

A TRANSIENT, NUTRIENT-BASED MODEL OF ARCTIC PLANT COMMUNITY RESPONSE TO CLIMATIC WARMING

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Abstract. We developed a nutrient-based, plant community and ecosystem model (ArcVeg) designed to simulate the transient effects of increased temperatures on the biomass and community composition of a variety of arctic ecosystems. The model is currently parameterized for upland, mesic ecosystems in high Arctic, low Arctic, treeline, and boreal forest climate zones. A unique feature of ArcVeg is that it incorporates up to 18 plant functional types including a variety of forbs, graminoids, shrubs, and nonvascular plants that are distinguished by a set of five parameters. Timing and rate of growth, as well as nutrient use, are particularly important in defining competitive interactions in the model and in explaining coexistence in complex communities.

Simulations of climatic warming, which increase nitrogen mineralization and growing season length, suggest an increase in total biomass for high and low Arctic zones over 200 yr, and an increase in shrub biomass at the expense of other plant functional types. The initial community response to warming was a function of the initial dominance structure, whereas the long-term response reflected adaptations of plant functional types to the new environment. Therefore, long-term responses (decades to centuries) differed in both direction and magnitude from initial responses. In addition, warming resulted in the formation of novel, stable plant communities after 200 simulation years that were not typical of current zonal vegetation types in the Arctic of northwestern North America.

Key words: *Arctic; climate change; dynamic vegetation modeling; moist acidic tundra; nitrogen; plant functional types; transient dynamics; tussock tundra.*

INTRODUCTION

Mean circumarctic air temperatures have increased by ~1.5°C since 1840, with much of this increase attributed to human-induced changes in atmospheric concentrations of greenhouse gases, such as carbon dioxide (CO₂) (Overpeck et al. 1997). Concomitant with these increases in air temperatures and atmospheric CO₂ are observed increases in annual precipitation (Maxwell 1997), and decreases in extent of snow cover (Robinson and Dewey 1990, Robinson et al. 1993) and sea ice (Chapman and Walsh 1993, Serreze et al., *in press*). General circulation models (GCMs) reproduce these empirical observations and predict substantial future increases in temperature and precipitation in the western North American Arctic (Maxwell 1992, Rowntree 1997). These changes in climate will likely have important effects on many properties of arctic terrestrial ecosystems (Chapin et al. 1992, Billings 1997); including soil carbon (C) and nitrogen (N) stocks (Shaver et al. 1992, McGuire et al. 1995, Johnson et al. 1996, McKane et al. 1997), permafrost distribution, the thickness of the soil active layer (Anisimov and Nelson

1996, Anisimov et al. 1997), and plant biomass and community composition (Chapin et al. 1995).

Direct effects of increased air temperatures on the photosynthesis of arctic plants may be limited (Miller et al. 1976, Stoner et al. 1978, Oechel and Billings 1992), and the same may be true for elevated CO₂ (Oberbauer et al. 1986, Tissue and Oechel 1987, Grulke et al. 1990). Yet several field studies do demonstrate positive effects of increased temperature on growth of arctic plants, particularly for dwarf evergreen and deciduous shrubs (Chapin et al. 1995, Graglia et al. 1997, Shevtsova et al. 1997). These results may be partially due to indirect effects of increased temperature by increasing nutrient mineralization rates (Post 1990, Nadelhoffer et al. 1992); responses of arctic plants to elevated CO₂ may also be dependent on nutrient availability (Oechel and Strain 1985).

Many studies have shown that increases in temperature yield greater nitrogen mineralization rates (e.g., Nadelhoffer et al. 1991, Binkley et al. 1994, Hobbie 1996) and greater levels of inorganic N (Chapin et al. 1995, Hobbie 1996) in arctic soils over annual time scales. Nutrient availability may be the most limiting factor for growth of arctic plants (Tissue and Oechel 1987, Chapin 1991), and it has been demonstrated that increased nutrient availability can lead to increased plant biomass and productivity (Chapin and Shaver 1985, Shaver and Chapin 1986, Shaver et al. 1996), as

Manuscript received 12 January 1999; 8 July 1999; accepted 8 July 1999.

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well as changes in species composition (Henry et al. 1986, Binkley et al. 1995, Chapin et al. 1995). Other indirect effects of increased temperatures on arctic ecosystems include greater nutrient uptake rates by plants (Chapin 1983) and possibly a lengthening of the growing season (Myneni et al. 1997). It is therefore likely that changes in climate will produce noticeable changes in arctic ecosystems over time scales of years to decades, and that these changes will be mediated in part by changes in nutrient dynamics.

Computer simulations suggest that global climatic change will lead to a reduction in the extent of arctic tundra and a northward movement of forested ecosystems (Prentice et al. 1992, Cramer and Leemans 1993, Lenihan and Neilson 1995). These predictions are based on current relationships between vegetation and climate, and the model output represents the equilibrium result of climatic changes. If biome shifts do occur, they would likely take centuries (MacDonald et al. 1993, Pastor and Post 1988). These equilibrium models are therefore not useful in predicting vegetation dynamics that occur over decades, a time scale that is relevant to the sustainability of grazing mammals (e.g., caribou [Russell et al. 1993]) and human populations (Kruse 1991) in the Arctic. Transient models of vegetation responses to climatic change will need to be developed to capture dynamics over decadal time scales and to assess the influence of other environmental constraints, such as substrate, disturbance, and migration (Starfield and Chapin 1996, Cramer 1997).

Our objective was to develop a model that would simulate temporal dynamics of arctic vegetation in response to climatic change. Earlier work on transient dynamics in northern ecosystems has either focused on successional changes within communities (Bonan et al. 1990) or has been at the level of community shifts (Pastor and Post 1988, Starfield and Chapin 1996). The paleorecord, however, clearly indicates that vegetation change results from the distinct responses of individual species to environmental forcings (Davis 1981, Brubaker et al. 1995). Simulations of temporal dynamics may therefore require more detailed plant components than those found in the currently available suite of ecosystem models (Starfield and Chapin 1996, Chapin et al. 1996, Shaver et al. 1997). The use of plant functional types facilitates the modeling of changes in community composition, particularly at spatial scales where it may not be practical to model dynamics of every species. Another motivation for focusing on the dynamics of plant functional types in regional-scale models is that it provides an opportunity to incorporate biogeochemical feedbacks between plant types and ecosystems (Pastor and Post 1988). Changes in plant functional type composition are also useful in evaluating implications of climatic change for wildlife.

METHODS

Model scope

We developed a nutrient-based, plant community and ecosystem model (ArcVeg) to simulate the transient

effects of climatic warming on the biomass and composition of a variety of arctic ecosystems. We decided that our model should be nutrient-based, because many arctic ecosystems are limited by plant-available nutrients, especially nitrogen (Shaver et al. 1992, Shaver and Chapin 1995, Schimel et al. 1996) and respond relatively quickly to changes in nutrient availability. The scope of the model is a latitudinal temperature gradient, encompassing five climatic-ecological zones: polar desert, high Arctic, low Arctic, treeline, and boreal forest. Our classification is similar to other schemes used for arctic zones (Bliss and Matveyeva 1992). We designed the initial version of the model to simulate only moist acidic vegetation, as this type has been well studied (e.g., Oechel et al. 1994, Chapin et al. 1986, Shaver and Chapin 1986) and thus offered the best prospects for data with which to parameterize and validate our model. Because the polar desert substrate is predominantly alkaline (Tedrow 1966, Bliss et al. 1984, Bay 1997), we have not fully parameterized the polar desert ecosystem type in this version of the model.

Because we were interested in the short-term (decadal) dynamics of vegetation, we designed the model to include a fairly detailed list of plant functional types (Table 1). Our main functional type groupings were identical to those derived by a cluster analysis of 37 species, based on over twenty plant attributes (Chapin et al. 1996). We used the cluster analysis of species in Chapin et al. (1996) to further subdivide the sedge, forb, deciduous shrub, and evergreen shrub groups into ecologically distinct subtypes. This was essential because one long-term objective of the model development was to estimate climatic effects on forage availability to caribou, a grazer that selects forage based on differences among species within the functional types of forbs, sedges, and deciduous shrubs (Russell et al. 1993). In addition, we distinguished groups of species whose distributions suggest strongly contrasting responses to climate and soil acidity.

Ecosystem properties along the temperature gradient

Spatial patterns of ecosystem attributes along the temperature gradient were used to generate model parameters and to develop model functions. Because our focus was on temperature change, we looked for data to support relationships between temperature and vegetation properties of arctic ecosystems. Spatial vegetation patterns show total biomass (above-plus belowground) in the circumpolar Arctic increasing exponentially with increasing summer temperature (data summarized by Gilmanov 1997). The mean and range in total biomass for vegetation in each of our five climate zones were calculated from this relationship (Table 2). For each of the climate zones along the temperature gradient, we additionally summarized data on plant community composition (Table 3) and aboveground biomass by plant functional type (Tables 3 and 4) from the literature. Data available from most studies were limited to aboveground biomass, or aboveground

TABLE 1. Plant functional types and associated model parameters.

Plant functional type	Mean biomass : nitrogen ratio (g biomass/g N)	Proportion of biomass senescing (annual)	Nutrient uptake efficiency (g N/g biomass) [†]
Moss	130 (91–159) [a,e,l]	0.10	0.0018
Lichen	200 (200–455) [a,e]	0.05	0.0006
Forb	(22–77) [a,e,k]	(0.83) [k]	
High Arctic acid	40	0.55	0.0400
Low Arctic acid	40	0.50	0.0400
Disturbance-related	40	0.55	0.0400
<i>Equisetum</i> spp.	45	0.55	0.0400
Sedge		(0.37) [k]	
<i>Eriophorum</i> spp.	70 (43–113) [c,d,l]	0.30	0.0350
<i>Carex</i> spp.	70 (32–102) [a,b,c,l]	0.35	0.0350
Grass	75 (56–90) [a,c,i]	0.40	0.0350
Deciduous shrub		(0.15) [k]	
<i>Salix</i> spp.	65 (61–65) [a,e]	0.20	0.0350
<i>Betula</i> spp.	90 (103) [l]	0.15	0.0350
<i>Alnus</i> spp.	110	0.10	0.0350
Evergreen shrub	(77–125) [a,d,e,i,l,k]	(0.10) [k]	
<i>Cassiope</i> and <i>Empetrum</i> spp.	100	0.15	0.0300
<i>Ledum</i> spp.	100 (85) [l]	0.15	0.0300
<i>Vaccinium</i> spp.	100 (87–125) [e,l]	0.15	0.0300
<i>Dryas</i> spp.	95 (80) [a]	0.17	0.0300
Deciduous tree	140	0.08	0.0250
Evergreen tree	150	0.05	0.0200

Note: Values in parentheses are ranges of data found in the literature. Letters in square brackets refer to references: (a) Babb and Whitfield (1977), (b) Muc (1977), (c) Bunnell (1981), (d) Heal et al. (1981), (e) Tieszen et al. (1981), (f) Wielgolaski et al. (1981), (g) Miller et al. (1982), (h) Tryon and Chapin (1983), (i) Aerts (1990), (j) Henry et al. (1990), (k) Shaver and Chapin (1991), (l) Hobbie (1996), (m) Hobbie and Chapin (1998).

[†] Varies throughout the growing season (N uptake efficiency is zero during PGPs below the minimum required for that plant type).

[‡] Minimum PGP for plant growth to occur (during PGPs below this value, the plant type does not take up nitrogen; the lower the value, the greater is the cold tolerance of the plant type).

biomass plus belowground stem and rhizome biomass. Data on root biomass for arctic ecosystems are scarce and highly variable (Shaver et al. 1996). However, there were a few studies that provided data for estimates of root biomass of plant functional types (Wielgolaski et al. 1981, Miller et al. 1982, Tryon and Chapin 1983, Henry et al. 1990, Hobbie and Chapin 1998). A comparison of these studies showed no consistent differences in above- to belowground biomass ratios across ecosystems for a given plant type, so we assumed that this ratio was constant along the temperature gradient for each functional type.

Total soil nitrogen to 20 cm depth increases along the temperature gradient from polar desert to low Arctic and then plateaus with greater temperatures (data from Viereck 1970, Chapin et al. 1980, Gersper et al. 1980, Dowding et al. 1981, McGuire et al. 1992, Ping et al. 1997, Shaver et al. 1997, Bockheim et al. 1998) (Table 2). Estimates of net N mineralization rates in the Arctic are sparse and variable (Kielland 1990, Giblin et al. 1991, Nadelhoffer et al. 1991, Schimel and Clein 1996), and many of the published values for net N mineralization do not adequately support plant production in models of arctic plant growth (Reynolds et al. 1996). A reasonable explanation is that soil inorganic N is only one source of N for arctic plants; other important sources include soil organic N in the form of amino acids (Kielland 1994, Kaye and Hart 1997) and resorption of N from senescing plant tissue (Jonasson and Chapin 1985, Schimel et al.

1996). To determine net N mineralization parameters for the model, we therefore calculated the annual quantity of N necessary to sustain the range of biomass for each of our vegetation types (Table 2). At an equilibrium biomass, it can be assumed that

$$\text{new biomass} = \text{biomass senescing.}$$

Therefore, in an N-limited ecosystem,

$$\begin{aligned} \text{available N} \times \text{biomass:N ratio} \\ = \text{total biomass} \times \text{proportion senescing} \end{aligned}$$

or

$$\begin{aligned} \text{available N} \\ = \text{total biomass} \\ \times \text{proportion senescing/biomass:N ratio} \end{aligned}$$

with biomass : N ratio and proportion senescing averaged across the plant community. We expressed available N as a proportion of the total soil N to 20 cm (Table 2). Inputs of N from biological N₂ fixation are added to this amount (see *Model structure* section). We do not consider resorbed N explicitly in our model.

Plant growth periods

Plant growth periods (PGPs) are a construct of the model that allows for intraseasonal and interseasonal

TABLE 1. Extended.

Probability of establishment (annual)			Growing season requirements (min. PGP) \ddagger	Proportion of live biomass aboveground
High Arctic	Low Arctic	Treeline		
0.30	0.50	1.00	1	1.00
0.20	0.20	0.20	1	1.00
0.30	0.50	1.00	1	0.30 (0.06–0.53) [f,g,j,m]
0.20	0.50	1.00	1–2	
0.30	0.50	1.00	1	
0.30	0.50	1.00	1	
0.05	0.25	0.50	2	0.20 (0.17) [f,m]
0.10	0.25	0.50	2	0.15 (0.04–0.17) [f,g,m]
0.20	0.50	0.50	2	0.40 (0.16–0.71) [g,j]
0.05	0.20	0.50	2–3	0.30 (0.28–0.33) [f,g]
0.05	0.20	0.50	3	0.20 (0.11–0.33) [f,g,m]
0.00	0.20	0.50	4	
0.10	0.20	0.50	3	0.40 (0.24–0.44) [f,g,m]
0.05	0.10	0.50	3	0.25 (0.24) [f,g]
0.10	0.20	0.50	3	0.40 (0.24–0.50) [f,g,m]
0.20	0.25	0.50	3	
0.00	0.00	0.00	5	0.60 (0.43–0.70) [f,h]
0.00	0.10	0.10	5	0.85 (0.85) [h]

variability in plant activity, climate, and nitrogen availability. Each growing season is subdivided into a maximum of five PGPs. PGPs can be thought of as discrete, temperature-related time periods within a growing season. The coldest (earliest) part of the growing season is PGP(1). The model includes a matrix of probabilities of each PGP occurring in a given year (this varies by climate zone), such that PGP(1) always occurs, and the occurrence of PGP(i) is conditional on the occurrence of PGP($i - 1$) (Table 5). The final PGP in a given year encompasses the time of peak temperatures and includes the remainder of the growing season. Therefore, we can simulate a relatively cold, short growing season (maximum PGP of 1; some years in polar desert climates) or a relatively warm, long growing season (maximum PGP of 5; most years in boreal forest climates).

The amount of soil nitrogen mineralized varies by PGP (Table 5). The proportion of total soil N mineralized annually (Table 2) was distributed among PGPs based on the assumptions that (1) PGP($i + 1$) is warmer than PGP(i), and (2) warmer PGPs are shorter in duration in cold climates compared to warm climates. The maximum number of PGPs achieved in a given year is therefore an indicator of annual temperatures and growing season length, and also determines the total N mineralized. A year with a low maximum PGP will have low total N mineralization and might not be conducive for growth of plants that require a long, warm growing season. In contrast, a year with a high maximum PGP will have high N mineralization, and should be conducive for growth of most plant types. Even though we divide the growing season into several time periods using the PGP construct, the model output is still generated on an annual timestep.

Plant functional type parameters

We distinguish among plant functional types in the model with a set of five parameters (Table 1): (1) mean biomass:nutrient ratio, (2) proportion of total biomass that senesces each year, (3) probability of establishment, (4) nutrient uptake efficiency, and (5) timing of growth/temperature tolerance. Our goal was to choose a simple set of plant parameters that would encompass a wide range of growth, competition and survival strategies, and also allow for the coexistence of many different plant functional types (see Savile 1960). Because plant growth is limited predominantly by available nitrogen in many arctic ecosystems (Shaver and Chapin 1995 and references therein), and data on N are relatively abundant for the region, we use N as our surrogate nutrient in the model. We first define each parameter then describe how parameter values were estimated for each plant functional type.

Mean biomass: nitrogen ratio is plant biomass divided by total mass of plant nitrogen (g biomass/g N). This is the inverse of average tissue N concentration and the conversion factor used to generate plant biomass from nitrogen taken up by the plant. These values remain constant throughout model execution.

Proportion of biomass senescing represents the proportion of biomass that is removed from total plant biomass pools as litterfall (all plant parts included) at the end of each growing season. These values also remain constant throughout model execution.

Probability of establishment is the annual probability of establishing new individuals for each plant functional type. Probability of establishment varies with climate zone (thus can change under a warming sce-

TABLE 2. Ecosystem properties along the temperature gradient.

Climate zone	Mean summer temperature range (°C)	Total biomass range (g/m ²) [†]	Total soil N to 20 cm (from literature) (g/m ²) [‡]	Calculated range of plant-available N (i.e., net N mineralized) (g·m ⁻² ·yr ⁻¹) [§]	Percentage of total soil N mineralized (annual)
Polar desert	<3	200–450	150	0.21–0.33	0.14–0.22
High Arctic	3–6	450–975	500	0.84–1.22	0.17–0.24
Low Arctic	6–9	975–2400	1000	2.14–2.74	0.21–0.27
Treeline	9–12	2400–4600	1000	3.64–4.14	0.36–0.41
Boreal forest	>12	4600–>10 000	1000	3.64–7.64	0.36–0.76

[†] Total biomass = $212.25 \times e^{0.267T}$, where T = mean summer temperature (Gilmanov 1997)

[‡] Sources: Viereck (1970), Chapin et al. (1980), Gersper et al. (1980), Dowding et al. (1981), McGuire et al. (1992), Ping et al. (1997), Shaver et al. (1997), and Bockheim et al. (1998).

[§] Calculated from total biomass (this table), proportion of biomass senescing (Table 1), and biomass:N ratio (Table 1). See *Methods: Ecosystem properties along the temperature gradient*.

^{||} Calculated from total soil N and plant available N (this table).

nario), but it is not affected by interannual variability in temperatures. The biomass of new individuals is also a parameter in the model and was set at 0.1 g/m² for all plant types.

Nitrogen uptake efficiency is the maximum mass of nitrogen that can be taken up per unit of plant biomass (g N/g biomass). This is a maximum value that may not be realized under conditions of nitrogen limitation or competition with other plants. Nitrogen uptake efficiency of each plant type can vary among PGPs (i.e., intraseasonally).

Timing of growth/temperature tolerance is represented by the minimum PGP at which a plant type is active. Nitrogen uptake efficiency for a plant type is zero during PGPs below the minimum required for ac-

tivity. This parameter allows for differences among plant functional types in cold tolerance and intraseasonal patterns of growth.

The model is currently parameterized for 18 plant functional types (Table 1). Values for plant functional type parameters are our best estimates based on the literature in combination with unpublished observations of plant attributes. Mean biomass:N ratio was calculated as the inverse of whole-plant nitrogen concentration (Babb and Whitfield 1977, Muc 1977, Bunnell 1981, Heal et al. 1981, Tieszen et al. 1981, Aerts 1990, Shaver and Chapin 1991, Hobbie 1996). Proportion of biomass senescing was assumed (at steady state) to equal net primary production divided by total biomass (Shaver and Chapin 1991). We estimated an-

TABLE 3. Data sources for moist upland ecosystems along a temperature gradient.

Climate zone	References		Biomass reference number
	Plant community composition	Plant functional-type biomass	
Polar desert	Bliss (1981)	Bliss et al. (1984)	1
	Bliss et al. (1984)	Henry et al. (1990)	2
High Arctic	Aleksandrova (1988)	Svoboda (1977) (non-acid)	3
	Muc and Bliss (1977)	Bliss (1977)	4
	Bliss (1981)	Walker (1985)	5
	Walker (1985)	Andreev (1966) [†]	5
	Walker (1990)	Aleksandrova (1958) [†]	6
	Jorgenson et al. (1994)		
Low Arctic	Elias et al. (1996)		
	D. Walker et al. (<i>unpublished data</i>)	Marion et al. (1982)	7
	D. Walker and N. Barry (<i>unpublished data</i>)	Stoner et al. (1982)	8
	Auerbach (1992)	Shaver and Chapin (1986)	9
	Walker et al. (1994)	Chapin et al. (1988) [‡]	10
		Hastings et al. (1989) [§]	11
Treeline	Drew and Shanks (1965)	Shaver and Chapin (1991)	12
	Brock and Burker (1980)	Chapin et al. (1979)	13
		Shaver and Cutler (1979)	14
		Shaver and Chapin (1986)	15
Boreal forest	Viereck (1970)	Cole and Rapp (1981)	16
	Viereck et al. (1983)	Van Cleve et al. (1983)	17
	Viereck et al. (1992)	Yarie and Van Cleve (1983)	18

[†] In Tikhomirov et al. (1981).

[‡] Only vascular biomass data.

[§] Only certain species sampled.

^{||} Tundra locations near treeline.

nual probability of establishment (from 0 to 1) based on unpublished, qualitative observations of seed production and seedling densities in the field, and on quantitative seedling densities recorded during biomass harvests (e.g., Shaver and Chapin 1991; D. Walker and N. Barry, *unpublished data*). Nitrogen uptake efficiency was calibrated from the other parameters and the expected plant community composition and biomass by plant functional type (Tables 3 and 4). We estimated the minimum PGP required for growth (timing of growth/temperature tolerance) based on the latitudinal distribution of functional types (Hultén 1968, Young 1971), assuming that the northern distributional limit of a plant functional type is related to the number of PGPs required to sustain biomass. For example, more PGPs (longer growing season) are required for boreal trees than for low arctic species which, in turn, require more PGPs than high arctic species.

Stochastic inputs: climate and disturbance

Climate is a qualitative variable in the model that is directly related to the number of PGPs. The mean number of PGPs for each climate zone was estimated based on a latitudinal gradient of plant functional type composition. The stochastic nature of the number of PGPs in a growing season allows for interannual variability in climate, with warm years (>average number of PGPs) and cool years (<average number of PGPs) occurring randomly based on the probabilities in Table 5. This qualitative index of climate is therefore directly related to plant functional type activity, as plant types differ in their minimum PGP required for growth (Table 1), and is also related to a quantitative rate of net nitrogen mineralization (Table 5).

The model simulates two types of stochastic disturbance. The first type removes a proportion of the biomass of each plant functional type. This is a selective disturbance in that the proportion of biomass removed decreases linearly with increasing plant biomass : N ratio (i.e., the disturbance is most intense for plants with the greatest N concentrations). Examples of this type of disturbance are caribou grazing (White and Trudell 1980) and frost damage (Walker and Walker 1991). The model user defines the probability of this disturbance occurring in a given year (same value for all plant functional types) and the maximum proportion of biomass removed. For this analysis, the probability of occurrence in a given year was 0.10, and the maximum proportion of biomass removed was 25%. Only 5% of the nitrogen in the disturbed biomass is considered lost from the system; the remaining 95% is returned to the total soil nitrogen pool. These values all remain constant throughout model execution.

The second type of disturbance is a non-selective, intense disturbance that exposes mineral soil. An example of this type of disturbance is a frost scar. The annual occurrence probability of this type of disturbance decreases from 0.10 in the polar desert to 0.01

in the boreal forest and therefore will change under a warming scenario. This type of disturbance results in the mortality of all live plant biomass, however, most of the nitrogen in the disturbed biomass (90%) is returned to the total soil nitrogen pool. In order to simplify our first analyses using this model, all disturbance parameters were set to be typical of native, moist acidic tundra.

Model structure

The model has three main pools (Fig. 1): (1) total soil organic nitrogen, (2) plant available nitrogen, and (3) total nitrogen in plant biomass for each of the 18 plant functional types. There are also three major processes in the model: (1) nitrogen mineralization, (2) plant uptake of nitrogen and the concomitant plant growth, (3) return of organic nitrogen to the soil via senescence and mortality of plant biomass. The model executes on an annual time step at a spatial scale of one square meter. The model can be run for up to one hundred independent square meter patches to incorporate spatial heterogeneity among patches. Differences among patches occur as a result of two spatially stochastic processes. First, during a year in which intense disturbances occur (e.g., frost scars), the probability of disturbance for each individual patch (i.e., the average proportion of area affected) was set to 0.10; therefore the simulated landscape will have spatial heterogeneity induced by differences in the time since last disturbance. Second, seedling establishment is determined each year on a patch by patch basis (probabilities in Table 1); therefore additional spatial heterogeneity will result from random differences in establishment of new individuals.

In each simulation year, the number of PGPs is determined stochastically based on probabilities appropriate for the current climate (Table 5). During each PGP, a proportion of the total soil nitrogen pool is mineralized, as a function of climate zone and PGP (Table 5). Inorganic N resulting from N₂ fixation is added to the mineralized N pool during each PGP. N₂ fixation increases linearly in the model with increasing biomass; maximum N₂ fixation in a PGP of 0.035 g N/m² (independent of climate zone) occurs at 1000 g biomass/m². The maximum possible annual value of 0.175 g N/m² (in a year with 5 PGPs and ≥1000 g biomass/m²) is consistent with values of N₂ fixation from other studies (Chapin et al. 1980, Gersper et al. 1980, Chapin and Bledsoe 1992, McKane et al. 1997).

During each PGP, plant functional types that are active compete for available soil nitrogen. The N demand for each plant functional type is calculated as the N uptake efficiency (g N/g biomass) times the total biomass of the plant type (g biomass). If the total N demand across all active plant functional types exceeds the available N during a PGP, then plant N uptake for each plant type is adjusted to be proportional to its demand. Plants increase biomass based on the N ac-

TABLE 4. Plant functional-type aboveground-biomass data (g/m²) from the literature.

Functional type	Polar desert		High Arctic				Low Arctic	
	1	2	3	4	5	6	7	8
Total biomass	261.08	65.70	257.54	280.00	124.00	185.00	1207.70	1436.87
Moss	222.45	18.60	77.30†	194.00	49.00	114.00††	607.70	1155.00
Lichen	5.38		70.80		1.00			50.50
Total vascular	33.25	47.10	109.40	86.00	65.00	71.00	600.00	231.37
Forb	15.22	0.50	36.00		22.00			
High-Arctic acid								
Low-Arctic acid								
Disturbance-related								
<i>Equisetum</i> spp.								
Monocots	11.13	41.50	5.60		42.00			17.90
Sedge					37.00			
<i>Eriophorum</i> spp.		13.20						11.60
<i>Carex</i> spp.		18.40	5.60					6.30
Grass		0.20		5.00				
Woody dicots	6.90	5.10	67.80	10.00				213.47
Deciduous shrub								
<i>Salix</i> spp.		0.60	4.40					
<i>Betula</i> spp.								31.70
<i>Alnus</i> spp.								
Evergreen shrub								
<i>Cassiope</i> and <i>Empetrum</i> spp.								20.30
<i>Ledum</i> spp.								51.77
<i>Vaccinium</i> spp.								105.80
<i>Dryas</i> spp.		3.50	63.40					
Trees								

Note: Numbers in column headings refer to biomass reference numbers in Table 3.

† Mainly on lower slopes

‡ Mosses and lichens.

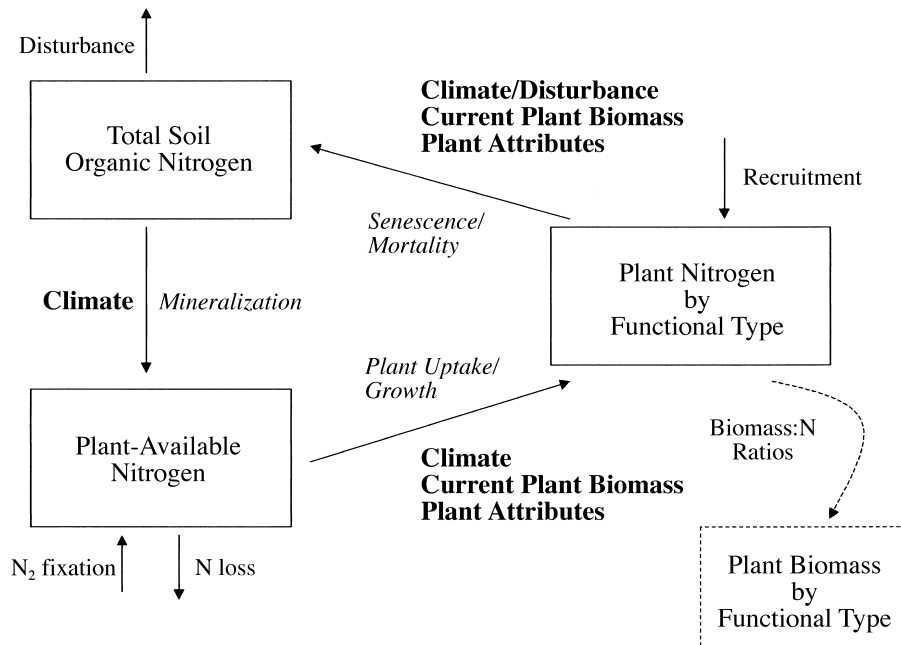


FIG. 1. ArcVeg flow diagram. Model pools are in boxes. The main processes are in italics inside the arrows, and the controls on these processes are in bold outside of the arrows. The dashed arrow and box represent the conversion of plant nitrogen to plant biomass in order to report the results as plant biomass.

TABLE 4. Extended.

Low Arctic				Treeline			Boreal forest		
9	10	11	12	13	14	15	16	17	18
465.71	186.00	546.65	637.94	549.00	654.00	300.90	9743.79	11 156.00	9840.00
248.20		414.00	248.20	225.00	288.30	64.00			
61.94			61.94	26.00	14.50	25.00			
155.57	186.00	132.65	327.80	298.00	351.20	211.90			
2.60			1.40						
2.30			1.40						
14.60	42.00	13.98	63.30	43.00	130.00	25.90			
10.20	36.00	10.36	55.30	30.00	122.70	18.70			
4.40	6.00	3.62	7.90	13.00	7.30	7.20			
			0.10						
138.37	144.00	118.67	263.10	255.00	221.20	186.00			
15.83	17.00	14.54	7.80		2.70				
48.70	51.00	42.08	76.10	5.00	18.90	28.60			
12.90	1.00		7.50	6.00	5.60	12.80			
26.20	30.00	29.26	84.30	92.00	97.80	107.10			
33.40	32.00	32.79	74.10	145.00	101.40	36.80			
							9734.29	11 156.00	9840.00

quired and the biomass:N ratio of the plant type. Establishment of new individuals can also augment plant functional type biomass.

Any available N not used in $PGP(i)$ remains available in $PGP(i + 1)$. Plant-available N that remains in the soil at the end of the growing season is assumed to be lost from the system. N losses in the model are minimal given that an average patch of low arctic tundra in the model will take up all of the available N when total biomass is greater than ~ 100 g biomass/m²; this value is small relative to the mean total biomass of low arctic tundra. Therefore most of the N lost will come from

recently disturbed patches with low plant biomass. Our low simulated N losses are also consistent with other findings (Chapin et al. 1980, Schimel et al. 1996). At the end of each growing season, a proportion of the total biomass senesces for each plant functional type. Organic nitrogen from senescent plant material is returned to the soil organic nitrogen pool. See the Appendix for a more detailed description of the model; the code for ArcVeg is available from the lead author.

Baseline climate and climate change simulations

Because the availability of data for parameterization and validation of the model was best for the high and

TABLE 5. Probability of $PGP(i)$ occurring given that $PGP(i - 1)$ occurs.

Climate zone	Probability					Mean no. of PGPs
	PGP 1	PGP 2	PGP 3	PGP 4	PGP 5	
Polar desert	1.0 (0.140) [0.000]	0.8 (0.060) [0.065]	0.1 (0.020) [0.030]	0.0 [0.026]	0.0	1.9
High Arctic	1.0 (0.042) [0.000]	1.0 (0.125) [0.000]	0.8 (0.050) [0.080]	0.1 (0.026) [0.009]	0.0 [0.025]	2.9
Low Arctic	1.0 (0.021) [0.000]	1.0 (0.063) [0.000]	1.0 (0.130) [0.000]	0.5 (0.035) [0.115]	0.1 (0.025) [0.025]	3.6
Treeline	1.0 (0.021) [0.000]	1.0 (0.063) [0.000]	1.0 (0.130) [0.000]	1.0 (0.150) [0.000]	0.8 (0.050) [0.350]	4.8
Boreal forest	1.0 (0.021)	1.0 (0.063)	1.0 (0.130)	1.0 (0.150)	0.9 (0.400)	4.9

Notes: Percentage of total soil N mineralized is in parentheses (see Table 2 for total annual ranges). Additional percentage of total soil N mineralized (under warming equivalent to the next warmest climate zone) is in brackets.

TABLE 6. Dominance rankings of plant functional type by total biomass.

Climate Zone	Scenario	Year	Dominant plant functional types (ranked by total biomass)			Occurrence percentage (across model runs)
			1	2	3	
High Arctic	baseline		Mosses	Sedges	Lichens	100
Low Arctic	baseline		Dec. Shr.	Ev. Shr.	Mosses	55
			Ev. Shr.	Dec. Shr.	Mosses	40
			Dec. Shr.	Mosses	Ev. Shr.	5
High Arctic	warming	10	Mosses	Sedges	Lichens	100
		25	Mosses	Sedges	Lichens	100
		50	Mosses	Sedges	Lichens	98
			Mosses	Sedges	Dec. Shr.	2
		75	Mosses	Sedges	Dec. Shr.	62
			Mosses	Sedges	Lichens	38
		100	Mosses	Sedges	Dec. Shr.	82
			Mosses	Dec. Shr.	Sedges	16
			Sedges	Mosses	Dec. Shr.	2
		125	Mosses	Dec. Shr.	Sedges	72
			Mosses	Dec. Shr.	Ev. Shr.	20
			Mosses	Sedges	Ev. Shr.	2
			Mosses	Sedges	Dec. Shr.	2
			Dec. Shr.	Ev. Shr.	Mosses	2
			Dec. Shr.	Mosses	Ev. Shr.	2
		150	Mosses	Dec. Shr.	Ev. Shr.	86
			Mosses	Dec. Shr.	Sedges	6
			Dec. Shr.	Mosses	Ev. Shr.	4
			Mosses	Dec. Shr.	Lichens	4
		175	Mosses	Dec. Shr.	Ev. Shr.	88
			Dec. Shr.	Mosses	Ev. Shr.	6
			Mosses	Dec. Shr.	Sedges	4
			Mosses	Dec. Shr.	Lichens	2
		200	Mosses	Dec. Shr.	Ev. Shr.	90
			Dec. Shr.	Mosses	Ev. Shr.	8
			Mosses	Dec. Shr.	Lichens	2
Low Arctic	warming	10	Dec. Shr.	Ev. Shr.	Mosses	100
		25	Dec. Shr.	Ev. Shr.	Mosses	94
			Dec. Shr.	Mosses	Ev. Shr.	4
			Ev. Shr.	Dec. Shr.	Mosses	2
		50	Dec. Shr.	Ev. Shr.	Mosses	96
			Ev. Shr.	Dec. Shr.	Mosses	4
		75	Dec. Shr.	Ev. Shr.	Mosses	96
			Ev. Shr.	Dec. Shr.	Mosses	4
		100	Dec. Shr.	Ev. Shr.	Mosses	96
			Ev. Shr.	Dec. Shr.	Mosses	4
		125	Dec. Shr.	Ev. Shr.	Mosses	100
		150	Dec. Shr.	Ev. Shr.	Mosses	98
			Ev. Shr.	Dec. Shr.	Mosses	2
		175	Dec. Shr.	Ev. Shr.	Mosses	98
			Ev. Shr.	Dec. Shr.	Mosses	2
		200	Dec. Shr.	Ev. Shr.	Mosses	100

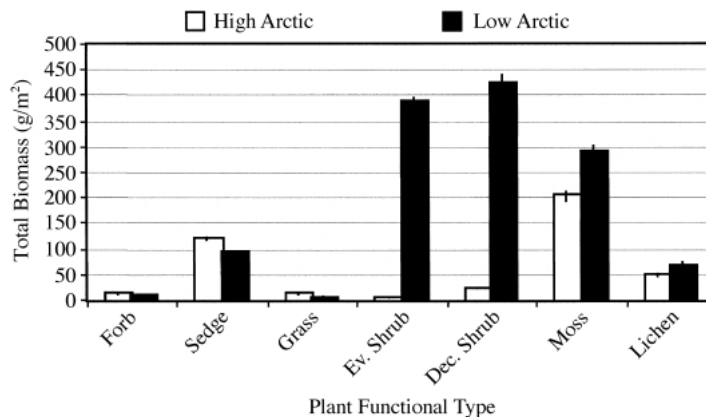
Note: "Dec. Shr." = deciduous shrub; "Ev. Shr." = evergreen shrub.

low Arctic, we present model output for these two climate zones. To determine the baseline biomass of each plant functional type at high and low arctic climates, we executed 20 separate simulations of the model for 1000 yr and 100 independent patches for each climate zone, starting with bare ground. Differences among model executions are a result of the stochastic nature of climate and disturbances in the model, in addition to all the patch-level stochasticity (frost scars and establishment of new individuals). Plant functional type biomass was averaged across the 100 patches for the last 200 yr of each simulation; this ensures that the model has reached a stochastic equilibrium plant community (after 800 yr) and incorporates interannual var-

iability into the mean. We then calculated mean biomass of each plant functional type across the 20 model runs and used these values for initial conditions in all simulations. We used two different methods to evaluate variability among model runs. The first method was to calculate the 95% confidence intervals for biomass of each plant functional type across the separate model runs. The second method was to examine the rank order of plant functional types based on their total biomass for the replicate runs of the model, essentially illustrating "alternative realities" of plant community composition.

Validation of plant functional type biomass was difficult considering the lack of data and the necessity to

FIG. 2. Simulated total biomass (g/m^2) of plant functional types in high and low Arctic under current climate. Values are means of 20 replicate model runs. Error bars are 95% confidence intervals across the 20 runs.



use most of the available data in model development. Six studies (two high Arctic and four low Arctic), not used in model development, were saved for model validation. We validated our regional representation of tundra vegetation (g biomass/ m^2) as simulated by ArcVeg against the six, site-specific observations. For the high Arctic, we compared our aboveground plant functional type biomass output to aboveground peak season biomass of plant types collected at the International Biological Program site in Barrow, Alaska (Webber 1978) and of plant types in the northern Yukon (Russell et al. 1993). We compared our low arctic model output to plant functional type data from several sources (Chapin et al. 1995, Shaver et al. 1996, Hobbie and Chapin 1998, Walker et al. 2000).

We conducted climate change (warming) runs for both high and low arctic ecosystems. To impose climate change, we shifted the climate to the next warmest climate zone (i.e., the high Arctic received a low Arctic climate, and the low Arctic received a treeline climate). The changes in climate were simulated to occur over a 100-yr transition period; during this period the probability of the new (warmer) climate occurring in a given year increases linearly from 0 to 1 over time (Starfield and Chapin 1996). For example, in year 40 of the 100-yr transition period, the probability of that year exhibiting the warmer climate is 0.4. After 100 yr, the probability of experiencing the warmer climate is 1. There are four important model elements that change with a changing climate: (1) the occurrence probabilities of PGPs (Table 5), (2) the proportion of the total soil nitrogen pool mineralized in each PGP (Table 5), (3) the occurrence probability of the second type of disturbance, and (4) the probabilities of plant functional type recruitment (Table 1).

All climate change runs started with the baseline functional type biomass values, identical for each of the 100 independent patches. Climate change was initiated in year 1 and was finalized after 100 yr. We performed 50 separate simulations for both the high and low Arctic warming scenarios. Plant functional type biomass values were averaged for the 100 inde-

pendent patches and were aggregated into the following seven types: mosses, lichens, forbs, sedges, grasses, deciduous shrubs, and evergreen shrubs. Means and 95% confidence intervals across the 50 replicate simulations were calculated for total biomass by plant functional type at year 10, and at 25-yr intervals through year 200. We additionally examined the variability in functional type rankings, as we did for baseline conditions. We also executed a single run of the model for both the high and low Arctic for 500 yr, again with warming transitioned from year 1 to year 100, to illustrate the interannual variability of model output associated with stochastic climate and disturbance regimes.

RESULTS

Current plant communities and biomass

ArcVeg simulates the equilibrium total biomass of high Arctic moist acidic tundra to be $424 \pm 18 \text{ g}/\text{m}^2$ (mean \pm 95% confidence intervals for 20 model runs), approximately $200 \text{ g}/\text{m}^2$ of which is moss biomass (Fig. 2). The next most dominant plant functional type is sedges with $121 \pm 3 \text{ g}/\text{m}^2$. Forb, grass, and shrub biomass are relatively low. The three dominant plant functional types, in rank order of total biomass, are mosses, sedges, and lichens for 100% of the model runs (Table 6). The equilibrium total biomass of low Arctic moist acidic tundra is simulated to be $1274 \pm 30 \text{ g}/\text{m}^2$. Most of this biomass is from mosses and from evergreen and deciduous shrubs, each of which is $>250 \text{ g}/\text{m}^2$. Sedge biomass is $92 \pm 4 \text{ g}/\text{m}^2$. Forb and grass biomass are again relatively low. Deciduous shrubs, evergreen shrubs, and mosses are the three dominant plant functional types, however, the rank order of dominance varied among model runs (Table 6).

Validation of current plant communities and biomass

The simulated range in total biomass of the high Arctic ($424 \pm 18 \text{ g}/\text{m}^2$) overlaps the low end of the expected range of values (Table 2), whereas the range in total biomass of the low Arctic ($1274 \pm 30 \text{ g}/\text{m}^2$)

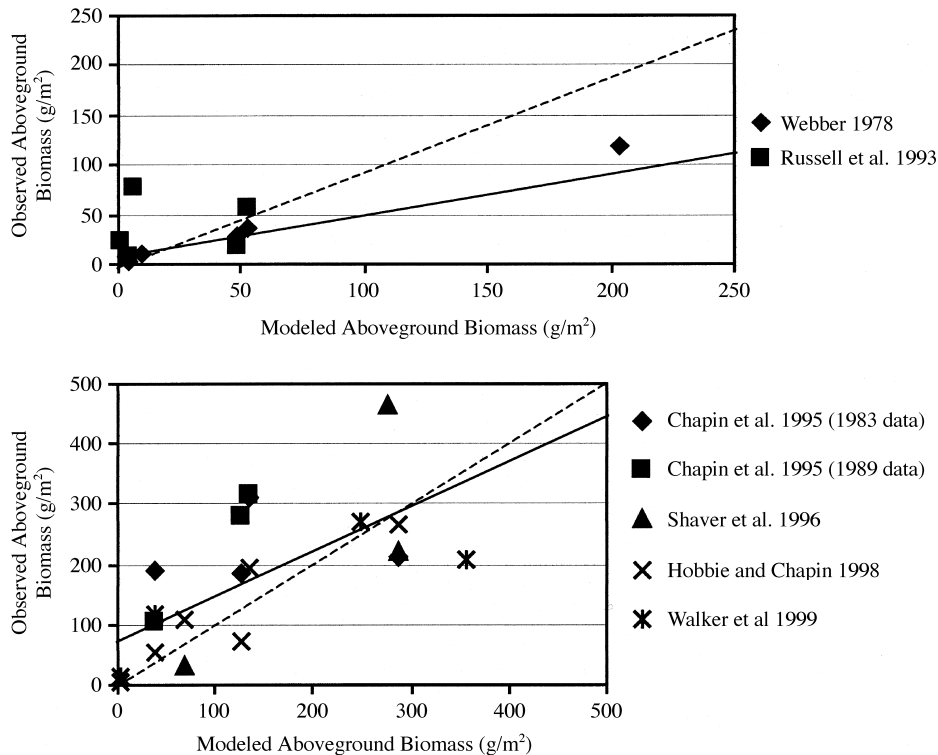


FIG. 3. Relationship between observed aboveground biomass for different plant functional types (g/m^2) and simulated aboveground biomass for plant functional types (g/m^2) for the (a) high and (b) low Arctic zone. The solid line is the regression line; the dashed line is the 1:1 line. Note that scales are different in the two panels.

falls within the expected range. There is a favorable correlation between modeled aboveground biomass by plant types and observed aboveground biomass by plant type ($r = 0.78$, $P < 0.01$) (Fig. 3a). Based on a regression analysis, the y intercept is not significantly different from zero. However, the model does overestimate values of aboveground biomass, possibly due in large part to a single point (mosses; with $>100 \text{ g/m}^2$ modeled and observed biomass) driving the regression.

There was also a favorable relationship between modeled biomass by plant type and observed biomass by plant type for the low Arctic ($r = 0.66$, $P < 0.01$) (Fig. 3b). Regression analysis showed the y intercept was significantly greater than zero, and the model slightly underestimated aboveground biomass values.

Responses of plant communities and biomass to climatic warming

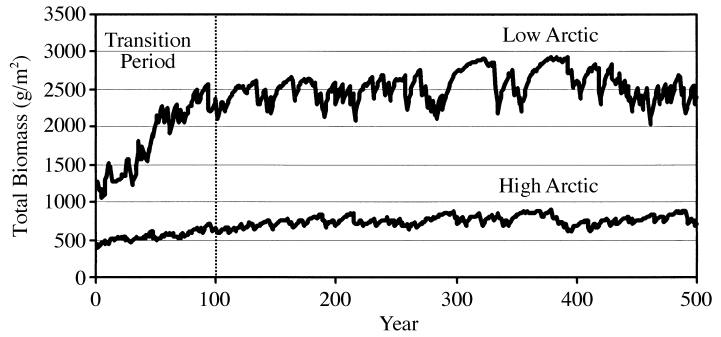
Simulated total biomass of both the high and low Arctic increases with warming. Total biomass of the high Arctic increases over 200 g/m^2 during the 100-yr transition period and continues to increase for approximately an additional 100 yr following this period (Fig. 4). Mean total biomass from years 200–500 (post climate change) in the single-run simulation is 771 g/m^2 ; however, the range is $\sim 600\text{--}900 \text{ g/m}^2$. Total biomass

of the low Arctic increases over 1000 g/m^2 during the 100-yr transition period (Fig. 4). Mean total biomass from years 200–500 is 2571 g/m^2 , and the range is from $\sim 2000 \text{ g/m}^2$ to 3000 g/m^2 .

Simulated warming altered the plant community composition (Table 6) and biomass (Fig. 5) of the high Arctic. Both mosses and sedges responded initially to warming with increased biomass, however their biomass began to decline after 50–75 yr. Sedge biomass declined to below its initial level, whereas moss biomass remained greater after warming compared to initial biomass. Mosses remained the dominant plant functional type in terms of biomass following climate change. Evergreen and deciduous shrubs were slow to respond, yet their biomass increased substantially between years 50 and 150. Biomass values of evergreen and deciduous shrubs were eventually both greater than sedge biomass after year 150. Lichen biomass increased slightly with warming, and there was little response of forbs and grasses.

Simulated warming in the low Arctic had large effects on biomass and some effects on plant functional type composition. Biomass of deciduous and evergreen shrubs increased substantially with warming (Fig. 6a), and deciduous shrubs remained the dominant plant functional type in terms of biomass (Table 6). Moss biomass increased slightly and then declined after year

FIG. 4. Simulated warming effects on total biomass (g/m^2) for high and low Arctic. Data represent a single run of the model. Climates are transitioned linearly from year 1 to year 100.



50 to initial levels. Lichen biomass increased, whereas sedge biomass declined (Fig. 6b). Grass biomass declined slightly, and forb biomass remained relatively unchanged.

Validation of responses to climatic warming

There are obvious constraints in validating a simulation of long-term ecosystem responses (Rastetter 1996). One common method, albeit insufficient to validate long-term models, is to compare short-term observations to short-term predictions of the model (Rastetter 1996). Given that this is our only reasonable option for validating predicted ecosystem responses, we compare 10-yr model results to data from temperature and nitrogen manipulation field studies. Experimental warming studies in the Arctic have produced a variety of results. One trend in the data is a growth response of shrubs to warming, demonstrated in several low arctic studies with treatment lengths ranging from 3 to 9 years (Chapin et al. 1995, Graglia et al. 1997, Shevtsova et al. 1997, Hobbie and Chapin 1998). In a meta-analysis of the International Tundra Experiment (ITEX) (Arft et al. 1999), near-surface air and soil warming induced a vegetative response in both the high and low

Arctic, for both woody and herbaceous species, after two years. However, by the fourth year of the warming treatments, there were no longer any significant responses of vegetative growth to increased temperatures. Robinson et al. (1998) found that increased temperatures yielded no change in plant community composition of a high Arctic semidesert after five years. Other observed effects of warming were decreases in moss and sedge biomass in the low Arctic after 3 and 9 years respectively (Chapin et al. 1995). The decrease in moss biomass may have been due in part to the exclusion of precipitation from the warming treatment.

Our model output concurs with the most common trend reported from field data, that shrub biomass increases in the low Arctic with increased temperatures. Based on 95% confidence intervals calculated over 50 runs, our model suggests a significant increase in deciduous shrub biomass in the low Arctic after 10 yr. By 25 yr after present, both deciduous and evergreen shrubs have significantly increased biomass with increased temperatures. Other significant trends for our low Arctic simulation after 10 yr are declines in forb and grass biomass, and an increase in moss biomass; our predicted increase in moss biomass is opposite the

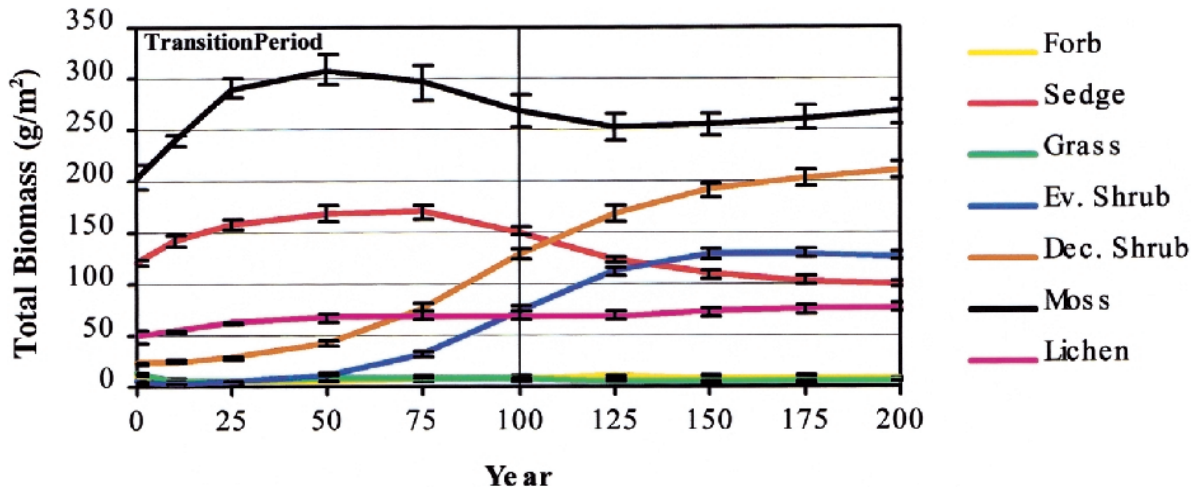


FIG. 5. Simulated warming effects on total biomass (g/m^2) of seven plant functional types in the high Arctic. Climates are transitioned linearly from year 1 to year 100. Data are averaged across 50 replicate runs of the model. Error bars represent 95% confidence intervals across the 50 replicate runs.

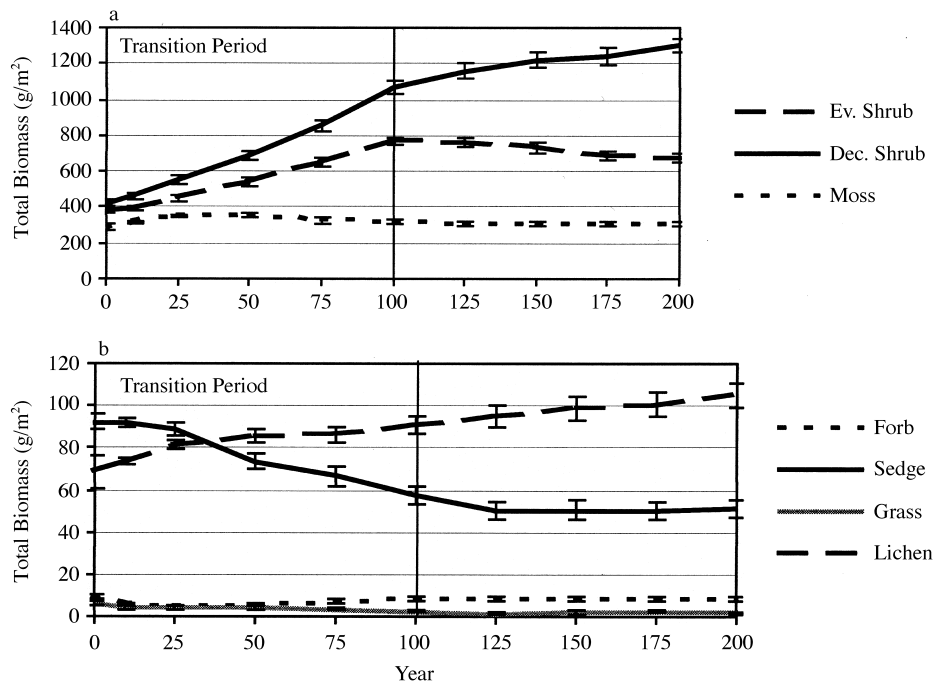


FIG. 6. Simulated warming effects on total biomass (g/m^2) of (a) dominant and (b) subdominant plant functional types in the low Arctic. Climates are transitioned linearly from year 1 to year 100. Data are averaged across 50 replicate runs of the model. Error bars represent 95% confidence intervals across the 50 replicate runs.

trend found for *Hylocomium splendens* by Chapin et al. (1995).

DISCUSSION

Comparison of ArcVeg to other plant community and ecosystem models

ArcVeg joins elements of plant community dynamics and biogeochemical cycling into a simple model that can be applied at a landscape to regional scale. Its structure is similar to those of existing gap models, however we have focused less on successional dynamics and more on the stochastic and transient nature of equilibrium communities. The combination of plant community dynamics and ecosystem processes is comparable to the approach being taken in the development of dynamic global vegetation models. However, our smaller spatial extent may allow us to simulate a more detailed plant community than global models.

Several features of our model make it unique in comparison to other models of arctic ecosystems. The first is its detail regarding plant functional types. Until recently, ecosystem models that focused on fluxes and stocks of carbon and nitrogen had generally considered vegetation as a single pool and, when parameterized for northern ecosystems, rarely distinguished beyond the vegetation types of polar desert, arctic tundra, and boreal forest (McGuire et al. 1995, McKane et al. 1997). These models considered species composition implicitly through differences in C:N ratio and allocation patterns. Models of arctic plant growth had pre-

viously been focused at wet meadow sites and often concentrated on a single plant species (Leadley and Reynolds 1992, Reynolds and Leadley 1992, Leadley et al. 1997). There were a few models developed that explicitly simulated a heterogeneous plant community in the arctic. Prentice et al. (in the physiologically based biogeographic model, BIOME 1.1 [1992]) defined six northern plant functional types; however, only two of these were tundra plant types. The GAS-FLUX model (Tenhunen et al. 1994), which simulated ecosystem gas exchange, used four plant functional types: deciduous shrubs, evergreen shrubs, graminoids, and mosses (Reynolds et al. 1996, and Miller et al. (1994) modeled tussock tundra with 10 plant species. Our model takes a more detailed approach to plant community dynamics, incorporating up to 18 plant functional types, allowing the opportunity to model processes such as herbivory that are sensitive to species traits or species diversity.

The second unique feature of the model is its transient nature. ArcVeg addresses the interannual dynamics of arctic plant communities, and it does so from a process-based, ecosystem perspective. Other models of northern vegetation responses to climate change largely focused on predicting the new equilibrium distribution of vegetation types (Lenihan and Neilson 1995, Cramer 1997). Starfield and Chapin (1996) modeled the transient dynamics of treeline vegetation in response to climate, focusing on switches among four major ecosystem types (upland tundra, grassland, coniferous for-

est, and broad-leaved deciduous forest) but ignoring the underlying biogeochemistry and species composition.

Nature of simulated vegetation change

There are several assumptions in our model that are crucial to understanding the predicted responses in our climate change simulations. First, warming increases the proportion of the total soil nitrogen pool that becomes available to plants each year. The response of nutrient mineralization rates to increased temperatures in the Arctic has been well documented (e.g., Nadelhoffer et al. 1991, Binkley et al. 1994, Hobbie 1996). While we do not explicitly model many soil pools and processes, we recognize that the additional mineralization can be achieved through several pathways. Increased nutrient mineralization can be caused by an increase in microbial activity and decomposition rates in the active layer as well as by an increase in the depth of the active layer, exposing more organic substrate. Increased temperatures may also increase the uptake of organic N by roots and root symbionts.

Second, climate change in the model incorporates an increase in the length of the growing season. Myneni et al. (1997) used remotely sensed, normalized difference vegetation index data to document a lengthening of the active growing season, with the greatest increase found between 45° N and 70° N. We express this in the model as an increase in the number of plant growth periods (PGPs) within a growing season; this situation favors plant functional types that are not very cold tolerant, but are good competitors for nutrients during longer, warmer growing seasons.

Third, there are no constraints on the migration or dispersal of plant functional types. A plant type can essentially be established in a community once the climate becomes suitable. The processes of migration and dispersal need to be incorporated into dynamic vegetation models in order to assess more accurately the plant community changes under new environmental conditions.

Fourth, climates are transitioned over a 100-yr period, and the probability of occurrence of the new climate increases linearly over this time period. Because each year during this period can be either the old or the new climate, the variability in climate is inherently greatest during this time.

Our model output suggests several points to consider regarding the nature of change in arctic ecosystems. The first is that climate change may induce the formation of an ecosystem that presently is absent or uncommon. For example, when a low Arctic climate was imposed on a high Arctic ecosystem, the new plant community composition and biomass were not representative of either the zonal low or high Arctic. This occurred because the soil nitrogen pool in the model imposed a constraint on the response of the high Arctic to warming, since initial soil N in the high Arctic was

parameterized to be 50% of the soil N in the low Arctic. Over millennia in our model, N₂ fixation may increase total soil N and eliminate this constraint. A deepening of the active layer as a result of warming may increase available soil nutrients more rapidly than predicted by our model, but it is still likely to be a long-term process.

The second point is that there may be lags in the response of vegetation, and initial responses may not reflect the long-term directional changes. For our high arctic simulations there were substantial lags evident, such that the short-term (0–50 yr) responses differ from the long-term (100–200 yr) effect. This is due to the nature of competition in our model, which gives the plants with greatest current biomass an advantage in obtaining nutrients. Therefore, plant types that are currently dominant have the best opportunity to capitalize initially on any increase in mineralization rates. Subdominant plant types may take some time to augment their biomass and increase their nutrient uptake capacity. Additionally, our model predicts changes in only 50% of the plant functional types simulated after 10 yr, and these changes are minimal. Combined with the potential for lags, this suggests that changes over decadal time scales may be difficult to predict.

Last, our model predicts long-term increases in total biomass and in shrub biomass for both the high and low Arctic, due to increased plant-available nitrogen and a longer growing season. Field studies on the effects of increased temperature have yielded a variety of results, however a common finding is a growth response of shrubs, which is consistent with our model output.

Next steps

Our model is simple, limited in environmental scope, and may or may not be lacking some important processes, such as light competition, soil organic matter transformations and functional type-specific N₂ fixation. Our immediate objectives for the model will be to further examine the sensitivity of the model output to plant attributes and disturbance parameters. We eventually hope to expand the environmental scope of the model to include variation in moisture and pH regimes. We also may be missing some key functionality regarding nutrient cycling, such as the allocation of carbon and nitrogen to different plant parts and the use of different forms of N by plants (NH₄⁺, NO₃⁻, amino acids, and resorbed N).

We hope, however, that our model will fill an important gap in efforts to predict arctic ecosystem dynamics by simulating the transient nature of arctic plant communities under scenarios of a changing climate. We believe our approach will also be applicable to ecosystems outside of the Arctic. Using a relatively simple set of parameters to define a comprehensive set of key plant functional types, in addition to simulating the spatial and temporal variability of a limiting resource, is a methodology that could advance the state

of dynamic vegetation modeling for a variety of ecosystems.

ACKNOWLEDGMENTS

This research was supported by the National Science Foundation (OPP-9521459). We thank Skip Walker and the participants in the Sustainability of Arctic Communities Project for stimulating discussions regarding the model. We also thank Lou Pitelka, Dave McGuire, and two anonymous reviewers for helping us improve the manuscript.

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APPENDIX

The ArcVeg program pseudo-code is available in ESA's Electronic Data Archive: Ecological Archives A010-004.