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EFFECTS OF DISTURBANCE ON ECOSYSTEM DYNAMICS
OF TUNDRA AND RIPARIAN VEGETATION:
A PROJECT IN THE R4D PROGRAM

Submitted by

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1 Introduction

A synthesis and integration of data gathered at the Imnavait Creek catchment in the form of up-to-date simulation models was one of the major goals of the Department of Energy-sponsored R4D program. Models were proposed as research tools to test our basic understanding of the structure and function of arctic ecosystems, as a means for providing initial management assessments of potential response to energy-related development, and as a vehicle for extrapolation of research results to other arctic sites and landscapes. Similar desires for the use of models as natural resource management tools have been expressed in ecosystem science for over 20 years. While significant progress has been made, much work is still required before truly integrated models will be able to effectively summarize and illustrate the complex interactions affecting physical-biological-social systems, particularly within a management framework. In this final summary report, I review progress made on models at a variety of scales, e.g., from nutrient uptake by individual roots to nutrient availability within arctic landscapes, and examine potentials and critical limitations of these models for providing insight on patch and landscape level function in tundra regions.

2 Process Models

2.1 Ecosystem gas exchange

Considerable effort has been devoted to the examination of ecosystem carbon dioxide exchange in tundra regions, beginning with investigations near Barrow, Alaska during the IBP. In spite of this, a general concept to explain the variation in observed flux rates based on physical and biological control mechanisms has been lacking. Phil Miller attempted to integrate information on microclimate, species composition, spatial structure, and gas exchange in ARTUS, but their approach was highly empirical and hence limited with respect to modeling the effects of disturbance on ecosystems. We developed the GAS-FLUX model to provide a mechanistic framework for integrating knowledge of tundra gas exchange (Reynolds *et al.* 1995). Our ultimate objective was to link this simulator with models of plant growth and nutrient availability in order to examine ecosystem dynamics under a wide range of conditions, including disturbance and climate change.

GAS-FLUX considers the gas exchange and the microclimate of three types of landscape patches or vegetation types in the Imnavait Creek watershed: moist Cassiope dwarf shrub (CDS) heath (upper slopes), tussock tundra (midslopes), and riparian (lower slopes). Each patch is considered to be homogeneous, but composed of a mixture of vascular and non-vascular (primarily Sphagnum mosses) plants. The vascular plant canopy is divided into a series of

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layers each containing leaf and stem material for one of three functional groups with a defined physiological response: deciduous shrubs, graminoids, and evergreen shrubs. Light interception by both stems and leaves is considered. Deciduous shrubs and graminoids occur in significant quantities in all three vegetation types, with their lowest leaf area index (LAI) in tussock tundra and highest LAI in the riparian meadows. Stem area index (SAI) of the deciduous shrubs plays an important role in light interception in all three vegetation types; evergreen shrubs are equally present in the upper and mid-slope locations but disappear in riparian sites. Light incident on the understory moss vegetation is computed as the light leaving the lowest layer of the vascular plant canopy. Sunlit and shaded leaf area is calculated for each canopy layer as well as sunlit and shaded portions of the ground surface. Leaf level photosynthesis for the vascular plants is described with the Farquhar equations, which are based on ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) kinetics as mediated by (1) the concentrations of competing gaseous substrates, CO₂ and O₂, and (2) the ratio of ribulose-1,5-bisphosphate (RuBP) concentration to enzyme active sites. CO₂ assimilation is linked to an empirical stomatal conductance model. Average hourly gas exchange rates for each canopy layer (vascular plants) and ground area (mosses) are obtained by weighting the sunlit and shaded area fluxes. Poikilohydric plants such as Sphagnum exhibit a dynamic response to slow changes in water content during the summer season, which presents added difficulties; we derived the parameters for the Farquhar model based on extensive measurements of CO₂ gas exchange over a range of water contents (Tenhunen et al. 1992, 1994).

Ecosystem efflux of CO₂ from tundra communities with deep organic soils varies primarily in response to changes in the depth to water table and/or soil moisture and temperature. Soil respiratory flux is determined using regression equations (Oberbauer et al. 1991). Net ecosystem gas exchange is computed by the balance of CO₂ flux rates from the aboveground (leaf, stem, moss) and soil components of the model. With GAS-FLUX, we are able to elucidate various abiotic and biotic interactions that contribute to ecosystem gas exchange. For example, the integrated daily CO₂ flux in tussock tundra on a clear day is 20 $\mu\text{mol m}^{-2}$ vs. -20 $\mu\text{mol m}^{-2}$ if the day is overcast, where the individual contributions of each system component can be quantified. Reynolds et al. (1995) used GAS-FLUX to examine the effect of similar short-term changes in microclimate vs. the effects of longer-term changes in seasonal soil moisture and in phenology. Since seasonal increases in mean soil temperature are small, the primary effect of temperature is seen in diurnal changes in CO₂ efflux. The balance between carbon fixation as influenced by phenology, LAI development, and radiation input and CO₂ efflux as determined by water table depth and soil aeration establishes tundra as either a source or sink for CO₂.

GAS-FLUX could be significantly improved with additional field data, including stem respiration, gas exchange of entire moss cushions, and whole-system gas exchange under a variety of conditions. Further work on lichen and ridgetop heath sites are needed to better represent these important arctic vegetation types in the model. Coupling of the abiotic-biotic interactions at the patch scale in GAS-FLUX presently occurs via water table fluctuations, which directly influences soil aeration, soil respiration, and thus carbon balance. While we do consider seasonal changes in phenology and LAI, interannual variations in environmental conditions that might alter these parameters and, ultimately, the magnitude of carbon dioxide uptake are not. As we continue to improve this model, our capability to better understand and predict the response of tundra ecosystems to climate change will also improve.

2.2 Plant Growth

As an initial step in developing a general framework for modeling arctic plant growth and development, we concentrated efforts on a single, ecologically important species, Eriophorum vaginatum. We selected E. vaginatum because it is widely distributed throughout arctic regions of the world, its tussock-forming habit affects ecosystem processes like soil nutrient cycling and

microclimate, and it is one of the principal invaders of disturbed areas. Consequently, a large amount of experimental data on its growth and physiology exists, perhaps more than for any other arctic species.

A complete description of the model, including validation and behavior, is given in Leadley and Reynolds (1992) and Reynolds and Leadley (1992). It utilizes a mechanistic framework and includes the effects of light, temperature, season length, nitrogen availability, and CO₂ concentration on growth dynamics. The temporal resolution is one year. Physiological activity is restricted to the arctic summer, defined as the time between spring snowmelt (late May) and before freezing of the soil (mid-September) in Imnavait Creek watershed. Carbon (C) and nitrogen (N) are divided into overwinter labile and structural components, where overwinter structure is the sum of overwinter leaf, root, plus other plant structures, e.g., stem, leaf sheath, and reproductive organs. Parameterization was based on physiological data from individual plants and by fitting observed, short-term responses of Eriophorum to nutrient additions. Validation was done with independent datasets of short-term Eriophorum response to increased temperature and shading, and the interaction of these with fertilization and to elevated CO₂ and temperature.

We used this model to examine the effects of simultaneous changes in temperature, season length, atmospheric CO₂ concentration, and N availability on biomass in E. vaginatum. Temperature, season length, and atmospheric CO₂ were found to have substantial effects on E. vaginatum but only indirectly through long-term changes in N availability (Leadley and Reynolds 1992). Simulated peak biomass responds linearly up to a doubling of current N levels; above this the relationship flattens out rapidly because the plant becomes limited by C. This emphasizes the importance of being able to describe any natural or anthropogenic effect on N cycling in tundra ecosystems.

Unforeseen competitive effects and other changes in the ecosystem that occur outside of expectation could, of course, make these predictions moot. Thermal erosion, loss of permafrost, and invasion of tussock tundra by shrubs or trees are examples of changes that may occur in a warmer climate or as a result of disturbance, but that are not considered. Another limitation of the model is its annual resolution, which limits the extent to which within-season variability may be examined. We have begun to compare the response of the annual model with a version of the model using a daily resolution (described in Reynolds and Leadley 1992). We hope in this way to determine the degree of potential error that is introduced by coarse time scaling. Another limitation is the lack of long-term validation data for disturbances, many of which may be expected to alter nutrient availability. In particular, there is not enough evidence from short-term experiments to exclude the possibility that other nutrients might become more limiting than nitrogen over the long-term.

Long-term studies will be crucial for resolving how nutrients and other environmental factors affect the productivity of E. vaginatum and other major tundra species. Short-term experiments and simulations miss many of the responses that are important in determining the ultimate consequence of disturbances and, therefore, great care should be used in extrapolating short-term responses over long periods. For example, elevated CO₂ will increase E. vaginatum photosynthesis in the short-term, but not the long-term; high nutrient availability does not affect root:leaf ratios in the short-term, but does in the long-term; mortality and senescence are poorly correlated with C and N status in the short-term, but are correlated in the long-term; and simulated productivity is highly dependent on season length in the short-term but independent of season length in the long-term. Models that are based on mechanism and designed for long-term simulations provide a basis for reconciling the apparent discrepancies between many short- and long-term responses to disturbance.

Our growth model (and experimental evidence) indicates that N availability is the factor that ultimately limits E. vaginatum productivity under a wide range of conditions. Some researchers have found that relative differences in photosynthetic rates, nutrient uptake, etc., between tundra species were not good predictors of whole-plant productivity. They suggested several mechanisms that have received little attention as potential regulators of the response of tussock tundra vegetation to increased nutrient availability: 1) plant allocation patterns, 2)

mortality of plant parts, and 3) controls on shoot density. Our model suggests that these are the principal mechanisms of response to nutrients. Increased productivity in response to N addition is caused by changes in allocation patterns and increases in overwinter biomass mediated by losses. These results are important in the context of future modeling efforts for other major tundra species.

2.3 Nitrogen Uptake

Nitrogen is one of the most important constraints on vascular plant productivity in tussock tundra. Tussock tundra occurs together with highly organic soils. Since external N inputs are very low, almost all of the N comes from the breakdown of organic compounds or from free living N-fixers. In addition, soil solution concentrations of NH_4^+ and NO_3^- in tussock tundra are far lower than those in agricultural systems. Therefore, factors regulating the uptake of nutrients by arctic plants may be very different from those that regulate nutrient uptake in mineral soils.

Given the importance of N dynamics in arctic ecosystems, we developed a mechanistic model to simulate N uptake by roots. The model, described in detail by Leadley *et al.* (1995), is again based on data from *E. vaginatum*. This sedge serves again (see also section 3.2.1) as an ideal model system because it has simple root morphology (e.g., unbranched cylinders without root hairs) and simple root demography (e.g., most roots are < 100 days old) It experiences low competition (comprises 80 - 100% of above- and belowground vascular biomass in tussocks; and it has no mycorrhizae. All of these characteristics simplify the task of developing a realistic model.

There is an unresolved debate concerning factors that regulate nutrient uptake by vegetation in terrestrial ecosystems. Plant physiologists and ecologists tend to emphasize the importance of root uptake kinetics and soil solution concentrations of nutrients. Many plant growth modelers have also explicitly or implicitly emphasized the importance of nutrient concentrations in regulating nutrient uptake. Others have argued that the supply rate of many soil nutrients is far more important than concentrations in determining total nutrient uptake. Simulation models of agricultural systems have emphasized soil factors and root morphology. However, there are no published studies that distinguish between these possible controls over uptake by natural vegetation in the field.

The root system of a plant is envisioned as a set of roots growing parallel to each other down into a soil cylinder that is divided into numerous concentric sub-cylinders. The model is conceptually similar to various nutrient flux models but has several technical differences (i.e., the use of a physical model of diffusion and discrete approximations of growth and uptake curves *vs.* analytical integration using splined fits) and includes a supply term for the addition or loss of nutrients by microbial activity (mineralization, immobilization, nitrification, etc.). The model was parameterized using field measurements of the properties of tussock tundra soils and field and laboratory measurements of *E. vaginatum* root uptake kinetics (details provided in Leadley *et al.* 1995). The model accounts for the supply, soil flux, and uptake of NH_4^+ , NO_3^- , and glycine by *E. vaginatum*. It can be used to examine factors likely to regulate the uptake from each of these sources of N and to estimate the relative contributions of each source to the overall N nutrition of this species.

The development and application of this model resulted in new perspectives concerning N uptake by plants that differ from conventional wisdom in several important ways: (1) calculations of N uptake based on soil solution concentrations and root uptake kinetics may have relatively large errors associated with them; (2) low soil solution concentrations of N do not necessarily indicate low supply or uptake; and (3) conclusions drawn from simulations of nutrient uptake in relatively fertile mineral soils cannot be extrapolated to poorly buffered, infertile soils. Using this model we found that soil solution concentrations of N and root uptake kinetics are not reliable predictors of N uptake in *E. vaginatum* in poorly buffered soils, where

root uptake kinetics and soil solution concentrations are inverse covariates (as root uptake capacity declines the soil solution concentration increases). Therefore, measurements of soil solution concentration and uptake kinetics that are not made at the same time or location will not account for this natural covariance. This is a particularly acute problem in tussock tundra because soil solution concentrations of NH_4^+ and NO_3^- vary dramatically over time and space. An additional problem is that the nutrient concentration in the bulk soil does not necessarily reflect the nutrient concentration at the root surface. Soil factors play an important role determining the relationship between bulk soil concentrations and concentrations at the root surface in these soils.

Based on an extensive set of simulations, we concluded that: (1) ammonium, glycine, and nitrate all probably make significant contributions to the N nutrition of *E. vaginatum*; (2) while the relative contribution of glycine is difficult to assess, it probably contributes in roughly equal proportions to ammonium; (3) the supply rate is the only factor that regulates nitrate uptake; and (4) the importance of factors that regulate ammonium and glycine uptake can be ranked as supply rate > (soil factors = root density) > uptake kinetics. Consequently, root uptake kinetics are not reliable predictors of whole-plant uptake in tundra (and other natural ecosystems where plant growth is N-limited) and the effects of plant species on nutrient cycling may depend at least as much on their effects on nutrient supply as on uptake. This conclusion, based on detail process-level mechanism, was used to simplify our growth model and to develop a simplified nutrient availability model for use at the landscape scale.

2.4 Decomposition

The uncertainties of interactions, combined with the dynamic nature of arctic soils, make it difficult to predict patterns of nutrient availability, especially so with regard to potential effects of disturbance. While not a substitute for data, mathematical models can aid in understanding the nature and behavior of such complex dynamics. Thus, we developed a general model to examine interactions between decaying litter, decomposer microorganisms, and C and N soil pools. Our approach was aimed to explore the mechanisms underlying observed patterns of decomposition using a model that balances simplicity with enough detail to suggest the reasons for system behavior.

Our model, GENDEC (Moorhead and Reynolds 1993) considers the effects of soil moisture, soil temperature, and season length on pools of carbon and nitrogen including labile plant compounds, holocellulose (cellulose + hemicellulose), resistant plant compounds (e.g., lignins), dead and live microbial mass, mineral N, and CO_2 . Nitrogen is assumed to balance carbon flows and the effect of N-limitation is determined by comparing available N to the amount required for maximum potential decay of a carbon pool based on temperature, moisture, and decay rate coefficient; actual decay of N-limited substrates is reduced in proportion to any existing deficit. Conversely, net N mineralization occurs when the quantities of N released from decomposition exceed microbial demands. The total quantities of carbon and N available for microbial use consist of the sum of all losses from the dead organic matter pools; available N includes mineral forms. Microbial growth and respiration are driven by C availability, i.e., total losses from C substrates given fixed assimilation efficiencies. Microbial turnover includes a fraction of the standing biomass, a portion of incremental growth, and a fraction of the standing biomass killed by wetting-drying events.

We used GENDEC to explore potential interactions of soil temperatures, season length, and soil moisture regimes on C and N dynamics of a tussock tundra soil, i.e., mineralization and immobilization independent of plant activities. In field situations, plants compete for N released during decomposition. In our simulations with the *E. vaginatum* growth model (Leadley & Reynolds 1992), we found that $9\text{--}18 \text{ g N m}^{-2} \text{ yr}^{-1}$ (within tussocks) was needed to obtain reasonable results, which converts to about $1.8\text{--}7.2 \text{ g N m}^{-2} \text{ yr}^{-1}$ at Imnavait Creek, where 20–40% of the soil surface is covered with tussocks. In comparison, other researchers have estimated that tussock tundra vegetation at the nearby Sagavanirktok River requires about 350

mg N m⁻² yr⁻¹ to realize aboveground production. If belowground production requires twice this amount, as much as 1.15 g N m⁻² yr⁻¹ could be needed to meet total plant demand. Some of the reported annual net N mineralization rates appear too small to support observed plant growth, although some species may also obtain amino acids directly from soil solution. Simulations under various climate change scenarios results suggest that there will be much variability compared to current levels depending on the rates and directions of changes in soil moisture and air temperature. Although data are limited, current levels of soil moisture appear close to optimum for decomposition, which indicates that any net changes in soil moisture may decrease C mineralization. More detailed soil profile descriptions and soil climate data are necessary to more accurately characterize both temporal patterns and net change in decomposition and nutrient dynamics in these systems.

3 Landscape Models

3.1 Hydrologic Transport

The strong relationship between water and plant structure/function in the Arctic is well known. Is there a predictive relation between soil water and vegetation type at Imnavait Creek, or between soil water and nutrient availability? These questions and others led to the development of simple hydrology models that could estimate soil water status for any pixel in the watershed.

We developed T-HYDRO, a spatially-explicit watershed model that utilizes a raster-based geographic information system (GIS) to generate a 2-dimensional water flow field for the Imnavait Creek watershed. Details are given in Ostendorf and Reynolds (1993). The watershed is subdivided into a grid of 10 x 10 m pixels and, for each pixel, we compute the total discharge (volume of water) leaving a pixel per year based on the difference between runoff, precipitation and evapotranspiration (units of m³ H₂O pixel⁻¹ y⁻¹). The centers of the pixels are connected by a network of nodes or "pipes" of equal diameter filled with soil; the elevational difference between pixels is the gravitational potential between nodes. Darcy's law is used to estimate the relative discharge through the connections and, ultimately, its routing through the landscape. The result is a "drainage area" map that shows the total upslope area that "drains" into a given pixel.

Ostendorf and Reynolds (1993) compared the predictions of T-HYDRO with a normalized difference vegetation index (NDVI) derived from a SPOT satellite image. NDVI is the difference between the infrared and red bands divided by the sum of the two spectral bands and is linearly related to the amount of photosynthetically active radiation (PAR) intercepted by vegetation. NDVI may provide an indirect measure of net primary productivity (NPP) since there is a close relationship between integrated intercepted PAR and NPP in many types of vegetation and is related to NPP on a biome scale. Comparing the drainage area map with the NDVI map using regression analysis, we were able to account for ca. 43% of the spatial variance in NDVI.

3.2 Topographically-derived Vegetation Classification Model (TVM)

As discussed above, we hypothesized that the general pattern of arctic vegetation might be explained by topographically-derived variables related to soil water. Based on a number of assumptions we developed several "topographically-derived" models, so-named since the only input variables are topographically-derived, i.e., discharge and/or slope. Topographically-derived models of moisture and nutrient availabilities and plant growth are described in Leadley et al. (1995). I describe a vegetation classification model below.

Ostendorf and Reynolds (1995) describe a topographically-derived model for vegetation classification (TVM) based on the relationships between slope (tan β), discharge (d), and plant community types. The objective is to predict plant community types at a particular location (pixel) based solely as a function of topographically-derived surrogates of soil moisture. Slope

determines the gravitational hydrological gradient and hence influences flow velocity; slope angle is inverse related to soil moisture. Discharge is estimated by either T-HYDRO. The (X,Y) coordinates corresponding to 21,250 10 m² pixels for the slope, discharge, and vegetation maps in the watershed were systematically scanned to determine the frequency of occurrence of each of six different community types associated with particular slope and discharge. The community type most closely associated with each slope and discharge was determined by either randomly selecting a community type based on relative frequencies or by selecting the community type with the highest frequency of occurrence; the latter approach gave slightly better results (see Ostendorf and Reynolds 1995 for details of the search algorithms, models and spatial error analysis).

We used five vegetation types: (1) heath (dry vegetation types), (2) tussock tundra (moist types), (3) riparian (wet types); (4) water and aquatic vegetation; and (5) barren/partially vegetated types. The first three types account for more than 95% of the vegetation in the Imnavait Creek and adjacent watersheds. The model was developed and parameterized using vegetation data from the Imnavait Creek watershed, an area equal to about 10% of the R4D region. It was then applied to the total R4D region (202,436 pixels) as a test of its validity.

The TVM model gives excellent predictions of the total percentage of the R4D region covered by each of the six vegetation types. In terms of spatial accuracy, the strength of the predictions is ca. 60%. While the general patterns of the major community types are reproduced, the absence of certain features in the Imnavait Creek watershed that occur in the larger R4D region, e.g., lakes and certain slope/discharge gradients, contribute to inaccuracies. TVM was inspired by the "hydroecological approach" of Molenaar, who distinguishes between operational and conditional functionality of environmental factors. Water is operational in the same sense that it serves as a "nutrient." In addition to this "direct, causal effect" of water, Molenaar lists several possible conditional or "physiological non-causal" functions, namely, water as a solvent for nutrients, as a factor regarding aeration, redox conditions and acidity, phosphorous supply, metal ion availability, humus formation and breakdown, and nutrient cycling and soil formation. These factors are especially important for arctic ecosystems. They co-vary via long-term interactions of vegetation and soil as controlled by hydrological processes, which in turn feed back to soil and vegetation. It appears impossible to separate such multiple factor interactions. By quantifying slope and discharge gradients in the TVM model, we lump a suite of conditional interrelated factors. Tan β and ∂ are continuous gradients and, as such, they serve as integrators of complex and long-term feedbacks between vegetation and the environment.

3.3 Topographically-derived T-MAP (Terrain Models for Arctic Processes)

Here I will briefly describe T-MAP (Terrain Models for Arctic Processes), a set of spatially-explicit landscape models for examining the effects of road construction on tundra ecosystems. T-MAP was motivated by the R4D goal of predicting the potential effects of energy-related development on ecosystems of the North Slope of Alaska. T-MAP predicts landscape patterns for water discharge, nitrogen (N) availability, vegetation type, plant biomass, and net primary productivity within the Imnavait Creek watershed. In Leadley et al. (1995) we present T-MAP and show comparisons of simulated ecosystem properties with a vegetation index determined from satellite measurements of spectral reflectance. We used T-MAP to explore the ecosystem consequences of several scenarios for hypothetical road construction through the Imnavait Creek watershed including (1) the obstruction of natural water drainage and (2) the deposition of dust originating from high-speed vehicle traffic. We focused on road-related disturbance because the Dalton Highway that serves the trans-Alaskan pipeline is one of the most prominent energy-related ecosystem disturbances in the foothills of the Brooks Mountain Range. Gravel roads built to support energy exploration in the Arctic alter ecosystem properties mainly via the disruption of water drainage patterns and through the dust deposition that accompanies high speed vehicle traffic. Dust

damages or eliminates most of the acidophyllic plant species such as Sphagnum mosses and lichens. The disruption of water drainage patterns can cause impoundments and thermal erosion (i.e., thermokarst), particularly in areas with massive ground ice. Our simulations with T-MAP provide preliminary information that may be useful for determining management options.

Roads that disrupt discharge may cause substantial disturbance to arctic ecosystems. Our simulations suggest that disturbance can be minimized by building roads in areas with the smallest effect on discharge patterns. Roads that ascend and descend slopes perpendicular to elevation contours and roads along ridges (i.e., watershed boundaries) are the least likely to cause vegetation disturbance through altered discharge. Dust from roads will have significant impacts regardless of road location.

Our conclusions and recommendations based on simulations with T-Maps are:

- (1) Any road construction has the potential to substantially alter vegetation biomass and community structure over large areas of the watershed. The net change in vegetation biomass and productivity is likely to be large and negative.
- (2) Roads through the basins of watersheds should be avoided because of the potential for severe discharge related damage to vascular plant and moss communities and the potential for widespread thermokarst erosion.
- (3) Roads along ridges may cause severe damage to lichens and mosses, and the effects of these roads propagate over large areas of the watershed and probably should also be avoided.
- (4) Roads placed perpendicular to the elevation contours are likely to cause the least damage, but these roads disturb small areas of the watershed that are likely to be susceptible to thermokarst erosion.

We show that a model based solely on elevation data and annual water budget can explain ca. 45% of the variation in observed NDVI and overlaps observed vegetation type in 76% of the watershed. Attempts to find direct correlations between ecosystem properties and remotely-sensed data often fail. Our approach demonstrates how a simulation model can be used to relate remotely-sensed vegetation indices to a wide range of important ecosystem properties and has potential to be developed into an applied management tool with further development and testing. Such models may serve as valuable tools for generating maps of risk potential of arctic landscapes to various types of disturbances.

3.4 A Model Simulation Of Megafaunal Impacts In The Far North

As an extension of our R4D research (with Terry Chapin), we initiated collaborations with S. Zimov, a Russian scientist in Siberia. We used our models to test ideas about historical changes in Siberian tundra. It has been hypothesized for Beringia that strong interactions among climate, animal grazing, and ecosystem processes lead to the extinction of the megafauna, which could cause a transition from predominance of steppe to predominance of moss-dominated tundra, i.e., tip the balance in favor of tundra. We address two questions with our modeling work (see Zimov et al. 1995): Was the climatic change at the end of the Pleistocene sufficient to cause transition from steppe to tundra? Are there plausible mechanisms by which loss of megafauna could cause a shift from steppe to tundra?

The model has three functional groups: "trees" (woody plants, including shrubs), "grasses" (herbaceous vascular plants), and "mosses" (nonvascular plants, including lichens). Each functional group has a characteristic maximum growth rate that is diminished when supplies of light, water, or nutrients are suboptimal. This growth rate, which determines a group's resource "demand," is further modified by competition coefficients that are determined by the priority of access of each group to a limiting resource (i.e., radiation or water). For example, mosses compete with trees and grass for water but not for light (because of their shorter stature); trees and grass compete with one another for light in the Far North where trees (=shrubs) are short, but elsewhere trees

are better competitors for light than are grasses and mosses. Comparable rules of competition for water are governed by rooting depth.

Nutrient supply, which is linked less directly to climate, is assumed to affect competition through differential effects on growth (i.e., response of grasses > trees > mosses) rather than being the resource for which plants compete. Nutrient supply can be varied in the model to simulate variation in soil fertility and the increased soil fertility associated with Pleistocene loess deposition. Mammalian grazers affect vegetation through consumption and destruction of biomass. We assume that grazers have no long-term detrimental effect on grass biomass in a steady state ecosystem controlled by climate and predators because 1) predators prevent overgrazing on the long time scales (centuries) simulated by the model and 2) grassland production in tundra compensates effectively for grazing through a variety of ecosystem feedbacks. Predictions of the model were qualitatively similar when this assumption was relaxed to allow grass response to grazing to range from moderately detrimental to moderately stimulatory, i.e., the range of grazing response observed in natural ecosystems.

Climatic data (radiation input and precipitation) were estimated for each terrestrial 5° grid point of longitude and latitude. The model, which includes grazing as a natural process, was solved for the equilibrium biomass (B) of each functional group ($dB/dt = 0$) at each 5° grid point, assuming each of four values of nutrient availability, to estimate patterns of functional-group composition. At the two intermediate soil-fertility levels the simulated distribution of functional groups closely matched observed vegetation patterns both within Beringia and globally, providing model validation. From these data we determined the combinations of Beringian climatic conditions that could be occupied by each functional group on infertile and fertile soils.

The model was then run to equilibrium with an annual time step to simulate patterns in productivity of each functional group on fertile and infertile soils under a representative Pleistocene Beringian scenario of cool climate, loess deposition, and presence of large grazers. We then ran four simulations of possible changes from Pleistocene to Holocene conditions: (1) the complex of conditions that changed at the end of the Pleistocene (climatic warming, elimination of grazers, and elimination of loess deposition), (2) climatic warming, (3) elimination of loess deposition, (4) elimination of large grazers. We did not include CO₂ effects in the model. Each of these simulations was run under two conditions of soil fertility (to represent topographic and geologic variation in nutrient supply) and two initial densities of colonizing species (i.e., mosses and trees) until biomass came to equilibrium with the new conditions. A 10-fold variation in initial rate of colonizer density altered the rate of vegetation change but not the equilibrium species composition, so we presented results from only the higher colonizer density.

When the model was run for all terrestrial climates (presented in Zimov et al. 1995), it gave a realistic geographic distribution of each functional group, giving us confidence that the model reasonably captures the general climatic controls over vegetation distribution, assuming a natural grazing regime. When the equilibrium biomass of major functional groups was calculated in Beringia under Pleistocene conditions, grasses were abundant under the entire range of climatic conditions, mosses were abundant in dry climates, and trees were restricted to the warmest, wettest climates, regardless of soil fertility. This pattern is consistent with the Pleistocene pollen record and with the maintenance of these grasslands by either climate, grazers, or loess deposition. When grazers were removed in the model, mosses expanded dramatically, grasses declined, especially at low fertility, and trees increased slightly. By contrast, a change in climate from Pleistocene to Holocene conditions resulted in a large increase in trees under moist conditions, a change in the moisture dependence of mosses, and modest changes in grasses. Loss of loess deposition under infertile conditions reduced grass growth and enhanced tree growth, but had no major effect on mosses. Under fertile conditions, loss of loess deposition had no major effect on species composition. Change from Pleistocene to present

conditions in all three parameters (grazers, climate, and loess) caused complete replacement of grasses by mosses and trees at low fertility and coexistence of all three types at higher soil fertility, patterns similar to those observed presently in northern Beringia. These results suggest that change in several factors, especially grazers and climate could cause a biome shift from dominance by grasses to dominance by mosses and shrubs, and that neither climate change nor loss of grazers was sufficient as a single factor in causing observed vegetation change from Pleistocene to Holocene vegetation.

In summary, the model suggests that many factors contributed to vegetation change at the Pleistocene-Holocene boundary, but that climate warming was particularly important to the invasion of woody plants and that loss of grazers had greatest effect on the balance between mosses and grasses. These results are consistent with paleorecords showing a switch to forest where climate permits a woody growth form to reach large size. However, it suggests that loss of grazers was critical to the switch from grass to moss dominance in areas presently occupied by tundra. Thus, the modeling supports our contention that extinction of the Pleistocene megafauna by human hunting in areas presently occupied by tundra could have caused a shift in the vegetation mosaic from predominance of grass-dominated steppe to predominance of moss-dominated tundra, even in the absence of a large climatic change. The model also suggests that other factors, particularly changes in climate and loess, contributed to this change and enhanced growth of woody plants.

4 Conclusions

Gaps in our knowledge suggest that it is still premature to expect fully integrated models of arctic ecosystem function and that the models described here must be understood as "next steps". In the absence of comprehensive understanding, there is a danger that largely untested hypotheses will become incorporated into models and influence our considerations. Such imperfections remain obscure because model testing and validation is often inadequate or impossible, particularly at larger spatial and temporal scales. Similarly, a wholly empirical approach to predicting arctic ecosystem responses to energy-related disturbances is impractical since it is impossible to design and conduct the many different combinations of experiments needed to sort out complex ecosystem interactions. Also, the size and expense of equipment restricts studies to relatively small spatial scales and the majority of experiments and field manipulations are short-term. Long-term changes that may lead to new feedbacks, homeostases, or shifts in species are not apparent. While simulation modeling cannot be a replacement for experiments, our limited body of empirical knowledge can be greatly extended when all assumptions and limitations are brought together in a best "state-of-the-art" formulation, as attempted in some of the R4D models. These models have the potential to provide important information and predictions that can help us link short-term, single factor experiments and our understanding of long-term, multi-factor disturbances.

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6 Springer-Verlag Book supported by DOE

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J F Reynolds and J D Tenhunen (eds)

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