Journal of Biogeography (J. Biogeogr.) (2005) 32, 863–878

ORIGINAL ARTICLE

Analysis of vegetation distribution in Interior Alaska and sensitivity to climate change using a logistic regression approach

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ABSTRACT

Aim To understand drivers of vegetation type distribution and sensitivity to climate change.

Location Interior Alaska.

Methods A logistic regression model was developed that predicts the potential equilibrium distribution of four major vegetation types: tundra, deciduous forest, black spruce forest and white spruce forest based on elevation, aspect, slope, drainage type, fire interval, average growing season temperature and total growing season precipitation. The model was run in three consecutive steps. The hierarchical logistic regression model was used to evaluate how scenarios of changes in temperature, precipitation and fire interval may influence the distribution of the four major vegetation types found in this region.

Results At the first step, tundra was distinguished from forest, which was mostly driven by elevation, precipitation and south to north aspect. At the second step, forest was separated into deciduous and spruce forest, a distinction that was primarily driven by fire interval and elevation. At the third step, the identification of black vs. white spruce was driven mainly by fire interval and elevation. The model was verified for Interior Alaska, the region used to develop the model, where it predicted vegetation distribution among the steps with an accuracy of 60–83%. When the model was independently validated for north-west Canada, it predicted vegetation distribution among the steps with an accuracy of 53–85%. Black spruce remains the dominant vegetation type under all scenarios, potentially expanding most under warming coupled with increasing fire interval. White spruce is clearly limited by moisture once average growing season temperatures exceeded a critical limit (+2 °C). Deciduous forests expand their range the most when any two of the following scenarios are combined: decreasing fire interval, warming and increasing precipitation. Tundra can be replaced by forest under warming but expands under precipitation increase.

Main conclusion The model analyses agree with current knowledge of the responses of vegetation types to climate change and provide further insight into drivers of vegetation change.

Keywords
Boreal forest, climate change, fire, Interior Alaska, logistic regression, modelling.

INTRODUCTION

Greenhouse gases released by human activities are the dominant forcing in anomalously high latter twentieth century temperatures in the Northern Hemisphere, overriding a millennial-scale cooling trend due to astronomical forcing (Briffa *et al.*, 1995; Mann *et al.*, 1998). At northern high latitudes this results in winter and spring warming accompanied

 doi:10.1111/j.1365-2699.2004.01185.x

by increased terrestrial precipitation (Houghton *et al.*, 1995). Seemingly in response, total plant growth (as estimated from satellite data) from 45 to 70° N has increased between 1981 and 1999 in most of Eurasia, parts of Alaska, boreal Canada and north-eastern Asia (Myneni *et al.*, 1997; Zhou *et al.*, 2001). There are also reports of increased shrubbiness in the northern Alaskan tundra (Sturm *et al.*, 2001) as well as increased shrubbiness combined with tree-line advances in north-west Alaska (Silapaswan *et al.*, 2001; Lloyd *et al.*, 2003). However, vegetation response to warming at high latitudes is complex, as increased warming does not lead to linear increases in vegetation biomass (Shaver *et al.*, 2000). Vegetation response may lag behind climate change depending on disturbance regime and the ability of species to disperse and establish themselves (Davis, 1989; Starfield & Chapin, 1996; Chapin & Starfield, 1997; Camill & Clark, 2000; Masek, 2001).

Boreal forests form a circumpolar belt spanning over 20° latitude covering North America and northern Eurasia, and contain one of the largest carbon reserves in the world in their water-logged and cold soils (Post *et al.*, 1982; Barbour *et al.*, 1987; Apps *et al.*, 1993; Ping *et al.*, 1997). Higher temperatures and increased precipitation in boreal and arctic Alaska in recent years have led to changes in sea ice, glaciers, permafrost and vegetation (Myneni *et al.*, 1997; Keyser *et al.*, 2000; Serreze *et al.*, 2000; Jorgensen *et al.*, 2001). Changes in ambient temperatures and precipitation patterns are also expected to affect fire frequency. There are indications that fire frequency has been increasing in western Canada (Stocks *et al.*, 1998; Chapin *et al.*, 2000c; Harden *et al.*, 2000) while decreasing in eastern Canada (Bergeron & Archambault, 1993; Flannigan *et al.*, 1998; Carcaillet *et al.*, 2001). Another concern is that changes in temperature, moisture and permafrost could lead to a release of carbon stored in boreal bogs (Yu *et al.*, 2001; Turetsky *et al.*, 2002). Indicators for warming-induced moisture limitations are the recent growth decline of white spruce near the timberline in Alaska (Lloyd & Fastie, 2002). This might explain the decoupling noted between warming and tree-ring width indicating an overall decrease in tree-ring width despite continued warming at high latitude sites in the Northern Hemisphere (Briffa *et al.*, 1998; Vaganov *et al.*, 1999; Barber *et al.*, 2000; Lloyd & Fastie, 2002). Considering the vast amounts of carbon stored in the boreal forest, future climate change at high latitudes may alter the global carbon budget with potentially important feedbacks between the boreal forest and global climate (Foley *et al.*, 1994; Chapin *et al.*, 2000c; Eugster *et al.*, 2000).

The boreal forest of Alaska is located in the state's Interior between the Alaska Range in the south, the coastal tundra to the west, the Brooks Range to the north, and continues eastward into Canada. In this study, we use a hierarchical logistic regression approach to evaluate the potential equilibrium response of the four major vegetation types of Interior Alaska (black spruce *Picea mariana* (Mill) B.S.P., white spruce *Picea glauca* (Moench) Voss, deciduous forest and tundra) to changes in growing season temperature, growing season precipitation and fire interval. Specifically, the following questions are addressed in this study: (1) What are the current controls on vegetation distribution? (2) What is the sensitivity of vegetation distribution to changes in climate? and (3) What is the sensitivity of vegetation distribution to changes in fire interval and how do the changes in the fire interval interact with changes in climate?

METHODS

Logistic regression is a statistical modelling tool that predicts the probability of a bivariate response variable based on a variety of explanatory variables. Logistic regression has been widely applied in ecological research, and has been used for risk assessment (Jalkanen & Mattila, 2000), habitat evaluations (Pearce & Ferrier, 2000), and the prediction of vegetation distribution (Hilbert & Ostendorf, 2001). We used logistic regression to predict the occurrence of the four major vegetation types tundra, deciduous forest, black spruce forest and white spruce forest in Interior Alaska. The model was based on the predictors elevation, aspect, slope, drainage, mean growing season (May–September) temperature, total growing season precipitation and fire interval. The importance of model predictors was evaluated based on *t*-values, *P*-values and standardized coefficient values during the three hierarchical regression runs. The predicted vegetation was first compared with a modified existing vegetation classification in Interior Alaska to verify the model for a region used to develop the model. The model was then independently validated for vegetation distribution in north-west Canada before it was applied to simulate changes in vegetation distribution for several different climate change scenarios involving changes in temperature, precipitation and fire interval to produce potential vegetation distribution in Interior Alaska in the future.

Logistic regression

Logistic regression is based on a transformation of a linear equation that uses a binomial logistic distribution where the probability of the response can be mathematically expressed as a function of several explanatory variables:

$$P(x) = \frac{e^{(\text{intercept}+a_1*\text{variable } 1+a_2*\text{variable } 2+\cdots+a_n*\text{variable } n)}}{1+e^{(\text{intercept}+a_1*\text{variable } 1+a_2*\text{variable } 2+\cdots+a_n*\text{variable } n)}}.$$

This equation estimates a probability value from 0 to 1.0 given the constants a_1 to a_n and any number of explanatory variables (Hosmer & Lemeshow, 2000). Depending on a chosen threshold probability value, everything above this threshold equals one state of the binomial response, while everything below equals the other state of the variable (e.g. tundra vs. forest). Depending on how this threshold value is increased or decreased, there will be more or less of either bivariate state in the outcome. By comparing estimated outcomes with known states, the value for the threshold with the highest prediction accuracy can be determined. Accuracy can be tested by running predictions over a range of threshold values and composing an accuracy table. Total accuracy can then be calculated as: Accuracy = (total true)/(total predicted) (Pearce & Ferrier, 2000).

We developed a logistic regression model for Interior Alaska (Fig. 1) using the following inputs as parameters: elevation, aspect, slope, drainage, mean growing season (May–September) temperature, total growing season precipitation and fire interval for each 1-km pixel. The total study area encompasses almost 300,000 km^2. While the logistic regression statistics were performed in SPLUS (MathSoft, Inc., Seattle, WA, USA), all data overlays and manipulations were done in a geographical information system (Arc/Info 8.02 by Environmental Systems Research Institute, Inc., Redlands, CA, USA). As logistic regression can only compare two outcomes at a time, the model was run in three hierarchical steps to predict the four major vegetation types:

1. Tundra or Forest → 2. Deciduous forest or Spruce forest → 3. Black spruce forest or white spruce forest.

Spatial data sets of explanatory variables

As none of the currently available 1-km resolution land cover classifications for Alaska distinguish between the two ecologically most important vegetation types, black and white spruce forests, we developed an algorithm that refines Fleming's (1997) land cover classification for Alaska. The algorithm defined the location of black spruce as spruce occurring on northern aspects and gentle to flat slopes based on generally accepted theories on the distributions of black and white spruce in Interior Alaska (Van Cleve *et al.*, 1986; Viereck *et al.*, 1992). The algorithm also used growing season temperature, aspect and slope to delineate black and white spruce in cells classified as woodland by the original classification (Fleming, 1997), i.e. cells near treeline. In interior Alaska, white spruce is the species that generally occurs at treeline. We used a 1-km resolution USGS global digital elevation model (DEM) to calculate elevation, slope (in per cent) and aspect (in degree). When aspect is treated as a continuous variable from 0 to 360°, it produces erroneous results because the two values at opposite ends of the gradient are actually the same in the landscape (i.e. northern aspect). Aspect values were therefore processed into two variables: southern vs. northern aspect and eastern vs. western aspect. In the first case, values increase from 0 at southern aspect to 180 at northern aspect with a value of 90 at western and eastern aspects. In the second case, eastern aspects were assigned zero and western aspects were assigned 180 with 90 at south and north aspects.

Soil drainage classes were imported from the USDA 1 : 1 million State Soil Geographic (STATSGO) data base and converted to 1-km pixels (Harden *et al.*, 2003). Drainage class reflects the speed at which water is removed from the soil after a rainfall event. Drainage values range from one ('excessive' meaning very rapid water loss after a rain event) to seven ('very poor' drainage leading to waterlogged soils).

Fire intervals are based on 50 years of historic fire data for Alaska compiled by the Alaska Fire Service (Murphy *et al.*, 2000). In the process of developing a regional data set, we applied a 150-km smoothing kernel (mean) to the actual fire data before summarizing the result at half-degree resolution. This smoothing kernel provided the best continuous data that reflected regional climate gradients rather than individual fires.

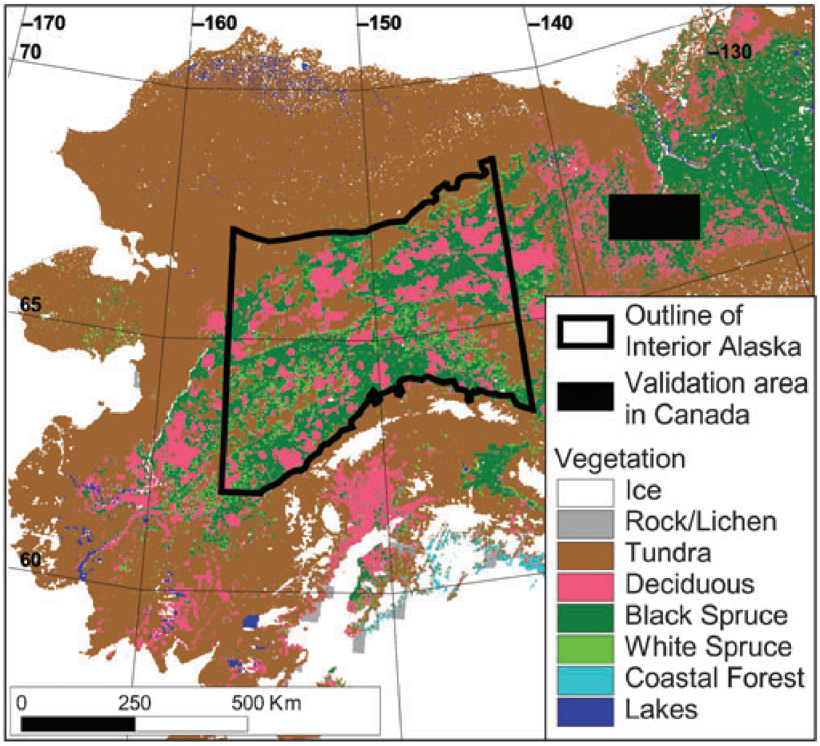

Figure 1 Delineation of Interior Alaska and location of validation area. This map shows the control vegetation used for model verification in Interior Alaska and model validation in north-west Canada.

For each half-degree cell, the proportion of annual area burned was calculated as: (area burned during 1950–2000)/(area of cell × 50 years). The fire interval was then calculated as the reciprocal. There is much disagreement in the literature on the use of terms such as fire interval, fire return interval, mean fire interval and fire frequency (Agee, 1993; Johnson, 1994). While 'fire interval' can be defined as 'the number of years between two successive fires,' 'mean fire interval' refers to the 'arithmetic average of all fire interval determined in a designated area during a specific time period' (Romme, 1980; Agee, 1993). Neither term correctly defines our fire data set of adjusted years between recurring fires. We decided to use the term 'fire interval' in this paper for simplicity rather than introducing a new term such as 'interpolated fire interval,' which would be more accurate.

Temperature and precipitation information for Interior Alaska were extracted from the Climatic Research Unit (CRU) 0.5° mean monthly climatology from 1961 to 1990 (New *et al.*, 1999) (Fig. 2a,b). Growing season temperature was calculated as the average temperature from the monthly temperatures for May to September. Precipitation was computed as the sum of precipitation over the growing season from May to September.

Model evaluation

The model was run for 1-km pixel sizes. Both *P*-values and *t*-values were used in evaluating variables that explain vegetation distribution. We set a *P*-value threshold of 0.05 for identifying variables that are significant in explaining vegetation distribution. *T*-values are calculated as the regression coefficient divided by the standard deviation of the coefficient and are considered significant above 1.96. High absolute *t*-values are indicative of variables that provide strong explanatory power, with positive *t*-values indicating a positive effect and negative *t*-values indicating a negative effect. Because the putative explanatory variables differ in their ranges (e.g.

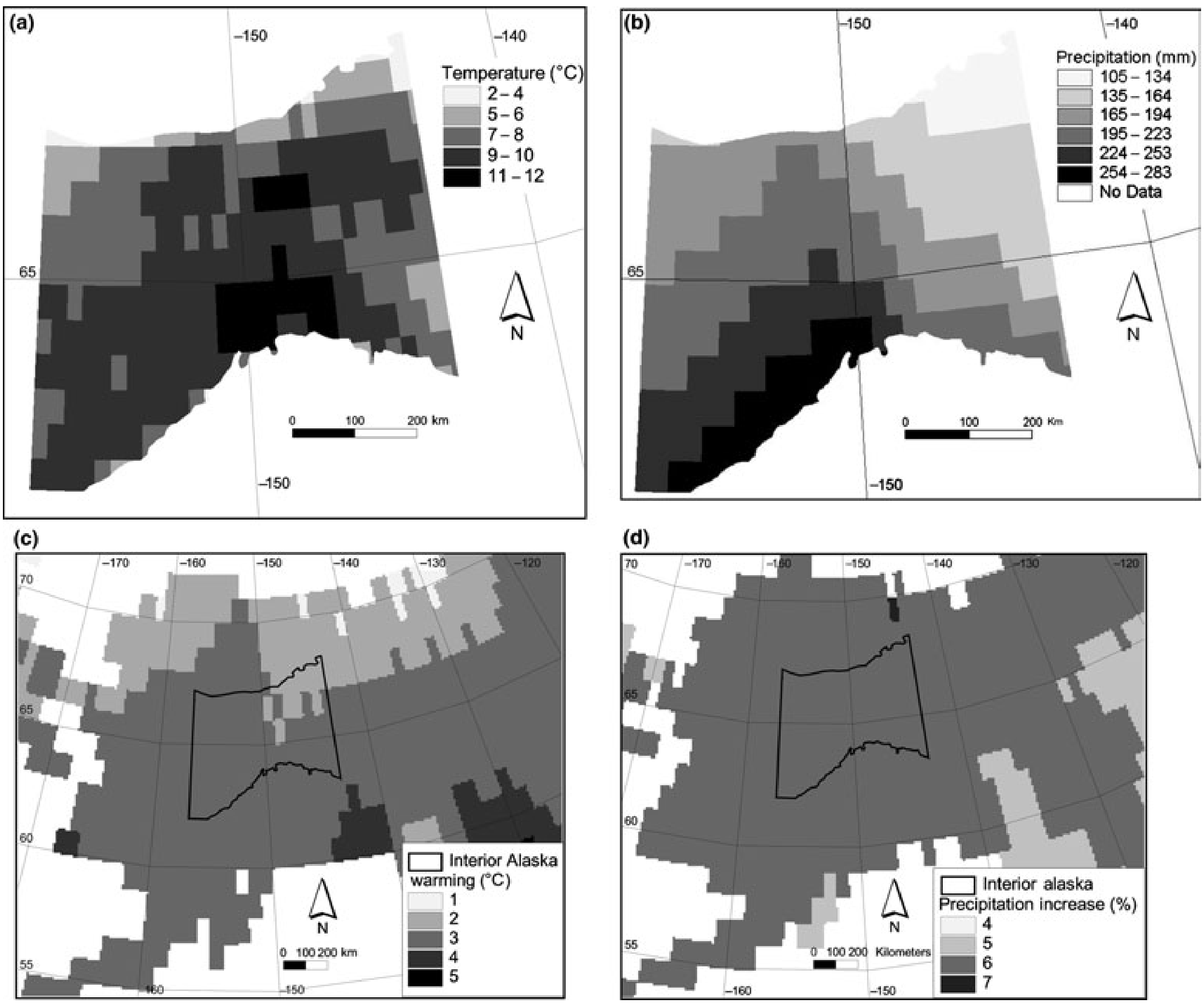

Figure 2 (a, b) Current climate for Interior Alaska from the CRU data base; (c, d) projected climate changes in Alaska according to the Hadley predictions for the year 2100. (a) Average growing season temperature (CRU); (b) total growing season precipitation (CRU); (c) growing season warming (Hadley); (d) growing season precipitation increase (Hadley).

elevation ranges from 18 to 1830 m while drainage ranges from 1 to 7), *t*-value coefficients of the regression are not directly comparable among explanatory variables. This difference in range among the input parameters can be adjusted by standardizing each of the input values using their means and standard deviations in the formula:

$$X_{\text{standardized}} = (X_i - X_{\text{mean}})/(\text{standard deviation } (X))$$

where X_i is the *i*th value for predictor X and X_{mean} the mean value for predictor X. This procedure does not affect the *P*-values and *t*-values of the logistic regression, and its primary value is in interpreting regression coefficients. Model predictions at each hierarchical step were compared with known vegetation over a range of threshold values. Using a classification or contingency table, the threshold with the highest accuracy was determined (Pearce & Ferrier, 2000). The logistic regression model was verified in Interior Alaska (Fig. 1), the region used to develop the model. We independently validated the model for vegetation distribution in north-western Canada to test its applicability to an area outside Interior Alaska (Fig. 1). Vegetation data for Canada were based on a 1995 map derived from Advanced Very High Resolution Radiometer (AVHRR) (Cihlar *et al.*, 1996), which was cross-walked to three major vegetation types: tundra, deciduous forest and spruce forest.

Climate change scenarios

For all climate and fire interval change simulations, input predictors were altered homogeneously, before the model simulated potential equilibrium vegetation under these new conditions in a total of 23 scenarios (Table 1). To be specific, the logistic regression equations and thresholds identified during model development were run using the changed input data sets for a prediction of equilibrium vegetation. In several scenarios, mean growing season temperature was increased by 1, 2 and 5 °C. A comparison of 19 global climate change simulations resulted in predicted warming in Interior Alaska to range between no warming to almost 10 °C warming of mean annual temperature with an average predicted warming of 2–3 °C (Källén *et al.*, 2001). Thus, a 5 °C growing season warming is slightly higher than expected warming. Annual precipitation is expected to increase an average of 11% for the entire area 60–90° N across the 19 models (Källén *et al.*, 2001). We included a larger range into our simulations by letting growing season precipitation increase and decrease by 10%, 20% and 30%. Temperature and precipitation scenarios were combined into scenarios for coupled climate change. Fire interval was both increased and decreased by 10%, 20% and 30% where an increase in fire interval represents a lengthening of the time between fires, thus allowing vegetation more time to recover between disturbances. While there are indications that fire interval is increasing in eastern Canada (Carcaillet *et al.*, 2001; Flannigan *et al.*, 2001), fire is becoming more frequent in north-western North America (Flannigan *et al.*, 1998). Fire interval was combined with warming where fire interval could increase or decrease by 30%, while temperature would rise by 5 °C. Fire interval was also combined with precipitation into four scenarios: fire interval could increase or decrease by 30%, while precipitation could increase or decrease by 30%.

Table 1 Summary of simulation scenarios

Temperature change (°C)	Precipitation change (%)	Fire interval change (%)
Individual change scenarios where one parameter is changed per simulation		
1. +1	4. −30	10. −30
2. +2	5. −20	11. −20
3. +5	6. −10	12. −10
	7. +10	13. +10
	8. +20	14. +20
	9. +30	15. +30
Combined change scenarios where two predictors are changed simultaneously		
16. –	−30	−30
17. –	−30	+30
18. –	+30	−30
19. –	+30	+30
20. +5	−30	–
21. +5	+30	–
22. +5	–	−30
23. +5	–	+30

These climate change scenarios are not directly based on expectations for future climate in Interior Alaska but serve as model sensitivity tests. To get a more realistic picture of future climate in Interior Alaska, we used the prediction for the year 2100 from the UK Hadley Center CM2 model in an additional equilibrium logistic regression model run (Johns *et al.*, 1997) (Fig. 2c,d). This transient model predicts future climate based on the combined effects of changes in greenhouse gases and sulphate aerosols. The Hadley predictions for 2100 were superimposed on the current climate file in the logistic regression model simulation. It is important to note that while we use the Hadley predictions for 2100 to drive the logistic regression model, model output should not be considered as predicting vegetation distribution in 2100 as the logistic regression approach produces equilibrium vegetation distribution.

RESULTS

Model verification and validation

In comparison with the *P*- and *t*-values of the logistic regression analysis, the standardized regression coefficients produce a slightly different ranking of the importance of explanatory variables (Table 2). The occurrence of tundra is strongly driven by elevation confirming that a majority of tundra in interior Alaska is alpine tundra rather than latitudinal tundra. Deciduous forest is associated with a decrease in fire interval and an increase in elevation. Black spruce is defined by a shorter fire interval and lower elevations than white spruce. Black spruce is also found on northern aspects and gentle slopes, criteria that were used to define black spruce *a priori*. Overall, *t*-values and standardized coefficients identified similar, ecologically significant drivers and seem to be both useful in analysing variables that explain vegetation distribution. Another issue that can affect model performance is the correlation among explanatory variables, however only slope vs. elevation and temperature vs. precipitation have absolute correlation values close to 0.5, which is less than our criteria of 0.7 for eliminating a correlated explanatory variable as redundant.

Verification of model predictions with vegetation distribution for Interior Alaska resulted in accuracies among the steps of the hierarchical logistic regression ranging from 68% to 83% (Table 3, Fig. 3a,b). In comparison with Interior Alaska, prediction accuracy for deciduous vs. spruce step of the hierarchical logistic regression declined from 68% to 53% in the validation analysis for north-west Canada, but there was little difference between analyses in the accuracy for the tundra vs. forest step (Table 3). As there was no separate white spruce class in the vegetation classification for Canada, the accuracies of the black vs. white spruce step could not be evaluated. When the hierarchical model was developed, thresholds were set so that the total area covered by white spruce was similar to observed values, which resulted in a large underestimation of deciduous forest and an overestimation of black spruce (Fig. 3b). In an analysis not presented in this study, the prediction of deciduous vs. spruce forest improved from 68% to 85% accuracy when historic fires since 1950 were added as an explanatory variable stand-age. We did not add the record of historic fires to our model for two reasons. First, definition of stand-age is incomplete because there is no spatially explicit record of fires before 1950. Secondly, the use of stand-age in the model would have required us to define stand-age in our future simulations.

Responses to changes in climate

Warming substantially influences potential equilibrium vegetation distribution of all vegetation types in Interior Alaska (Fig. 4). The area for tundra decreases under all warming scenarios, and tundra almost disappears when present temperatures increase by 5 °C (Fig. 4a). Deciduous forest and black spruce forest, on the contrary, continue to expand their potential range with rising ambient temperatures (Fig. 4b,c). The potential extent of white spruce increases at +1 and +2 °C, but decreases when temperatures continue to rise (Fig. 4d). Under 5 °C warming over current temperatures, deciduous forest could expand to 450% of its current distribution primarily by invading black spruce habitat, while black spruce forest could increase to 128% its current distribution by replacing upland tundra and white spruce areas.

Warming by 5 °C could lead to a replacement of the current vegetation types in 29% of Interior Alaska (Fig. 3c). In this scenario, higher elevations serve as refuges for deciduous forest and white spruce while black spruce remains in flat areas below *c.* 500 m (Fig. 3d). When 5 °C warming is imposed, areas of change are concentrated at 200–800 m (73% of the area of change), N and W aspect (64%), and 1–7% slope (65%). Ninety-eight per cent of the area currently covered by tundra could be converted to a different vegetation type as well as 76% of the current white spruce forest.

All four vegetation types show a strong response to precipitation change (Fig. 4). Increasing precipitation by 30% results in a change in vegetation type in 22% of the area (Fig. 3e), compared with a 14% change caused by decreasing precipitation by 20%. Both tundra and white spruce could increase to roughly 150% of their current distribution under

Table 2 *t*-values, *P*-values and standardized coefficient values for model parameters. Bold *P*-values are ≥ 0.05 and not significant. The sign of the *t*-values and standardized coefficient values is associated with the first vegetation type in the simulation, e.g. tundra in 'tundra vs. forest'. Drainage is represented as values from 1 (very rapid water runoff) to 7 (waterlogged soil). E–W and S–N aspect range from 0 (east or south) to 180 (west or north, respectively). Fire interval represents the number of years between burns. For example, a decrease in temperature is the most significant parameter for predicting tundra according to the unmodified *t*-values, while increasing elevation is the most important parameter when using standardized coefficient values (inputs are normalized for each parameter to account for differences in parameter ranges)

	P-values			*t*-values			Standardized coefficient values		
	Tundra vs. forest	Deciduous forest vs. spruce	Black vs. white spruce	Tundra vs. forest	Deciduous forest vs. spruce	Black vs. white spruce	Tundra vs. forest	Deciduous forest vs. spruce	Black vs. white spruce
Drainage	< 0.01	< 0.01	< 0.01	−51	0	30	0	0	0
Elevation	< 0.01	< 0.01	< 0.01	91	51	−7	11,752,480	8,334,067	−1,501,024
E–W aspect	**0.57**	< 0.01	< 0.01	1	9	−3	425	5,734	−2,883
Fire interval	**0.96**	< 0.01	< 0.01	0	−69	−22	−9984	−34,432,270	−7,051,116
Precipitation	< 0.01	< 0.01	< 0.01	76	−11	−47	33,895	−3,768	−25,319
Slope	< 0.01	< 0.01	< 0.01	36	−27	−75	16	−14	−52
S–N aspect	< 0.01	**0.17**	< 0.01	−22	1	70	−20,081	1,064	83,802
Temperature	< 0.01	**0.19**	< 0.01	−156	0	24	−6	0	1

Table 3 Model verification and validation accuracy (%). The logistic regression model was verified by comparing predicted vegetation with actual vegetation in Interior Alaska. The validation was performed by comparing model predictions with actual vegetation in north-western Canada

Simulations	Verification (%)	Validation (%)
Tundra vs. forest	83	85
Deciduous vs. spruce	68	53
Black vs. white spruce	80	N/A

30% precipitation increase. This causes a decrease of deciduous forest to 34% of its current distribution and a decrease of black spruce by 75%. Precipitation decrease leads to the opposite result as the area of deciduous forest doubles and the area of black spruce increases slightly. White spruce and tundra potentially decrease to 54% and 67%, respectively, of their current ranges. Under a 30% precipitation increase, *c.* 50% of the areas currently covered by either deciduous forest or white spruce are converted to tundra while precipitation decrease leads to an invasion of black spruce into former tundra and white spruce forest. These results might in part be due to a spurious correlation between regional precipitation patterns and vegetation (precipitation is lower in the north and north-east than in the south-west while tundra is mostly concentrated on the northern part of Interior Alaska). Ecologically, summer precipitation is very important, especially for black and white spruce, and we feel that justifies keeping it in the model despite this potentially spurious correlation.

When changes of temperature and precipitation are combined, one factor seems to drive the vegetation change more than the other, indicating that it is a stronger driver in the simulation scenario (Fig 4). Vegetation changes across the precipitation gradient are no longer linear when precipitation interacts with temperature increases. Under the combined warming and precipitation change scenarios, deciduous forest shows the greatest relative increase although it never achieves dominance in Interior Alaska. At 5 °C warming and 30% precipitation decrease, deciduous forest could expand more than 500% over its current range, while 30% precipitation increase could lead to deciduous forest expansion to 354% of its current range. Expansion of spruce and deciduous forest leads to the elimination of tundra when temperatures reach 5 °C regardless of the precipitation regime although precipitation increase leads to a slower replacement. Although a 30% precipitation decrease by itself could lead to a decrease in black spruce area, black spruce expands its range when combined with warming. This vegetation type shows a more positive association with precipitation increase and warming than precipitation decrease and warming. White spruce displays a constant decline under warming and/or precipitation decrease. This decline is hastened with greater reductions in precipitation. However, if precipitation increases with temperature, white spruce could expand to roughly twice its current distribution at 1, 2 and 5 °C warming, with a peak at +2 °C.

In comparison to current climate, the Hadley CM2 model (Johns *et al.*, 1997) predicted a 6% increase in total growing season precipitation for basically all of Alaska accompanied by 1–5 °C warming in growing season temperature (Fig. 2c,d), with an average growing season temperature increase of 2.8 °C for Interior Alaska by 2100. The potential equilibrium vegetation distribution under this scenario creates a landscape consisting mostly of black spruce forest with some deciduous forest and very little white spruce at intermediate elevations, and tundra at high elevations (Fig. 3f). Under these conditions, black spruce habitat expands from 67% to 89% of Interior Alaska and deciduous forest increases from 1% to 5% while white spruce area decreases from 9% to 2%. All three vegetation types replace current tundra, which decreases drastically from 23% to only 2% of Interior Alaska. Black spruce not only extends into more than half of the area currently covered by tundra, but it also almost completely covers the sites that currently support white spruce. White spruce and deciduous forest in turn expand into tundra sites by raising the treeline along the elevation gradient. Thus, the alpine tundra on low elevation hills in the centre of Interior Alaska is primarily replaced by deciduous forest.

Responses to changes in fire interval and interactions with changes in climate

Except for deciduous forest, changes in fire interval alone cause minor changes in the potential equilibrium distribution of vegetation types in Interior Alaska. When fire interval lengthens by 30% over current levels, white spruce area expands slightly, while deciduous forest area potentially shrinks to less than half its current area (Fig. 5). When fire interval decreases, deciduous forest can increase to 233% of its current distribution, while white spruce experiences a decrease to 90% of its current area. Tundra and black spruce vegetation remain essentially stable through all six fire interval scenarios (Table 1).

While changes in the fire interval have little effect on the response of tundra and white spruce to 5 °C warming, decreases in the fire interval could cause deciduous forest to expand to nearly double the area under 5 °C warming alone, a response that appears to be primarily at the expense of black spruce (Fig. 5 compared with Fig. 4). In contrast to changes in temperature, changes in the fire interval interact substantially with changes in precipitation. In comparison with a wetter climate with no changes in fire interval, increases and decreases in the fire interval accompanying a wetter climate can lead to a substantial decline in the area of white spruce, a slight decrease in the area of tundra, and increases in the area of deciduous forest and black spruce, in which case deciduous forest is more responsive to decreases in the fire interval (Fig. 5). In comparison with a drier climate with no change in the fire interval, increases or decreases in the fire interval cause substantial declines in white spruce extent and a slight decline in tundra (Fig. 5). In contrast, the area of black spruce under a drier climate is little affected by decreases in fire interval, but increases

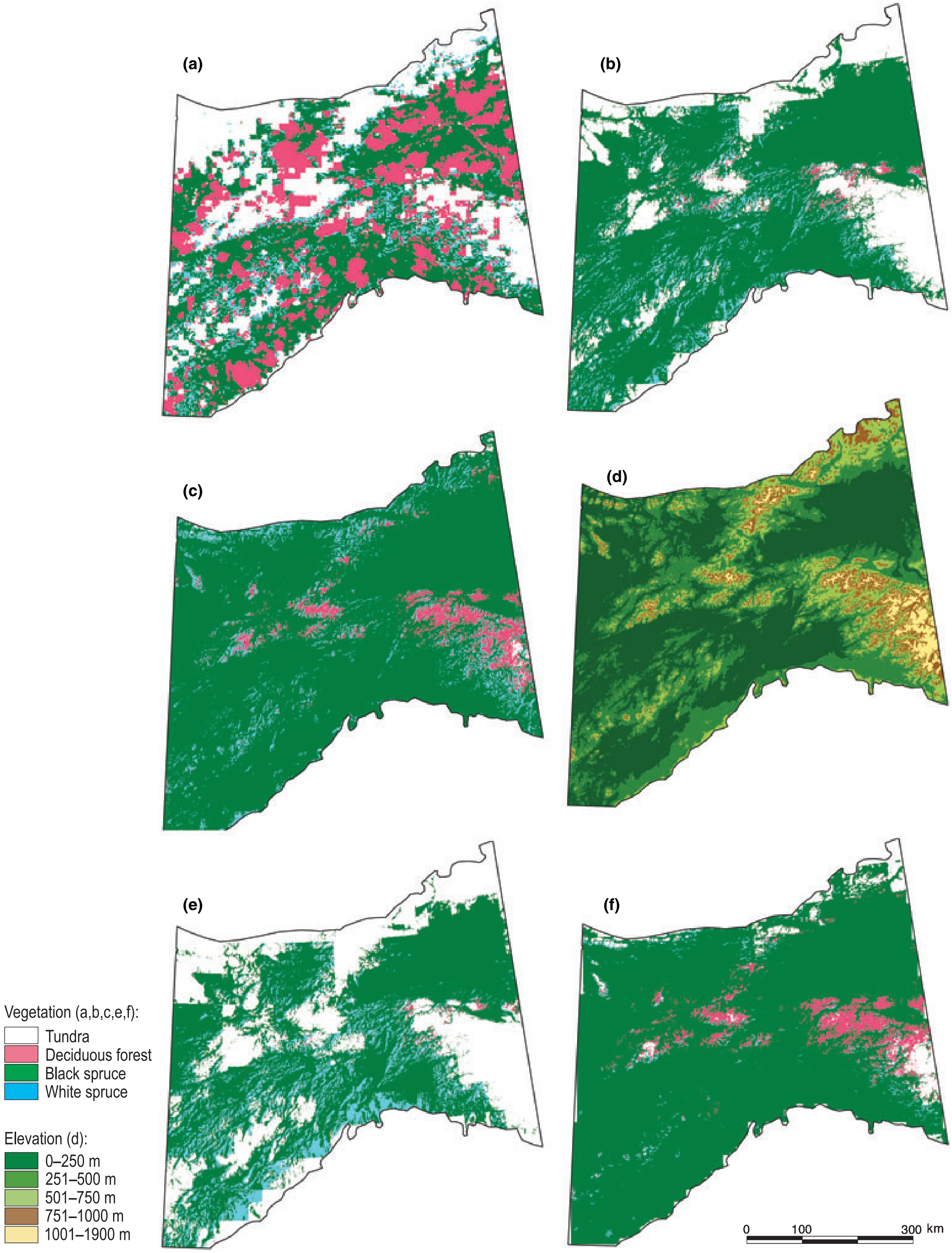

Figure 3 Simulated and observed vegetation under several scenarios in Interior Alaska compared with elevation. (a) Observed vegetation *c.* 1991: 27% tundra, 24% deciduous forest, 39% black spruce, 10% white spruce. (b) Simulated vegetation *c.* 1991: 23% tundra, 1% deciduous forest, 68% black spruce, 9% white spruce. (c) Simulated vegetation under a 5 °C growing season temperature increase. (d) Elevation (m). (e) Simulated vegetation under 30% precipitation increase. (f) Simulated vegetation *c.* 2100 (Hadley scenario).

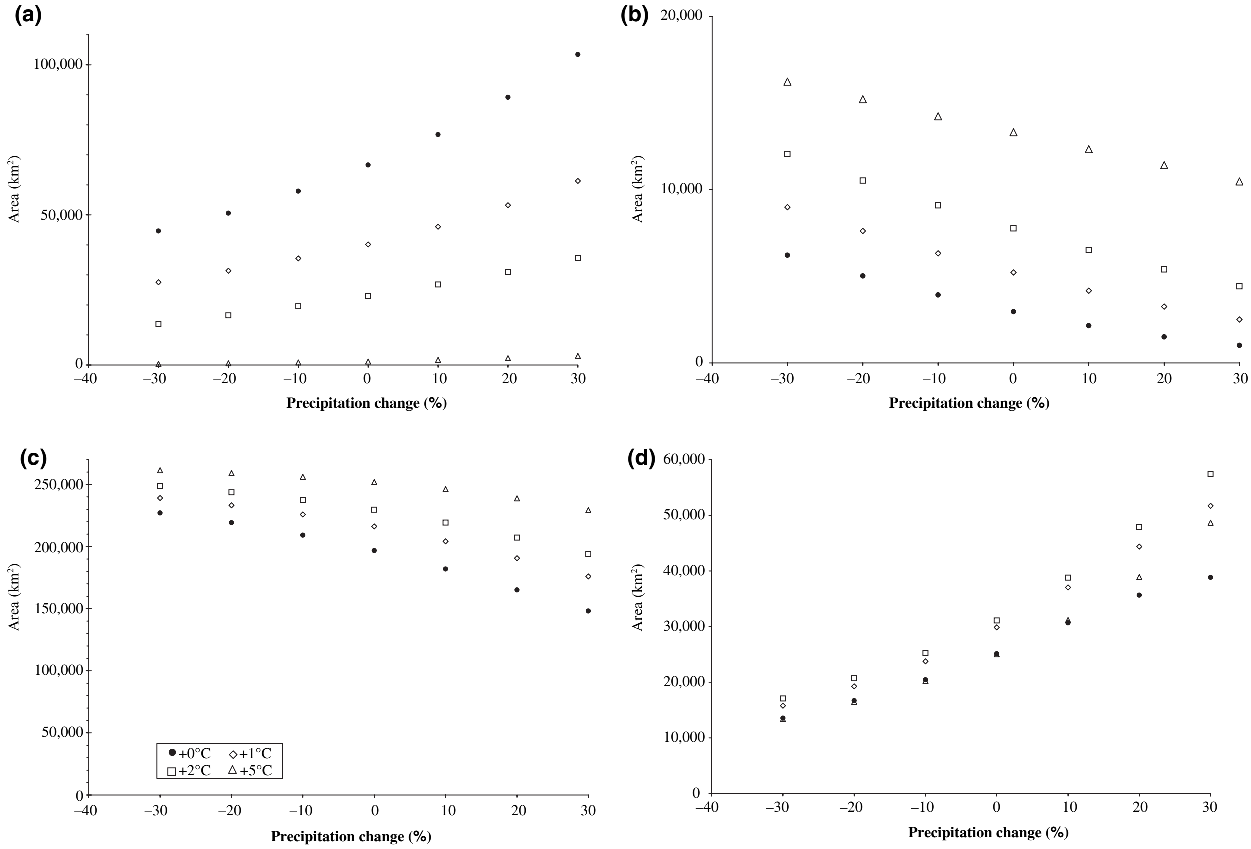

Figure 4 Climate response of the four major vegetation types. These figures show how the spatial extent (in km^2) of each of the four major vegetation types in Interior Alaska responds to changes in precipitation and temperature: (a) tundra; (b) deciduous forest; (c) black spruce; (d) white spruce.

with an increasing fire interval (Fig. 5). Deciduous forest shows the opposite pattern as its potential area under a drier climate increases substantially with decreases in the fire interval, but is little affected by increases in the fire interval (Fig. 5).

DISCUSSION

North-western North America has been experiencing substantial changes in climate over the last several decades. Meteorological records since the 1940s for Alaska and north-western Canada show an increase in spring minimum temperature by an average 0.47 °C per decade and a lengthening of the growing season by 2.6 days per decade, which is reflected in the advance of leaf onset date by an average of 1.1 days per decade and advanced onset of spring ice breakup on the Tanana River in Interior Alaska by 0.7 days per decade (Keyser *et al.*, 2000). The response of vegetation distribution in high latitudes has several implications for the climate system (Chapin *et al.*, 2000c; McGuire *et al.*, 2002). First, expansion of boreal forest into regions now occupied by tundra reduce growing season albedo and increase spring energy absorption, which may enhance atmospheric warming (Bonan *et al.*, 1992; Thomas & Rowntree, 1992; Foley *et al.*, 1994; McFadden *et al.*, 1998; Chapin *et al.*, 2000b). In contrast, an increase in the proportion of deciduous forests at the expense of conifers has the potential to reduce energy absorption and work against atmospheric warming (Chapin *et al.*, 2000a). Secondly, changes in vegetation distribution in high latitudes may influence the atmospheric concentrations of carbon dioxide (Smith & Shugart, 1993; Chapin *et al.*, 2000a; McGuire *et al.*, 2000a,b), as high latitude ecosystems contain *c.* 40% of the world's soil carbon inventory that is potentially reactive in the context of near-term climate change (McGuire *et al.*, 1995; Melillo *et al.*, 1995; McGuire & Hobbie, 1997). The replacement of tundra with boreal forest will likely eventually increase carbon storage in high latitudes (Smith & Shugart, 1993; McGuire & Hobbie, 1997), while decreases in fire interval in north-western North America will likely decrease carbon storage in boreal forest ecosystems (McGuire *et al.*, 2002).

Our analysis of current controls on vegetation distribution in the boreal forest of Interior Alaska and vegetation sensitivity to expected future changes in climate and fire interval in this study have implications for feedbacks to the climate system of water, energy, and carbon exchange responses in Interior Alaska. Below we first discuss the limitations of our approach followed by insights from our analysis of controls over vegetation distribution in Interior Alaska in the context of other studies that have evaluated these controls using different analytical tools and from different perspectives. We then discuss insights that emerged from our analysis of the

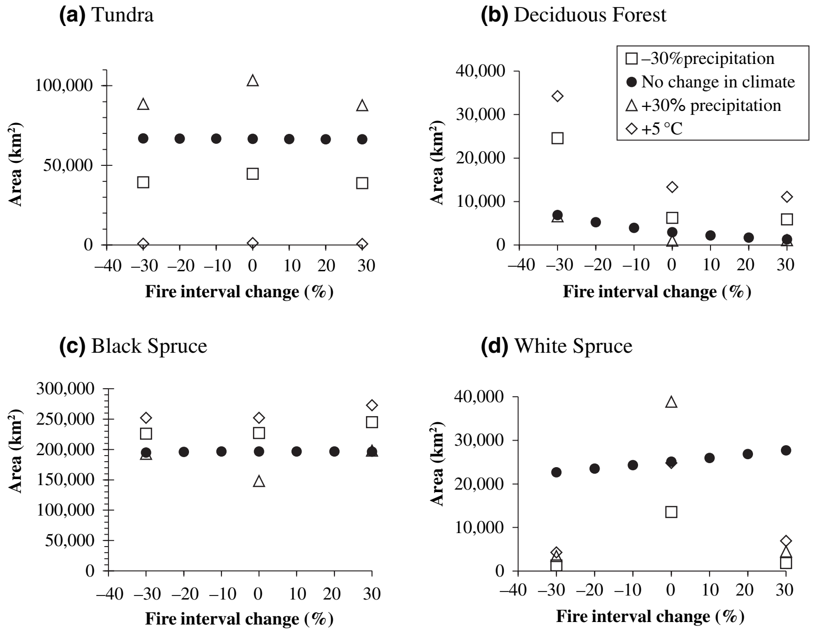

Figure 5 Interactions between climate and fire changes. These figures show how the spatial extent (in km^2) of each of the four major vegetation types in Interior Alaska responds to changes in fire interval individually and when combined with changes in precipitation and temperature. (a) Tundra; (b) deciduous forest; (c) black spruce; (d) white spruce.

sensitivity of vegetation distribution in Interior Alaska to scenarios of changes in climate and fire interval. Finally, we discuss some of the next steps in improving understanding of controls over vegetation distribution and the sensitivity of vegetation distribution to environmental changes in high latitudes. Our model is based on 1-km pixel sizes and our findings are only applicable at a regional scale.

Limitations of the empirical statistical approach

The logistic regression model is an empirical approach that describes the statistical manifestations of processes rather than explaining underlying mechanisms or detailed causality. Confidence in this approach is highest for interpolation rather than extrapolation of results. Our analysis of climate space indicates that all our chosen fire interval and precipitation simulations are well within the limits of the climate space used to create the model, while the 5 °C warming scenario had less than 50% overlap. We also have to keep in mind that we are using an equilibrium model that does not account for transient dynamics as the vegetation responds to a new climate. The response of processes such as dispersal, establishment, changes in soil conditions (temperature, moisture, nutrients), and the thawing of permafrost have great potential to influence the trajectory of vegetation change and it is not clear to what extent these processes are captured in the empirical approach we used in this study. The model thus simulates potential vegetation which might be unrealistic as species assemblages could change under new climate conditions (Davis, 1989; Kirilenko & Solomon, 1998; Epstein *et al.*, 2000). While we need to be cautious about interpreting the time-scale of our simulations, the results are not dissimilar to the end-points of dynamic approaches simulating vegetation responses in high latitudes. For example, a transient model for Alaska showed that it would take 150 years for the conversion of tundra to forest after a 3 °C instantaneous warming and 80 years after a 6 °C warming (Starfield & Chapin, 1996). In addition, a dynamic global vegetation model predicted a loss of 50% of all tundra north of 50° N by 2100 using the same Hadley CM2 climate scenario we used (White *et al.*, 2000).

Controls over vegetation distribution in Interior Alaska

Tundra in Interior Alaska is largely alpine, and our analysis indicates that its distribution is strongly related to elevation. The location of tundra in the landscape was also dictated by temperature, which was likely the proximate driver for the distribution of tundra. The reason that elevation had a stronger effect than temperature in our analysis was because the underlying resolution of the elevation data set was finer than the climate data sets we used in this analysis. Increasing precipitation and south to north aspect have negative association with tundra, suggesting that alpine tundra is mostly located on dry southern aspects, with forest on northern aspects (Edwards & Armbruster, 1989). This might be explained by moisture limitations for forests on southern exposures (Lloyd & Fastie, 2002) or higher fire incidence on southern slopes due to higher temperatures and lower soil moisture (Bonan & Shugart, 1989).

The distinction between deciduous and spruce forest was almost exclusively driven by fire history. Deciduous trees and shrubs establish first after a severe fire, while spruce requires several decades before it dominates the canopy (Van Wagner, 1983; Viereck, 1983). Model bias towards white spruce caused large areas of observed deciduous forest to be simulated as black spruce. This bias is due to the hierarchical nature of the model where thresholds between vegetation types had to be adjusted so that there were sufficient pixels left at the end of the sequence that could be designated as white spruce. Some of the deciduous forest pixels that the logistic regression model misclassified as spruce might consist of successional deciduous forest that will eventually become spruce. A stand-age variable would have improved deciduous forest prediction but could not be used for the simulations for several reasons.

In spruce communities, black spruce statistically gives way to white spruce as fire interval increases and as elevation increases. Black spruce forests are characterized by higher fire frequency than white spruce forests due to their topographic location and tree structure (Viereck *et al.*, 1986). When the Fleming (1997) vegetation classification was reduced to fewer classes, we assigned black spruce to bottomland spruce forests and northern aspects. In contrast, the timberline in Alaska is primarily composed of white spruce (Lloyd & Fastie, 2002). Slope and S–N aspect are also important drivers that distinguish black and white spruce, where black spruce is associated with gentle slopes and northern aspects. The slope and elevation data sets of our analysis were correlated and thus represent similar environmental locations, as most flat bottomlands (at 1-km resolution) are located at low elevations in Interior Alaska. While the logistic regression model confirmed some of the rules we implemented to separate white and black spruce, it also recognized fire interval as the most important driver between the putative locations of black and white spruce.

Sensitivity of vegetation distribution to changes in climate

Spruce

In our evaluation of the sensitivity of vegetation distribution to scenarios of climate change, black spruce always remains the most dominant vegetation type in Interior Alaska regardless of the scenario. While warming generally improves tree growth in the temperature-limited boreal zone (Grossnickle, 2000), warming-induced soil moisture deficit can reduce the growth of white spruce (Szeicz & MacDonald, 1995; Barber *et al.*, 2000). Climate change predictions for the area above 60° N averaged across several models indicate 3.4 °C annual warming and 11% increase in precipitation, which will take mostly in fall and winter and less so in the summer and varies widely among models (Räisänen, 2001). In comparison, our model only evaluated growing season precipitation. In north-west Canada, climate warming seemed to lead to lower minimum annual river and lake levels, more forest fires and lower yields from softwoods (Lange 2001). Our logistic regression model identifies that decreases in precipitation cause a reduction in white spruce area when accompanied by warming greater than 2 °C. In contrast to white spruce, other forest types continue to expand with warming. Black spruce may be buffered from decreases in precipitation because it tends to grow in poorly drained flat areas and on north slopes. In contrast, from a regional perspective, deciduous forests tend to grow on drier, steeper slopes than spruce forests and our analysis suggests that they have the potential to replace white spruce as the climate warms and dries. The response of white spruce to warming and drying is supported by field observations of white spruce growth at treeline in various regions of Alaska (Lloyd & Fastie, 2002) and on southern slopes in Interior Alaska (Szeicz & MacDonald, 1995; Barber *et al.*, 2000). In simulations by Bonan *et al.* (1990), white spruce could only grow successfully at 1 °C warming, while under the 3 and 5 °C climatic warming none of the tree species currently found in the typical white spruce-hardwood forest uplands of interior Alaska were able to grow due to soil moisture limitations. In northern Manitoba, modelling analyses suggest that net primary productivity (NPP) has increased between 1900 and 1990, while southern Saskatchewan experienced a drastic reduction of woody biomass and a conversion of boreal forest to grassland, which was attributed to temperature-induced moisture stress (Peng & Apps, 1999; Price *et al.*, 1999). Simulations with both the CENTURY model and FORSKA2 indicated that boreal forest vegetation is very sensitive to changes in precipitation (Price *et al.*, 1999). In our simulations, black spruce expanded its range when precipitation decreases because it was able to move into areas currently covered by tundra or white spruce. When precipitation increase is coupled with a 5 °C warming, black spruce replaces tundra areas. However black spruce areas are invaded by white spruce and tundra under increasing precipitation by itself. In contrast, simulations in central Canada's southern boreal zone produce a decline in black spruce with monthly precipitation decrease (Price *et al.*, 1999). This difference between modelled responses of black spruce is likely associated with the presence of permafrost in Interior Alaska, which may better buffer black spruce to a drying climate in comparison with black spruce in the southern boreal zone of Canada.

Tundra

Alpine tundra is the second most dominant vegetation type in Interior Alaska and disappears whenever warming is imposed. This trend is not offset by increasing precipitation, although tundra reaches its largest extent under 30% precipitation increase. This detected relationship between tundra and precipitation could be the result of a spurious correlation between regional vegetation and precipitation patterns. Although it is not yet possible to detect advances in elevational tree-line with 30–79 m resolution Landsat images (Masek, 2001; Silapaswan *et al.*, 2001), shrub invasion into arctic tundra has been noticed on aerial photographs (Sturm *et al.*, 2001) and with 30-m resolution Landsat Thematic Mapper images (Silapaswan *et al.*, 2001). Warming experiments at Toolik Lake, Alaska, have resulted in enhanced shrub production with decreases in non-vascular plants (Chapin *et al.*, 1995). The conversion of tundra to spruce and deciduous forest under a warming climate has been simulated in several studies (Starfield & Chapin, 1996; Rupp *et al.*, 2000b, 2001; White *et al.*, 2000).

Deciduous forest

While the logistic regression approach identifies only a small percentage of the actual deciduous forest in Interior Alaska, our analysis suggests that it is one of the most dynamic vegetation types in response to changes in climate. This vegetation type responds well to warming and low precipitation under separate simulations, where it responds up to five times more strongly to combinations of these change scenarios than to individual changes.

Sensitivity of vegetation distribution to changes in climate and fire interval

Vegetation response to combined scenarios involving changes in precipitation regime potentially include implicit changes in the fire regime. Simulations by Rupp *et al.* (2000a) show that climate warming induced increases in fire frequency and extent, which resulted in more early successional deciduous forest on the landscape at any given time. Bonan *et al.* (1992) concluded from their simulations that the biomass of trembling aspen and paper birch increase with warming, reaching maxima at 5 °C and 60% precipitation increase. Based upon the Hadley CM2 climate scenario, the hypothetical potential vegetation for Interior Alaska in 2100 is mostly black spruce forest with some deciduous forest; however, this simulation does not explicitly account for changes in fire regime.

For no change in climate, our analyses indicate that deciduous forest responds to a decrease in the fire interval by expanding at the expense of white spruce. Deciduous forest is an early successional stage in areas outside active floodplains (Mann *et al.*, 1995), which over time is replaced by either black or white spruce (Van Cleve *et al.*, 1986; Viereck *et al.*, 1986). Clearly, a decrease in recovery time between burns would improve the competitive ability of deciduous forest over spruce in the landscape. Our model simulations confirm that this vegetation type is associated with a shorter fire interval. When warming is accompanied by a decrease in the fire interval, our analyses indicate that deciduous forest generally expands at the expense of black spruce. This result agrees with model analyses for north-west Alaska in which warming led to an increase in the number and size of fires and resulted in a conversion of spruce to deciduous forest (Rupp *et al.*, 2000b). Decreases in precipitation generally cause a decrease in the area of white spruce. When precipitation decrease is accompanied by a decrease in the fire interval, deciduous forest primarily expands into regions vacated by white spruce. In contrast, when precipitation decrease is accompanied by an increase in the fire interval, black spruce expands into regions vacated by white spruce, indicating that white spruce is more moisture limited than black spruce (Barber *et al.*, 2000). It seems unlikely that drier growing seasons would be accompanied by less fires in Alaska; however, when groundwater levels were decreased during the medieval warming period in Alberta, birch was replaced by the less fire-prone aspen leading to an overall decrease in fire frequency (Campbell & Campbell, 2000).

Fire interval is most interactive for responses of black and white spruce for increases in precipitation. For no change in fire interval, increased precipitation causes white spruce and tundra to expand at the expense of black spruce and deciduous forest. However, when precipitation increases are accompanied by changes in the fire interval, white spruce declines substantially, black spruce recovers, and tundra still expands to a lesser degree. Our model simulations indicate that vegetation responds to changes in fire frequency; however, vegetation clearly affects fire regime through flammability and fuel loads (Lynch *et al.*, 2003). While we do not fully understand the mechanisms that might be responsible for this interaction between precipitation increase, change in the fire interval, and vegetation distribution, the result suggests the potential for nonlinear dynamics among climate, fire interval, and vegetation dynamics.

Limitations and next steps

Our logistic regression model simulated potential equilibrium vegetation and does not account for changes in soil properties or the addition of new vegetation types. There are indications that soil moisture limitations in Interior Alaska could potentially lead to the formation of a steppe-like vegetation type (Viereck & Van Cleve, 1984; Rupp *et al.*, 2000a). Warming may also be enhancing large-scale permafrost degradation in the Tanana Flats of Interior Alaska, which has been occurring since the mid-1700s and is currently causing ecosystem conversions from birch forests to fens and bogs (Jorgensen *et al.*, 2001). These changes in the boreal forest can have far-reaching effects on climate through changes in albedo and other surface properties, potentially leading to new feedbacks among vegetation, disturbance and climate (Bonan *et al.*, 1992; Chapin *et al.*, 2000c; Zhao *et al.*, 2001).

Although our model was run at 1-km pixel sizes, its predictive ability is limited by the coarseness of some of the input data, especially fire interval and soil data. While the current model showed drainage as a minor predictive factor, fire interval appeared to be associated with regional variability in vegetation. There is a strong need for higher resolution soil/drainage data for Alaska as there is indication for a relationship between soil drainage and fire regime (Harden *et al.*, 2003). Another issue is that changes in regional climate in Interior Alaska are affecting soil dynamics and therefore indirectly vegetation (Jorgensen *et al.*, 2001). As we are unable to include detailed soil dynamics in the model, we rely on the driving climate data sets for analysis and interpretation of future vegetation composition. This leads to spurious correlations in model results between vegetation types and climate variables. In reality, climate changes indirectly affect vegetation through alterations to soil and fire regimes.

Even greater is the need for a black vs. white spruce validation data set at the regional scale. We have searched extensively for validation data for the black vs. white spruce model step but it simply does not exist. Although the two species have slightly different growth forms, they sometimes mimic each other and it is not possible to distinguish them without a detailed on-the-ground analysis. Therefore, there is no remote sensing-based or otherwise extrapolated large-scale data set available that could be used to validate our 1-km data. Using our expert knowledge in aggregating an existing remote sensing classification as model input seems the best possible way at this point. Despite the circularity of the argument, our model provides interesting insights into black and white spruce dynamics.

While the logistic regression approach has limitations, it has allowed us to evaluate formally the potential controls over vegetation distribution. Our analysis has revealed controls that are consistent with insights that have been gained from studies that have used very different techniques, e.g. dendrochronological techniques (Barber *et al.*, 2000), to study how vegetation responds to spatial and temporal environmental variability in Alaska. We feel that these analyses provide insights into the potential implications of structural and functional responses of ecosystems in Interior Alaska to regional climate change. These insights can be incorporated into regional dynamic vegetation models that may then be used to inform climate models. Logistic regression is a tool that can be effectively used in other high latitude regions to reveal how controls might change with spatial variability in environmental factors, which is an important step in improving mechanistic understanding about controls over the structure and function of high latitude ecosystems throughout the circumboreal region. This improved understanding should promote progress in elucidating the role of high latitude ecosystems in the climate system.

ACKNOWLEDGEMENTS

We would like to thank Matt Macander, Catherine Thompson, Cherie Darnel and Rose Meier for creating some of the input data sets. We are very grateful to Edward Debevec for helping with the statistics. This research was supported by the Department of Environmental Sciences at the University of Virginia and grants through NSF under the ARCSS program (OPP-0095024 and OPP-9908829).

REFERENCES

Agee, J.K. (1993) *Fire ecology of Pacific Northwest forests*. Island Press, Washington, DC.

Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R., Simpson, L.G. & Vinson, T.S. (1993) Boreal forest and tundra. *Water, Air, and Soil Pollution*, **70,** 39–53.

Barber, V.A., Juday, G.P. & Finney, B.P. (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, **405,** 668–673.

Barbour, M.G., Burk, J.H. & Pitts, W.D. (1987) *Terrestrial plant ecology*, 2nd edn. Benjamin/Cummings Publishing, Menlo Park, CA.

Bergeron, Y. & Archambault (1993) Decreasing frequency of forest fires in the southern boreal zone of Quebec and its relation to global warming since the end of the 'Little Ice Age'. *The Holocene*, **3,** 255–259.

Bonan, G.B., Shugart, H.H. (1989) Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*, **20,** 1–28.

Bonan, G.B., Shugert, H.H. & Urban, D.L. (1990) The sensitivity of some high-latitude boreal forests to climatic parameters. *Climatic Change*, **16,** 9–29.

Bonan, G.B., Pollard, D. & Thompson, S.L. (1992) Effects of boreal forest vegetation on global climate. *Nature*, **359,** 716–718.

Briffa, K.R., Jones, P.D., Schweingruber, F.H., Shiyatov, S.G. & Cook, E.R. (1995) Unusual twentieth-century summer warmth in a 1,000-year temperature record from Siberia. *Nature*, **375,** 156–159.

Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G. & Vaganov, E.A. (1998) Reduced-sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature*, **391,** 678–682.

Camill, P. & Clark, J.S. (2000) Long-term perspectives on lagged ecosystem response to climate change: permafrost in boreal peatlands and the grassland/woodland boundary. *Ecosystems*, **3,** 534–544.

Campbell, I.D. & Campbell, C. (2000) Late Holocene vegetation and fire history at the southern boreal forest margin in Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **164,** 279–296.

Carcaillet, C., Bergeron, Y., Richard, P.J.H., Fréchette, B., Gauthier, S. & Prairie, Y.T. (2001) Change in fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? *Journal of Ecology*, **89,** 930–946.

Chapin, F.S., III & Starfield, A.M. (1997) Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change*, **35,** 449–461.

Chapin, F.S., III, Shaver, G.R., Giblin, A.E., Neilson, R.P., Nadelhoffer, K.J. & Laundre, J.A. (1995) Response of arctic tundra to experimental and observed changes in climate. *Ecology*, **76,** 694–711.

Chapin, F.S., III, Eugster, W., McFadden, J.P., Lynch, A.H. & Walker, D.A. (2000a) Summer differences among arctic ecosystems in regional climate forcing. *Journal of Climate*, **13,** 2002–2010.

Chapin, F.S., III, McGuire, A.D., Randerson, J.T., Pielke, R., Sr, Baldocchi, D.D., Hobbie, S.E., Roulet, N.T., Eugster, W., Kasischke, E.S., Rastetter, E.B., Zimov, S.A., Oechel, W.C. & Running, S.W. (2000b) Feedbacks from arctic and boreal ecosystems to climate. *Global Change Biology*, **6,** 211–223.

Chapin, F.S., III, McGuire, A.D., Randerson, J., Pielke, R.A., Sr, Baldocchi, D.D., Hobbie, S.E., Roulet, N.T., Eugster, W., Kasischke, E.S., Rastetter, E.B., Zimov, A. & Running, S.W. (2000c) Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology*, **6,** 211–223.

Cihlar, J., Ly, H. & Xiao, Q. (1996) Land cover classification with AVHRR multichannel composites in northern environments. *Remote Sensing of Environment*, **58,** 36–51.

Davis, M.B. (1989) Lags in vegetation response to greenhouse warming. *Climatic Change*, **15,** 75–82.

Edwards, M.E. & Armbruster, W.S. (1989) A tundra-steppe transition on Kathul Mountain, Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research*, **21,** 296–304.

Epstein, H.E., Walker, M.D., Chapin, F.S. & Starfield, A.M. (2000) A transient, nutrient-based model of arctic plant community response to climatic warming. *Ecological Applications*, **10,** 824–841.

Eugster, W., Rouse, W.R., Pielke, R.A., Sr, McFadden, J.P., Baldocchi, D.D., Kittel, T.G.F., Chapin, F.S., Liston, G.E., Vidale, P.L., Vaganov, E.A. & Chambers, S. (2000) Land-atmosphere energy exchange in Arctic tundra and boreal forest: available data and feedbacks to climate. *Global Change Biology*, **6,** 84–115.

Flannigan, M.D., Bergeron, Y., Engelmark, O. & Wotton, B.M. (1998) Future wildfire in circumboreal forests in relation to global warming. *Journal of Vegetation Science*, **9,** 469–476.

Flannigan, M., Campbell, I., Wotton, M., Carcaillet, C., Richard, P. & Bergeron, Y. (2001) Future fire in Canada's boreal forest: paleoecology results and general circulation model – regional climate model simulations. *Canadian Journal of Forest Research*, **31,** 854–864.

Fleming, M.D. (1997). A statewide vegetation map of Alaska using phenological classification of AVHRR data. *Proceedings of the second circumpolar arctic vegetation mapping workshop and the CAVM-North America workshop* (ed. by D.A. Walker and A.C. Lillie), pp. 25–26. USGS, Anchorage, AK, USA.

Foley, J.A., Kutzbach, J.E., Coe, M.T. & Levis, S. (1994) Feedbacks between climate and boreal forests during the Holocene epoch. *Nature*, **371,** 52–54.

Grossnickle, S.C. (2000) *Ecophysiology of northern spruce species: the performance of planted seedlings*. NRC research Press, Canada.

Harden, J.W., Trumbone, S.E., Stocks, B.J., Hirsch, A., Gower, S.T., O'Neill, K.P. & Kasischke, E.S. (2000) The role of fire in the boreal carbon budget. *Global Change Biology*, **6,** 174–184.

Harden, J.W., Meier, R.A., Darnel, C., Swanson, D.K. & McGuire, A.D. (2003) Soil drainage and its potential for influencing wildfire in Alaska. *Studies by the US Geological Survey in Alaska, 2001* (ed. by J.P. Galloway). US Geological Survey Professional Paper 1678. USGS, Menlo Park, CA, USA.

Hilbert, D.W. & Ostendorf, B. (2001) The utility of artificial neural networks for modelling the distribution of vegetation in past, present and future climates. *Ecological Modelling*, **146,** 311–327.

Hosmer, D.W. & Lemeshow, S. (2000) *Applied logistic regression*, 2nd edn. John Wiley & Sons, New York, NY.

Houghton, J.T., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg, A. & Maskell, K. (eds) (1995) *Climate change 1995: the science of climate change*. Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK.

Jalkanen, A. & Mattila, U. (2000) Logistic regression models for wind and snow damage in northern Finland based on the National Forest Inventory data. *Forest Ecology and Management*, **135,** 315–330.

Johns, T.C., Carnell, R.E., Crossely, J.F., Gregory, J.M., Michell, J.F.B., Senior, C.A., Tett, S.F.B. & Wood, R.A. (1997) The second Hadley Centre coupled ocean-atmosphere GCM: spinup and validation. *Climate Dynamics*, **13,** 103–134.

Johnson, E.A. (1994) Fire frequency models, methods and interpretations. *Advances in Ecological Research*, **25,** 239–287.

Jorgensen, M.T., Racine, C.H., Walters, J.C. & Osterkamp, T.E. (2001) Permafrost degradation and ecological changes associated with a warming climate in Central Alaska. *Climatic Change*, **48,** 551–579.

Källén, E., Kattsov V., Walsh J. & Weatherhead E. (2001) *Report from the arctic climate impact assessment modeling and scenarios workshop*. Arctic Climate Impact Assessment Secretariat, Fairbanks, AK.

Keyser, A.R., Kimball, J.S., Nemani, R.R. & Running, S.W. (2000) Simulating the effects of climate change on the carbon balance of North America high-latitude forests. *Global Change Biology*, **6,** 185–195.

Kirilenko, A.P. & Solomon, A.M. (1998) Modeling dynamic vegetation response to rapid climate change using bioclimatic classification. *Climatic Change*, **38,** 15–49.

Lange, M.A. (2001) *Regional climate impact studies in the Arctic. Report from the Arctic climate impact assessment modelling and scenarios workshop* (ed. by E. Källén, U. Kattsov, J. Walsh, E. Weatherhead). Arctic Climate Impact Assessment Secretariat, Fairbanks, AK.

Lloyd, A.H. & Fastie, C.L. (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, **52,** 481–509.

Lloyd, A.H., Rupp, T.S., Fastie, C.L. & Starfield, A.M. (2003) Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska. *Journal of Geophysical Research*, **108**(D2), 8161, doi: 10.1029/2001JD000852.

Lynch, J.A., Clark, J.S., Bigelow, N.H., Edwards, M.E. & Finney, B.P. (2003) Geographic and temporal variations in fire history in boreal ecosystems of Alaska. *Journal of Geophysical Research*, **108,** FFR 8.

Mann, D.H., Fastie, C.L., Rowland, E.L. & Bigelow, N.H. (1995) Spruce succession, disturbance, and geomorphology on the Tanana River floodplain, Alaska. *Ecoscience*, **2,** 184–199.

Mann, M.E., Bradley, R.S. & Hughes, M.K. (1998) Global scale temperature patterns and climate forcing over the past six centuries. *Nature*, **392,** 779–787.

Masek, J.G. (2001) Stability of boreal forest stands during recent climate change: evidence from Landsat satellite imagery. *Journal of Biogeography*, **28,** 967–976.

McFadden, J.P., Chapin, F.S., III & Hollinger, D.Y. (1998) Subgrid-scale variability in the surface energy balance of arctic tundra. *Journal of Geophysical Research*, **103,** 28, 947–961.

McGuire, A.D. & Hobbie, J.E. (1997) Global climate change and the equilibrium responses of carbon storage in arctic and subarctic regions. *Modeling the Arctic System: a workshop report of the Arctic System Science Program* (ed. by Arctic Research Consortium of the US), pp. 53–54. Arctic Research Consortium of the United States, Fairbanks, AK.

McGuire, A.D., Melillo, J.M., Kicklighter, D.W. & Joyce, L.A. (1995) Equilibrium responses of soil carbon to climate change: empirical and process-based estimates. *Journal of Biogeography*, **22,** 785–796.

McGuire, A.D., Melillo, J.M., Randerson, J.T., Parton, W.J., Heimann, M., Meier, R.A., Clein, J.S., Kicklighter, D.W. & Sauf, W. (2000a) Modeling the effects of snowpack on heterotrophic respiration across northern temperate and high latitude regions: comparison with measurements of atmospheric carbon dioxide in high latitudes. *Biogeochemistry*, **48,** 91–114.

McGuire, A.D., Clein, J.S., Melillo, J.M., Kicklighter, D.W., Meier, R.A. & Serreze, M.C. (2000b) Modeling carbon responses of tundra ecosystems to historical and projected climate: the sensitivity of pan-arctic carbon storage to temporal and spatial variation in climate. *Global Change Biology*, **6,** 141–159.

McGuire, A.D., Wirth, C., Apps, M.J., Beringer, J., Clein, J.S., Epstein, H.E., Kicklighter, D.W., Bhatti, J., Chapin, F.S., III, de Groot, B., Efremov, D., Eugster, W., Fukuda, M., Gower, T., Hinzman, L.D., Huntley, B., Jia, G.J., Kasischke, E.S., Melillo, J.M., Romanovsky, V.E., Shvidenko, A., Vaganov, E.A. & Walker, D.A. (2002) Environmental variation, vegetation distribution, carbon dynamics, and water/energy exchange in high latitudes. *Journal of Vegetation Science*, **13,** 301–314.

Melillo, J.M., Kicklighter, D.W., McGuire, A.D., Peterjohn, W.T. & Newkirk, K.M. (1995) Global change and its effects on soil organic carbon stocks. *Role of nonliving organic matter in the Earth's carbon cycle* (ed. by R.G. Zepp and C. Sonntag), pp. 175–189. John Wiley & Sons, New York, NY.

Murphy, P.J., Mudd, J.P., Stocks, B.J., Kasischke, E.S., Barry, D., Alexander, M.E. & French, N.H.F. (2000) Historical fire records in boreal forest. *Fire, climate change, and carbon cycling in the boreal forest* (ed. by E.S. Kasischke and B.J. Stocks), pp. 274–288. Springer-Verlag, New York, NY.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R. (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386,** 698–702.

New, M., Hulme, M. & Jones, P. (1999) Representing twentieth-century space-time climate variability. Part I: development of a 1961–90 mean monthly terrestrial climatology. *Journal of Climate*, **12,** 829–856.

Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133,** 225–245.

Peng, C. & Apps, M.J. (1999) Modelling the response of net primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. *Ecological Modelling*, **122,** 175–193.

Ping, C.L., Michaelson, G.J. & Kimble, J.M. (1997) Carbon storage along a latitudinal transect in Alaska. *Nutrient Cycling in Agroecosystems*, **49,** 235–243.

Post, W.M., Emanuel, W.R., Zinke, P.J. & Stangenberger, A.G. (1982) Carbon pools and world life zones. *Nature*, **298,** 156–159.

Price, D.T., Halliwell, D.H., Apps, M.J. & Peng, C.H. (1999) Adapting a patch model to simulate the sensitivity of Central-Canadian boreal ecosystems to climate variability. *Journal of Biogeography*, **26,** 1101–1113.

Räisänen, J. (2001) Intercomparison of 19 global climate change simulations from an Arctic perspective. *Report from the Arctic Climate Impact Assessment Modeling and Scenarios Workshop* (ed. by E.V. Källén, V. Kattsov, J. Walsh and E. Weatherhead), pp. 11–13, Arctic Climate Impact Assessment Secretariat, Fairbanks, AK.

Romme, W.H. (1980) Fire history terminology: report of the ad hoc committee. *Proceedings of the Fire History Workshop* (ed. by M.A. Stokes and J.H. Dieterich), pp. 135–137. USDA Forest Service General Technical Report RM-81. Fort Collins, CO.

Rupp, T.S., Chapin, F.S. & Starfield, A.M. (2000a) Response of subarctic vegetation to transient climatic change on the Seward Peninsula of north-west Alaska. *Global Change Biology*, **3,** 541–555.

Rupp, T.S., Starfield, A.M. & Chapin, F.S. (2000b) A frame-based spatially explicit model of subarctic vegetation response to climatic change: comparison with a point model. *Landscape Ecology*, **15,** 383–400.

Rupp, T.S., Chapin, F.S. & Starfield, A.M. (2001) Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in northwestern Alaska. *Climatic Change*, **48,** 399–416.

Serreze, M.C., Chapin, F.S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W.C., Morison, J., Zhang, T. & Barry, R.G. (2000) Observational evidence of recent change in the northern high-latitude environment. *Climatic Change*, **46,** 159–207.

Shaver, G.R., Canadell, J., Chapin, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L. &

Rustad, L. (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience*, **50,** 871–882.

Silapaswan, C.S., Verbyla, D.L. & McGuire, A.D. (2001) Land cover change on the Seward Peninsula: the use of remote sensing to evaluate the potential influences of climate warming on historical vegetation dynamics. *Canadian Journal of Remote Sensing*, **27,** 542–554.

Smith, T.M. & Shugart, H.H. (1993) The transient response of terrestrial carbon storage to a perturbed climate. *Nature*, **361,** 523–526.

Starfield, A.M. & Chapin, F.S. (1996) Model of transient changes in arctic and boreal vegetation in response to climate and land use change. *Ecological Applications*, **6,** 842–864.

Stocks, B.J., Fosberg, M.A., Lynham, T.J., Mearns, L., Wotton, B.M., Yang, Q., Jin, J.-Z., Lawrence, K., Hartley, G.R., Mason, J.A. & McKenney, D.W. (1998) Climate change and forest fire potential in Russia and Canadian boreal forest. *Climatic Change*, **38,** 1–13.

Sturm, M., Racine, C. & Tape, K. (2001) Increasing shrub abundance in the Arctic. *Nature*, **411,** 546–547.

Szeicz, J.M. & MacDonald, G.M. (1995) Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. *Journal of Ecology*, **83,** 873–885.

Thomas, G. & Rowntree, P.R. (1992) The boreal forests and climate. *Quarterly Journal of the Royal Meteorological Society*, **118,** 469–497.

Turetsky, M.R., Wieder, R.K. & Vitt, D.H. (2002) Boreal peatland C fluxes under varying permafrost regimes. *Soil Biology and Biochemistry*, **34,** 907–912.

Vaganov, E.A., Hughes, M.K., Kirdyanov, A.V., Schweingruber, F.H. & Silkin, P.P. (1999) Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, **400,** 149–151.

Van Cleve, K., Chapin, F.S., Flanagan, P.W., Viereck, L.A. & Dyrness, C.T. (1986) *Forest ecosystems in the Alaskan taiga*. Springer-Verlag, New York, NY.

Van Wagner, C.E. (1983) Fire behaviour in northern conifer forests and shrublands. *The role of fire in northern circumpolar ecosystems* (ed. by R.W. Wein and D.A. MacLean), pp. 65–80. John Wiley & Sons, New York, NY.

Viereck, L.A. (1983) The effects of fire in black spruce ecosystems of Alaska and northern Canada. *The role of fire in northern circumpolar ecosystems* (ed. by R.W. Wein and D.A. MacLean), pp. 201–220. John Wiley & Sons, New York, NY.

Viereck, L.A. & Van Cleve, K. (1984) Some aspects of vegetation and temperature relationships in the Alaska taiga. *The potential effects of carbon dioxide-induced climatic changes in Alaska* (ed. by J.H. McBeath), pp. 129–142. University of Alaska, Fairbanks, AK.

Viereck, L.A., Van Cleve, K. & Dyrness, C.T. (1986) Forest ecosystem distribution in the taiga in interior Alaska. *Forest ecosystems in the Alaskan taiga* (ed. by K. Van Cleve, F.S. Chapin, P.W. Flanagan, L.A. Viereck and C.T. Dyrness), pp. 22–43. Springer-Verlag, New York, NY.

Viereck, L.A., Dyrness C.T., Batten A.R. & Wenzlick K.J. (1992) *The Alaska vegetation classification*. USDA Forest Service PNW GTR 286. Portland, OR, USA.

White, A., Cannell, M.G.R. & Friend, A.D. (2000) A high-latitude terrestrial carbon sink: a model analysis. *Global Change Biology*, **6,** 227–245.

Yu, Z., Campbell, I.D., Vitt, D.H. & Apps, M.J. (2001) Modelling long-term peatland dynamics. I. Concepts, review, and proposed design. *Ecological Modelling*, **145,** 197–210.

Zhao, M., Pitman, A.J. & Chase, T. (2001) The impact of land cover change on the atmospheric circulation. *Climate Dynamics*, **17,** 467–477.

Zhou, L., Tucker, C.J., Kaufman, R.K., Slayback, D., Shabanov, N.V. & Myneni, R.B. (2001) Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research-Atmospheres*, **106,** 20,069–20,083.

BIOSKETCHES

Monika Calef is interested in vegetation dynamics in the boreal forest of Alaska. This includes vegetation patterns due to topography, succession, and fire and responses to high latitude climate change.

David McGuire works on the role of terrestrial biological processes in the function of the earth system, with a primary focus on the role of biological processes in high latitude terrestrial ecosystems.

Howard Epstein's research focuses on plant ecology of arctic tundra of North America, savannas and grasslands of southern Africa, and successional fields of the Virginia Piedmont.

Scott Rupp's interests are in ecosystem and landscape ecology, emphasizing secondary succession, regeneration, and disturbance dynamics in subarctic and boreal forests.

Herman Shugart is a systems ecologist whose primary research interests focus on the simulation modelling of forest ecosystems, including biogeochemical cycles, energy flow, secondary succession, growth, birth and death of trees.

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