Twenty-Five Year Record of Changes in Plant Cover on Tundra of Northeastern Alaska

Authors: Jorgenson, Janet C., Raynolds, Martha K., Reynolds, Joel H., and Benson, Anna-Marie

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Janet C. Jorgenson[1,6]
Martha K. Raynolds[2]
Joel H. Reynolds[3,5] and
Anna-Marie Benson[4]

[1]Arctic National Wildlife Refuge, U.S. Fish and Wildlife Service, 101 12th Avenue, Fairbanks, Alaska 99701, U.S.A.
[2]Institute of Arctic Biology, University of Alaska Fairbanks, Box 757000, Fairbanks, Alaska 99775, U.S.A.
[3]Division of Natural Resources, National Wildlife Refuge System, U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503, U.S.A.
[4]Division of Natural Resources, National Wildlife Refuge System, U.S. Fish and Wildlife Service, 101 12th Avenue, Fairbanks, Alaska 99501, U.S.A.
[5]Present address: Western Alaska Landscape Conservation Cooperative, 1011 East Tudor Road, MS 281, Anchorage, Alaska 99503, U.S.A.
[6]Corresponding author: janet_jorgenson@fws.gov

Abstract

Northern Alaska has warmed over recent decades and satellite data indicate that vegetation productivity has increased. To document vegetation changes in the Arctic National Wildlife Refuge, we monitored plant cover at 27 plots between 1984 and 2009. These are among the oldest permanently marked and continuously monitored vegetation plots in the Arctic. We quantified percent cover of all plant species by line-point intercept sampling and assessed change over time for seven plant growth forms. Cover of bryophytes and deciduous shrubs showed slight decreasing trends. Evergreen shrubs, horsetails, and depth of thawed soil above permafrost had no trends. For lichens, graminoids, and forbs, trends varied by plant community type. Overall, vegetation in the plots changed little over the study period, in contrast to results from other studies in northern Alaska. A few plots had dramatic changes, however, which we attributed to subsidence from melting ground ice or to floodplain dynamics. Our results demonstrate that vegetation change on the Arctic Refuge coastal plain over the past quarter century has been spatially heterogeneous and facilitated by disturbance. The findings highlight the need for greater work linking plot-level and regional remote sensing measurements of change.

Introduction

The climate of northern Alaska has been changing for the past three decades (Hinzman et al., 2005). Summer temperatures have increased 4 °C since the early 1980s (Bhatt et al., 2010) and spring snow melt is occurring earlier, leading to a longer growing season (Hinzman et al., 2005). Warming is projected to continue in the future (ACIA, 2005). Arctic vegetation is strongly limited by direct and indirect effects of temperature (Chapin et al., 2005) and will change greatly if temperatures continue to rise, as evidenced by past changes documented in the paleorecord (Anderson and Brubaker, 1994) and current latitudinal gradients in vegetation (Lantz et al., 2010; Walker et al., 2012). We expect tundra plant communities to change composition under warmer growing conditions, with different plant species responding at different rates because of their individual traits and habitat preferences (Chapin, 2003).

Most evidence for changing vegetation in the Arctic comes from remote sensing, because of the remoteness of most of the Arctic and the scarcity of vegetation plots established before the rapid warming of the 1990s. The normalized difference vegetation index (NDVI), an index of quantity of green vegetation derived from satellite data, has increased Arctic-wide since the 1970s, with the greatest increases in northern Alaska (Bhatt et al., 2010; Epstein et al., 2012). The increase has generally been attributed to broad-scale increases in shrubs (Jia et al., 2003; Stow et al., 2004). Advanced Very High Resolution Radiometer (AVHRR) satellite records consistently show increases in NDVI in our study area (Bhatt et al., 2013). Repeat aerial photography

has shown increases in shrub cover at some tundra sites between the 1950s and the present (Tape et al., 2006; Frost and Epstein, 2014).

Warming experiments on Arctic tundra have shown large changes within artificially warmed enclosures. General patterns are usually a decrease in lichens and bryophytes and an increase in deciduous shrubs (Sistla et al., 2013; Hollister et al., 2005; Wahren et al., 2005) or graminoids (van Wijk et al., 2003). Manipulating the soil nutrient regime also caused differential responses (Bret-Harte et al., 2004). In a synthesis of 61 tundra warming experiments, Elmendorf et al. (2012a) found that experimental warming increased shrub abundance and decreased lichens and bryophytes. There was heterogeneity across sites and response changed over time.

Ground-based data documenting change over time in unmanipulated vegetation plots in the Arctic have begun to accumulate in the past decade. Myers-Smith et al. (2011) listed sites across the Arctic with evidence of change in shrub abundance. Elmendorf et al. (2012b) reported a synthesis of vegetation changes over time in plots at 46 locations across the Arctic, including the plots in our study. They found great heterogeneity of response, but did find Arctic-wide trends of increasing abundance for evergreen shrubs and low and tall shrubs, but not for total deciduous shrubs or any other plant growth form. Among-site comparisons showed that deciduous shrubs increased more in the warmest parts of the Arctic and at the wettest sites. Low and tall shrubs increased more at sites that had experienced recent warming

In this study, we monitored plant cover on the coastal plain of the Arctic National Wildlife Refuge from 1984 to 2009. These are among the oldest permanently marked and continuously monitored

vegetation plots in the Arctic. The plots span a large area (75 km by 50 km), and represent all of the major tundra community types in this region, ranging from upland tundra to wetlands to riparian shrublands. The study was initially designed to document disturbance and recovery from vehicle traffic in the winters of 1984 and 1985 (Felix and Raynolds, 1989; Jorgenson et al., 2010). The control plots adjacent to the vehicle trails also provide an excellent long-term data set for examining changes in undisturbed tundra vegetation over a period of rising ambient temperatures and increasing tundra greenness as detected by satellites.

Methods

STUDY AREA

The study area spans the coastal plain and Brooks Range foothills on the North Slope of the Arctic Refuge (Fig. 1). It is mainly in the warmest bioclimatic subzone of the Arctic (Subzone E with some Subzone D; CAVM Team, 2003). Distinct plant communities form an intricate mosaic on the landscape with distribution determined mainly by topographic position due to control of soil moisture (Table 1). The tundra has a nearly continuous carpet of plants less than 0.5 m tall, mainly sedges, shrubs, and mosses. Shrubs are taller along drainages. Soils are underlain by permafrost and the seasonally thawed surface layer that supports plant growth is usually less than 40 cm deep in midsummer. Permafrost-related topographic features are common, including ice-wedge polygons and frost boils.

The climate warmed on the North Slope of Alaska and in our study area over the 25-year study period. Kuparuk, Alaska, is approximately 190 km to the west and has the closest climate station, with records covering the entire study period. In addition its distance from the sea coast is similar to that of most of our study plots. The records show a mean annual temperature of –11 °C and mean annual precipitation of 10 cm. Mean annual temperature increased by 2.5 °C between 1984 and 2009 (Western Regional Climate Center, 2010, http://www.wrcc.dri.edu). Precipitation records are less reliable (McAfee et al., 2013) but show an increase in total yearly precipitation from 7 to 12 cm. The greatest warming occurred in spring and fall, but summer growing season temperatures also increased by 1.5 °C (June to August). This was due mainly to an increase in June temperatures, indicating a lengthening of the growing season.

SAMPLING DESIGN

Twenty-seven permanent vegetation plots were established in 1984 and 1985 (Fig. 1). These are the undisturbed control plots for a study of tundra recovery after vehicle traffic from oil exploration (Jorgenson et al., 2010). Plot locations were targeted to represent the primary plant communities of the area (Table 1). Elevation ranged from 5 m to 275 m. Plots were sampled six times between 1984 and 2009.

Line-point intercept sampling was used to quantify percent cover of plant species in the 4 m × 30 m plots (Bonham, 2013). A vertical point frame was positioned to sample 20 points (spaced at 20-cm intervals) on each of 10 evenly spaced 4-m-long permanent transects, for a total of 200 points per plot. A vertical pin was lowered from the frame at each point and every plant species intercepted by the pin was recorded. The percent cover for each species was calculated as the number of pin "hits" divided by 200. Each plot was first sampled in two consecutive years: 12 plots in 1984 and 1985, 12 plots in 1985 and 1986, and 3 plots in 1986 and 1987. They were then resampled in 1988, 1991, 2002, and 2009. Sampling dates ranged from July 1 to August 29. Data collected before July 10 or after August 13 were dropped from the analyses (18% of original data points) to reduce confounding effects of changing plant phenology on plant species percent cover (e.g., leaf growth or senescence). We aggregated plant species into seven growth forms (also known as plant functional groups) for analysis: bryophytes, lichens, graminoids, deciduous shrubs, evergreen shrubs, forbs, and horsetails. Plant nomenclature followed the USDA Plants Database (USDA, 2013). Depth of seasonally thawed soil above permafrost (thaw depth) was measured by probing with a rod at 30 systematic points per plot each year
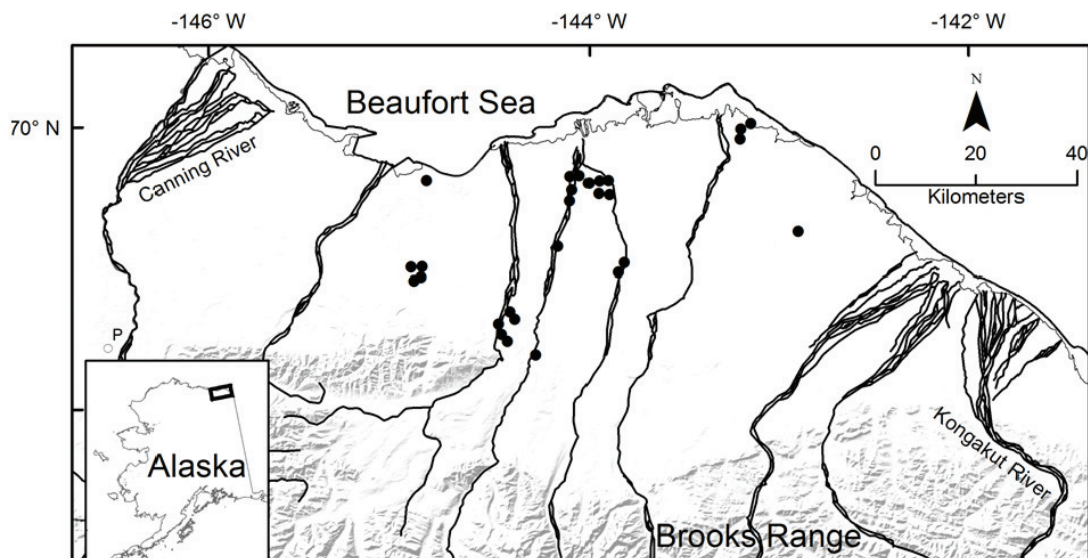

FIGURE 1.   Map of 1984–2009 vegetation plots on the coastal plain of the Arctic National Wildlife Refuge, Alaska. Dot labeled "P" is location of Figure 8.

TABLE 1

Plant community types of the north slope of the Arctic NWR, Alaska, based on Walker et al. (1982), with codes for graphs in parentheses, percent of study area, and number of study plots in each type.

Type	% of study area[a]	# of plots	Description
Wet Graminoid Tundra (WG)	13	1	Low-lying flats and drainages with the sedges *Carex aquatilis* and *Eriophorum angustifolium* and little moss or shrub cover. The poorly drained soils are saturated throughout the summer and have a thick, fibrous organic horizon.
Sedge-Willow Tundra (MS)	30	5	Low-lying flats and gentle slopes with the sedges *Eriophorum angustifolium* and *Carex aquatilis* and the willows *Salix pulchra* and *S. reticulata*. Mosses include *Tomentypnum nitens, Hylocomium splendens*, *Aulacomnium* sp., *Sphagnum* sp., and *Campylium stellatum*. On moist, fine-grained, retransported, glaciofluvial, and abandoned floodplain deposits. Soils are somewhat poorly drained, have a moderately thick organic layer, and are saturated at intermediate depths but generally free of surface water.
Sedge-Dryas Tundra (MNT)	13	6	Somewhat poorly drained sites dominated by the dwarf shrub *Dryas integrifolia* and the sedge *Carex bigelowii*, with the willows *Salix reticulata, S. phlebophylla,* and *S. richardsonii* and mosses such as *Tomentypnum nitens, Hylocomium splendens, Distichium capillaceum*, and *Ditrichum flexicaule*. Forbs (e.g., *Lupinus arcticus*), lichens (e.g., *Cetraria* sp.), and horsetails (e.g., *Equisetum variegatum*) are common. Found on moist calcareous slopes, pebbly marine sediments, and glacial deposits. Notable for a hummocky surface topography, patches of exposed mineral soil and extremely variable organic horizons resulting from active and stabilized frost boils.
Tussock Tundra (TT)	28	5	Dominated by the tussock-forming sedge *Eriophorum vaginatum* and shrubs *Salix pulchra, Betula nana, Rhododendron tomentosum (Ledum decumbens),* and *Vaccinium vitis-idaea*. Bryophytes included *Hylocomium splendens, Sphagnum* sp., *Aulacomnium turgidum, Ptilidium ciliare,* and *Tomentypnum nitens*. Soils are somewhat poorly drained, on deposits of loess or colluvial material on top of coarser, residual materials, or on old, weathered glacial deposits.
Shrub Tundra (ST)	5	2	Dominated by the same shrubs as Tussock Tundra. Species composition is similar to Tussock Tundra, but with few tussocks. In the study area, occurs only on raised areas with high-centered polygon surface morphology. Soils are somewhat poorly drained.
Riparian Shrublands (RS)	2	5	Willow shrublands on river floodplains and stream banks, dominated by *Salix alaxensis, S. glauca,* and *S. richardsonii*, commonly with a moss and forb understory. Willow height usually less than 0.5 m. Occurs on both young floodplain deposits with mixed gravel and fine-grained material, and older terraces with a thin fine-grained alluvium layer over gravel. Soils are well drained.
Dryas Terrace (DT)	3	3	Infrequently flooded river terraces with the evergreen shrub *Dryas integrifolia* and dwarf willow, forb, horsetail, moss, and lichen species similar to Sedge-Dryas Tundra. Well-drained soils with a very thin organic mat over river deposits.

[a]From Jorgenson et al. (1994)

between July 26 and August 13. The thaw depth analysis included one more year of data than the plant cover data (1998).

DATA ANALYSIS

To address a null hypothesis of no trend in plant percent cover over time, we analyzed changes in cover of seven different plant growth forms and four plant community types (Table 1). Community types with small sample sizes were aggregated with other types that had similar species composition and landscape positions: the two Shrub Tundra plots were included with Tussock Tundra, the one Wet Graminoid plot was included with Sedge-Willow Tundra, and the three Dryas Terrace plots were combined with the Riparian Shrublands plots.

We used linear mixed-effect models to incorporate both fixed-effect parameters and random effects (Pinheiro and Bates, 2000). The fixed effects (year and plant community type) quantified how these attributes influenced the mean response (i.e., percent cover). Note that the fixed-effect parameters are interpreted in the same manner as a multiple regression analysis that does not incorporate

a random effect. We modeled plot as a random effect to account for the repeated measurements on each plot (i.e., the "within-plot" temporal dependence structure of the observations). By averaging over the distribution of the plot-specific random effects, we obtained the mean response of the population, expected percent cover, characterized by the fixed effects.

We originally fit the models using a binomial response, but the models were overdispersed and diagnostics indicated poor model fit. Instead, we transformed percent cover using $\sin^{-1}\sqrt{}$. The transformation is frequently used for "percent data" because it is variance stabilizing (Zar, 2010); moreover, the transformed normal response fit our data.

We fit the following five models to seven plant growth forms:

$$\sin^{-1}\sqrt{peccent\,cover} = \alpha_{Plot} + \beta_0 + \in$$
$$\sin^{-1}\sqrt{peccent\,cover} = \alpha_{Plot} + \beta_1 Year + \in$$
$$\sin^{-1}\sqrt{peccent\,cover} = \alpha_{Plot} + \beta_2 + \beta_2 PlantComm + \in$$
$$\sin^{-1}\sqrt{peccent\,cover} = \alpha_{Plot} + \beta_0 + \beta_1 Year + \beta_2 PlantComm + \in$$
$$\sin^{-1}\sqrt{peccent\,cover} = \alpha_{Plot} + \beta_0 + \beta_1 Year + \beta_2 PlantComm + \beta_3 Year * \beta_4 PlantComm + \in$$

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where percent cover was the percentage of hits from 200 pins in a vertical point frame, with the transformation $\sin^{-1}\sqrt{}$ (Zar, 2010).

α_{Plot} was the intercept for the plot random effects.

Year was fitted as a linear trend.

PlantComm: This covariate included four different plant community types that represented factors that could influence plant response through time, including site conditions (e.g., depth of the soil active layer above permafrost, moisture regime, nutrient availability) and biological conditions (e.g., vegetation structure, plant community composition, competing species).

$\in$ was random error.

We examined standard diagnostics for multiple regression analyses and also examined whether the distribution of the random intercepts (plot effects) were approximately normal. We examined residual plots for the fixed effects and for the random effects and found no evidence of nonconstant variance. We examined normal probability plots of residuals and did not find any evidence of departure from a normal error distribution for cover data. Normal probability plots and residual plots were examined and we found no data points were overly influential in our models.

To select the best model, we used an information theoretic approach where the "best" model had the smallest AIC (Akaike's Information Criterion; Burnham and Anderson, 2002).

Depth of seasonal soil thaw above permafrost (thaw depth) was modeled as with the plant cover data. Only the three upland community types were included, because soil was too rocky for probing in the riparian types. The thaw depth analysis included one more year of data than the plant cover data (1998).

All analyses were conducted in Program R 3.1.1 (R Development Core Team, 2010).

In addition to the analyses by plant growth form, we examined plant cover data for vascular plants, nonvascular plants, some individual species, and more narrowly defined plant growth forms: some dominant deciduous shrub species as well as erect versus prostrate deciduous shrub species; bryophytes divided into pleurocarpous mosses (feathermosses), acrocarpous mosses, *Sphagnum* mosses, and liverworts; lichens divided into foliose, fruticose, and crustose species; and sedges vs. grasses. These taxa are discussed in the supplementary materials.

Results

Trends in plant cover over the 25-year study period were detected for five of the seven plant growth forms. Changes varied among plant community types for three of these growth forms.

For lichens, the best model included an interaction between year and community type (Table 2). There were decreasing trends in lichen cover in the three upland community types. Our model estimated decreases in Sedge-Dryas Tundra (22% to 9% cover) and Tussock Tundra/Shrub Tundra (17% to 10%), with changes of only 2% in the other two community types (Fig. 2). This model had 100% of the weight in the model set, indicating strong support for it compared with the other fitted models (Table 2).

For bryophytes, the best model included a year effect, and the change in percent cover did not vary by community type. This model estimated a 4% decrease in percent cover during the years of this study from 60% to 56% (Fig. 2). We consider this year effect to be weak because the best model containing a year effect was only a small improvement over the null model (0.8 AIC value).

For deciduous shrubs, the best model included a year effect. Our model estimates a 3% decrease in cover, from 19% to 16% (Fig. 3). Examination of raw percent cover data for species and

subgroups of deciduous shrubs that have shown trends in other studies revealed no patterns of increasing abundance over all plant community types, or within specific community types. For example, Appendix Fig. A1 shows no increases for diamondleaf willow (*Salix pulchra*), shrub birch (*Betula nana*), or total erect deciduous shrubs.

For evergreen shrubs, we found no evidence of any trend in percent cover over the study period (Fig. 3). The best model for this growth form contained only community type.

For graminoids, there was strong support for the model that included a year and community type interaction; this model contained 100% of the weight of the model set. There was an increasing trend over time in percent cover of graminoids in Sedge-Dryas Tundra (from 9% to 16%) (Fig. 4). There were declining trends for graminoids in the other three community types: 16% in 1984 to 11% in 2009 for Sedge-Willow/Wet Graminoid and small changes for the other two community types.

For forbs, there was strong support for the model with a year and community type interaction. Percent cover of forbs changed over the study period, mainly in combined Riparian Shrublands/Dryas Terrace communities, where the percent cover declined from 12% to 5% (Fig. 4). This was due to decreases in cover of legumes.

For horsetails, we found no evidence of change over the study period (Appendix Fig. A2). The best model for horsetails contained only the community type.

For soil thaw depth, there was no trend over time (Fig. 5). We fit an additional model with the year term squared because the high thaw depth values in 1998 indicated that a polynomial term might fit the data better than a linear relationship. The null model fit our data better than the other models.

Discussion

This study provides evidence for changes in abundance of lichens, graminoids, and forbs in some plant community types on the coastal plain of the Arctic Refuge between 1984 and 2009. Where trends in percent cover were detected, they were generally modest and decreasing over time. The only large increase in cover was for graminoids in the Moist Sedge-Dryas community type, but it decreased in three other communities. Lichen cover decreased in the upland plant community types. Forb cover decreased in the riparian type. Cover of bryophytes and deciduous shrubs showed slight decreasing trends over the study period, while evergreen shrubs and horsetails had no trends.

Changes in plant communities were smaller than would be expected based on results from other studies in northern Alaska, including remote sensing (Bhatt et al., 2013), repeat aerial photography (Tape et al., 2006), long-term vegetation plots (Mercado-Díaz and Gould, 2010), and experimental warming plots (Sistla et al., 2013).

The lack of an increasing trend for cover of shrubs in these plots was unexpected. Burgeoning deciduous shrubs are believed to be driving a major vegetation transition in northern Alaska (Chapin et al., 2005; Jia et al., 2003; Tape et al., 2006). That view is supported by two nearby studies whose locations bracket our study area. Permanent plots 225 km to the southwest at Toolik Lake Long Term Ecological Research Station showed increased cover and height of shrubs and graminoids between 1989 and 2009 (Mercado-Díaz and Gould, 2010). At Herschel Island, 155 km east of our area, Myers-Smith et al. (2011) observed increases in abundance of all dominant willow canopy species in similar vegetation types to our study and over the same time period.
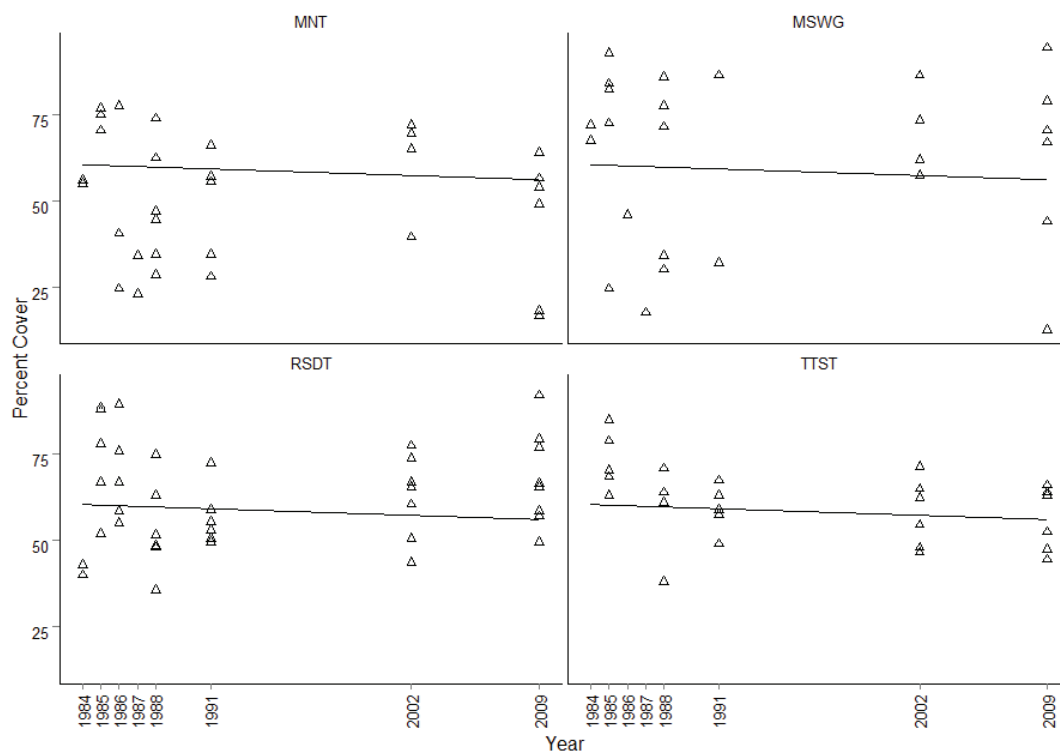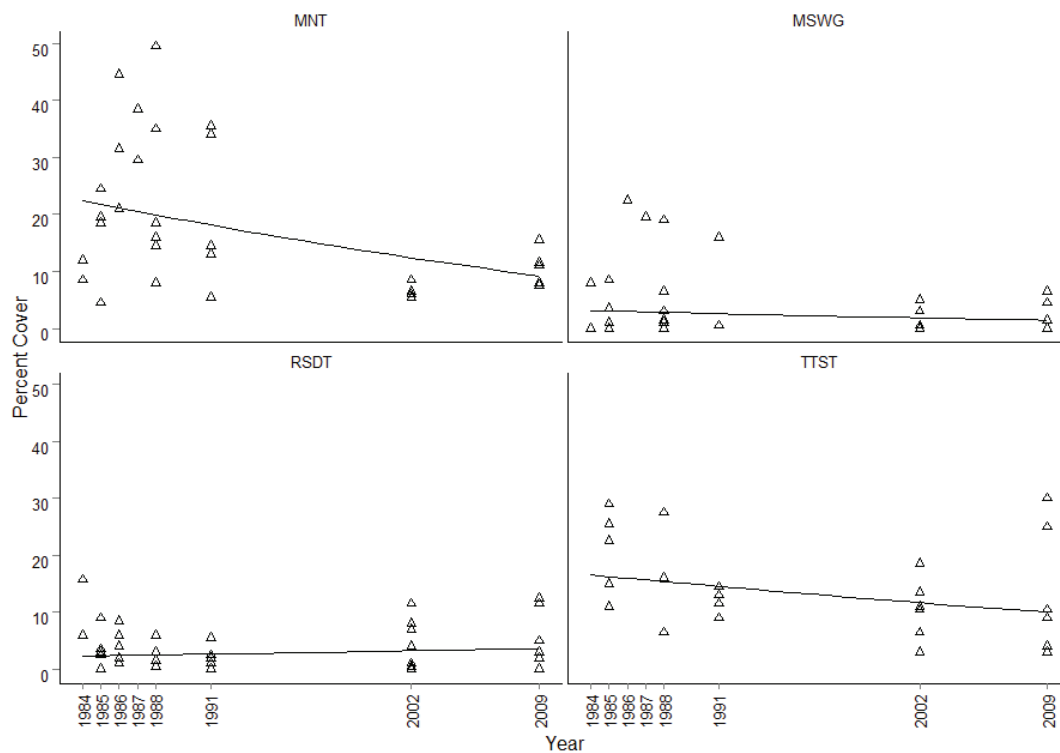
FIGURE 2. Trends in percent cover for lichens (top) and bryophytes (bottom) in plots in northeastern Alaska. Triangles represent raw data, and trend lines represent model predictions from a linear mixed-effect model containing an interaction between year and plant community. Panels show data and trends within four plant community types: MNT = Sedge-Dryas tundra, MSWG = Sedge-Willow/Wet Graminoid tundra, RSDT = Riparian Shrubland/Dryas Terrace, TTST = Tussock Tundra/Shrub tundra.

The decreases for bryophytes and lichens that we found in the study area are consistent with results reported elsewhere in the Arctic (e.g., Cornelissen et al., 2001; Pajunen, 2009; Wahren et al., 2005). Tundra warming experiments have also caused reductions in bryophytes and lichens (Elmendorf et al., 2012a; Hollister et al., 2005). Most of these studies attributed the decreases to shad-

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TABLE 2

Results from five models fitted to percent cover data from seven plant growth forms. Data were collected from 1984 to 2009 in the Arctic National Wildlife Refuge, Alaska.

Growth form		Null	Year	Plant Comm	Year + PlantComm	Year – PlantComm Interaction
Lichens	ΔAIC	37.0	29.0	23.5	14.9	**0.0**
	Weight	0	0	0	0	**1.00**
Bryophytes	ΔAIC	0.8	**0.0**	4.3	3.4	2.1
	Weight	0.29	**0.43**	0.05	0.08	0.15
Deciduous Shrubs	ΔAIC	2.2	**0.0**	3.4	1.3	2.6
	Weight	0.15	**0.44**	0.08	0.22	0.12
Evergreen Shrubs	ΔAIC	12.9	14.7	**0.0**	1.9	7.0
	Weight	0	0	**0.70**	0.28	0.02
Graminoids	ΔAIC	25.1	27.1	12.7	14.7	**0.0**
	Weight	0	0	0	0	**1.00**
Forbs	ΔAIC	39.1	38.1	21.7	20.8	**0.0**
	Weight	0	0	0	0	**1.00**
Horsetails	ΔAIC	23.4	25.2	**0.0**	1.8	5.7
	Weight	0	0	**0.69**	0.28	0.04
Degrees of Freedom		3	4	6	7	10

The header "Model descriptions" spans the five model columns.

Results from six models fitted to the thaw depth data.

	Null	Year	PlantComm	Year + PlantComm	Year – PlantComm Interaction	Year^2
ΔAIC	0	1.6	1	2.6	4.9	1.2
Weight	0.34	0.15	0.21	0.09	0.03	0.19

ing and litter accumulation from increasing vascular plants. In our study, lichens decreased most where there were large increases in graminoids.

There was no trend for depth of the soil active layer above permafrost, but depths were greatest in 1998, when the summer was unusually warm. Data from the Prudhoe Bay area (approximately 200 km west of the study area) show exceptionally warm summers in 1989 and 1998, with correspondingly deeper thaw depths (Streletskiy et al., 2008). Plant cover data were not collected in 1998, but sedge growth was notably lush in our plots that summer (e.g., Fig. 6).

A cool summer climate may be one reason for the few vegetation changes shown by this study. Elmendorf et al. (2012a, 2012b)

suggested that substantial vegetation changes, driven by shrub increase, may be most likely in warmer parts of the Arctic. Such areas are ecological transition zones and therefore prone to change. There are no long-term climate stations in our area and few on the North Slope of Alaska, but gridded climate data indicate that our study area may be cooler during the growing season than the more inland parts of the North Slope, probably because of proximity to the Beaufort Sea coast (Comiso, 2006; PRISM Climate Group, 2008). Growing season temperatures are higher in places on Alaskan tundra that have shown the most vegetation change, such as the foothills of the central North Slope (Mercado-Díaz and Gould, 2010; Tape et al., 2006) and the Seward Peninsula of western Alaska (Joly et al., 2009; Silapaswan et al., 2001).
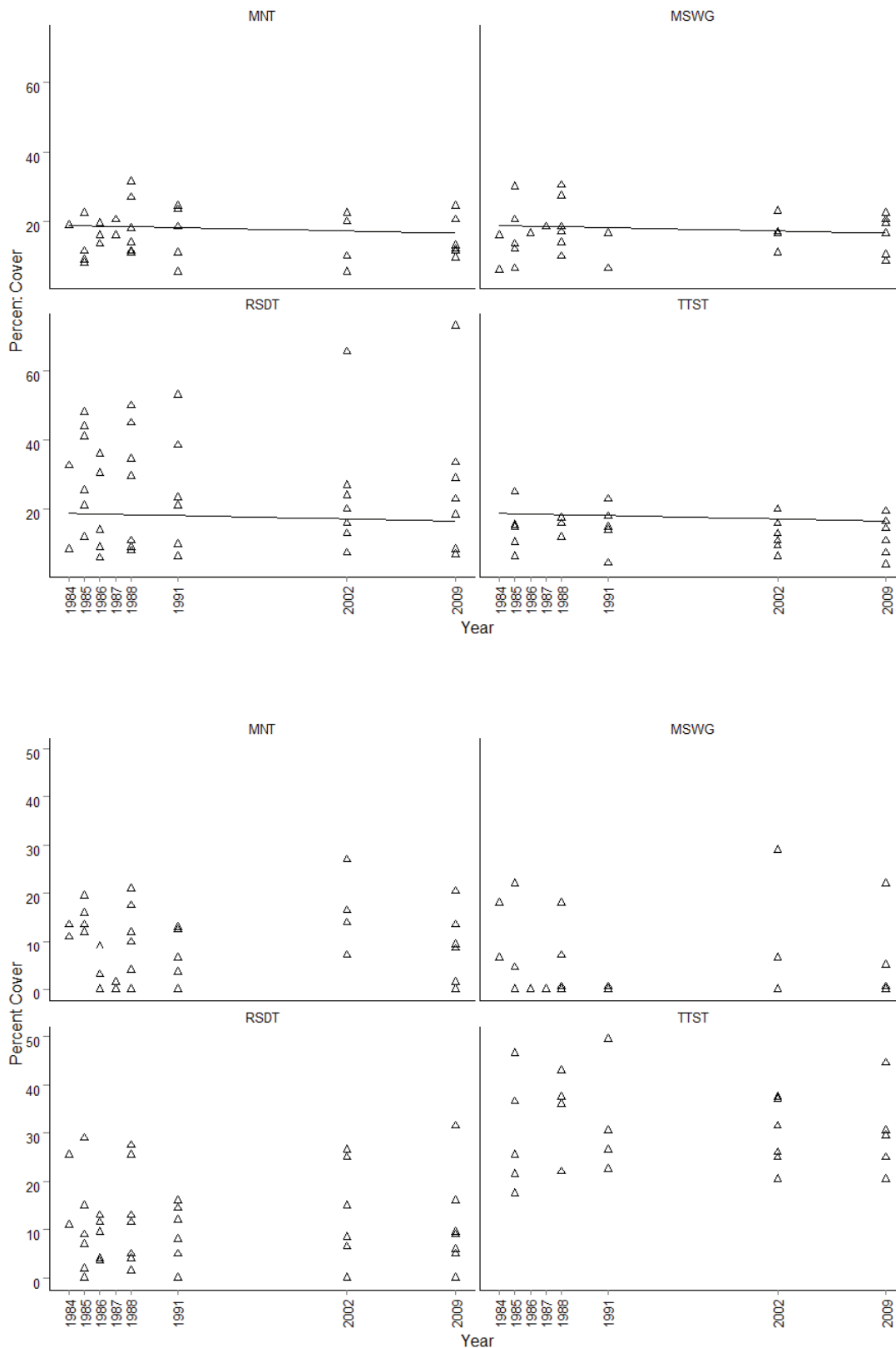
FIGURE 3. Percent cover of deciduous shrubs (top) and evergreen shrubs (bottom) in plots in northeastern Alaska. The decrease for deciduous shrubs did not vary by plant community. No trends were detected for evergreen shrubs. See Figure 2 for abbreviations.

Our results suggest spatial heterogeneity in the response of vegetation to climate change. Instead of broad-scale changes in vegetation predicted by NDVI, we found differing patterns in different plant community types. Response to climate change is not likely to be uniform across a mosaic of different plant communities, whose distribution at the local scale are determined not by air
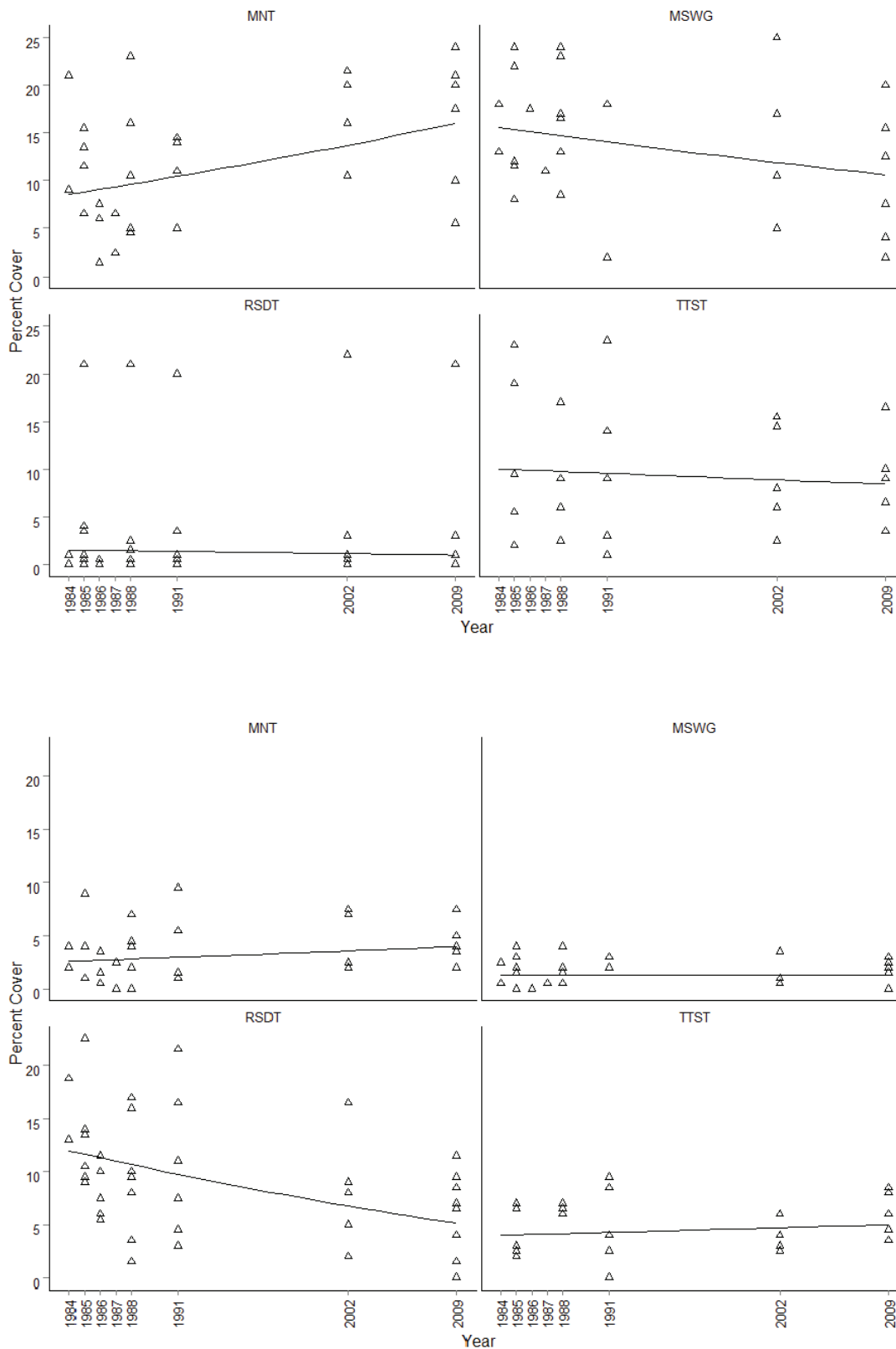
FIGURE 4. Percent cover of graminoids (top) and forbs (bottom) in plots in northeastern Alaska. The models contained interactions between year and plant community. See Figure 2 for abbreviations.

temperature but by topographic position as it controls factors such as soil moisture, texture, ground ice, and nutrient status. In addition, we found that vegetation change in our area has been patchy.

In most individual plots, plant community composition showed few directional changes over the 25-year period. In contrast, 3 of the 27 plots had dramatic changes.
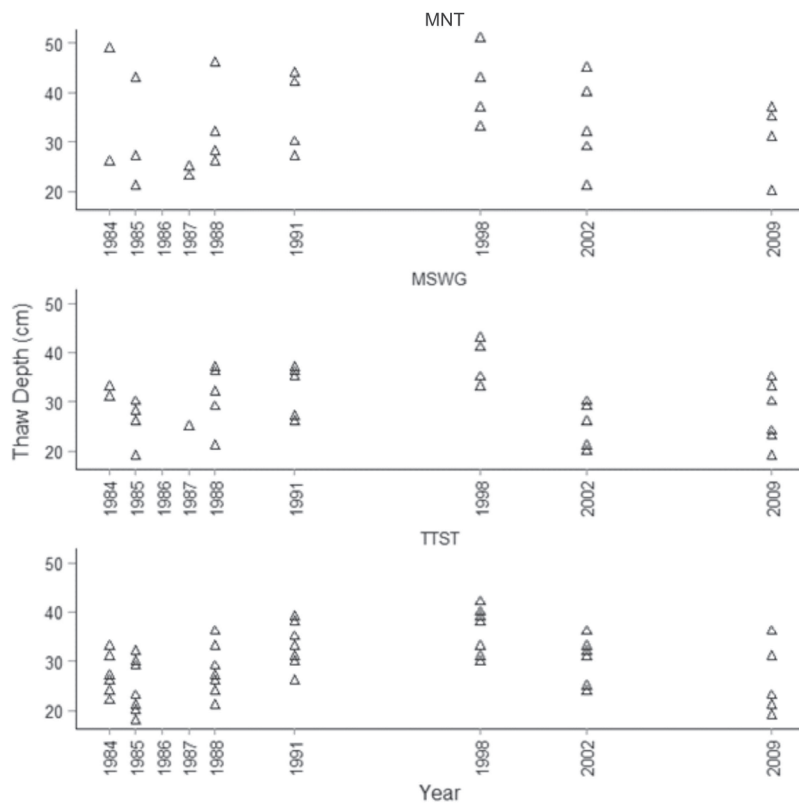
FIGURE 5. Thaw depth in plots in northeastern Alaska. No trends were detected. The best model did not include a year term with either a linear or polynomial model. Thaw depths were not measured in the RSDT community type. See Figure 2 for abbreviations.

Ground ice, which varies by landscape age, soil texture, and drainage (Jorgenson et al., 1998), is likely a large factor in the patchy vegetation change, since many of our plots had high soil ice content. Sampling done at 18 of our 27 plots showed that excess ice in the top 30 cm of the permafrost ranged from 2% to 45% by volume (Jorgenson et al., 2010). In addition to this ice in the soil matrix, vertical ice wedges form massive ice just below the thawed soil layer and are very sensitive to disturbance and climate change (Jorgenson et al., 2006; Raynolds et al., 2014). Ice wedges commonly occupy 10%–15% of the volume of the top 3 m of permafrost, but can be highly variable depending on surficial geology (Kanevskiy et al., 2013). Fifteen of our plots had patterned ground indicative of subsurface polygonal networks of ice wedges. Two plots showed extreme changes in microtopography and vegetation over the study period. Melting of ground ice caused soil subsidence, surface wetting, and large increases in graminoids and decreases in lichens and bryophytes. Ponds formed above melting ice wedges in one plot, covering 22% of the plot area with water by the later years of the study (Figs. 6 and 7). Obvious melting of ground ice did not occur at most plots with polygonal patterned ground, but instead occurred more at polygonized plots that had a discontinuous vegetative mat, which therefore had less insulation against summer warmth.

Floodplain dynamics were another source of patchy vegetation change. In one Riparian Shrubland plot, which was in a more frequently flooded topographic position than the other riparian plots, the willow canopy became denser and taller (Figs. 3 and A7).

An analysis of NDVI patterns at our plots also suggests that what vegetation change has been observed in the area has not been uniform. Pattison et al. (2015) found that the general increase in NDVI detected by AVHRR satellite data for our area was not supported by NDVI derived from finer-scale LANDSAT-TM imagery (30-m pixels). This agrees with Raynolds et al. (2013), who report-ed that a general increase in coarse-scale (AVHRR) NDVI in an area 225 km southwest of our study area, previously interpreted as a tundra-wide increase in plant productivity, consisted of patches of NDVI increase within a matrix of nonchange, when mapped with finer-scale satellite data (LANDSAT-TM). Only 5% of that area had increasing LANDSAT NDVI, which was generally related to disturbance. Fraser et al. (2011) found that LANDSAT NDVI increased on only 6% of an area in the Yukon Territories just east of our study area.

Ecological lags and buffers may slow the response of tundra vegetation to climate change. Plant species characteristics and interactions likely prevent plant community composition from shifting rapidly in response to annual changes in weather or to a climate warming trend. Dominant species in our study area are long-lived perennials, often with conservative growth strategies for survival in a harsh and unpredictable climate (Bliss and Petersen, 1992). Most plots were completely covered in live vegetation and associated plant litter. An increase in any plant species would probably be at the expense of other species, unlike in the high Arctic where plant cover is sparse. Species interactions likely provide negative feedbacks that slow vegetation change (Camill and Clark, 2000; Dormann and Woodin, 2002).

We have no evidence that herbivory affected our results; however, long-established relationships between plants and herbivores control plant community composition and could cause unexpected responses to changing climate (Gough et al., 2007; Pajunen, 2009). Tundra exclosure studies demonstrate the impacts of herbivory by large and small mammals, particularly on lichens, deciduous shrubs, and other deciduous plants (Olofsson et al., 2009; Post and Pedersen, 2008). The Porcupine Caribou Herd moves through the study area in the summer and herd size increased from an estimated 135,284 in 1983 to 169,000 in 2010 (Caikoski, 2011). The main forage for caribou in our study area is deciduous plants: graminoids
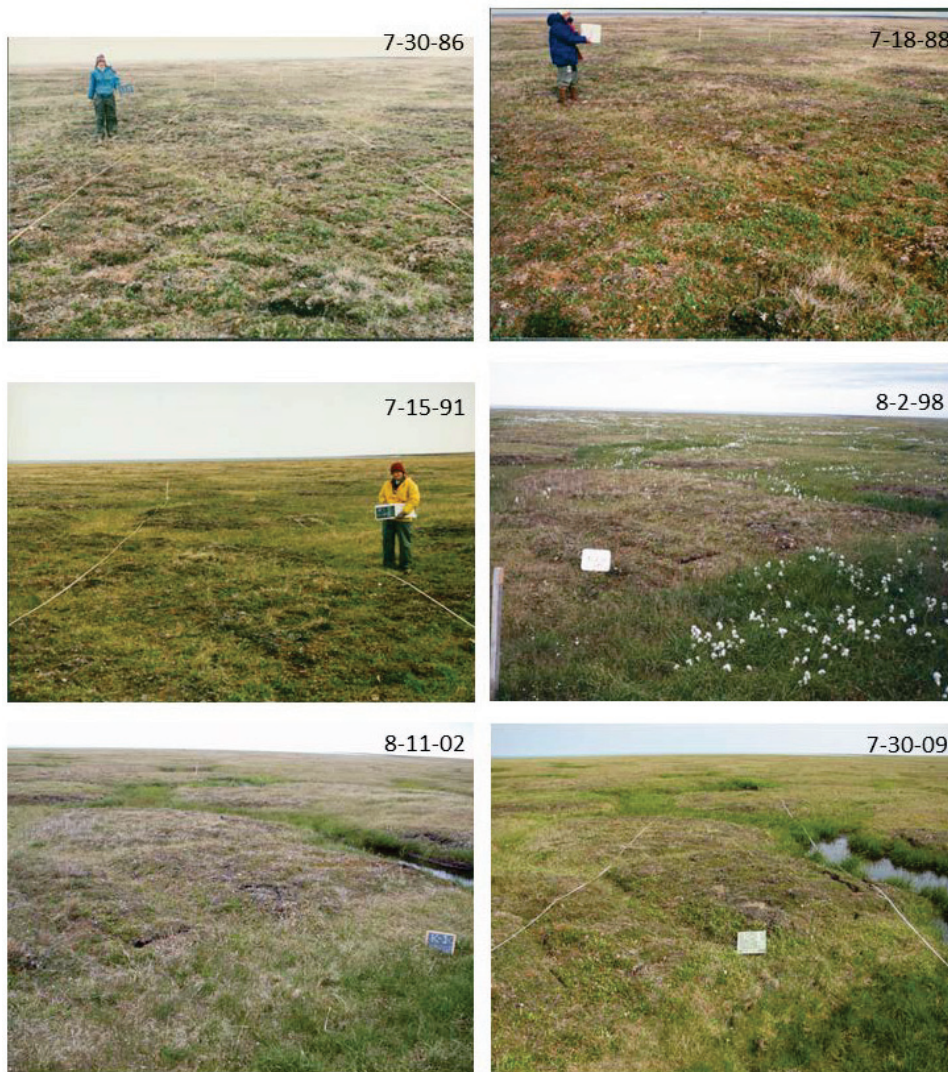
FIGURE 6. Photo series of a Sedge-Dryas plot showing subsidence of polygon troughs due to melting of ground ice over 25 years.

and willows during snow melt and willows and forbs for the rest of the summer (Griffith et al., 2002). They leave the area for the winter, seeking lichens elsewhere. Impacts on plants from caribou foraging are surprisingly hard to see in our plots, perhaps because the caribou move through the area quickly and strip flowers and leaves, rather than biting shrub stems. Signs of foraging by birds are sometimes visible, such as willow bud removal by ptarmigan. Heavy ptarmigan browsing during the snow season may limit erect shrub growth, unless snow depths increase and cover apical buds (Tape et al., 2010).

The link between a changing climate and plant community composition is mediated by physical factors that have longer response time than the direct effects of air temperature (Shaver and Kummerow, 1992; Camill and Clark, 2000). Edaphic conditions are particularly important. Soil temperature is likely more important to plant growth in the Arctic than air temperature (Chapin et al., 2005) and is buffered by the insulating dense moss mat present on almost all of our plots and the presence of continuous permafrost within 0.2 to 1 m of the surface. Plant species composition may be slow to shift until temperatures in the plant rooting zone increase. Snow depth and soil moisture, for which we have no trend data, are also major factors controlling plant productivity (Gamon

et al., 2013). In an experiment by Wahren et al. (2005), increased snow depth had a greater positive impact on vegetation than experimental summer warming.

A change in disturbance regime may be required to overcome the stabilizing feedback effects that maintain Arctic ecosystems, in order for large vegetation changes to occur in as few as 25 years. Jorgenson et al. (2015) identified a number of disturbance-related drivers that affected vegetation change in northern Alaska, but projected only modest shifts in vegetation communities over the next 100 years. Within a localized area, however, changes can be dramatic. For example, plots established on tundra disturbed by vehicle traffic in our study area showed large changes in vegetation over the period of this study (Jorgenson et al., 2010). Trails that subsided due to melting ground ice had greatly increased sedge cover, while some trails without subsidence had a short-lived flush of grass growth. While monitoring of disturbed plots in this study clearly showed these and other plant cover changes over time, including changes in dominant plant growth forms as disturbance levels worsened or recovered, most of the adjacent control plots remained quite stable. This and the vegetation changes documented on our plots where ice wedges melted show that vegetation in our study area is capable of rapid change if microtopography and soil
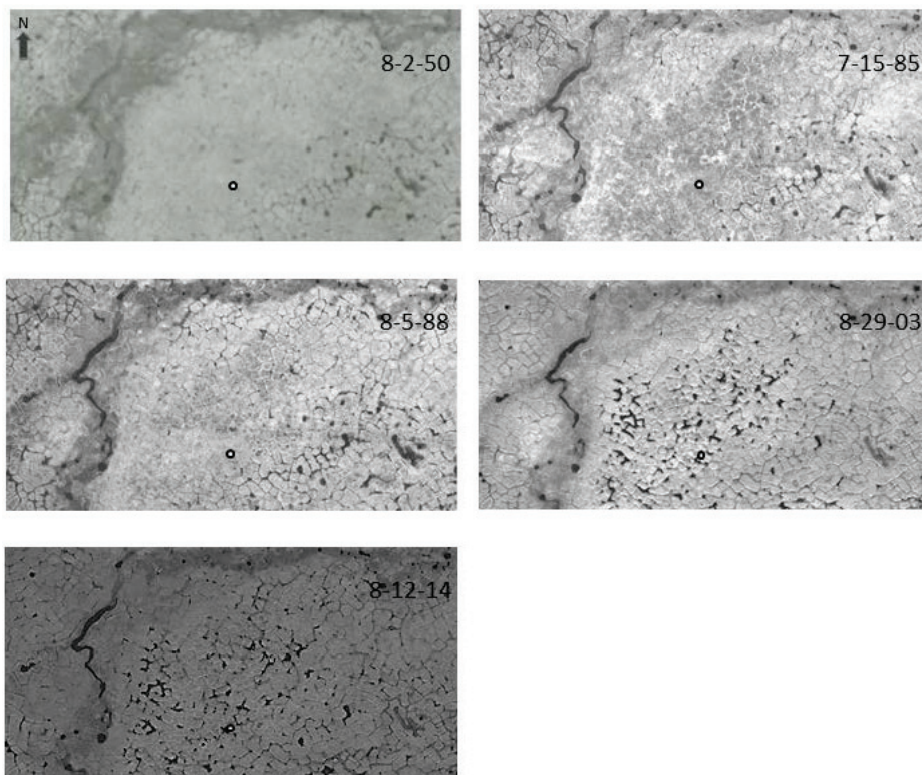
FIGURE 7. Location of the plot shown in Figure 6. Note increase of water on the landscape, especially north and west of the plot (circle). The polygonal networks of wet troughs visible on the images are caused by a buried ice wedge under each trough. Aerial photographs from first three years are 1 m, 0.6 m, and 0.4 m resolution, respectively. Resolution is 0.6 m for 2003 and 2014 satellite imagery.

moisture are altered. Tape et al. (2011) documented the patchiness of shrub increase in northern Alaska, with greater shrub increase in high-resource environments, often riverine sites disturbed by flooding, and little change in low-resource environments, including most of the tundra vegetation not situated along rivers or in drainages. Walker et al. (2009) and Lantz et al. (2009) also pointed out the importance of disturbance to vegetation change, including permafrost thawing and landslides. A case of shrub invasion at the western edge of our study area highlights the importance of disturbance. Willows have grown tall around a gravel pad constructed in the early 1970s (Fig. 8). The striking difference between the tall willows and the low vegetation of the surrounding tundra is probably not due to climate change but instead to altered growing conditions from soil disturbance and greater winter snow depth.

Conclusions

Monitoring of 27 permanent vegetation plots over a quarter century showed that changes in plant cover were usually modest, in contrast to other studies indicating there have been large vegetation changes across Arctic Alaska over this time period. We found no increasing trends for percent cover of shrubs and few for other plant growth forms. Vegetation change was patchy, with most plots changing little over the study period but dramatic changes in three of the plots. Those three experienced disturbances linked to ground ice melting or floodplain dynamics.

This study provides "ground-truth" data for quantifying current patterns and rates of change of Arctic tundra and highlights the need for greater work linking plot-level and regional remote

FIGURE 8. Tall willows at edges of gravel pad constructed near the study area during oil exploration in 1972–1974, photographed in 2005. Location is on Figure 1. The difference between the tall willows and the low vegetation of the surrounding tundra is probably due to altered growing conditions including protection afforded by deeper snow accumulation in winter (late-melting snow banks visible on summer satellite images), as well as disturbance of the soil temperature, moisture, texture, and thaw depth from soil subsidence and gravel inputs from the pad. Site is about same elevation as our highest elevation study plots.

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sensing measurements of change. Such work is essential to correctly identify local-scale factors controlling expected regional-scale vegetation transitions, and thus provide further insight into likely spatial and temporal variability of those transitions. This study contributes to this essential step toward realistic regional and circumpolar projections of climate change impacts, future plant communities, and vegetation feedbacks to climate.

Acknowledgments

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APPENDIX

Online Supporting Information

In this supplement, we provide more information on the plant composition of the study area. In addition, we examine changes over time in plant cover data for some individual species and more narrowly defined plant growth forms. These include the following: bryophytes divided into pleurocarpous mosses (feathermosses), acrocarpous mosses, *Sphagnum* mosses, and liverworts; lichens divided into foliose, fruticose, and crustose species; some dominant deciduous shrub species as well as erect vs. prostrate deciduous shrub species; and sedges vs. grasses. These results are limited because they do not test statistical significance, but they provide information on ecological relationships. We also summarize trends over time for each plant community type.

Supporting Information by Plant Growth Form

BRYOPHYTES

Bryophytes (mosses and liverworts) carpeted the study area, with higher cover than all vascular plants combined. Pleurocarpous mosses (feathermosses) formed dense mats and provided over three-quarters of the bryophyte cover. The remainder was made up of acrocarpous mosses, most common in Sedge-Dryas Tundra, Tussock Tundra, and Shrub Tundra; liverworts, most common in

Salix pulchra (Diamondleaf willow)
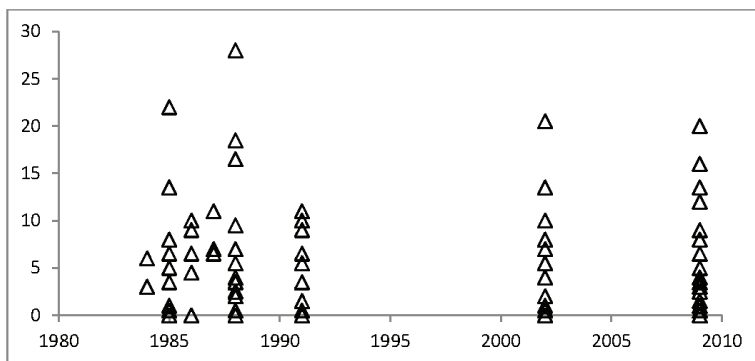
Betula nana (Shrub birch)
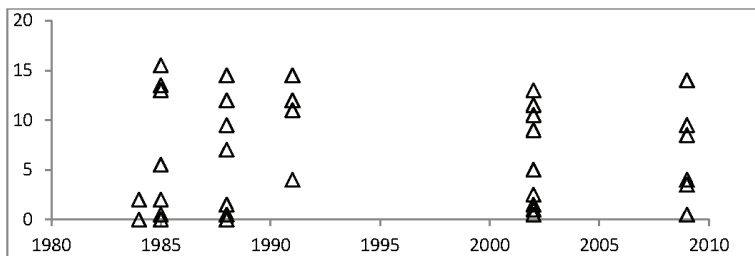
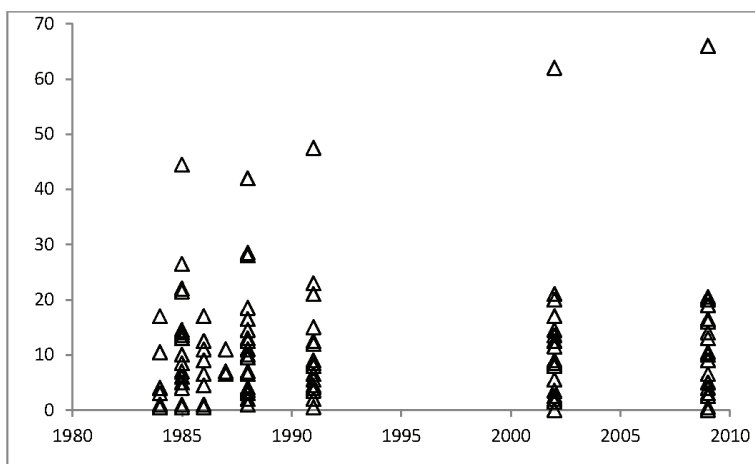Erect deciduous shrubs (all deciduous shrubs except prostrate species)

FIGURE A1. Percent cover data for some types of deciduous shrubs that have shown increases in other studies in northern Alaska. Data include all plant community types.
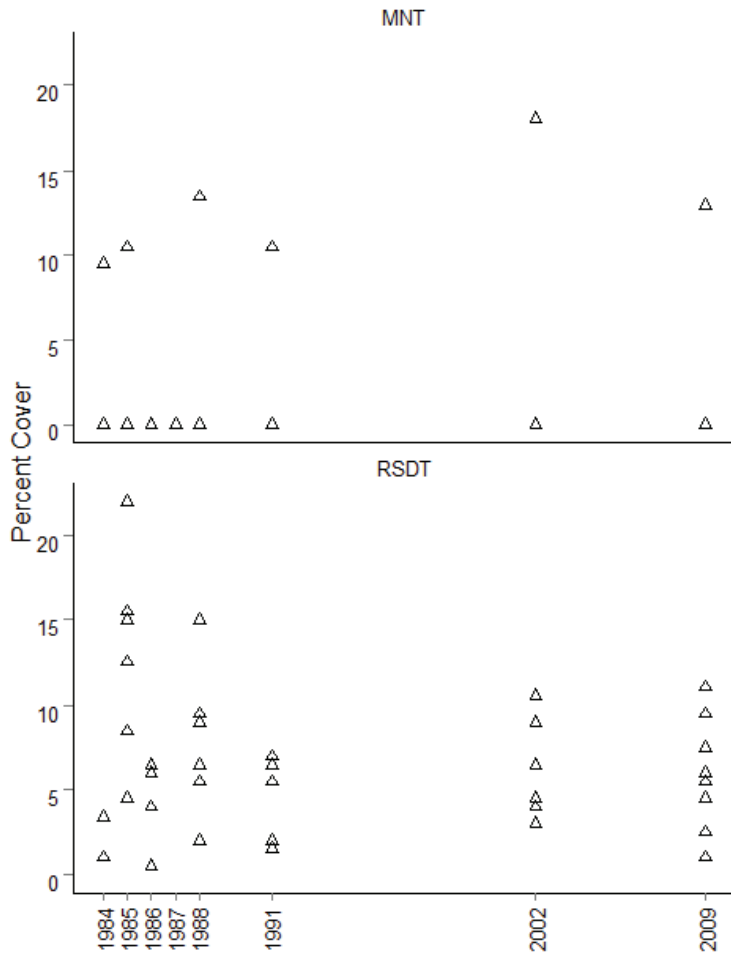
FIGURE A2. Percent cover of horsetails in plots in northeastern Alaska. No trends were detected. Horsetails were not present in MSWG and TTST. Figures for other growth forms are in the main paper.

Sedge-Dryas; and *Sphagnum* mosses, most common in Sedge-Willow and Tussock Tundra. The most common taxa in descending order were *Tomentypnum nitens, Hylocomium splendens, Aulacomnium turgidum, Dicranum* species, *Sphagnum* species, and *Aulacomnium palustre*.

Bryophyte cover decreased slightly during the study period (Fig. 2). Based on raw data summaries for narrowly defined growth forms, acrocarpous mosses, and liverworts decreased, while feathermosses and *Sphagnum* moss did not. Also, while most species decreased over time, the most common species did not. For the two most common feathermosses, *Hylocomium splendens* changed little and *Tomentypnum nitens* usually increased over time, especially in plots where it was the dominant bryophyte. *Sphagnum* increased at 11 of the 12 plots where it had more than 1% cover. This is consistent with Lang et al. (2012), who found that while most bryophytes declined with experimental or naturally warmer temperatures, *Sphagnum* and common pleurocarpous mosses responded positively.

In plots that had very large decreases in bryophyte and lichen cover during the study, acrocarpous mosses and liverworts were the common species in the early years and decreased greatly over time. Pleurocarpous mosses were nearly absent. It appears that acrocarpous mosses were most common in environments that were in transition and pleurocarpous mosses dominated in environments that were more stable.

LICHENS

Lichen cover was much lower than bryophyte cover. Because of the dense vegetative cover in this low-Arctic study area, the most common species were foliose lichens, which apparently tolerate shading by vascular plants better than the other lichens. The most common taxa were, in order of abundance, *Peltigera aphthosa*, other *Peltigera* species (mainly *P. canina* and *P. malacea*), crustose lichens (*Ochrolechia frigida* and others), *Cladonia* species, *Cetraria* species, *Flavocetraria* species, and *Dactylina arctica*. The foliose *Peltigera aphthosa* thrived in moist, partly shady microhabitats, with an affinity for evergreen shrubs. The other lichen species grew in more exposed microsites. Lichens were most abundant and diverse in the Sedge-Dryas community type, where they were associated with greater bare soil.

Lichens decreased over time in the three upland plant community types, with large decreases in some Sedge-Dryas plots (Fig. 2). The decline in lichens held true for all types of lichens, foliose, fruticose, and crustose. Fruticose lichens (e.g., *Cladonia*) declined in almost every plot, but increased in the three Dryas Terrace plots. Crustose lichens declined in almost every plot where present. Crustose lichens form a delicate crust on disturbed ground and were most common in the Sedge-Dryas plant community type, which had bare soil due to active frost boils. Decreases in crustose lichens may indicate stabilization of frost boils by graminoids, due
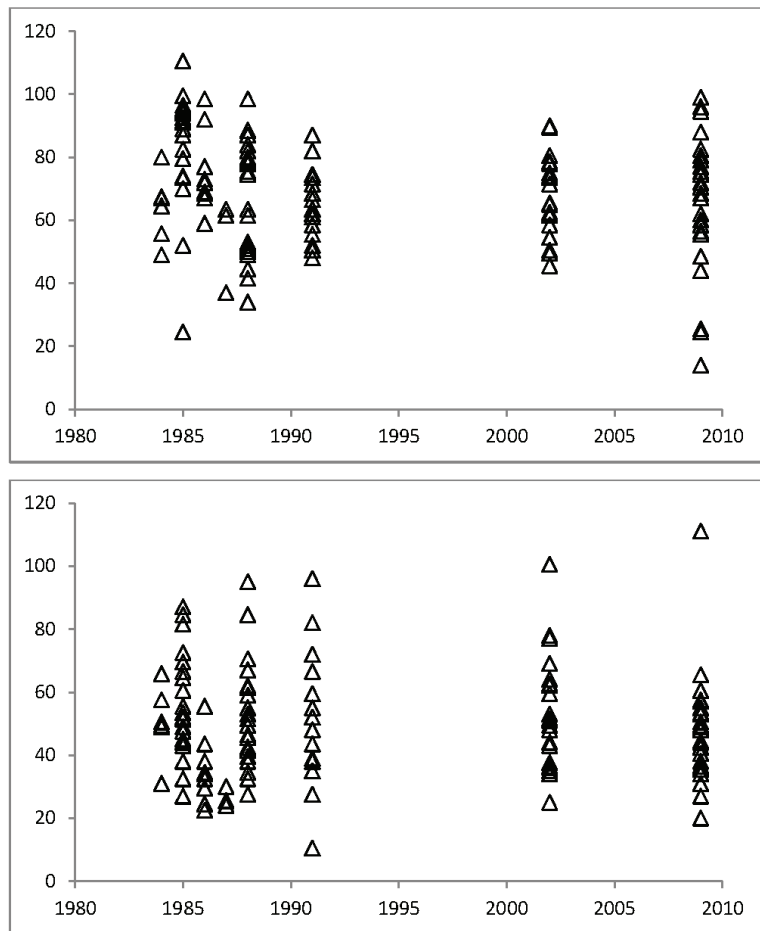
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FIGURE A3. Percent cover data summed for all nonvascular plants (top) and all vascular plants (bottom). Data include all plant community types.

to increased soil moisture after ground subsidence. Foliose lichens decreased less over time than the fruticose and crustose lichens.

In a synthesis of tundra experiments and natural environmental gradients, Cornelissen et al. (2001) found that in the low Arctic, where vegetation is dense and layered, lichen abundance was inverse to vascular plant abundance and predicted that climate warming will lead to reduced lichen abundance due to competition from taller plants. In our plots, lichen abundance was usually not lower in plots with higher vascular plant cover, probably because of the abundance of the shade-tolerant lichen *Peltigera aphthosa*.

Joly et al. (2010) reported that lichens decreased as graminoids increased on tundra in western Alaska. In our study, this occurred in the Sedge-Dryas community type. Ground subsidence and soil wetting probably explain the decreasing lichen cover in Sedge-Dryas, but subsidence was not evident in other plant community types.

DECIDUOUS SHRUBS

Thirteen species of willow (*Salix*) provided more than three-quarters of the deciduous shrub cover. The most common species in descending order were: *Salix pulchra*, the most abundant vascular plant species in this study, especially common in Sedge-Willow and Wet Graminoid; *Salix reticulata*, widespread and most common in Riparian Shrubland and Dryas Terrace; *Salix phlebophylla*, most common in Sedge-Dryas; and *Betula nana*, most common in Tussock Tundra and Shrub Tundra.

Deciduous shrub cover did not show an increasing trend (Fig. 3). Because some deciduous shrub species have shown evidence of increasing abundance over time in other studies, even if total cover of deciduous shrubs did not (e.g., Elmendorf et al., 2012b), we graphed data for important species and physiognomic groups of deciduous shrubs and found no increases over the course of the study, either over all plots or in specific plant community types. Data for *Salix pulchra* (diamondleaf willow) and *Betula nana* (shrub birch), the most commonly increasing species in other studies, and for total erect deciduous shrub cover are shown in Figure A1. The lack of increase for shrub birch in particular was unexpected because of the exuberance with which that species sometimes responds to tundra warming experiments (Bret-Harte et al., 2001) and the large shrub birch increases predicted to occur with climate change in northern Alaska by integrated ecosystem models, such as in Euskirchen et al. (2009).

In a synthesis of experimental warming plots throughout the Arctic, Elmendorf et al. (2012a) found that warming caused shrub increase mainly in parts of the Arctic with higher ambient temperatures and dominance by taller shrubs. In contrast, graminoid increase was greater in colder areas. Our study area may have a cooler summer climate than other parts of the Alaska North Slope where shrub increases have been found.

With warming growing conditions, shrubs are expected to out-compete other growth forms by shading them (Chapin, 2003). Shrubs in the study area are not presently taller than the graminoids, except in the riparian zone. At a different set of plots in this study area where canopy height was measured, canopy deciduous shrubs
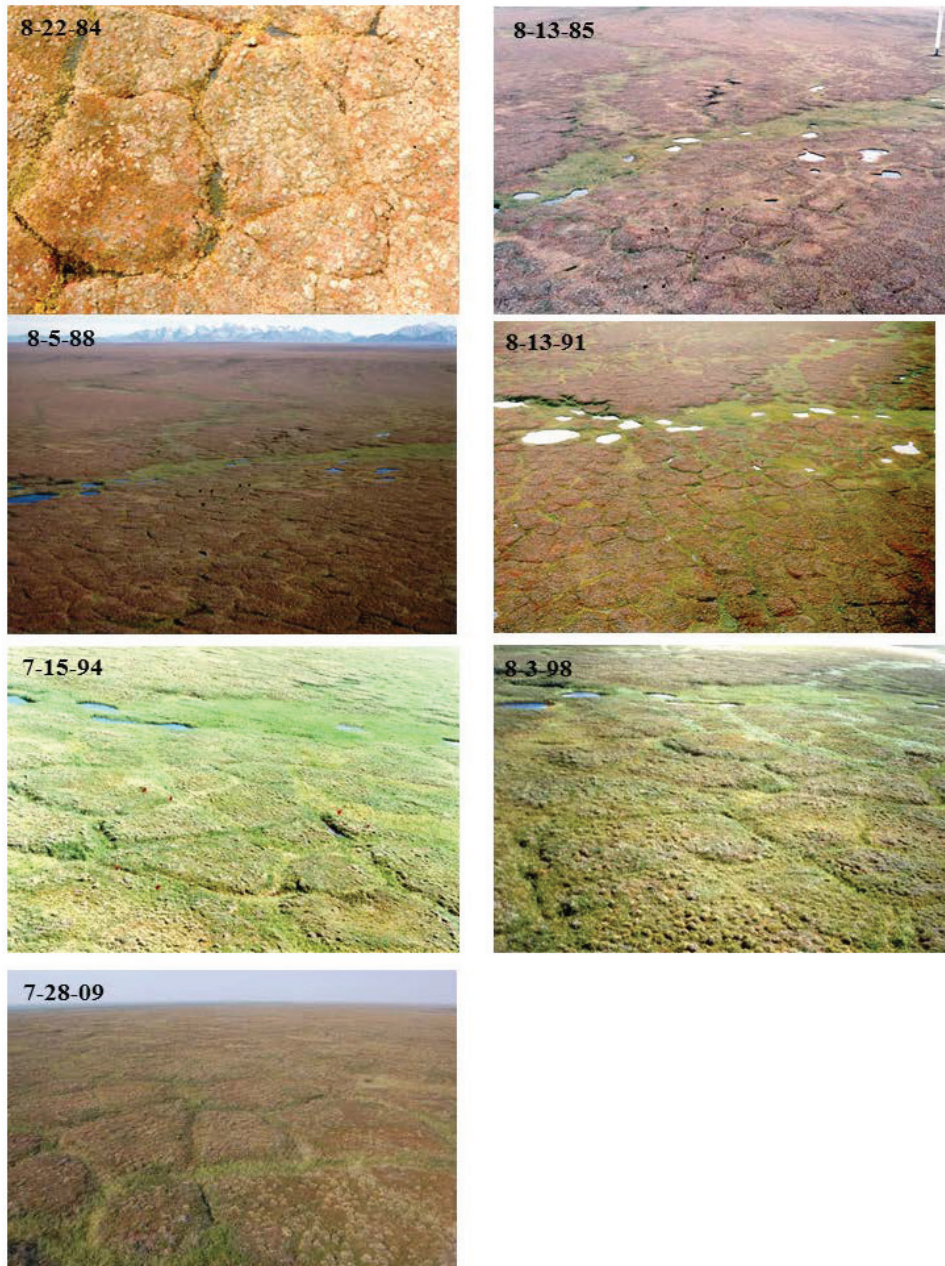
FIGURE A4. A plot on Shrub Tundra on high-centered ice wedge polygons that showed little change in vegetation or topography over 25 years. Dates are given as m-dd-yy.

were about equal in height to the graminoids while evergreen shrubs were less than half as tall (unpublished data). The balance between shrub and graminoid dominance may in many cases be more affected by soil moisture than shading. Shrubs in our study area tend to grow on more well drained microsites and graminoids on wetter, poorer drained microsites, so a shift in dominance from graminoids to shrubs may occur sooner if soil moisture decreases. Soils could become better drained in the future if higher air temperatures increase potential evapotranspiration, with or without increased precipitation, or if increased thaw depths or differential thaw settlement cause a lowering of the water table on parts of the landscape.

EVERGREEN SHRUBS

The main evergreen shrubs in the study area, all dwarf species, were *Dryas integrifolia, Vaccinium vitis-idaea, Rhododendron tomentosum (Ledum decumbens)*, and *Cassiope tetragona*, in descending order of abundance. Evergreen shrub cover was greatest in Tussock Tundra/Shrub Tundra and lowest in Sedge-Willow/ Wet Graminoid. *Dryas integrifolia* grew with dwarf willows and was common in Riparian Shrubland, Dryas Terrace, and Sedge-Dryas. The other evergreen shrubs were common in Tussock Tundra and Shrub Tundra, usually with *Betula nana*. Evergreen shrub cover was greater in plots with abundant lichens and bryophytes and lower in plots dominated by erect willows and graminoids.

Cover values for evergreen shrub species were more constant year to year than other growth forms and showed no trend over time (Fig. 3). When graphed separately, neither ericaceous shrubs nor *Dryas* shrubs showed a trend.

In leaf productivity and nutrient tests at plots disturbed by vehicles in our study area, the evergreen shrubs *Vaccinium vitis-idaea* and *Rhododendron tomentosum* showed less response to the post-

FIGURE A5. Moist Sedge-Willow plot on polygonized tundra where polygon troughs did not subside and vegetation did not change greatly over the 25 year period. The 1988 photograph shows undisturbed plot on the right. Plot on left was on a winter ice airstrip made in 1985.

disturbance nutrient flush than the deciduous shrubs *Salix pulchra* and *Betula nana*, indicating a more conservative growth strategy (Emers et al., 1995).

GRAMINOIDS

Graminoids, mainly sedges, co-dominated in the plant canopy with deciduous shrubs in the upland plant community types. The most common species in descending order were *Eriophorum angustifolium*, present in all upland types; *Eriophorum vaginatum*, the tussock former in Tussock Tundra and Shrub Tundra; *Carex bigelowii*, dominant in Sedge-Dryas; and *Carex aquatilis*, co-dominant with *Eriophorum angustifolium* in Sedge-Willow and Wet Graminoid.

Graminoid cover increased over time in the Sedge-Dryas community type and decreased in the other types (Fig. 4). In Sedge-Dryas, the graminoids *Eriophorum angustifolium* and *Carex aquatilis* increased in cover because of wetting of the soil due to ice wedge polygon subsidence. In Sedge-Willow the graminoids, mainly those same two species, decreased in all plots. The other common sedge species changed less over time. The response of vegetation to vehicle disturbance in our study area showed that sedge species varied

in their ability to respond quickly to changing growing conditions (Emers et al., 1995). The rhizomatous sedges *Eriophorum angustifolium* and *Carex aquatilis* had increases in foliar biomass and nutrient content (nitrogen and phosphorus) after vehicle disturbance caused a transient nutrient flush and increased soil moisture and depth of the soil active layer. In comparison, the tufted sedges *Eriophorum vaginatum* and *Carex bigelowii* showed less increase in biomass and nutrient content in response to disturbance.

Grasses showed no consistent patterns over time. Kennedy et al. (2001) reported increases of the grass *Arctagrostis latifolia* over a 13 year period on nearby Herschel Island, Canada. In our area there was a flush of growth of this species only on plots disturbed by vehicle traffic and only for the first five years after disturbance (Jorgenson et al., 2010). This showed that *Arctagrostis latifolia* was capable of responding rapidly to changing soil conditions, but did not persist when conditions recovered.

Plots with high graminoid cover also had high cover of litter, because most litter was dead graminoid leaves. Litter may be a main way graminoids suppress other plants, by covering the ground with a thatch of dead leaves that decomposes slowly and dries quickly, providing a poor substrate for plant germination and persistence.

Data from multiple years in close succession (six sampling years between 1984 and 1991) showed that graminoid cover varied more year to year than other growth forms except forbs. Graminoids and forbs evidently responded more quickly to yearly differences in weather and growing conditions. There were years with unusually lush graminoid growth observed in the study area (e.g., 1998, 2000), although not sampled in this study. In the Arctic, estimates for graminoid abundance and height are probably less stable than for other growth forms and more affected by the years that data are collected.

FORBS

Forbs included many species with different habitat requirements and large year to year variability. The most common of the 50+ forb species in the study area were legumes (12 species, e.g., *Oxytropis, Hedysarum*, and *Astragalus* species), *Bistorta plumosa, Rubus chamaemorus, Pyrola grandiflora, Bistorta vivipara, Tephroseris atropurpurea*, and *Petasites frigidus*.

Forb cover decreased in Riparian Shrub/Dryas Terrace (Fig. 4). There were no clear trends for most forb species except the legumes, which decreased in all Riparian Shrublands and Dryas Terrace plots and in most other plots where present. Legumes are nitrogen-fixers and are generally common on disturbed soil (Campbell, 1927). They may be pioneer species in these communities and the decrease in riparian plots may be due to natural succession on floodplains.

HORSETAILS

Almost all horsetails in the plots were of decumbent evergreen species, mainly *Equisetum variegatum*. Horsetails were most common in Riparian Shrub/Dryas Terrace and Sedge-Dryas, the types with the deepest soil active layer. Cover changed little over time (Fig. A2).

SOIL THAW DEPTH

The study area is in the zone of continuous permafrost, but approximately 30 cm of soil thaws at the surface each summer. The depth of thawed soil above the permafrost varies based on

FIGURE A6. Same plot as Figure A5. This is a typical Moist Sedge–Willow plot, dominated by the sedges *Eriophorum angustifolium* and *Carex aquatilis* and the willow *Salix pulchra*, without trends in plant cover over the period of the study.

soils and vegetation. Our study does not include thaw depth data from Riparian Shrublands or Dryas Terrace plots, because gravel soils impeded measurement. However, a few samples indicate that thaw depth was greatest on gravel along rivers, in Riparian Shrublands vegetation with a thin and discontinuous organic soil layer (>45 cm). As the insulating organic soil layer accumulates, soils cool and thaw depth decreases (38 cm for one Dryas Terrace plot). Mean thaw depth was 34 cm for Sedge-Dryas plots, which had a thin and discontinuous insulating organic layer due to active frost boils, 33 cm for Wet Graminoid, 31 cm for Tussock Tundra, and 29 cm for Sedge-Willow. It was 24 cm for Shrub Tundra, where the soil is cooled by shading from dense evergreen shrubs. Thaw depths did not increase over the course of our study, but were greatest in 1998, which had a very warm summer (Fig. 5).

Vascular vs. Nonvascular Plants

Data by plant growth forms were summed into nonvascular and vascular plant cover (Fig. A3). Nonvascular plant cover was driven by bryophytes because bryophytes had much higher cover in the study area than lichens. Bryophyte cover decreased slightly over time. In contrast, overall vascular plant cover showed little change over time.

Supporting Information by Plant Community Type

SEDGE-DRYAS TUNDRA

Sedge-Dryas Tundra covers 13% of the study area and is most prevalent near the coast and on glacial deposits (Jorgenson et al., 1994). It has moist soils like the other upland types, but different soil properties. Active frost boils disturb soil horizons and soils are nonacidic and ice-rich, with deep annual thaw. Dominant plants are usually *Dryas integrifolia* and *Carex bigelowii*. Sedge-Dryas plots had less bryophyte and deciduous shrub cover than the other three types and more lichen and bare soil. Lichens were mainly fruticose and crustose, unlike the other plant community types that had mainly foliose lichens.

Sedge-Dryas was the least stable plant community over time. Polygon troughs in some plots had high sedge cover and standing water, indicating active ice wedge thawing. These plots had the greatest increases in graminoid cover and greatest decreases in lichen and bryophyte cover over time of any plot. This plant community type was also the most susceptible to vehicle damage in a related study, probably due to high soil
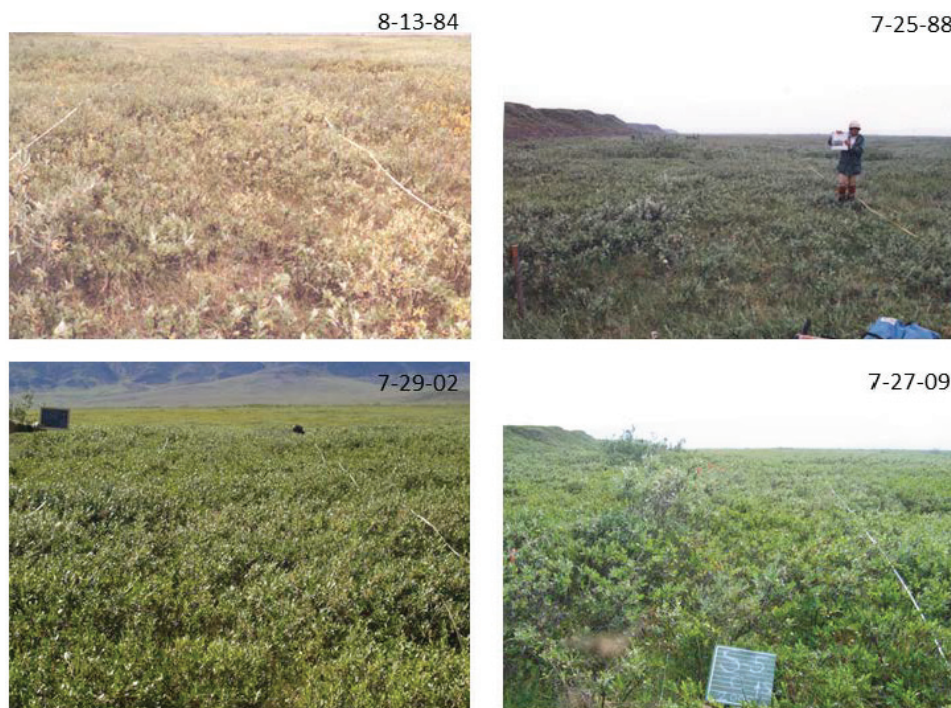
FIGURE A7. Riparian Shrublands plot that had deciduous shrub cover increase from 44% to 73% between first and last year of the study. Almost all shrubs were willows, with *Salix richardsonii* the most abundant. Average canopy willow height in this plot increased from 31 to 46 cm.

ice content and disruption of the thin and discontinuous vegetative mat, causing deeper soil thaw in the summer (Jorgenson et al., 2010).

For Sedge-Dryas, models showed large decreases in lichen cover, large increases in graminoids, and little change for other growth forms (Figs. 2–4). Lichens decreased greatly at five of the six Sedge-Dryas plots. At most plots, this was accompanied by increase in graminoids and a decrease in some bryophytes. The increasing graminoids were *Eriophorum angustifolium* and *Carex aquatilis*. The decreasing lichens were fruticose and crustose species. The decreasing bryophytes were acrocarpous mosses and hepatics. Pleurocarpous mosses were common in some plots, but seldom decreased.

Two plots on highly polygonized tundra showed extreme changes in microtopography and vegetation over the study period (e.g., Figs. 6–7). Melting of ground ice caused soil subsidence, surface wetting, and large increases in graminoids and decreases in lichens and bryophytes. Thermokarst ponds formed in one plot, covering 20% of the plot area with water by the later years, where none was present in the early years. These plots had twice the lichen cover of other plots in the early years of the study. Unlike most plots, the lichens were mainly fruticose lichens, rather than foliose. Bryophytes were mainly acrocarpous mosses, with almost none of the pleurocarpous mosses that dominated all other plots in the study. Graminoids were the wet-site sedges, mainly *Eriophorum angustifolium* and *Carex aquatilis,* instead of *Carex bigelowii*. The unusual plant species composition at these plots was probably because they were already subsiding before this study began, as can be seen in the time series of aerial photos of this area from 1950 to 2010 (Fig. 7).

Jia et al. (2003) reported that the wide-spread NDVI increase on North Slope tundra varied by plant community type, with the greatest increase for Sedge-Dryas tundra (referred to as Moist Nonacidic Tundra). This agrees with our assessment that this type is very susceptible to climate change, due to more ex-

posed mineral soil, less protective moss mat, and greater soil ice than other types.

TUSSOCK TUNDRA/SHRUB TUNDRA

Tussock Tundra (28% of study area) dominates the inland foothills landscape. Shrub Tundra (5% of area) develops on high-centered ice-wedge polygons, often from tussock tundra that became better drained, favoring shrubs over tussocks. This occurs where melting of tops of ice wedges causes polygon troughs to deepen and polygon centers to become drier.

Tussock tundra was dominated by *Eriophorum vaginatum, Salix pulchra, Rhododendron tomentosum (Ledum decumbens)*, and *Vaccinium vitis-idaea*. Bryophytes were mainly pleurocarpous mosses and lichens were mainly foliose. Plots were more similar in species composition to each other than in other plant community types. Shrub Tundra plots were similar but had fewer and less robust tussocks. The greatest difference from other plant community types was that Tussock Tundra/Shrub Tundra had three times more cover of evergreen shrubs. It also had more complex physical structure, with more layers of vegetation than the other plant community types.

Models showed decreasing cover of lichens and little change in other growth forms (Figs. 2–4). All narrowly defined growth forms of lichens and bryophytes decreased, except *Sphagnum* moss increased.

Shrub Tundra plots were highly polygonized but, unlike polygonized Sedge-Dryas plots, had few vegetation changes (Fig. A4). Gamon et al. (2012) also found long-term stability (>80 years) for polygonized tundra with similarities to Shrub Tundra, which they attributed to the stabilizing feedbacks from the different albedo characteristics of the polygon centers and troughs. Our Shrub Tundra plots had the shallowest mean thaw depths of any plant community type (24 cm), compared to 34 cm for Sedge-Dryas plots, indicating that the dense vegetation insulated the soil better than the discontinuous vegetation and exposed mineral soil of the Sedge-Dryas plots.
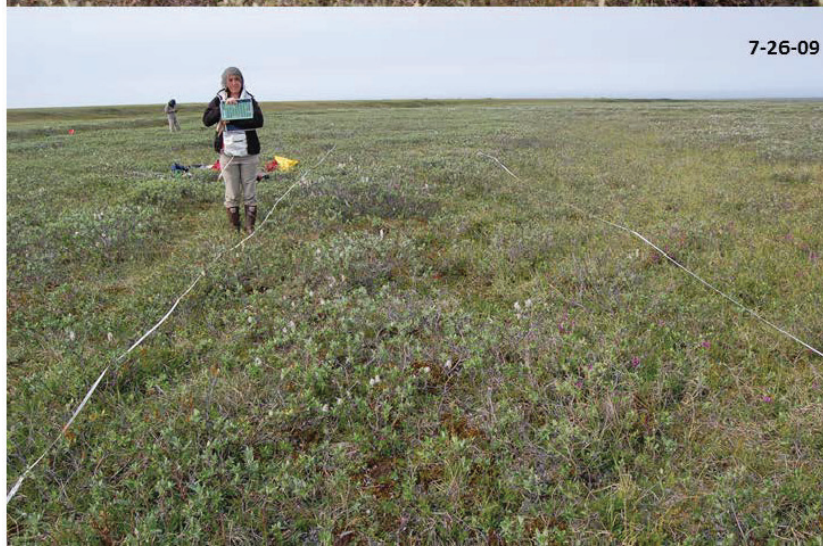
FIGURE A8. In contrast to Figure A7, the other four Riparian Shrubland plots did not have increasing trends for deciduous shrub cover or height. The dominant shrub in this plot was *Salix richardsonii*.

SEDGE WILLOW/WET GRAMINOID TUNDRA

Sedge-Willow and Wet Graminoid plots were on an ecological continuum from moist to wet tundra. Sedge-Willow plots (30% of study area) had high cover of the sedges *Eriophorum angustifolium* and *Carex aquatilis* and willows, mainly *Salix pulchra*. The single Wet Graminoid plot (13% of study area) was similar, but with less willow cover due to saturated surface soil. The models showed decreasing graminoids and little change for other growth forms (Figs. 2–4). Figs. A5 and A6 show a typical Sedge-Willow plot, with few changes over time.

Wet Graminoid tundra was undersampled in this study, but the one plot showed little vegetation change, indicating that this type may have been stable during the study period. Elmendorf et al. (2012b) found that deciduous shrub abundance increased over time more often at wet sites in the Arctic than at moist or dry sites. We do not have enough data to address that question.

RIPARIAN SHRUBLANDS/DRYAS TERRACE

The synthesis of long-term vegetation plots in the circumpolar Arctic included no other Riparian Shrublands plots (Elmendorf et al., 2012b). Riparian Shrublands (2% of area) devel-

op as erect willow species and forbs colonize river bars, taking advantage of the bare well-drained gravels and deep summer soil thaw. Shrublands where surface soils remain coarse, without accumulation of paludifying sand and silt layers, develop over time into Dryas Terrace vegetation (3% of area). Flooding becomes infrequent, a moss and soil organic layer develops, permafrost begins to aggrade, nutrient status decreases, and erect willows with deep root systems are gradually replaced by dwarf shrubs.

In these plots, soils were well-drained and the landscape too young to have developed ice wedge polygons. The five Riparian Shrublands plots were densely vegetated with little exposed gravel, indicating they were stabilizing. The canopy willows were species that grow much taller in central Alaska but are low in the north. In only one plot did the mean willow canopy height exceed 15 cm. Riparian Shrublands had more deciduous shrubs and forbs than other plant community types, with fewer graminoids and lichens. The three Dryas Terrace plots were similar to Riparian Shrublands, but the dominant shrubs were the dwarf evergreen *Dryas integrifolia* and dwarf willows, with almost no erect willows remaining.

The models showed only slight changes over time in these plant community types, except for a large decrease in forbs, mainly

legumes (Figs. 2–4). Deciduous shrub cover decreased in six of eight plots but increased greatly in one plot (Figs. A7 and highest percent cover values visible in Figs. 3 and A1).

The changes in the individual plots were likely related to primary succession on river bars. Successional stages in Arctic Alaska were described by Bliss and Cantlon (1957), but the rate of succession is not known. Viereck (1966) suggested that the riparian shrubland stage can last for 100–200 years in alpine Alaska. The development of willows over a 25 year period at one of our plots demonstrates that succession can occur rapidly under optimal conditions. That plot, shown in Figure A7, was in a moist abandoned river channel on a terrace, likely close to the water table. It had high cover of willows, graminoids, and feathermosses and almost no lichens or evergreen shrubs. Willows became denser and taller over the study period and cover of most other growth forms also increased. That contrasted with the other Riparian Shrublands plots that were on drier terraces and changed less over time (Fig. A8).

Mean height of the canopy-forming deciduous shrubs was measured in the five Riparian Shrublands plots, as part of the vehicle disturbance study. There were too few data to analyze or draw conclusions for this study, but four of the five undisturbed control plots changed little over time. In contrast, in the plot mentioned above (Fig. A7) mean height increased from 31 to 46 cm between the first and last years of the study.

Repeat photography by Tape et al. (2006) indicated that riparian areas experienced some of the fastest shrub increases on the Alaska North Slope over a 60 year period. Only one of our five Riparian Shrublands plots showed that, perhaps due to our shorter time frame. Another influence may be that primary succession on river bars may obscure any shrub gains caused by climate change, because the successional trajectory for these sites would be for taller willow species to die out as permafrost aggrades and the shrublands shift from erect shrub to dwarf shrub dominance. In addition, alders were prominent in the shrub expansion documented by Tape et al. (2006), but are absent from our study area. This is an indication that our area, closer to the coast, has different growing conditions than areas of the North Slope that have shown greater changes in vegetation in recent decades.

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