

# Detecting changes in arctic tundra plant communities in response to warming over decadal time scales

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## Abstract

Detecting the response of vegetation to climate forcing as distinct from spatial and temporal variability may be difficult, if not impossible, over the typical duration of most field studies. We analyzed the spatial and interannual variability of plant functional type biomass from field studies in low arctic tussock tundra and compared these to climate change simulations of plant community composition using a dynamic tundra vegetation model (ArcVeg). Spatial heterogeneity of peak season live aboveground biomass was estimated using field samples taken from low arctic tundra at Ivotuk, Alaska (68.5°N, 155.7°W) in 1999. Coefficients of variation for live aboveground biomass at the 1 m<sup>2</sup> scale ranged from 14.6% for deciduous shrubs, 18.5% for graminoids and 25.3% for mosses to over 57% for forbs and lichens. Spatial heterogeneity in the ArcVeg dynamic vegetation model was simulated to be greater than the field data, ranging from 37.1% for deciduous shrubs to 107.9% for forbs. Disturbances in the model, such as caribou grazing and freezing–thawing of soil, as well as demographic stochasticity, led to the greater variability in the simulated results. Temporal variances of aboveground live biomass over a 19-year period using data from Toolik Lake, AK fell within the range of field and simulation spatial variances. However, simulations using ArcVeg suggest that temporal variability can be substantially less than site-scale spatial variability. Field data coupled with ArcVeg simulations of climate change scenarios indicate that some changes in plant community composition may be detectable within two decades following the onset of warming, and shrubs and mosses might be the key indicators of community change. Model simulations also project increasing landscape scale spatial heterogeneity (particularly of shrubs) with increasing temperatures.

*Keywords:* arctic tundra, global warming, plant community dynamics, spatial and temporal heterogeneity, vegetation dynamics model

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## Introduction

A current major focus in earth and environmental sciences is detecting the effects of a warming planet. Several studies confirm a global increase in mean near-surface air temperatures and implicate anthropogenic emissions of CO<sub>2</sub> as a factor contributing to the

warming trend (Mann *et al.*, 1998; Hansen *et al.*, 1999; Crowley, 2000). While it is challenging enough to observe a global warming trend, detecting earth-system responses to warming may be difficult or impossible. Areas most appropriate for detecting ecosystem responses to climate warming and for projecting future responses of other regions are those that are currently warming most rapidly (Overpeck *et al.*, 1997; Hansen *et al.*, 1999; Giorgi *et al.*, 2001; Vaughan *et al.*, 2001). Arctic Alaska is one region that has experienced more rapid recent warming than the global mean, increasing approximately 2–3 °C over the past 3–4 decades

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(Hansen *et al.*, 1999; Barber *et al.*, 2000; Oechel *et al.*, 2000; Serreze *et al.*, 2000).

Northern ecosystems in western North America are also experiencing other physical changes related to warming (Serreze *et al.*, 2000) such as increases in precipitation (Maxwell, 1997; Oechel *et al.*, 2000), decreases in snow cover (Robinson *et al.*, 1993) and sea ice extent (Vinnikov *et al.*, 1999) and increased permafrost thawing (Osterkamp and Romanovsky, 1999). Recent biological changes include an increase in peak season plant biomass (as indicated by the remotely sensed normalized difference vegetation index), and a longer growing season that begins earlier (Myneni *et al.*, 1997; Zhou *et al.*, 2001). Many of these changes collectively result in Arctic terrestrial ecosystems shifting between sinks of carbon and sources of carbon to the atmosphere, with some evidence of multiple directional shifts over the past 40 years (Oechel *et al.*, 1993; Oechel *et al.*, 2000). Given that arctic soils contain a substantial fraction of the world's belowground carbon, these changes could have major effects on the global carbon budget (Post *et al.*, 1985).

In addition to responses at the ecosystem level, some changes in terrestrial plant communities have occurred. Sturm *et al.* (2001) showed evidence in repeat photo-pairs that the abundance of three dominant deciduous shrub species has increased on the North Slope of Alaska over the past 50 years. Repeated sampling of 1 km<sup>2</sup> grids in the eastern Low Arctic of Alaska since 1989 also revealed increases in shrubs (M. D. Walker unpublished data), and indigenous observations suggest that this increase in shrub abundance is widespread throughout northwestern North America (Krupnik and Jolly, 2002). In addition to these 'control' observations, warming experiments have shown some responses of tundra plants to short-term increases in temperatures. While in many cases, vegetation properties did not change with warming over periods up to 9 years (Chapin *et al.*, 1995; Hobbie and Chapin, 1998; Shaver *et al.*, 1998), some effects of higher temperatures were increases in shrub biomass and growth (Chapin *et al.*, 1995; Graglia *et al.*, 1997; Shevtsova *et al.*, 1997; Hobbie and Chapin, 1998; Hartley *et al.*, 1999; Hobbie *et al.*, 1999) and decreases in non-vascular plant biomass (Chapin *et al.*, 1995; Hobbie *et al.*, 1999; Cornelissen *et al.*, 2001). Using a dynamic vegetation model, Epstein *et al.* (2000) projected increases in tundra shrub biomass over several decades with a simulated 3 °C warming of mean summer temperatures.

The International Tundra Experiment (ITEX) consists of a set of circumpolar and alpine tundra sites that uses open top chambers as a common means for implementing warming treatments. Arft *et al.* (1999) conducted the first meta-analysis of ITEX data and found some

common plant-level responses within 4 years of the onset of warming, such as increases in vegetative growth and earlier leaf bud burst and anthesis. Given the potentially high degree of landscape-scale spatial variability in tundra ecosystems (Walker *et al.*, 1994; Shaver *et al.*, 1996; Riedel *et al.*, in press) and the relatively few observed temporal responses of arctic vegetation to warming over the last two decades (Chapin *et al.*, 1995; Hobbie and Chapin, 1998; Shaver *et al.*, 1998), the probability of the presence, and concomitant detection, of an effect might be rather small. The goal of this paper was to examine the spatial and short-term temporal variability of arctic tundra vegetation with both field and simulation data, and address the following question: Will changes in plant community composition occur in arctic tundra as a result of warming, and, if so, should we expect to be able to detect these changes over the time frames that we typically conduct field observations or experiments?

## Materials and methods

In order to examine the spatial and short-term temporal variability of arctic tundra, we took advantage of existing field data (some published, others unpublished) and an existing model of arctic tundra vegetation dynamics (ArcVeg; Epstein *et al.*, 2000). We focused this study on a single tundra vegetation type, low arctic moist acidic tundra (MAT), because this tundra type has the greatest wealth of field data, several manipulation experiments, and the ArcVeg model is parameterized for this vegetation.

### Observed spatial variability

To analyze the spatial variability of low arctic MAT, we used a dataset of aboveground plant biomass collected during the growing season of 1999 at Ivotuk, Alaska (68.5°N, 155.7°W) (Riedel *et al.*, submitted for publication). Ivotuk is located on the North Slope of the Brooks Range at an elevation of approximately 550 m and is characterized by a mean July maximum temperature of 12 °C and green vegetation for ~110 days (Jia *et al.*, 2002). MAT at Ivotuk is dominated by the deciduous shrub, *Betula nana*, the tussock-forming sedge *Eriophorum vaginatum* and *Sphagnum* mosses, and is representative of the zonal vegetation type (Walker *et al.*, 2003).

In the summer of 1999, we harvested 10 random 20 × 50 cm (0.1 m<sup>2</sup>) plots of vegetation from a 1 ha section of MAT at Ivotuk at six different times during the growing season. Aboveground vascular plant biomass was clipped at the top of the moss layer, and all green moss biomass was harvested. Vegetation was oven dried at 55 °C for 48 hr and sorted into six plant

functional types (mosses, lichens, forbs, graminoids, evergreen shrubs and deciduous shrubs). Shrubs were divided into woody and foliar material, and graminoid and shrub foliar biomass was separated into live and dead components. Peak aboveground live plant biomass of  $722 \text{ g m}^{-2}$  was found on the fifth sampling period (July 29) for MAT. The subsequent (last) sampling period indicated minimal senescence from peak ( $697 \text{ g m}^{-2}$  of live phytomass on August 13); we therefore used the 20 samples collected during these two periods for our analysis of spatial heterogeneity.

In order to match spatial scales with the ArcVeg model ( $1 \text{ m}^2$ ), we used a Monte Carlo approach to generate a distribution of  $1 \text{ m}^2$  plots from the 20  $0.1 \text{ m}^2$  plots sampled. We randomly selected 10  $0.1 \text{ m}^2$  plots to generate  $1 \text{ m}^2$  and then continued generating  $1 \text{ m}^2$  plots randomly until the means and variances of biomass for all six plant functional types converged on values; this occurred after approximately 20  $1 \text{ m}^2$  plots were generated. We calculated the final means and spatial coefficients of variation for the plant functional types mentioned above from this distribution of 20  $1 \text{ m}^2$  plots.

#### *Simulated spatial variability*

We used the ArcVeg tundra vegetation and ecosystem dynamics model (see Epstein *et al.*, 2000 for model description) to simulate the landscape scale spatial heterogeneity of low arctic MAT. The ArcVeg model consists of a set of equations that operates on nitrogen (N) mass balance in plants and soil, with nitrogen cycling among soil organic matter, plant-available N and plant biomass pools. Fifteen possible plant types compete for available nitrogen in the model and produce new biomass as a simple function of the nitrogen acquired multiplied by the plant-specific nitrogen use efficiency of production. The results for the 15 plant types were pooled following the simulations to match the plant functional types sampled in the field.

Spatial heterogeneity in the model is simulated with gap dynamics processes in addition to preferential foraging by large herbivores such as caribou. The ArcVeg model simulates multiple, spatially independent  $1 \text{ m}^2$  patches of vegetation (i.e. there is no simulation of seed dispersal or vegetation growth from one patch into an adjacent patch). There is an annual probability of a freeze-thaw disturbance associated with colder climates that kills all the vegetation on a patch. During the years in which this disturbance occurs, a certain proportion of patches is affected at random, thus inducing spatial heterogeneity. In the current parameterization of the model, there is a 0.05 probability that this disturbance will occur in a given

year and, for those years, a 0.10 probability that a given patch will be affected. The annual probability of establishment for new individuals in low arctic MAT ranges from 0.10 to 0.25 for sedges and shrubs to 0.50 for mosses, lichens, grasses and forbs. Also, in the current parameterization, there is a 0.10 probability that a caribou herd will forage on the landscape in a given year. The caribou selectively forage on the plants with the greatest nitrogen concentrations and remove a maximum of 25% of the total live biomass of a plant type. The processes described here are all of those that contribute to the simulated spatial heterogeneity of low arctic MAT in ArcVeg.

We performed a single execution of the model for a 520-year period in order to ensure that the simulation had reached a stochastic equilibrium by year 500. For the year 500, we selected 20 patches at random and calculated the mean and coefficients of variation for the six plant functional types.

#### *Observed Temporal Variability*

In order to analyze the observed temporal variability of low arctic MAT vegetation, we reviewed the few datasets from the literature that present changes in the biomass or composition of tundra plant types under a control environment over time (Shaver and Chapin, 1991; Chapin *et al.*, 1995). We accessed relevant information online for an analysis of the Toolik Lake Long-Term Ecological Research site data. Data on the aboveground plant biomass for the six plant functional types being examined were available for the years 1982, 1983, 1989, 1995 and 2000 for a common set of sites established in 1981. Twenty,  $20 \times 20 \text{ cm}$  quadrats were harvested during each year, five quadrats in each of four blocks; blocks were 20 m transects that have been treated as replicates (no significant block effects) in other biomass analyses (Shaver *et al.*, 2001). We calculated the means and coefficients of variation for total live aboveground biomass of the six plant functional types (mosses, lichens, forbs, graminoids, evergreen shrubs and deciduous shrubs) over time.

#### *Simulated temporal variability*

To analyze the simulated temporal variability in MAT vegetation, we again used the ArcVeg tundra vegetation dynamics model. We used the same model run of 520 years as that used to analyze simulated spatial variability. We chose 20 patches at random and then analyzed the temporal variability of a 5-year sequence consistent with the sequence of years for which we had field data (i.e. simulation years 500, 501, 507, 513, 518),

calculating the means and coefficients of variation for plant functional type aboveground biomass over time.

#### *Statistical comparison of field data vs. model output*

We conducted a single factor analysis of variance (ANOVA) to determine statistically significant differences ( $P < 0.05$ ) in plant functional type biomass between field data and model output, using the Iivotuk 1999 field data and ArcVeg spatial data simulations; each dataset had 20 observations. We also analyzed statistically significant differences ( $P < 0.05$ ) over time between Toolik Lake field data and the ArcVeg temporal simulations, using a repeated measures ANOVA, with Year as the repeated independent variable; again there were 20 observations in each dataset per year.

#### *Simulating decadal scale variability as a result of warming*

We conducted additional ArcVeg simulations to examine the decadal scale variability in plant community composition associated with climate warming. Again, we ran the ArcVeg model for 500 years to equilibrate and then in year 500, we imposed one of three warming treatments: no warming (i.e. no change in climate), a warming of 3 °C mean growing season temperatures ramped linearly over a 50-year period, an instantaneous warming of 3 °C mean growing season temperatures. We continued the simulations for an additional 100 years. We performed 5 replicates for each of these three treatments for a total of 15 model executions.

We conducted a detrended correspondence analysis (DCA) with the model output from years 480 (20 years prior to the onset of warming treatments) to 520 (20 years after the warming treatments), in order to examine changes at the plant community level. We analyzed the DCA scores for the first two axes over time for each treatment as a means of examining changes in plant community composition. We also analyzed the mean DCA scores (across 20 years for the no warming treatment) for seven plant functional types (graminoids were split into sedges and grasses for this analysis) individually in order to identify the plant types that had the greatest influence on the aggregate DCA scores. Then we analyzed the change in these plant functional types over time with warming as simulated by ArcVeg. In an additional analysis, we examined the frequency distributions of plant functional type biomass by 1 m<sup>2</sup> patches in ArcVeg every 5 years between years 500 (warming onset) and 600 to determine the effects of warming on spatial variability in low arctic MAT.

## Results

### *Spatial and short-term temporal variability*

Both the field data and the modeling output suggest a substantial degree of spatial heterogeneity in functional type composition of low arctic MAT at the landscape scale (Table 1), with spatial coefficients of variation ranging for 14.6% for deciduous shrubs (field data) to 107.9% for forbs (modeled data). Model estimations of heterogeneity, the coefficients of variation in plant type biomass, were consistently greater than field estimations; however, there were some similarities. Both model and field data showed high variability in forbs and lichens, and the least variability in deciduous shrubs. The ArcVeg model also suggested relatively high variability for graminoids and evergreen shrubs. Mean biomass values were statistically similar ( $P > 0.05$ ) for forbs, deciduous shrubs and lichens between field and model data, however, the ArcVeg model simulated less aboveground live graminoid and evergreen shrub biomass, and greater moss biomass than was observed ( $P < 0.05$ ). The Iivotuk dataset represents an independent test of the ArcVeg model and gives us some confidence that we can simulate the dynamics of MAT beyond the region for which the model was parameterized (Kuparuk River Basin).

The temporal field variability is unavoidably affected by some spatial heterogeneity, because plots are destructively sampled at each harvest. The ArcVeg model simulated temporal (interannual) variability as being somewhat more constrained than the spatial variability, with lower coefficients of variation for all plant types relative to the spatial data and the temporal field data from Toolik Lake. This suggests that comparing field experiments sampled in different years should not greatly compromise the utility of these comparisons. The field data and model output for temporal patterns of plant functional type biomass were statistically similar for forbs, mosses and lichens ( $P > 0.05$ ) and different for graminoids, deciduous shrubs and evergreen shrubs. Keep in mind though, that the simulations were under a 'no warming' scenario, whereas the field control plots may have experienced some warming over the 19 years of the sample period.

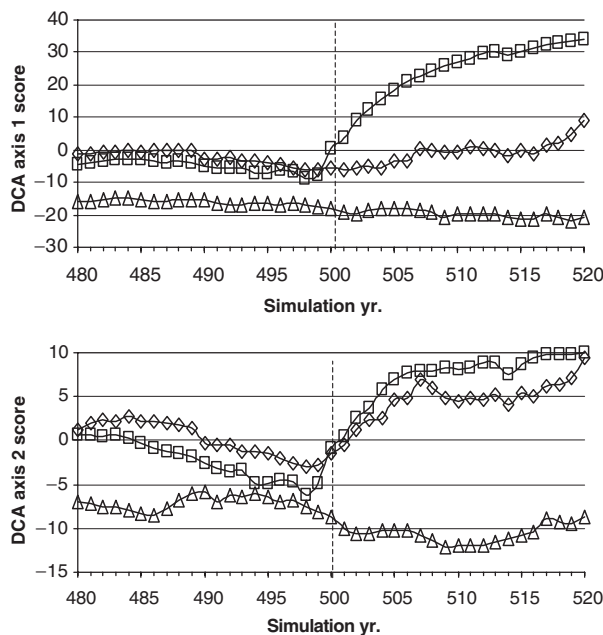
### *Simulations of climate change*

DCA scores (used as indices of plant community composition) for the first two axes were altered by a simulated warming of 3 °C, either instantaneous or ramped over a 50-year period (Fig. 1). DCA axis 1 scores increased immediately with the onset of

**Table 1** Spatial and temporal means ( $\text{g m}^{-2}$ ) and coefficients of variation (CV; %) for plant functional types in low arctic tundra as estimated by field data and simulated by the ArcVeg model

	Forbs	Graminoids	Dec. shrubs	Ev. shrubs	Mosses	Lichens	Total
		S,T	T	S,T	S		
<b>Spatial field</b>							
Mean	3.1	75	160	189	222	45	694
CV	57.7	18.5	14.6	18.0	25.3	72.7	
<b>Spatial model</b>							
Mean	2.3	19	139	88	313	44	605
CV	107.9	86.4	37.1	88.9	53.7	78.1	
<b>Temporal field</b>							
Mean	0.8	141	173	242	180	52	789
CV	26.4	53.2	48.4	33	34.1	67.4	
<b>Temporal model</b>							
Mean	1.9	17	128	82	305	44	578
CV	17.0	6.9	4.4	3.4	12.5	10.2	

Spatial field data are generated from 20  $0.1 \text{ m}^2$  plots within a 1 ha site at Ivotuk, Alaska, and temporal field data are from years 1982, 1983, 1989, 1995 and 2000 at Toolik Lake, Alaska. An 'S' under the variable name indicates that spatial means were significantly different between field data and model output (ANOVA,  $P < 0.05$ ); a 'T' under the variable name indicates that temporal patterns were significantly different between field data and model output (repeated measures ANOVA,  $P < 0.05$ ).



**Fig. 1** Detrended correspondence analysis (DCA) scores (for the first two axes) of plant community composition in ArcVeg using the biomass of seven plant functional types (mosses, lichens, forbs, sedges, grasses, deciduous shrubs and evergreen shrubs). Three climate scenarios were simulated (no warming, immediate warming of  $3^\circ\text{C}$  mean growing season temperatures and warming of  $3^\circ\text{C}$  mean growing season temperatures linearly ramped over 50 years); warming scenarios were initiated in simulation Year 500.

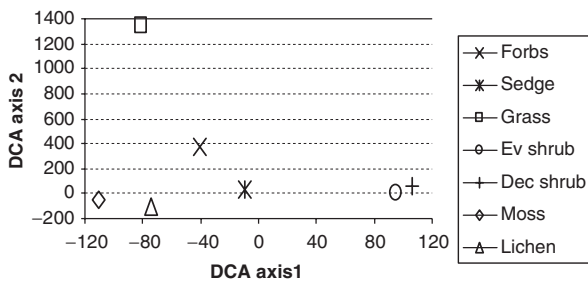
instantaneous warming and appear to be reaching a new equilibrium point by 20 years after warming. For the 50 years ramped warming, the axis 1 scores

increased gradually and were noticeably different from baseline at the end of the 20-year period of analysis. Axis 2 scores increased rather rapidly for both ramped and instantaneous warming, appearing to equilibrate at some point close to 10 years following the onset of warming.

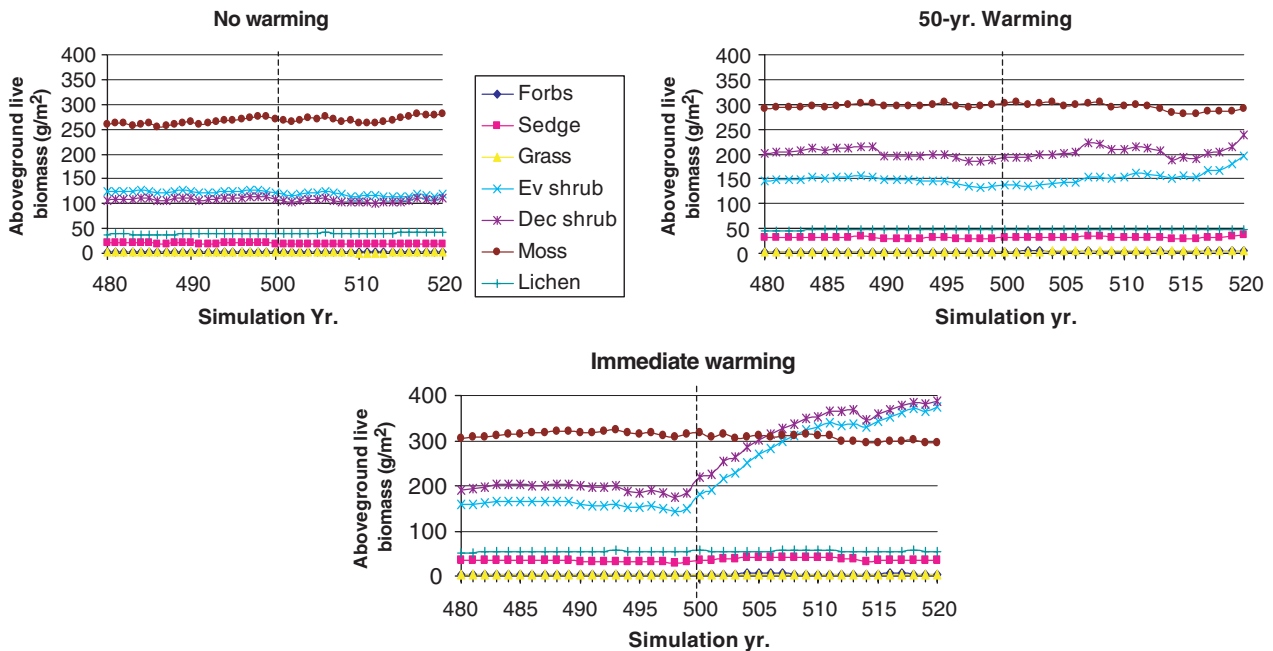
DCA axis 1 scores were strongly, positively correlated with deciduous and evergreen shrub biomass, and negatively correlated with non-vascular, moss and lichen, biomass (Fig. 2). Axis 2 scores were strongly positively correlated with the plant types comprising a rather small proportion of community biomass, namely forbs and grasses. Based on the DCA scores, we examined more closely the dynamics of shrubs, non-vascular plants and minor community components, such as forbs and grasses.

Both deciduous and evergreen shrubs increased immediately with the onset of instantaneous warming, reaching somewhat of a plateau after approximately 10 years (Fig. 3); after 20 years, evergreen shrub biomass had increased 137% from baseline, whereas deciduous shrub biomass increased 93%. With warming ramped over a 50-year period, increases in evergreen and deciduous shrub biomass were noticeably different from baseline values only after approximately 15–20 years; after 20 years, evergreen shrub biomass had increased 47% from baseline, whereas deciduous shrub biomass increased 28%. Under typical climatic conditions, mosses and lichens in the ArcVeg model exhibit gradual increases in biomass over time, with periodic drops due to physical disturbances. In both warming

scenarios (instantaneous and 50 years ramped), moss biomass showed significant declines following the onset of warming, however in the control (no warming) scenario, moss biomass continued its gradually increasing trend (Fig. 4). The same situation occurred for lichens (not shown in the figures); increases prior to the onset of climate change were replaced by decreases in the two warming scenarios following climate change. Aboveground live biomass for grasses and forbs ranged between 1 and 4 g m<sup>-2</sup> both prior to and after the onset of warming. Coefficients of variation were high for both plant types and changes as a result of warming were not statistically or ecologically significant.



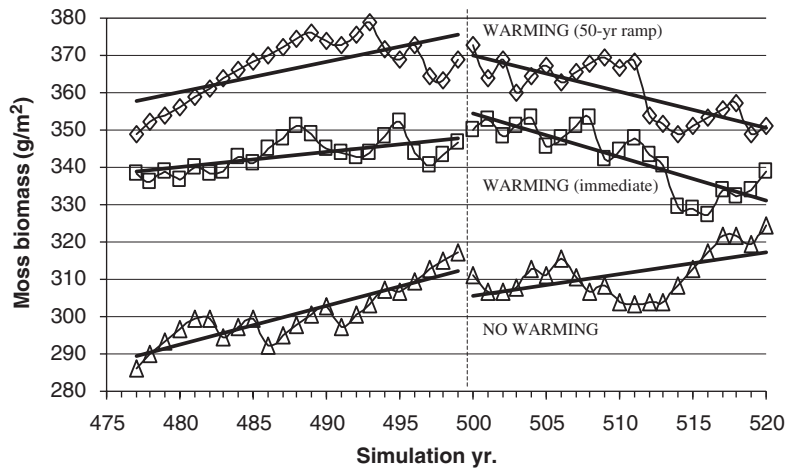
**Fig. 2** Mean detrended correspondence analysis (DCA) scores (for the first two axes) of seven individual plant functional types (mosses, lichens, forbs, sedges, grasses, deciduous shrubs and evergreen shrubs), averaged over 20 simulation years in ArcVeg using a current climate scenario.



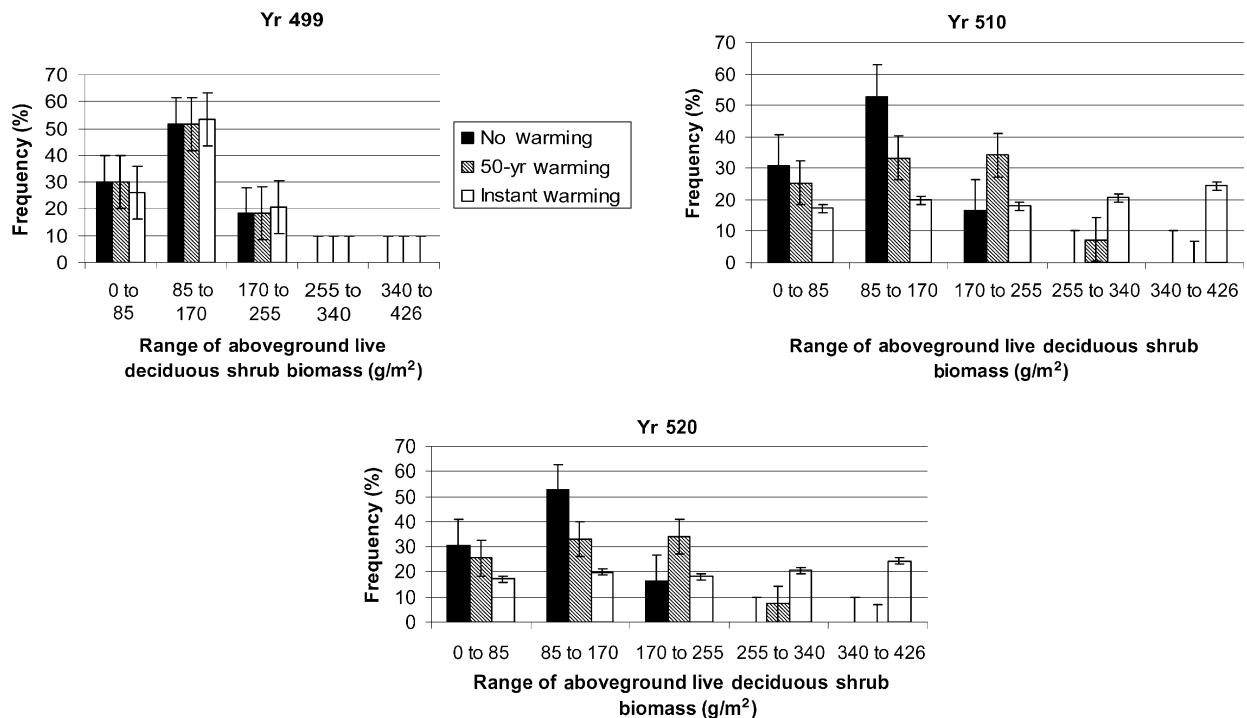
**Fig. 3** Simulated aboveground live biomass (g m<sup>-2</sup>) of seven plant functional types (mosses, lichens, forbs, sedges, grasses, deciduous shrubs and evergreen shrubs) in ArcVeg for three climate scenarios (no warming, immediate warming of 3 °C mean growing season temperatures and warming of 3 °C mean growing season temperatures linearly ramped over 50 years); warming scenarios were initiated in simulation Year 500.

*Simulations of interactions between temporal and spatial variability*

For most of the plant functional types there was a simulated interaction between the temporal variability of biomass and the spatial heterogeneity of biomass with climate change. The spatial heterogeneity of shrub biomass changed most strikingly. Not only did mean aboveground live deciduous and evergreen shrub biomass increase with warming, but the spatial variance increased as well (shown for deciduous shrubs in Fig. 5). Standard deviation of deciduous shrub aboveground live biomass across ArcVeg plots increased from 76 g m<sup>-2</sup> in year 500 (when the simulated warming began) to 123 g m<sup>-2</sup> 25 years after instantaneous warming. It remained around this level for the next 75 simulated years. In the ramped warming scenario, it took between 50 and 75 years for the standard deviation to increase by a similar magnitude (67 g m<sup>-2</sup> in year 500 to 119 g m<sup>-2</sup> in year 550). Standard deviation of evergreen shrub biomass increased from 115 g m<sup>-2</sup> in year 500 to 233 g m<sup>-2</sup> in year 525 and remained at this level for the next 75 simulation years. In the ramped warming scenario, it again took between 50 and 75 years to realize a similar change in spatial variability compared to instantaneous warming (95 g m<sup>-2</sup> in year 500 to 223 g m<sup>-2</sup> in year 550). Forbs, sedges, grasses and mosses all exhibited decreases in



**Fig. 4** Simulated live moss biomass ( $\text{g m}^{-2}$ ) in ArcVeg for three climate scenarios (no warming, immediate warming of  $3\text{ }^{\circ}\text{C}$  mean growing season temperatures and warming of  $3\text{ }^{\circ}\text{C}$  mean growing season temperatures linearly ramped over 50 years); warming scenarios were initiated in simulation Year 500.



**Fig. 5** Frequency (%) of simulated  $1\text{ m}^2$  patches in ArcVeg with aboveground live deciduous shrub biomass in different quantitative categories for three climate scenarios (no warming, immediate warming of  $3\text{ }^{\circ}\text{C}$  mean growing season temperatures and warming of  $3\text{ }^{\circ}\text{C}$  mean growing season temperatures linearly ramped over 50 years), prior to the onset of climate treatment (Year 499), 10 years into the treatment (Year 510) and 20 years into the treatment (Year 520).

spatial variability with warming, whereas spatial variability of lichens increased with warming.

**Discussion**

Results from ArcVeg simulations suggest that some changes in plant community composition of low arctic,

MAT could be detectable over a 20-year period. Given that temperatures in the Arctic of northern Alaska have been warming for several decades (Serreze *et al.*, 2000), and are projected to continue warming (Hansen *et al.*, 1999), the 50 years ( $3\text{ }^{\circ}\text{C}$ ) ramped warming scenario may be the most realistic for this region. These simulations in ArcVeg show certain plant

community dynamics being apparent within 20 years, whereas others may take more than a few decades to observe (Fig. 1), depending on the component of the plant community being monitored. Shrubs appear to be a dominant component of change, and based on the model results it could take 20 years to detect changes in shrub biomass above baseline levels (Fig. 3); after 20 simulation years the changes (%) above baseline values were comparable to spatial and temporal coefficients of variation observed under control conditions. Observing declines in moss biomass as a result of warming may take equally as long (Fig. 4), as slow growth rates combined with the inherent spatial variability may make detecting changes over time even more difficult. The relatively low temporal variability simulated by ArcVeg suggests that standardized non-destructive measurements may be particularly useful in detecting long-term changes in experimental manipulations.

Only a few field studies have detected recent, 'naturally' forced changes in plant community composition in the Arctic of northern Alaska within one or two decades as a result of warming (Chapin *et al.*, 1995; Walker *et al.*, unpublished data). However, several warming experiments using greenhouses and open top chambers have induced plant community composition changes over several years (Chapin *et al.*, 1995; Hobbie and Chapin, 1998; Hobbie *et al.*, 1999). These and other studies (Graglia *et al.*, 1997; Shevtsova *et al.*, 1997; Hartley *et al.*, 1999) seem to support the modeling conclusions that shrubs and non-vascular plants may be the most responsive to decadal warming in addition to being ecologically significant components of change. The ITEX meta-analysis (Walker *et al.*, in press) revealed a circumpolar trend of increased deciduous shrub cover and declining cover of mosses and lichens.

Not only should changes in the mean abundances of plant community components be expected, but changes in spatial variability of plant community composition are projected as well. The ArcVeg model output suggests that the spatial variance of deciduous and evergreen shrub biomass (1 m<sup>2</sup> resolution) will increase over time; however, it may also take several decades to detect this change in spatial heterogeneity (Fig. 5). The reason for increased spatial variance of shrubs in the model is that although the mean biomass of shrubs increases as a result of warming (due to increased nitrogen availability and a longer growing season), the minimum biomass values of shrubs do not increase similarly. Disturbance processes in the model, such as cryoturbation and grazing, maintain the presence of patches with low shrub biomass through either removal of aboveground plant tissue or mortality of plants,

whereas the mean and maximum values for shrub biomass among patches increased with warming.

An increase in the length of the growing season and increased net nitrogen mineralization rates (or plant-available N), as results of warming, drive the changes in plant community composition as simulated by ArcVeg. Several remote sensing studies have shown recent increases in the length of the growing season in the Arctic, particularly an earlier date of onset (Myneni *et al.*, 1997; Zhou *et al.*, 2001). A few studies have shown increased rates of net N mineralization with warming (Chapin *et al.*, 1995; Hartley *et al.*, 1999; Schmidt *et al.*, 2002), and several have shown the effects of increased N on plant community composition (Shaver and Chapin, 1991; Shaver *et al.*, 1998, 2001). Shaver *et al.* (2001) found large increases in the deciduous shrub *Betula nana* with N fertilization over a 15-year time period at Toolik Lake, Alaska. The degree to which changes in temperature alter the nitrogen cycle in arctic tundra will likely play an important role in eliciting or constraining changes in plant community composition.

A simplification within the ArcVeg model assumes a single, conceptual pool of plant-available nitrogen that includes ammonium, nitrate and amino acids, such as glycine, that are used by arctic plants (Kielland, 1994; Kaye and Hart, 1997). The model state variable is essentially plant-available N and makes no distinction among the different forms of N or available N at different soil depths. In the field, these different N sources vary throughout the growing season, and plant types differ in their use of the different forms of N (McKane *et al.*, 2002). In fact, evergreen shrubs were found to use more glycine (which comprises >60% of plant-available N) than deciduous shrubs (McKane *et al.*, 2002), which could explain some of the discrepancies between our field and model results. If warming alters the seasonal patterns of availability and the relative abundances of these forms of N (e.g. increasing the conversion of amino acids to inorganic N), this might alter the community composition in ways that are not currently simulated by ArcVeg.

Growth of evergreen shrubs has increased in several warming experiments in the Arctic (Chapin *et al.*, 1995; Graglia *et al.*, 1997; Shevtsova *et al.*, 1997; Hartley *et al.*, 1999; Hobbie *et al.*, 1999), and evergreen shrub biomass exhibited large projected increases in the ArcVeg model simulations. Evergreen shrubs, however, did not respond significantly in the ITEX meta-analysis of circumpolar warming experiments (Walker *et al.*, in press). Evergreen shrubs have increased growth in response to fertilizer additions (Graglia *et al.*, 1997); however, Shaver *et al.* (2001) clearly demonstrated that long-term additions of nitrogen and phosphorus fertilizer strongly favored deciduous shrubs over ever-

green shrubs. The discrepancy between the mixed and minimal response of evergreen shrubs in field studies and the strong increase with warming as simulated by the model may be due to several factors. The simplified nitrogen cycle in ArcVeg (discussed above) may not distinguish responses of deciduous and evergreen shrubs to changes in the N cycle, including any differences in N retranslocation between these two shrub types. Competition for light is also not directly simulated in ArcVeg, and the deciduous shrubs in this ecosystem tend to be more erect than the evergreen shrubs and may reduce light levels in the subcanopy. It is also possible that a short-term increase in evergreen shrubs in response to warming is eventually offset by a longer-term decline.

The reduction in mosses and lichens with warming, which is simulated by ArcVeg, is consistent with field observations (Chapin *et al.*, 1995; Hobbie *et al.*, 1999; Cornelissen *et al.*, 2001; Walker *et al.*, in press). In the model, this results from competition with vascular plants for nitrogen. The decline of non-vascular plants with warming in the field has also been assumed to reflect competition with vascular plants, although the specific resources for which these plants are competing have not been identified.

To summarize, the output from the ArcVeg model suggests that a 3 °C increase in mean summer temperatures ramped linearly over a 50-year period will elicit detectable changes in plant community composition over two decades. Given the sample sizes and time frames that are commonly used in the Arctic, community changes should be observed, and, if they are not detectable, there must be feedbacks or buffering processes in place that are currently not understood or incorporated into models (e.g. Oechel *et al.*, 2000). The likely changes in tundra plant community composition with warming will be an increase in shrubs and a decline in mosses. These projections are consistent with many of the recent field experiments and observations in dwarf-shrub and graminoid-dominated arctic tundra. The projection of increased evergreen shrubs by ArcVeg is inconsistent with the ITEX meta-analysis of warming experiments and the 15 years fertilization experiment of Shaver *et al.* (2001). The simplified N cycle and the lack of light competition in ArcVeg may be responsible for these discrepancies.

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### References

- Arft AM, Walker MD, Gurevitch J *et al.* (1999) Response patterns of tundra plant species to experimental warming: a meta-analysis of the International Tundra Experiment. *Ecological Applications*, **69**, 491–511.
- Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. *Nature*, **405**, 668–672.
- Chapin III FS, Shaver GR, Giblin AE *et al.* (1995) Responses of Arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.
- Cornelissen JHC, Callaghan TV, Alatalo JM *et al.* (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, **89**, 984–994.
- Crowley TJ (2000) Causes of climate change over the past 1000 yr. *Science*, **289**, 270–277.
- Epstein HE, Walker MD, Chapin III FS *et al.* (2000) A transient, nutrient-based model of arctic plant community response to climatic warming. *Ecological Applications*, **10**, 824–841.
- Giorgi F, Whetton PH, Jones RG *et al.* (2001) Emerging patterns of simulated regional climate changes for the 21st century due to anthropogenic forcings. *Geophysical Research Letters*, **28**, 3317–3320.
- Graglia E, Jonasson S, Michelsen A, Schmidt IK (1997) Effects of shading, nutrient application and warming on leaf growth and shoot densities of dwarf shrubs in two arctic-alpine plant communities. *Ecoscience*, **4**, 191–198.
- Hansen JR, Ruedy J, Sato M *et al.* (1999) GISS analysis of surface temperature change. *Journal of Geophysical Research*, **104**, 30997–31022.
- Hartley AE, Neill C, Melillo JM *et al.* (1999) Plant performance and soil nitrogen mineralization in response to simulated climate change in subarctic dwarf shrub heath. *Oikos*, **86**, 331–343.
- Hobbie SE, Chapin III FS (1998) The response of tundra plant biomass, aboveground production, nitrogen, and CO<sub>2</sub> flux to experimental warming. *Ecology*, **79**, 1526–1544.
- Hobbie SE, Shevtsova A, Chapin III FS (1999) Plant responses to species removal and experimental warming in Alaskan tussock tundra. *Oikos*, **84**, 417–434.
- Jia GJ, Epstein HE, Walker DA (2002) Spatial characteristics of AVHRR-NDVI along latitudinal transects in northern Alaska. *Journal of Vegetation Science*, **13**, 315–326.
- Kaye JP, Hart SC (1997) Competition for nitrogen between plants and soil microorganisms. *Trends in Ecology and Evolution*, **12**, 139–143.
- Kielland K (1994) Amino acid absorption by arctic plants: implications for plant nutrient and nitrogen cycling. *Ecology*, **75**, 2373–2383.
- Krupnik I, Jolly D (2002) *The Earth is Faster Now: Indigenous Observations of Arctic Environmental Change*. Arctic Studies Center, Smithsonian Institution and Arctic Research Consortium of the United States, Fairbanks, Alaska.
- Mann ME, Bradley RS, Hughes MK (1998) Global-scale temperature patterns and climate forcing over the past six centuries. *Nature*, **397**, 779–787.

- Maxwell B (1997) Recent climate patterns in the Arctic. In: *Global Change and Arctic Terrestrial Ecosystems* (eds Oechel WC, Callaghan T, Gilmanov T, Holten JJ, Maxwell B, Molau U, Sveinbjörnsson B), Springer-Verlag, New York pp. 21–46.
- McKane RB, Johnson LC, Shaver GR *et al.* (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, **415**, 68–71.
- Myneni RB, Keeling CD, Tucker CJ *et al.* (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.
- Oechel WC, Hastings SJ, Vourlitis G *et al.* (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature*, **361**, 520–523.
- Oechel WC, Vourlitis GL, Hastings SJ *et al.* (2000) Acclimation of ecosystem CO<sub>2</sub> exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, **406**, 978–981.
- Osterkamp TE, Romanovsky VE (1999) Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes*, **10**, 17–37.
- Overpeck J, Hughen K, Hardy D *et al.* (1997) Arctic environmental change over the last four centuries. *Science*, **278**, 1251–1256.
- Post WM, Pastor J, Zinke PJ (1985) Global patterns of soil nitrogen storage. *Nature*, **317**, 613–616.
- Robinson DA, Dewey KF, Heim Jr RR (1993) Global snow cover monitoring: an update. *Bulletin of the American Meteorological Society*, **74**, 1689–1696.
- Schmidt IK, Jonasson S, Shaver GR *et al.* (2002) Mineralization and distribution of nutrients in plants and microbes in four arctic ecosystems: responses to warming. *Plant and Soil*, **242**, 93–106.
- Serreze MC, Walsh JE, Chapin III FS *et al.* (2000) Observational evidence of recent change in the northern high-latitude environment. *Climatic Change*, **46**, 159–207.
- Shaver GR, Bret-Harte MS, Jones MH *et al.* (2001) Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology*, **82**, 3163–3181.
- Shaver GR, Chapin III FS (1991) Production: biomass relationships and element cycling in contrasting Arctic vegetation types. *Ecological Monographs*, **61**, 1–31.
- Shaver GR, Johnson LC, Cades DH *et al.* (1998) Biomass and CO<sub>2</sub> flux in wet sedge tundras: responses to nutrients, temperature, and light. *Ecological Monographs*, **68**, 75–97.
- Shaver GR, Laundre JA, Giblin AE *et al.* (1996) Changes in live plant biomass, primary production, and species composition along a riverside toposequence in Arctic Alaska, USA. *Arctic and Alpine Research*, **28**, 363–379.
- Shevtsova A, Haukioja E, Ojala A (1997) Growth response of subarctic dwarf shrubs, *Empetrum nigrum* and *Vaccinium vitis-idaea*, to manipulated environmental conditions and species removal. *Oikos*, **78**, 440–458.
- Sturm M, Racine C, Tape K (2001) Increasing shrub abundance in the Arctic. *Nature*, **411**, 546–547.
- Vaughan DG, Marshall GJ, Connolley WM *et al.* (2001) Climate change: devil in the detail. *Science*, **293**, 1777–1779.
- Vinnikov KY, Robock A, Stouffer RJ *et al.* (1999) Global warming and Northern Hemisphere sea ice extent. *Science*, **286**, 1934–1937.
- Walker DA, Epstein HE, Jia GJ *et al.* (2003) Phytomass, LAI, and NDVI in northern Alaska: relationships to summer warmth, soil pH, plant functional types and extrapolation to the circumpolar Arctic. *Journal of Geophysical Research – Atmospheres*, 0.1029/2001JD000986.
- Walker MD, Walker DA, Auerbach NA (1994) Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science*, **5**, 843–866.
- Zhou L, Tucker CJ, Kaufmann RK *et al.* (2001) Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research – Atmospheres*, **106**, 20069–20083.