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Plant community responses to experimental warming across the tundra biome

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Recent observations of changes in some tundra ecosystems appear to be responses to a warming climate. Several experimental studies have shown that tundra plants and ecosystems can respond strongly to environmental change, including warming; however, most studies were limited to a single location and were of short duration and based on a variety of experimental designs. In addition, comparisons among studies are difficult because a variety of techniques have been used to achieve experimental warming and different measurements have been used to assess responses. We used metaanalysis on plant community measurements from standardized warming experiments at 11 locations across the tundra biome involved in the International Tundra Experiment. The passive warming treatment increased plant-level air temperature by 1–3°C, which is in the range of predicted and observed warming for tundra regions. Responses were rapid and detected in whole plant communities after only two growing seasons. Overall, warming increased height and cover of deciduous shrubs and graminoids, decreased cover of mosses and lichens, and decreased species diversity and evenness. These results predict that warming will cause a decline in biodiversity across a wide variety of tundra, at least in the short term. They also provide rigorous experimental evidence that recently observed increases in shrub cover in many tundra regions are in response to climate warming. These changes have important implications for processes and interactions within tundra ecosystems and between tundra and the atmosphere.

arctic and alpine ecosystems | biodiversity | climate change | vegetation change

Detecting biotic responses to a changing environment is essential for understanding the consequences of global climate change (1–4). Shifts in the composition and abundance of plant species will have important effects on ecosystem processes, including net primary production and nutrient cycling, and on organisms at all trophic levels (5). Vegetation changes are expected to be large in tundra regions (1, 4, 6) in response to predicted warming, although the variability in tundra vegetation at local and regional scales makes it difficult to predict these changes. Arctic regions have been warming since the mid-1800s (7), but the warming has accelerated in recent decades (1, 7, 8) and is expected to continue throughout this century (1, 4). Model projections show that the warming could result in the loss of as much as 40% of the current tundra area by the year 2100 as it is replaced by boreal forest (1). Observational studies have found that leaf-out is earlier (9) and shrub cover has increased in areas such as northern Alaska (10). Many observed biotic changes are consistent with expected responses to increasing temperature (11, 12); however, experimental warming provides a direct test of the effect of temperature on plant communities.

Over the past two decades, experimental studies have shown that tundra plants can respond strongly to environmental manipulations, including warming (e.g., refs. 13–16), and there have been a few syntheses of these studies (17–20). However, most of the previous studies were conducted at single sites for relatively short periods using methods unique to the study. The restricted geographic coverage, short duration, and variability in experimental design hinder the general conclusions from syntheses of these studies. These shortcomings were highlighted in the recent synthesis of responses of arctic terrestrial ecosystems to climate change completed for the Arctic Climate Impact Assessment (1), which recommended better coordination of research throughout the Arctic. Here, we report whole plant community results from standardized warming experiments conducted at 11 locations throughout the tundra biome (Fig. 1). The studies are part of the International Tundra Experiment (ITEX), which is a network of arctic and alpine sites throughout the world where experimental and observational studies have been established by using standardized protocols to measure responses of tundra plants and plant communities to increased temperature (16, 17, 21–28). The use of standardized protocols helps to ensure data are comparable among sites and increases the strength and reliability of conclusions based on analyses of the data. In a previous synthesis of short-term plant responses at ITEX sites (17), we found that graminoid and forb species showed the strongest growth responses to experimental warming, and these were greatest in the

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Abbreviation: ITEX, International Tundra Experiment.

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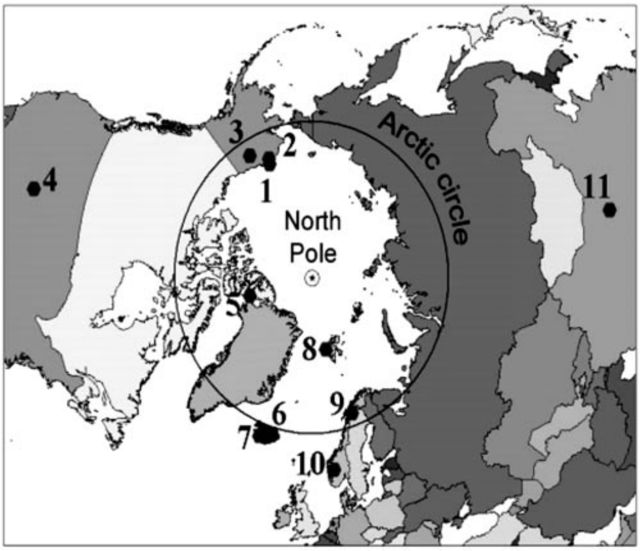

Fig. 1. Location of the sites included in this analysis: 1, Barrow, United States; 2, Atqasuk, United States; 3, Toolik Lake, United States; 4, Niwot Ridge, United States; 5, Alexandra Fiord, Canada; 6, Audkuluheidi, Iceland; 7, Thingvellir, Iceland; 8, Svalbard, Norway; 9, Latnjajaure, Sweden; 10, Finse, Norway; and 11, Tibetan Plateau, China. Basic site characteristics are given in Table 1.

Low Arctic. In High Arctic sites, warming increased reproductive effort in many plant species. In the present study, we examine the consequences of these responses for tundra plant communities.

Results

Across all sites, moderate increases in temperature caused significant changes in tundra vegetation. Vascular plants grew significantly taller under the warming treatment (Fig. 2). The cover (a proxy for biomass) of deciduous shrubs and graminoids increased, whereas cryptogams (lichens and bryophytes) decreased. Overall species composition and abundance was significantly changed (as described by ordination scores), and species diversity, evenness, and richness decreased in response to warming.

The changes were rapid, and effects of warming on species composition (ordination scores), litter cover, and species diversity were evident after only two growing seasons (Fig. 3). In most cases, three to four growing seasons of experimental warming yielded a significant change in cover and height of growth forms.

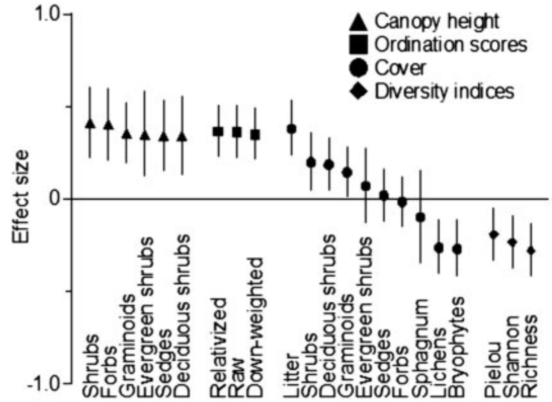

Fig. 2. Response of tundra plant community variables to experimental warming. The values represent the mean effect size and 95% confidence interval from metaanalyses of the 22 variables measured in all studies, where studies consisted of the site and each of the growing seasons in which measurements were made. Effect sizes for cover were in the range considered small by metaanalysis convention, indicating a small magnitude of response. Moderate effect sizes were found for canopy height, ordination scores, and diversity indices, indicating a larger magnitude of response. Note that only the magnitude is important for the ordination scores.

Once achieved, the changes were sustained over the length of the record of studies.

Observed changes in cover were not primarily caused by increases in the dominant species at each site. The three most abundant species did not show a consistent response to warming [nonsignificant mean effect size of -0.01 ± 0.13 (95% confidence interval)]. There was an equal likelihood of increasing or decreasing cover of the most abundant species [significant heterogeneity in effect ($P < 0.05$) with a mean of essentially zero]. Thus, we do not believe the community-level results represent a transient response where the dominant species initially takes advantage of the more favorable microenvironment.

For the variables that showed different responses to warming among sites, we found that the geographic region or soil moisture regime helped to explain these differences (Fig. 4). In most cases, High Arctic sites were less responsive to warming. Warming had the greatest effect on canopy height in Low Arctic sites and the cover of deciduous shrubs in alpine sites. When the studies were partitioned by soil moisture regime, the effect of warming on plant height and cover was greatest in mesic sites. Growth form,

Table 1. Environmental description of the study locations

Location*	Country	Region†	Temperature, °C‡	Latitude	Elevation, m	Moisture regime§	Seasons of warming, y
Barrow (1)	U.S.A.	High Arctic	3.7	71°19′	3	Dry, wet	6
Svalbard (8)	Norway	High Arctic	5.3	78°56′	22	Dry	4
Finse (10)	Norway	Alpine	6.5	60°37′	1,500	Dry	4
Alexandra Fiord (5)	Canada	High Arctic	6.7	78°53′	50	Dry, moist, wet	4
Latnjajaure (9)	Sweden	Low Arctic	7.9	68°21′	1,000	Dry, moist	4
Niwot Ridge (4)	U.S.A.	Alpine	8.0	40°03′	3,500	Dry	3
Audkuluheidi (6)	Iceland	Low Arctic	8.5	65°16′	490	Dry	3
Atqasuk (2)	U.S.A.	Low Arctic	8.9	70°29′	15	Dry, wet	5
Tibetan Plateau (11)	China	Alpine	10.0	37°37′	3,200	Moist	3
Thingvellir (7)	Iceland	Low Arctic	11.0	64°17′	120	Dry	5
Toolik Lake (3)	U.S.A.	Low Arctic	12.0	68°38′	760	Dry, moist	6

*Number in brackets refers to location in Fig. 1.
†Regional classifications were based on a combination of climate and geography.
‡Mean July air temperatures.
§Sites consisted of the combination of location and soil moisture regime. In total 17 sites were represented in the analysis.

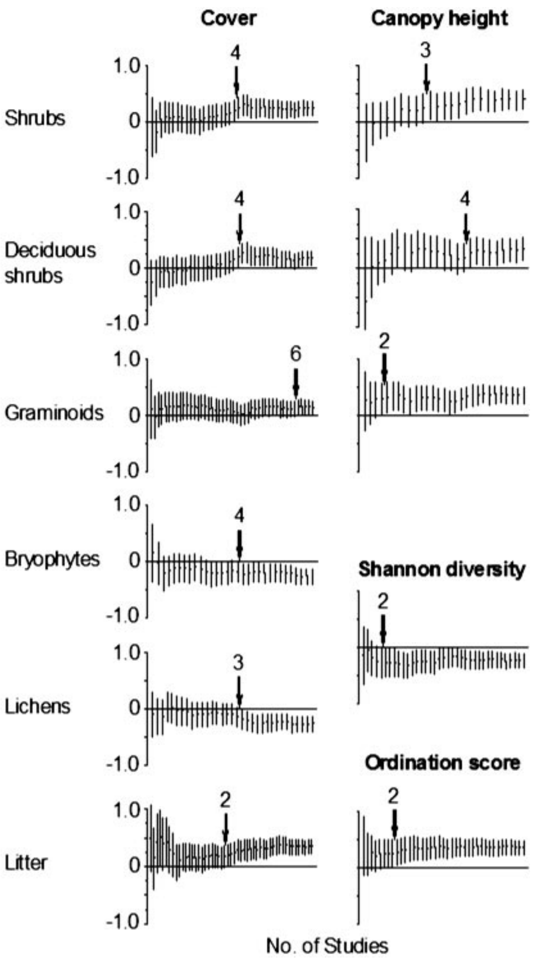

Fig. 3. Response of tundra plant community variables that showed a significant main response to warming partitioned by duration of the warming experiments. The values represent the mean effect size and 95% confidence interval of a series of metaanalyses where studies were added successively to the analysis based on the number of growing seasons of warming. The arrows indicate the growing season of warming in which the effect became significant. The ordination score is based on the raw cover values. The number of seasons of warming at each site is given in Table 1.

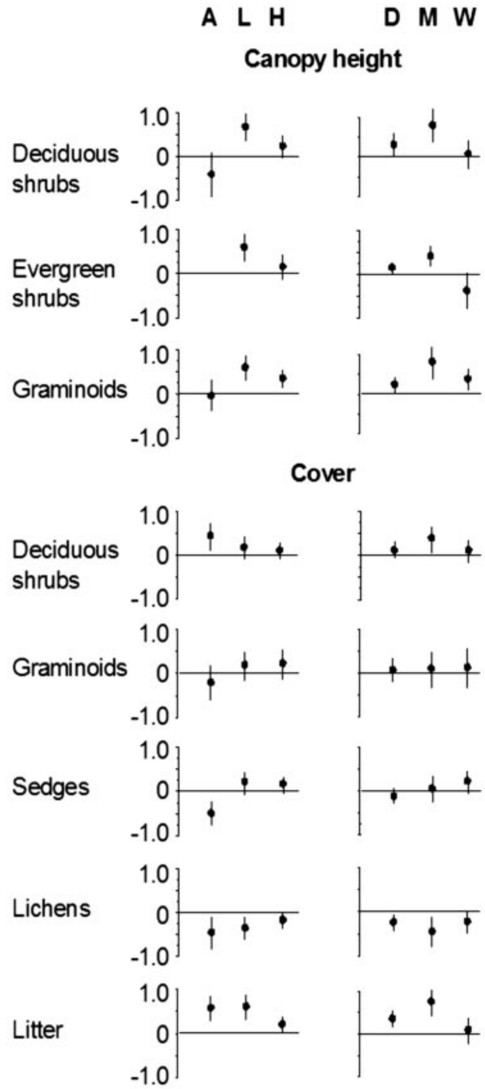

Fig. 4. Response of tundra plant community variables that showed significant differences in response among sites partitioned by region (A, alpine; L, Low Arctic; H, High Arctic) or moisture regime (D, dry; M, moist; W, wet). The values represent the mean effect size and 95% confidence interval. The classification of the sites by region and the soil moisture regimes at each site are shown in Table 1.

geography, and soil moisture are not entirely independent, so these results do not necessarily suggest causation.

Discussion

Across the wide variety of tundra sites represented in our study, plant communities responded strongly to moderate increases in temperature caused by experimental warming. Increases in the height and cover of graminoids and shrubs were generally found in all sites across the network. The rapid and sustained response by graminoid species was predicted from a previous synthesis of plant responses (17) that showed strong increases in growth in warmed plots after 1 year. The increase in woody plant dominance in response to experimental warming, especially deciduous shrub cover and height, is consistent with observations from the paleoecological record (31, 32), natural temperature gradients (33), and tundra areas currently experiencing climate change (8–10). A shift from herbaceous to woody tundra will have important consequences for ecosystem processes. For example, increased shrub height and cover will change the surface energy budget, mainly through changes in albedo and increased surface roughness (34, 35). The greater leaf density in a shrub dominated canopy will likely amplify atmospheric warming by increasing net (absorbed) radiation (2, 35). The shift to woody tundra will also alter the ecosystem carbon balance (27, 35, 36) and nutrient dynamics, mainly through changes in litter composition and amounts (36).

The decrease in species diversity we observed was somewhat surprising and is inconsistent with the broad patterns of increasing diversity along natural gradients of increasing temperature (33). The decline in species diversity may result from differences between long-term and short-term warming effects, as local extinctions and shifts in dominance are likely to occur before immigration (37). The changes in diversity in our plots were caused by shifts in relative abundance of extant species. The increased height and density of shrubs, graminoids, and forbs resulted in decreased cover of shade-intolerant lichens and bryophytes. A decline in lichen cover in response to warming was also noted in a recent review of experimental studies in northern systems (38). The decrease in evenness indicates a change in the dominance structure of the plant communities, where fewer species produce a larger proportion of the cover. This consistent response may represent a first step toward local species extinction.

The response to warming is influenced by the initial community composition and ecosystem characteristics, as seen by the variability in response among sites for several variables. The lack of strong responses in the High Arctic sites indicates a possible link between ability to respond and growing season temperature and length (39). Soil nutrient availability is lowest in these sites (40) and would likely limit the growth response to warming (41). The lower diversity in the High Arctic (33) may also limit the response at the community level, with fewer responsive species and phenotypes. The smaller response in the High Arctic is supported by a previous metaanalysis of ITEX results (17), where we found short-term growth responses in High Arctic plants were lower than those in Low Arctic or alpine plants. Soil moisture is an important determinant of community composition, and generally mesic sites have the greatest species diversity and are most responsive to environmental change (42). The Low Arctic mesic sites showed the greatest increases in canopy height in response to warming, which is most likely a function of the density of plants in these tundra communities. With very little room for lateral expansion, the response is concentrated in vertical growth.

The variability in response among sites illustrates the shortcomings of using data from a few sites to parameterize vegetation models for the tundra biome and indicates that such models will likely be inaccurate for some regions (1, 43). Although we are able to show important common responses across tundra sites, our study is also biased by their distribution. The sites were relatively evenly distributed among alpine, Low Arctic, and High Arctic areas and greatly increased the geographic scope of previous studies; however, the majority of our sites had a dry soil moisture regime. In addition, results from short-term experiments are not generally good predictors for longer-term changes (14, 23). For example, a previous metaanalysis of species responses to as many as 4 years of warming at ITEX sites (17) showed that graminoids and forbs had the greatest initial growth responses, yet here we show graminoids and shrubs had larger changes over the 6 years included in our study. Thus, coordinated experimentation and long-term monitoring networks similar to the ITEX network are essential for detecting and understanding biotic change in response to climate warming.

The results presented here are from a coordinated approach to examine species (16, 17), plant community (23–25), and ecosystem-level (27) response to experimental warming. Although increases in shrubs (10, 35) and declines in lichens (38) have been shown in response to warming in prior studies, our results indicate that the changes are widespread and applicable to the tundra biome as a whole. Thus, our analysis provides strong verification that observed increases in woody species in tundra regions are a result of warming. Finally, the decline in species diversity at all sites supports the assertion that climate change will, at least initially, reduce biodiversity in tundra regions (33, 44). We predict continued trends in warming of the tundra biome will cause species loss and shift vegetation toward increased shrub dominance.

Methods

The coordinated warming experiments were started in the early 1990s and followed the standardized protocols in the ITEX manual (22). At the study sites, transparent circular or hexagonal open-top chambers (OTCs) ranging in diameter from 0.5 to 1.5 m and up to 0.5 m high were used to raise mean growing season air temperature by 1–3°C (21–28). OTCs are considered to be the warming manipulation best suited for most tundra environments (26) and have been found to be a reasonable analogue of regional climate change (28).

At each site the vegetation was sampled during midsummer by using standardized methods (22) to detect changes caused by warming. Vegetation cover and height were measured with a 0.6- to 1-m^2 point frame that could be relocated over the same area of each plot. The first and last vertical "hits" of vascular plant species, lichens, bryophytes, litter, or bare ground intercepting each of 100 points were recorded. The variables derived included: the height and cover of the major vascular plant growth forms (shrub, graminoid, and forb); cover of bryophytes, lichen, and litter; species richness (the number of species recorded); Pielou diversity index (an estimate of species evenness); Shannon diversity index (a combination of species richness and evenness); and cover of the three most dominant species. For some analyses, the growth forms were further subdivided: shrubs included all shrubs and were also partitioned into deciduous and evergreen shrubs; bryophytes were analyzed both collectively and separately for *Sphagnum*; and sedges were analyzed separately from graminoids, which included grasses and rushes. Although standing dead hits were recorded if they occurred, only live hits were included in the analyses, except for the calculation of litter cover, where litter was considered dead, unattached plant material on the ground.

To examine the absolute changes based on all of the vegetation data, we calculated ordination scores for each plot at each site for each year. To minimize bias caused by the ordination method, three separate detrended correspondence analyses (DCAs) were performed by using raw cover values, relativized cover values, and cover values where rare species were down-weighted. The DCA was done by using PC-ORD (version 4.10) (29).

We conducted a metaanalysis on the vegetation measurements collected at each site, and >40 studies were included (studies consisted of the site and each of the growing seasons in which measurements were made). The metaanalysis was performed by using METAWIN (version 2.0) (30), and we used the normalized difference between experimental and control means adjusted for sample size (hedges *D*). A series of separate metaanalyses, where studies were systematically added to the analysis based on the number of seasons of warming (cumulative metaanalysis), were used to determine the number of growing seasons necessary to detect a significant effect. The variables were further analyzed by the categories moisture regime (dry, moist, wet) and geographic region (alpine, Low Arctic, High Arctic) when there was a significant difference in the response to warming between sites (measured by the total heterogeneity of the metaanalysis; Qt).

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