CHAPTER 1

Forest Ecosystem Analysis at Multiple Time and Space Scales

I. INTRODUCTION

Forests currently cover about 40% of Earth's ice-free land surface ($52.4 \times 10^6\,km^2$), a loss of $10 \times 10^6\,km^2$ from that estimated were it not for the presence of humans (see Chapter 9). Although a large fraction of forestland has been converted to agricultural and urban uses, we remain dependent on that remaining for the production of paper products, lumber, and fuelwood. In addition to wood products, forested lands produce freshwater from mountain watersheds, cleanse the air of many pollutants, offer habitat for wildlife and domestic grazing animals, and provide recreational opportunity. With projected increases in human population and rising standards of living, the importance of the world's remaining forests will likely continue to increase, and, along with it, the challenge to manage and sustain this critical resource.

Humans affect forests at many scales. In individual stands, our activities influence the composition, cover, age, and density of the vegetation. At the scale of landscapes, we alter the kinds of stands present and their spatial arrangement, which influences the movement of wind, water, animals, and soils. At the regional level, we introduce by-products into the air that may fertilize or kill forests. At the global scale, our consumption of fossil fuels has increased atmospheric carbon dioxide levels and possibly changed the way that carbon is distributed in vegetation, soils, and the atmosphere, with implications on global climate. The worldwide demand for forest products has stimulated not only the transfer of processed wood products from one country to another, but also the introduction of nonnative tree species, along with associated pests, that threaten native forests and fauna. While the management of forested lands is becoming increasingly important, it is also becoming more contentious because less land is available for an increasing range of demands. Pressure to extract more resources from a dwindling base is leading to a number of challenging questions. Is it possible to maintain wildlife habitat and timber production on the same land unit, and still retain the land's hydrologic integrity? Where should forested land be preserved for aesthetic values, and where should it be managed for maximum wood production? How can an entire watershed be managed so that the availability of water to distant agricultural fields and cities is assured?

This book does not provide specific answers to these management questions, as each situation is unique. Rather, it offers a framework for analyses and introduces a set of tools that together provide a quantitative basis for judging the implications of a wide variety of management decisions on the natural resource base, viewed at broader spatial scales and longer time dimensions than was previously possible. It is our supposition that if we are to be successful stewards of forests we must find a way to integrate what is known into predictive models and apply new methods to validate or invalidate the predictions of these models over Earth's broad surface. We believe that advances in modeling provide such a basis for the analysis of forest ecosystems at multiple scales and strive to illustrate the underlying principles and their application.

One of the major concessions in scaling that we are required to accept is the need to reduce the amount of detail to a minimum. This requirement has the advantage of reducing the cost and complexity of analyses, but it demands insights into which ecosystem properties are critical and then determining how they may be condensed into integrative indices and monitored at progressively larger scales. By modeling ecosystem behavior at different scales we gain confidence in the appropriateness of key variables, when those variables should best be monitored, and the extent to which the analyses apply generally.

This book is structured to start the analysis of forest ecosystems at the level of individual stands and gradually expand the time and space scales. In doing this, we have incorporated throughout the text many of the principles presented in the U.S. Ecological Society of America report on "the scientific basis for ecosystem management" (Christensen *et al.,* 1996). We emphasize quantifying our present understanding of ecosystem operation with soundly based, tested ecological models, but we also identify some important gaps in research. When covering the breadth of topics needed for multiscale analysis, we are unable to review all topics comprehensively but provide over a thousand references to original sources. Although we incorporate how human activities and forested ecosystems interact, we do not advocate specific management policies. We believe, however, that sounder decisions are possible by projecting the implications of various management policies at a variety of scales when models rest on common underlying biophysical and ecological principles.

II. THE SCIENTIFIC DOMAIN OF FOREST ECOSYSTEM ANALYSIS

A forest ecosystem includes the living organisms of the forest, and it extends vertically upward into the atmospheric layer enveloping forest canopies and downward to the lowest soil layers affected by roots and biotic processes. Ecosystem analysis is a mix of biogeochemistry, ecophysiology, and micrometeorology that emphasizes "the circulation, transformation, and accumulation of energy and matter through the medium of living things and their activities" (Evans, 1956). For example, rather than concentrating on the growth of individual trees, the ecosystem ecologist often expresses forest growth as net primary production in units of kilograms per hectare per year. Ecosystem ecology is less concerned with species diversity than with the contribution that any complex of species makes to the water, carbon, energy, and nutrient transfer on the landscape.

Ecosystem studies consider not only the flux of energy and materials through a forest, but also the transformations that occur within the forest. These transformations are an index of the role of biota in the behavior of the system. Forest ecosystems are open systems in the sense that they exchange energy and materials with other systems, including adjacent forests, aquatic ecosystems, and the atmosphere. The exchange is essential for the continued persistence of the ecosystem. A forest ecosystem is never in complete equilibrium, a term appropriate only to closed systems in the laboratory. An excellent primer on ecosystem analysis terminology and principles is a textbook by Aber and Melillo (1991).

Although we are studying forest ecosystems across multiple time and space scales, we initiate our analysis at a forest stand, a scale where most of our measurements and understanding originated (Burke and Lauenroth, 1993). A hierarchical structure is common to all of science in that a reference level of interest is first defined where patterns are observed and described. A causal explanation is sought for these patterns at a finer resolution of detail, while their implications and broader interactions become apparent at a level above (Passioura, 1979; O'Neill *et al.,* 1986). This book is based on a hierarchical structure of studying ecosystems. For example, in evaluating net primary production, we explore details of photosynthesis, respiration, and carbon allocation at the canopy level in the first section of the book to understand the causal mechanisms and their controls. In Section II, we follow stand development through time, evaluating how net primary production changes. In Section III, the effects of photosynthesis combined with other ecosystem properties are shown to interact across the landscape, modifying the local climate, the flow of rivers, and the seasonal variation in regional atmospheric CO_2.

An initial step in ecosystem analysis is to measure the amount of material stored in different components of the system, for example, the carbon stored in stem biomass, water stored in the snowpack, and nutrients stored in the soil. In systems terminology, these are the *state variables* that can be directly measured at any given time. Innumerable studies have been published measuring the current state of forest ecosystems. Frequently, however, the rates of change of these system states, or *flows of material,* are of greatest interest. What is the rate of snowmelt, stem biomass accumulation, or nutrient leaching in a particular system? These questions require study of the processes controlling energy and matter transfer, a much more difficult undertaking. In these process studies, we wish to identify the *cause–effect relationships* controlling system activity, which is often called a mechanistic approach. This identification of system states and multiple cause–effect relationships that operate in a forest ecosystem to regulate material flows can be quantified and organized with an ecosystem simulation model. This type of model becomes the starting point of our space/time scaling of ecosystem principles.

III. THE SPACE/TIME DOMAIN OF ECOSYSTEM ANALYSIS

A. Seasonal Dynamics Operating in Individual Forest Stands

We begin multiscale analysis of forest ecosystems with the *stand* as our reference level, which includes the vegetation and surrounding physical environment, linked together through a variety of biological, chemical, and physical processes. Most scientific understanding of ecosystem processes has been gained by direct field measurements and experiments on small study plots usually <1 ha (10,000 m^2) over a period from a few days to at most a few years (Levin, 1992; Karieva and Andersen, 1988). From an ecological scaling point of view, we like to refer to these studies as the *stand/seasonal* level of analysis (Fig. 1.1). Such studies are designed to clarify the ecological processes and controls on the forest without regard to the spatial heterogeneity of the surrounding landscape, or the temporal changes that forests have undergone or will undergo in future years. In the first section of the book (Chapters 2–4) we review forest ecosystem processes and the mechanisms controlling their activity.

Unfortunately, many of the major ecological concerns facing natural resource managers and policy makers are not tractable at the spatial and time scales within the stand/seasonal domain where we have the most direct insights. Forest managers are generally responsible for decisions that affect large and diverse areas, and policy makers must visualize *future* conditions and ecosystem responses that may result from policies made *today*. Consequently, to make forest ecosystem analyses more relevant it is essential that stand/seasonal understanding of ecosystem processes be extrapolated in space and forward in time. Attempts to execute direct studies over large regions (Sellers *et al.,* 1995) or for long periods (Magnuson, 1990) cost tens of millions of dollars, so are rarely attempted. We must search for an alternative means by which knowledge gained at the stand/seasonal level can be expressed in a quantitative way to serve as a platform for extrapolation to larger space and time scales. A set of conceptually linked computer simulation models offer a valid alternative to large-scale ecosystem experiments if they can represent the mechanisms coupling biogeochemical processes in a realistic way yet not require an exorbitant amount of data that are difficult or impossible to acquire.

B. Role of Models in Ecosystem Analysis

Models have been an integral tool of ecosystem analysis since the earliest days of systems ecology (Odum, 1983). Ecosystems are too complex to describe by a few equations; current ecosystem models have hundreds of equations which present interactions in noncontinuous and nonlinear ways. Furthermore, these models provide the organizational basis for interpreting ecosystem behavior. Swartzman (1979) identified six primary objectives for ecosystem simulation models: (1) to replicate system behavior under normal conditions by comparison with field data, (2) to further understand system behavior, (3) to organize and utilize information from field and laboratory studies, (4) to pinpoint areas for future field research, (5) to generalize the model beyond a single site, and (6) to investigate effects of manipulations or major disturbances on the ecosystem over a wide range of conditions. Active ecosystem modeling programs pursue all of these objectives, although relevance to land management is attained only in objectives 5 and 6.

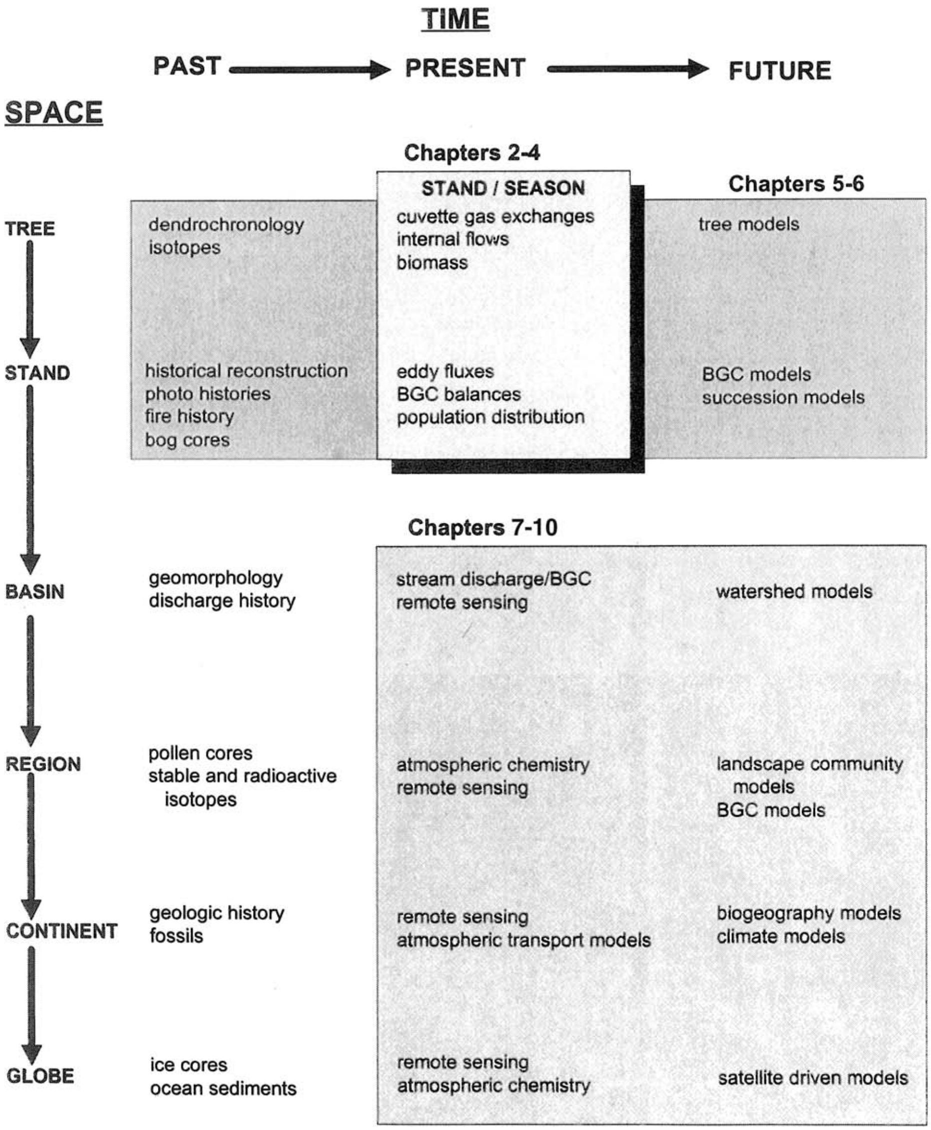

FIGURE 1.1. Examples of measurement techniques available for forest ecosystem analysis at different time and space scales. Temporal analysis of past ecosystem activity is possible from quasi-permanent records obtained by tissue or elemental analysis, such as tree rings, isotopic ratios, and pollen records from ice and bog cores. Spatial analysis beyond the stand level requires some type of remote sensing technology, and temporal analysis into the future requires some form of modeling. The scales and measurements depicted in the shaded boxes are the subject of this book. The stand/seasonal demarcation represents the space/time scale where most ecological understanding has been attained.

A comprehensive biogeochemical model should treat all of the processes presented in Table 1.1, although we are aware of no current model that does so completely. It is essential that energy, carbon, water, and elemental cycles all be represented, even if simplistically. It is precisely the interactions among the cycles that are the core of ecosystem analysis. The inherent differences in time dynamics among these cycling processes should also be acknowledged, although not necessarily by explicit calculations. Leaf energy balances change within minutes, system gas fluxes change diurnally, tissue growth and carbon

TABLE 1.1
Component Processess of a Comprehensive Ecosystem Biogeochemical Model

- Energy balance
  - Short-wave radiation balance (incoming—outgoing)
  - Long-wave radiation balance (incoming—outgoing)
  - Sensible heat flux
  - Latent heat flux
  - Soil heat flux
- Water balance
  - Precipitation partitioning (snow versus rain)
  - Canopy and litter interception and storage
  - Soil surface infiltration
  - Soil water content
  - Subrooting zone outflow
  - Hill slope hydrologic routing
  - Evaporation
  - Transpiration
- Carbon balance
  - Photosynthesis, gross primary production
  - Maintenance respiration
  - Growth respiration
  - Photosynthate storage
  - Net primary production
  - Carbon allocation
    - Leaves, stem/branches, roots, defensive compounds, reproduction
  - Phenological timing
    - Canopy growth/senescence
    - Litterfall of leaves, turnover of stems and roots
  - Decomposition
  - Net ecosystem production
- Elemental balance
  - Sources (atmosphere, rock weathering, biological fixation)
  - Soil solution transformation
  - Immobilization, nitrification, denitrification
  - Mineralization
  - Root uptake
  - Tissue storage
  - Internal recycling
  - Volatilization
  - Leaching
  - Export through harvesting and erosion

allocation dynamics are observable at weekly to monthly intervals, whereas nutrient mobilization may be measurable seasonally. Different forest ecosystem models have time steps ranging from an hour to a year, and newer models contain sections that represent processes at different time steps.

Of equal importance is that each process is treated with approximately the same level of detail. A model that computes photosynthesis of each age class of needles but fails to couple the nitrogen cycle to photosynthetic capacity is not balanced. Most forest biogeochemical models suffer some deficiencies in balance because they began as single process models and only later, often in much less detail, added other processes critical to ecosystem operation. Beyond some of these basic properties of good ecosystem modeling, every model differs depending on the specific objectives pursued. Some ecosystem models optimize energy partitioning as part of a climate model, whereas others focus on forest productivity, hydrology, or elemental cycles.

Ecosystems, because of their dynamic and interconnected properties, cannot be subjected to classic experimentation where one variable at a time is modified (Rastetter, 1996). Computer simulation models of ecosystem behavior offer a valuable experimental alternative because they allow multivariant interactions to be traced and analyzed. With simulated experiments, the accuracy with which different variables need to be measured can also be estimated. Such ecosystem models establish mathematical relationships in a simple but increasingly mechanistic way, to clarify causal connections and integrate system operation. On this basis, models can *predict responses to new conditions* that do not yet exist. For example, computer simulation models can predict how stream discharge may respond to harvesting in a watershed and identify possible flood problems before any logging commences. Computer simulation models have been the primary means for evaluating potential responses of natural ecosystems to future climate changes. For example, the Vegetation/Ecosystem Modeling and Analysis Program (VEMAP) has simulated ecosystem biogeographical and biogeochemical responses to climatic change for the entire continental United States (VEMAP, 1995). This project relied almost exclusively on computer simulations to provide a reasonable estimate of future conditions.

1. Example of a Scalable Ecological Model

Because a primary theme of this book is scaling in space and time, we will frequently use a model originally designed for multiscale applications, the FOREST-Bio-Geo-Chemical simulation model (FOREST-BGC) to explore ecosystem interactions. FOREST-BGC originated as a stand-level model of forest biogeochemical cycles, in effect, a model quantifying our understanding of the mechanistic processes of energy and mass fluxes in the stand/season space/time domain. Other forest ecosystem models are also available, and results from these will be illustrated (see reviews by Ågren *et al.,* 1991; Tiktak and van Grinsven, 1995; Ryan *et al.,* 1996a; Thornley and Cannell, 1996). FOREST-BGC is a process-level simulation model that calculates the cycling of carbon, water, and nitrogen through forest ecosystems (Fig. 1.2; Running and Coughlan, 1988; Running and Gower, 1991). FOREST-BGC calculates most of the important ecosystem processes covered in this book. The model has both daily and annual time steps, recognizing the substantial differences in the response of different ecosystem processes. Hydrologic and canopy gas

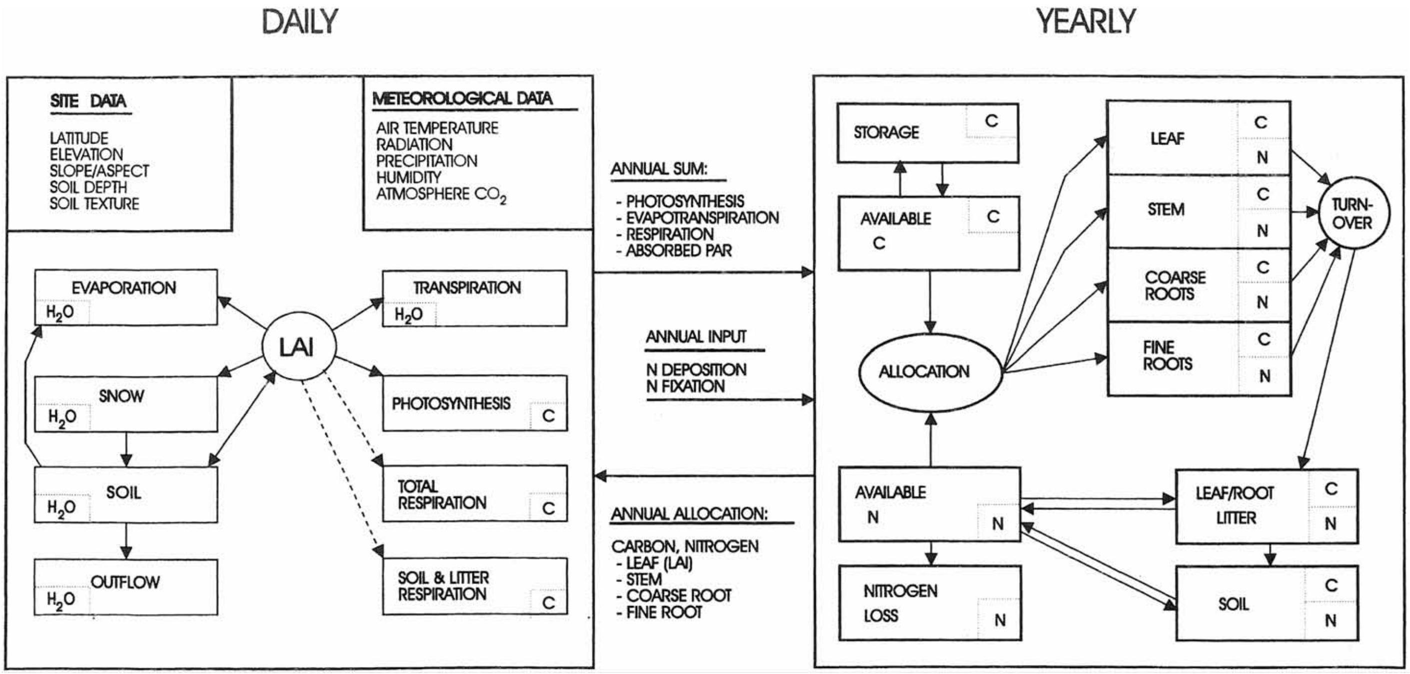

FIGURE 1.2. Compartment flow diagram for the FOREST-BGC ecosystem simulation model. This diagram illustrates the state variables of carbon, water, and nitrogen, the critical mass flow linkages, the combined daily and annual time resolution, and the daily meteorological data required for executing the model. The major variables and underlying principles associated with the model were developed specifically for application at multiple time and space scales, and for compatibility with remote-sensed definition of key ecosystem properties.

exchange processes are calculated daily, while ecosystem carbon and nitrogen processes are computed annually.

The model structure of FOREST-BGC is based on some key simplifying assumptions that have proved particularly valuable in extending ecosystems analyses to regional levels (Chapters 7–9). These simplifying assumptions give us examples of how much ecological detail must be sacrificed in an ecosystem model to attempt regional scaling. Trees are not defined individually as in a typical forest stand growth model, only the cycling of carbon, water, and nitrogen is expressed in mass units. Species also are not explicitly identified, although species-specific physiological characteristics can be represented. Geometric complexities of different tree canopies are reduced to a simple quantification of the sum of all leaf layers as leaf area index (LAI). Treatments of internal tree physiology such as carbohydrate and water transport are minimized. Belowground root system and soil processes are treated in a simplified way to reduce requirements for difficult to obtain field data. Finally, FOREST-BGC was designed to require only standard meteorological data, namely, daily maximum–minimum temperature and precipitation, so that the model might be applied beyond those few sites with sophisticated instrumentation. Many of the other models presented in this book make different assumptions of model structure that are valid for other objectives but do impede spatial applications.

Even more simplifying assumptions are incorporated in a Light Use Efficiency (LUE) model of forest productivity we present in Chapter 3 (Landsberg and Waring, 1997). This model estimates forest productivity simply by quantifying the photosynthetically active radiation absorbed by a forest canopy, and then places some climatological and physiological restrictions on the conversion of that solar energy into above- and belowground biomass, thus bypassing all of the complexity of quantifying carbon, water, and nitrogen cycles found in FOREST-BGC. The LUE models can appropriately be operated with satellite data only, and hence they provide a global estimate of primary productivity, the ultimate spatial scaling exercise (see Chapters 9 and 10).

2. Importance of Model Validation

Because the initial stand/seasonal ecosystem model is a vehicle central to the success of the space/time scaling to follow, high confidence in the validity of this first type of simulation model is essential. How well does the model capture the structure, controls, and dynamics of a real forest ecosystem? Obviously that question can never be answered for all forests and circumstances, but by testing some of the key assumptions, and finding good agreement between predicted and measured values for a wide range of systems, a basis is provided for judging the model's soundness. Rykiel (1996) formalized the steps required in ecological model validation as beginning with evaluation of the theoretical basis of the model, then testing the operational integrity of the computer code, and finally making comparisons of model output with measured data relevant to the intended domain and purpose of the model.

Some parts of FOREST-BGC have undergone considerable testing, particularly the hydrologic and carbon cycle components (Running, 1984a,b; Knight *et al.,* 1985; McLeod and Running, 1988; Nemani and Running, 1989a; Hunt *et al.,* 1991; Korol *et al.,* 1991; Band *et al.,* 1993; Running, 1994; White and Running, 1994; Korol *et al.,* 1995). It is difficult, however, to validate every aspect of an ecosystem model. We recommend a group of variables that can be accurately measured in the field and reflect a range of ecosystem interactions linked to carbon, water, and nutrient cycles. These include

- snowmelt
- soil moisture depletion
- predawn leaf water potential
- leaf area index
- net primary production
- stem biomass
- leaf litterfall
- leaf nitrogen content
- leaf litter nitrogen content

Throughout this book we will present results of studies that confirm the ability of forest ecosystem models to predict these variables, often within the accuracy that can be obtained with direct field measurements. Confidence in ecosystem models is best developed at the stand level first, where a wealth of data exists. Tests of model predictions at larger space and time scales are much more difficult, although new technologies are providing a means of validation at these scales also.

IV. TIME AND SPACE SCALING FROM THE STAND/SEASONAL LEVEL

Once we have gained some confidence in our understanding of how major processes interact in a single stand seasonally, we can begin to extrapolate principles to larger space and time scales required for land management. Making these extrapolations, however, requires a much wider array of tools, including multiple models that demand different input data. FOREST-BGC evolved first as a stand/season model, but, because of our interest in space and time extrapolation, a family of conceptually related models was produced (see Sections II and III). The logical connections among this family of models allow the validation activity from one model to improve our confidence in a subsequent model designed for larger spatial scales, Because FOREST-BGC has undergone validation tests at the stand level for many years, we have higher confidence in simulations extrapolated forward in time, or spatially to a region, despite the validation not being at the same scale as the current model implementation.

A. Scaling in Time

Section II of this book (Chapters 5 and 6) concentrates on temporal scaling of our stand-level understanding. Looking back in time allows us to develop an appreciation and understanding of the temporal dynamics previously experienced by an ecosystem. We can quantify the ecological history of a forest through analysis of tree ring growth increments, fire scars, tissue stable isotope composition, and a variety of other methods including written and photographic records (Fig. 1.1). While we can measure current activity of ecosystem processes with gas exchange cuvettes, water budgets, and biomass analysis, to project into the future we must rely on computer models, which justifies care in constructing them and testing them as widely as possible (Dale and Rauscher, 1994).

1. Stable Isotopes

Stable isotope analyses provide one of the few consistent and available methods for *temporal scaling backward in time.* In this book we make an effort to illustrate opportunities for greater use of stable isotope analyses in nearly every chapter. Many elements are composed of multiple isotopes differing slightly in atomic mass because of extra neutrons but possessing nearly identical chemical activities (Table 1.2; Schimel, 1993). These elements with higher atomic mass do not decay radioactively, so are known as stable isotopes. Kinetic reactions, such as diffusion, and biochemical reactions, such as photosynthesis, slightly discriminate against these heavier isotopes, causing subtle variations in the concentrations of the stable isotope relative to the standard isotope for each element (Fig. 1.3). For example, although the standard carbon in any biological tissue is ^{12}C, some fraction less than 1% will be ^{13}C, depending on the kinetic and biochemical reactions that occurred to synthesize a carbon-bearing molecule such as cellulose. Carbon also exists in an unstable radioactive form as ^{14}C, whose half-life is 5715 years. In biological material, the decay of ^{14}C since its incorporation provides a means of dating the age.

The natural abundances of stable isotopes found in rocks, plants, animals, atmosphere, and water bear witness to their origin. Improvements in the sensitivity of mass spectrometers have allowed detection of isotopic ratios that previously could not be done, and have opened an entire new array of retrospective ecosystem analysis. As ecosystem studies have expanded in scope to assess changes over landscapes and geologic time scales, analyses of multiple isotopes of C, N, S, H, O, Sr, and Pb have provided integrated, long-term records on the frequency and extent of drought, documented shifts in the diets and distribution of animals, and provided a quantitative record of the amount of anthropogenic pollutants deposited on forests, fields, and water bodies throughout the world.

When analyses are extended across ecosystems that include urban areas, our increasing dependence on fossil fuels becomes clear through changes recorded in the isotopic composition of $^{13}CO_2$ in the atmosphere and in the annual rings of trees. Organic matter contains hydrogen and oxygen derived from water which shows through its isotopic composition the temperature at which precipitation fell, so that climatic changes also can be assessed through isotopic analyses. Rocks, and soils derived from them, differ in the isotopic composition of sulfur, strontium, and lead. These differences are reflected in the

TABLE 1.2

Percent Abundance of Stable Isotopes Commonly Employed in Ecosystem Studies[a]

Carbon	Oxygen	Hydrogen	Nitrogen	Sulfur	Strontium	Potassium	Magnesium
^{12}C 98.89	^{16}O 99.763	H 99.9844	^{14}N 99.64	^{32}S 95.02	^{84}Sr 0.56	^{39}K 93.08	^{24}Mg 78.8
^{13}C 1.11	^{17}O 0.0375	D 0.0156	^{15}N 0.36	^{33}S 0.75	^{86}Sr 9.86	^{40}K 0.0119	^{25}Mg 10.15
	^{18}O 0.1995			^{34}S 4.21	^{87}Sr 7.00	^{41}K 6.91	^{26}Mg 11.06
				^{36}S 0.02	^{88}Sr 82.58		

[a] Adapted from Schimel (1993).

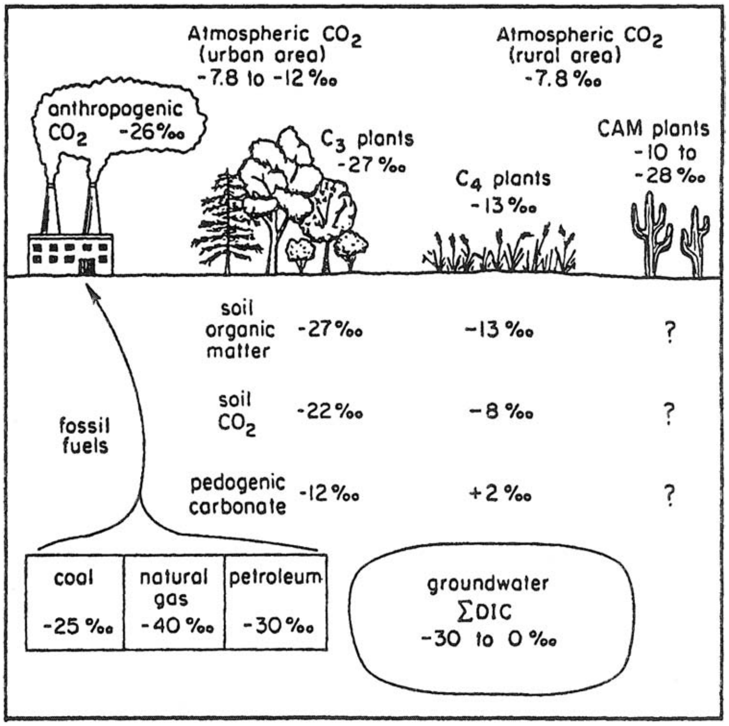

FIGURE 1.3. The concentration of the stable isotope carbon-13 expressed as a reduction in ^{13}C relative to a background reference (standard delta $^{13}C = 0$, with units of parts per thousand, or δ‰) shows that trees, tropical grasses, and desert cacti produce biomass with distinctly different isotopic composition from that of CO_2 in the atmosphere as a result of differences in photosynthetic pathways. Further isotopic discrimination occurs as organic matter is decomposed or converted to various fossil fuels. Combustion of fossil fuels and burning of biomass cause a reduction in the $^{13}C/^{12}C$ ratio of CO_2 in the atmosphere which, through analysis of trapped gases in dated ice cores, provides a quantitative record of anthropogenic activities for many centuries into the past. Similar isotopic fractionations occur with other elements, which provide ecologists quantitative estimates of the diets and home ranges of animals, the rates of nitrogen fixation and mineral weathering, and the amounts of nitrogen and sulfur deposited as pollutants. (From Boutton, 1991.)

tissue composition of plants and the bones and other tissues of all animal life, which provides a basis for locating the origin of elephant tusks and the ranges of other animals in geologically variable landscapes. Stable isotope analyses also play a role at regional and global scales in verifying model assumptions concerning the movement of pollutants and the relative importance of terrestrial and oceanic production on the global carbon balance.

2. Range of Ecosystem Time Dynamics

Many ecosystem processes occur continuously, although the process rates are controlled by prevailing conditions. One can consider litter decomposition to occur almost continuously except under extreme conditions of temperature and aridity. Litter decomposition can be described based on cause–effect relationships between the temperature and hydration of the substrate tissues and observed rates of litter decay. Other processes occur in predictable cycles; daily photosynthesis begins every morning at sunrise, or seasonally with canopy leaf emergence every spring. Because of the high level of regularity and predictability, these process activities can be treated as a straightforward *deterministic* relationship in a simulation model. Other ecosystem processes, however, are initiated by discrete events that can be highly unpredictable in time, originate well beyond the boundaries of the ecosystem, yet produce major consequences. Major disturbances such as forest fires and hurricanes are good examples, and these are often treated as random events with *stochastic* models. A model is stochastic if even only one process is described mathematically as a random event in the system.

Considering the time domain of tree life cycles, what we find in the historical development of most forests is a progression of phases following establishment. Without disturbance the progression is fairly predictable, but disturbance is a part of forest history, although its occurrence is not necessarily random. Disturbance that leads to change in structure often occurs when competition for resources becomes intense and the ability of trees to withstand fire, insect, or disease outbreaks approaches a minimum. At such time, a disturbance is likely to open the forest canopy and improve conditions for surviving trees and their replacements.

To project a forest ecosystem response forward in time, we use models that simulate forest development and vegetation dynamics (Shugart *et al.,* 1992). Such models are able to predict the expected changes in biogeochemical cycling, and the progressive life cycle of species through their recruitment, growth, death, and ultimate replacement, following specified kinds and intensities of disturbance. The models, to accommodate current conditions, must also account for introductions and extinctions of species of plants, animals, and pathogens that alter normal competitive relations. In Chapter 5, examples of models predicting stand development and vegetation dynamic are presented.

In Chapter 6, stress in forest development is specifically linked to disturbance. Experiments and observations are reported which quantify changes in resource availability and subsequent system response to fire, insects, and disease. A general measure of ecosystem carbon stress is the growth efficiency by which sunlight is captured through photosynthesis and transformed into stem growth. Other indices related to nutrient and water availability provide explanations to observed changes in growth efficiency. These *stress indices* can be predicted with ecosystem process models such as FOREST-BGC, or with more simplified LUE models, and thus serve as a type of validation. In addition, some indices derived from dendrochronology and stable isotope analyses provide retrospective information about disturbances that occurred over the life span of the trees.

B. Scaling in Space

In Section III, we focus on spatial scaling. Chapter 7 presents a hierarchical framework for integrating the tools of remote sensing, geographic information systems (GIS), topographic climatic extrapolation, and ecosystem modeling to analyze current ecosystem activity over large areas and to project ecosystem responses into the future. The Regional

Ecosystem Simulation System, RESSys, is introduced, and some of the component models for local climate extrapolation, topographic partitioning, and hydrologic routing are discussed (Running *et al.,* 1989; Band *et al.,* 1993). The necessity for using a forest ecosystem model with carefully simplified input variables becomes evident, for how could one obtain data of leaf age distribution or root lengths for simulations over a 100,000-ha forest?

The integration of remote sensing, GIS, and computer modeling has proved essential for regional scale ecosystem analysis, and we describe some of the latest examples in Chapters 8 and 9. The most advanced regional analyses drive sophisticated ecosystem process models forward in both time and space, providing simulations of vegetation dynamics and biogeochemistry covering whole continents for hundreds of years into the future (VEMAP, 1995). Validation of these large-scale computer model projections is becoming one of the biggest challenges in ecology. It is from these space/time integrated modeling tools, however, that ecology is able to offer a major advance in resource analysis. An important decision in the spatial representation of landscapes is whether the smallest recognizable elements (or cells) are considered connected or unconnected in the horizontal dimension. The question asked is, Does the ecosystem activity in one cell influence the activity in adjacent cells? Depending on the answer to this seemingly mundane question, the tools and theory for landscape representation are substantially different, as illustrated in Chapters 8 and 9. For example, if decomposition can be considered spatially independent of the surrounding mosaic of forest ecosystems, it greatly simplifies the subsequent spatial analyses.

On the other hand, processes that control the spread of fire, outbreaks of insects and diseases, or the transport of water and sediment in streams require an explicit spatial understanding of surrounding ecosystems, which greatly complicates the analyses. The discipline of landscape ecology has evolved numerous methods to quantify and interpret spatial connectiveness. These techniques attempt to describe the pattern of the landscape by defining the spatial arrangements of different ecosystem types, and by recording changes in the sizes and shapes of those recently disturbed. We introduce techniques for evaluating landscape structure, heterogeneity, vegetation redistribution, and disturbance processes in Chapters 7 and 8. However, because the focus of this book is primarily on ecosystem structure and function rather than pattern and interpretation, we leave the detailed treatment of these geographic topics to others (Forman, 1995; Turner and Gardner, 1991).

V. MANAGEMENT APPLICATIONS OF ECOSYSTEM ANALYSIS

Management applications of ecosystem analysis commonly encompass large areas, which imposes a requirement that the types and accuracy of data match the available sources. Ecosystem analysis can provide through model simulations some estimates of important variables that are difficult to measure directly. For example, using hydrologic equilibrium theory, one can infer a balance that is commonly established among climatic properties, soil water holding capacity, and the maximum leaf area that forests will support. It is a seeming contradiction that these rather sophisticated ecosystem models and analytic tools are particularly valuable in data-poor areas. A handful of key measurements, some acquired by satellite and synthesized with a model, can allow an inference of ecosystem activity that would be nearly impossible to acquire through standard ground surveys. The first requirement in preparing for regional scale assessments is to construct a coordinated, geographically specific information base that includes the most important system attributes such as weather data, satellite imagery of the mosaic of vegetation and soils, snowpack depth, streamflow, and location of wildlife populations. Most established land management agencies have acquired a tremendous amount of these kinds of data, but they are often not available in a consistent, geographically referenced format. The second requirement is to maintain the array of ecosystem and environmental data in an immediately accessible form. Finally, ecological process models are needed that use the archived data sets and real-time information to project both near and long-term ecosystem responses. We will illustrate how these data sets are developed, archived, and utilized in models developed specifically for projecting regional ecosystem responses to changing conditions, including both natural disturbances and those associated with management policies.

Many of the concepts and analyses presented in this book come from studies conducted across the Oregon transect (Fig. 1.4). The 250-km transect provides a climatic gradient for the distribution of temperate evergreen forests that encompasses the full range in productivity represented by this biome (Waring and Franklin, 1979). Because of this unique compression of ecological diversity and the commercial value of the Pacific Northwestern

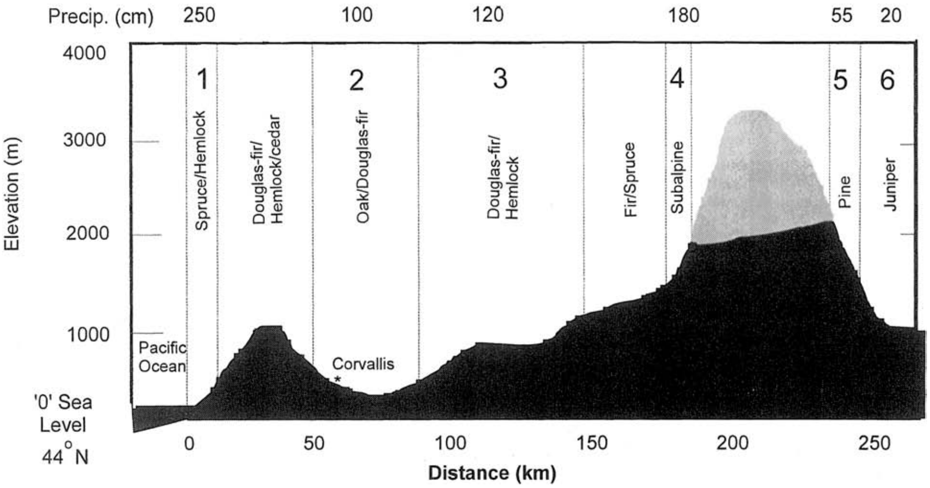

FIGURE 1.4. Graphic depiction of the elevational and climatic gradient across the Oregon transect, the location of many studies cited in this book. The transect begins in the temperate rain forests along the Pacific Ocean and ends in juniper woodland only 250 km to the east after crossing two mountain ranges. The transect encompasses virtually the global range of structure and productivity of evergreen coniferous forests. A long history of forest ecosystem research makes this region one of the most studied and best understood forest landscapes on Earth (Waring and Franklin, 1979; Gholz, 1982; Edmonds, 1982; Peterson and Waring, 1994). Competing socioeconomic values for timber production, wildlife habitat, anadromous fish populations, hydroelectric power production, and recreation also make this region ideal for testing the soundness of multiresource ecosystem management principles.

forests, a long and rich history of forest research is available from which to draw examples (Edmonds, 1982; Peterson and Waring, 1994). This text will highlight the many innovations in forest ecosystem research that have come from studies in this region.

VI. RELATED TEXTBOOKS

This text would not be possible without the historical development of forest ecosystem analysis. Important books on forest ecosystems were published under the auspices of the International Biological Program (Reichle, 1981; Edmonds, 1982) and precursors to that program (Bormann and Likens, 1979). More recent texts related to forest ecosystem analysis include *Forest Stand Dynamics,* emphasizing species-specific stand development and individual species (Oliver and Larson, 1996). *Terrestrial Ecosystems* by Aber and Melillo (1991) has a particularly good chapter on ecosystem analysis principles. Principles of landscape analysis which emphasize the quantification and interpretation of landscape patterns are well treated in publications by Formann (1995) and Turner and Gardner (1991). Ecophysiology of forests are covered by Smith and Hinckley (1995a,b). *Biogeochemistry* at the global scale is the topic of a valuable book by Schlesinger (1991, 1997). Two other texts on forest ecosystems have been published that contain additional information and offer somewhat different perspectives (Perry, 1994; Landsberg and Gower, 1997).

VII. WEB SITE FOR UPDATED MATERIALS

In the second edition of the textbook, we provided a CD-ROM on which additional images and computer code for two models were provided. To keep up to date, we have established a web site to replace the CD-ROM: http://ntsg.umt.edu/textbooks/. There you will find animated illustrations of daily, seasonal, and interannual variation in ecological and meteorological conditions at the landscape, regional, continental, and global scales, along with codes and tutorials for various simulation models.