

Plant Species Composition and Productivity following Permafrost Thaw and Thermokarst in Alaskan Tundra

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ABSTRACT

Climate warming is expected to have a large impact on plant species composition and productivity in northern latitude ecosystems. Warming can affect vegetation communities directly through temperature effects on plant growth and indirectly through alteration of soil nutrient availability. In addition, warming can cause permafrost to thaw and thermokarst (ground subsidence) to develop, which can alter the structure of the ecosystem by altering hydrological patterns within a site. These multiple direct and indirect effects of permafrost thawing are difficult to simulate in experimental approaches that often manipulate only one or two factors. Here, we used a natural gradient approach with three sites to represent stages in the process of permafrost thawing and thermokarst. We found that vascular plant biomass shifted from graminoid-dominated tundra in the least disturbed site to shrub-dominated tundra at the oldest, most subsided site, whereas the inter-

mediate site was co-dominated by both plant functional groups. Vascular plant productivity patterns followed the changes in biomass, whereas nonvascular moss productivity was especially important in the oldest, most subsided site. The coefficient of variation for soil moisture was higher in the oldest, most subsided site suggesting that in addition to more wet microsites, there were other microsites that were drier. Across all sites, graminoids preferred the cold, dry microsites whereas the moss and shrubs were associated with the warm, moist microsites. Total nitrogen contained in green plant biomass differed across sites, suggesting that there were increases in soil nitrogen availability where permafrost had thawed.

Key words: tundra; vegetation; biomass; net primary productivity; permafrost; Alaska; thermokarst; climate change; nitrogen; soil moisture.

INTRODUCTION

Climate change scenarios predict that the greatest magnitude of warming will occur at high latitudes (Houghton and others 1996; IPCC 2001). This predicted warming is supported by observational

evidence over the last 25 years (Serreze and others 2000), and is associated with warmer ground temperatures and permafrost (permanently frozen soil) thawing (Lachenbruch and Marshall 1986; Osterkamp and Romanovsky 1999). Changes in arctic tundra plant community composition, biomass, and productivity as a result of a warming climate are expected to have strong feedbacks to climate change both through controls over eco-

system C storage (Billings 1987; Shaver and others 1992, 2001; Mack and others 2004), and through changes in energy balance (Liston and others 2002; Chapin and others 2005). Understanding the response of plant communities to the direct and indirect effects of a warmer climate will be important for predicting future feedbacks, and indeed, a widespread increase in arctic shrubs abundance demonstrates that these changes are already underway (Sturm and others 2001).

Changes in plant community composition, biomass, and productivity as a result of climate change can either occur directly as a result of warmer air and soil temperatures, or indirectly through changes in soil resources such as water and nutrient availability. Increased air temperature directly stimulates plant growth and plant species shifts across a range of tundra ecosystems (Arft and others 1999; Jonasson and others 1999; Dormann and Woodin 2002; van Wijk and others 2003; Walker and others 2006), and also stimulates soil warming, heterotrophic decomposition, and nutrient release from soil organic matter. Increased nutrient availability, in particular nitrogen (N), increases plant growth and shifts species composition in many well-drained tundra ecosystems (Jonasson and others 1999; Shaver and others 2001; Dormann and Woodin 2002; van Wijk and others 2003; Mack and others 2004; Walker and others 2006). Although experimental manipulations of temperature and nutrient availability often stimulate productivity, with nutrients typically having a much stronger effect than temperature, changes in plant species composition have been more variable among different tundra sites (van Wijk and others 2003). Some studies have shown that shrub abundance and growth increase in experimental manipulations of air temperature and nutrient availability, often at the expense of graminoid species and/or nonvascular abundance (Shaver and others 2001; Jonsdottir and others 2005). Other studies show many or all plant functional groups including graminoids responding positively to the manipulated variables (for example, Walker and others 2006).

Complicating our understanding of the links between climate warming and vegetation change is the occurrence of thermokarst, ground subsidence that can occur when ground ice wedges thaw. This effect of warming acts on vegetation indirectly by creating localized variability in moisture conditions as lower karst areas accumulate moisture and may have the water table near the soil surface, while nearby higher areas become drier. This has direct effects on plant species composition and growth

that follows the altered moisture regime, which promotes mesophilic mosses (Camill 1999) and vascular plants in some areas (Lloyd and others 2003), while preventing growth of other species (Jorgenson and others 2001). The indirect effect of changing moisture regime on soil nutrient availability is also likely to affect plant growth and species composition. These types of changes in surface topography and hydrology are common where permafrost is thawing (Davis and others 2000), but are conspicuously absent from experimental warming studies because manipulated plot sizes are relatively small and heat is transferred laterally to unmanipulated areas rather than warming the permafrost within the plot (Marion and others 1997; Hobbie and Chapin 1998; Osterkamp and Romanovsky 1999; Shaver and others 2000). Therefore, it is unclear how results from experimental warming studies in northern ecosystems will translate to the reality of permafrost thawing and thermokarst development.

In areas where ice-rich permafrost has disappeared, thermokarst scars are ubiquitous on the landscape, suggesting it is a critical mechanism by which vegetation and ecosystem change will occur with climate warming (Vitt and others 2000; Jorgenson and others 2006). There have been large-scale observational studies of thermokarst development and vegetation change in forested peatland areas in Canada (Camill and Clark 1998; Camill 1999, 2000; Turetsky and others 2000; Bartleman and others 2001). These studies have focused on the development of thermokarst bogs within permafrost plateaus that are themselves raised above the water table of surrounding fens. In that geographic region, landscape-scale relief is minimal such that local permafrost thawing causes waterlogged bogs to form as water is trapped within the surrounding unthawed permafrost (Vitt and others 2000). The net effect of warming on vegetation and ecosystem dynamics is likely to be strongly dependent on moisture status following thaw (Oechel and others 1994; Camill 1999), but much less is known about thermokarst effects in upland areas that are relatively well drained due to local topographic relief.

In this study, we made use of a naturally occurring area of permafrost thaw that has been monitored over the past several decades (Osterkamp and Romanovsky 1999). This study differs from most previous research on thermokarst in boreal peatland because it is in an area with relatively good drainage and is focused on upland moist acidic tundra (MAT). The MAT vegetation association is the most common in arctic Alaskan tundra (Epstein and others 2004), and is also extensive in

subarctic areas in the zone of discontinuous permafrost (CAVM Team 2003). Both the vegetation and permafrost are expected to be highly sensitive to climate warming in the discontinuous permafrost zone. Our study area provided a natural gradient ranging from relatively undisturbed moist tundra, to tundra where the permafrost has thawed, ice wedges have melted, and changes in plant species composition have occurred. Our objectives were (1) to describe the changes in plant species composition and productivity that have occurred as the result of permafrost thawing and thermokarst, and (2) to quantify changes in soil microclimate and nutrient availability that are expected to be the proximal drivers of vegetation change. This study provides an important contrast to thermokarst areas that develop into waterlogged ecosystems, and to experimental studies that manipulate single or several factors.

MATERIALS AND METHODS

Site Description

This study was conducted near Healy, Alaska, at a location in the foothills north of the Alaska Range, just outside of Denali National Park. Ground temperature has been monitored for several decades in this area in a deep borehole, before and after the permafrost was observed to thaw on a gentle ($<5^\circ$) north-facing slope (Osterkamp and Romanovsky 1999). This is a unique data set that closely documented the thermal erosion of permafrost as it started in the mid to late 1980s until the present. In this area ($63^\circ52'42.1''N$, $149^\circ15'12.9''W$), we have selected three sites that represent differing amounts of disturbance from permafrost thaw: (1) relatively undisturbed tussock tundra, dominated by the tussock-forming sedge *Eriophorum vaginatum* with *Sphagnum* spp. mosses and shrubs (hereafter called 'Tussock'), (2) a site adjacent to the borehole that started documented permafrost thawing in 1985 ('New Karst'), and (3) a site located where permafrost appeared to have thawed more than three decades prior to the thawing at the borehole based on visual observation of thermokarst features from 1951 aerial photographs ('Old Karst') (Figure 1). The warming ground temperature and loss of ice wedges from these sites has had multiple direct and indirect effects on the tundra ecosystem. In addition to warmer soil temperature and deeper thaw depth, soil moisture and the overall hydrology of the area has been altered where ice wedges have thawed and drained away (Table 1). The soil surface collapsed in areas overlying ice wedges, and

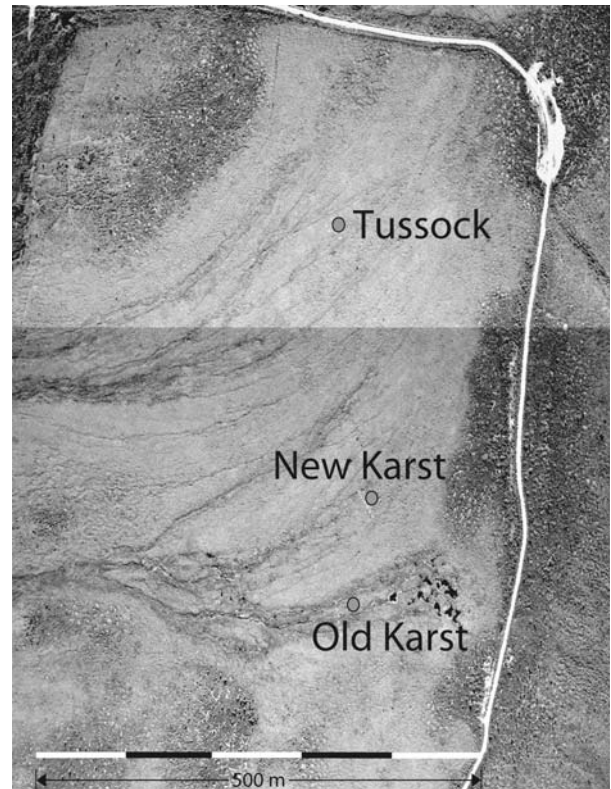


Figure 1. Aerial photograph of study area near Healy, Alaska with the locations of the three sites. The *white line* is a road surrounded by *dark patches* of shrubs and trees. *Light patches* represent moist acidic tundra; thermokarst areas are the dark drainage network leading down slope to Eight Mile Lake, which is off the left side of the photo.

the undulating surface microtopography (thermokarst) caused water to accumulate in lower areas, leaving higher areas dry. Although there are no significant differences among sites in the mean moisture, the coefficient of variation in moisture is higher where subsidence is more pronounced. These thermokarst features are most dramatic in the Old Karst site, are just starting to develop in the New Karst site, and are largely absent in the Tussock site. Together, these three sites are a natural experimental gradient that appear to represent the long-term effects of permafrost thawing and thermokarst on ecosystem dynamics in areas that are relatively well drained. As such, this study area captures direct and indirect effects of warming that are difficult to replicate with small-scale experimental manipulations.

Biomass and ANPP

We quantified differences in plant species composition, aboveground biomass, and aboveground NPP among these three sites to determine how

Table 1. Environmental Characteristics for Sites that Differed in the Degree of Permafrost Thawing

	Old Karst	New Karst	Tussock	<i>P</i> value
Summer mean soil moisture (gH ₂ O gdw soil ⁻¹)	2.1 (0.3)	2.1 (0.2)	1.9 (0.2)	0.603
Summer mean soil temperature (°C)	11.3 (0.2) ^a	10.2 (0.2) ^a	8.7 (0.2) ^b	<0.001
Maximum thaw depth (cm)	65.3 (7.5) ^a	49.7 (2.0) ^{ab}	45.9 (2.4) ^b	0.065

Soil moisture was measured for the surface 5 cm of organic soil/moss, and temperature was measured at 10 cm. Maximum thaw depths were measured in mid-September. Different letters denote statistically significant pairwise difference among sites, within a measurement type. Values are summer averages (\pm standard error)

vegetation could change in response to permafrost thawing. To do this, we coupled intensive destructive harvests of the tundra vegetation with more extensive surveys of plant biomass distribution at the sites. For the harvests, we separated the aboveground tundra ecosystem by plant species and plant part, and then used allometric relationships that we derived to extend this information to the broader surveys.

At the time of peak aboveground plant biomass in late July of 2004, we randomly selected twelve 21 × 21 cm quadrats at each of the three sites. These quadrats were arrayed along a 40 m transect that was perpendicular to the slope at the site, and was paired with another 40 m transect where the more extensive plant biomass surveys were conducted. The plant species composition in each quadrat was first quantified nondestructively using a point-intercept sampling method to determine the presence of specific plant species and tissue types (Shaver and others 2001). The goal of the point-intercept sampling in the destructive-harvest quadrats was to construct relationships between the number of contacts and the biomass of each species, determined subsequently by destructive harvest. Plant species composition was quantified in each quadrat using a frame with a fishing line grid size of 7 × 7 cm (Walker 1996). At each of the 16 intersections of the grid within the quadrat, a metal rod (diameter = 1 mm) was placed vertically through the plant canopy. We recorded species identity and tissue type (leaf, stem, or fruit) for every plant that touched the rod. When the point-intercept sampling was finished, we cut the intact quadrat from the tundra down to 20 cm below the soil surface and returned it to the lab for further processing.

We then separated the whole aboveground tundra ecosystem for all harvested quadrats into live and dead plant parts over a 3-day period in the lab. Belowground was defined for this ecosystem as anything located below the bottom of the green portion of the moss, which can form an almost continuous carpet on the soil surface around the base of the vascular plants. Live biomass was then

sorted to the species level for vascular plants. Each vascular species was further separated by tissue type: flowering or fruiting structures, new (current year) leaves, new stems, old (all previous years) leaves, and old stems. Nonvascular plant species were sorted into moss and lichen functional groups, and the visibly green portion was sampled as live biomass. All plant components were dried at 60°C and weighed.

Aboveground vascular net primary production (ANPP) was estimated as the sum of the current year's apical and secondary growth. Apical growth was defined as the sum of new leaves, new stems, flowers and fruits that grew in 2004. The difference between previous year-old stem weight and current year-old stem weight was defined as secondary growth. Because we did not measure the previous year stem weight directly, we estimated that component using the secondary growth rate measured in another tussock tundra site at Toolik Lake, Alaska. Secondary growth of stems, a relatively small component of total vascular ANPP, was calculated for the three species that have significant stem thickening: *Vaccinium uliginosum*, *Betula nana*, and *Ledum palustre*, using growth rates of 36.2, 15.8, and 7.9%, respectively (Shaver and others 2001; Bret-Harte and others 2002).

Using the information from the point-intercept sampling and the biomass harvest, we constructed linear regressions between the number of hits per point for each species and their corresponding total biomass on an area basis. Additionally, we calculated ratios that related component plant tissues to total biomass based on the destructive harvest data so that we could calculate how much of the total biomass ANPP comprised. The allometries and ratios were applied to point-intercept data measured on another set of quadrats as a nondestructive means of estimating biomass and ANPP distribution among species on a larger area than could be effectively destructively harvested. Twelve larger quadrats per site were sampled using a 70 × 70 cm frame in a 40 m transect directly upslope of the harvested quadrats. Grid spacing within the larger

quadrats was the same as the smaller harvested quadrats. Using the larger quadrats, we quantified vegetation composition over a total area 11.1 times larger than using the destructively harvested quadrats alone. Allometries were used to convert the point-intercept data to total biomass and component parts for individual species with the exception of *Oxycoccus microcarpa*, which occurred in such small amounts that a suitable allometry could not be constructed. Although the frequency of occurrence of *Andromeda polifolia* was enough to construct an allometric equation, this species was not itemized in summary tables due to its relatively minor contribution to total biomass (less than 2% of total biomass in each of the five quadrats in which it occurred). All calculations of total biomass and ANPP for the sites did include this minor contribution from *A. polifolia*.

Moss NPP was estimated using the cranked wire method that measures the vertical growth of moss as referenced to a wire inserted at the moss surface (Clymo 1970). A 20 cm wire with two opposing 90° angles was inserted into the moss such that a 5 cm length of wire in between the two angles paralleled and sat on the moss surface. Eight centimeters of wire went into the moss to provide stability while 7 cm protruded upwards and was used to reference growth. Between 6 and 15 wires were placed in five different moss types (defined below) during the last week of May, and total moss growth was measured nondestructively during the second week of September. To convert moss vertical growth (mm) to moss NPP (g m^{-2}), the vertical growth was multiplied by the mass of a known volume of new growth. This mass estimate was obtained by harvesting five 8 × 8 cm plots for each moss type at each site and measuring the mass associated with a 3 mm growth increment. These point-based estimates of moss NPP were multiplied by the ground area occupied by the different moss types in the 12 large quadrats at each site. We did this scaling using a line-intercept method to quantify the five dominant moss groups: *Sphagnum fuscum*, *S. magellanicum*, hydrophilic *S. spp.* (which included *S. girgenhornii*, *S. lenense*, *S. warnstorffii*, and *S. aongstroemii*), *Dicranum spp.* (primarily *D. eolongatum*, and *D. undulatum*), and feathermoss (primarily *Hylocomium splendens*, but also included *Pleurozium schreberi*).

We measured the concentration of foliar N from six vascular species common to all sites as an index of changes in ecosystem nutrient availability among sites. To compare leaves among sites, we analyzed the fully developed, new leaf cohort for each species (Reich and others 1992). Each sample was the composite of mature leaves from multiple individ-

ual plants within a quadrat, and there were six quadrats analyzed at every site, with the exception of *B. nana* in the Old Karst and New Karst sites, which was only found and analyzed in three and four quadrats, respectively. Leaves were dried at 60°C and ground, and the N concentration was measured using a Costech elemental analyzer. Because increased plant growth can sometimes offset increases in soil N availability, we multiplied the concentration of foliar N by the green photosynthetic biomass (total canopy N) as another metric of change in nutrient availability across sites.

Data Analysis

Vascular plant species were grouped as deciduous, evergreen, and graminoid functional groups (Table 2). Nonvascular mosses and lichens each comprised their own functional group for biomass (Table 2). Differences among sites were analyzed using a single factor ANOVA ($n = 12$ quadrats per site) (SYSTAT). Where differences among groups were detected by ANOVA, post hoc pairwise comparisons were made using the relatively conservative Tukey's HSD test. In some cases, biomass data were square root or natural log transformed to meet the assumptions of ANOVA. We reported Pearson's coefficients for correlations among species if the data were normally distributed, or could be transformed to meet this criterion. In half of the species where this assumption could not be met we reported the nonparametric Spearman's Rho instead. Principle component analysis was performed on the covariance of percent cover data for vegetation, where assumptions of normality are not required.

RESULTS

Aboveground Biomass

The eight major vascular plant species that comprised more than 95% of the aboveground vascular biomass were common to all three sites (Table 2). There were significant positive relationships between the point-frame number of hits and the aboveground biomass (AGB) for all plant species and functional groups with the exception of *O. microcarpus*, which occurred very rarely and had little biomass (Table 3). These relationships were best described by linear functions that could explain between 49 and 80% of the variance in biomass for vascular plant functional groups. Nonvascular biomass was also best described by linear functions, which explained 70% of the lichen biomass variance but only 33% of the moss biomass variance (Table 3). Moss biomass per unit area differed

Table 2. Plant Species Composition at Moist Acidic Tundra Site near Healy, Alaska

Vascular species	Nonvascular species		
Graminoid	Mosses	Mosses	Mosses
<i>Eriophorum vaginatum</i>	<i>Sphagnum cuspidatum</i>	<i>Polytrichum commune</i>	<i>Racomitrium lanuginosum</i>
<i>Carex bigelowii</i>	* <i>S. lenense</i>	<i>P. strictum</i>	
Deciduous	* <i>S. magellanicum</i>	* <i>Pleurozium schreberi</i>	Lichens
<i>Betula nana</i>	<i>S. angustifolium</i>	* <i>Hylocomium splendens</i>	<i>Cladina mitis</i>
<i>Rubus chamaemorus</i>	* <i>S. girgensohnii</i>	<i>Orthotrichum speciosum</i>	<i>Cladonia amaurocraea</i>
<i>Vaccinium uliginosum</i>	* <i>S. fuscum</i>	<i>Tomentypnum nitens</i>	<i>Cladonia arbuscula</i>
Evergreen	* <i>S. warnstorffii</i>	<i>Meesia uliginosa</i>	<i>Cladonia chlorophaea</i>
<i>Empetrum nigrum</i>	* <i>S. aongstroemii</i>	<i>Brachyphyllum cirrosom</i>	<i>Cladonia rangiferina</i>
<i>L. decumbens</i>	<i>Aulacomnium turgidum</i>	<i>Brachythecium salebrosum</i>	<i>Cladonia deformis</i>
<i>V. vitis-idaea</i>	<i>Aulacomnium palustre</i>	<i>Rhytidium rugosum</i>	<i>Icmadophila ericetorum</i>
<i>Andromeda polifolia</i>	* <i>Dicranum elongatum</i>	<i>Rhytidium rugosum</i>	
<i>Oxycoccus microcarpa</i>	* <i>D. undulatum</i>	<i>Ditrichum flexicaule</i>	

The most abundant nonvascular species that were measured for annual growth are marked with an asterisk.

Table 3. Linear Regressions describing the Relationship between the Proportion of Point Frame Hits and Total Aboveground Biomass and Aboveground Net Primary Production (ANPP) (sum of leaf, stem, and reproductive) in Units of g m⁻² for Plant Species and Functional Groups

	Slope	Intercept	R ²	P value	New leaf	New stem	Secondary growth	Fruit
Graminoid	223.42	-45.87	0.802	<0.001	-	-	-	-
<i>C. bigelowii</i>	63.21	8.38	0.402	<0.001	0.6985	0.2471	-	0.0543
<i>E. vaginatum</i>	243.16	-34.61	0.792	<0.001	0.5541	0.4039	-	0.0420
Deciduous	163.35	39.47	0.656	<0.001	-	-	-	-
<i>B. nana</i>	254.68	17.21	0.778	<0.001	0.3373	0.0806	0.0074	0.0145
<i>R. chamaemorus</i>	74.07	9.53	0.475	<0.001	0.9151	0.0849	-	-
<i>V. uliginosum</i>	176.31	22.52	0.589	<0.001	0.2809	0.1137	0.1586	0.0088
Evergreen	145.39	27.04	0.485	<0.001	-	-	-	-
<i>Empetrum nigrum</i>	210.15	8.22	0.348	0.016	0.1792	0.0537	-	0.0604
<i>L. decumbens</i>	157.68	11.22	0.512	0.002	0.2286	0.0753	0.0390	0.0137
<i>V. vitis-idaea</i>	126.95	6.47	0.461	<0.001	0.3790	0.0875	-	0.0294
Moss	147.51	22.99	0.324	<0.001	-	-	-	-
Lichen	411.59	-4.87	0.708	<0.001	-	-	-	-

For all regressions, n = 36 quadrats.

widely depending on the species present, but the point-framing method was not able to resolve these differences very well due to the very short stature of moss. These regression relationships were used to estimate AGB and ANPP for the 36 large quadrats that were point-framed at all sites. These more extensive estimates of biomass were used to explore differences in vegetation AGB and ANPP among sites in response to permafrost thawing.

There was a significant difference in the total AGB among sites ($P = 0.009$), with Tussock having about 75% of the biomass of the other two sites on average (Table 4). Of the biomass, vascular plant species comprised 69–76% of the total amount at

each site with moss and lichen species making up the remainder. The pattern of total AGB among sites was similar to the pattern of vascular plant biomass alone, with Tussock having about 71% of the vascular biomass of the other two sites on average. Within functional groups, the identity of the dominant species remained the same across sites (Table 4), but there were changes in the abundance of different functional groups among sites (Table 4; Figure 2A). Biomass of both evergreen shrubs (dominated by *L. decumbens*) and deciduous shrubs (dominated by *V. uliginosum*) was highest at Old Karst and lowest at Tussock (evergreen $P < 0.001$, deciduous $P = 0.004$). In contrast,

Table 4. Total Aboveground Biomass of Plant Species and Functional Groups at Three Sites that Differ in Degree of Permafrost Thawing

	Old Karst (g/m ²)	New Karst (g/m ²)	Tussock (g/m ²)	P value
Graminoid	38.54 ± 14.21 ^a	145.33 ± 31.95 ^b	97.31 ± 19.46 ^{ab}	0.004
<i>E. vaginatum</i>	21.96 ± 12.19 ^a	129.79 ± 30.74 ^b	79.22 ± 19.38 ^b	0.002
<i>C. bigelowii</i>	16.58 ± 3.63	15.54 ± 1.91	18.09 ± 2.11	0.794
Deciduous	150.23 ± 13.62 ^a	116.31 ± 10.92 ^{ab}	88.86 ± 11.15 ^b	0.004
<i>B. nana</i>	36.67 ± 5.68	30.23 ± 7.03	26.51 ± 8.34	0.597
<i>R. chamaemorus</i>	28.25 ± 2.74 ^a	20.91 ± 1.32 ^a	12.29 ± 1.90 ^b	<0.001
<i>V. uliginosum</i>	85.30 ± 11.84 ^a	65.17 ± 5.36 ^{ab}	50.06 ± 4.74 ^b	0.015
Evergreen	142.16 ± 9.79 ^a	108.86 ± 14.94 ^a	62.72 ± 9.59 ^b	0.002
<i>Empetrum nigrum</i>	35.29 ± 10.07	26.19 ± 11.70	14.50 ± 6.63	0.329
<i>L. decumbens</i>	83.93 ± 10.52 ^a	67.90 ± 7.06 ^a	33.47 ± 2.27 ^b	<0.001
<i>V. vitis-idaea</i>	21.93 ± 2.99	14.76 ± 3.88	14.45 ± 3.01	0.212
All vascular	330.93 ± 17.48 ^a	370.50 ± 37.72 ^a	248.89 ± 12.44 ^b	0.005
Mosses	99.24 ± 9.74 ^a	90.52 ± 8.34 ^a	64.38 ± 10.45 ^b	0.001
Lichens	55.55 ± 14.46	26.83 ± 7.33	47.73 ± 10.96	0.193
All nonvascular	154.79 ± 10.16 ^a	117.35 ± 10.89 ^{ab}	112.12 ± 14.01 ^b	0.031
All growth forms	485.72 ± 17.23 ^a	487.85 ± 36.65 ^a	361.01 ± 15.81 ^b	0.001

Different letters denote significance pairwise differences among sites, within a species or functional group. Species without letters did not differ significantly among sites. Values are averages (± standard error)

graminoid biomass (dominated by *E. vaginatum*) was lowest at Old Karst and highest in the other two sites ($P = 0.005$). There was 28% less non-vascular biomass at Tussock relative to the Old Karst site ($P = 0.031$), and this was driven by differences in moss biomass ($P = 0.001$). In relative terms, the functional group shift in contribution to total AGB from graminoids to shrubs is even clearer (Figure 2B). Graminoid biomass was equally dominant at New Karst and Tussock comprising almost 25% of the AGB, whereas it was significantly less important at Old Karst, there contributing less than 8% of the total ($P = 0.001$). In contrast, deciduous and evergreen shrubs each contributed about 30% of the total AGB in Old Karst, whereas evergreen shrub biomass declined in importance in the other two sites to about 15% of the total ($P = 0.002$). In relative terms, moss and lichen abundance alone or in combination did not differ greatly among sites.

Patterns of photosynthetic tissue biomass alone (green plant biomass) help demonstrate the potential importance of nonvascular plant species to ecosystem carbon uptake (Figure 3A), although other factors such as instantaneous photosynthetic rate and length of the growing season for different functional groups are important too. At Old Karst, the moss and lichen groups each contributed about a quarter of the total photosynthetic aboveground biomass (Figure 3B). At New Karst and Tussock, however, graminoids still dominated the photosynthetic AGB, contributing more than 25% of the

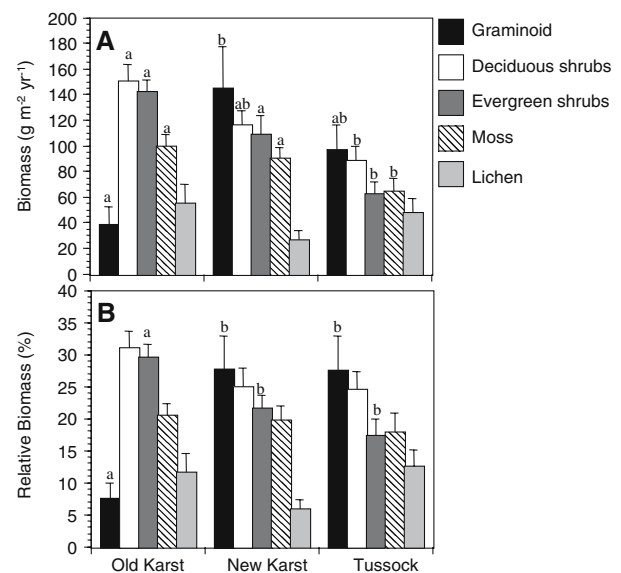


Figure 2. Aboveground biomass (A) and relative abundance aboveground biomass (B) by functional group for the three sites that differ in degree of permafrost thawing and thermokarst. Different letters denote significant pairwise differences among sites, within a species or functional group. Species without letters did not differ significantly among sites.

total, whereas the proportional contribution from mosses and lichens were together equal to or more important than the contribution from the shrubs.

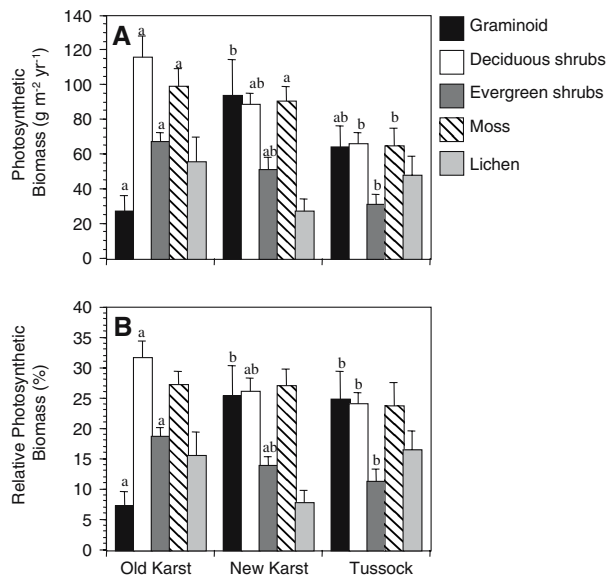


Figure 3. Photosynthetic biomass (**A**) and relative abundance photosynthetic biomass (**B**) by functional group for the three sites that differ in degree of permafrost thawing and thermokarst. Different letters denote significant pairwise differences among sites, within a species or functional group. Species without letters did not differ significantly among sites.

Aboveground Net Primary Production

Patterns of total vascular ANPP were influenced greatly by graminoid ANPP, as all leaf blade and leaf sheath tissue (measured as AGB) was produced in the current year (Figure 4). New Karst had the largest graminoid AGB and the highest vascular ANPP whereas Old Karst had the least graminoid ANPP. Old Karst vascular ANPP was dominated instead by deciduous and evergreen shrubs, whereas each of those functional groups contributed less than half the ANPP of the graminoids in the other two sites. Tussock had high graminoid ANPP but lower total vascular ANPP compared to New Karst, while Old Karst had vascular ANPP intermediate between the two (Figure 4, $P = 0.029$).

Measurements of vascular ANPP alone do not account for the contribution of nonvascular growth, which can be significant especially for mosses. We found from direct measurements that moss productivity was highest at Old Karst, intermediate at New Karst, and lowest at Tussock (Figure 4, $P = 0.01$). In fact, moss productivity at Old Karst was as high as deciduous shrubs, the most productive vascular functional group at that site. Adding moss productivity to vascular NPP made Old Karst the most productive site, although not

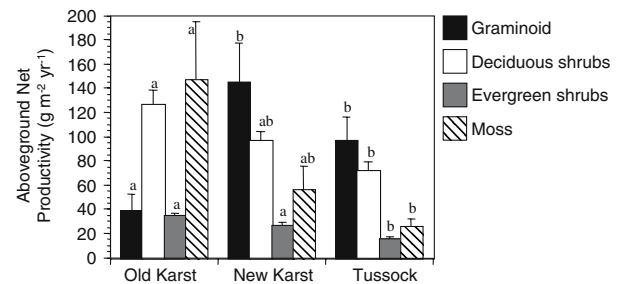


Figure 4. Annual net primary productivity by functional group for the three sites that differ in degree of permafrost thawing and thermokarst. Different letters denote significant pairwise differences among sites, within a species or functional group. Species without letters did not differ significantly among sites.

significantly different from New Karst. Moss productivity measurements showed that green moss biomass turned over in less than a year at the Old Karst site, in approximately 2 years at New Karst, and 3 years for Tussock.

Species Dominance

Although all vascular plant species were observed at all sites, changes in species abundance among the sites could also be observed at the level of individual quadrats due to the microsite heterogeneity at the sites. Across all quadrats at all three sites, the proportion of *E. vaginatum* AGB was significantly negatively correlated with the aboveground biomass of the shrubs, including *Rubus chamaemorus* (Figure 5A; $r = -0.650$, $P < 0.001$), *V. uliginosum* ($r = -0.419$, $P = 0.011$), and *B. nana* ($r = -0.526$, $P = 0.001$). Along with this tradeoff between graminoid and shrub dominance, several of the shrub species, *R. chamaemorus* and *V. uliginosum*, were positively correlated with one another (Figure 5B; $r = 0.645$, $P < 0.001$). Nonvascular plants also responded strongly to changes in vascular plant species. Moss biomass was positively correlated with increases in biomass by the shrubs *R. chamaemorus* (Figure 5C; $r = 0.664$, $P < 0.001$), *B. nana* ($r = 0.478$, $P = 0.003$), and *V. uliginosum* ($r = 0.472$, $P = 0.004$), but negatively correlated with *E. vaginatum* ($r = -0.557$, $P < 0.001$). Lichen biomass responded less strongly to the presence of other species than moss in general, but did correlate positively with the shrub *V. vitis-idea* ($r = 0.656$, $P < 0.001$), and negatively with moss biomass ($r = -0.424$, $P = 0.01$), and weakly with *V. uliginosum* ($r = -0.305$, $P = 0.07$). These patterns of tradeoffs in species abundance were similar when considering photosynthetic biomass alone. This

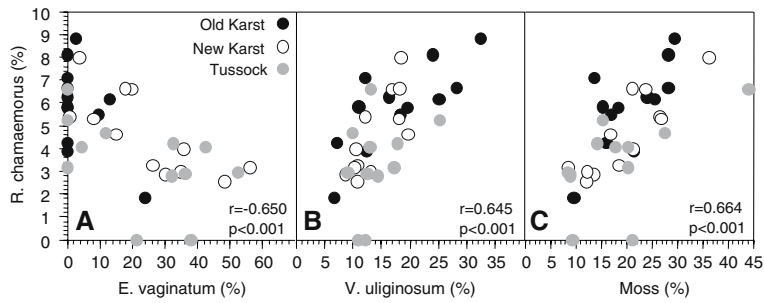


Figure 5. Correlations between the relative biomass of the deciduous shrub, *Rubus chamaemorus*, and three other species representing different plant functional groups: graminoids (A), deciduous shrubs (B), and moss (C).

quadrat-level analysis demonstrates that plant species and functional group shifts among sites are driven by changes occurring at the microsite level. The microsite changes that occur within sites are likely linked to the heterogeneous spatial pattern of ground subsidence.

Principle component analysis of vegetation composition within quadrats further demonstrates differences across quadrats and across sites (Figure 6). Principle component axis 1 described 59% of the total variance and was positively weighted by the graminoids (in order of decreasing importance): *E. vaginatum* and *Carex bigelowii*, and negatively weighted by shrub species and nonvascular functional groups: moss, *B. nana*, *V. uliginosum*, *E. nigrum*, lichen, and *R. chamaemorus*. Principle component axis 2 described 18% of the variance and was positively weighted by: lichen, *V. vitis-idaea*, and *L. decumbens*, whereas negatively weighted by: moss, *V. uliginosum*, *B. nana*, and *E. vaginatum*. Quadrat values for these principle component axes were correlated with environmental measurements of soil temperature and moisture (Table 1). The vegetation PCA 1 correlated negatively with maximum moisture ($r = -0.441$, $P = 0.008$), and temperature at 5 and 10 cm ($r < -0.440$, $P < 0.01$ for both). The vegetation PCA axis 1 was also negatively correlated with a principle component axis 1 that was comprised by all the environmental variables ($r = -0.475$, $P = 0.004$). This environmental PCA 1 described 64% of the variance in environmental conditions, largely describing warm and moist conditions as it was positively weighted by moisture and temperature measurements. Principle components axis 2 for the environmental variables described 30% of the variance and described cold and moist conditions, being positively weighted for all moisture variables whereas negatively weighted by both temperature variables. This environmental PCA 2 was negatively correlated with the vegetation PCA 2 ($r = -0.614$, $P < 0.001$), and with all the moisture variables ($r > -0.480$, $P < 0.005$ for all).

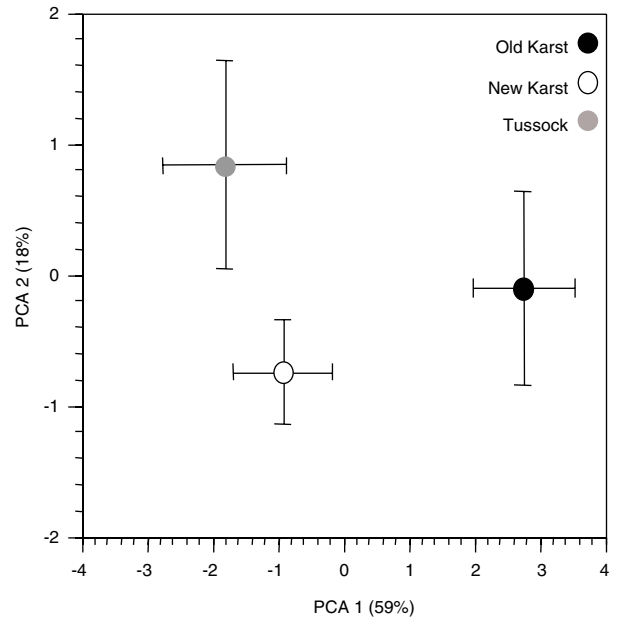


Figure 6. Principle component analysis for relative aboveground biomass of the different plant species and functional groups showing the difference in vegetation communities among sites. The first two principle component axes explained 77% of the total variance in vegetation structure.

Nutrient Availability

Changes in soil temperature, moisture, and permafrost are likely to impact species composition and productivity directly, but perhaps more importantly, indirectly through changes in nutrient availability. Foliar N concentration varied among species and sites by a factor of 2 (Table 5), with differences among species being highly significant ($P < 0.001$) but no trend across sites ($P = 0.395$). Even though foliar N concentration did not differ across sites, total canopy N (green biomass multiplied by foliar N) was significantly higher at Old Karst and New Karst compared to Tussock ($P = 0.001$), suggesting that more soil N was available at those sites.

Table 5. Percent Nitrogen in New Foliage of Vascular Plant Species Common to all Three Sites

Species	N (%)		
	Old Karst	New Karst	Tussock
Graminoid			
<i>E. vaginatum</i>	1.58 ± 0.06	1.60 ± 0.09	1.55 ± 0.08
<i>C. bigelowii</i>	1.77 ± 0.14	1.84 ± 0.17	2.10 ± 0.15
Deciduous			
<i>B. nana</i>	2.16 ± 0.14	2.10 ± 0.34	1.97 ± 0.08
<i>R. chamaemorus</i>	1.92 ± 0.04	2.28 ± 0.14	2.04 ± 0.05
<i>V. uliginosum</i>	1.89 ± 0.06	1.98 ± 0.08	1.95 ± 0.08
Evergreen			
<i>E. nigrum</i>	1.64 ± 0.03	1.72 ± 0.17	1.70 ± 0.09
<i>L. decumbens</i>	1.17 ± 0.08	1.22 ± 0.08	1.23 ± 0.11

n = 6 per species per site, with the exception of *B. nana* with *n* = 3 and 4 at Old Karst and New Karst sites, respectively.

DISCUSSION

In this upland tundra ecosystem where permafrost has been thawing over the past several decades and thermokarst has developed, we observed large differences among our sites in plant community composition. Aboveground plant biomass ranged from being dominated by sedges, to becoming increasingly dominated by deciduous and evergreen shrubs across our sites as thermokarst became more developed (Figure 2). Aboveground vascular net primary productivity followed this same pattern, with graminoids dominating productivity in the Tussock and New Karst sites, whereas Old Karst productivity was dominated by shrubs (Figure 4). Nonvascular plant productivity was an important component of plant biomass, especially when considering the apparently photosynthetic (green) biomass alone (Figure 3). And, nonvascular productivity contributed significantly to total aboveground plant growth, especially at the Old Karst site where moss growth equaled the production of the deciduous shrubs, likely as a result of favorable moisture conditions.

Although our sites differed from one another in terms of soil environmental variables, plant biomass, and ANPP based on comparisons of means, it was also clear that the effects of permafrost thawing and thermokarst acted on plant species composition at a very local (quadrat) level via changes in microclimate that accompanied ground subsidence (Figure 5). Across all quadrats, there was a tradeoff between graminoid and shrub biomass whereas deciduous shrubs, evergreen shrubs, and mosses all increased in abundance together. This pattern held across all sites and was likely related to the soil

conditions of a particular quadrat and the small stature of tundra ecosystems where many individuals occupy a single 70 × 70 cm quadrat. The shrubs and moss preferred the warm and moist quadrats, whereas the graminoids dominated cold and dry quadrats. At the site scale, increased abundance of quadrats with particular microclimates produced the overall vegetation differences among sites (Figure 6).

Independent from microclimate, N is known to play a strong role in plant productivity and plant species composition in moist tundra, and may increase in availability as permafrost thaws (Shaver and others 2001; Mack and others 2004). Across these sites, changes in the N cycle as reflected by foliar N concentration patterns did not necessarily follow our straightforward expectation. Plant species trended towards higher N concentration in the Tussock and New Karst site and lower N concentration in the Old Karst site, but were not significantly different across sites, opposite to our hypothesis. Although foliar N concentration has been observed to increase in fertilizer addition experiments (Shaver and others 2001), other studies have shown that the increased growth stimulated by increased N availability can actually dilute the N concentration leaving foliar N concentration values the same (Shaver and Laundre 1997). Indeed, when foliar N concentrations were multiplied by total photosynthetic biomass the pattern reversed; Old Karst and New Karst both contained significantly higher total N in green tissue compared to Tussock. Because N availability is typically a limiting nutrient in this type of tundra, we interpret increased canopy N as an increase in the supply rate of N from the soil in the sites with greater thermokarst.

Because permafrost thawing and thermokarst development has multiple direct and indirect effects on patterns of plant biomass and species composition via changes in temperature regime, soil moisture status and distribution, and nutrient availability, it is difficult to identify single experimental manipulations that have recreated the effects that we observed. However, similar patterns of increased shrub abundance have been observed in other manipulative and observational studies in tussock tundra ecosystems most similar to ours. Fertilizer addition studies conducted in moist tussock tundra at Toolik Lake, Alaska found increased shrub biomass and productivity after 20 years of fertilization (Chapin and Shaver 1996; Shaver and others 2001). Initially, graminoid biomass and productivity increased with fertilization for several years, as that was the dominant functional group. Over time, increased shrub productivity and abundance came at the expense of decreased graminoid abundance and eventually graminoid abundance declined to zero. In that study, a different deciduous shrub, *B. nana*, dominated after fertilization whereas changes in *V. uliginosum*, *L. decumbens*, and *R. chamaemorus* biomass across sites were most important in our study, while *B. nana* was only a minor component of total biomass and did not change in abundance across sites. In contrast to our site, increased shrub abundance in the fertilizer treatment correlated with decreased moss abundance as canopy closure decreased growth and survival of nonvascular mosses and lichens. Across our Healy sites, moss biomass was positively correlated with shrub abundance. Differences in the identity of dominant species could either be a result of initial differences in vegetation composition, or a result of the particular environmental conditions created as a result of natural permafrost thawing as compared to experimental manipulations. Likewise the co-existence of species combinations could be influenced by the nature of perturbation, which in terms of the timing and spatial location of increased N availability is much different in a fertilizer study compared to changes in N cycling due to natural warming.

Although fertilizer addition studies in MAT at Toolik Lake produced similar patterns in vascular functional group abundance as we observed at our site, results from other air warming treatments differed. A meta-analysis of the International Tundra Experiment, consisting of small passive greenhouses that warmed the near-surface air in 13 different circumpolar sites (including Toolik Lake), found that increases in deciduous shrub and graminoid cover together occurred across sites,

whereas nonvascular cover decreased (Arft and others 1999). Our New Karst site may be most similar to the meta-analysis results, where graminoid productivity was still high even as shrubs were increasing. However, changes in species dominance at the Old Karst site suggests that competition by shrubs and mosses eventually will decrease graminoid abundance and productivity given a longer time interval. The results from our study and the manipulative experiments suggest that initial responses in productivity may not entirely reflect the long-term trajectory of species dominance due to successional processes (Hollister and others 2005).

Increased shrub abundance has also been documented in large-scale observational studies across Alaska and Canada. Invasion of upland tundra by shrubs was documented in repeat photographs of the North Slope of Alaska over a 50-year time interval (Sturm and others 2001; Tape and others 2006). In that study, the deciduous shrub green alder (*Alnus crispa*) showed the largest increase in abundance, whereas the deciduous shrubs willow (*Salix* spp.) and dwarf birch (*B. nana*) increased in abundance to a lesser degree, although the contribution of the latter two shrub genera may have been underestimated from air photos due to their relatively small and inconspicuous stature. Observations of permafrost bogs in the forested peatlands of Canada also showed increased productivity of the understory (combined for shrubs, moss, graminoids) across a wide range of collapse scar sites (Camill and others 2001). There, increased shrub productivity came at the expense of decreased black spruce (*Picea mariana*) production as the trees could not grow in the waterlogged conditions that characterized these bogs after permafrost thawed.

The change in hydrology produced by ground subsidence creates a wide range of microenvironments that affect plant species composition and growth. One reason why our site features increased moss biomass and production with permafrost thawing in contrast to the experimental manipulations may be a function of increased moss growth in quadrats where the water table is near the soil surface. These waterlogged microsites are a common feature of Old Karst and to a lesser degree in New Karst, even though our sites are characterized as relatively well drained. Indeed, the increased moss NPP at Old Karst was more a function of increased growth per moss area (Figure 4) rather than any strong increase in moss abundance and biomass (Table 4), which could be due to more moist and favorable conditions for moss growth.

The same wet and warm microenvironment that favored moss was negatively associated with graminoid biomass, which may explain why graminoids strongly decrease in abundance with increased thermokarst. These wet and dry microenvironments created by permafrost thawing and thermokarst development are typically not reproduced to this degree in experimental manipulation of climate change factors because of experimental artifacts.

Plant species composition, aboveground biomass, and net primary productivity in our three sites are most likely related to the difference in disturbance history that resulted from the timing of permafrost thaw and ground subsidence. Although we have an incomplete history of the site in terms of disturbance age, the fact that these sites are undergoing change from disturbance is demonstrated by the widespread abundance of dead moss on the soil surface, and by the degree of ground subsidence. Other work has showed that at the end of the little Ice Age (mid-nineteenth century) a period of permafrost thawing ensued that coincided with thermokarst development in areas of interior Alaska (Jorgenson and others 2001, 2006), which may have also triggered thawing in the Old Karst site (T. Jorgensen, personal communication). A cooling period followed, before regional climate warming began again in the 1960s and 1970s, leading to more widespread thawing in the same time frame as the development of the New Karst site (Osterkamp and Romanovsky 1999; Serreze and others 2000). Although the Tussock site would clearly be affected by regional warming, it has not undergone the ground subsidence and thermokarst of the other two sites. Permafrost thawing often remains localized because lateral heat transfer is limited, thus the depth of thaw is roughly equivalent to the lateral distance at the surface that is affected (Romanovsky and Osterkamp 2000). In other words, thawing permafrost to 2 m depth affects a 2 m wide patch at the surface. Subtle differences in microtopography and drainage, then, can lead to areas undergoing thermokarst and loss of permafrost, whereas adjacent areas retain permafrost. However, if regional warming is the ultimate trigger of this observed permafrost thawing, even our Tussock site is likely to be undergoing change, albeit not to as great a degree as the other two sites.

In conclusion, our sites appear to represent a gradient in time since disturbance by permafrost thawing and thermokarst development in upland tundra. Although permafrost thawing and ther-

mokarst at this site was likely triggered by increases in regional air temperature or winter precipitation (Romanovsky and Osterkamp 2000), changing soil moisture distribution and nutrient availability are likely to have a stronger effect on plant biomass and productivity compared to the effect of changes in regional climate. These changes in soil resources appeared to be particularly important in shifting this graminoid-dominated tundra ecosystem to one dominated by shrubs and moss.

ACKNOWLEDGEMENTS

We would like to thank Terry Chapin and the personnel of BNZ-LTER for the use of equipment and laboratory space. This research is based upon work supported by: NSF EAR Grant #0223193 to EAGS; NASA New Investigator Award to EAGS; a NSF LTER Grant #0080609 to EAGS; a NSF DEB Grant #0516326 to EAGS; and a A.W. Mellon Foundation grant to EAGS.

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