James F. Reynolds John D. Tenhunen (Eds.)

Landscape Function and Disturbance in Arctic Tundra

With 109 Figures, 11 in color
and 47 Tables

To Harbin,
With best regards and
compliments —
Jim

Springer

14 Patch and Landscape Models of Arctic Tundra: Potentials and Limitations

J. F. REYNOLDS, J. D. TENHUNEN, P. W. LEADLEY, H. LI, D. L. MOORHEAD, B. OSTENDORF, and F. S. CHAPIN III

14.1 Introduction

A synthesis and integration of data gathered at the Imnavait Creek catchment in the form of up-to-date simulation models was a major goal of the R4D program sponsored by the Department of Energy (Chap. 1, this Vol.). 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 (NRC 1982). Similar desires for the use of models as natural resource management tools have been expressed in ecosystem science for over 20 years (Hammond 1972; Cooper 1976; Loucks 1985; Slocombe 1993; Kaufmann et al. 1994). 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 (e.g., Pickett et al. 1994).

In this chapter, we present a summary of some of the models that were developed as part of the R4D program. We 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 the potentials and limitations of these models for providing insight on patch and landscape level function in tundra regions.

Our approach to modeling arctic systems has been to focus in each instance on a single phenomenon and scale (both temporal and spatial) in order to clearly define the system of interest (O'Neill 1988). We agree with Starfield and Bleloch (1991) that models should be constructed for a particular purpose, based on assumptions and data relevant for that purpose, rather than attempting to serve "all purposes" and include everything known about a subject. Different types of models are needed, ranging from simple phenomenology to detailed mechanisms. Each model type is used at the scale for which it is best suited (e.g., whole plant growth, ecosystem productivity, watershed discharge, etc.). Knowledge generated from a model at one level may contribute to our total system understanding and, thus, help build or alter a model at another level (Reynolds and Leadley 1992; Reynolds et al. 1993).

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14.2 Modeling Framework

14.2.1 Spatial Simulation Units

The arctic landscape is a rich mosaic of soil types, topography, lakes, creeks and vegetation (Chap. 4, this Vol.). Such heterogeneity must be considered when modeling the effects of disturbance on landscape function (DeAngelis et al. 1985; Turner 1989; Turner and Dale 1991; Hannsson et al. 1994). In this context – and consistent with our theme of avoiding complex, "all purpose models" – three distinct tasks were addressed by our modeling efforts: (1) the description of processes that occur at *specific* locations or patches in the landscape; (2) characterization of energy and material transport *between* patches; and (3) interfacing of patch and transport processes in a *landscape* framework. These modeling tasks were accomplished using the spatial "simulation units" defined in Table 14.1. This scheme illustrates important spatial and temporal linkages in arctic landscapes and provides a framework for integrating structural, functional, and transport linkages within and across ecosystem boundaries in the watershed.

The smallest simulation unit is at the scale of an individual plant. Plants are coupled to their environment via numerous plant-soil-atmosphere-animal vectors (Table 14.1). We define "patch" ecosystems as relatively discrete and internally homogeneous units of land, e.g., the biotic community residing on a particular soil type. While true homogeneity is rarely observed in nature (Kotliar and Wiens 1990), we view patches as parcels of land that have similar responses to energy and water inputs, regardless of their spatial location. These physically and biologically homogeneous areas may be identified on the basis of similar soil, vegetation, slope, and aspect and are conceptually identical to "hydrologic response units," which are land areas that respond similarly throughout when subjected to hydrologic events, e.g., precipitation (Battaglin et al. 1993).

A series of connected and interrelated patches form a flow path (Woodmansee 1988, 1990). An example is Walker's toposequence in the Imnavait Creek watershed (see Fig. 4.8, this Vol.), which identifies five patches – crest, shoulder, upper backslope, lower backslope, and footslope – on the basis of differences in soils, vegetation physiognomy, geologic surface forms, and plant community types. Another example is the toposequence defined by Schimel et al. in the nearby Sagavanirktok River valley, (see Fig. 10.1, this Vol.), which consists of six ecosystem types running from tussock tundra on upland sites, down through a series of floodplain terraces, to the river. Typically, water, atmospheric turbulence, and animals are the main vectors of transport of materials and energy between patches. Field studies at the level of flow paths correspond to examining the degree of "connectedness" between patches (examples given in Chaps. 5, 8, 13, this Vol.). Understanding flow paths is important since ecosystem processes are directly affected by transfers of mate-

Table 14.1. Spatial simulation units

Spatial simulation unit			Typical coupling vectors	
Name	Spatial scale[a] (m^2)	Structural components	Water	Energy/nutrients
Plant	10^{-4}–10^{-1}	Leaves Stems Roots Soil volume	Soil water Transpiration Water uptake	Photosynthesis Respiration Nutrient uptake Herbivory
Patch	10^{0}–10^{4}	Plants Soil Microbes Animals	Precipitation Infiltration Discharge/run-on Evapotranspiration Soil water balance	Net carbon balance Nutrient cycling Decomposition Trace gas flux
Flow path	10^{2}–10^{5}	Patch ecosystems Toposequences or soil catenas	Soil water flux and discharge [Hillslope Darcian flow dominant]	Mass flux of sediment Mass flux of dissolved nutients Aeolian transport
Landscape	10^{6}–4×10^{6}	Flow-path ecosystems Groundwater; channel storage	Channel flow [Turbulent flow dominant]	Dispersal Trace gas flux
Region[b]	10^{7}–10^{10}	Landscapes (= integrative flow systems) Lakes; rivers		Hydrologic transport of sediments Hydrologic transport of dissolved nutrients Aeolian transport Migration

[a] Examples of "typical" values for arctic tundra; based on Osmond et al. (1980), Woodmansee (1988, 1990) and Walker and Walker (1991).
[b] "Mesoscale" in Walker and Walker (1991), which includes 2nd-order watersheds.

rials across system boundaries (Forman and Gordon 1986) and these boundaries may vary in response to disturbance (Wiens et al. 1985).

The Imnavait Creek watershed consists of an assemblage of flow path ecosystems that deliver mass and energy (mainly by gravitational processes) to the stream. The sum total of these flow paths corresponds to our use of the term "landscape." This simple definition is based on the concept of an "integrated flow system," which is analogous to a specific drainage basin associated with a water gauging station (Li et al. 1977). Thus, at the landscape scale of interest, the entire Imnavait Creek watershed is the simulation unit.

The largest spatial unit is a region (Table 14.1). Regional studies involve a mixture of integrated flow systems or landscapes that make up the scale of interest, e.g., the 22-km^2 R4D region (see Fig. 1.1, this Vol.) or the entire North Slope (Walker and Walker 1991).

Table 14.2. Types of models developed in the R4D program. Numbers 1–9 correspond to those shown in Fig. 14.1 [chapters cited are in this volume]

Types of models	References
Mechanistic	
① Photosynthesis, respiration (GAS-FLUX)	Chap. 5 (5.5); Chap. 14 (14.3.1); Tenhunen et al. (1992, 1994)
Decomposition and mineralization (GENDEC)	Chap. 16 (16.3.4, 16.5); Chap. 14 (14.3.4); Moorhead and Reynolds (1992, 1993)
Plant growth	Chap. 14 (14.3.2); Leadley and Reynolds (1992); Reynolds and Leadley (1992)
Nutrient uptake	Chap. 14 (14.3.3); Leadley et al. (1996)
Soil respiration	Chap. 5 (5.5); Chap. 17; Oberbauer et al. (1991)
Soil thermal regime (TDHC)	Chap. 6 (6.4.1); Hinzman et al. (1991); Kane et al. (1991, 1992)
Surface energy budget	Chap. 6 (6.2.1); Kane et al. (1991, 1992)
Transport	
② Hydrology (discharge, soil water storage; TOPMODEL)	Quinn et al. (1995); Chap. 17
③ Hydrology (discharge; T-HYDRO)	Chap. 14 (14.4.1); Chap. 18 (18.3.1.1); Ostendorf and Reynolds (1993, 1995)
Hydrology (snowmelt)	Chap. 6 (6.4.2); Kane et al. (1992)
Hydrology (runoff; HBV)	Chap. 6 (6.4.3); Hinzman and Kane (1991); Hinzman et al. (1993); Kane et al. (1991, 1992)
④ Dust deposition	Chap. 15
Topographically derived	
⑤ T-VEG	Chap. 18 (18.3.1.2)
⑥ T-NUT, T-PLT	Chap. 18 (18.3.1.3, 18.3.1.4)
⑦ TVM	Chap. 14 (14.4.2); Chap. 17 (17.3.1); Ostendorf and Reynolds (1995)
Landscape	
⑧ GAS-FLUX/TOPMODEL	Chap. 17
⑨ T-MAP	Chap. 18

14.2.2 Types of Models

Reynolds and Leadley (1992) described numerous ecological models developed for arctic tundra. One of these, the arctic tundra simulator (ARTUS), was specifically designed to address effects of disturbance on tussock tundra (Miller et al. 1984). These models – restricted mainly at the plant or patch scale – were largely motivated by research interests in the International Biome Program (IBP) (Wielgolaski 1975; Miller et al. 1975, 1978, 1979, 1984; Chap. 2, this Vol.). Reynolds and Leadley (1992) concluded that most of these models

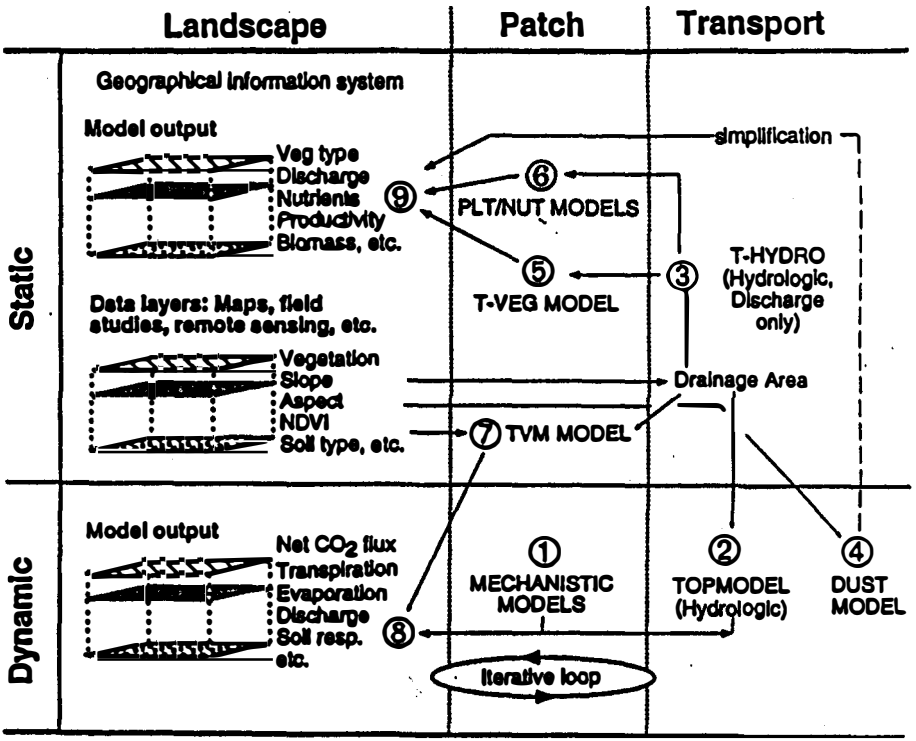

Fig. 14.1. Framework for integrating structural and transport linkages within and across ecosystem boundaries. Illustrated are "building blocks" for landscape models described in Chap. 17 (*8*) and Chap. 18 (*9*). Some of these models (i.e., *1–7*) were used directly as submodels; others served to generate information that led to simplifications or assumptions. See Table 14.2 for further details

were either too complex for long-term simulations or were too empirical for extrapolation. Nevertheless, these models provided an excellent baseline for model development in arctic ecosystems.

Examples of the various types of models developed in the R4D program that are based on these previous efforts are given in Table 14.2 and Fig. 14.1. These models are referred to as mechanistic, transport, topographically derived, and landscape. Our mechanistic models may be viewed as "bottom-up" models in that they employ information and relationships from below the scale of focus and are generally based on processes or mechanisms that link or relate various elements to one another. We constructed mechanistic models for a range of arctic phenomena at the scale of organs, individuals, and patches (Table 14.1) as part of our effort to obtain fundamental understanding of biotic and abiotic controls on carbon, nutrient, and water fluxes in arctic ecosystems. Our transport, topographically derived, and landscape models – at the scale of flow paths and landscapes (Table 14.1) – are, on the other hand, best viewed as

examples of "top-down" approaches. The fundamental difference to bottom-up models is the extent to which information is used from hierarchies below the level of focus. That is, in top-down models processes that occur below the scale of interest are subsumed into derived variables that relate to, or correlate with, the variable of focus. Of course, to the extent that these newly derived relationships are representative of processes, interactions, and feedbacks among real parts of the system, we can say that these models are also mechanistic (Reynolds et al. 1993).

In the next section, we review select models developed in the R4D. This overview, illustrated in Fig. 14.1, is intended to elucidate both potentials and limitations of these models and to suggest where further work is needed. Some of these models were used directly as submodels in higher-order models; others served to generate information that led to simplifications or assumptions in higher-order models. Various simplification and aggregations schemes may be used in translating information from these models. For example, in Chapters 17 and 18 (this Vol.), we present two landscape models indicated by #8 and #9, respectively, in Fig. 14.1; the "building blocks" for these models are indicated by the various arrows.

14.3 Bottom-Up Models

14.3.1 Ecosystem Gas Exchange

14.3.1.1 Motivation

Considerable effort has been devoted to the examination of ecosystem carbon dioxide exchange in tundra regions (Chap. 11, this Vol.), beginning with investigations near Barrow, Alaska, during the IBP (Chap. 2, this Vol.). 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. Miller et al. (1984) 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 (Tenhunen et al. 1994). Our ultimate objective is 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.

14.3.1.2 Description

GAS-FLUX considers the gas exchange and the microclimate of three types of landscape patches or vegetation types in the Imnavait Creek watershed: moist

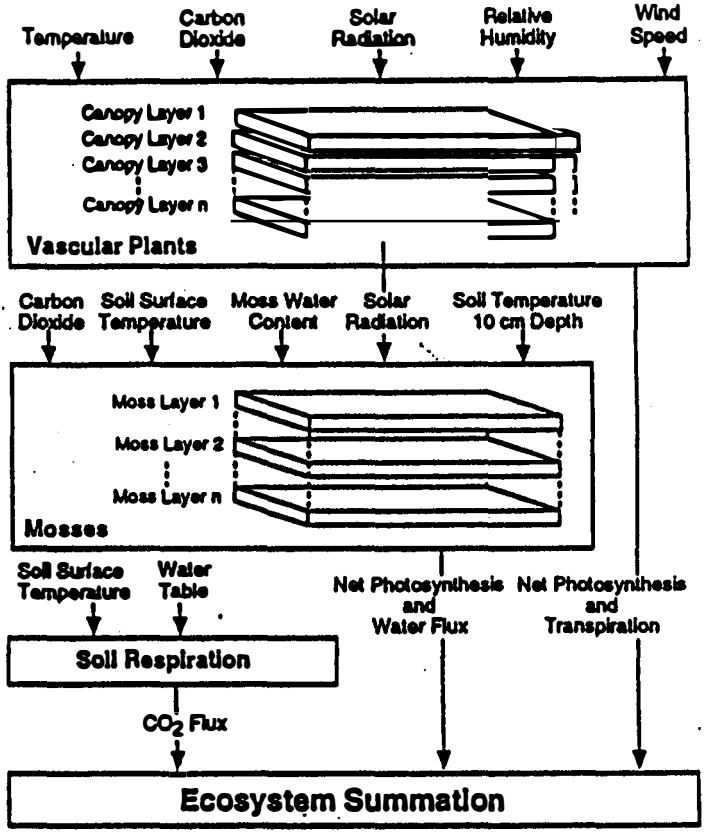

Fig. 14.2. Structure of the GAS-FLUX model as applied to tundra plant communities. Summation of CO_2 and water-exchange processes in vascular plant *canopy layers*, *moss layers*, and *soil* provides estimates of ecosystem water and carbon balance. (Modified from Tenhunen et al. 1994)

Cassiope dwarf shrub (CDS) heath (upper slopes), tussock tundra (midslopes), and riparian (lower slopes) (cf. Chaps. 4, 5, 17, this Vol.). Each patch is considered to be homogeneous, but composed of a mixture of vascular and nonvascular (primarily *Sphagnum* mosses) plants. The vascular plant canopy is divided into a series of layers each containing leaf and stem material for one of three functional groups with a defined physiological response: deciduous shrubs, graminoids, and evergreen shrubs (Fig. 14.2, Table 14.3).

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 midslope 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

Table 14.3. Simplified canopy characteristics used in GAS-FLUX for vascular plants in three community types distributed along a topographic and water-availability gradient in the Imnavait Creek watershed. Structure indicated was assumed to occur during the midseason or mature stage of phenological development from ca. July 15–August 1

	Moist CDS heath (upslope)		Tussock tundra (midslope)		Riparian (lower slope)	
	LAI[a] (angle)	SAI[b] (angle)	LAI (angle)	SAI (angle)	LAI (angle)	SAI (angle)
Deciduous shrub (D)	0.24 (45)	0.174 (50–80)	0.12 (45)	0.174 (50–80)	0.35 (45)	0.151 (50–80)
Graminoid (G)	0.24 (85)	-	0.12 (85)	-	0.6 (60–85)	-
Evergreen shrub (E)	0.2 (30)	0.016 (30)	0.2 (30)	0.016 (30)	-	-
Total vascular plant LAI	0.68		0.44		0.95	

[a] Leaf area index ($m^2 m^{-2}$); average angles from the horizontal in degrees; average leaf widths of D = 1.0 cm, G = 0.3 cm and E = 0.3 cm, considered the same in all three vegetation types; all leaves and stems considered to be alive and non-clustered.
[b] Stem area index ($m^2 m^{-2}$); all stems ≤6 mm diameter and photosynthetically active.

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 et al. (1980) equations, which are based on ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) kinetics as mediated by (1) the concentrations of competing gaseous substrates, CO_2 and O_2, and (2) the ratio of ribulose-1,5-bisphosphate (RuBP) concentration to enzyme-active sites. CO_2 assimilation is linked to an empirical stomatal conductance model (Collatz et al. 1991). 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 (Chap. 11, this Vol.); we derived the parameters for the Farquhar et al. model based on extensive measurements of CO_2 gas exchange over a range of water contents (Tenhunen et al. 1992, 1994).

Ecosystem efflux of CO_2 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 (Chaps. 11, 17, this Vol.). Soil respiratory flux is determined by using regression equations (Chap. 11, this Vol.); Oberbauer et

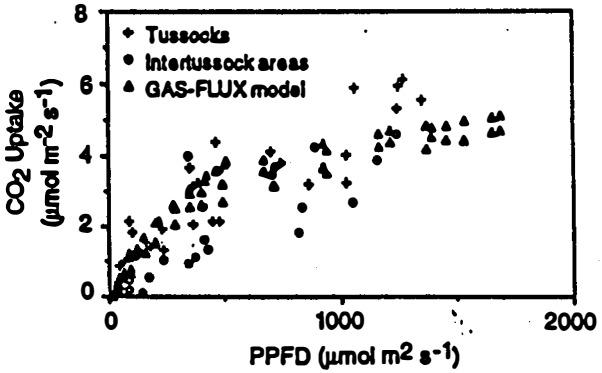

Fig. 14.3. Estimated CO_2 uptake of *Eriophorum vaginatum* tussocks and intertussock areas as a function of PPFD at the time of measurement. Comparison with the mean tussock tundra ecosystem uptake estimated from GAS-FLUX under a variety of weather conditions. (Tenhunen et al. 1994, 1995)

al. 1991, 1992). Net ecosystem gas exchange is computed by the balance of CO_2 flux rates from the aboveground (leaf, stem, moss) and soil components of the model. A comparison of net CO_2 uptake as described by GAS-FLUX and measured with small chambers in tussock tundra of the Imnavait Creek catchment is shown in Fig. 14.3.

14.3.1.3 Potentials and Limitations

With GAS-FLUX, we are able to elucidate various abiotic and biotic interactions that contribute to ecosystem gas exchange. For example, the integrated dally CO_2 flux in tussock tundra on a clear day is 20 μmol^{-2} vs. -20 μmol m^{-2} if the day is overcast, where the individual contributions of each system component can be quantified (Fig. 14.4). Tenhunen et al. (1992) 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 CO_2 efflux (Chap. 17, this Vol.). As described in Chapters 11 and 17 (this Vol.), the balance between carbon fixation as influenced by phenology, LAI development, and radiation input and CO_2 efflux as determined by water table depth and soil aeration establishes tundra as either a source or sink for CO_2.

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 ridge-top 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, directly

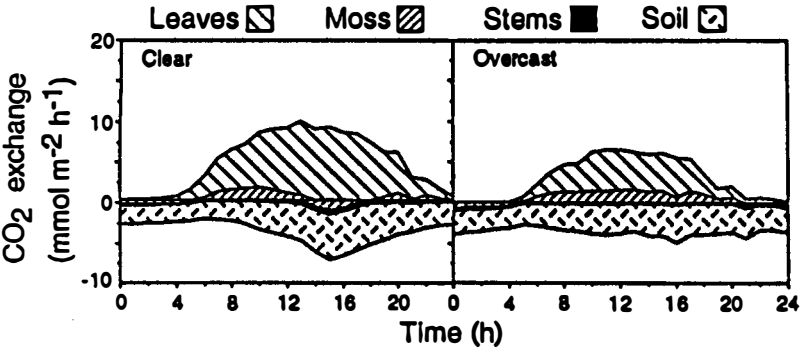

Fig. 14.4. Simulated CO_2 gas exchange of tussock tundra vegetation on a warm, clear day at midseason. The fluxes for leaves, *Sphagnum* moss, twigs, and soil are shown, additively, with carbon fixation by leaves and moss shown as positive fluxes and respiration of moss, twigs, and soil as negative. *Left* Simulations for a clear day at midseason (integrated daily CO_2 flux = $20\,\mu mol\,m^{-2}$); *right* for an overcast day (integrated daily CO_2 flux = $-20\,\mu mol\,m^{-2}$). Soil was considered to be moist and well aerated. *Sphagnum* water content was set at 750% of dry weight. (Modified from Tenhunen et al. 1995)

influencing 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. In Chapter 17 (this Vol.), we describe an exploratory study to link GAS-FLUX with a watershed model in order to consider interactions between carbon balance and spatial aspects of water table variability.

14.3.2 Plant Growth

14.3.2.1 Motivation

A number of vascular and nonvascular whole-plant growth models have been developed for arctic ecosystems (reviewed in Reynolds and leadley 1992). These models range from: (1) budget-type models where plants are treated as "black boxes", i.e., plant biomass is lumped into a single box and growth is described as the difference between inputs and outputs (usually fixed values); (2) flux-type models that contain a high degree of comprehensiveness in terms of gas exchange processes per se, but have a highly empirical treatment of plant growth processes; and (3) mechanistic models that range greatly in terms of the degree of phenomenology and mechanism used. Because of the emphasis on modeling at the IBP wet meadow sites (especially Barrow, Alaska), most of these models were developed for mesic tundra ecosystems. Recently, Rastetter

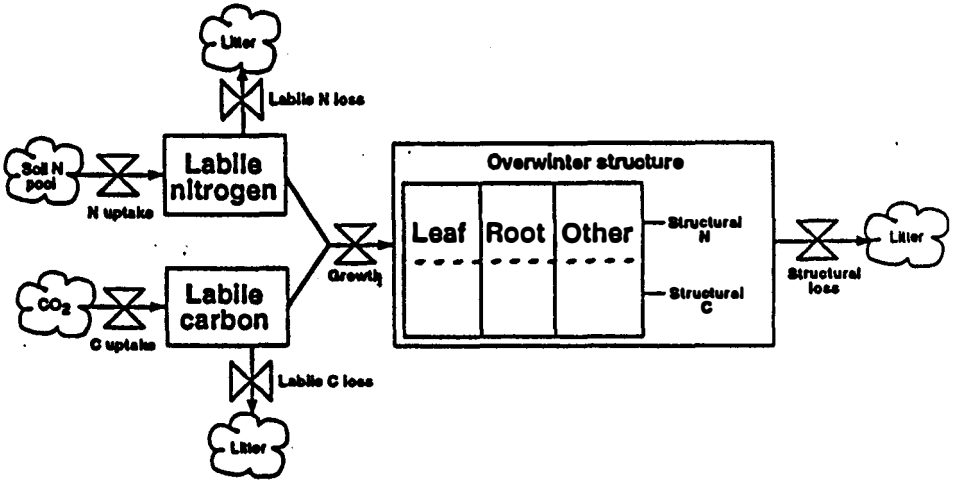

Fig. 14.5. Conceptual diagram of plant growth model. *Boxes* represent state variables, *arrows* are fluxes, *valves* signify control over fluxes, and *clouds* represent infinite sinks or sources. (From Leadley and Reynolds 1992)

et al. (1991) applied a biogeochemical model to arctic tundra; this model is mechanistic but highly aggregated, treating all plants as a single entity.

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 one of the dominant vascular plant species in tussock tundra. It is found in many arctic and subarctic ecosystems, and microclimate and soil processes are profoundly affected by the tussocks that it forms (Chapin et al. 1979; Bliss 1981). Consequently, a large amount of experimental data on its growth and physiology exists, perhaps more than for any other arctic species.

14.3.2.2 Description

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 CO_2 concentration on growth dynamics. The spatial simulation units are plants (Table 14.1) contained in a core in the center of a tussock that is 3.3×10^{-3} m^2. The temporal resolution is 1 year. A diagram of the model is shown in Fig. 14.5 where the variables represent the overwinter status of the plant, i.e., January 1 of each 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 (Fig. 14.5). Parameterization was based on physiological data from individual plants and by fitting observed, short-term responses of *Eriophorum* to nutrient additions (Chapin et al. 1986; Shaver et al. 1986). Validation was done with independent data sets of short-term *Eriophorum* responses to increased temperature and shading, and the interaction of these with fertilization (data from Chapin et al. 1986; Shaver et al. 1986), and to elevated CO_2 and temperature (data from Tissue and Oechel 1987).

14.3.2.3 Potentials and Limitations

We used the growth model to examine the effects of a 50-year period of climate change on peak biomass (overwintering biomass plus seasonal production) in *E. vaginatum*. Three scenarios (see Fig. 14.6) were simulated. In scenario 1, the model predicts that a simultaneous increase in the direct effects of temperature, season length, and CO_2, with no change in N availability, would result in a slight decrease in peak biomass. This is a result of decreasing overwinter biomass that is not offset by a slight increase in seasonal production. In scenario 2, a simulated long-term doubling of N availability resulted in a ca. 70% increase in peak biomass, whereas with concurrent changes in climate and N availability (scenario 3), the model predicted a slight decline in peak biomass compared to increases in N alone. In essence, the model predicts that climate change will have substantial effects on *E. vaginatum* only indirectly through changes in N availability, which emphasizes the importance of being able to describe any natural or anthropogenic effect on N cycling in tundra ecosystems (see below).

Our model and experimental evidence (e.g., Shaver and Chapin 1986) indicate that N availability is the factor that ultimately limits *E. vaginatum* productivity under a wide range of conditions. In addition, both the model and data suggest that allocation patterns and mortality are much more important than physiological factors such as photosynthesis rates and nutrient uptake kinetics in determining the growth and biomass of *E. vaginatum*. These results are important in the context of future modeling efforts for other major tundra species.

The ability of the model to predict the responses of *E. vaginatum* to climate change or other disturbances is limited by the assumptions (1) that competitive relationships with other plants species remain unchanged, (2) that all of the factors that potentially limit growth are included in the model (e.g., nutrients other than nitrogen are not important), and (3) that there will be no profound changes in environment such as the loss of the permafrost layer. In addition, the model cannot account for within-season changes in environment because it has a very coarse time resolution. As described in Reynolds and Leadley (1992), we are examining this potential error by comparing it with

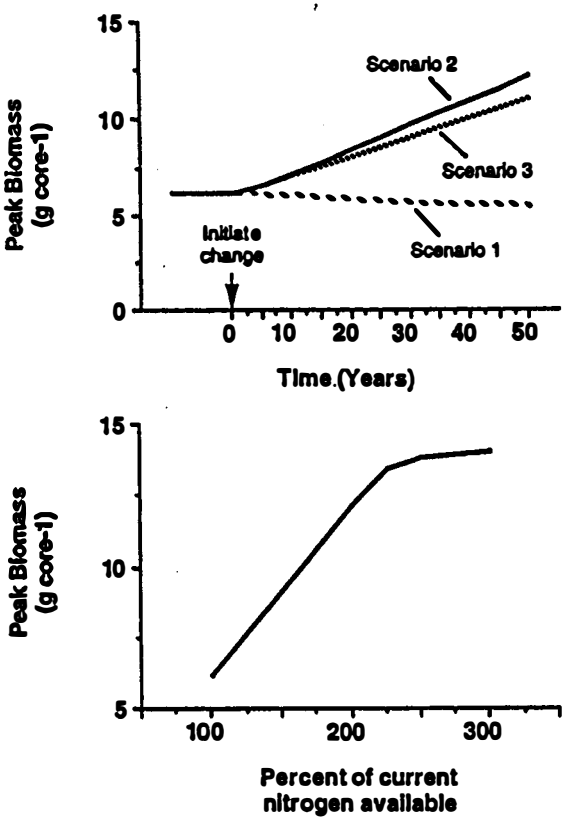

Fig. 14.6. *Above* Response of *E. vaginatum* biomass (core = 3.32×10^{-3} m^{-2}) to long-term climate change simulated by linear increases over a 50-year period in temperature (8–13 °C), season length (100–120 days), atmospheric CO_2 concentration (340–680 μl/l). Nitrogen availability varied from 9–18 g m^{-2} year^{-1}. *Scenario 1* Climate change with no change in N availability; *2* an increase in N availability with no change in climate; *3* climate change with an increase in N availability. *Below* Simulated response of *E. vaginatum* to long-term changes in N availability. (From Leadley and Reynolds 1992)

another model of *E. vaginatum* that uses a daily time step. Another caveat is that we have attempted to model the long-term responses of *E. vaginatum* to environmental variation, but we were only able to validate it using relatively short-term data sets. Thus, the predictions made for the climate change scenarios in Fig. 14.6 must be viewed as extrapolations well outside the range of validation. These long-term simulations are important, however, because they show that the long-term responses of arctic plants to environmental change are potentially very different than those predicted by short-term simulations (see Reynolds and Leadley 1992 for specific examples).

In addition to these limitations of the model, we have also made several important simplifying assumptions about the regulation of nitrogen uptake in

E. vaginatum. In particular, we have assumed that nitrogen uptake is limited only by nitrogen availability and that it is not limited by root biomass, nitrogen uptake kinetics, or soil properties. These assumptions were tested using a highly detailed model of nitrogen uptake described in Section 14.3.3.

14.3.3 Nitrogen Uptake

14.3.3.1 Motivation

Nitrogen is one of the most important constraints on vascular plant productivity in tussock tundra (Shaver et al. 1986; Chaps. 11, 16, this Vol.; see above). Tussock tundra occurs together with highly organic soils (Chapin et al. 1979; Chap. 4, this Vol.). 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 (Nadelhoffer et al. 1992). In addition, soil solution concentrations of NH_4^+ and NO_3^- in tussock tundra are far lower than those in agricultural systems (Marion et al. 1989). 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. (1996), is also based on data from *E. vaginatum*. This sedge is well suited to simulation of nitrogen uptake because its growth habit permits a number of simplifying assumptions. In particular, the roots of *E. vaginatum* grow relatively straight down into the soil without branching, are not heavily suberized, are nonmycorrhizal, and experience only intraspecific competition for nitrogen.

14.3.3.2 Description

The root system of a plant is envisioned as a set of roots growing parallel to each other down into soil cylinders. Each soil cylinder is divided into numerous concentric sub-cylinders around an individual root (Fig. 14.7). The model is conceptually similar to the Barber and Cushman (1981) model, but has several technical differences and includes a term for the supply of nutrients from microbial mineralization and immobilization of nutrients ("S" in Fig. 14.7) that is not included in the Barber and Cushman model. 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. 1996). 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.

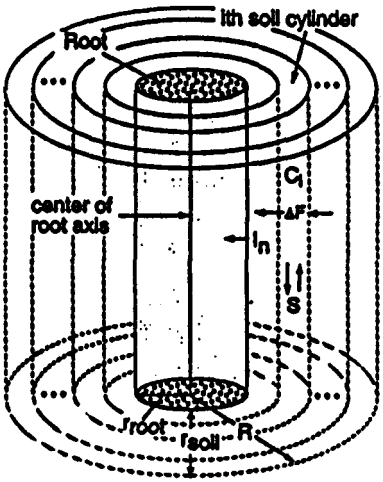

Fig. 14.7. Diagram of root segment and surrounding soil cylinder divided into numerous concentric subcylinders. Net exchange of nutrients in *ith* subcylinder by diffusion and mass flow (ΔF), C_i is concentration of soil solution, S is supply rate of nutrients (gain or loss) from microbial activity, I_n is flux into root, and R is radius from center of root axis to outer soil cylinder. (Modified from Leadley et al. 1996)

14.3.3.3 Potentials and Limitations

Extensive sensitivity analysis using this model suggests that ammonium, nitrate, and even small molecular weight amino acids can make significant contributions to the nitrogen nutrition of *E. vaginatum*. The sensitivity analysis also suggests that the rate of supply of nitrogen compounds through microbial mineralization is the most important factor in determining the rate of nitrogen uptake by *E. vaginatum* and that soil properties, the intensity of root exploration of the soil, and root uptake kinetics play minor roles. As a consequence, it was concluded that nitrogen uptake in arctic ecosystems is sensitive to factors different to those in fertile agricultural systems. Specifically, root morphology and soil factors are very important in determining nitrogen uptake in agricultural systems (Barber and Siblerbush 1984), but are not important in *E. vaginatum*. Because of this, efforts to predict nitrogen uptake by *E. vaginatum* and other arctic plants based on root uptake kinetics, soil solution concentrations, and root length (e.g., the model of Marion and Everett 1989), puts an inappropriate emphasis on factors that are poorly correlated with nitrogen uptake. These conclusions, based on a detailed, process-level mechanism, were used to justify the simplifications made in the *E. vaginatum* plant growth model (Sect. 14.3.2) and to develop a simplified nutrient availability model for use at the landscape scale (Sect. 14.4.2).

14.3.4 Decomposition

14.3.4.1 Motivation

Nitrogen dynamics in arctic soils, especially the relationships between nutrient mineralization, microbial immobilization, and plant uptake, are still not well

understood (Kielland and Chapin 1992; Chap. 10, this Vol.). Low temperatures, permafrost, low nutrient inputs, and frequently water-logged conditions reduce the rate of organic matter turnover and cycling of organically bound nutrients; furthermore, many of the conditions inhibiting decomposition are enhanced by the accumulation of dead organic matter, so that turnover rate may actually decrease with increasing organic matter accumulation (Oechel and Billings 1992; Tenhunen et al. 1992; Nadelhoffer et al. 1992). Rates of net N mineralization seem relatively insensitive to changes in soil temperature and moisture content within the normal range of tussock tundra conditions (2–10 °C, <0.4 bar; Marion and Miller 1982; Marion and Black 1987; Nadelhoffer et al. 1991, 1992). In contrast, respiration in tundra soil (an index of decomposition) is greatly influenced by soil temperature and water regimes (Bunnell et al. 1977; Flanagan and Bunnell 1980; Peterson et al. 1984; Oberbauer et al. 1991; Nadelhoffer et al. 1992; Chaps. 11, 17, this Vol.). Although these observations seem contradictory, nutrients released from decaying organic matter may be immobilized by decomposer microorganisms so that the net mineralization rate is more dependent on litter quality and microbial carbon:nutrient balance than the overall decay rate.

The dynamic physiochemical nature of arctic soils, combined with the uncertainties of biological interactions, makes it difficult to predict patterns of nutrient availability, especially so with regard to potential effects of disturbance. Mathematical models can aid in understanding the nature and behavior of such complex dynamics. 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.

14.3.4.2 Description

Our model, GENDEC (Moorhead and Reynolds 1991, 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 (Fig. 14.8). 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 (C) 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

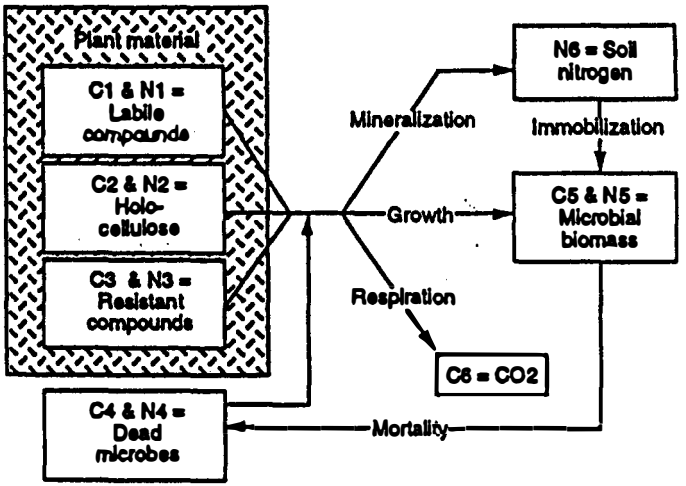

Fig. 14.8. Carbon and nitrogen flows in the GENDEC decomposition model. (From Moorhead and Reynolds 1993)

given fixed assimilation efficiencies. Microbial turnover includes a fraction of the standing biomass, a portion of incremental growth, and a portion of the standing biomass killed by wetting-drying events.

14.3.4.3 Potentials and Limitations

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. Three major conclusions were reached: (1) the amount of simulated N turnover from decaying organic matter is sufficient to meet plant demands, hence, the model exhibits reasonable behavior under current environmental conditions; (2) previously reported inconsistencies in patterns of C and N mineralization for organic arctic soils likely result from different fates of mineral forms of C (lost from the system as CO_2) and N (rapidly immobilized within the system) – an insight that would be difficult to gain from experiments utilizing common incubation methods; and (3) response of N dynamics to changes in climate regimes is unpredictable, given uncertainties in climate change scenarios for this region (Moorhead and Reynolds 1993).

Under current climate conditions, simulated mineral N pools are very small in tussock tundra soils, maximum values averaging $<26\,mg\,N\,m^{-2}$, which is equivalent to ca. $1.52\,\mu g\,N\,g^{-1}$ soil organic matter (SOM) (assuming soil organic matter is ca. 50% carbon) and is slightly lower than extractable nitrate + ammonia concentrations generally reported for tussock tundra soils (Marion and Black 1987; Kielland 1990; Giblin et al. 1991; Nadelhoffer et al. 1991). The

reason for such a small mineral N pool is usually attributed to rapid immobilization by microorganisms. In our simulations, immobilization accounted for all of the N released by decay since decomposition is so strongly N-limited, amounting to 5.28 g N m^{-2} $year^{-1}$ (310 μg N g^{-1} SOM $year^{-1}$) under current climatic conditions. It is misleading to compare these results to estimates of net N mineralization reported by experimental studies using incubation and leaching methodologies. For example, the overall C:N ratios of the soil organic matter examined by Nadelhoffer et al. (1991) and Giblin et al. (1991) are relatively low (16:1 –220:1), yet ratios of C:N mineralization are high (≥450:1). In general, decomposer microorganisms require a balance of C and N that requires a far greater turnover of N accompanying CO_2 production than these mineralization ratios suggest. This implies strong N limitation and tight cycling within the decomposer community in spite of low overall C:N ratios of soil organic matter.

In field situations, plants compete for N released during decomposition. In our simulations with the *E. vaginatum* growth model (Sect. 3.2), we found that 9–18 g N m^{-2} $year^{-1}$ (within tussocks) was needed to obtain reasonable results, which converts to about 1.8–7.2 g N m^{-2} $year^{-1}$ at Imnavait Creek, where 20–40% of the soil surface is covered with tussocks. In comparison, Shaver et al. (1990) estimated that tussock tundra vegetation at the nearby Sagavanirktok River requires about 350 mg N m^{-2} $year^{-1}$ to realize aboveground production. If belowground production requires twice this amount, as much as 1.15 g N m^{-2} $year^{-1}$ could be needed to meet total plant demand. The amount of N turnover estimated by GENDEC exceeds this quantity. In contrast, many of the reported annual net N mineralization rates are too small to support observed plant growth (e.g., Giblin et al. 1991; Nadelhoffer et al. 1991), although some species may also obtain amino acids directly from soil solution (Kielland 1990; Keilland and Chapin 1992).

Insight to this apparent paradox can be gained by comparing observed and simulated patterns of C and N mineralization. Efflux of carbon dioxide from tundra soils appears more closely related to decomposition than many estimates of net N mineralization. Our simulations produced 79.5 g CO_2-C m^{-2} $year^{-1}$ (4.7 mg CO_2-C g^{-1} SOM), which is comparable to observations reported for tussock tundra soils (Poole and Miller 1982; 127 g CO_2-C m^{-2} $year^{-1}$, Giblin et al. 1991; 68 g CO_2-C m^{-2} $year^{-1}$, Nadelhoffer et al. 1991; 8 mg CO_2-C g^{-1} SOM $year^{-1}$). Ratios of C mineralization:N mineralization in our simulations – based on cumulative CO_2-C efflux and average size of the N-mineral pool – are much higher (ca. 3550:1 to 5000:1) than those reported by Nadelhoffer et al. (1991; 800:1) and Giblin et al. (1991; 450:1), although these field measurements probably represent five separate extractions of a smaller, transient mineral pools. Also, Nadelhoffer et al. (1991) and Giblin et al. (1991) found no correlation between soil respiration and N-mineralization rates. Similarly, there was no constant relationship between the size of the mineral N pool and either CO_2 efflux or net N immobilization in simulations. However, the quantity of C mineralized as CO_2 in GENDEC was directly proportional to net N

immobilized because decomposer microorganisms require a balance of C and N to simultaneously meet energetic and nutritional needs. This means that N release from dead organic matter must balance C flux, but such a relationship is difficult to demonstrate by experimentally extracting a small, transient mineral N pool from incubated soils under conditions of rapid N immobilization (e.g., Giblin et al. 1991; Nadelhoffer et al. 1991). Both experimental and simulation data indicate that N is tightly cycled within organic arctic soils. We suggest that N availability to plants is proportionally related to the cumulative turnover of N from decaying organic matter rather than any static measure of soil mineral N pool size.

Results of simulations under various climate change scenarios suggest large potential variability compared to current C and N dynamics, depending on the rates and directions of changes in soil moisture and temperature regimes. Although increasing temperatures increased estimated N turnover, 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.

14.4 Top-Down Models

14.4.1 Hydrologic Transport

14.4.1.1 Motivation

The strong relationship between water and plant structure/function in the Arctic is well known. Numerous researchers have found strong correlations between both patterns and productivity of tussock tundra vegetation and moisture gradients (e.g., Bliss et al. 1984; Jasieniuk and Johnson 1982; Jorgenson 1984; Peterson and Billings 1980; Webber 1978; Chapin et al. 1988; Matthes-Sears et al. 1988; Murray et al. 1989; Gebauer et al. 1995; Chaps. 4, 5, 11, this Vol.) and an array of chemical, physical, and biological variables, e.g., thaw depth and heat input (Webber 1978; Walker et al. 1989; Hastings et al. 1989; Shaver et al. 1990). The importance of water is illustrated in Webber's (1978) conceptual model of the principal environmental variables affecting vegetation at Barrow, Alaska (Fig. 14.9). While the role of topography on the water regime at the patch scale is explicit in Fig. 14.9, the importance of this relationship may be implied as well when we consider vegetation patterns and landforms at larger spatial and temporal scales. Over longer periods of time, integrated, complex feedbacks among a number of processes often govern the performance of arctic plants under natural circumstances more strongly than do short-term responses of individual processes per se (Chapin et al. 1992).

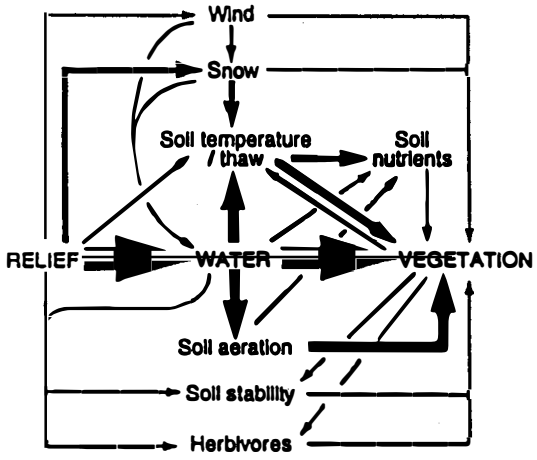

Fig. 14.9. Principal environmental variables that control vegetation at Barrow, Alaska. Strength of control indicated by *thickness of line*. Redrawn from Webber (1978)

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. This was seen as a first step in developing landscape models for tundra ecosystems. We used two models, TOPMODEL and T-HYDRO (#2 and #3, respectively, Fig. 14.1 and Table 14.2). TOPMODEL, which predicts both water routing and soil water deficits, was linked to the GAS-FLUX model to simulate landscape patterns of ecosystem gas exchange (#8, described in Chap. 17, this Vol.). The water routing algorithm used in TOPMODEL was also used in a vegetation typing scheme (#7). T-HYDRO, which only computes water routing, was used in vegetation typing model (#5) and in landscape models for nutrient availability and growth (#6), the latter as part of the landscape model T-MAPS (#9, described in Chap. 18, this Vol.). TOPMODEL is described in Chapter 17, this Vol.; our work with T-HYDRO is described below.

14.4.1.2 Description

T-HYDRO is a spatially explicit watershed model that utilizes raster-based topographic information to generate a two-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 21 250 square pixels with 10-m side length and, for each pixel, we compute the total discharge (volume of water) leaving a pixel per year based on the difference between run-on, precipitation, and evapotranspiration (units of m^3 H_2O $pixel^{-1}$ $year^{-1}$) (Fig. 14.10). The water-routing algorithm arrived at using this approach differs slightly from that used by Quinn et al. (1991) in TOPMODEL. The result is a "drainage area" map that shows the total upslope area that "drains" into a given pixel. The map for Imnavait Creek is shown in Fig. 18.4 in Chapter 18 (this Vol.).

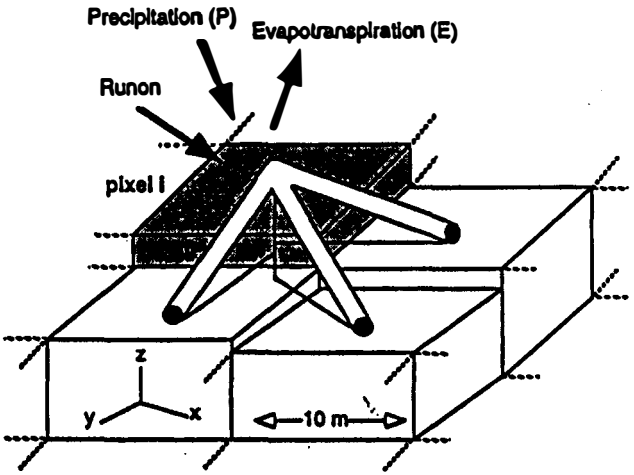

Fig. 14.10. Water-routing scheme used in T-HYDRO. Centers of pixels are connected by a network of nodes or "pipes" of equal diameter filled with soil; the elevational difference between pixels is the gravitational potential between nodes. Darcy's law is used to estimate the relative discharge through the connections and, ultimately, its routing through the landscape. Redrawn from Ostendorf and Reynolds (1993)

14.4.1.3 Potentials and Limitations

We compared the drainage area map produced by T-HYDRO with a normalized difference vegetation index (NDVI) map 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 (White and Running 1994) and is linearly related to the amount of photosynthetically active radiation (PAR) intercepted by vegetation (Sellers 1987). 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 (Monteith 1981) and NDVI is related to NPP on a biome scale (Goward et al. 1985). 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 (see Fig. 18.8, this Vol.).

To examine the spatial relationships between the NDVI and discharge, we constructed semivariograms of the maps. Since semivariance may not only depend upon the lag distance but also on direction (Cressie 1991), we examined *directional* semivariograms coinciding with the major environmental gradients in the Imnavait Creek watershed – N75°E (northeast to southwest, i.e., perpendicular to the stream channel) and N15°W (northwest to southeast, i.e., parallel to the main stream channel) – as well as those without reference to direction (*omnidirectional*). When two or more directional semivariograms differ significantly, the spatial structure of the system is called *anisotropic*. Anisotropic semivariograms occur when there is a strong gradient in the landscape. We used the anisotropy ratio to characterize the anisotropic structure of the NDVI and discharge maps (Trangmar et al. 1985):

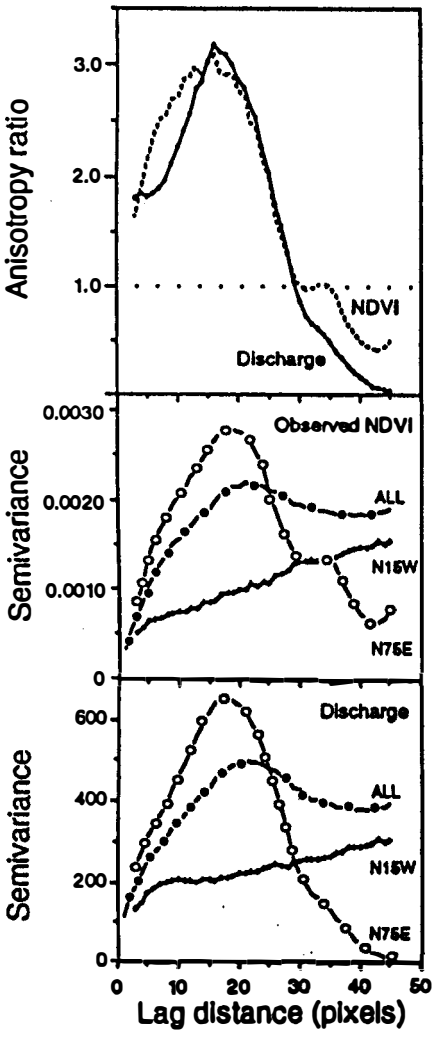

Fig. 14.11. *Directional* (N75°E, N15°W) and *omnidirectional* (all directions) semivariograms of the NDVI and discharge maps for the Imnavait Creek watershed. Anisotropy ratio defined in text

$$k(h) = \frac{\gamma(h,\theta_1)}{\gamma(h,\theta_2)}, \quad (1)$$

where k(h) is the anisotropy ratio at lag distance h, and $\gamma(h, \theta_1)$ and $\gamma(h, \theta_2)$ are semivariance in two directions, θ_1 = N75°E and θ_2 = N15°W, respectively. If k(h) is equal or close to 1, spatial heterogeneity is defined as *isotropic*.

The semivariograms of the maps are quite similar: omnidirectionals peak at ca. 21 pixels, N75°E directionals peak at ca. 18, and N15°W directionals show strong trend effects (Fig. 14.11). Both maps have an apparent anisotropic structure since the anisotropy ratio is above the isotropic line over most spatial scales. Strong anisotropy suggests that the tundra landscape portrayed by the

two maps is structured differently in the two directions, which is consistent with our field experience. Anisotropy is expected because the watershed has distinct vegetation zones in the N75°E direction and, generally in the same direction, gradients of elevation and drainage. Thus, the differences between semivariograms in the two directions likely represent real differences in the landscape.

T-HYDRO is parameterized with an estimate of the water budget based on a single year and our regression model is based on a single NDVI scene; a multi-year data set would be valuable in order to test the generality of these relationships. Nevertheless, these results support Webber's conceptual model (Fig. 14.9) and our hypothesis that the influence of topography on the local water regime can be used as a tool to predict vegetation patterns in the landscape. There are of course numerous, complex interactions and feedbacks that exist in arctic ecosystems that contribute to the high variability of the vegetation patterns, including soil properties, slope, radiation, temperature, and the glaciation history or the age and successional state of the evolving landscape (Walker and Walker 1991; Chap. 4, this Vol.). Extensions of this analysis are described below and in Chapters 17–18 (this Vol.).

14.4.2 Topographically Derived Vegetation Model

14.4.2.1 Motivation

As discussed above, we hypothesized that the general pattern of arctic vegetation – and other important long-term processes as shown in Fig. 14.9 – might be explained by topographically derived variables related to soil water. In our efforts to build simple landscape models, we made a number of assumptions directly related to Fig. 14.9. These assumptions included: average soil moisture during the growing season may be derived from local water discharge and slope; vegetation types are predictable from soil moisture and slope; the productivity and biomass of poikilohydric plants are related to soil moisture; and N availability is related to soil moisture. Based on these assumptions, we developed several "topographically derived" models (#5–#7, Fig. 14.1 and Table 14.2), so named since the only input variables are topographically derived, i.e., discharge and/or slope. Topographically derived models of moisture and nutrient availability and plant growth are described in Chapter 18 (this Vol.). We describe a vegetation model (#7) below.

14.4.2.2 Description

Ostendorf and Reynolds (1995) describe a topographically derived model (TVM) for predicting vegetation types based on the relationships between slope (tan β), discharge (δ), and plant vegetation. A general overview of the approach is given in Fig. 14.12. The objective is to predict plant vegetation

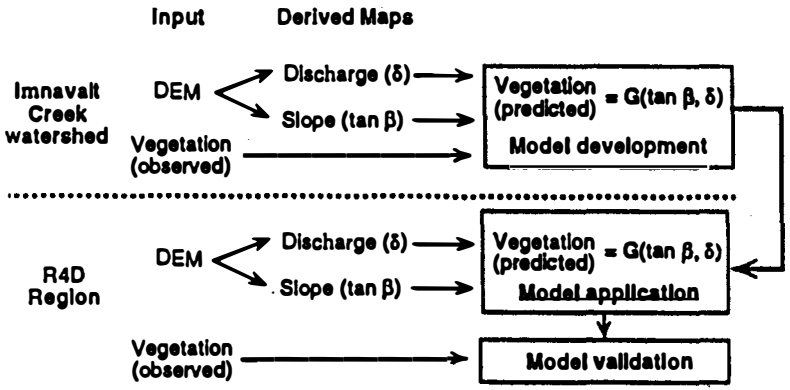

Fig. 14.12. Scheme for TVM based on functional relationships (*G*) between slope (*tan β*), discharge (δ), and plant vegetation types. The model was developed and parameterized using data from the Imnavait Creek watershed and then tested against the larger R4D region. (From Ostendorf and Reynolds 1996)

types at a particular location (pixel) based solely on a function of topographically derived surrogates of soil moisture. Slope determines the gravitational hydrological gradient and hence influences flow velocity; slope angle is inversely related to soil moisture. Discharge is estimated by the water-routing algorithm used in TOPMODEL (Quinn et al. 1991). Slope, discharge, and vegetation maps in the watershed were systematically scanned to determine the frequency of occurrence of each of five different vegetation types associated with particular slope and discharge (an example is shown in Fig. 17.3, this Vol.). The vegetation type associated with each slope and discharge combination was determined by one of two functions (G, Fig. 14.12): (1) randomly selecting a community type based on relative frequencies or (2) selecting the community type with the highest frequency of occurrence. The latter gave slightly better results (see Ostendorf and Reynolds 1996 for details of the search algorithms, functions, and spatial error analysis).

We used five vegetation types: (1) *aquatic types* dominated by sedges, grasses, or forbs; (2) *water track/riparian* tundra; (3) *moist types* (= tussock tundra) dominated by mesic dwarf shrubs, sedges, and mosses; (4) *dry types* (= heath tundra) dominated by ericaceous dwarf shrubs and lichens; and (5) *barren* or partially vegetated areas. Types 2–4 account for more than 95% of the vegetation in the Imnavait Creek and adjacent watersheds (Walker et al. 1989; see Chaps. 4 and 11, this Vol.). The model was developed and parameterized using vegetation data from the Imnavait Creek watershed, an area equal to about 10% of the R4D region (Fig. 1.1, this Vol.). It was then applied it to the total R4D region (202436 pixels) as a test of its validity.

14.4.2.3 Potentials and Limitations

The TVM model gives excellent predictions of the *total* percentage of the five vegetation types in the R4D region (compare measured vs. predicted areas in

Table 14.4. Validation of the TVM model for R4D region (22km²). The $\hat{k}$ statistic evaluates the overall accuracy of spatial predictions. Z-values based on a standardized sample number of 457 spatially independent pixels. (Modified from Ostendorf and Reynolds 1996)

Vegetation type	Measured area	Predicted area	Spatial accuracy
	(%)	(%)	(%)
Aquatic types	0.8	0.7	3.0
Water track/riparian	20.8	17.3	57.1
Moist types	58.1	63.6	75.9
Dry types	20.1	18.3	44.4
Barren	0.2	0.1	0.3
		Goodness of fit	59.3
		$\hat{k}$ =	0.29
		Z =	7.9*

*$P < 0.001$ such that $\hat{k} = 0$.

Table 14.4). 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, is a major source of error.

TVM was inspired by Webber's (1978) model and the "hydroecological approach" of Molenaar (1987). Molenaar distinguishes between operational and conditional functionality of environmental factors. Water is operational in the sense that it serves as a "nutrient." In addition to this "direct, causal effect" of water, Molenaar lists several possible conditional or "physiological noncausal" functions, namely, water as a solvent for nutrients, and as a factor regulating aeration, redox conditions and acidity, phosphorus supply, metal ion availability, humus formation and breakdown, and nutrient cycling and soil formation. These functions are especially important for arctic ecosystems as shown in Webber's (1978) model. They are a result of the long-term interactions of vegetation, soil, and hydrological processes (Fig. 14.9). It appears impossible to separate such multiple factor interactions. However, by quantifying slope and discharge gradients in the TVM model, we lump a suite of 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.

The TVM model represents a top-down approach based on topography, but it may be linked to small-scale, bottom-up models of arctic plants (e.g., Leadley and Reynolds 1992). With slope and discharge, we are able to account for a large proportion of the variance in vegetation patterning and, hence, this model could be used to delineate areas where we might expect similar ecosystem behavior at the patch scale. Further work is warranted to examine the generality of Webber's model (Fig 14.9) and the potential of TVM-type models as scaling tools.

14.5 Conclusions

One limitation to developing integrated models for the arctic is that we still do not understand many of the basic processes that control ecosystem responses to multiple stresses. An example is the role of individual species in ecosystem function. Within a given climate regime, different vegetation types exhibit different rates of carbon and nutrient cycling, water balance, and energy balance largely because of the effects of individual species on resource supply, trophic structure, and/or disturbance regime. In the arctic, ecophysiological studies show that plant species differ substantially in growth rate, nutrient uptake, tissue turnover, and litter quality (e.g., Chapin 1980; Chapin et al. 1992), processes that determine productivity and nutrient cycling. However, such detailed species-specific information for all of these processes has never been incorporated into an ecosystem model because of our lack of understanding of the specific linkages and feedback mechanisms involved. Perhaps the best alternative is to identify and employ functional groups – i.e., species that share a similar physiology or growth form, etc. – traits that can have important ecosystem consequences (Chapin 1993). Another limitation is our lack of understanding of how the destruction and fragmentation of natural habitats affect different components of a ecosystem. Individual organisms may modify their behavior, community and population dynamics can shift, and system-level fluxes of carbon, water and nutrients may be impacted in complex ways (Sousa 1984; Goigel-Turner 1987; Pickett et al. 1989; Dunning et al. 1992; DeAngelis and White 1994). Field measurements taken only at one level, e.g., the community, may belie effects on individual species, functional groups, and populations, which in turn may occur at different spatial and temporal scales (see Robinson et al. 1992).

These gaps in our knowledge – as well as many others – 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 are often inadequate or impossible, particularly at larger spatial and temporal scales (Oreskes et al. 1994; Reynolds et al. 1996). 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, homeostasis, or shifts in species are not apparent.

Models are based on assumptions and conceptualizations about how ecosystems behave and on important factors, relationships, and interactions that

must be considered. While simulation modeling has limitations, 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 described in this book. These models have a great potential to provide important information and predictions that can help us link short-term, single-factor experiments to our understanding of long-term, multifactor disturbances.

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