Characteristics that predict success for warmed tundra vegetation

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INTRODUCTION

The Arctic is more profoundly affected by climate change than lower latitude regions. Warming has been more pronounced in the Arctic and this trend is expected to continue; vegetation in high latitude regions is also expected to respond to climate change more than vegetation in other parts of the world. Tundra plants have had to adapt to the severity of the Arctic climate order to successfully colonize the region. Thus small changes in climate could have a large impact on the plant community. This study seeks to predict the response of plant species to climate change in association with the International Tundra Experiment (ITEX), by using experimental warming to simulate climate change at four study sites in northern Alaska.

The prevailing wisdom is that species that are predominantly distributed in low Arctic regions will respond faster to warming. These low Arctic species are expected to increase in cover and distribution, and as this happens, cover and distribution of species primarily found in the high Arctic will decrease. Previous studies have found that when compared to the control treatment, the warming treatment results in an overall increase in absolute cover of vascular plants, and a change in relative cover of some individual species. When looking at each of the four sites individually, the overall warming trend is upheld at some sites but not at others. However, sites with a decrease or with no change in overall absolute cover still experienced changes in the community. We used a variety of grouping methods based on geography, morphology, and phenology of the plants to analyze how different groups of plants were responding to the warming treatment. Groupings were determined using both observations collected in the field and observations reported in the literature. The goal of this study is to determine which grouping schemes are best able to predict trends in changing Arctic vegetation communities.

METHODS

Seventeen grouping schemes were developed using both the literature about arctic vegetation, and data collected from the field. These grouping schemes fall into two general groups: those relating to geographic distribution of the species (FIG 2), and those relating to morphology, development, and phenology (FIG 3).

The species present were classified using each of these grouping schemes. Occasionally we had insufficient data to classify a species, such as when measurements were not taken or when an author did not encounter a certain species, and in these cases we removed those species from the analysis of that grouping scheme. We used R version 2.10.1 to compare absolute cover of each group in each treatment through a two-way ANOVA.

RESULTS

Out of the seventeen grouping schemes used in this study, most were shown to be useful for at least one site (Table 1). We looked for a significant interaction between the grouping scheme and the warming treatment, because that indicated that the grouping scheme was a useful predictor of the plants' response to warming. The interaction between the warming treatment and the grouping scheme was significant for ten of the classifications ($p < 0.05$). Five of the remaining groups showed potential trends ($p < 0.10$). The grouping scheme that was significant at the most sites was Greenland Distribution (FIG 2). That interaction was significant at the Barrow Wet, Atqasuk Wet, and Atqasuk Dry sites, as well as overall, for all sites combined. Two other sites, High Arctic/Low Arctic and Alaskan distribution, also had significant interactions overall, and the group Biome Distribution showed a trend.

CONCLUSIONS

The grouping schemes used in this study were useful, though further study is needed to determine which grouping schemes are the most valuable for predicting plant response. Previous studies of these four sites have also shown that the sites respond differently to warming; a site that is more responsive will have the potential to show a stronger treatment effect in the interaction between warming and grouping.

Grouping schemes related to geography and distribution were in general better predictors of species' response to warming than grouping schemes related to morphology and development. The significant interactions for the four sites combined all came from geographic grouping schemes. Of these, the Greenland Distribution scheme showed the greatest number of significant interactions with the warming treatment. At our sites, species present chiefly in the north of Greenland (label "N," see Fig 2) increased at a higher rate than other species in response to warming. This result agrees with the results of another of the groups that is significant for all sites combined, the High Arctic/Low Arctic grouping scheme; plants labeled "High Arctic" increased in cover, while plants labeled "Low Arctic" decreased in cover. Though we would expect an increase in cover from plants labeled as southerly species, this increase in northerly species is due to the way the plants are grouped. Our study sites exist within the boundaries of northern zones; the "N" label includes more southerly species than the "NN" label. These same "N" species also fall in the "High Arctic" group.

In some grouping schemes, one responsive group is dominated by one responsive species. The dry heath study sites were chosen because of the presence of the evergreen shrub *Cassiope tetragona. C. tetragona* is either the dominant species or the only species in the most responsive group in Wintering State of Buds and Plant Family. The same is true at the wet site for *C. aquatilis* in the group Alaskan Distribution. The two are both labeled as group "N" from the Greenland Distribution scheme, the most responsive group with the largest number of significant interactions.

Several of the geographic grouping schemes showed that groups with the largest range had the greatest increase in cover in response to warming. Thus those species that are already adapted to greater variations in habitat are successful under warmed conditions.

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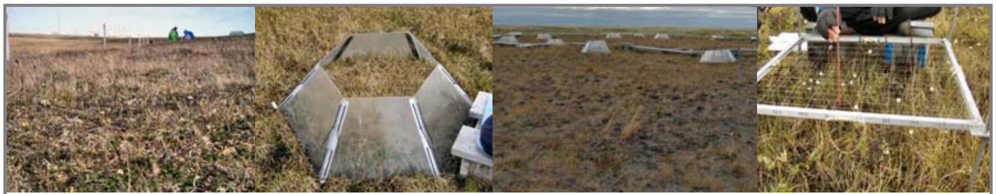
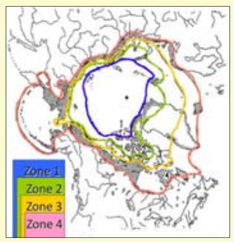


Barrow Dry Heath Site — Barrow Wet Meadow Site (*with OTC*) — Atqasuk Dry Heath Site — Atqasuk Wet Meadow Site (*with point frame*)

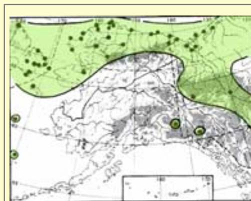
FIG 1. Sites were established at the coastal city of Barrow, Alaska (71°17′44″N 156°45′59″W) in 1994 and at the inland village of Atqasuk (70°28′40″N 157°25′5″W) in 1996. At each location a site was established in a dry heath community and in a wet meadow community. At each of these four sites there are 24 control plots and 24 plots under Open-Topped Chambers (OTCs). The OTCs warm the experimental plots on average between 1° and 3° Celsius for the growing season, depending on the site and weather conditions for the year. Plant community data was collected using a point frame method in 2007 and 2008. At each intersection of a 75cm x 75cm 100 point grid, a ruler was dropped. Every occurrence of a plant species was identified by species and recorded as alive or dead (C). This was done for all control and experimental plots.

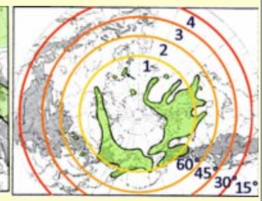
FIG 2. Grouping schemes related to geographic distribution

Young Zones
Young 1971



Young initially described these zones using his observations from St. Lawrence Island. He combined this with the research of others to create these circumpolar zones. Species with a northern limit within the blue line are labeled Zone 1; those with a northern limit within the green line are Zone 2, etc.





Alaskan Distribution
Hultén 1968

1: present throughout Alaska
2: present on north and south coasts
3: southern limit is north of southern coast
4: present in central AK, not at N or S coasts
5: northern limit is south of northern coast

Hultén included distribution maps of both Alaska and the northern hemisphere with his descriptions of each plant species. On the left is *Carex aquatilis* sub. *stans,* in group 3. At right is *Cassiope tetragona* in Latitude group 2, Longitude group 1.

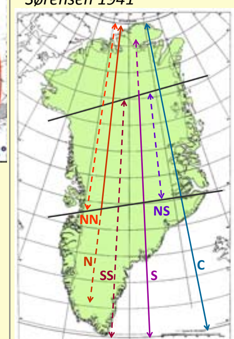
Latitudinal Distribution
Hultén 1968

1: Southern limit north of 60°N
2: Southern limit between 60°N and 45°N
3: Southern limit between 45°N and 30°N
4: Southern limit between 30°N and 15°N

Longitudinal Distribution
Hultén 1968

1: Present at all longitudes
2: Not present at all longitudes

Greenland Distribution
Sørensen 1941



Species classified by their distribution in Greenland in these groups described by Sørensen
NN: Distinct southern limit, no northern limit
N: No distinct limits, present mostly in north
SS: Distinct northern limit, no southern limit
S: No distinct limits, present mostly in south
NS: Distinct northern and southern limits
C: Circumgreenlandic species

High Arctic/Low Arctic Distribution
Edlund & Alt 1989 and Gould & Walker 1999

Consists of only two groups, high arctic and low. Arctic. Defining high and low is necessarily relative, so for the purposes of this study, the division between the two categories is approximately the northern limit of erect dwarf shrubs such as *Salix pulchra* (Gould & Walker 1999). High arctic plants are more northerly, and low arctic plants are more southerly.

Biome Distribution

All plants are tundra plants. This grouping scheme describes the primary biome of the species using these five labels:
Arctic
Arctic alpine
Alpine
Boreal
Cosmopolitan

FIG 3. Grouping schemes related to morphology and development

Family

These 16 families are present at the sites:

Asteraceae	Betulaceae
Brassicaceae	Caryophyllaceae
Cyperaceae	Diapensiaceae
Ericaceae	Juncaceae
Papaveraceae	Poaceae
Polygonaceae	Primulaceae
Ranunculaceae	Salicaceae
Saxifragaceae	Scrophulariaceae

Monocot/Dicot

Number of cotyledons

Cassiope tetragona: Evergreen shrub present at the dry sites.

Group labels for *C. tetragona* (Counterclockwise starting top left):

Ericaceae
Dicot
Evergreen
Floral Wintering Stage 7
Late Bud Burst (Barrow)
Early Bud Burst (Atqasuk)
Early Flower Burst
TDD_{sm}
Thawing Type 2
Chamaephyte

Wintering State of Leaves
Sørensen 1941

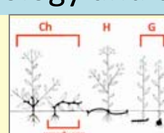
S: Summer-green; leaves function only in the summer
W: Winter-green; leaves function in two growing seasons, with winter between
E: Evergreen; leaves function more than two summers

Wintering State of Buds
Sørensen 1941

A: active bud protection
P: passive bud protection
U: Unprotected buds

Floral Wintering Stage
Sørensen 1941

State of individual over winter, with 1 being the least developed and 7 being the most developed
1: Purely vegetative. Some leaf primorida to form in summer, along with floral primordia.
2: All leaf primordia formed. Floral primorida to form in summer.
3: Not purely vegetative. Inflorescence without differentiated floral primordia.
4: Floral parts in incipient differentiation.
5: Calyx, anthers formed. Ovary developing.
6: Flower buds large and roughly developed.
7: Flower buds fully developed. Anthers with pollen
8: Floral development aperiodical. Buds at stages 3-7.



Raunkiær Life Form
Sørensen 1941

CH: Chamaephyte; buds on persistent shoots near ground
G: Geophyte; Buds resting in dry ground
H: Hemicryptophyte; Buds at or near soil surface

Thawing Type *Sørensen 1941*

Grouped by thawing type of the ecosystem in which the species is naturally included
1: Snow covering ceases June 1 at the latest
2: Snow covering ceases between June 1-15
3: Snow covering ceases June 15- July 1
4: Snow covering disappears after July 1
Some species are classified as between groups; 1-2, 2-3, and 3-4 are also used.

Early/Late Leaf Bud Burst
ITEX phenology data

Means were taken from observations of phenological responses collected since establishment of sites
E: Spp mean leaf bud burst is before mean leaf bud burst for all spp at that site
L: Spp mean leaf bud burst is after mean leaf bud burst for all spp at the site

Early/Late Flower Burst
ITEX phenology data

E: Spp mean flower burst is before mean flower burst for all spp at that site
L: Spp mean flower burst is after mean flower burst for all spp at the site

TDD_{sm}/Julian Day
Hollister 2003

Whether or not TDD_{sm} is a better predictor of flower burst than Julian Day
T: Thawing degree days from snowmelt. TDD refers to the number of days with a mean daily temperature above 0°C. Flower burst in spp labeled T is a reaction to temperature
J: Day of the year. Flower burst in spp labeled J is a reaction to day length rather than temperature.

	Young Zones *Young 1971* 42/72	High Arctic / Low Arctic *Gould and Walker 1999* 40/72	Biome Distribution 54/72	Latitudinal Distribution *Hultén 1968* 72/72	Longitudinal Distribution *Hultén 1968* 72/72	Alaskan Distribution *Hultén 1968* 72/72	Greenland Distribution *Sørensen 1941* 41/72	Family 72/72	Monocot/Dicot 72/72	TDD_{sm} / Julian Day *Hollister 2003* 10/72	Raunkiær's Life Forms *Sørensen 1941* 41/72	Thawing Type *Sørensen 1941* 41/72	Wintering State of Leaves *Sørensen 1941* 41/72	Wintering State of Buds 41/72	Floral Wintering Stage *Sørensen 1941* 42/72	Early / Late Leaf Bud Burst *ITEX phenology data* 52/72	Early / Late Flower Burst *ITEX phenology data* 39/72
All Sites Considered		*	·			*	*										
Barrow Wet							*									*	·
Barrow Dry	*	*	·		*	*		*					*	*			
Atqasuk Wet				·		*	*						*		*		
Atqasuk Dry							*			·		·					

TABLE 1. Each of the seventeen grouping schemes at each of the four study sites. Light green schemes are related to geography and distribution; light blue schemes are related to morphology and development. Asterisks and dots indicate a significant interaction between the grouping scheme and the warming treatment. *p<.05, ·p<.10. Trends and significant interactions are also reported for all sites combined. Fraction represents number of species out of the total 72 that were defined under each grouping scheme.