



Sustainability of Managed Temperate Forest Ecosystems

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We would expect foresters to know a lot about sustainable management. Forests take long periods of time to develop, and foresters have been managing temperate forest ecosystems for several centuries. They are used to taking a long view, planning for forests and planting trees that are not likely to be harvested within their professional, and often personal, life span. At the same time, the concept of sustainability in forestry has often been narrow and limited to continued production of wood fiber. Similarly, our scientific understanding of the basis for forest productivity and techniques for assessing trends in productivity, especially of the entire ecosystem and over long periods of time, is not very robust.

This chapter reviews what we know about the sustainability of managed temperate forest ecosystems. Since this is such an immense topic, the review is primarily an overview with an emphasis on recent knowledge and emerging concepts of the productivity and maintenance of forest ecosystems rather than a comprehensive review of the last 100 years of forest science.

The chapter begins with a definition of sustainability, taking a broad view of forest productivity and sustainability rather than simply focusing on the production of wood products. The first major section considers the status of our knowledge of major ecosystem processes related to sustainability; it will be clear that much critical information on long-term productivity is lacking, particularly on the soil ecological subsystem, and other data, such as on respiration, are nearly impossible to gather. Next, biophysical measurements of sustainability are considered along with

some suggestions for a minimal monitoring program. An extensive section on alternative management approaches follows; development and application of alternative silvicultural and landscape practices offer immense potential for integrating sustainable production of environmental goods and services with commodities. A section describing existing approaches, models, and data sets follows. The review concludes with a series of proposals for managed temperate forests to (a) develop critical scientific information, (b) implement and test new management systems, and (c) assess long-term productivity.

Definition of sustainability

Sustainability refers to the maintenance of the *potential* for our forest and associated aquatic ecosystems to produce the same quantity and quality of goods and services in perpetuity. Potential is emphasized since it makes implicit the option to return to alternative conditions rather than focusing exclusively on current conditions. This concept of sustainability considers a broad range of goods and services. It includes, for example, retaining the forest's capacity to provide functional services, such as regulating the flow of streams and minimizing the loss of nutrients and soil as a result of erosion. It means an ability to provide habitat, either currently or at some future time, for the full array of animal and plant organisms on the site. And, of course, sustainability means the continuing capacity to provide the same quantity and quality of products for human consumption.

The basis for sustainability lies in maintaining the physical and biological elements of productivity. Hence, sustainability requires that we prevent the following:

- Degradation of the productive capacity of our forest lands and the associated water bodies, that is, net loss of productivity, and
- Loss of genetic diversity, including extirpation of species, that is, net loss of genetic potential.

Each of these principles has both an ecological and an ethical basis; even though they are human constructs, they can be objectively defined in ecological terms. Principle two—no net loss of genetic potential—is probably the most fundamental, since we can sometimes restore productive capacity to degraded ecosystems but have only very limited capacity to restore lost genetic potential. No principle, in my view, is absolute or inviolate. There will be times when rational, even ecologically sensitive, human beings will violate either principle. But when such violations occur, they should be done with society's full knowledge of the act and its consequences, not as a result of ignorance and not in secrecy.

Sustainability absolutely should *not* be viewed exclusively or primarily in terms of the short-term production of specific commodities, such as sawlogs or trophy ungulates, although such concerns are an appropriate component of a concept of sustainable forestry. Assuming the above, sustainable practices for managed temperate forest ecosystems should place a very high priority on practices that meet the dual standards of maintaining (a) productive capacity and (b) genetic diversity. It is essential to maintain a broad view of productivity—goods and services—and of the spatial and temporal scales to which it is to be applied rather than to adopt a narrow construct that focuses solely on the production of wood fiber.

Status of knowledge of major ecosystem processes

There is a substantial base of knowledge on the components and processes that are the basis of productivity in temperate forest ecosystems. Foresters and forest scientists have contributed substantially to this base during the last century, although their contributions have tended to be narrowly focused on trees, wood production, and managed forests. Furthermore, the ecosystem

paradigm is of relatively recent origin. Major boosts to our understanding of forests have come as a result of recent research programs that have focused on forests as ecosystems. The contributions of the International Biological Programme are particularly notable at both the international and national levels (Reichle 1981; Edmonds 1981). Programs centered on individual sites, such as Coweeta Hydrologic Laboratory (North Carolina; Swank and Crossley 1988), the Hubbard Brook (New Hampshire; Bormann and Likens 1981), and H. J. Andrews (Oregon; Edmonds 1981) experimental forests, have also contributed major advances to the knowledge of forest ecosystems.

A general review of the major components and processes of ecosystems that underline productivity is provided in this section, which considers the physical and biotic elements that are essential to the productivity of temperate forests. The physical variables that act directly on the biota (the operational environment) are distinguished from second- and third-order environmental variables, such as elevation and aspect, which are indirect influences. Although a secondary variable, soils are considered in some detail because of their influence on moisture and nutrient regimes, their importance to sustainability, and their susceptibility to human influences, both positive and negative. The biotic components of productivity, including the "ecosystem support staff" of smaller organisms, such as decomposers, are considered along with the photosynthetically active primary producers, such as trees.

Identification and discussion of important ecosystem processes, such as productivity and decomposition, are also covered. Ecological definitions of productivity are presented and contrasted with traditional forestry definitions. Natural variation in rates of ecosystem processes and recovery rates are also considered.

Physical components of productivity

Productivity comprises physical elements (the operational environment) and physical variables (such as soil and elevation).

THE OPERATIONAL ENVIRONMENT

At the most fundamental level, the biota respond to a relatively small set of physical factors: light, carbon dioxide, temperature, moisture, nutrients, mechanical forces, and toxic chemicals. This includes that part of the biota responsible for providing the energy base for the whole ecosystem,

for example, organisms with chlorophyll that are capable of photosynthetically capturing the sun's energy. These physical elements are sometimes referred to as the operational environment in an effort to distinguish them from physical variables, such as soil, elevation, or aspect, that indirectly influence biotic activity through their effect on these operational factors, the ones that the biota are actually sensing and to which they are responding (Waring and Major 1964).

Several of these variables can be quickly disposed of in this review since they are generally viewed as constants in temperate forest regions. Light, for example, is typically not a limiting factor in temperate forest regions. Sufficient light is generally available throughout the year even though the intensity is obviously greater in the summer than in the winter. Hence, light does not seriously constrain photosynthetic activity even during winter months, assuming that temperature and moisture conditions are suitable. Temperate forests in northwestern North America provide a good example of this, since mild, wet winters allow a substantial amount of the annual photosynthesis to occur outside the growing season (Edmonds 1981, chapter 10; Waring and Franklin 1979).

The carbon dioxide content of the atmosphere is, in contrast, often viewed as a limiting factor for productivity and, over the short term, as a constant. The atmospheric concentration of carbon dioxide is, of course, gradually increasing, and the potential impact of this increase on productivity of green plants is a controversial topic currently discussed and debated by scientists and participants attempting to assess impacts of global change on productivity. Predictions vary from little or no response to the increased levels of carbon dioxide to predictions of significant increases in plant productivity. An analysis of how productivity responds to increases in carbon dioxide is beyond the scope of this review and is not considered further here; the reader is referred to Adams and others 1990; Bazzaz 1990; Easmus and Jarvis 1989; and Jarvis 1989 for discussions of this topic.

Mechanical forces actually cover a variety of mechanical effects that can limit productivity through their direct impact on the green plants or other ecosystem processes. Examples include heavy snow or ice loads that damage or break trees; powerful winds that break twigs, branches, and boles of trees; and floods. Excluded from the

endemic operational environment are catastrophic mechanical disturbances that essentially destroy the existing ecosystem and initiate a new one, such as an intense wildfire or volcanic eruption.

Toxic materials provide a chemical equivalent to the physical forces in the operational environment of the forest. These can be natural materials that are found in the soil or atmosphere of a region. For example, excessive magnesium levels in the ultrabasic metamorphosed type of rock known as serpentine effectively exclude many organisms and retard growth of many others. High atmospheric levels of sulphur compounds associated with hydrothermal vents might be another example of a natural chemical toxin. However, most of the toxic chemicals that are discussed today are of anthropogenic origin (Aber and others 1989), such as concentrations of atmospheric ozone and acid fogs. As with elevated levels of carbon dioxide, an analysis of the effects of various atmospheric and soil pollutants of anthropogenic origin is beyond the scope of this review and are not considered here.

MAJOR OPERATIONAL VARIABLES

The operational environmental elements of temperature, moisture, and nutrients stand out as variables responsible for most of the variability in productivity among temperate forest ecosystems. Levels of these variables vary widely among temperate forest sites on continental, regional, and even local scales. Multivariate analyses of the operational environment invariably identify some combination of temperature, moisture, and nutrients as major controllers of distribution and productivity of the forest community (see Gholz 1982; Zobel and others 1976).

Temperature is typically the primary operational physical factor controlling the distribution and productivity of forest ecosystems over regions and elevational gradients. Local variations in temperature regimes can also be substantial, however, such as on steep slopes of contrasting aspect or as a result of topographic conditions, such as a depression that accumulates and forms a frost pocket. Temperature directly controls various chemical and physical processes (such as photosynthesis, decomposition, and water uptake) and, indirectly, through its effects on moisture regime, controls potential evapotranspiration.

Moisture, as an operational element, is sensed by trees and other plants in terms of internal plant moisture stress (Waring and Schlesinger 1985).

The moisture regime is, however, the result of a complex interaction involving the balance between water uptake, which is generally from water stored in the soil, and water loss, which is primarily the result of loss to the atmosphere through stomata or openings in the leaves. Hence, daily and seasonal patterns in the intensity of the gradient from soil to plant to atmosphere are critical. Many indirect measures are used to provide an integrated index to overall moisture conditions of a forested site. Direct measurements typically mark internal plant moisture stress at selected times of year using pressurized chambers.

Nutrients are a third operational variable that typically controls forest productivity. Indeed, nutrients have received an extraordinary amount of attention from foresters because this is often the only environmental variable that is readily subject to human manipulation. Included here would be all of the macro- and micronutrients that green plants require, although some, such as nitrogen, have received much more attention than others. There is substantial regional variance in the relative importance of nutrients and moisture as limiting factors on productivity. In much of the world's temperate mesic forests, moisture is available throughout most of the summer; analyses of such areas, such as eastern North America and eastern Asia, including Japan, typically identify nutrients as a more important variable than moisture. In contrast, moisture is typically ranked as more important than nutrients in northwestern North America, where there is substantial moisture deficit in summer (Edmonds 1981; Waring and Franklin 1979; Zobel and others 1976).

In conclusion, the physical operational environment of a forest can be defined in terms of relatively few variables. The most important of these in influencing productivity are temperature, moisture, and nutrients.

SOIL AS AN ELEMENT OF PRODUCTIVITY

Foresters often focus on soil as the physical basis for productivity, which is reasonable given the direct relationship that soil has to two of the three operational variables: moisture and nutrients. It is the amount and condition of the soil that largely control the moisture and nutritional regime to which the tree is subjected. Consequently, human impacts on the soil's ability to provide water and nutrients can have a dramatic impact on forest productivity and may be either positive or negative (Grier and others 1989; Harvey and Neuenschwander 1991). Furthermore, impacts

can be very long lasting.

As a physical medium, soils provide several functions: storage of moisture (a portion of which is available to plants), source and storage of nutrients, site for anchorage by plants, and habitat for critical plant symbionts, such as mycorrhizal-forming fungi and other organisms essential to ecosystem processes. Both physical and chemical aspects of the soil are important. Physical aspects include such variables as depth, drainage, bulk density, porosity (especially macropores), texture, and temperature; these variables, in turn, influence conditions critical to the biota, such as aeration (oxygen content), capacity to hold moisture, and availability of moisture. Important chemical aspects of the soil include quantities and qualities of the various macro- and micro-nutrients and the rates at which they are made available.

Biotic components of productivity

From a perusal of any soil textbook, it is clear that we know quite a bit about the chemical and physical processes of soil, but not nearly as much about their biota and biological functioning (Jenny 1980). Biota provide the other essential components of productivity. This includes the primary producers of the ecosystem—the organisms with chlorophyll that are capable of capturing the sun's energy through photosynthesis—and the most important of these in forest ecosystems are the trees. It also includes many other essential organisms that support the ecosystem: plants, animals, fungi, monera (such as bacteria), algae, and protozoa that decompose organic substances, make nutrients available, and assist the primary producers. Fungi that form mycorrhizae with vascular plants, thereby facilitating moisture and nutrient uptake from the soil, are a classic example of the latter, although other relationships may be of comparable importance, as in the case of the endophytic communities found on leaves and needles (Carroll 1980).

The importance of the biotic components to sustained productivity of the ecosystem should be obvious; nevertheless, it seems to be absent from many discussions of productivity and sustainability and is not made explicit in many others. The principle that sustainability requires maintenance of genetic diversity explicitly recognizes the importance of the biotic components and may be, in fact, the most important practical reason for conserving biological diversity in all of its forms.

PRIMARY PRODUCERS

Relatively little needs to be said about the importance of green plants to the productivity of our forest ecosystems. Green plants, and specifically trees, are the basic agents for capturing energy, the energetic base on which the entire ecosystem operates. Forest ecologists generally recognize that different species of trees, either singly or in combination, have different capabilities to capture the potential productive capacity of a site. The fact that different genotypes of the same species may differ markedly in their productivity on the same site is also generally understood and is the basis for various tree breeding programs to develop genotypes that have improved capabilities, such as more rapid growth or greater resistance to disease.

Nevertheless, there are many important gaps in our understanding of how species composition affects either short- or long-term forest productivity. For example, definitive theoretical and empirical information is still lacking on the relative yield of mixtures of species versus a single-species monoculture. This is also true of contrasting forest structures: yields from an even-aged stand with a single canopy layer versus an uneven-aged stand with multiple layers of canopy.

The fact that trees and their production are typically used to assess potential productivity of a forest site creates further complications. For example, trees and genotypes indigenous to a locality may not be as capable of exploiting the productive resources of a site as exotic species. New Zealand provides some outstanding examples of this phenomenon. *Pinus radiata*—a pine endemic to a small area in California—grows very rapidly in New Zealand and is highly productive of commercial wood products. Many of these exotic pine forests are grown on sites that were originally grasslands. Another North American pine, *Pinus contorta*, has escaped from cultivation in New Zealand and is forming forests at elevations substantially above the original timberline formed by native trees; this ability to grow at lower temperatures obviously has the potential to alter drastically the structure and function of these previously alpine habitats. Again, the point is that trees or other plants native to a habitat may not be the genotypes capable of achieving maximum short- or long-term productivity on the site. At the same time, local species or genotypes may well be optimal for other ecosystem functions, including the provision of habitat for native species.

Besides determining the rate of energy fixation or production for the site, primary producers also have the potential to alter significantly the soil's physical and chemical conditions. This can have either positive or negative effects on the long-term potential of a site and obviously should be considered in selecting genotypes, species, or combinations of species for management purposes. The ability of some families or genera of vascular plants to support nitrogen-fixing symbionts in root nodules is a well-known example; representative tree genera with this ability are *Acacia*, *Alnus*, and *Robinia*. Some tree species, such as members of the *Cupressaceae*, as well as many deciduous hardwoods, produce a base-rich litter that, among other things, reduces acidity, increases levels of nutrients, and results in richer and more active communities of organisms in the soil. Other tree species produce litter that increases soil acidity and decreases availability of soil nutrients. *Picea* and *Tsuga* are well-known coniferous examples. An extreme example of the negative effect of specific tree species on soil properties is *Eucalyptus*, which, over time, generates beneath it a bleached, nutrient-poor zone sometimes referred to as an eggcup podzol.

Clearly, we need to recognize explicitly (a) the importance of the genetic component of the primary producers at both the specific and intraspecific levels in influencing attainable short- and long-term productivity and (b) the circular problems inherent in using the productivity of trees as the measure of productivity of a site.

TREE SYMBIONTS AND DECOMPOSERS

The support staff of an ecosystem include many other organisms that carry out important functions, such as facilitating primary producers (the fungi that form mycorrhizae) or participating in the decomposition of organic materials and release of the nutrients they contain (many invertebrates, bacteria, and fungi). These organisms make up the bulk of the biological diversity found in forest ecosystems but are rarely explicitly recognized; hence, they are sometimes referred to as the invisible or hidden biodiversity of ecosystems (Franklin 1992).

Many of these groups are represented by several species, which may provide some functional redundancy, but also an array of genetic types that are closely adapted to specific niches. As a result, dominance among these organisms can shift seasonally or over longer periods in response to environmental changes and maintain a

high level of functioning. For example, we know how fungi capable of forming mycorrhizae with trees shift dominance seasonally with soil moisture and temperature conditions, thereby maintaining optimal mycorrhizal function for the tree symbionts.

Although we have begun to appreciate the importance of such "lesser" organisms to ecosystem function, detailed knowledge of their distribution, community structure, ecology, functioning and, importantly, response to disturbances that disrupt or destroy the forest is not available. Developing this information is a high priority for scientists; in the meantime, applying management practices that are likely to conserve this functionally important diversity is a high priority for foresters.

HERBIVORES AND PATHOGENS

Herbivores and pathogens are a group of organisms that feed on and sometimes damage or kill the primary producers. Although foresters have tended to focus on the negative impacts that these organisms have on short-term productivity, herbivores and pathogens also make important functional contributions to the ecosystem.

Herbivores can have very important influences on productivity over either short- or long-term periods. For example, epidemic-level outbreaks of moths can defoliate forests for one or more seasons, drastically reducing tree growth and increasing mortality. Bark beetles are another common cause of death in trees. Grazing by ungulates, such as deer or elk, can alter the composition and structure of forests, significantly affecting their ability to regenerate and produce.

Disease organisms (rusts and various fungi capable of infecting living trees) as well as decomposers and herbivores can also reduce growth and cause the decay and death of trees and other plants. Yet many of the effects of herbivores and pathogens are essential to the long-term functioning of the ecosystem. They contribute to the natural thinning process, for example, by reducing vigor or killing individual trees. A continuing flow of dead trees is essential to provide the coarse woody debris essential to a variety of ecosystem functions (Franklin, Shugart, and Harmon 1987). Similarly, decay organisms may create cavities and other habitat niches in living trees. There is some suggestion that moderate levels of herbivory may actually contribute to overall productivity of an ecosystem by increasing the availability of nutrients and reducing competition.

Herbivores and pathogens are clearly important biotic elements that influence the productivity and sustainability of forest ecosystems. A substantial base of information exists on the negative impacts of pathogens and herbivores, and it is clear that, in some places and at some times, these may be a dominant influence. Very little quantitative data are available on the positive contributions these organisms may make to the productivity and sustainability of ecosystem.

Major ecosystem processes associated with productivity

A great deal of research has been conducted on the function and structure of forest ecosystems during the last three decades, with the International Biological Programme providing much of the impetus. Much of this work has dealt with the capture and fixation of energy through photosynthesis (primary productivity) and with cycles of material (carbon, nutrients, and water): pathways, rates, and controls. An important result of this research has been a new appreciation of the importance of structure and structural complexity to ecosystem function, including long-term productivity and the provision of habitat for a variety of forest-dwelling organisms. We now recognize, for example, that dead trees and tree parts are as important to the functioning of the forest as live trees (Franklin, Shugart, and Harmon 1987).

DEFINITION OF ECOSYSTEM PRODUCTIVITY

Various measures of ecosystem productivity and associated formulas are used by ecologists in assessing ecosystem productivity. These are substantially different from measures used by foresters, as will be discussed in a following section. Unrecognized, these differences are frequently the basis for significant, often public, disagreements among ecologists and foresters about the productivity of natural forests. Productivity is a rate and is typically measured on a yearly basis as mass per unit of area per year. In these formulas, autotrophs are organisms that capture energy from primary sources (primary producers or green plants), while heterotrophs are organisms that use organic compounds created by the primary producers as their source of energy (all animals).

The most common measures of productivity used by ecologists are gross primary productivity (GPP), net primary productivity (NPP), and net ecosystem productivity (NEP; Kimmins 1987). Gross primary productivity encompasses all of

the productivity of (energy captured by) an ecosystem, forest or otherwise. The formula for GPP is

$$GPP = NPP + R_a$$

where R_a is the respiration of the autotrophs in the ecosystem. Net primary productivity is

$$NPP = \Delta B + L + C$$

where ΔB is the change in biomass, L is total litter production (including tree mortality), and C is consumption of green plants by herbivores. Net ecosystem productivity is calculated as

$$NEP = NPP - R_e$$

where R_e is the respiration of the entire ecosystem (both autotrophs and heterotrophs). Values for these formulas are typically reported as grams per square meter per year or metric tons per hectare per year.

These formulas contrast markedly with foresters' calculations of productivity, which typically involve only the production of bole or wood volume and are based on measures of tree growth, mortality, and, sometimes, birth (ingrowth). The differing viewpoints on productivity have profound consequences for examining older forest ecosystems where both GPP and NPP may remain high even though increments of additional wood mass have fallen to low or negative levels.

Although the concepts and formula may be quite clear, actually calculating the productivity of forest ecosystems is extremely difficult. Estimating respiration is one of the serious problems in determining either GPP or NEP; although respiration can be estimated for individual components, developing reasonable estimates for the entire ecosystem is impossible with existing technologies.

PRIMARY PRODUCTIVITY

The environmental factors controlling primary productivity in forest ecosystems have been extensively studied (Waring and Schlesinger 1985). As noted earlier, temperature, moisture, and availability of nutrients are the key variables.

Estimates of NPP have been calculated for numerous forest ecosystems (see, for example, Cannell 1982; Reichle 1981). The NPP variables of living biomass increment, litter production, and consumption by herbivores aboveground are all susceptible to measurement, albeit with some difficulty in the case of litter production and consumption. But perhaps the most difficult aspect of measuring NPP is the productivity that occurs belowground.

Most estimates of NPP for forest ecosystems

are only for the aboveground portion because of the immense technical difficulties associated with estimating belowground productivity. Not only is there no easy method of observing and measuring belowground, but there is also considerable controversy about the accuracy of the labor-intensive approaches currently under use (Kimmins 1987).

The difficulty of measuring belowground productivity is extremely unfortunate because of the supposed overall importance of belowground productivity to the carbon budget of the forest. Recent research has shown that the belowground portion of the ecosystem is very dynamic, with high rates of turnover in fine roots and mycorrhizal fungal hyphae. Only 20 percent of the biomass is found belowground in a typical forest, and earlier studies assumed that belowground productivity was proportional to the mass. Unfortunately, energy demands may be as high as 50 to 70 percent of the photosynthate produced by the forest due to the high turnover of roots and hyphae.

It is also known that the energy requirements belowground increase on sites that are deficient in nutrients or water, because more fine roots and hyphae must be produced to exploit the soil mass for the required materials. One very important implication of this finding is that some or all of the increases in productivity associated with forest fertilization may represent shifts in the allocation of energy from belowground to aboveground; hence, the observed increases in aboveground productivity may not represent increases in total productivity of the ecosystem.

These discoveries about the energetic requirements and productivity of the belowground portions of terrestrial ecosystems, including forests, are forcing drastic reassessments. First, they have made clear that basing conclusions about total NPP only on aboveground measurements is highly questionable, if not dangerous. Today, any estimates of ecosystem productivity that do not include the belowground portion of the forest are open to challenge. This specifically includes any assessment of long-term trends in productivity and responses to experimental treatments, such as thinning and fertilization. Consequently, valid observational and experimental studies are relatively rare, and almost all of the older literature on productivity of the forest ecosystem is open to question.

A second important implication is that the trees and other green plants are critical sources of energy to sustain the extremely dynamic

belowground ecosystem. In effect, the tree has been shown to be as important to the vitality of the soil as the soil has traditionally been viewed to be to the tree. Loss of this source of energy as a result of forest removal, even for short periods, is hypothesized to cause the failure of reforestation efforts and long-term loss of forestland to vegetation other than forests (Perry and others 1988).

Calculating NPP requires an estimation of litter production over the period of measurement. This is generally done by periodically collecting and weighing litterfall within the forest stand of interest. Numerous well-documented techniques involve litter traps placed on the forest floor that collect insect frass, flowering parts, leaves, twigs, and branches.

Few litterfall studies and calculations include the largest pieces of litter: dead trees. Current tree mortality is technically part of the litter factor in the NPP equation. Long-term studies of tree populations are necessary to obtain accurate data on annual rates of mortality because of high year-to-year variability, which often includes a major stochastic, or random, component (Franklin, Shugart, and Harmon 1987). For this reason, many studies of ecosystem productivity ignore tree mortality even though tree death may contribute as much organic material as the smaller, traditional components of litterfall (Sollins 1982).

Obtaining accurate measures of consumption by herbivores, the third element of the NPP equation, is very difficult although some techniques provide an approximation. Fortunately, aboveground herbivory is relatively insignificant in healthy forest ecosystems (Kimmins 1987). Hence, assumed values are unlikely to produce major errors in calculating NPP. Herbivory belowground is much more poorly understood, however, and could be a major factor in any calculation of NPP.

DECOMPOSITION AND SECONDARY PRODUCTIVITY

Decomposition is probably second only to primary production as the most important ecosystem process. Decomposition is carried out by a variety of organisms that break down organic materials to release energy and nutrients:

organic compounds + decomposition = energy
+ carbon dioxide + water + nutrients.

Most of the secondary producers (organisms that use existing organic carbon compounds as their base of energy) found in forest ecosystems are decomposers or detritivores (organisms that

feed on organic litter), and most of the secondary productivity in forest ecosystems is associated with decomposition or detritivory. Much information has been developed on rates and pathways of and controls on decomposition during recent years. Important environmental variables include the moisture and temperate conditions found on the site; both can limit rates of decomposition. Chemical attributes of the detritus or litter have a major influence on rates of decomposition. Lignin and nitrogen contents of leaf litter, for example, both have been shown to be important variables and are used in general equations for predicting rates of decomposition. The available biota is another critical variable. For example, soil arthropods play critical roles in fragmenting larger organic materials while feeding on and consuming portions of them, providing large surface areas for colonization by other decomposer organisms. Consequently, excluding or eliminating segments of the soil fauna can have significant impacts on rates of decomposition.

Decomposition of large or coarse woody debris, such as large standing dead trees (known as snags) and logs on the forest floor, is particularly complex and has only recently become the subject of intensive study (see, for example, Harmon and others 1986; Harmon and Chen 1992).

OTHER CRITICAL ECOSYSTEM PROCESSES

Primary production and decomposition have been singled out for attention in this review because of their importance to the sustained productivity of all ecosystems, including forests. Many other ecosystem processes are important, however, some of which have already been identified, such as consumption by herbivores. The identification and elaboration of these processes alone could fill several pages.

Nitrogen fixation is one additional process that requires mention, however, because of its importance to fertility of the soil and site. It has also been the subject of important recent discoveries. Nitrogen fixation involves the conversion of elemental nitrogen in the atmosphere to the biologically useful forms of ammonia or nitrate. Although physical processes such as lightning discharges can produce this conversion, much, if not most, of the nitrogen is fixed biologically.

Relatively few organisms are capable of nitrogen fixation (cyanobacteria). Although some of these are free-living organisms, many of the most important nitrogen fixers live in association with other organisms. Well-known examples are ni-

nitrogen-fixing organisms that live in root nodules of legumes (the pea family) or in several other genera of vascular plants, such as alder, and as components of lichens.

Forest ecosystem studies during the last decade have identified at least four additional locales for nitrogen fixation. An early discovery during the International Biological Programme was fixation by large foliose lichens, primarily *Lobaria oregana*, living in canopies of old-growth Douglas fir trees (Carroll 1980; Denison 1979). Current estimates place annual nitrogen fixation at 5 to 9 kilograms per hectare in a typical 500-year-old forest. Rotting wood, particularly large logs, can also be the site of significant nitrogen fixation (Harmon and others 1986), as can areas of rot within living trees; current estimates of annual nitrogen fixation in intact, natural old-growth forests are typically 3 to 5 kilograms per hectare. Two other sites discovered to be sites of nitrogen fixation in intact forest stands are the rhizosphere (regions immediately adjacent to tree roots in the soil) and leaf litter (Heath and others 1987).

Rates of nitrogen fixation can be very high during early stages of succession on forest sites, when legumes or other trees and shrubs with nitrogen-fixing symbionts are dominant elements. For example, annual rates of nitrogen fixation in young *Alnus rubra* stands can exceed 200 kilograms per hectare (Trappe and others 1967).

This discussion of spatial and temporal locales for nitrogen fixation is essential to any analysis of forest sustainability because of nitrogen's importance as a nutrient. Although some forest systems may actually have an excess of nitrogen as a result of chemically enriched rainfall, this is not generally the case. Hence, in designing sustainable forest management systems, foresters must consider the need to maintain organisms, structures, and successional stages that contribute to nitrogen fixation.

Structural aspects of forest ecosystems related to sustainability

Structural complexity is the critical link in ecosystem function, whether the manager is concerned with productivity, maintenance of other ecosystem processes, such as nitrogen fixation, or provision of habitat for wildlife and other elements in biodiversity. Structure provides a surrogate for many processes and organisms that would otherwise be difficult to measure (Franklin and others 1981). Structure is also the major ecosystem attribute that foresters can manipulate directly.

Structural attributes of ecosystems involve both individual categories of structures, such as living trees and snags, and their collective arrangement, that is, structural attributes of the stand.

INDIVIDUAL STRUCTURES

Dominant trees are major structural components of forests, particularly in older stands (Franklin and others 1981). Shade-intolerant or pioneer species are often prominent in this role. Dominant trees carry out critical processes, such as much of the photosynthesis, as well as provide diverse and essential habitat for other organisms. In older natural forests, the dominant trees may attain very large sizes (for example, 1 to 2 meters in diameter and 50 to 90 meters in height in northwestern North America). Their canopies and boles provide habitat for a large number of epiphytic organisms, such as mosses and lichens, and habitat for a large and diverse community of invertebrates. Dominant trees are also the source of two other key structural components of the forest: large standing dead trees and large logs on the forest floor.

Intermediate-sized trees of shade-tolerant species are also important structural components of forests. They create a range of tree sizes and typically contribute to intermediate levels of canopy, producing a stand that has a many-layered canopy extending from the ground to the top of the crowns.

Large snags and fallen logs, typically larger than 10 to 15 centimeters in diameter and collectively known as coarse woody debris, represent two other important individual structures found in natural forests (Franklin and others 1981; Harmon and others 1986; Maser and others 1988). Biologists have recognized the importance of snags to many species of wildlife for some time (Hunter 1990) but only recently began to recognize the numerous ecological benefits of coarse woody debris on the forest floor and in associated streams. These benefits range from geomorphic functions, in influencing erosional processes, to biological diversity, in providing habitat for a broad array of animal and plant organisms, to providing sources of energy and nutrients for these systems.

The change in attitude toward coarse woody debris reflects a dramatic new recognition that dead trees are as important as live trees to ecological functioning in a forest (Franklin and others 1987). Moreover, the dead tree structures may perform terrestrial or aquatic functions for many

centuries because they decay or disappear from ecosystems slowly (Harmon and others 1986). Furthermore, functions change throughout the lifetime or gradual decay of a snag or log.

OVERALL STAND STRUCTURE

Overall structural heterogeneity is an important feature of almost all natural forests. The forest as a whole cannot be reduced simply to individual structures and aggregated into a whole. Heterogeneity in both the horizontal and vertical dimensions is a hallmark of natural and, especially, older forests.

Variations in the density of the overstory canopy, including complete gaps in the canopy, are an important element in stand-level structural diversity. A natural stand typically has locales where levels of light are higher and vegetation on the forest floor is better developed than in other areas, where dense tree foliage, especially of shade-tolerant species, produces a heavily shaded environment from which understory plants may be absent or nearly so.

The variability in light conditions, as well as belowground competition for moisture and nutrients, contributes to the complexity and richness of understories in many late-successional forests. These diverse understories can be critical for some organisms; for example, the old-growth *Picea sitchensis*-*Tsuga heterophylla* forests of the Alaskan panhandle provide essential habitat for Sitka black-tailed deer (*Odocoileus hemionus sitkensis*; Alaback 1984; Schoen and Kirchoff 1990). Research throughout the temperate forest regions of the world is showing that developing and maintaining diverse understory plant communities in forest stands are an important and complex undertaking, not simply a matter of manipulating crown density or levels of light.

STRUCTURES IN TRADITIONAL MANAGED STANDS

Structural attributes of temperate forest stands subject to traditional management are typically very different from those of natural stands. The most common managerial system has been the creation of even-aged, even-sized stands using clear-cutting and artificial reforestation (Oliver and Larson 1990). Such stands are highly simplified and lack many structural components, such as snags and logs, as well as stand-level structural complexity, such as multiple levels of canopy, chaotic tree spacing, and gaps.

Managed stands have been simplified in response to economic criteria—efficient manage-

ment and high productivity of target tree species—in the belief that much of the structural complexity found in natural stands is not essential to sustained productivity of the site. The recent research, briefly reported here, on the role of structural diversity in maintaining the processes and organisms essential to forest sustainability is a major challenge to those assumptions.

Disturbances and ecosystem recovery rates

Responses of forest ecosystems to disturbances, including the pattern and rate of recovery, are highly dependent on the intensity and type of disturbance, which, in turn, determine the carryover of biological materials from the old or disturbed to the new or recovering ecosystem. This section briefly reviews disturbances, biological legacies, and rates of ecosystem recovery. A great deal of literature is available on disturbances and their effects, including effects on at least some aspects of productivity.

DISTURBANCES

Forest ecosystems are subject to a wide variety of disturbances that influence both immediate and long-term productivity. The important variables in determining impacts on sustainability are the type, intensity, size, and frequency of disturbance. Among the important types of natural disturbances are fires, windstorms, floods, landslides, epidemic outbreaks of insects or disease, and volcanism. Forest cutting by humans is probably the most important single disturbance globally.

Each of these types of disturbance does, of course, display a range of intensities. For example, wildfires can be intense, stand-consuming crown fires, such as the 1989 fires in Yellowstone National Park, or low-intensity, creeping groundfires that leave most of the forest intact. Wind displays a similarly wide range of behaviors, often generating intense damage at a regional level in the form of a hurricane or typhoon or, at a more local level, in the form of a tornado; however, wind most often disturbs chronically and at the smaller spatial scale, blowing over or breaking individual or small groups of trees. Other natural disturbances illustrate a similar gradient from slight to intense effects on the forest ecosystem. This gradient is typically found within a single disturbance, such as a fire or windthrow, especially if it occurs on a larger scale.

Disturbances occur over a very wide spatial scale. Wildfires and windstorms can range from a few square meters to thousands of hectares. Some types of disturbances, such as floods and landslides, are constrained to certain scales by landforms; these may have an extensive linear (downstream) dimension, however, even if limited in width. Again, the larger the disturbance, the more heterogeneous it will be in terms of intensity; for example, larger wildfires almost always include areas of intense and very light burning.

Disturbances are sometimes characterized as being either stand regenerating or intrinsic to the within-stand dynamic of a forest. Such a categorization includes consideration of both size and intensity of a disturbance. A very low-intensity disturbance, such as a groundfire, is often considered to be an integral part of the environment of a forest stand, even if it is of large extent. Creation of a gap in a forest canopy by the uprooting of one or several trees is also typically considered to be part of a stand dynamic despite its intensity within a small area.

Frequency of disturbance is a fourth and extremely important variable. Many disturbances are highly episodic, occurring at infrequent intervals. In the case of some disturbances, such as wildfires, long intervals between occurrences tend to result in much more intense events than where short intervals are involved; this is typically related to the period available for fuels to accumulate. Frequent disturbances can also have very negative effects on productivity and the process of recovery, however, where they result in the loss of nutrients, soil organic matter, or organisms; repeated disturbances can, for example, eliminate or dramatically reduce the level of biological legacies, such as sources of mature tree seed, at each iteration. Hence, repeated intensive crown fires can produce large areas that are very slow to reforest. One of the reasons for the rapid recovery of ecosystems at Mount St. Helens (Washington State) in 1980 was the absence of a second major eruption over most of the area; therefore, the legacy of surviving organisms was not subject to further death and burial (Franklin, Frenzen, and Swanson 1988).

Human-induced disturbances exhibit all of the same variables as natural disturbances: type, size, intensity, and frequency. Indeed, forest harvest activities can be considered and scaled with regard to each of these. Types of activities can be as variable as felling and removal of timber and nondestructive removal of forest crops, such as

rubber or nuts. Sizes can range from the small patch to thousands of hectares, as in the case of some forest cutting. Intensity, as noted later, can vary from intense clear-cutting followed by slash burning to selective cutting of individual trees. Finally, human disturbances can recur each year or after many decades or even centuries.

Disturbances do have contrasting impacts on the productivity of a site, and even a single type of disturbance can have either positive or negative effects, depending on the nature of the forest ecosystem and the intensity of the disturbance. For example, wildfire negatively affects ecosystem productivity by volatilizing significant amounts of nitrogen as the organic matter is consumed. Positive effects include short-term release of soil nutrients, particularly basic elements, as the organic matter is consumed; on some sites, accumulations of organic matter may be excessive from the standpoint of site nutrition. Wind-driven disturbances rarely result in short-term losses or gains in nutrients. Geomorphic disturbances, such as floods or landslides, can have positive or negative benefits, depending on whether nutrient-rich materials are removed, added, or buried by erosional or depositional processes.

BIOLOGICAL LEGACIES

Studies of early-successional recovery of ecosystems following disturbances generally give little attention to the influence of the ecosystem before the disturbance (Franklin 1990; Franklin, Frenzen, and Swanson 1988). The role of migration or reinvasion of organisms is typically emphasized, while surviving organisms and structures are largely ignored. However, disturbances are increasingly recognized as processes that leave behind varying levels of organisms, structures, and patterns. These biotically derived legacies from predisturbance ecosystems have important influences on the paths and rates of recovery.

As defined here, biological legacies are living organisms that survive a disturbance, particularly a catastrophic or stand-regenerating disturbance, organic debris, particularly the large organically derived structures, and biotically derived patterns in soils and understories. The living legacies may take a variety of forms, including intact plants and animals, perennating structures (rhizomes), and dormant spores and seeds. Important biotically derived structures include dead trees (snags) and fallen logs, large soil aggregates, and dense mats of fungal hyphae. These

structures are appreciated more and more for their role in ecosystem functioning, such as the importance of large woody structures as wildlife habitat (Harmon and others 1986; Maser and others 1988). Pattern legacies include those created in soil properties—chemical, physical, and microbiological—through the action of plants and their litter, and patterns in understory vegetation associated with variations in the conditions of canopy light. These patterns can be either positive or negative; for example, patches of soil associated with some tree species may be enriched in nitrogen or various bases, while others may be leached of nutrients and acidified.

Disturbances of various types, intensities, spatial scales, and frequencies produce different types and levels of biological legacies. Some of the relationships are obvious. More intense or frequent disturbances tend to have lower levels of living legacies; however, disturbances vary widely in the types of living legacies they leave behind. For example, wildfires are most likely to kill smaller and thin-barked trees and spare large, thick-barked dominant trees. Windthrow, however, typically eliminates dominant trees, leaving behind the largely intact understory of tolerant tree seedlings and saplings. In northwestern North America, fire and wind differ dramatically in their compositional or successional consequences; wildfire favors the shade-intolerant pioneer, Douglas fir, while wind favors survival and subsequent dominance of the shade-tolerant western hemlock and western red cedar.

Almost all intense disturbances in forest ecosystems tend to leave behind large legacies of dead organic material, including structures (snags and logs); this is because most natural forest disturbances, such as wildfire and windthrow, kill trees but consume or remove relatively little of the material. This legacy provides a continuity of wildlife habitat, bridging the two generations of ecosystems as well as providing long-term transfer of organic material and nutrients.

Traditional intensive harvest of forests by humans has typically left a much smaller biological legacy than have natural disturbances. Although many of the original plant and animal species may survive, the intensity of management practices has a strongly negative influence on the level of living legacies (Halpern 1988, 1989). Legacies of large organic structures, such as snags and fallen logs, are also drastically reduced under most current silvicultural practices, which include both harvest and slash disposal operations.

As a result, the young forests that develop following traditional clear-cutting practices are typically much simpler in composition and structure than those that develop following natural disturbances.

The types and relative levels of biological legacies following a catastrophic disturbance, then, are extremely important in determining the rate at which the new forest ecosystem will recover and, perhaps even more important, the diversity of organisms, processes, and structures that it will contain. Many of these have direct significance for sustained levels of productivity. An outstanding example is the retention of organisms capable of fixing nitrogen and providing appropriate habitat for their propagation and functioning. In forest ecosystems, this retention may encompass a wide range of forms; in old-growth Douglas fir forests, for example, it includes canopy-dwelling lichens with cyanobacteria elements and microorganisms that live in decaying wood, such as fallen logs and snags (Franklin 1992).

The types and quantities of biologically derived materials persisting through a disturbance generated by either natural or human causes have a powerful influence on the levels of nutrients and organic matter present in the recovering ecosystem. Nature generally provides for high levels of legacies and for other mechanisms that retain nutrients. However, traditional forest harvest practices, such as clear-cutting, tend to minimize biological legacies and maximize nutrient losses, as in the volatilization of nitrogen that occurs during slash burning.

ECOSYSTEM RECOVERY TIMES

There have been numerous studies of succession in forest ecosystems, but very few actually investigate or predict compositional, structural, or functional recovery, except as it relates to production and standing crops of wood. Models and data related to production of wood are considered later in this report.

Recovery rates in forests are actually considered to be quite slow compared with other major types of ecosystems, such as grasslands, deserts, or tundra (MacMahon 1981). This relates in large measure to the structural complexity of forests and the long period of time required to reestablish a diverse and fully functional forest ecosystem.

Foresters have focused heavily on regeneration of trees and reestablishment of a forest canopy (forest dominance) on a site. Regeneration of trees can occur immediately under managed con-

ditions as a result of planting but is highly variable under natural succession; it may be essentially instantaneous where an abundant source of tree seeds is present or may require many decades where environmental conditions are severe or seed sources are distant. Growth of the regenerated trees to the point where the tree canopy becomes continuous is also highly variable, depending on the productivity of the site. In the case of temperate hardwood forests, rapid growth of pioneers, such as *Prunus* or *Alnus*, may produce canopy closure in two or three years (Reiners 1992). Among the coniferous forests, moist and warm regions dominated by *Pinus* (such as the southeastern United States or the exotic plantations of New Zealand) are the fastest to return to tree dominance. In northwestern North America, closure of the forest canopy may require a decade for completion, even on productive sites; twenty to thirty years of succession may be required on typical sites following either logging or natural disturbance (Halpern 1988, 1989).

Much more is involved in ecosystem recovery, however, than simply tree dominance or even achievement of some level of biomass. A diverse array of structures, processes, and organisms must reestablish themselves at some level approximating the original forest. Significant biological legacies, such as snags and fallen logs, largely determine how rapidly recovery of the full functional ecosystem will take place. If such legacies are absent so that new structures have to be grown to desired sizes (and, in the case of dead wood structures, killed and decayed to particular states), the recovery process can be extremely slow, perhaps involving many centuries in some types of forest. If such legacies are retained on the disturbed sites, recovery can be much more rapid.

There is increasing evidence that some elements of the ecosystem are very slow to recover. One study in the Appalachian Mountains of eastern North America, for example, has shown that some understory plant species—mosses, herbs, and shrubs—may not have recovered to their natural levels even 100 years after logging. In the temperate rain forests of southeastern Alaska, development of a compositionally diverse understory of the type required as winter range by Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) typically requires 200 years following logging (Alaback 1984).

If a late-successional forest is taken as the end point of successional recovery, it appears that several centuries are required for composition

and most structural and functional features to recover. In the temperate hardwood forests of northeastern North America, 150 to 200 years may suffice for recovery, but in the coniferous forests of northwestern North America, as many as 250 to 450 years appear to be necessary to fully achieve late-successional forest conditions (Franklin and others 1981; Franklin and Spies 1991).

RESTORATION OF SOIL PROPERTIES

Restoration of soil properties almost certainly requires even longer time periods than does recovery of the biological elements of the ecosystem (Grier and others 1989; Jenny 1980). Very little good information is available on the rates of soil formation, or even on the rate at which organic matter typically accumulates in the soil. Nevertheless, it is clear that soil typically develops at a very slow rate.

In fact, much (and possibly most) accumulation of soil parent material on a site results from episodic depositions of materials from adjacent sites and not the weathering of parent materials in place. The majority of deep forest soils are composed of alluvial, colluvial, glacial, aeolian, and volcanic materials that were moved to the site by water, gravity, ice, wind, or eruptions. Hence, the frequency and type of episodic events (primarily geomorphic) are extremely influential in determining both the depth of existing parent material and the probability for replenishment. This is an important point: replacement of soil parent materials on many sites may depend primarily on the recurrence of infrequent and highly episodic geomorphic process, such as a volcanic eruption; hence, soil conservation should have a high priority among forest management considerations.

Once in place, biological processes are critical in the evolution of the soil parent materials into an organically and nutritionally rich medium for growth. As noted earlier, this can be a slow process. It is probable that most forest soils are continuously and gradually accumulating soil organic matter under natural successional regimes. Although the available information is inconclusive, soil organic matter is probably not accumulating—and may be declining—under many forest management regimes currently in use (Kimmins 1987).

Perhaps the most difficult problem in soil restoration is the reintroduction and establishment of critical soil organisms, such as fungi, invertebrates, and bacteria, once they have been elimi-

nated. There is good evidence that significant elements of the soil biota can be lost with the elimination of host tree species from the site (Perry and others 1989); this can lead, in turn, to serious problems in the reestablishment of forest cover.

Natural variation in ecosystem productivity

Significant variation in both space and time exists in the productivity of forest ecosystems. Spatial (site-to-site) variability has already been discussed and can effectively span two-and-a-half orders of magnitude in production of wood, from less than 10 to more than 250 square meters per hectare a year.

A forest ecosystem on a specific site can also experience substantial year-to-year variation in productivity, quite aside from long-term trends associated with successional development of the forest. The greatest variability—certainly in terms of percentages and, often, in absolute values as well—occurs on sites that are subject to major environmental stresses. These include marginal forests on hot, droughty sites, such as those found at lower timberline, and on cold arctic and alpine timberline. Productivity is typically low on these sites, and growth is responsive to variations (either positive or negative) in climatic conditions. Dendrochronology, the analysis and interpretation of tree rings, is based on the sensitivity of tree productivity to climatic fluxes, especially on severe sites. Productivity might easily span two orders of magnitude on sites with major environmental limitations. Although annual and periodic variability in the productivity of temperate forest ecosystems is present on moderate sites as well, it is smaller in magnitude than year-to-year variation.

Changes in local or global environmental and climatic conditions can be expected to produce major changes in the productivity of forest ecosystems. Effects of local pollutants, such as emissions from smelters, have been well documented. Effects of regional changes in pollutants or in climatic conditions are less clear but are currently the subject of intense scientific interest (Franklin and others 1991). Such changes clearly have the potential to produce major changes in the productivity of forest ecosystems; the direction of the change will, of course, depend on the current circumstance. If changes in environmental and climatic conditions produce additional drying in a forest ecosystem already moisture-limited, the resulting

effect would probably be negative; conversely, increased levels of atmospheric carbon dioxide may result in increased productivity and more efficient use of available moisture.

Episodic and stochastic processes and thresholds

Forest ecosystems are subject to many important processes that are either episodic or stochastic or both. Some of these have already been discussed in earlier sections, particularly with regard to disturbances. Disturbances are among the most important of the processes that are, in the majority of cases, both episodic and stochastic, or random. Variation in environmental conditions (climate) is another example.

Two important aspects of the dynamics of tree populations central to forests and forest productivity—birth and death—can be episodic or stochastic processes or both. Birth, the successful establishment of new tree seedlings, may require a major (stand-regenerating) disturbance, which is typically both episodic and stochastic. It may also depend on the production of a bumper seed crop, another process that is at least episodic, and possibly stochastic. Finally, successful regeneration of trees on sites with severe environmental conditions may depend on the occurrence of one or two years with an unusually favorable climate. Regeneration of *Pinus ponderosa* forests in central Arizona, for example, requires the combination of two unusually moist springs and a bumper seed crop; these conditions occur only every two or three decades.

Scientific knowledge of tree death or mortality is surprisingly poor, considering its importance in forest ecology and productivity (Franklin, Shugart, and Harmon 1987). Some mortality is quite regular and predictable, particularly the natural thinning that occurs early in development of the stand. Much mortality, however, including such events as an outbreak of pests and pathogens or a major windstorm, is highly episodic. Generally, mortality of established trees (above the seedling and sapling stage) in forest stands is both episodic and stochastic, impeding our ability to predict rates, causes, and spatial patterns of mortality in mature and late-successional stands.

One of the major needs in forest management is to recognize the highly stochastic na-

ture of most natural ecosystems. More management plans need to consider the potential for stochastic disturbances. More management decisions need to consider probabilities, such as in the potential for successful natural regeneration. Far too many management decisions are based on a deterministic view of forest ecosystem responses and an unwillingness to accept outcomes with less than 100 percent probability of success.

Thresholds have not been a major topic in considerations of the productivity of temperate forest ecosystems. Nevertheless, the occurrence of thresholds is implicit in many discussions, since so many processes fit the traditional logistic curve. However, few interpretations of physiological, population, community, or ecosystem phenomena have been explicitly made in terms of thresholds; they could be, however, and resource managers often assume that there are such points beyond which responses accelerate or decelerate. Threshold phenomena have been explicitly recognized in the area of landscape ecology. One example is the effect of dispersed patch clear-cutting on various landscape measures, such as mean patch size (see, for example, Franklin and Forman 1987).

Biophysical measurements for temperate forests

Many approaches to predicting the productivity of forests and forest sites have been developed over the last century. These include direct measurements of tree and stand growth and many indirect approaches, such as those using soils, landforms, and plant communities. Most of the approaches focus ultimately on the arboreal component as the measure of productivity and, often, only on bole (wood) production, rather than on all ecosystem components. This is acceptable to at least some degree, since many capabilities of a forested site (such as processes and organisms) are related to or indexed by the ability of the site to grow a tree to a maximum size at a particular rate. However, focusing exclusively on trees in assessing productivity ignores many elements essential to sustainable forestry.

Techniques for direct assessment or measurement of long-term trends in site productivity, as opposed to the modeling approaches discussed later, are not well advanced. Most of the existing

measures show a high rate of error when applied to specific sites and stands. This natural variability makes it extremely difficult to identify long-term signals or trends in site productivity, a common problem with many ecological phenomena (Likens 1989).

Biological measurements

Biological measures used in assessing forest productivity include direct measures of forest yields and tree growth, measures of total ecosystem productivity, rates of key ecosystem processes, and vegetational associates or plant communities as indicators.

TREE PRODUCTIVITY AND WOOD PRODUCTION

The yield of a fully stocked forest stand over a given time period is the ultimate measure of arboreal productivity for a site (Daniel, Helms, and Baker 1979). Since such a measure is rarely possible, traditional approaches to predicting forest site potential and forest growth have been combined in a tree-based growth measurement called site index with yield tables of various types.

Site index is the height to which a tree of a given species will grow within a specific time period. Site index is typically based on height growth curves developed using empirical data on cumulative height attained by dominant and codominant trees over time. The index age varies with tree species; 50 years is a common age for fast-growing species, such as *Pinus sp.* in the southeastern United States, while 100 years is a common index age in western North America, where initial growth rates are slower. A site index is typically assessed by obtaining height and age on a sample of dominant and codominant trees from the site and projecting height to the index age using a set of site curves; the selected trees are typically assumed to have grown naturally.

Height growth rate of free-growing trees was selected and has been defended by foresters on the basis that it is relatively unaffected by stocking levels or tree density, whereas other measures of growth, such as diameter, are. Hence, it is considered to be a direct indicator of site potential, irrespective of stand conditions. Studies have shown significant effects of stand density on height growth, however, with considerable variability among species (Daniel, Helms, and Baker 1979). Furthermore, growth curves (patterns of height growth over time) may differ among sites for the same species and site index; that is, even where

tree heights on two sites are identical at the index age, patterns of height growth both prior to and after the index age may differ. This has encouraged the development of more localized, or polymorphic, site curves as an alternative to the creation of a generalized set of site curves for a large region (Daniel, Helms, and Baker 1979).

Yield tables are the other half of the traditional approach to predicting forest productivity. Most yield tables, including all of the older ones, are constructed by sampling fully stocked stands of one (usually) or two or more (rarely) tree species that represent different ages and levels of productivity as measured by site index. The empirical data are used to develop comprehensive tables that predict the volumes of wood (cubic meters per hectare or board-feet per acre) to be expected from fully stocked stands of those species at various ages and on sites with different site indexes. Yield bulletins typically include much other tabular and graphical information as well, such as calculations of increment per unit of time and changes in tree density. Yield tables can be viewed fundamentally as tree population or demographic models. Early yield tables were almost entirely for stands of natural origin, but more recently, many have been developed for managed stands, such as plantations, and include effects of thinning and other management activities.

Yield tables have been superseded in many regions by computerized growth models that have the ability to incorporate substantially more variables, including effects of variable stand densities. These are discussed later, since they are not direct measurements of productivity. Most direct measurements of the productivity of a forest site are based on site index, which is then coupled with yield tables or yield models. Other techniques, such as projecting growth on the basis of recent patterns of tree growth, are occasionally used for estimating growth over the near future.

ECOSYSTEM PRODUCTIVITY

Ecological measures of productivity—gross primary productivity, net primary productivity, and net ecosystem productivity—are much more comprehensive than the traditional forestry measures. At least conceptually, they include all components of the ecosystem. Unfortunately, accurate estimates of total ecosystem productivity are extremely difficult, if not impossible, to obtain, particularly the respiration component and almost all measurements belowground. This calls

into doubt the accuracy of most available estimates of gross primary productivity and net ecosystem productivity for forest ecosystems.

Estimates of net primary productivity of forest ecosystems can and have been made for research sites. However, obtaining the necessary measurements requires heroic physical, as well as conceptual and financial efforts, so as a routine measure of ecosystem productivity, estimating net primary productivity is impractical. The conceptual contribution of ecosystem productivity is probably the aspect most relevant to this review. It recognizes explicitly the productivity of all parts of the ecosystem rather than focusing exclusively on trees and volume of wood. As a result, it provides us with a very different point of view on the health and productivity of an older forest ecosystem than do measures of productivity that are based on additional increments of wood or biomass.

PROCESSES AS INDEXES

Although not widely accepted, rates of key ecological processes, such as decomposition or mineralization of organic matter, are sometimes proposed as indexes to overall health or productivity of an ecosystem. One variable that seems to have a high level of sensitivity to pollutants and some other stresses is the time that evergreen trees retain needles or leaves.

SITE COMMUNITY CLASSIFICATIONS

Plant communities and vegetative indicator plants have been proposed and are sometimes used to assess the productivity of a forest site. Such approaches are based on the concept that specific plants—singly, in sets, or as communities—are indicative of specific environmental conditions, such as moisture, temperature, and nutrient regimes. Hence, inferences about site conditions and overall productivity can be drawn from their presence or abundance on a site.

The Finnish types of forest site represent the earliest development of this concept. These were based on the belief that empirical relationships exist between plant cover and tree growth. The presence of a certain plant species in the understory was assumed to indicate a particular quality of site.

Many vegetation-based approaches have been developed and are widely applied throughout the world. In Scandinavia, most vegetational approaches follow the original model pioneered by Cajander. The vegetation classification system developed by Braun-Blanquet dominates in cen-

tral Europe and many other parts of the world. In western North America, Daubenmire pioneered the approach with his habitat-type concept, which is now widely applied to national forestlands.

Many other approaches have used plants as indicators of site environment and productivity, including the use of vegetative indicators to define the operational environment (see, for example, Waring and Major 1964). Most plant community or plant indicator approaches ultimately return to traditional forestry measures—site index and stand yields—to rate productivity of a site.

Physical measurements

Many scientists have proposed that measurements of physical site conditions, rather than trees or other biota, be used to rate potential productivity of a site. One advantage is that such approaches do not require the presence of any particular organism or stand condition in order to rate productivity; this also can (using some approaches) avoid biasing productivity estimates toward any particular genotype, species, or life-form. Biotic productivity is, however, the ultimate measure of sustainability, so that most physical measures are, in fact, referenced back to plant production.

ENVIRONMENTAL REGIME

Occasional proposals have been made to assess potential productivity of a forest site using direct measures of environmental variables, such as mean temperature, frost-free days, precipitation, and so forth. As noted earlier, there are strong correlations between overall productivity and environmental variables, such as moisture and temperature. Most of these studies are based on measures of the operational environment, however, and not on measurements of the regional climate.

Although climatological indexes have been developed for temperate regions, they are not currently used in assessing forest productivity. Indeed, the life zone approaches used in the United States early in this century might fall into this category. Holdridge's life zone concept is one environmental indexing scheme that is widely used for tropical forest areas.

SOIL PROPERTIES

Foresters have made considerable use of soils as a basis for predicting forest productivity (Daniel, Helms, and Baker 1979; Pritchett and Fisher 1987).

The need to predict yields on sites lacking the trees or the tree species of interest has been a particular stimulus to the use of soils. Soils are also viewed as a permanent feature of the site, in contrast to vegetative cover.

Soil taxonomic units or types have been one basis for predicting forest yields. Exclusive dependence on soil types has had limited success, however. This is related, in part, to variability in the soil mapping units. Site curves are typically used as a basis for rating soil productivity, but using inappropriate curves may create another problem, although one of the major uses of soil types has been in developing stratified management plans. Finally, soils are only one part of the environment to which the forest is responding.

Predictive equations based on combinations of soil properties—soil-site indexes—have been widely used. These are typically localized, empirical relationships. Data are collected on a variety of physical and chemical properties of soil and then subjected to multiple regression analysis with a site index as the response variable. Representative properties that have been used in equations include thickness of the A horizon, moisture-holding capacity, and total soil depth (Daniel, Helms, and Baker 1979). Currently, soil-site index approaches do not appear to be in wide use.

Site classification systems

Various site classification schemes attempt to combine elements of geology, physiography (land-forms), soils, and vegetation for predicting the management potential, including productivity, of forest sites. These include the physiographic types of site developed in Ontario, Canada, by Hills, the classification of biogeocoenoses developed in British Columbia by Krajina, classifications developed for the Great Lakes region of the United States by Barnes and associates, and forest site classifications developed for New England by Leak and his associates.

Alternative management options

Traditional approaches to forest management in temperate regions focus on economically efficient production and harvest of wood products and reforestation of the site with a new generation of trees. The dominant paradigm is production of even-aged plantations of a single species with final harvest accomplished by clear-cutting.

Precommercial thinning and, in some cases, herbicide treatments are used to maintain rapid growth in crop trees and to free them from competing herbs, shrubs, or trees viewed as weeds. Some management regimes use fertilization to stimulate growth. Commercial thinnings may also be carried out. Rotation ages are determined primarily by economic analysis or, in the case of some government forests, by some biological criterion, such as culmination of mean annual increment. Levels of use vary but typically do not involve the removal of needles and twigs from the harvest site, although subsequent slash disposal activities, such as broadcast slash burning, may consume much of this material. Traditionally, all structural material that can be used is removed, and the remainder is disposed. The site is assumed to be capable of sustaining productivity levels under this regime.

Such an approach to forest management is fundamentally agricultural: it aims to maximize the desired output by simplifying the ecosystem of interest and subsidizing it with energy inputs, such as fertilizers. Implicit in this approach is a belief that what is good for wood production is good for other resource values. The tendency toward simplification is of particular concern because it traditionally occurs at many levels in temperate forest management in terms of genotype, species, product, stand structure, landscape pattern, and successional stage (Franklin and others 1986). Foresters sometimes persist in simplifying forest ecosystems even when doing so is not essential to management objectives and is done at substantial expense.

Development of alternative management paradigms is clearly appropriate, with the increased emphasis placed on the sustained production of all forest values, including wood products, and with our vastly greater knowledge of forest ecosystems and their functioning (Hopwood 1991). Traditional practices, which had their genesis 50 to 100 years ago, do not reflect either the broadened societal objectives for forest land or the scientific findings of the last twenty to thirty years. Returning to my initial commentary defining sustainability and its basis, it seems that sustainable forest management practices should emphasize the maintenance of the productive capacity of the forest land (principle 1) and of the biota that are the engines of the ecosystem (principle 2).

The question, then, is what form the new alternatives to traditional practices should take. The answer involves considerations and alternative

approaches at the level of both the stand and the landscape. The stand level is considered first with the focus on management approaches in stands that are to be managed for some level of commodity production. A consideration follows of landscape-level approaches that involve both managed and reserved areas.

The central concept of alternative approaches for managed stands of temperate forest is to maintain or recreate stands that are structurally and compositionally diverse. That is, within the constraints of objectives and stand conditions, the effort is to maintain as much of the structural and compositional diversity as possible rather than to simplify the stand. Structural diversity is usually the goal, because structure is normally closely correlated to organisms and processes; that is, structure provides the necessary conditions or habitat for desired organisms and processes. The general principle of maintaining structural diversity should be kept in mind during the following discussion. The exact set of silvicultural practices—the treatments developed to create or maintain structural diversity—will vary with the type, condition, and environment of the forest and, of course, with the specific set of management objectives.

Creation of young stands

Young stands provide many opportunities for developing elements or attributes that are important in enhancing ecosystem processes and biodiversity. Aggressive efforts to create stands of mixed composition are one initial step. Plantings of single species and weeding by either chemical or mechanical means strongly direct the managed forest toward a monoculture. Plantings of multiple species and efforts to retain species mixtures in precommercial thinning or weeding exercises will, however, create compositionally diverse forests. Maintaining a mixture of species can greatly enhance a variety of ecological values, such as the ability to provide habitat for a broad array of organisms. For example, an occasional hardwood can add significant structural and species diversity (as host to a variety of plant epiphytes and animal species) to a conifer-dominated stand; this would include substantial heterogeneity in microclimatic and edaphic conditions. Hardwoods such as *Alnus* sp. and *Robinia* bring an additional benefit of nitrogen fixation.

Richer mixtures of conifers can also provide valuable diversity. For example, species belonging to the *Cupressaceae* (cypress or false cedar

family), such as *Thuja* and *Chamaecyparis*, improve the quality of soil in addition to producing valuable wood products. All *Cupressaceae* accumulate calcium and other bases in their foliage, which produces high-quality litter (Kiilsgaard, Greene, and Stafford 1987). This litter contributes, in turn, to higher base saturation, higher rates of nitrogen mineralization, reduced acidity, and production of more biologically active mull humus conditions (Alban 1969; Turner and Franz 1985).

Delaying the process of canopy closure can also have environmental benefits in some young stands. Canopy closure is probably the most dramatic and, for some organisms and processes, the most traumatic single event in the life of the stand, other than its ultimate destruction by some catastrophe. Many aspects of the forest, including its composition and functioning, change rapidly and significantly at the time of canopy closure. Intensive forest management has traditionally sought to achieve rapid closure of the canopy (early full occupancy of the site by commercial trees) following a disturbance, such as clear-cutting. Yet the open conditions prior to closure of the tree canopy are important ecologically. The stage prior to canopy closure is rich in plant and animal species, including many game species, that are valued by humans (Hunter 1990; Thomas 1979). Vascular plant species with nitrogen-fixing symbionts are most common during this period. Hence, maintaining open conditions farther into the rotation—delaying full canopy closure—can provide ecological benefits.

Canopy closure can be delayed by maintaining wider spacings between trees. Reducing the planting densities between trees and undertaking heavy precommercial thinning achieve this objective. Furthermore, studies show that wide spacing can be maintained in young stands with little or no sacrifice in the volume of commercial wood produced (for example, Reukema 1979; Reukema and Smith 1987). Trees can be pruned to produce high-quality wood in the open-grown stands. Such prescriptions are used in management of *Pinus radiata* plantations in New Zealand.

Structural retention at harvest

Structural diversity is emerging from forest ecosystem research as a critical attribute in providing for a diversity of processes and organisms. Furthermore, it is some of the large structures—large living trees, large snags, and large fallen boles—that are typically absent from managed stands,

since stands have traditionally been clear-cut. Retaining some of the structures from the old stand at the time of final harvest is one of the best ways to provide the new stand with a high level of structural diversity, including larger structures.

COARSE WOODY DEBRIS

Coarse woody debris, including large standing dead trees and fallen boles, are extremely important to ecosystem function. They provide habitat for many elements of biological diversity and essential processes. Rotting wood is also important to maintenance of site productivity by contributing nutrients and organic matter to the soil; even the identifiable wood fragments incorporated into the soil—soil wood—play a distinctive role (see, for example, several papers in Harvey and Neuenschwander 1991). Practices that contribute to maintenance of coarse woody debris include the retention of such material at the time of harvest cutting and the creation of snags and logs from trees reserved for that purpose.

Retention of snags and logs is particularly effective for maintaining coarse woody debris when harvesting trees in young and mature stands of natural origin and old-growth forests. Natural stands typically have significant amounts of coarse woody debris that can be used as a biological legacy. Retention of snags is more controversial and less effective than maintenance of logs for a variety of reasons. There are concerns for the safety of forest workers because of the potential for structural failure in snags. Retention of snags increases logging costs. Snags also create potential problems in fire protection because they tend to produce firebrands once ignited. Snags are a potential hazard to aircraft involved in management activities. Furthermore, many snags have relatively short life spans, especially if they are heavily rotted. Nevertheless, efforts to maintain snags on cutover forestlands are increasing because of their importance to many animal species. Two approaches used to reduce hazards associated with snag retention are (a) clustering of snags in small groups or patches and (b) creating snags from living trees following harvest cutting. Silvicultural prescriptions can be designed to maintain a given number and distribution of snags over the rotation. A common objective in *Pseudotsuga* forests in northwestern North America, for example, is the continuous availability of five large (more than 50 centimeters in diameter) snags per hectare.

Living trees can be used as sources for coarse woody debris in stands that lack either large snags or logs, as is the case for stands currently under intensive management. This is a particularly valuable practice for restoring structure to stands and landscapes that have been simplified by past practices.

Maintenance of appropriate quantities and qualities of coarse woody debris in managed stands is, of course, much more complex than simply providing periodically for a few dead trees. Different tree species provide snags and logs with substantially different characteristics and ecological potential. All tree species are not equal in terms of their behavior as coarse woody debris! Furthermore, coarse woody debris needs to be present in various stages of decay. Material of greater structural soundness may be important for geomorphic and some animal habitat roles, for example, while highly decayed wood is of greater value as a component of soil. Numerous questions exist as to the quantities and spatial distribution of coarse woody debris required to achieve specific management objectives; how much is enough? Developing the specific data ultimately needed for silvicultural prescriptions will be a challenge to scientists and managers for many years to come (Maser and others 1988).

RETENTION AND PARTIAL CUTTING OF GREEN TREES

Retention of green trees on cutover areas is another practice that can create higher levels of structural diversity on managed stands. This approach can be referred to as partial cutting, partial retention, or green tree retention, in an effort to distinguish it from both clear-cutting and selective cutting (Franklin 1990). Retention of green trees involves reserving a significant percentage of the living trees, typically including some of the larger or dominant individuals, at the time of harvest for retention through the next rotation. The density, composition, condition, and distribution of the reserved trees vary widely, depending on management objectives, initial stand conditions, and other constraints. The general objective is, however, to sustain a more structurally diverse stand than could be obtained through even-aged management. Partial cutting has not been widely used or recognized in forestry. Some silvicultural textbooks briefly discuss related concepts such as shelterwood with reserve, but these approaches have not been widely taught or applied in forestry.

Many ecological objectives, including several that contribute to sustainability, can be achieved

by retaining living trees on harvested areas while simultaneously producing and removing wood products. First, living trees can be used as sources of coarse woody debris—snags and logs—especially where safety concerns or logging methods make retention of snags difficult. Living trees can also be retained to provide wildlife habitat.

Living trees can function as refugia and inocula for many of the smaller organisms or hidden diversity mentioned early in this review. For example, many species of the rich invertebrate fauna found in forests have poor dispersal capabilities (Lattin 1990). Such organisms typically do not recolonize areas once their habitat has been eliminated by clear-cutting. Refugia for these kinds of organisms can be provided by leaving host trees, which then become an inoculum or source of seeds for the new stand. The same concept is applicable to mycorrhizae-forming fungal species. At least some of these fungi can disappear from cutover areas if all potential host species are eliminated (Perry and others 1988). When some of their hosts are left behind, the fungal communities are conserved and can inoculate the young stands. This concept is a counterpoint to the forester's common complaint that living trees cannot be retained because they are sources of pests and pathogens, such as invertebrates and fungi. Most invertebrates and fungi in forest stands are, in fact, essential components that should be retained, and maintaining living trees on the site is one important tool for achieving this objective.

Retention of living trees, especially dominants, also alters the microclimate of the cutover area. That is what traditional shelterwood cutting is all about: the overstory moderates the microclimate, encouraging regeneration of trees where the environment on a clear-cut would be too severe due to heat or frost (Daniel, Helms, and Baker 1979). Obviously, what works for tree seedlings will work for other forest organisms as well: they would also be expected to survive better on partial cuttings than on clear-cuts. Perhaps as important, many organisms will move more readily through a patch or landscape that has at least some living trees than through a clear-cut environment because of the ameliorated climate or protective cover or both. Replacement of clear-cutting with partial cutting on a managed landscape matrix could dramatically improve overall connectivity and reduce the isolation of islands of natural habitat.

Retention of green trees can be used as a strategy to grow large, high-quality wood during the

next rotation. For example, mature (80- to 250-year-old) *Pseudotsuga menziesii* are still capable of substantial growth (Williamson 1973). Hence, large living trees could provide both economic and ecologic benefits in scenarios involving management of a mixed stand with a low density of large, slower growing trees of one species on a long rotation, while simultaneously growing several rotations of a rapidly growing second species.

Partial cutting could be used to create mixed-structure stands that provide critical wildlife habitat. For example, in northwestern North America, numerous natural stands represent mixtures of young and old structures; the stand may be relatively young (for example, eighty years) but also contain a significant component of large, old trees, large snags, and large logs. Such stands are typically the consequence of wildfires or windstorms that left behind a large legacy from the original stand. Forests of this type often provide suitable habitat for animal species generally associated with old-growth forests (Ruggiero and others 1991). Partial cutting systems could be used to create comparable mixed-structure stands, which would provide late-successional forest habitat conditions in one-quarter to half of the time that would be required following traditional clear-cutting.

Partial cutting could also be used to reduce the impact that harvesting the forest has on hydrologic and geomorphic processes. For example, retention of living trees can reduce the potential for landslides by maintaining root strength, which is critical to maintaining the stability of soils on steep slopes. Retention could also be used to reduce the impact of cutting where harvesting the forest contributes to the frequency and intensity of flood flows. In northwestern North America, for example, maintaining a sufficient number of large trees to intercept snow and maintain the thermal balance on cutover areas will reduce the intensity of the rain-on-snow floods that are common in this region.

Prescriptions for partial cutting vary widely, depending on many factors, including management objectives and stand conditions. For example, providing a minimal number of snags and logs may require retention of as few as ten to eighteen trees per hectare. Creation of mixed-aged, mixed-structure forests suitable for late-successional forest species may require twenty to forty retained trees per hectare, depending on age of the forest.

The appropriate spatial distribution of retained living trees—whether to disperse them or con-

centrate them in patches—is another important issue in partial cutting. The answer depends partially on objectives and constraints. For example, when small patches of living trees are retained, they may be more effective as refugia for invertebrates; aggregating them may also minimize impacts on logging and other forestry operations. At the same time, well-distributed snags and logs are desirable because they maintain productivity of the soil and provide habitat for some wildlife species.

SELECTIVE CUTTING

Selective cutting involves the removal of individual or small groups of trees at relatively frequent intervals (every ten years). This system is typically aimed at creating or perpetuating uneven-aged stands (more than three age classes) and always maintains a protective cover at the site. In the last several decades, large industrial forest landowners and government forest agencies have rarely used selective cutting as a major approach to forest management, although there have been exceptions. Its unpopularity is due to the high costs, inefficiency, technical difficulty in application, and potential damage to stands and sites when applied to large trees on steep mountainous topography.

Selective cutting can, however, be an effective technique for maintaining compositional and structural diversity in stands that are managed for low to moderate levels of wood production (Daniel, Helms, and Baker 1979). Of all the cutting systems, it provides the highest level of biological legacies of all types and, under some circumstances, minimizes impacts on the long-term productive potential of the site.

Selective cutting is not a panacea, however. It is a difficult system to apply and requires the forester to have a high level of technical competence, particularly if a high-grading approach, in which only the most valuable trees are removed, is to be avoided. It can be very difficult to apply when the preferred species of tree crop is intolerant of shading, and potential shade-tolerant competitors are present. The potential is also very high for damage to residual stands and for accelerated erosion and soil degradation when applied to stands on steep mountain topography; this is because selective cutting requires frequent entries to the stand, which, in turn, may necessitate creation and maintenance of a dense system of roads and skid trails. Use of aerial logging techniques can reduce some of these impacts, but their high cost may be prohibitive.

It also appears that selective cutting may not maintain conditions suitable for many interior or late-successional animal species, despite the high levels of structural retention. For example, at least some of the neotropical migrant songbirds that use the eastern North American deciduous forests respond negatively to the creation of even small openings within the large intact forest areas they require (Terborgh 1992). In another example from the tropics, selective logging has had significant and pervasive impacts on animal species of the interior forest. Hence, it is not safe to assume that selective cutting is the best approach to integrating forest harvest and environmental values, including sustainability.

Much more extensive use of selective cutting is appropriate in future efforts to develop forest management approaches that are more ecologically sensitive. It will be most applicable on areas where there is less emphasis on commodity production and where the species and topography are appropriate to frequent light-harvest entries. In contrast, partial cutting, as presented earlier, is typically designed around a single-harvest entry per rotation.

LONG ROTATIONS

The practice of using long rotations has a high potential as an alternative management approach that would reduce the impacts of harvest cutting on environmental values, including site productivity and biodiversity. This might involve increasing rotation ages by a factor of 1.5 to 2.0 over current rotations, which have been based on economic factors or biological maturity of crop trees (the culmination of mean annual increment). As a specific example, the rotation age (frequency of final harvest cut) on national forests in the northwestern United States might be shifted from the current 80 to 100 years to 160 to 200 years.

Such shifts in rotation age can have numerous environmental benefits, including reduced impacts on soils and biological diversity. They can drastically reduce the proportion of a managed landscape that is in a recently cutover condition, which, in turn, can reduce the risk to soils and water quality since, for example, recently cutover areas are much more subject to erosion and landslides. A higher percentage of the landscape would be in forest cover under long rotations, and some of this forest would include later stages of forest succession that would not be present in a landscape managed under short rota-

tions. Overall, long rotations help to maintain a greater diversity of organisms and processes.

Most large industrial forest landowners view long rotations as an anathema, but only from an economic standpoint. In their view, the return on their investment is simply not acceptable in managed forests with rotations longer than fifty to sixty years. Such strictly economic criteria are rarely applied to government forest lands, however.

Amelioration and restoration practices

The potential for restoring structures, organisms, and processes to forest stands that have been simplified or degraded warrants mention. There are many situations where silviculture can contribute to the restoration of degraded sites, the creation of habitat (such as snags and other structures), and the reintroduction of organisms. For example, in the Northwestern United States, workshops, experiments, and pilot tests are underway aimed at restoration of structural complexity in simplified young stands developed following earlier logging. Specific objectives typically include provision of habitat for species associated with mature and old-growth forests.

Existing materials for assessing sustained productivity

Productivity is a topic that has concerned foresters and forest scientists for several centuries. Numerous approaches have been developed to assess productivity and numerous datasets have been collected that vary widely in terms of their formality, levels of sophistication, effort, etc. Not surprisingly, there are great differences in approaches, both between different countries and regions within countries. In general, uniform approaches have not been developed and adopted, except in countries where a national forestry organization has had the ability to define and push adoption of a countrywide approach. There have been attempts through organizations like the International Union of Forest Research Organizations (IUFRO) to at least develop and adopt standardized terminology and explore common methodological approaches (AAAS 1967 and Newbould 1967). However, uniform methods do not generally exist even among adjoining regions, let alone countries.

Numerous other problems are associated with existing methodologies, predictive tools, and data sets in addition to this general lack of uniformity. For example, the vast majority deal only with the production of wood or biomass and do not address total productivity of the ecosystem. Further, even when a methodology purports to address productivity of the forest ecosystem, significant components, such as the productivity belowground, are ignored (Harris, Sanantonio, and Mc Ginty 1980). Hence, a wealth of material exists for assessing productivity of temperate forests, but little of it can be directly adapted to address the primary issue in this volume: measuring the productivity of ecosystems over long periods of time.

Measurement programs

Sample plots placed in forest stands have been a primary tool of foresters almost since the inception of the forestry profession. Although they vary widely in size, layout, permanence, and almost all other features, sampling plots have been around for a long time and have provided the bulk of the empirical data for estimating forest productivity.

Most countries, agencies, or corporations that are involved in management of significant forest properties have some kind of continuing forest inventory program that uses a system of sample plots. Continuous forest inventory is a central concept in forestry that generally involves the establishment of permanent sample plots over the forest property, usually using some systematic sampling design. The specifics of these plots vary widely with the organization, but the use of plot clusters is common. Measurement intervals also vary; however, five-year remeasurements are common.

In some countries, national organizations have responsibility for conducting forest inventories. In the United States, for example, the Department of Agriculture Forest Service takes periodic inventories of resources on all publicly owned forests. Regional experiment stations design and conduct this inventory, except on national forest lands, where it is carried out by the National Forest Management Organization. This inventory system, as with many directed to forest lands, is beginning to broaden its focus beyond the counting of standing live trees and calculation of wood volumes to the acknowledgment of other forest attributes (structures such as snags and fallen logs) and resources.

Such traditional inventories typically have numerous deficiencies that drastically limit their potential value as models for a system to assess long-term productivity. Foremost among these is that they are typically designed to provide a statistical sample of an entire forest ownership, state, region, or country. They do not provide estimates of standing crops (let alone productivity) at the level of an individual stand; the data cannot be related to some spatial data base. Hence, it is possible to infer that there are x hectares of stands of y age and z volume, but there is no way to determine where they are located within the sampling area.

Because forest sampling is conducted at very low densities and is not stand-specific, interpreting the causes of changes in stand volumes and growth rates between remeasurement periods is very difficult. The phenomenon of declining productivity in the third generation of forests in the southeastern United States provides an excellent example; in the 1970s and 1980s, growth rates appeared to have declined, leading to suggestions that site productivity might also be declining. Several alternative hypotheses were proposed, however, and resolution of this issue has been rendered difficult by the low density and geographical resolution of the sample.

Stand-based inventory systems do exist in some ownerships and provide a better opportunity to identify changes, and their causes, in the productivity of a forest over time. Clearly, none of these systems is designed to measure changes in the inherent productivity of a site. They are simply approaches to estimating standing volumes of wood or aboveground organic material and to calculating rates of accumulation or loss; that is, growth or productivity of the current stand.

A protocol or set of protocols to assess changes in long-term forest productivity has not yet been designed nor, obviously, implemented. The forestry organization that has gone the furthest in this direction, so far as I know, is the group in New Zealand concerned with management of the exotic *Pinus radiata* forests.

Long-term experiments are being developed and implemented by forest research and management organizations to address the specific issue of long-term forest ecosystem productivity under varying management regimes. Examples exist in many temperate forest regions. These are research projects, not routine operational activities; the investment in data collection is high, and the

geographic scope is typically low. Nevertheless, these experiments will provide the most definitive information on long-term productivity and will almost certainly provide useful insights into the design of broader schemes for assessing the productivity of forest ecosystems.

Existing data sets

An immense number of data sets address the issue of forest productivity over a variety of spatial and temporal scales. The forestry literature is full of data on productivity, as are the files of forest research and management agencies. As noted earlier, the concept of continuous forest inventory is generally followed in most countries that have significant forestry programs.

It would be impossible to describe or list this immense body of data in a short review. Many reviews and directories are already available, several of which are cited below. Unfortunately, much of this information has limited value. As noted earlier, these data sets typically focus only on the tree and often only on the wood component. They do not address productivity of the ecosystem as it is currently defined.

The fact that these data sets consider only the aboveground portion of the tree or forest is a serious deficiency. When monitoring changes in forest productivity, this approach is unacceptable, particularly since shifts in the relative productivity of aboveground and belowground components can occur with changes in site conditions. In temperate regions, the proportion of photosynthate used belowground tends to increase substantially with increased nutrient or water stress (Kimmins 1987). Finally, these data sets have rarely been designed to assess long-term changes in productivity. Not only are essential elements missing, but the methods used have often been modified over decades of remeasurement, making comparisons of data difficult.

During the last few decades, various data sets on the productivity of temperate forest ecosystems have been developed that do attempt to address overall, rather than just wood, productivity. Even these are far too numerous to compile in this review. There are, however, some major references that provide access to many of these data sets and a great deal of the literature.

One of the best compilations of data on productivity of temperate forest ecosystems is the synthesis volume on forests generated by studies

of the International Biological Programme (Reichle 1981). This volume summarizes most of the research on forest productivity conducted during a global ten-year effort. Included are numerous data sets from intensive study sites throughout (primarily, but not exclusively) the northern temperate region. Although incomplete for some variables, the focus is on ecosystem productivity.

Numerous research data sets have been generated since the 1960s, when studies of ecosystem productivity first became popular. Cannell (1982) has compiled many of these in a book, *World Forest Biomass and Primary Production Data*. Other important compilations and discussions of forest productivity are Eckardt (1968, a volume published as part of a UNESCO series), the proceedings of several conferences (International Union of Forest Research Organizations 1971, 1973), and a summary of research, *Productivity of the World Ecosystems* (Reichle, Franklin, and Goodall 1975). No list of major publications on forest productivity would be complete without mention of the Russian classic, *Productivity and Mineral Cycling in Terrestrial Vegetation*, by Rodin and Bazilevich (1967), which includes many tables of data on forests as well as other types of terrestrial ecosystems.

On an operational rather than a research level, the most comprehensive data sets on forest productivity are probably those associated with very intensive management of plantations. Examples include the exotic *Pinus radiata* plantations in New Zealand, Australia, and South Africa and hybrid *Populus* plantations worldwide. Forestry agencies in at least some of these locales have given substantial attention to long-term productivity and its measurement, including belowground components in a few cases.

As noted, innumerable data sets on forest productivity address the production of wood. Although essentially no data sets were designed specifically to address forest ecosystem productivity over long time periods, some major forest research projects have been or currently are being established throughout the northern temperate zone that should correct many of these deficiencies.

Predictive models

It is not surprising that many models of various types are aimed at predicting forest productivity; this is, after all, one of the major concerns of foresters and forest management organizations. Many approaches have been taken, including traditional forest yield tables and computerized

growth and yield models of highly varied constructs. A growing number of forest succession models include predictions of overall changes in forest structure as well as biomass.

WOOD YIELD TABLES AND MODELS

Yield tables have been the most traditional form of forest production models (see, for example, Society of American Foresters, *Forestry Handbook*, 1984). These models typically have been developed using data collected from a large number of forest plots located in forest stands of relative species composition, stocking levels, geography, and so on. Through a variety of mathematical, statistical, and subjective analyses, such data are used as a basis for constructing tables that indicate the wood yields that should be expected at various time intervals on sites of varying productive potential. Productive potential is typically indexed by the site index criterion discussed earlier (heights achieved by dominant trees by some index age). Most yield table publications also include many other tables relating stocking density, periodic growth and mortality, and other stand variables to stand age.

Forest yield tables have most commonly been developed for well-stocked, even-aged stands of a single species. Such tables exist for almost every important species and type of forest in the northern temperate zone, and, typically, there are several yield tables (often representing different geographic regions or management intensities) for very important commercial tree species. As very general models to predict forest growth, yield models have major limitations, particularly in their ability to predict accurately the growth of specific stands.

The prediction of forest growth has shifted toward computer-based growth and yield models with the development of computer technologies. These tend to be much more sophisticated and deal with a larger set of variables than was possible with traditional yield tables. However, as with yield tables, they are normally based on empirical data sampled from some forest population.

Many such growth and yield models use a wide variety of approaches and assumptions. Early yield tables and growth simulation models focused on natural stands, but development of growth simulators for managed stands has been particularly popular with forestry agencies during the last several decades. This has allowed managers to consider the effects of various management regimes. ORGANON, a model devel-

oped at Oregon State University, is a good example of a state-of-the-art model of growth and yield (Hann, Olsen, and Hester 1992). FORTNITE is one of the few examples of a growth model designed to look at forest productivity as it is affected by various manipulations over long time periods (Kimmins 1987).

The limited empirical data bases from which yield tables and models have been constructed have been one of their major limitations. Mortality, the most difficult variable to estimate, creates the greatest degree of uncertainty in predicting yields.

ECOSYSTEM MODELS

During the last twenty years, a new class of forest growth model has emerged that focuses on predicting successional changes in forests over very long time periods. These models are based on the dynamics of tree populations, but they also provide output on stand-level attributes, such as accumulations of organic matter. Many of these forest ecosystem models are conceptually related and are sometimes referred to as the FORET family of forest growth models (Shugart 1984). The first of these models was JABOWA, which was developed for the Hubbard Brook Experimental Forest (New Hampshire). Its primary focus is on the processes of birth, growth, and death of the tree population. These processes are driven, in turn, by environmental conditions, including temperature and moisture at the site and light within the stand. The birth and death processes are based on probability functions. A variety of model outputs—tree density, biomass, leaf area, and so forth—is possible, depending on the interests of the scientist or manager.

Extensive work is under way to improve the capabilities of FORET-type models, including the development of spatially explicit versions, which keep track of the location of individual trees, incorporate the dynamics of coarse woody debris (standing dead trees, fallen logs, and so forth), and incorporate more realistic probability functions, such as for tree mortality. Versions have been developed that focus on the nutrient status of the site as well as forest structure.

Current models of this type have some limitations. Because they are designed to simulate changes in a variety of ecosystem attributes over very long time periods and for diverse sites, predictions of tree growth or wood production for specific stands may not be as good as for the traditional, and much more specific, growth and yield models.

An important attribute of these models is that they are stochastic or probabilistic rather than deterministic. Most forest growth and yield models are deterministic: only one solution is possible with an initial set of conditions. But, with the FORET family of models, an infinite number of solutions is possible. Hence, numerous, even hundreds of, simulations may be run for a given stand to produce an array of predicted outcomes: in effect, a probability distribution for future conditions of the stand.

Conclusions and recommendations

Assessing the long-term productivity or sustainability of temperate forest ecosystems represents a major challenge. Currently, this is not being adequately accomplished anywhere, nor does a suitable model or prototype exist for such a program. Hence, development of a protocol or, better still, a series of protocols for measuring the sustainability of forest ecosystems should have very high priority. Existing research and management programs can provide useful information and guidance in this effort.

The most important points in designing the assessment program are (a) recognizing the necessity of assessing several variables and (b) identifying those variables. Clearly, no single variable will adequately assess sustainability. Monitoring sustainability of forest lands and associated waters will require periodic assessments of a broad array of variables from the landscape to populations of specific organisms. Specifically, a monitoring program should assess the following:

- Forest cover and condition at the landscape level
- Flow and quality of water
- Structural conditions, including live and dead trees, of the forest stand
- Physical, chemical, and biological condition of the soil and
- Populations and trends in indicator organisms.

A program that covers such a broad range of parameters will require programs of highly varied spatial and temporal scale. An approach based on a single measurement, index, or sampling strategy is not going to be successful. Admittedly, giving up the notion of such a simple monitoring program creates greater complexities and much higher costs; nevertheless, it is an essential first

step for a program that truly intends to monitor sustainability. Fortunately, such a strategy is consistent with the emerging interest in adaptive management of resources. This approach requires comprehensive monitoring to provide the resource management system with corrective feedback.

Once a decision has been made to proceed with a multi-factor monitoring program, the specific variables can be chosen and protocols developed by working with appropriate scientific teams. There will undoubtedly be substantial variation among forested regions, both in terms of variables and sampling techniques—another blow, unfortunately, to the notion of a singular global scheme. In the following sections, some candidate variables are proposed for a minimal monitoring program to assess productivity of the forest ecosystem.

Minimal program for monitoring sustainability of the forest ecosystem

A minimal program should incorporate the following measures: forest cover and condition at the landscape level, system losses and hydrologic controls, biological condition of the forest, condition of the soil, and biological diversity.

FOREST COVER AND CONDITION AT THE LANDSCAPE LEVEL

Periodic assessments of the extent of forest cover, and some interpretation of its condition (age and stocking density), are the variables of interest in this segment of the monitoring program. These assessments would probably be made at five-year intervals and use various types of data obtained by remote imagery, satellites, or aircraft. The assessments would probably be made at the level of regions, in the case of large countries, or at the level of small countries.

SYSTEM LOSSES AND HYDROLOGIC CONTROL

Aquatic systems—streams, rivers, and lakes—are probably the best integrators of the effects of human activities on terrestrial landscapes. The system losses referred to here are primarily losses of soil and nutrients that can be measured within aquatic systems as suspended or dissolved sediments and materials. Hence, a monitoring element that addresses the production or accumulation of sediments and the quality of water is important. Note that this monitoring occurs in the aquatic environment rather than in upland forest areas. The production of water—the total amount, seasonal distribution, and frequency and

level of flood flows—is also extremely important, especially when water is recognized as one of the major products of a forest ecosystem. Both system losses and water production are probably best monitored by creating a system of benchmark watersheds in forested regions where the flow and quality of water are sampled on a more-or-less continuous basis. Techniques for such measurement programs are well known and should be easily adapted. The biggest problems are the initial cost of such installations and the continuing costs in funds and technical personnel of maintaining and analyzing data generated by such a monitoring program. However, government organizations such as the U.S. Geological Survey have extensive experience with these activities.

BIOLOGICAL CONDITION OF THE FOREST

The primary focus of this portion of the monitoring program is on some measure of productivity at the level of the individual forest stand. Tree growth per unit of time under some specified conditions, such as dominant free-grown individuals, still appears to be the best measure for integrating the overall effect of all variables influencing productivity. A direct measure of net primary productivity is beyond the scope of a routine monitoring program.

The use of tree growth per unit of time is conceptually the same approach that is used with the site index concept reviewed earlier. An alternative approach might be some measure of overall productivity of the stand; however, this can be very strongly influenced by stand conditions, so the problem of standardization is greater than where individual trees are used.

In addition to a measure of site productivity, it may also be important to monitor the structural diversity found within forest stands. Levels of standing dead trees (snags) and fallen logs on the forest floor are an example of an important structural element that has often been ignored in programs to monitor the condition of a forest. Because such material is extremely important as animal habitat, and can be important in maintaining site productivity, it should be an element of any scheme for monitoring forest ecosystems.

CONDITION OF THE SOIL

The soil is, in terms of human life spans, a largely nonrenewable resource. It is important, therefore, to monitor specifically the physical, chemical, and biological state of this basic resource. Although it can be argued that the use of some

biological measure of site productivity negates the need to monitor soil parameters directly, there is the possibility of doing irreversible harm to forest soils before that harm is reflected in declining productivity of the site. There is also the possibility of biological compensations for declining soil condition.

A soil monitoring program should include assessments of loss (due to erosional processes), physical conditions (bulk density and physical conditions), chemistry (primarily levels of critical nutrients with consideration of trace and toxic elements), and biota of the soil. One specific element of the soil biota that should receive attention in a monitoring program is the diversity of mycorrhizae-forming fungal species that are present.

BIOLOGICAL DIVERSITY

General measures of biological diversity, in terms of overall species richness, are probably not of much value in a monitoring program. Diversity indexes tend to assume that all species are of equal interest and that the richer the ecosystem, the better. This is clearly not the case with forested and, probably, most other natural or semi-natural ecosystems.

It will often be appropriate to include monitoring of selected organisms, however, because they have intrinsic importance to the ecosystem as indicator and keystone species or because they have high interest and significance to *Homo sapiens*. Species chosen for monitoring will have to be carefully selected based on scientific and societal considerations; however, monitoring at the level of individual species, guilds, functional groups, and so forth must almost inevitably be part of a comprehensive monitoring program.

This is probably the most difficult and, in terms of criteria for selecting organisms or organismal groups, the most poorly developed assessment approach. Although techniques exist for monitoring many vertebrate groups, such as birds, mammals, and amphibians, they may require high levels of technical expertise. More critical is the lack of developed approaches to the monitoring of functionally important groups such as invertebrates, including insects, and fungi.

Any monitoring program that purports to address sustainability of the forest ecosystem must, of necessity, address organisms as species or groups of species; it cannot be based totally on a single measure or integrated index of ecosystem function, such as productivity. Biodiversity is basic to long-term sustainability or productive potential.

Implementing a monitoring program

Generic plans for monitoring forest sustainability can be developed at the global and continental levels, but details of parameters and sampling techniques will have to be adapted to the particular conditions of regions and individual countries. Establishment of a global advisory body to develop general guidelines and assist in planning and implementing monitoring programs at the level of countries, regions, and continents would certainly be useful, so long as the equally critical elements of flexibility in design and scientific integrity and credibility are maintained.

Residents of rural environments in and around forests should be given special consideration for employment in the monitoring program. Traditionally, monitoring programs are assigned to professional and technical personnel within established agencies, who often live outside the affected region and are subject to frequent transfers. Resident populations have long-term familiarity with the region, including appropriate work experience, and they intend to reside in the locale. Necessary scientific and technical training could be provided for selected residents who could then be incorporated into the long-term monitoring program.

Accelerated research program

It should be clear from this review that research based on the productivity of forest ecosystems and their maintenance needs to be drastically expanded. Forest science, in particular, needs to broaden its view from the level of the tree (or just the bole) to that of the whole ecosystem. The following categories of research are critically in need of attention:

- Productivity of belowground portions of forest ecosystems
- Canopy architecture and its effect on productivity, particularly the relative effectiveness of multilayered and multispecies canopies
- Dynamics of soil organic matter and chemistry over long time periods, including rates of soil development under natural regimes
- Ecological role and dynamics of coarse woody debris across a full range of ecosystems and
- Improved understanding of causes and patterns of tree mortality and other stochastic processes in forest ecosystems.

For other suggestions on research programs, see *Forestry Research: A Mandate for Change* (National Research Council 1990).

References

- AAAS (American Association for the Advancement of Science). 1967. *Primary Productivity and Mineral Cycling in Natural Ecosystems*. New York.
- Aber, J. D., K. J. Nadelhoffer, P. Steudler, and J. M. Melillo. 1989. "Nitrogen Saturation in Northern Forest Ecosystems." *BioScience* 39, pp. 378-86.
- Adams, R. M., C. Rosensweig, R. M. Peart, J. T. Ritchie, B. A. McCarl, J. D. Glyer, R. B. Curry, J. W. Fones, K. J. Boote, and L. H. Allen, Jr. 1990. "Global Climate Change and U.S. Agriculture." *Nature* 345, pp. 219-24.
- Alaback, P. B. 1984. "A Comparison of Old-growth Forest Structure in the Western Hemlock-Sitka Spruce Forests of Southeast Alaska." In W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley, eds., *Fish and Wildlife Relationships in Old-Growth Forests*, pp. 219-25. Bronx, N.Y.: American Institute of Fisheries Research Biologists.
- Alban, D. H. 1969. "The Influence of Western Hemlock and Western Red Cedar on Soil Properties." *Proceedings of the Soil Science Society of America* 33, pp. 453-57.
- Bazzaz, F. A. 1990. "The Response of Natural Ecosystems to the Rising Global CO₂ Levels." *Annual Review of Ecology and Systematics* 21, pp. 167-96.
- Bormann, F. H., and G. E. Likens. 1981. *Pattern and Process in a Forested Ecosystem*. New York: Springer-Verlag.
- Cannell, M. G. R. 1982. *World Forest Biomass and Primary Production Data*. New York: Academic Press.
- Carroll, G. C. 1980. "Forest Canopies: Complex and Independent Subsystems." In R. H. Waring, ed., *Forests: Fresh Perspectives from Ecosystem Analysis*, pp. 87-107. Proceedings of the fortieth annual Biological Colloquium. Corvallis, Oreg.: Oregon State University Press.
- Daniel, T. W., J. A. Helms, and F. S. Baker. 1979. *Principles of Silviculture*. 2d ed. New York: McGraw-Hill Book Company.

- Denison, W. C. 1979. "Lobaria oregana, A Nitrogen-fixing Lichen in Old-growth Douglas Fir Forests." In J. C. Gordon, C. T. Wheeler, and D. A. Perry, eds., *Symbiotic Nitrogen Fixation in the Management of Temperate Forests*, pp. 266-75. Corvallis, Oreg.: Oregon State University Forest Research Laboratory.
- Easmus, D., and P. G. Jarvis. 1989. "The Direct Effects of Increase in the Global Atmospheric CO₂ Concentration on Natural and Commercial Temperate Trees and Forests." *Advances in Ecological Research* 19, pp. 1-55.
- Eckardt, F. E., ed. 1968. *Functioning of Terrestrial Ecosystems at the Primary Production Level*. Proceedings of the Copenhagen Symposium. New York: United Nations Educational, Scientific, and Cultural Organization.
- Edmonds, R. L., ed. 1981. *Analysis of Coniferous Forest Ecosystems in the Western United States*. United States/International Biosphere Program Synthesis Series 14. Stroudsburg, Penn.: Hutchinson Ross.
- Franklin, J. F. 1990. "Biological Legacies: A Critical Management Concept from Mount St. Helens." In *Transactions of the Fifty-fifth North American Wildlife and Natural Resources Conference*, pp. 216-19. Washington, D.C.: Wildlife Management Institute.
- . 1992. "Scientific Basis for New Perspectives in Forests and Streams." In R. J. Naiman, ed., *Watershed Management: Balancing Sustainability and Environmental Change*, pp. 25-72. New York: Springer-Verlag.
- Franklin, J. F., and R. T. T. Forman. 1987. "Creating Landscape Patterns by Forest Cutting: Ecological Consequences and Principals." *Landscape Ecology* 1, pp. 5-18.
- Franklin, J. F., P. M. Frenzen, and F. J. Swanson. 1988. "Re-creation of Ecosystems at Mount St. Helens: Contrasts in Artificial and Natural Approaches." In J. Cairns, Jr., ed., *Rehabilitating Damaged Ecosystems*, vol. 2, pp. 1-37. Boca Raton, Fla.: CRC Press.
- Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. "Tree Death as an Ecological Process." *BioScience* 37, pp. 550-56.
- Franklin, J. F., and T. A. Spies. 1991. "Composition, Function, and Structure of Old-growth Douglas Fir Forests." In L. F. Ruggerio, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords., *Wildlife and Vegetation of Unmanaged Douglas Fir Forests*, pp. 71-80. PNW-GTR-185. Portland, Oreg.: U.S. Forest Service, Pacific Northwest Research Station.
- Franklin, J. F., and others. 1981. "Ecological Characteristics of Old-growth Douglas Fir Forests." General Technical Report PNW-118. U.S. Department of Agriculture, Forest Service, Northwest Forest Range and Experiment Station, Portland, Oreg.
- . 1986. "Modifying Douglas Fir Management Regimes for Nontimber Objectives." In C. D. Oliver, D. P. Hanley, and J. A. Johnson, eds., *Douglas Fir: Stand Management for the Future*, pp. 373-79. Contribution 55. Seattle, Wash.: University of Washington, College of Forest Resources.
- . 1991. "Effects of Global Climate Change on Forests in Northwestern North America." *Northwest Environmental Journal* 7, pp. 233-54.
- Gholz, H. L. 1982. "Environmental Limits on Aboveground Net Primary Production, Leaf Area, and Biomass in Vegetation Zones of the Pacific Northwest." *Ecology* 63:2, pp. 469-81.
- Grier, G. C., and others. 1989. "Productivity of the Forests of the United States and Its Relation to Soil and Site Factors and Management Practices: A Review." General Technical Report PNW-222. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oreg.
- Halpern, C. B. 1988. "Early Successional Pathways and the Resistance and Resilience of Forest Communities." *Ecology* 69, pp. 1703-15.
- . 1989. "Early Successional Patterns of Forest Species: Interactions of Life History Traits and Disturbance." *Ecology* 70:3, pp. 704-20.
- Hann, D. W., C. L. Olsen, and A. S. Hester. 1992. *ORGANON User's Manual*. Oregon State University, Department of Forest Resources, Corvallis, Oreg.
- Harmon, M. E., and H. Chen. 1992. "A Comparison of Coarse Woody Debris Dynamics in Two Old-growth Forest Ecosystems: Chanbai Mountain, PRC, and H. J. Andrews Experimental Forest, U.S.A." *BioScience* 41, pp. 604-10.
- Harmon, M. E., and others. 1986. "Ecology of Coarse Woody Debris in Temperate Ecosystems." In A. MacFadyen and E. D. Ford, eds., *Advances in Ecological Research* 15, pp. 133-302. Academic Press.

- Harris, W. F., D. Santantonio, and D. McGinty. 1980. "The Dynamic Belowground Ecosystem." In R. H. Waring, ed., *Forests: Fresh Perspectives from Ecosystem Analysis*, pp. 119-29. Corvallis, Oreg.: Oregon State University Press.
- Harvey, A. E., and L. F. Neuenschwander, eds. 1991. "Proceedings: Management and Productivity of Western-montane Forest Soils." General Technical Report INT-280. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah.
- Heath, B., P. Sollins, D. A. Perry, and K. Cromack, Jr. 1987. "Asymbiotic Nitrogen Fixation in Litter from Pacific Northwest Forests." *Canadian Journal of Forest Research* 18, pp. 68-74.
- Hopwood, D. 1991. *Principles and Practices of New Forestry*. Land Management Report 71. Victoria, B.C.: British Columbia Ministry of Forests.
- Hunter, J. L., Jr. 1990. *Principles of Managing Forests for Biological Diversity*. Englewood Cliffs, N.J.: Prentice-Hall.
- International Union of Forest Research Organizations. 1971. *Working Party on the Forest Biomass Studies. Section 25, Growth and Yield*. Gainesville, Fla.: University of Florida.
- . 1973. *Working Party on the Mensuration of Forest Biomass. 54.01 Mensuration, Growth, and Yield*. Vancouver, B.C., Canada.
- Jarvis, P. G. 1989. "Atmospheric Carbon Dioxide and Forests." *Philosophical Transactions of the Royal Society of London B* 324, pp. 369-92.
- Jenny, H. 1980. *The Soil Resource Origin and Behavior*. New York: Springer-Verlag.
- Kiilsgaard, C. W., S. E. Greene, and S. G. Stafford. 1987. "Nutrient Concentrations in Litterfall from Some Western Conifers with Special Reference to Calcium." *Plant and Soil* 102, pp. 223-27.
- Kimmins, J. P. 1987. *Forest Ecology*. New York: Macmillan Publishing Company.
- Lattin, J. D. 1990. "Arthropod Diversity in Northwest Old-growth Forests." *Wings* 15:2, pp. 7-10.
- Likens, G. E., ed. 1989. *Long-Term Studies in Ecology: Approaches and Alternatives*. New York: Springer-Verlag.
- MacMahon, J. A. 1981. "Successional Processes: Comparisons among Biomes with Special Reference to Probable Roles of and Influences on Animals." In D. C. West, H. H. Shugart, and D. B. Botkin, eds., *Forest Succession: Concepts and Application*, pp. 277-304. New York: Springer-Verlag.
- Maser, C., R. F. Tarrant, J. M. Trappe, and J. F. Franklin, eds. 1988. "From the Forest to the Sea: A Story of Fallen Trees." General Technical Report PNW-GTR-229. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oreg.
- National Research Council. 1990. *Forestry Research: A Mandate for Change*. Washington, D.C.
- Newbould, P. J. 1967. *Methods for Estimating the Primary Production of Forests*. Oxford, England: Blackwell Scientific Publications.
- Oliver, C. D., and B. C. Larson. 1990. *Forest Stand Dynamics*. New York: McGraw-Hill Book Company.
- Perry, D. A., and others. 1988. *Maintaining the Long-Term Productivity of Pacific Northwest Forest Ecosystems*. Portland, Oreg.: Timber Press.
- . 1989. "Bootstrapping in Ecosystems." *BioScience* 39, pp. 230-37.
- Pritchett, W. L., and R. F. Fisher. 1987. *Properties and Management of Forest Soils*. 2d ed. New York: John Wiley and Sons.
- Reichle, D. E., ed. 1981. *Dynamic Properties of Forest Ecosystems*. International Biological Programme 23. Cambridge, England: Cambridge University Press.
- Reichle, D. E., J. F. Franklin, and D. W. Goodall, eds. 1975. *Proceedings of a Symposium on Productivity of World Ecosystems*. Washington, D.C.: National Academy of Sciences.
- Reiners, W. A. 1992. "Twenty Years of Ecosystem Reorganization Following Experimental Deforestation and Regrowth Suppression." *Ecological Monographs* 63:4, pp. 503-23.
- Reukema, D. L. 1979. "Fifty-year Development of Douglas Fir Stands Planted at Various Spacings." Research Paper PNW-254. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest Range and Experiment Station, Portland, Oreg.
- Reukema, D. L., and J. H. G. Smith. 1987. "Development over Twenty-five Years of Douglas Fir, Western Hemlock, and Western Red Cedar Planted at Various Spacings on a Very Good Site in British Columbia." Research Paper PNW-381. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oreg.
- Rodin, L. E., and N. I. Bazilevich. 1967. *Production and Mineral Cycling in Terrestrial Vegetation*. London: Oliver and Boyd.

- Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff, eds. 1991. "Wildlife and Vegetation of Unmanaged Douglas Fir Forests." General Technical Report PNW-285. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oreg.
- Schoen, J. W., and M. D. Kirchoff. 1990. "Seasonal Habitat Use by Sitka Black-tailed Deer on Admiralty Island, Alaska." *Journal of Wildlife Management* 54, pp. 371-78.
- Shugart, H. H. 1984. *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*. New York: Springer-Verlag.
- Society of American Foresters. 1984. *Forestry Handbook*. New York: John Wiley and Sons.
- Sollins, P. 1982. "Input and Decay of Coarse Woody Debris in Coniferous Stands in Western Oregon and Washington." *Canadian Journal of Forest Research* 12, pp. 18-28.
- Swank, W. T., and D. A. Crossley, Jr., eds. 1988. *Forest Hydrology and Ecology at Coweeta*. New York: Springer-Verlag.
- Terborgh, J. W. 1992. *Diversity and the Tropical Rain Forest*. New York: Scientific American Library.
- Thomas, J. W., ed. 1979. *Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington*. USDA Agricultural Handbook 553. Washington, D.C.: U.S. Department of Agriculture.
- Trappe, J. M., J. F. Franklin, R. F. Tarrant, and G. M. Hansen. 1967. *Biology of Alder*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oreg.
- Turner, D. P., and E. H. Franz. 1985. "The Influence of Western Hemlock and Western Red Cedar on Microbial Numbers, Nitrogen Mineralization, and Nitrification." *Plant and Soil* 88, pp. 259-67.
- Waring, R. H., and J. F. Franklin. 1979. "Evergreen Coniferous Forests of the Pacific Northwest." *Science* 204:4400, pp. 1380-86.
- Waring, R. H., and J. Major. 1964. "Some Vegetation of the California Coastal Redwood Region in Relation to Gradients of Moisture, Nutrients, Light, and Temperature." *Ecological Monographs* 34, pp. 167-215.
- Waring, R. H., and W. H. Schlesinger. 1985. *Forest Ecosystems Concepts and Management*. Orlando, Fla.: Academic Press, Inc.
- Williamson, R. L. 1973. "Results of Shelterwood Harvesting of Douglas Fir in the Cascades of Western Oregon." Research Paper PNW-161. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oreg.
- Zobel, D. B., A. McKee, G. M. Hawk, and C. T. Dyrness. 1976. "Relationships of Environment to Composition, Structure, and Diversity of Forest Communities of the Central Western Cascades of Oregon." *Ecological Monographs* 46, pp. 135-56.

**DEFINING AND MEASURING
SUSTAINABILITY**

The Biogeophysical Foundations



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