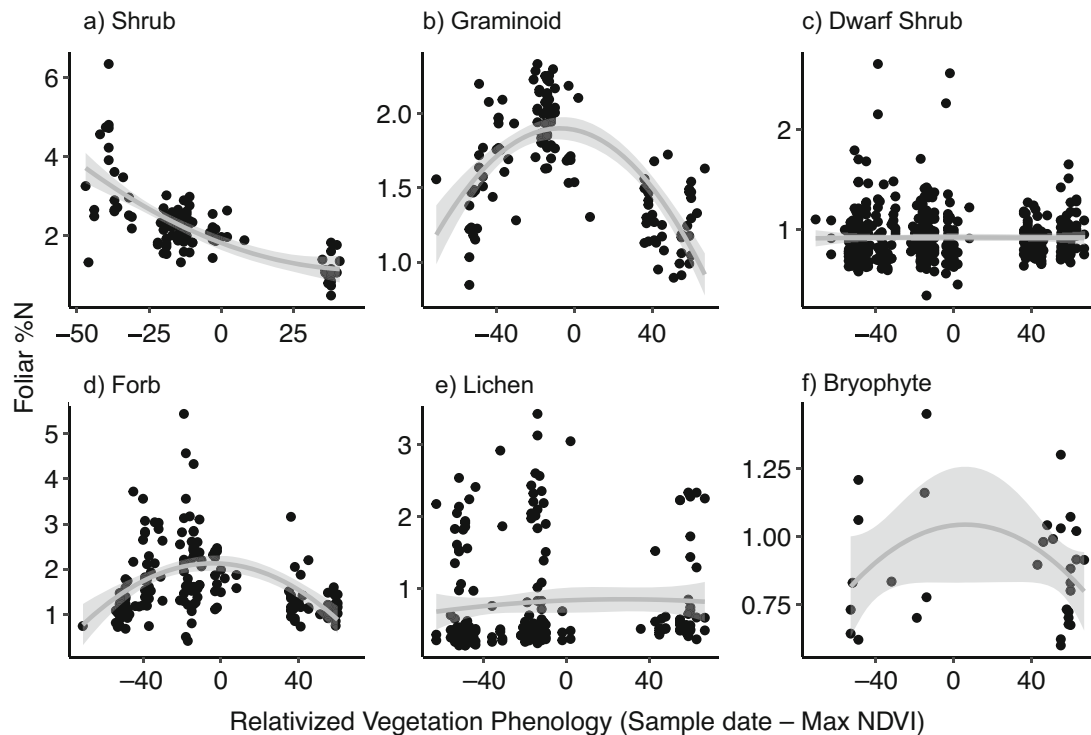


FIGURE 2 Association between leaf N concentration and relative vegetation phenology for (a) shrub ($n = 122$), (b) graminoid ($n = 133$), (c) dwarf shrub ($n = 536$), (d) forb ($n = 173$), (e) lichen ($n = 237$), and (f) bryophyte ($n = 35$) functional groups. Shading represents 95% confidence intervals. NDVI, normalized difference vegetation index.

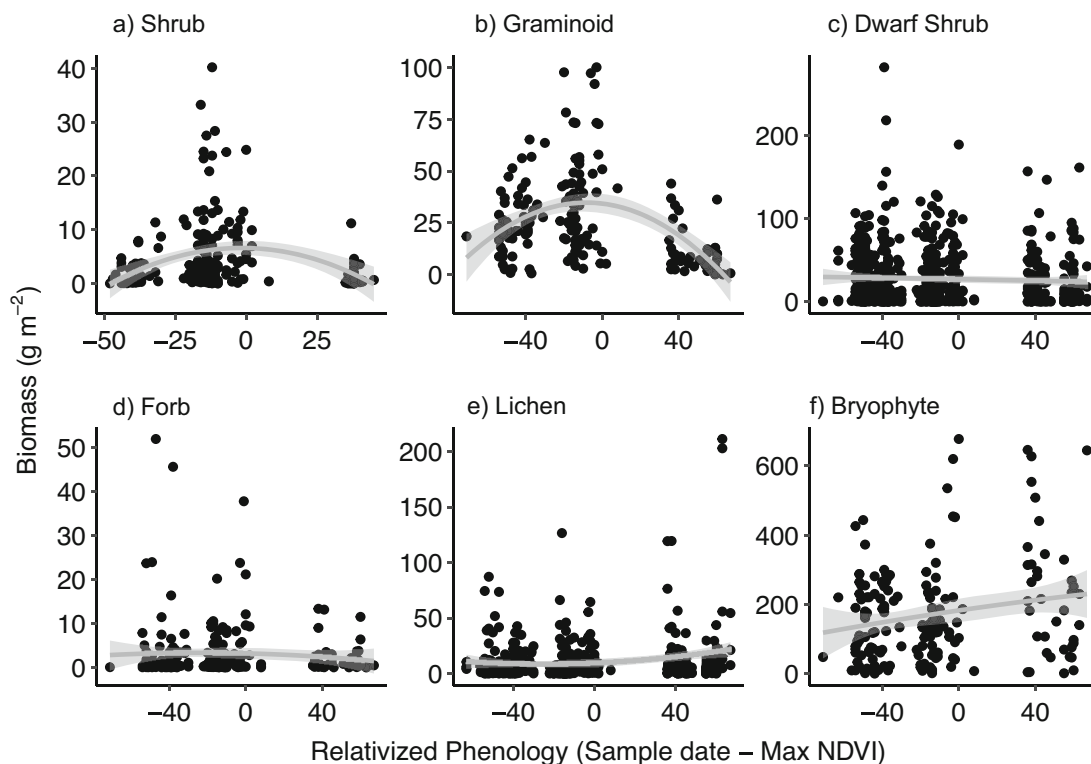


FIGURE 3 Association between biomass and relative vegetation phenology for (a) shrub ($n = 188$), (b) graminoid ($n = 163$), (c) dwarf shrub ($n = 637$), (d) forb ($n = 241$), (e) lichen ($n = 397$), and (f) bryophyte ($n = 180$) functional groups. Shading represents 95% confidence intervals. NDVI, normalized difference vegetation index.

TABLE 2 Best performing models ($\Delta AIC < 2$) of foliar %N by functional group.

Model	AIC _c	ΔAIC_c	Weight	Marginal R^2
Shrub				
Snow phenology ² + veg. phenology	32.0	0.00	0.05	0.53
Veg. phenology + veg. phenology ²	32.1	0.06	0.05	0.53
Veg. phenology	32.64	0.60	0.04	0.52
Snow phenology ²	33.11	1.06	0.03	0.52
Veg. phenology + NDVI + NDVI ²	33.4	1.35	0.03	0.53
Veg. phenology + veg. phenology ² + NDVI	33.57	1.53	0.03	0.53
Veg. phenology + veg. phenology ² + NDVI ²	33.85	1.81	0.02	0.53
Snow phenology ² + coast + veg. phenology	33.85	1.81	0.02	0.53
Veg. phenology + veg. phenology ² + NDVI + NDVI ²	33.93	1.88	0.02	0.54
Snow phenology ² + veg. phenology + veg. phenology ²	33.97	1.92	0.02	0.53
Dist to coast + veg. phenology + veg. phenology ²	34.02	1.97	0.02	0.53
Snow phenology + snow phenology ² + rel. phen.	34.03	1.99	0.02	0.53
Snow phenology + veg. phenology + veg. phenology ²	34.03	1.99	0.02	0.53
Graminoid				
Snow phenology + snow phenology ² + veg. phenology + veg. phenology ²	24.66	0.00	0.15	0.54
Snow phenology + snow phenology ² + veg. phenology	26.07	1.41	0.07	0.53
Snow phenology + veg. phenology + veg. phenology ²	26.39	1.73	0.06	0.53
Dwarf shrub				
Coast	−667.97	0.00	0.13	0.07
Coast + veg. phenology ²	−665.99	1.97	0.05	0.07
Snow phenology + coast	−665.97	1.99	0.05	0.07
Forb				
Snow phenology + veg. phenology ²	149.08	0.00	0.08	0.20
Snow phenology ² + veg. phenology ²	149.44	0.35	0.07	0.20
Veg. phenology + veg. phenology ²	149.45	0.37	0.07	0.20
Snow phenology + coast + veg. phenology ²	150.53	1.44	0.04	0.21
Snow phenology ² + coast + veg. phenology ²	150.82	1.73	0.03	0.21
Coast + veg. phenology + veg. phenology ²	150.82	1.74	0.03	0.21
Snow phenology + snow phenology ² + veg. phenology ²	150.84	1.76	0.03	0.21
Veg. phenology ²	151.05	1.97	0.03	0.18
Lichen				
Veg. phenology ² + NDVI + NDVI ²	392.61	0.00	0.14	0.10
Snow phenology ² + veg. phenology ² + NDVI + NDVI ²	393.51	0.90	0.09	0.11
Veg. phenology + veg. phenology ² + NDVI + NDVI ²	393.55	0.94	0.08	0.11
Snow phenology + veg. phenology ² + NDVI + NDVI ²	393.56	0.95	0.08	0.11
Bryophyte				
Snow phenology ² + NDVI ²	−8.51	0.00	0.11	0.18
Snow phenology + NDVI ²	−8.20	0.31	0.09	0.16
Veg. phenology + NDVI ²	−8.05	0.46	0.09	0.16
Veg. phenology ² + NDVI + NDVI ²	−6.56	1.96	0.04	0.18

Abbreviations: AIC, Akaike information criterion; NDVI, normalized difference vegetation index; rel. phen., relative phenology; veg. phenology, vegetation phenology.

included in the top models of shrubs, graminoids, forbs, and bryophytes, and relative vegetation phenology stage was included in the top models of shrubs, graminoids, forbs, and lichen. NDVI or NDVI² is present in the top models of %N of lichen and bryophytes. The top model of %N of dwarf shrubs includes only the distance from the coast. The proportion of variation explained by the fixed effects in the top models of shrubs and graminoids was 0.53 and 0.54, respectively, and was lower for dwarf shrubs, forbs, lichen, and bryophytes (0.07, 0.20, 0.10, and 0.18, respectively; Table 2).

The top models of biomass included relative phenology stage of snow or vegetation in all vegetation functional groups except dwarf shrubs and forbs. Relative snow phenology stage (either standard or quadratic form) appeared in the top models of shrubs and lichen, and relative vegetation phenology stage appeared in the top models of shrubs, graminoids, lichen, and bryophytes (Table 3). The top model for forbs included only NDVI², and the top model for dwarf shrubs was the null model. The proportion of variation explained by the fixed effects in the top models of biomass was much lower than that of foliar %N. Like for the models of foliar %N, the proportion of variation explained was highest in the models of shrubs and graminoids (0.27 and 0.21, respectively), and lower for dwarf shrubs, forbs, lichen, and bryophytes (0, 0.06, 0.10, and 0.16, respectively; Table 3).

Based on model-averaged estimates, foliar %N of shrubs predicted by relative vegetation phenology stage declined through the growing season, while forb %N peaked mid-season and lichen and bryophyte %N remained consistently low through the season (Figure 4; Appendix S1: Table S1). Graminoid foliar %N predicted by snow phenology peaked mid-season, and dwarf shrub %N declined with greater distance from the coast (lower in the southern and more mountainous portion of the study area). Model-average estimates of the seasonal patterns of biomass differed from seasonal patterns of leaf %N. Shrub biomass predicted by relative vegetation phenology stage increased throughout the growing season, graminoid biomass peaked mid-season, and bryophyte biomass primarily increased in the latter portion of the growing season (following peak NDVI; Figure 5; Appendix S1: Table S2). Forb biomass increased with greater NDVI, and lichen biomass increased with greater distance from the coast. Dwarf shrub biomass was predicted best by the null model.

DISCUSSION

We found that relative vegetation and snow phenology stage predicted seasonal patterns of leaf %N, particularly in graminoid and shrub functional groups, although the most

important predictors of leaf %N varied by functional group. For all groups except for dwarf shrubs, both vegetation and snow phenology were included in the top models of seasonal foliar %N. Models with relative phenology stage were particularly good for explaining seasonal variability of %N in shrubs, graminoids, and forbs. Similarly, both vegetation and snow phenology were also included in the top models of seasonal biomass for shrubs and graminoids; however, only a small amount of variability in biomass was explained by the models for all groups. Overall, phenology and environmental variables predicted foliar %N more strongly than biomass in all functional groups. Relative phenology stage calculated at the 500-m scale was a stronger predictor than broad geographic position (distance from coast) for both %N and biomass, indicating that local snow and environmental conditions controlling phenology are critical to understanding %N, biomass, and local C cycling.

Plant tissue %N observed in our study is similar to, but generally slightly lower than, that observed in other regions of the Arctic. For deciduous shrubs, dwarf shrubs, and graminoids, our observations of mean tissue %N were slightly lower than those observed at Toolik Lake, Alaska, in moist and dry tundra species (Leffler et al., 2016; Richert et al., 2021; Welker et al., 2005) and shrubs and graminoids of northeast Alaska (Walsh et al., 1997). Shrub leaf %N was also lower than *Salix arctica* in NW Greenland (Leffler & Welker, 2013) and lower than *Betula glandulosa* in the Canadian low Arctic (Zamin et al., 2017). The difference may be in part because our samples were collected over a large area and over the course of the entire growing season, and consequently, our mean observations include a wider range of %N values. Our observations of shrub and dwarf shrub %N were comparable to those observed in subarctic Swedish Lapland (Hansen et al., 2006), and dwarf shrub tissue %N in our study was slightly higher than that observed at a Swedish subarctic site (Michelsen et al., 1996). Our biomass observations were similar to other observations from Arctic Alaska (Shaver & Chapin, 1991) and particularly consistent with other low Arctic sites with relatively warmer summers (Epstein et al., 2008).

Each functional group displayed distinct seasonal patterns of leaf %N and biomass, particularly when observed against relative vegetation phenology stage, with the strongest patterns evident in deciduous shrubs and graminoids. Maximum %N for shrubs occurred nearly two months before peak vegetation productivity and then declined exponentially (Figure 2), consistent with the physiology of Arctic deciduous shrubs and in accordance with Körner's postulate of leaf %N investment and C dilution during growth in tundra plants (Körner, 2003). Directly following snowmelt, shrubs transfer N from stems and large roots to leaves, yielding high foliar %N in the early season (Chapin

TABLE 3 Best performing models ($\Delta AIC < 2$) of biomass by functional group.

Model	AIC _c	ΔAIC_c	Weight	Marginal R^2
Shrub				
Snow phenology ² + coast + veg. phenology + NDVI	735.77	0.00	0.10	0.27
Snow phenology ² + coast + veg. phenology + NDVI ²	737.14	1.38	0.05	0.26
Snow phenology ² + coast + veg. phenology + NDVI + NDVI ²	737.43	1.66	0.04	0.27
Graminoid				
Veg. phenology + veg. phenology ² + NDVI	592.05	0.00	0.09	0.21
Snow phenology ² + veg. phenology ² + NDVI	592.58	0.53	0.07	0.20
Snow phenology + veg. phenology ² + NDVI	592.86	0.81	0.06	0.20
Veg. phenology + veg. phenology ² + NDVI ²	593.44	1.39	0.04	0.21
Coast + veg. phenology + veg. phenology ² + NDVI	593.84	1.78	0.04	0.21
Snow phenology + veg. phenology + veg. phenology ² + NDVI	593.86	1.80	0.04	0.21
Dwarf shrub				
Null model	2311.09	0.00	0.07	0
Snow phenology + veg. phenology	2312.65	1.56	0.03	0.01
Snow phenology	2312.65	1.56	0.03	0.001
Snow phenology ²	2312.67	1.59	0.03	0.001
Coast	2312.94	1.86	0.03	0.001
NDVI ²	2312.96	1.87	0.03	0.001
Veg. phenology	2312.97	1.88	0.03	0.000
Veg. phenology ²	2313.00	1.91	0.03	0.000
NDVI	2313.01	1.92	0.03	0.000
Forb				
NDVI ²	846.26	0.00	0.09	0.06
Coast + NDVI ²	847.74	1.48	0.04	0.07
Snow phenology ² + NDVI ²	847.79	1.53	0.04	0.06
Veg. phenology + NDVI ²	847.83	1.57	0.04	0.06
Snow phenology + NDVI ²	847.91	1.65	0.04	0.06
NDVI + NDVI ²	848.00	1.74	0.04	0.06
Lichen				
Snow phenology + coast + veg. phenology + veg. phenology ²	1433.87	0.00	0.08	0.10
Coast + veg. phenology ²	1434.04	0.16	0.08	0.09
Snow phenology + snow phenology ² + coast + veg. phenology	1434.51	0.64	0.06	0.10
Snow phenology + coast + veg. phenology + veg. phenology ² + NDVI ²	1435.46	1.59	0.04	0.11
Snow phenology + snow phenology ² + coast	1435.49	1.62	0.04	0.09
Snow phenology + coast + veg. phenology + veg. phenology ² + NDVI ²	1435.56	1.69	0.03	0.11
Coast + veg. phenology + veg. phenology ²	1435.64	1.77	0.03	0.09
Coast + veg. phenology ² + NDVI ²	1435.84	1.97	0.03	0.09
Bryophyte				
Coast + veg. phenology + veg. phenology ² + NDVI	984.25	0.00	0.08	0.16
Snow phenology ² + coast + veg. phenology ² + NDVI	984.65	0.39	0.07	0.16
Snow phenology + coast + veg. phenology ² + NDVI	985.02	0.76	0.06	0.16
Snow phenology + coast + veg. phenology + veg. phenology ² + NDVI	985.48	1.23	0.04	0.17
Coast + veg. phenology + veg. phenology ² + NDVI ²	985.68	1.42	0.04	0.17
Snow phenology ² + coast + veg. phenology ² + NDVI ²	986.17	1.92	0.03	0.16

Abbreviations: AIC, Akaike information criterion; NDVI, normalized difference vegetation index; veg. phenology, vegetation phenology.

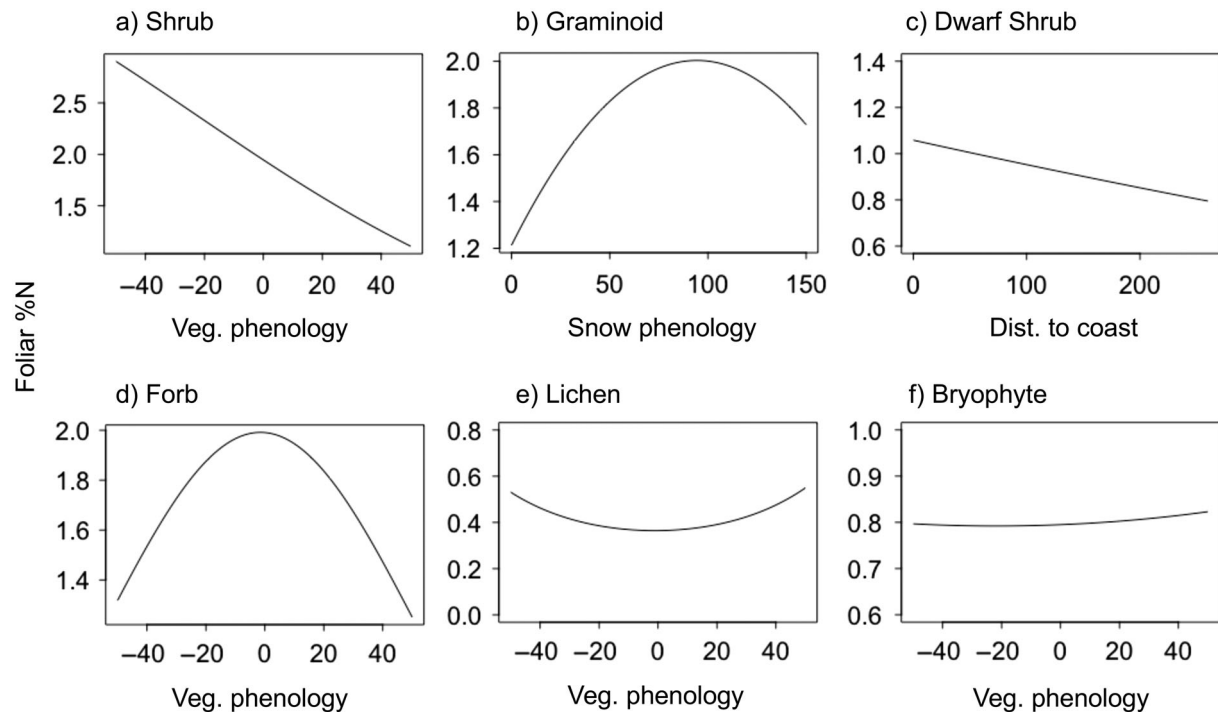


FIGURE 4 Model-averaged effects of the association between leaf N concentration and the strongest predictor for each functional group: (a) shrub, (b) graminoid, (c) dwarf shrub, (d) forb, (e) lichen, and (f) bryophyte functional groups. Dist. to coast, distance to coast; snow phenology, relative snow phenology stage; veg. phenology, relative vegetation phenology stage.

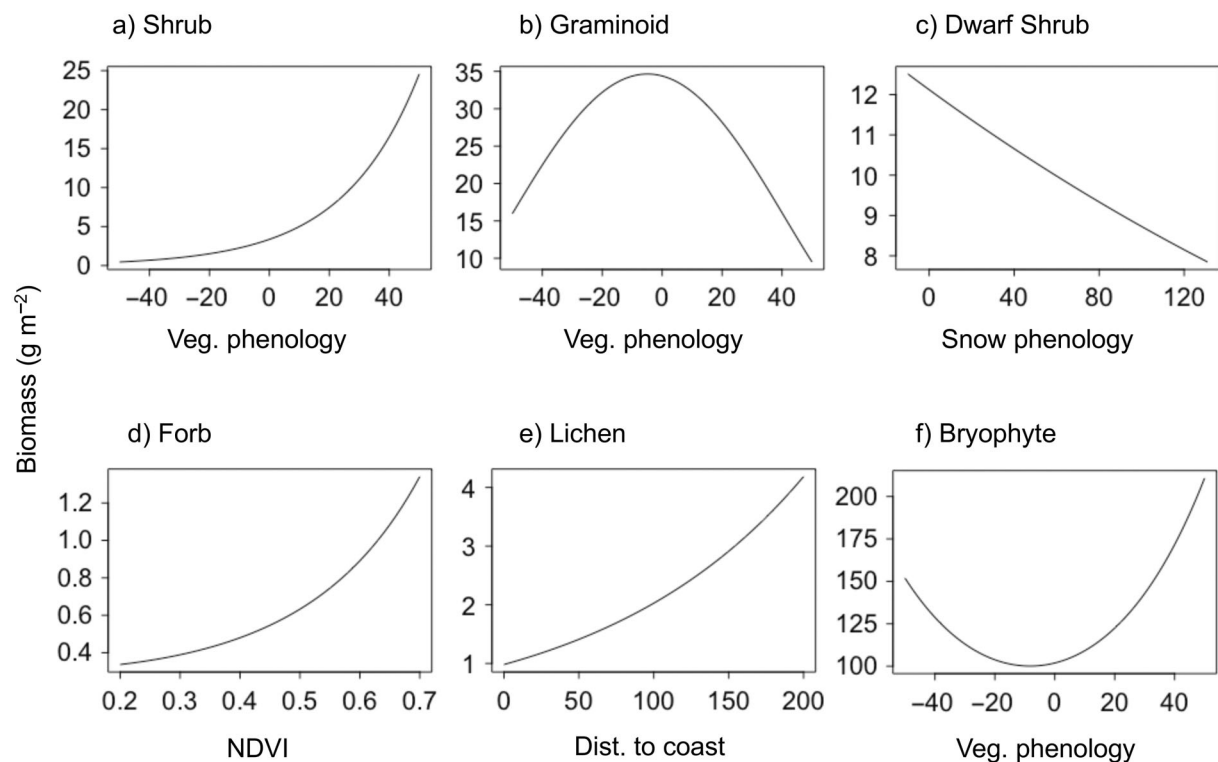


FIGURE 5 Model-averaged effects of the association between biomass and the strongest predictor for each functional group: (a) shrub, (b) graminoid, (c) dwarf shrub, (d) forb, (e) lichen and (f) bryophyte functional groups. Dist. to coast, distance to coast; NDVI, normalized difference vegetation index; snow phenology, relative snow phenology stage; veg. phenology, relative vegetation phenology stage.

et al., 1980). Leaf %N then declines through time due to the dilution of the growing tissue with structural carbohydrates (Greenwood et al., 1990), and during senescence, N is transferred back to stems and roots, a key nutrient use efficiency strategy for tundra plants (Aerts & Chapin, 1999). In contrast, evergreen dwarf shrubs maintained low leaf %N content through all phenological stages, consistent with a gradual translocation of N to leaves throughout the growing season (Chapin et al., 1980). The trend we observed of increasing %N in graminoids in the first part of the growing season and a decline before peak productivity is also like trends observed elsewhere (Sedinger & Raveling, 1986). Consistent with these observations, peak %N in graminoids in northern Alaska occurred when NDVI was approximately 50% of its seasonal maximum (Hogrefe et al., 2017). Lichens and bryophytes also maintained relatively low leaf N throughout the growing season, which is typical for these functional groups (Chapin & Shaver, 1989). Mosses often have low N use efficiency (Turetsky et al., 2012), although in some species the upper green portion of the tissue has higher N concentrations than the brown portion (Pakarinen & Vitt, 1974), indicating some seasonal movement of N between photosynthesizing versus supporting tissue (Chapin et al., 1980).

Relative vegetation and snow phenology stage were among the most important determinants of tissue %N in every functional group examined, except dwarf shrubs. The importance of relative vegetation phenology stage in predicting plant seasonal N dynamics is an intuitive result of the seasonal translocation of N among different parts of a plant and its sensitivity to interannual variations in plant phenology (in contrast to a predictor, such as day of year). The utility of relative vegetation phenology stage for predicting plant nutritional dynamics in Northern Alaska has previously been highlighted by Johnson et al. (2018), who found this metric useful for modeling the spatial and temporal variability in caribou forage quality through the growing season. Our results specifically identify the importance of early-season phenology as a control on seasonal patterns of vegetation %N, which vary strongly among Arctic vegetation functional groups. End-of-season phenology of Arctic vegetation, while not explored in this study, is also responsive to climate conditions (Kelsey et al., 2021) and may have significant consequences to Arctic ecosystems, particularly nutrient content and biomass. Our results indicate that local-scale (500 m) variation in phenology is more predictive than the broad geographic-scale (10–100 km) proxies, such as distance from the coast. This result emphasizes the importance of local conditions on phenology (Borner et al., 2008) and therefore on the critical plant properties of %N, biomass, and C cycling.

Relative snow phenology is important to Arctic plant tissue %N because of the multitude of environmental

changes plants experience during and after snowmelt. The timing of snowmelt controls the timing of warming and a plant's access to direct sunlight, while water released from melting snow drives nutrient availability and soil moisture during the growing season (Jespersen et al., 2018). Both the timing of snowmelt and the amount of water present in the snowpack are known to influence the timing of vegetation phenological events (Assmann et al., 2019; Grippa et al., 2005; Pedersen et al., 2018; Zeng & Jia, 2013). The relative snow phenology stage metric is also likely important in predicting tissue %N because of the important role that snow plays in facilitating soil microbial activity during winter months by insulating soil from low temperatures (Bilbrough et al., 2000; Elberling, 2007; Schimel et al., 2004) and the subsequent effects on vegetation phenology and biomass (Kelsey et al., 2021). Because snow modeling tools and remote sensing data sets can generate information on snow-free dates throughout the Arctic, even for regions that are typically logistically difficult to sample, relative snow phenology stage may be an important avenue for understanding and anticipating plant seasonal N dynamics in this and other Arctic environments. Further, relative snow phenology stage offers an advantage over the use of relative vegetation phenology stage based on NDVI, as the latter can only be modeled after the growing season when the timing of the seasonal NDVI peak has been established.

Climate and phenology of the Arctic are changing. Air temperatures are increasing, particularly in the winter (Box et al., 2019; Gulev et al., 2021; Walsh et al., 2011), and in some regions, snow accumulation may also be increasing (Khani et al., 2022; Stuefer et al., 2020; Thackeray et al., 2019). Advancing Arctic plant phenology in response to these changes has been observed in both in situ investigations and remotely sensed observations (Ju & Masek, 2016; Myers-Smith et al., 2019). Current phenology of northern ecosystems is such that the date of peak photosynthetic activity occurs after the summer solstice (date of maximum insolation), suggesting that advancing phenology could improve the alignment of plant phenology with the conditions for maximum C uptake. Indeed, advancing dates of peak photosynthetic activity are already associated with increased primary productivity in the northern hemisphere (Gonsamo et al., 2018; Park et al., 2019). Our results add a deeper understanding to this result, indicating that productivity responses to phenological change are likely dependent on local conditions as local phenology is a stronger predictor of critical plant properties than large-scale geographic position (distance to the coast), which determines variation at the 10–100 km scale.

Further, our results suggest that changes in vegetation productivity in response to shifting seasonal patterns of %N also vary among vegetation functional groups. Defoliart et al. (1988) found that in the Arctic sedge

Eriophorum vaginatum, maximum photosynthetic rates followed a similar pattern to %N, which peaks after the summer solstice. In this case, our results suggest that advancing phenology has the potential to increase C uptake by improving the alignment of maximum %N with the date of greatest insolation. In contrast, no consistent relationship between %N and photosynthesis or primary productivity was observed by Chapin and Shaver (1996) in several Arctic graminoid, deciduous shrub, and evergreen shrub species in response to manipulations of temperature, snow, and light. Leffler and Welker (2013) found that snow addition changed the magnitude, but not the timing, of maximum %N and maximum photosynthetic rates in an Arctic deciduous shrub. Taken together, these findings suggest the effect of advancing vegetation phenology on Arctic vegetation C uptake and primary productivity may vary both with local conditions and by Arctic vegetation functional group.

Vegetation phenology is also critical to Arctic herbivores as a control on the timing of availability of high-quality (high N content) forage. Advancing vegetation phenology is driving changes for many Arctic herbivores, including changes in muskox abundance (Post et al., 2019), range shifts for caribou (Severson et al., 2021), and decreased fitness of goslings (Doiron et al., 2015). Phenological mismatch among herbivores and vegetation can affect other ecosystem processes, including nutrient cycling (Beard et al., 2019). Our results suggest that effects of vegetation phenology on forage quality for Arctic herbivores will also likely vary among vegetation functional groups and on small (500 m) spatial scales.

Projections and observations of changes in snow phenology are much more varied than those for vegetation phenology, and currently there are relatively few consistent trends of changing snow conditions (Richter-Menge & Druckenmiller, 2020; Walsh et al., 2011). Warming may bring greater snowpack (Krasting et al., 2013), which in turn could delay snowmelt and potentially exert an opposing pressure on seasonal %N trends from that of advancing date of POS. However, if spring air temperature also increases, then snowmelt may not be delayed even with a greater snowpack, in which case an advancing POS would be the dominant phenological change driving the seasonality of tissue %N within Arctic vegetation functional groups. Either way, our results highlight the role of localized conditions controlling phenological response in determining the critical plant properties of %N, biomass, and subsequent changes to C cycling.

CONCLUSION

Understanding the seasonal trends of leaf %N and biomass is a critical component of anticipating future C

cycling in Arctic environments. Our work explored seasonal trends in %N and biomass among Arctic vegetation functional groups across a broad geographical area to determine what environmental, modeled, or remotely sensed variables can be used to understand these trends at large scales. Our research recognizes that relative phenology stage is a strong predictor of Arctic vegetation %N and specifically suggests that local conditions (~500 m spatial scale) are critical to predicting seasonal patterns in these important plant properties and in anticipating future C cycling in this rapidly changing biome.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Arctic Data Center: <https://doi.org/10.18739/A2B27PS63>.


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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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