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# Phytomass patterns across a temperature gradient of the North American arctic tundra

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[1] Only a few studies to date have collectively examined the vegetation biomass and production of arctic tundra ecosystems and their relationships to broadly ranging climate variables. An additional complicating factor for studying vegetation of arctic tundra is the high spatial variability associated with small patterned-ground features, resulting from intense freeze-thaw processes. In this study, we sampled and analyzed the aboveground plant biomass components of patterned-ground ecosystems in the Arctic of northern Alaska and Canada along an 1800-km north-south gradient that spans approximately 11°C of mean July temperatures. Vegetation biomass was analyzed as functions of the summer warmth index (SWI−sum of mean monthly temperatures > 0°C). The total absolute biomass (g $m^{-2}$) and biomass of shrubs increased monotonically with SWI, however, biomass of nonvascular species (mosses and lichens), were a parabolic function of SWI, with greatest values at the ends of the gradient. The components of plant biomass on patterned-ground features (i.e., on nonsorted circles or within small polygons) were constrained to a greater degree with colder climate than undisturbed tundra, likely due to the effect of frost heave disturbances on the vegetation. There were also clear differences in the relative abundances of vascular versus nonvascular plants on and off patterned-ground features along the SWI gradient. The spatial patterns of biomass differ among plant functional groups and suggest that plant community responses to temperature, and land-surface processes that produce patterned-ground features, are quite complex.

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## 1. Introduction

[2] Regional-scale patterns of vegetation have been analyzed along a number of climate gradients throughout the world [*Canadell et al.*, 2002]; these spatial patterns provide important insights into the controlling factors of vegetation and the potential plant responses to environmental change [*Epstein et al.*, 1996; *Barrett et al.*, 2002; *Jia et al.*, 2002; *Jobbagy et al.*, 2002; *Scanlon et al.*, 2002; *Zhou et al.*, 2002]. Only a few studies to date have collectively examined the vegetation biomass and production of arctic tundra ecosystems and their relationships to broadly ranging climate variables [e.g., *Gilmanov and Oechel*, 1995]. No prior study has taken a systematic and consistent approach to examining vegetation biomass patterns along the full temperature gradient of the arctic biome, particularly for the different plant types that comprise the arctic tundra.

[3] The arctic tundra is a vast biome; its extent ranges from just south of 60° N latitude in some places to approximately 83° N latitude, a distance well over 2500 km. Mean July temperatures across the latitudinal gradient of the Arctic can range from approximately 1–12°C, and the structure and function of the vegetation varies in response to this broad climate gradient [*Walker et al.*, 2005]. Numerous studies have sampled and estimated arctic tundra vegetation biomass for single locations (some of which contain multiple sites with different vegetation types), and many of these have been in the Low Arctic, or the more southern arctic tundra [*Hastings et al.*, 1989; *Shaver and Chapin*, 1991; *Chapin et al.*, 1995; *Shaver and Chapin*, 1995; *Hobbie and Chapin*, 1998; *Shaver et al.*, 1998; *Boelman et al.*, 2003; *Thompson et al.*, 2004; *Riedel et al.*, 2005]. Fewer studies have estimated the vegetation biomass for High Arctic [*Aleksandrova*, 1958; *Andreev*, 1966; *Bliss*, 1977; *Svoboda*, 1977] and polar desert ecosystems [*Bliss et al.*, 1984; *Henry et al.*, 1990].

[4] With respect to biomass along environmental gradients, *Shaver et al.* [1996] examined phytomass along a topographic sequence in northern Alaska, and some studies have examined tundra vegetation biomass (or proxies) across pieces of the full arctic climate gradient. Essentially all of these gradient studies have occurred on the North

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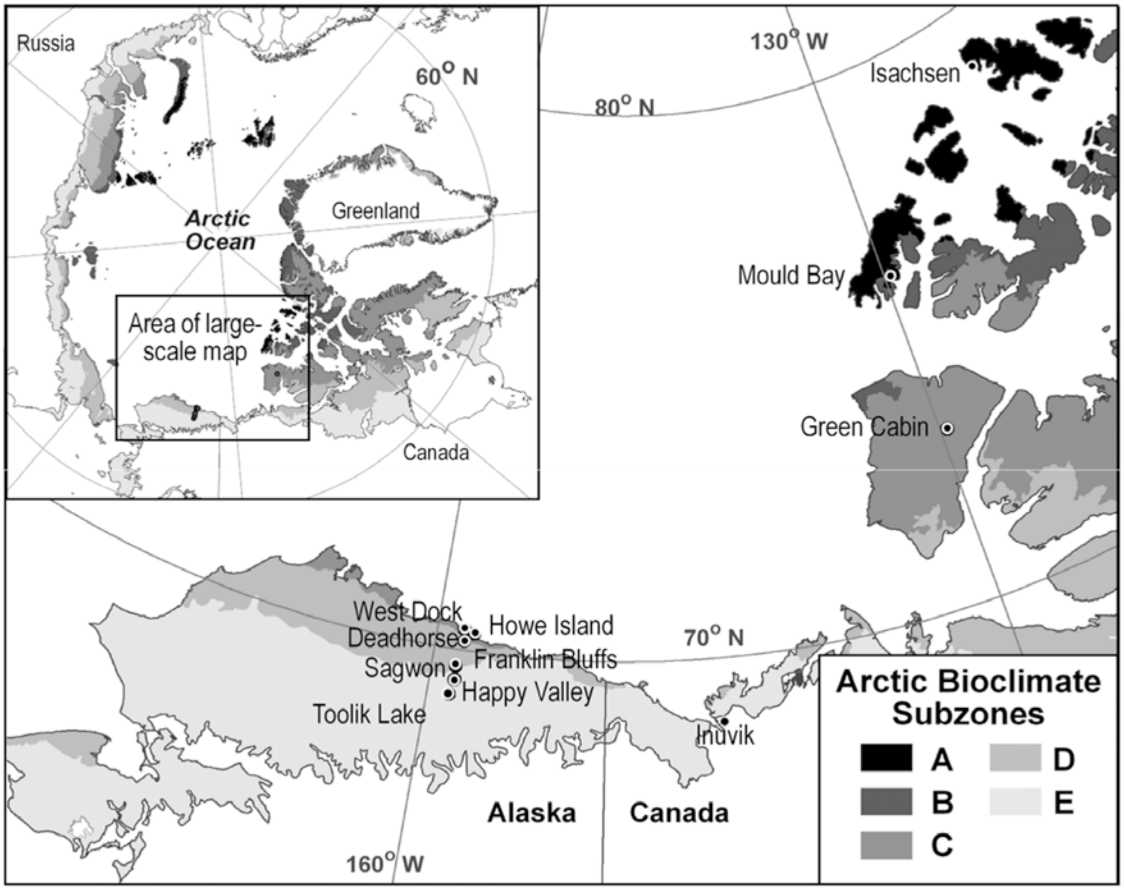

**Figure 1.** Map of the study sites along the North American Arctic Transect.

Slope of Alaska and include only the warmest parts of the arctic tundra (i.e., the Low Arctic), with a few data points for some High Arctic locations in the northernmost parts of Alaska (e.g., Barrow and Howe Island) [*Williams et al.*, 2000; *Jia et al.*, 2002; *Walker et al.*, 2003a, 2003b]. *Kelley et al.* [2004] extended her analysis of the Normalized Difference Vegetation Index (NDVI) north to Green Cabin, a High Arctic location (73°08′N) on Banks Island, Northwest Territories, Canada.

[5] Two of the above mentioned studies [*Walker et al.*, 2003a, 2003b] examined trends in the aboveground biomass of different plant functional types along the temperature gradient of the Alaskan North Slope. *Walker et al.* [2003b] found that aboveground shrub biomass increased exponentially with summer warmth index (SWI–sum of mean monthly temperatures > °C), but only for sites with acidic soils; aboveground shrub biomass increased linearly with SWI for the nonacidic sites and did not increase strongly compared to the acidic sites. They also found that mosses increased more strongly on the nonacidic sites with SWI than on the acidic sites.

[6] Only a few studies have gone further in examining vegetation along geographic or environmental gradients in the Arctic. *McGuire et al.* [2002] conducted a review of data from five arctic transects throughout Alaska, Canada, Scandinavia and Siberia. They found consistent and nonlinear declines in the NDVI and vegetation carbon with increasing latitudes from 50 to 75°N; however their data on vegetation carbon are not expressed for any categories more resolute than arctic tundra and forest-tundra. Perhaps the most comprehensive studies of plant biomass and productivity along climate gradients in the Arctic were conducted by *Gilmanov and Oechel* [1995], and *Gilmanov* [1997]. These studies effectively used all of the available data on phytomass and net primary productivity for arctic and subarctic ecosystems globally, and developed phenomenological relationships between these vegetation variables and climate/soils variables. They found that climate alone was insufficient to explain the patterns of aboveground net primary productivity (ANPP) in these systems, yet the combination of mean annual temperature, soil nitrogen and green phytomass explained 87% of the variability in ANPP.

[7] An additional complicating factor for studying vegetation of arctic tundra is the high spatial variability associated with small patterned-ground features (e.g., nonsorted circles and small nonsorted polygons), resulting from intense freeze-thaw processes [*Walker et al.*, 2003b, 2004; *Kelley et al.*, 2004]. Patterned ground features are quite common throughout the Arctic, yet plant biomass has never been examined explicitly with respect to these features, and never have they been incorporated into a landscape or regional scale study on vegetation patterns. In this study, we sampled and analyzed the aboveground plant biomass components of patterned-ground ecosystems in the Arctic of northern Alaska and Canada along an 1800-km north-

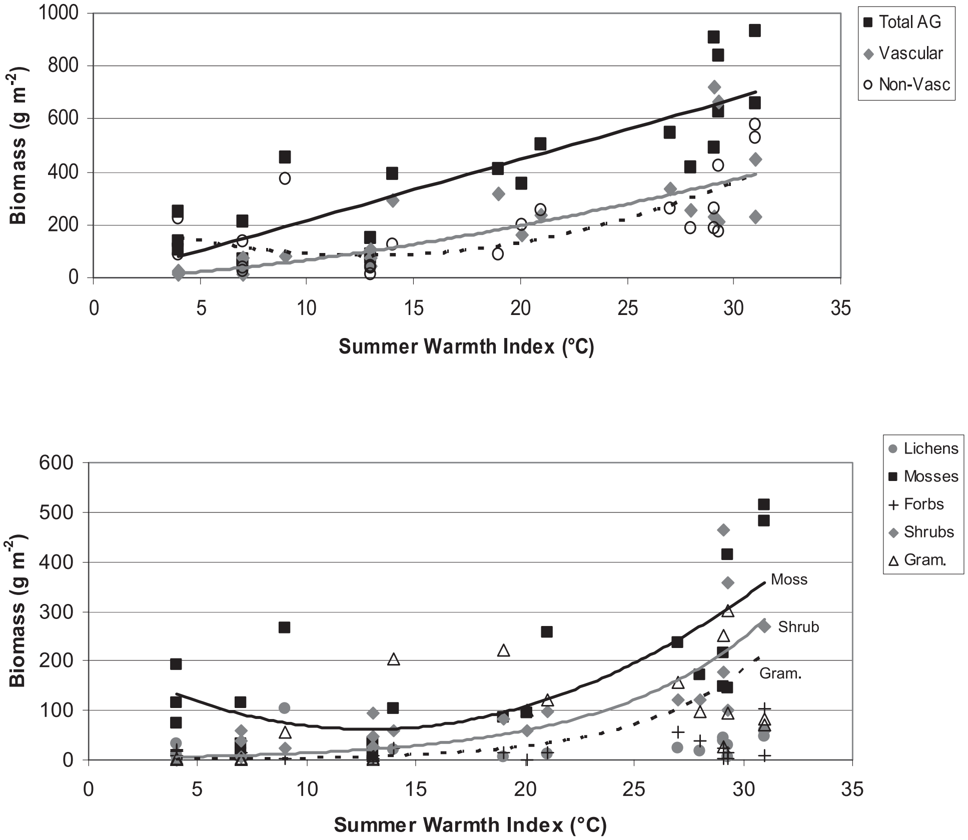

**Figure 2.** (a) Aboveground biomass (g m$^{-2}$) and (b) aboveground biomass of the major plant functional types (g m$^{-2}$) as functions of Summer Warmth Index (SWI–the sum of monthly mean temperatures > 0°C); data were collected from random tundra plots across our study sites.

south gradient that spans approximately 11°C of mean July temperatures.

## 2. Methods

[8] For sites along the full arctic bioclimate gradient, from the Low Arctic shrub tundra in northern Alaska to the polar desert of the Canadian Archipelago (Figure 1), we collected several different data sets of aboveground plant biomass and plant functional type composition. The first data set utilized measurements from a prior NSF-funded study within the Arctic Transitions of the Land-Atmosphere System (ATLAS) program [*Walker et al.*, 2003a, 2003b]. Study sites were located along two regional-scale, north-south gradients within the North Slope of Alaska. For the western locations which included, from north to south, Barrow, Atqasuk, Oumalik, and Ivotuk, biomass was collected from 10 random 20 × 50 cm plots within 100 m$^2$ grids. For the eastern locations which included, from north to south along the Dalton Highway, Howe Island, West Dock, Deadhorse, Franklin Bluffs, Sagwon and Happy Valley, two 50m line-transects were located in representative tundra areas. At 5, 25 and 45 m along each transect, one 20 × 50 cm plot was harvested for aboveground plant biomass. As part of our NSF Biocomplexity project, we added three locations within the High Arctic and the polar desert, including Green Cabin on Banks Island (arctic subzone C [*Walker et al.*, 2005]), Mould Bay on Prince Patrick Island (arctic subzone B) and Isachsen on Ellef Ringnes Island (arctic subzone A). Methods for biomass collection were identical to the transect approach used for locations along the Dalton Highway in northern Alaska. In all cases, plant biomass was clipped at the base of the green moss layer, and was sorted into the following categories: lichens, mosses, graminoids, forbs, and shrubs. Sorted plant material was then dried to constant weight.

[9] Because patterned-ground was a focus of this study, biomass was also collected from a series of plant communities both on and between patterned-ground features [*Kade et al.*, 2005; *Vonlanthen et al.*, 2008]. Using the Braun-Blanquet approach [*Dierschke*, 1994], 117 plots (relevés) were analyzed for Low Arctic, northern Alaska locations, and 75 plots were analyzed for the High Arctic, Canada locations (see Figure 1). For each relevé plot, the entire aboveground plant community within a 20 × 50 cm area was removed intact, including any organic soil layers and 2 cm of the mineral soil. These tundra samples were placed in plastic bags, transported back to the laboratory in Fairbanks, and frozen until analysis. After thawing, plants were clipped at the base of the green vegetation and sorted into the plant functional groups listed above. Sorted plant material was dried to a constant weight.

[10] Our sampling methodology, as detailed above, was stratified random, and we pooled the biomass data, calculating plant biomass means for each of the sampling locations, and for plant biomass on patterned-ground features and in undisturbed tundra (in between patterned-ground features). Total aboveground plant biomass, vas-

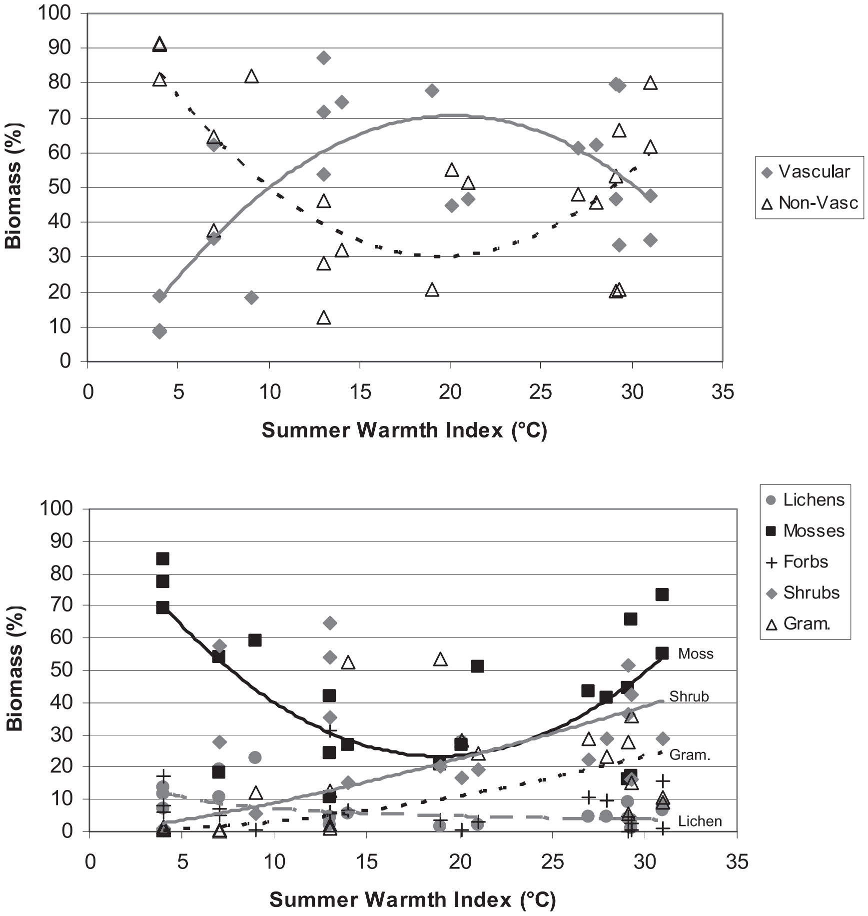

**Figure 3.** (a) Relative abundance (% biomass) and (b) relative abundance of the major plant functional types (% biomass) as functions of Summer Warmth Index (SWI–the sum of monthly mean temperatures > 0°C); data were collected from random tundra plots across our study sites.

cular and nonvascular plant biomass, as well as the biomass of each individual plant functional type were regressed against the summer warmth index (SWI–sum of mean monthly temperature > 0°C) for random plots, plots in between patterned-ground features, and plots on patterned-ground features. In this manner, we developed regional scale relationships between aboveground plant biomass and an important index of summer temperatures across the full climate gradient of the Arctic.

## 3. Results

### 3.1. Random Tundra Plots Along the North American Arctic Transect

[11] Total aboveground biomass increased linearly with summer warmth index (SWI) across the North American Arctic Transect (NAAT), ranging from approximately 100 g $m^{-2}$ in the polar desert to 700–1000 g $m^{-2}$ in the Low Arctic tundra; most of the variability in total aboveground biomass (71%) was explained by SWI. Aboveground biomass of vascular plants was strongly related as a power function to SWI ($r^2$ = 0.80), and biomass of nonvascular plants exhibited parabolic behavior as a function of SWI ($r^2$ = 0.52) (Figure 2a). Biomass of lichens and aboveground biomass of forbs were not significantly related to SWI along the NAAT. Aboveground biomass of both shrubs and graminoids increased exponentially with SWI ($r^2$ values = 0.64 and 0.61, respectively). Moss biomass exhibited parabolic behavior as a function of SWI ($r^2$ = 0.56). Moss biomass ranged from <100 g $m^{-2}$ in the High Arctic to >500 g $m^{-2}$ in the Low Arctic tundra (Figure 2b).

[12] In terms of relative abundance, or more specifically the percent of aboveground biomass, the patterns were somewhat different. The percent of vascular and nonvascular biomass exhibited parabolic behavior along the SWI gradient. Nonvascular biomass was clearly more representative in the polar desert and colder High Arctic systems than vascular biomass, less abundant than vascular biomass in the warmer parts of the High Arctic, and essentially similar to vascular biomass in the Low Arctic (Figure 3a). Similarly, moss biomass showed parabolic variation across the SWI gradient, however, lichen relative abundance declined as a negative power function with increasing SWI. Shrub and graminoid relative abundances increased as power functions with SWI, whereas forbs showed no significant relationship along the temperature gradient (Figure 3b).

### 3.2. Undisturbed Tundra Plots Along the North American Arctic Transect

[13] Total aboveground biomass increased linearly with SWI for the zonal, undisturbed tundra biomass ($r^2$ = 0.84).

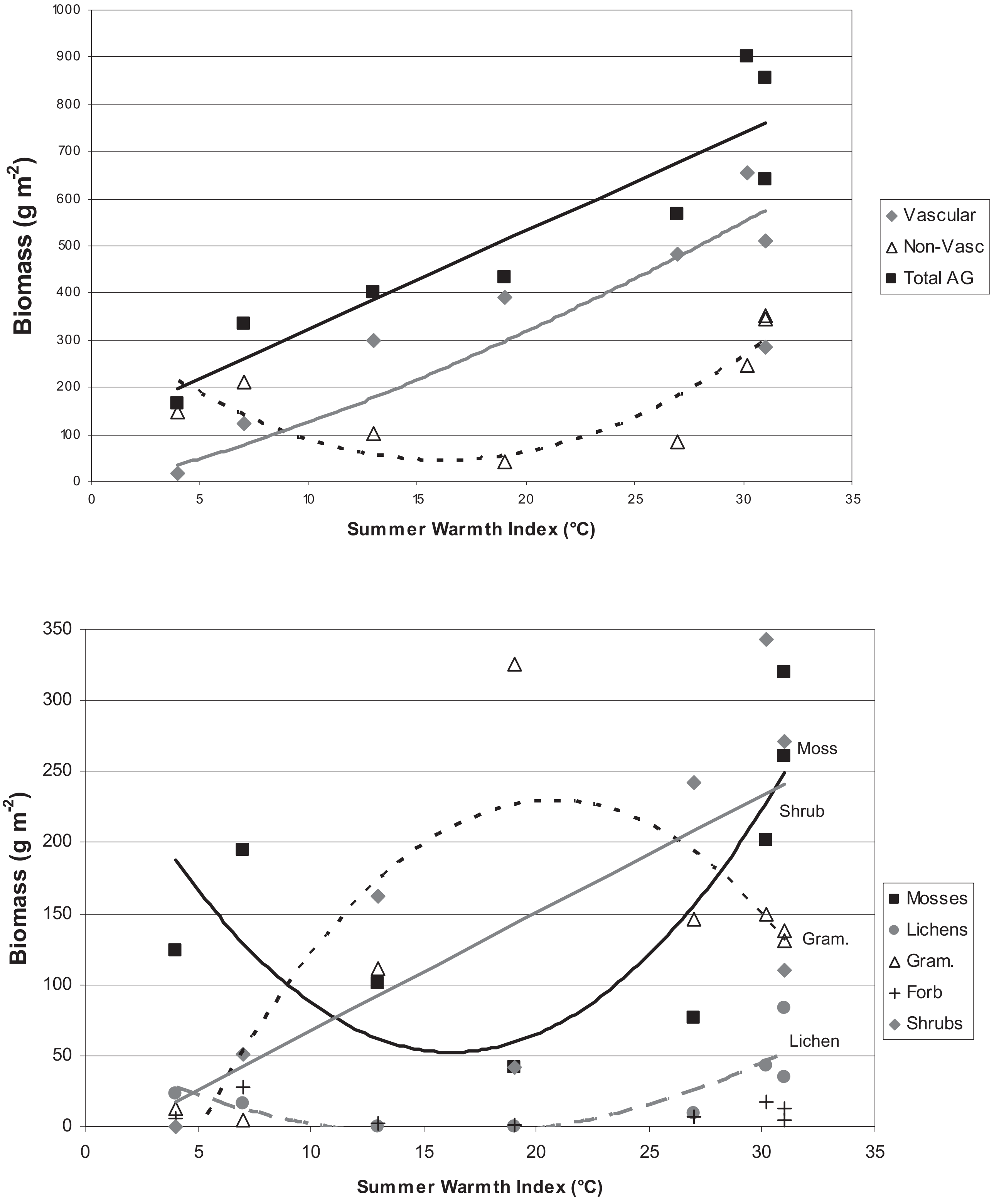

**Figure 4.** (a) Aboveground biomass (g m$^{-2}$) and (b) aboveground biomass of the major plant functional types (g m$^{-2}$) as functions of Summer Warmth Index (SWI–the sum of monthly mean temperatures > 0°C); data were collected from undisturbed tundra relevés across our study sites.

Total aboveground biomass ranged from <200 g m$^{-2}$ in the north to 900 g m$^{-2}$ at the southern end of the gradient. Vascular plant biomass increase as a power function with SWI ($r^2$ = 0.84), whereas nonvascular plant biomass exhibited parabolic behavior along the SWI gradient ($r^2$ = 0.73), with the least amount of biomass in the center of the gradient (Figure 4a). Shrub biomass for zonal, undisturbed tundra sites increased linearly with SWI. Graminoid

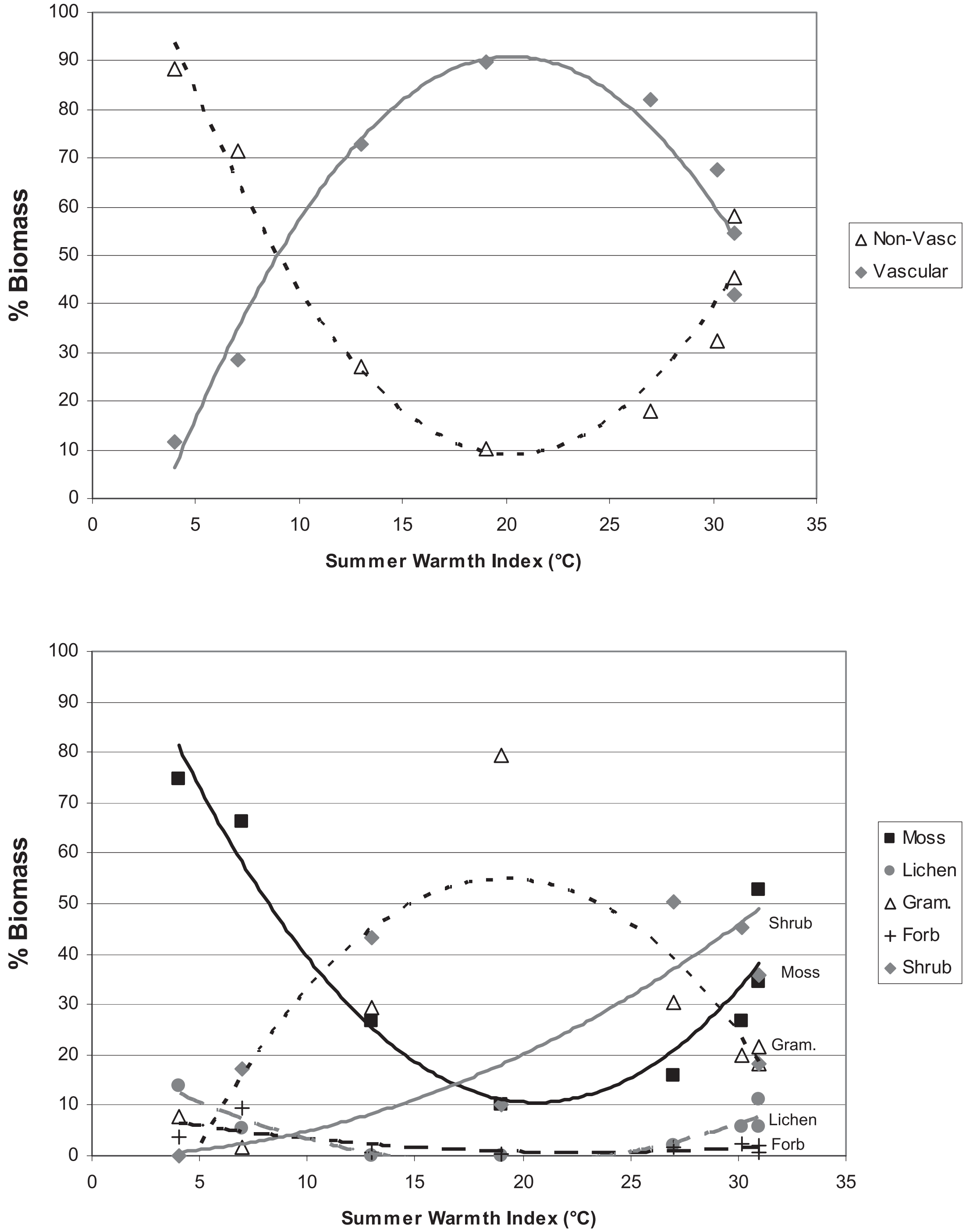

**Figure 5.** (a) Relative abundance (% biomass) and (b) relative abundance of the major plant functional types (% biomass) as functions of Summer Warmth Index (SWI−the sum of monthly mean temperatures > 0°C); data were collected from undisturbed tundra relevés across our study sites.

biomass was greatest in the middle of the gradient, whereas mosses and lichens had their greatest biomass values at the ends of the gradient. Forb biomass did not vary significantly across the gradient (Figure 4b).

[14] In terms of relative abundance, vascular and nonvascular biomass were parabolic functions of SWI ($r^2$ = 0.94) with vascular biomass being a low proportion of the total biomass in the coldest areas and most of the biomass in areas with moderate temperatures. In the warmest parts of the tundra along the gradient, vascular and nonvascular biomass had similar proportions of the total biomass (Figure 5a). Percentage of shrub biomass increased as a power function along the gradient of SWI ($r^2$ = 0.59). Graminoids exhibited their greatest percentage of biomass at the center of the SWI gradient, whereas moss, lichen and forb relative abundances all varied parabolically with

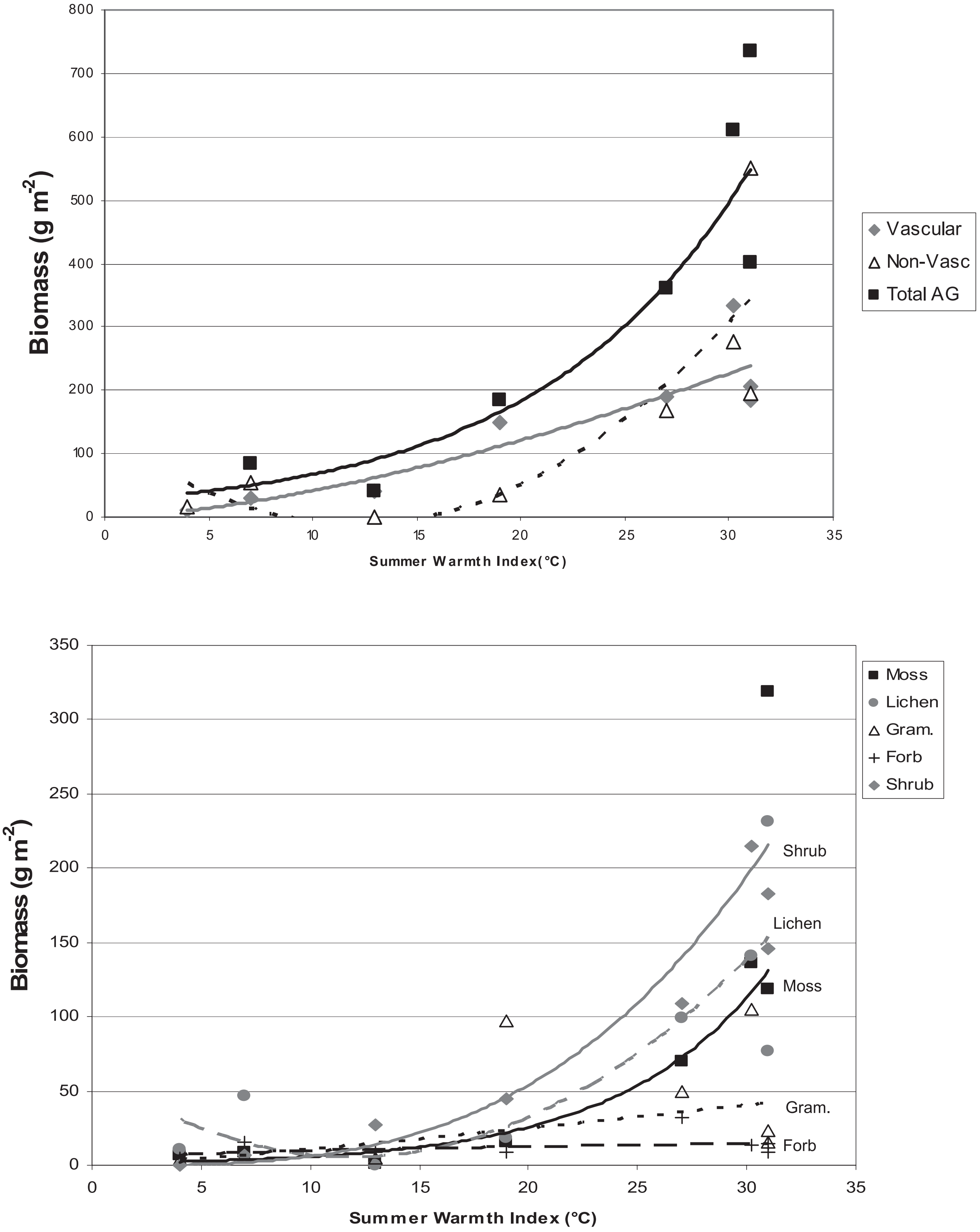

**Figure 6.** (a) Aboveground biomass (g $m^{-2}$) and (b) aboveground biomass of the major plant functional types (g $m^{-2}$) as functions of Summer Warmth Index (SWI–the sum of monthly mean temperatures > 0°C); data were collected from patterned-ground feature relevés across our study sites.

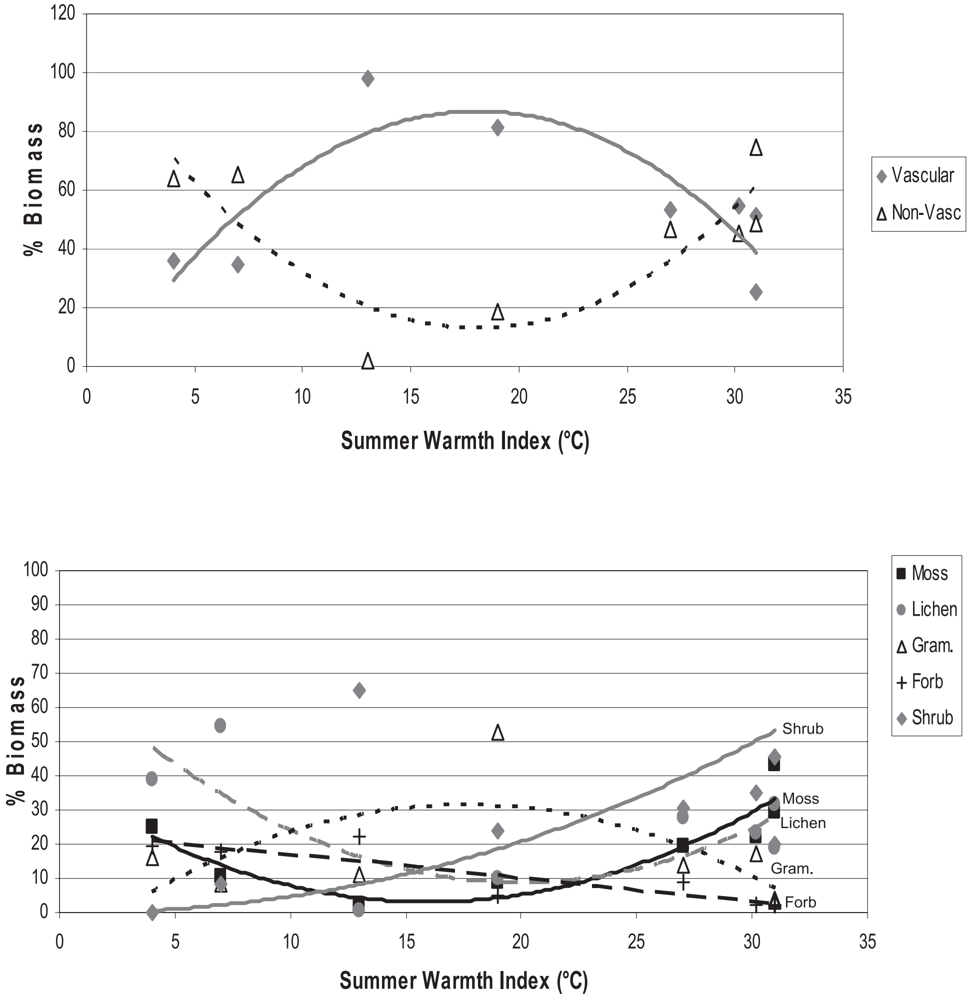

**Figure 7.** (a) Relative abundance (% biomass) and (b) relative abundance of the major plant functional types (% biomass) as functions of Summer Warmth Index (SWI–the sum of monthly mean temperatures > 0°C); data were collected from patterned-ground feature relevés across our study sites.

temperatures, having their greatest values at the cold and warm ends of the gradient (Figure 5b).

### 3.3. Patterned-Ground Tundra Plots Along the North American Arctic Transect

[15] The spatial dynamics of plant biomass along an arctic temperature gradient differed substantially on pattern-ground features compared to undisturbed tundra. Total aboveground biomass on patterned-ground features increased exponentially with increasing SWI ($r^2$ = 0.83), ranging from <100 g $m^{-2}$ in the north to >700 g $m^{-2}$ in the southern tundra. Nonvascular biomass was a parabolic function of SWI ($r^2$ = 0.70), however, with much greater values in the southern Low Arctic tundra than in the north, and vascular biomass was an increasing power function of SWI ($r^2$ = 0.95) (Figure 6a). Shrub, graminoid, and forb biomass all increased as power functions of SWI ($r^2$ values were 0.92, 0.51, and 0.26, respectively). Moss biomass increased exponentially with SWI, and lichen biomass was a parabolic function of SWI, however with its greatest values on patterned-ground features in the southern tundra (Figure 6b).

[16] In terms of relative biomass, the percentage of vascular biomass on patterned-ground features was less than that of nonvascular biomass at the cold end of the gradient, greater than that of nonvascular biomass in the center of the gradient, and similar to nonvascular biomass at the warm end of the gradient (Figure 7a) ($r^2$ = 0.70). Percentage of shrub biomass on patterned-ground features increased as a power function of SWI, whereas percentage of forb biomass on patterned-ground features declined linearly with SWI. Graminoids had their greatest relative abundance at the center of the gradient, whereas mosses and lichens had their greatest percentage of biomass at the ends of the gradient (Figure 7b).

## 4. Discussion

[17] Although the arctic tundra biome exists across a broad temperature gradient, to date there have been no regional-scale, quantitative studies of arctic tundra biomass and how it relates to temperature. There have been a number of studies examining certain community and population properties of tundra vegetation and their relationship to environmental factors at broad spatial scales [*Walker et*

**Table 1.** Regression Equations for Plant Biomass Along a Gradient of Summer Warmth Index

| Biomass Variable | Equation | $r^2$ |
|---|---|---|
| *Absolute Biomass (g $m^{-2}$) for Random Tundra Plots* | | |
| Total Aboveground | $y = 22.98x - 13.05$ | 0.71 |
| Vascular | $y = 1.86x^{1.56}$ | 0.80 |
| Nonvascular | $y = 0.93x^2 - 23.82x + 235.54$ | 0.52 |
| Moss | $y = 0.90x^2 - 23.05x + 209.79$ | 0.56 |
| Shrubs | $y = 3.48e^{0.14x}$ | 0.64 |
| Graminoids | $y = 0.69e^{0.19x}$ | 0.61 |
| *Relative Biomass (%) for Random Tundra Plots* | | |
| Vascular | $y = -0.20x^2 + 8.16x - 11.47$ | 0.53 |
| Nonvascular | $y = 0.22x^2 - 8.54x + 113.29$ | 0.51 |
| Moss | $y = 0.21x^2 - 7.94x + 98.27$ | 0.48 |
| Shrubs | $y = 0.42x^{1.33}$ | 0.44 |
| Graminoids | $y = 0.05x^{1.84}$ | 0.54 |
| Lichens | $y = 26.99x^{-0.57}$ | 0.21 |
| *Absolute Biomass (g $m^{-2}$) for Undisturbed Tundra Plots* | | |
| Total Aboveground | $y = 20.88x + 114.12$ | 0.84 |
| Vascular | $y = 5.65x^{1.35}$ | 0.84 |
| Nonvascular | $y = 1.15x^2 - 37.07x + 345.20$ | 0.73 |
| Moss | $y = 0.90x^2 - 29.28x + 290.17$ | 0.65 |
| Shrubs | $y = 8.29x - 15.35$ | 0.56 |
| Graminoids | $y = -0.94x^2 + 39.05 - 175.02$ | 0.70 |
| Lichens | $y = 0.25x^2 - 7.79x + 55.03$ | 0.70 |
| *Relative Biomass (%) for Undisturbed Tundra Plots* | | |
| Vascular | $y = -0.32x^2 + 12.95x - 40.29$ | 0.94 |
| Nonvascular | $y = 0.32x^2 - 12.96x + 140.41$ | 0.94 |
| Moss | $y = 0.26x^2 - 10.56x + 119.38$ | 0.89 |
| Shrubs | $y = 0.05x^{2.04}$ | 0.59 |
| Graminoids | $y = -0.26x^2 + 10.11x - 41.96$ | 0.66 |
| Lichens | $y = 0.06x^2 - 2.41x + 21.03$ | 0.86 |
| Forbs | $y = 0.02x^2 - 0.75x + 9.31$ | 0.45 |
| *Absolute Biomass (g $m^{-2}$) for Patterned-Ground Feature Plots* | | |
| Total Aboveground | $y = 24.95e^{0.10x}$ | 0.84 |
| Vascular | $y = 1.19x^{1.54}$ | 0.95 |
| Nonvascular | $y = 0.99x^2 - 23.80x + 132.56$ | 0.70 |
| Moss | $y = 1.33e^{0.15x}$ | 0.68 |
| Shrubs | $y = 0.004x^{3.16}$ | 0.92 |
| Graminoids | $y = 0.71x^{1.19}$ | 0.51 |
| Lichens | $y = 0.41x^2 - 9.64x + 62.89$ | 0.69 |
| Forbs | $y = 4.38x^{0.35}$ | 0.26 |
| *Relative Biomass (%) for Patterned-Ground Feature Plots* | | |
| Vascular | $y = -0.29x^2 + 10.43x - 7.45$ | 0.70 |
| Nonvascular | $y = 0.29x^2 - 10.44x + 107.56$ | 0.70 |
| Moss | $y = 0.13x^2 - 4.27x + 37.25$ | 0.82 |
| Shrubs | $y = 0.03x^{2.14}$ | 0.64 |
| Graminoids | $y = -0.14x^2 + 4.82 - 10.92$ | 0.40 |
| Lichens | $y = 0.15x^2 - 6.17x + 70.31$ | 0.53 |
| Forbs | $y = -0.69x + 23.92$ | 0.80 |

*al.*, 1994; *Jónsdóttir et al.*, 1999; *Virtanen et al.*, 1999, 2006]; however, these studies typically examined species richness data and plant cover percentages. *Gilmanov and Oechel* [1995] gathered what was likely most (if not all) of the available data on the phytomass and productivity of arctic tundra sites. These existing phytomass and productivity data vary considerably even within specific vegetation types, and much of this variability is probably due to numerous methodological differences.

[18] Nevertheless, *Gilmanov and Oechel* [1995] focused their analyses on both total and aboveground net primary productivity (ANPP), and found that across arctic ecosystems primary productivity was related to temperature, the quantity of soil organic matter, and the current amount of live green biomass [see also *Gilmanov*, 1997]. These variables explained up to 73% of the variability in ANPP, and the relationship between ANPP and mean annual temperature was an exponential one. Relationships between biomass and environmental variables were not published in these papers, even though the biomass data were collected. However, *Epstein et al.* [2000] evaluated the relationship using these data as part of a model development project and found that total biomass was also an exponential function of mean annual temperature.

[19] In this study, using a consistent sampling methodology, we found good linear fits between total aboveground biomass and the summer warmth index (SWI) for both random plots and plots of undisturbed tundra along a gradient of SWI from 4°C-months to 31°C-months; SWI explained up to 84% of the variability in total aboveground biomass. For total aboveground biomass on patterned-ground features, the relationship with SWI was an exponential one. At the southern end of our SWI gradient, the total aboveground biomass on patterned-ground features is not much less than that found in undisturbed tundra. However, in colder sites, the disturbance associated with patterned-ground features (i.e., frost heave) reduces the biomass to a greater extent than just the colder temperatures, thus yielding the observed exponential decline in biomass with decreasing SWI [*Walker et al.*, 2008].

[20] Vascular and nonvascular biomass (g $m^{-2}$) both exhibit similar patterns across random, undisturbed, and patterned-ground plot. Vascular biomass increases as a power function with SWI, whereas nonvascular biomass is a parabolic function of SWI. Some of the lowest values of nonvascular biomass occur in the center of the SWI gradient, with arctic subzones C and D [*Walker et al.*, 2005]; higher values occur to the north in subzone B and in the polar desert (subzone A). Similarly, moss biomass has a parabolic relationship with SWI for both random plots and undisturbed plots, and lichen biomass has a parabolic relationship with SWI for undisturbed and patterned-ground plots. No other plant functional type exhibits this kind of behavior along the SWI gradient. This suggests that while nonvascular plants tend to dominate the plant communities in the polar desert and northern High Arctic (subzones A and B, respectively), as the climate warms to the south, the nonvascular plants are likely being outcompeted (possibly for light and nutrients) by taller vascular plants. Several recent studies have indicated that increased temperatures can lead to a reduction in mosses in favor of vascular plants such as shrubs [*Chapin et al.*, 1995; *Hobbie and Chapin*, 1998; *Epstein et al.*, 2004; *Walker et al.*, 2006]. At the southern end of the gradient (subzone E) there are sufficient resources to support a plant community that includes an overstory of vascular plants and an understory of nonvascular plants. Our data on relative (%) biomass clearly illustrate the changing dominance of vascular versus nonvascular plants across the arctic temperature gradient.

[21] Forb biomass was not significantly related to SWI for either random or undisturbed plots; however it increased as a power function with SWI for patterned-ground plots. Graminoid biomass typically increased with SWI; however in undisturbed plots it had a negative parabolic relationship with SWI (i.e., greatest at intermediate values). This also

might suggest competition between graminoids and shrubs in the Low Arctic (subzones D and E).

[22] In terms of relative abundance (% biomass) of the different plant functional types, shrub biomass increased as a power function of SWI for all plot types (random, undisturbed and patterned-ground). Moss and lichen relative abundance were parabolic functions of SWI, except for the random plots where lichen biomass declined as a power function of SWI. Graminoid biomass was a negative parabolic function of SWI for both undisturbed plots and patterned-ground plots, and increased as a power function of SWI for the random plots (although there were some plots with high graminoid biomass toward the center of the gradient). Relative abundance of forbs declined as a power function of SWI for random and patterned-ground plots, and was a parabolic function of SWI for the undisturbed plots. This is expected as the absolute biomass of forbs (g $m^{-2}$) essentially does not vary across the SWI gradient.

[23] The strength of the relationships between plant functional type biomass and SWI was quite surprising with $r^2$ values generally >0.50 and ranging up to 0.94. It was also interesting that the spatial dynamics were so consistent across plot types, especially between the undisturbed tundra and the patterned-ground features. The spatial patterns of plant functional type relative abundance were effectively the same between undisturbed tundra and patterned-ground features; there was only a slight difference in the spatial pattern of forb relative abundance between the two plot types. In the High Arctic and polar desert, mosses made up a larger portion of the plant community in undisturbed tundra, and lichens were more dominant on patterned-ground features. In the Low Arctic, lichens were more dominant on patterned-ground features compared to undisturbed tundra. For absolute abundance (g $m^{-2}$), the spatial dynamics were quite different, with most of the plant functional types exhibiting different spatial patterns between undisturbed tundra and patterned-ground features. The most striking difference in absolute biomass between undisturbed tundra and patterned-ground features is the reduction of biomass on patterned-ground features that begins in the northern part of the Low Arctic (subzone D) and continues through the polar desert, with the most dramatic reduction toward the center of the gradient in subzone C.

[24] The equations presented here (Table 1) can be used to make baseline projections of how tundra biomass and plant communities will respond to changes in climate, particularly warming, as is predicted by general circulation models [*Christensen et al.*, 2007]. Total aboveground biomass and shrub biomass are projected to increase with increasing temperatures; these changes are likely already being observed remotely [*Sturm et al.*, 2001; *Jia et al.*, 2003; *Goetz et al.*, 2005], however actual increases in biomass have yet to be confirmed on the ground [see *Chapin et al.*, 1995; *Hobbie and Chapin*, 1998; *Shaver et al.*, 2001; *Walker et al.*, 2006]. Our regression models suggest that the responses of nonvascular plants and graminoids to warming will differ depending on the location along the regional climate gradient. Clearly the effects of warming on plant growth will interact with competitive relationships among plant functional types to determine the ultimate responses.

[25] Warming may have a greater effect on arctic tundra plant biomass on patterned-ground features than in undisturbed tundra. Plant biomass on patterned-ground features is presently limited by surface disturbances, such as frost heave [*Walker et al.*, 2004, 2008], which in turn is facilitated by the absence of insulation by vegetation at the surface [*Kade and Walker*, 2008]. If increasing temperatures were to increase plant biomass on patterned-ground features, this may generate a positive feedback, whereby the frost heave disturbance is reduced and more vegetation is able to colonize and/or grow on the patterned-ground features. The relationships between plant biomass and plant community composition along the arctic temperature gradient are in many cases nonlinear, and these relationships are influenced by the presence of patterned-ground features on the arctic tundra landscape. The response of tundra vegetation to climate warming is therefore likely to be complex, and an understanding of plant responses, competition and physical processes will be necessary to improve on the projections made here with these first-order relationships.

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