

# 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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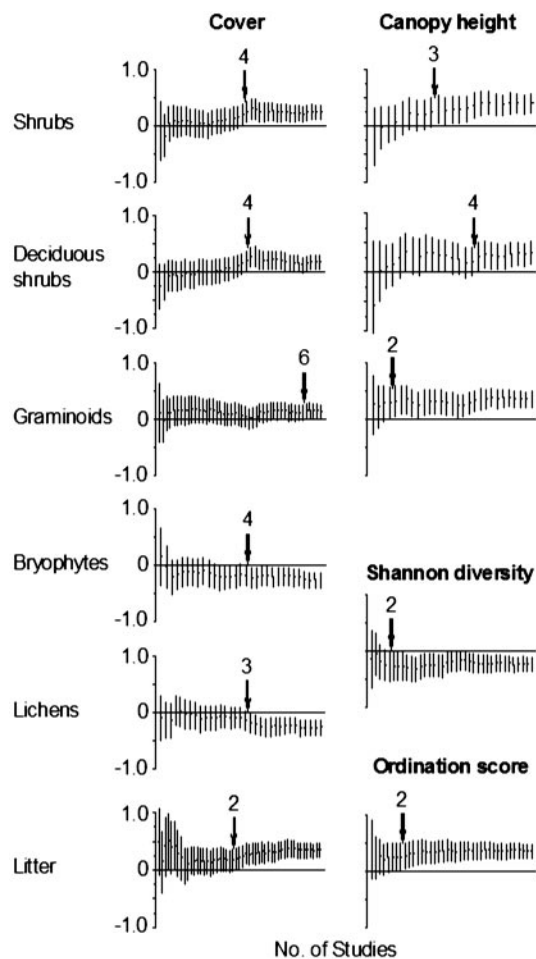
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Abbreviation: ITEX, International Tundra Experiment.

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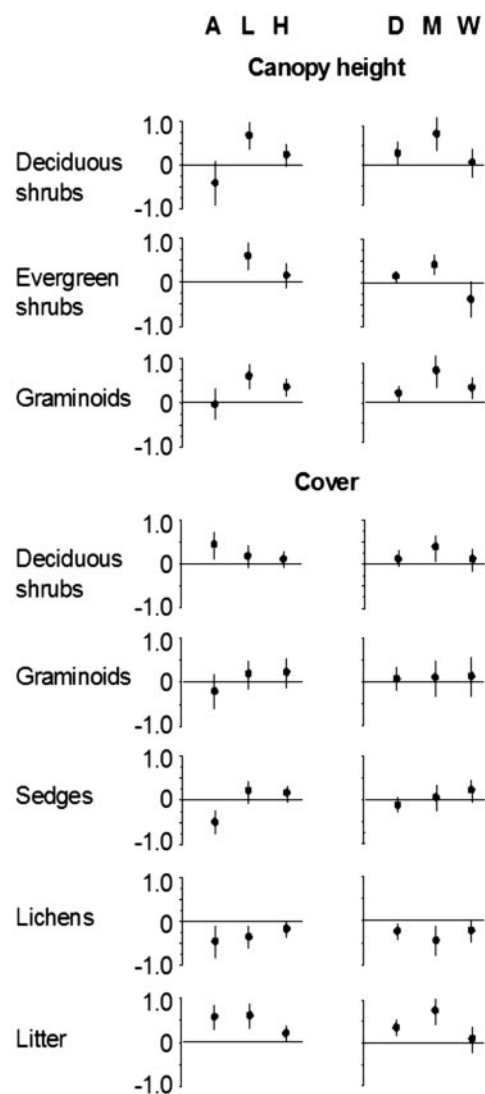


**Fig. 3.** Response of tundra plant community variables that showed a significant main response to warming partitioned by duration of the warming experiments. The values represent the mean effect size and 95% confidence interval of a series of metaanalyses where studies were added successively to the 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.

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 warm-



**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.

ing 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





