CHAPTER 5

Temporal Changes in Forest Structure and Function

I. INTRODUCTION

In Chapters 2–4, we presented details about the way forest ecosystems operate at the stand level throughout the year. We now add a longer time dimension to our perspective. Most of our understanding of forest dynamics comes from retrospective analysis from looking at the way past events and stand structure lead to the development of the forests that we can see and measure today. To capture and to quantify that understanding is the role of various forest models, of which a variety exist with different assumptions and limitations. By careful application of these models we can project our knowledge forward in time to visualize how forests may appear and function in the future.

Historically, stand growth models have been developed by statistical analyses of large quantities of forest inventory data (Stage, 1977). These models assume implicitly that conditions in the future will be the same as those under which the measured forests developed. More theoretical but less quantitative models were introduced by ecologists such as Cowles (1899) and Clements (1936) who observed trends in species composition in chronosequences that began on fresh substrates. They noted that soil conditions improved in time as nutrients and organic matter accumulated, and they envisioned that early combinations of plants were replaced by other "communities," one after another in succession until a semistable *climax* type of vegetation appeared. The climax vegetation was thought to replace itself continuously in the absence of disturbance or a major change in climate. The entire sequence from bare substrate to steady-state climax vegetation was termed *primary succession.* If the steady-state community was disturbed, the sequence was not set back to the beginning because of soil development. Instead, a *secondary succession* of plant communities was envisioned that paralleled later phases in primary succession. Although ecologists debated the concept of plant communities (Gleason, 1926) and the idea of a single climatic climax (Tansley, 1935; Whittaker, 1953), the general theory of succession toward a stable end point was accepted in most textbooks until fairly recently (see review by Cook, 1996).

Since the 1960s, however, it has become apparent that the concept of a predictable succession of vegetation types is too simplistic, to the extent that modern ecological texts tend to avoid the term succession and replace it with "vegetation dynamics" (Cook, 1996). There are now many new theories that include more mechanistic and stochastic processes than found in earlier schemes (Pickett, 1976; Connell and Slatyer, 1977; Grime, 1977; Tilman, 1985; Huston and Smith, 1987). Most modern theoretical models recognize that the type of disturbance (fire, flood, windstorm, insect outbreak, etc.), and its intensity and timing, have important consequences that affect vegetation dynamics and ecosystem performance. Modern theories recognize the importance of (a) timing of species establishment, (b) differential abilities of species to compete for space and resources, and (c) tolerance of species to persist under adverse conditions (Cook, 1996).

Models that correctly predict historical patterns of forest growth and vegetation dynamics may still be unable to predict future responses where new conditions affect both growth and the mix of species (Bossel, 1991). During the twentieth century gypsy moth, chestnut blight, Dutch elm disease, and kudzu vine have altered the composition of forests throughout much of the eastern United States, with significant effects on forest stand dynamics. Over the same period, pesticides, herbicides, and atmospheric pollutants have modified conditions from those that occurred previously (Braun, 1950). Also, climatic conditions appear to be changing. Clearly, statistically based forest growth models or classic succession models would be inadequate for predictions; models that can represent ecosystem processes and the changing biosphere are required.

In this chapter, we begin by analyzing how forest ecosystems change in the course of undisturbed stand development and how those changes may be measured retrospectively. We then consider an array of new, mechanistic forest models that provide a means of projecting forest development forward in time. Models such as FOREST-BGC compute the changes in stand biogeochemistry through time. *Gap-phase* vegetation models incorporate patch-sized disturbance events, recruitment, and mortality processes and project their effects on the future composition and structure of the forest. Models which combine biogeochemistry with the dynamics of competition and tolerance among trees hold promise for more realistic projections of forest stand dynamics (Huston, 1991; Cook, 1996). Of course, disturbance is part of any realistic analysis of forest development, as considered in detail in Chapter 6. We do not know specifically what future climatic conditions will be like, nor what natural disturbances or human activity will occur, so we can only test scenarios with these models. These modeled scenarios, however, when done carefully, provide the most realistic method available for assessing the implications of management decisions in a changing future environment.

II. STRUCTURAL STAGES IN STAND DEVELOPMENT

As trees grow, they alter their environment and demands for resources; some trees gain resources at the expense of others. Competition is particularly intense when only one species is present because requirements for resources and the adaptations available to obtain them are nearly identical for all individuals. When more than one species is present, access to resources differs as a result of variable rooting depths and selective patterns of nutrient accumulation (Schulze *et al.,* 1994b). A few colonizing species grow rapidly to become dominant, while the majority of species, particularly in tropical rain forests, remain almost static until a gap in the canopy opens above them. Although mortality occurs, the leaf area index of such stands remains almost constant from year to year. In terms of ecosystems, it is important to recognize changes in canopy level competition that occur over long periods because these affect nutrient cycling, carbon uptake and allocation, as well as water flow through forests.

In only a few places have long-term records of species composition and growth been obtained from repeated measurements on the same plots of ground (Leak, 1987; Harcombe *et al.,* 1990; Fain *et al.,* 1994). More often, changes in forest structure and growth have been inferred from contemporary surveys that represent a wide range of forest age classes (Christensen and Peet, 1981). Scientists have made stem analyses of many trees (including dead standing and fallen stems) to provide a reconstructed history of particular stands (Oliver and Stephens, 1977; Bradshaw and Zackrisson, 1990; Abrams *et al.,* 1995). Changes in aboveground carbon and nutrient stores can be calculated from repeated measurements of stem numbers and diameters using allometric relationships (Chapter 3). Estimating complete forest life cycles, however, requires the construction of dynamic models that can predict tree growth and changes in composition over centuries.

The initial sequence of stand development can be extended to another generation of trees. If the replacement process occurs slowly, LAI and other properties, such as decomposition rates and stand water use, may remain stable from one generation to another (Bormann and Likens, 1979). Underlying the smooth progressive replacement of one species by another are important phases in ecosystem development that reflect subtle differences in the efficiency of operation and the relative importance of various processes. At least four idealized stages in stand development can be defined when a new forest replaces a previous one: (1) initiation, (2) stem exclusion, (3) understory reinitiation, and (4) an old-growth phase (Oliver, 1981; Fig. 5.1). We will describe each of these in some detail and then relate changes in ecosystem processes to each stage, and to repeated sequences to provide a long-term perspective.

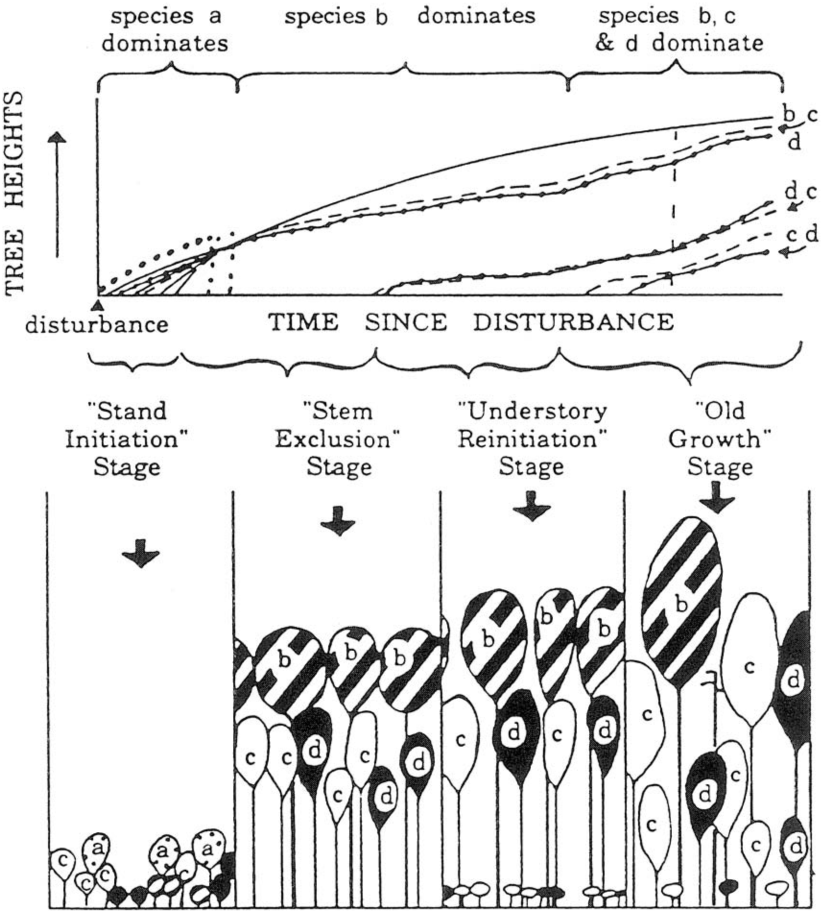

FIGURE 5.1. Four idealized stages in stand development can be recognized from structural features alone. At initiation, seedlings are rarely affected by competition with other trees. At canopy closure, stem exclusion begins. As the overstory trees approach maximum height, the canopy opens and an understory is reinitiated. In the old-growth stage a multilayered canopy develops. (Modified from *Forest Ecology and Management,* Volume 3, C. D. Oliver, "Forest development in North America following major disturbances," pp. 153–168, 1981, with kind permission of Elsevier Science–NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.)

A. Initiation Stage

After a major disturbance, seeds, spores, or other regenerating parts of plants are usually available to germinate or sprout. Seedlings quickly respond to improved light conditions and reduced competition for moisture and nutrients. This is true whether the disturbance results from the death of a single tree or arises from destruction of the entire stand. Where fresh substrate is deposited from floods, landslides, or volcanic eruptions, the biotic links from one generation to another are reduced but may still contribute to the rapid reestablishment of vegetation (Franklin *et al.,* 1985).

Animals are present in all stages of forest development, but their activities in the initiation stage are particularly significant. Wide-ranging birds and large vertebrates play an important role in distributing seeds across areas separated by inhospitable environments. Animals also improve the chances of seed germination by partially digesting seed coats and by preparing the soil in various ways. Some tree species have seeds that only certain kinds of vertebrates can disseminate successfully. The tree *Calvaria major,* a native on the island of Mauritius in the western Indian Ocean, has had no natural regeneration (without the assistance of humans) for 300 years because its seeds needed to be processed through the extinct dodo bird, *Raphus cucullatus* (Temple, 1977). In Africa, elephants consume great quantities of the fruits of *Balanities willsoniana;* when elephants are absent, the fruits, which are toxic to smaller animals, rot. Janzen (1979) observed that *Simaba cedron* trees growing in tropical forests of Central America share fruit characteristics with *Balanities* and concluded that the present restricted distribution of *Simaba* is related to the extinction of mastodons in the last 10,000 years. Some seed coats are so hard that only a few animals can crack them. The reintroduction of the horse into Central America by Spaniards increased dispersal of the seeds of a number of species with extremely hard seed coats (Janzen and Martin, 1982).

Rapid recolonization of forest sites following fire or other major disturbance may well depend on the presence of certain vertebrates. Truffles, fungi that produce potato-shaped fruiting bodies underground, form important symbiotic mycorrhizal associations with tree roots (Chapters 3 and 4). These fungi are almost exclusively hunted for, stored, and dispersed by small mammals (Maser *et al.,* 1978). Loss of small mammals from an ecosystem would reduce the likelihood of barren areas being revegetated with mycorrhizae of the truffle group.

Besides humans, birds have the greatest impact on long-distance seed dispersal. Blue jays (*Cyanocitta cristata*) cached more than 50% of the entire mast crop of an oak forest in Virginia an average distance of more than 1 km from the source (Darley Hill and Johnson, 1981). The ability of birds and small mammals to cache large nuts may help explain how hazelnut (*Corylus*) was able to colonize the landscape after retreat of the continental glaciers in Europe as fast and sometimes faster than species with wind-dispersed seeds such as birch and pine (Walter, 1954). Insects, birds, and bats also play important roles as pollinators (Crawley, 1983). Animals, through their eating habits and movement may concentrate nutrients within one system or distribute them between ecosystems (McClelland, 1973). Large vertebrates also affect forest ecosystems by changing the microhabitat through trampling, burrowing, or, in the case of animals such as beavers, felling trees. The absence of large animals can, therefore, indirectly limit the populations of other animals and plants. For example, when 10-ha segments of Amazon forests were isolated, peccaries no longer provided wallows, and three species of frogs disappeared, along with other types of flora and fauna (Lewin, 1984).

Although the initiation stage in stand development is simple to define on the basis of the limited height and age of trees present, predicting which species of tree seedlings will survive is extremely difficult, because of local variation in resource availability and selective herbivory by animals.

B. Stem Exclusion Stage

When only one tree species is present, competition is particularly intense as stand development enters the "stem exclusion" stage. In extreme cases, stem numbers may be reduced by nearly 90% in 50 years (Tadaki *et al.,* 1977). A "self-thinning" rule defines an upper limit for the number of stems as a function of the average biomass of individual trees (Drew and Flewelling, 1977; White, 1981; Westoby, 1984). This empirical relation is usually presented with a log–log plot that has a nearly constant slope of −3/2 that defines a decrease in maximum stem biomass ($W_{\mathrm{s.max}}$, kg) as stem population per hectare (p) increases:

$$W_{\mathrm{s.max}} = k_s p^{-3/2} \tag{5.1}$$

where k_{s} is a coefficient that increases with the maximum stem biomass of individual trees, obtained either from empirical data such as yield tables or from simulation models that calculate maximum accumulation of (live) stem biomass.

To take an empirical example, a stand at maturity with 150 stems and maximum stand biomass of 600 Mg ha^{-1} gives $k_{\mathrm{s}} = 7.3 \times 10^6$. To apply the formula, initial stand mass and stocking density must he provided, and the mean stem mass (W_{s}) generated by a growth model tested against $W_{\mathrm{s.max}}$ for the current population [$p(W_{\mathrm{s.max}})$]. If $W_{\mathrm{s}} > W_{\mathrm{s.max}}$, Eq. (5.1) solves for $p(W_{\mathrm{s}})$ and predicts that stem numbers will be reduced by $\Delta p = [p(W_{\mathrm{s}}) - p(W_{\mathrm{s.max}})]$, where Δp is stem mortality. By the end of the next year, if total stem biomass has increased, the procedure is repeated. The biomass in annual mortality (or harvest) is an important ecosystem variable required to estimate the return (or removal) of organic matter to the soil in large woody debris. The results of applying the −3/2 self-thinning rule to three hypothetical pine plantations with initial stocking at 1000, 2500, and 5000 stems ha^{-1} show that self-thinning occurs first in the stand with the highest initial stocking; eventually, however, all three stands reach similar stem numbers in later stages of stand development (Landsberg and Waring, 1997; Fig. 5.2).

The LAI of the overstory reaches its maximum during the stem exclusion stage. Because there is no net addition of foliage to the canopy, only a transfer of leaf area from less competitive to more competitive individuals can occur. Leaf area, not biomass of stems, is the underlying principle behind the operation of the self-thinning rule (Westoby, 1977; Landsberg, 1986a). The self-thinning rule is widely applied in forestry (Tang *et al.,* 1994), mainly because it does not require information on leaf area, but this makes the rule empirical (Weller, 1987). Ecologists have extended the application of the rule to simulate the optimum stocking and thinning regime required to produce large woody debris as quickly as possible from young, fast growing forests (Sturtevant *et al.,* 1997).

Growth efficiency, defined as stem wood production per unit of leaf area (Chapter 3), is another widely applied measure of the intensity of competition among individual trees that foresters and ecologists share. Between the initiation stage and the stem exclusion stage, growth efficiency often decreases by more than 90% (Fig. 5.3). At canopy closure, trees readily separate into classes (dominant, codominant, intermediate, and suppressed) that reflect the amount of sunlight captured by individual crowns (Oliver and Larson, 1996). Trees of mean diameter (average basal area) usually represent codominant individuals. Trees of below average diameter display below average growth efficiencies because of their less favorable competitive position (Oren *et al.,* 1985; O'Hara, 1988). The tallest,

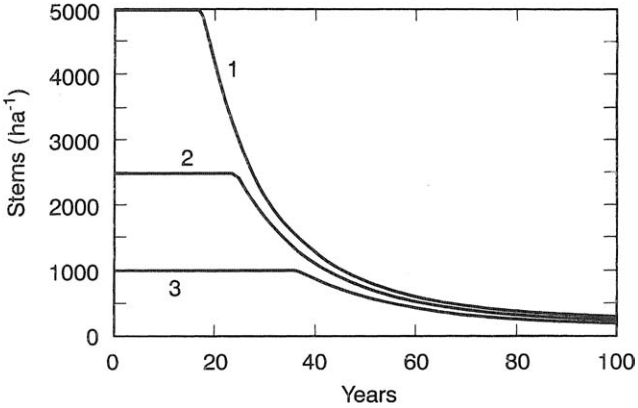

FIGURE 5.2. Application of the self-thinning rule in hypothetical pine stands with initial stem numbers of (1) 5000, (2) 2500, and (3) 1000 stems ha^{-1} shows that stem mortality is proportionally much higher in (1) than (2) or (3). After 50 years, however, tree numbers begin to approach similar values regardless of initial stocking. (Modified from *Forest Ecology and Management,* Volume 95, J. J. Landsberg and R. H. Waring, "A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning," pp. 205–215, 1997, with kind permission of Elsevier Science–NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.)

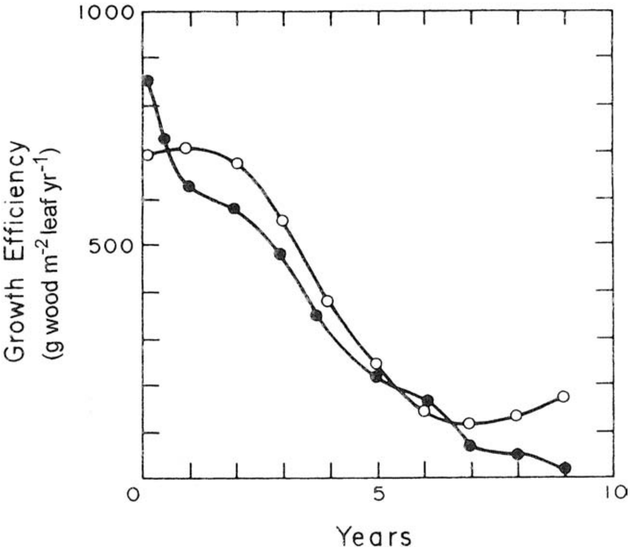

FIGURE 5.3. Two 20-year-old Scots pines with approximately similar dimensions showed more than a 90% reduction in growth efficiency in less than a decade. During the last 3 years, canopy closure occurred and one tree (●) was overtopped. The other tree (○) achieved a position of dominance and increased its growth efficiency. Allometric equations developed from trees in the same stand were used to estimate growth from changes in stem diameter. Leaf area was calculated from sapwood area present each year. (Data from R. H. Waring, B. Axelsson, and S. Linder, Swedish University of Agricultural Sciences, Uppsala, Sweden. Figure from Waring and Schlesinger, 1985.)

dominant trees in unthinned forests usually produce the most growth per unit of leaf area. Dominant trees in thinned stands, however, may develop extensive crowns, which result in below average growth efficiencies (O'Hara, 1988).

If frequent thinning is practiced within the stem exclusion stage, canopy closure is avoided and the LAI of the overstory remains below the maximum. With a more open canopy, however, understory vegetation, including other tree species, can become established and create conditions similar to the next stage in stand development. The combined LAI of all vegetation remains similar over a broad range in stocking density of overstory trees. This tendency to display a common LAI from initiation through later stages in stand development is a key feature of forest ecosystems that will have important implications for scaling as discussed in Chapters 7–10.

Practices that modify the potential of a site will alter the maximum LAI. This axiom was demonstrated in a series of replicated experiments on young pine forests in Sweden, which received a combination of irrigation and nutrient additions for more than a decade (Axelsson and Axelsson, 1986). In all treatments, including the control, mean tree growth efficiency showed an exponential decrease with time (Fig. 5.4a). Treatment effects could be compared (1) in relation to growth efficiency at a common and necessarily low LAI (1.0) or (2) as a function of total aboveground stem wood production at canopy closure (Fig. 5.4b). The upper limits on wood production tend to approach an asymptote at an LAI of 5 to 6, which corresponds to interception of more than 90% of all visible radiation (Chapters 2 and 3). Considerable flexibility exists in how forests are managed through the control of the spatial distribution of leaf area on trees and understory vegetation.

C. Understory Reinitiation Stage

As trees approach their maximum height, growth slows; however, mortality still occurs, and gaps are created in the canopy that cannot be filled completely by branch extension. The gaps allow sunlight to penetrate to the forest floor and stimulate the reinitiation of understory vegetation that was largely excluded in the previous stage. The reintroduction of an understory provides more opportunity for diverse animal populations to increase as both cover and forage are available. The increase in diversity of habitats and food supply has been suggested as an important feature for supporting a host of controlling agents (arthropods, ants, small rodents, and birds) that reduce the dangers of insect herbivory so common to the previous stage in stand development (Holmes *et al.,* 1979; Price *et al.,* 1980; Doane and McManus, 1981; Schowalter, 1989; Torgersen *et al.,* 1990; Perry, 1994). More complex forests would, according to this reasoning, have greater inherent resistance to insect herbivory, a subject discussed in Chapter 6.

Stem mortality in this stage of stand development provides the first large pieces of organic debris to the forest floor that are likely to persist through the next stage. Foresters are often concerned about the accumulation of woody debris at this time as a potential fuel hazard, breeding site for bark beetles, or habitat for other potentially damaging insects and pathogens. Ecologists, on the other hand, have begun to investigate the significance of woody debris as a potentially important contributor to species diversity and nutrient cycling, and a component of long-term carbon storage (Thomas, 1979; Harmon *et al.,* 1986; McComb *et al.,* 1986; Perry, 1994; Cohen *et al.,* 1996).

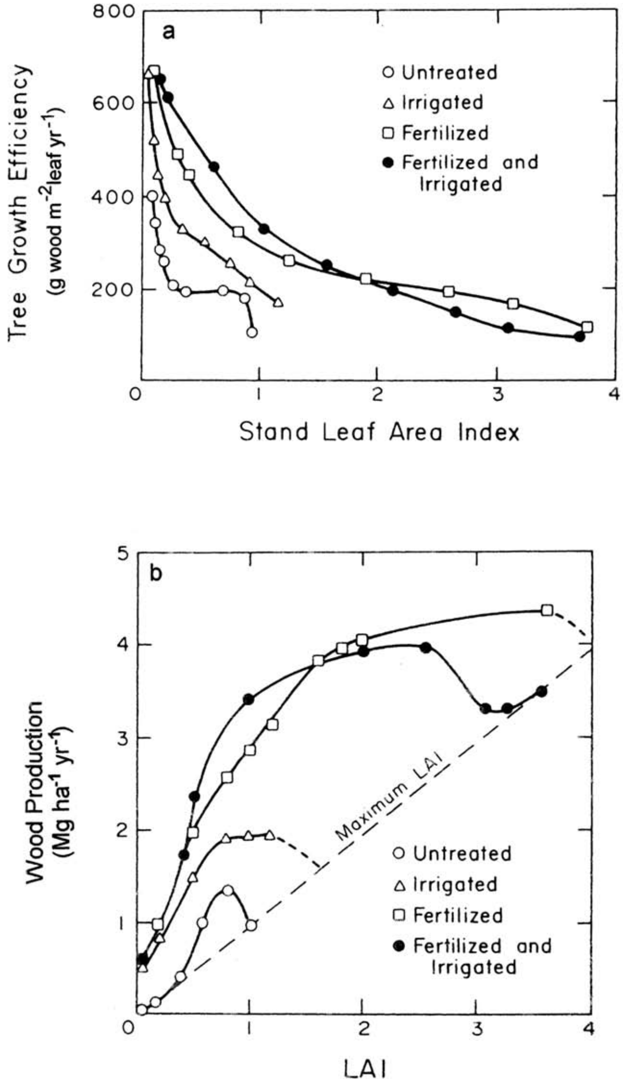

FIGURE 5.4. (a) Saplings of Scots pine grown over a decade under different nutrient and water regimes showed large differences in growth efficiency at a comparable LAI of 1.0. As the stands approached their maximum leaf area after 10 years, however, growth efficiencies approached similar values. At that time LAI differed by more than threefold. (b) As Scots pine plantations approached their maximum LAI determined by experimental treatments, stem wood production per hectare became closely related to maximum LAI because stem wood production per unit of leaf area was similar, regardless of the environment at canopy closure. (From Waring and Schlesinger, 1985.)

D. Old-Growth Stage

Dominant trees in an old-growth forest show little if any height growth. In many cases, treetops have died, but diameter growth still continues. As a result, the total live biomass usually reaches a maximum in the early old-growth stage. In boreal forests, maximum biomass approaches 400 Mg ha^{-1} although the average biomass is only about 40 Mg ha^{-1} (Botkin and Simpson, 1990). In dry to wet tropical regions, forest biomass ranges from 160 to 690 Mg ha^{-1}, with an average of about 330 Mg ha^{-1} (Brown *et al.,* 1991). Standing biomass in the temperate old-growth coniferous forests of the Pacific Northwest averages between 800 and 1000 Mg ha^{-1}, with a maximum of 2500 Mg ha^{-1} reported in coastal redwood forests (Waring and Franklin, 1979).

Tree species composition and structural diversity may reach maximum levels in the old-growth stage, although the number of species of plants and animals together may be higher at stand initiation (Oliver and Larson, 1996). Species of trees adapted to growing in shaded conditions require less sapwood to support a given amount of leaf area than those adapted to more exposed situations (Chapter 3). The reduction in sapwood volume may reduce stem and branch maintenance respiration by as much as 50% (Edwards and Hanson, 1996).

In general, all trees present in old-growth forests tend to have lower growth efficiencies than at earlier stages in stand development (Waring, 1983; Waring *et al.,* 1992; Kaufmann, 1996). Usually a large amount of woody debris is present in various decay classes, which together with variation in vertical structures provides habitat for many organisms, so that food chains are extremely varied. This variation tends to favor an even flow of resources through the ecosystem, although by increasing the total number of species, the probability of local extinction may actually increase (Moffat, 1996; Tilman, 1996). Species extinction, however, is a subject best evaluated at a larger spatial scale (Chapter 9).

Although old-growth forests might be assumed to be free of disturbance, they are not. Wind periodically uproots trees and creates larger gaps than present in previous stages of stand development. Fires frequently burn through old-growth eucalyptus forests in Australia and are a key factor in sustaining nutrient cycling (Burgman, 1996; Chapter 6). Even in 1000-year-old stands of coastal redwood (*Sequoia sempervirens*), many floods have occurred so that the original ground level on which trees were first established is now buried beneath >10 m of silt (Stone and Vasey, 1968). The presence of an overstory that has attained maximum height is one general feature of old-growth forests that can be evaluated across landscapes through the application of various remote sensing techniques (Wallin *et al.,* 1996).

Some forest stands, particularly in arid climates with incomplete canopy closure and frequent historic ground fires, develop multiple age classes growing interspersed on the site. O'Hara (1996) studied ponderosa pine stands in Oregon and Montana and found that they naturally contained two to five cohorts, or age classes of trees, ranging from 22 to 220 years. These multiaged stands were found to have the same volume increment productivity as equivalent even-aged stands in the area. O'Hara also concluded that volume productivity was better predicted when stand structure was included in the algorithms than with LAI alone.

III. FUNCTIONAL RESPONSES OF STANDS AT DIFFERENT STAGES IN DEVELOPMENT

Studies that provide measures of functional changes over a complete range in stand development are rare. It is necessary, therefore, to piece together information from a variety of studies. In this section we present examples which emphasize production, nutrient uptake, and accumulation in biomass and organic matter over time.

A. Production of Biomass

Production of biomass, as shown in earlier chapters, can be predicted as a function of stand structure, the availability of critical resources, and climatic restrictions. Mencuccini and Grace (1996) compared structural and functional changes in tree carbon, water, and nutrient status of 10 plantations of Scots pine which ranged in age from 7 to 59 years and grew in a deep sandy soil in southeast England. Although the study included only the first three phases of stand development, it provides important insights.

At age 7 the pine plantation had a leaf area index far below the maximum that the site could support (Fig. 5.5a). Bracken fern (*Pteridium aquilinum*) formed a dense understory. By age 20, stem exclusion began and density decreased from above 3200 trees ha^{-1} to less than half that number. As LAI peaked, the fern understory was completely shaded out. A plateau in LAI was maintained until about age 35, by which time trees had attained nearly 90% of the height recorded at age 60 (Mencuccini and Grace, 1996). Beyond age 40, overstory LAI began to decrease so that, by age 60, LAI was about half of that at age 20. The opening of the canopy at ages beyond 50 years permitted ferns to reappear (understory reinitiation stage).

Aboveground net primary production ($\mathrm{NPP_A}$) initially increased in parallel with canopy leaf area index but decreased more rapidly as the stands aged (Fig. 5.5b). This pattern is general for most even-aged forests (Ryan *et al.,* 1997b). An increase in maintenance respiration cannot account for more than a 10% change in growth rates, according to reviews by Ryan *et al.* (1997b) and Gower *et al.* (1996). The study by Mencuccini and Grace offers an alternative explanation for the rapid decrease in $\mathrm{NPP_A}$ with stand age. They measured water conducting properties in stems and branches for the full range of age classes and from these data calculated stand hydraulic conductance (G_{st}) (Fig. 5.5c). The relation between $\mathrm{NPP_A}$ and G_{st} is linear, with $r^2 = 0.88$. This analysis supports the hypothesis that hydraulic limitations on photosynthesis and the amount of LAI that can be supported are sufficient to account for most of the observed decrease in tree and stand growth with age (Ryan and Yoder. 1997). An alternative hypothesis, namely, that nutrient limitations arise from a reduction in the rates at which minerals are recycled, may apply in some systems (Gower *et al.,* 1996), but no variations in foliar nutrient concentrations were reported across the full range of stand ages by Mencuccini and Grace (1996).

B. Accumulation of Nutrients and Soil Organic Matter

Patterns of nutrient accumulation are roughly similar to those of biomass because nutrient concentrations in wood do not change appreciably as trees age (Fig. 5.6). Some species

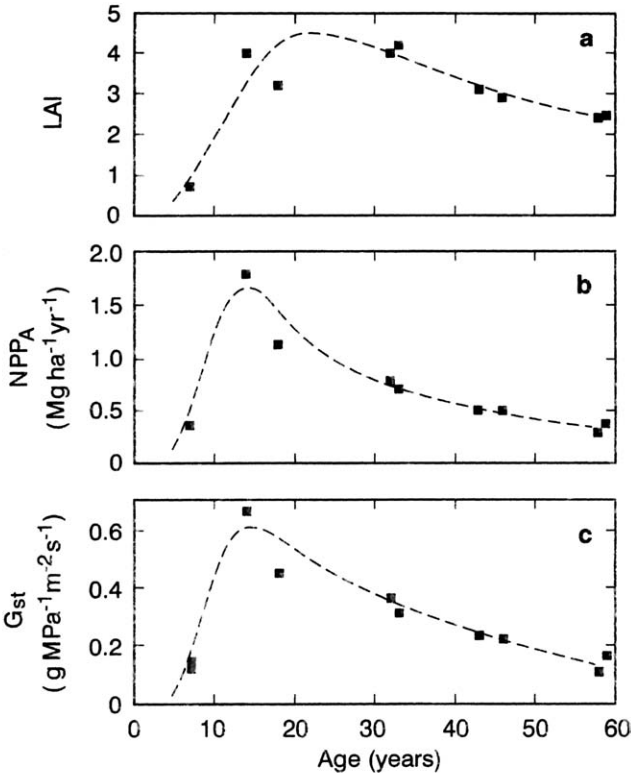

FIGURE 5.5. (a) Leaf area index (LAI) in plantations of Scots pine increases rapidly following establishment, peaking at stand closure, about age 20. In later phases of stand development, the overstory LAI decreases slowly, which permits the understory ferns (and other life forms) to increase their LAI. (b) Aboveground net primary production (NPP_A, $Mg\,ha^{-1}\,year^{-1}$) tends to follow overstory LAI with stand development but decreases much more abruptly in later phases. (c) Total stand hydraulic conductance (G_{st}, g H_2O $MPa^{-1}\,m^{-2}\,s^{-1}$) was based on average dimensions of height, diameter, and branch length for all trees present in each stand. Changes in stand hydraulic conductance directly parallel changes observed in NPP_A as pine stands develop. (After Mencuccini and Grace, 1996.)

in the initiation stage, however, have particularly high concentrations of nutrients in their biomass after forest burning or cutting (Marks, 1974). As canopy leaf area approaches a maximum, fine-litter accumulations on the forest floor approach equilibrium. The relatively rapid decomposition of these nutrient-rich materials allows recirculation through the ecosystem.

There is a similar pattern of nutrient storage as the forest floor and soil organic matter accumulate when forests develop on fresh substrate (primary succession). Sometimes the organic C and N in the forest floor peak early and then slowly decrease to an equilibrium value after a few centuries. This was the case for forest soils that developed on volcanic mudflows in northern California (Fig. 5.7). A rapid accumulation of N and C in the soil was presumably aided by early colonizing vegetation, which included N-fixing shrubs. On the other hand, C and N may accumulate more rapidly in soils where decomposition rates

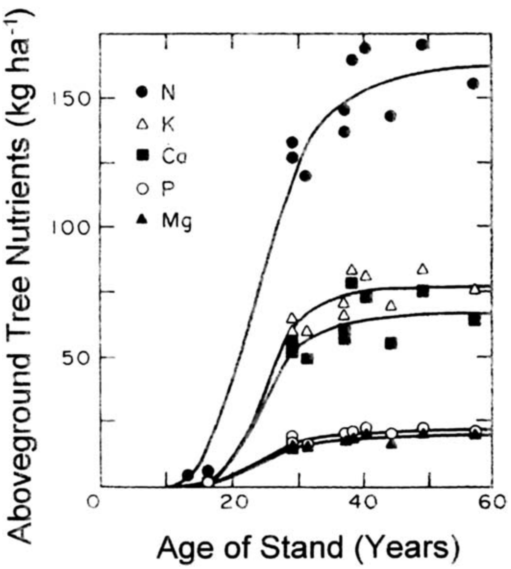

FIGURE 5.6. Accumulation of nutrients in tree biomass during the postfire development of jack pine (*Pinus banksiana*) in New Brunswick, Canada. (From MacLean and Wein, 1977; drawing from Waring and Schlesinger, 1985.)

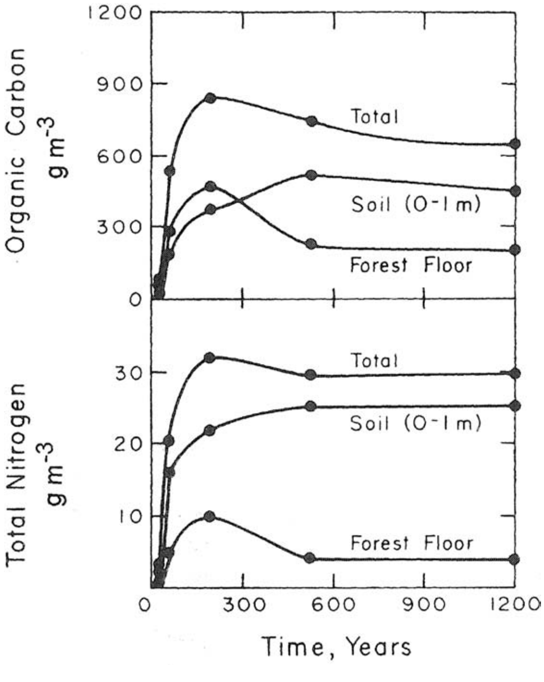

FIGURE 5.7. Accumulation of organic C and N in soil developed on volcanic mudflows of varying age on Mount Shasta, California. (Modified from Dickson and Crocker, 1953; drawing from Waring and Schlesinger, 1985.)

are slow than where rates are rapid (Gower and Son, 1992; Binkley and Valentine, 1991).

As the overstory canopy begins to open at the understory reinitiation stage, more woody debris accumulates on the forest floor, which may result in slowing the turnover of organic residues. The increased carbon: nutrient ratio in the organic substrate, combined with a development of an understory, usually captures nutrients that might otherwise be lost through leaching in the less demanding old-growth stage. When a forest reaches the old-growth stage, 20% of the total N in litterfall may be woody material, with the Ca fraction much higher (Harmon *et al.,* 1986). In situations where atmospheric deposition of nitrogen and sulfur is high, leaching of inorganic nutrients from old-growth stands may exceed losses from earlier stages in development as a result of reduced uptake (Bormann and Likens, 1979; Bormann, 1985). In unpolluted regions, however, the large store of decaying woody detritus immobilizes inorganic nitrogen and cations, to the extent that losses may be less than in earlier stages of stand development (Sollins *et al.,* 1980; Binkley and Brown, 1993; Hedin *et al.,* 1995; Allen *et al.,* 1997; Clinton *et al.,* 2002).

IV. LOOKING BACK IN TIME

A. Paleoecology

The longest continuous record of changes in the local composition of forests derives from an analysis of tree pollen grains and other organic residues collected from bogs and lake bottoms (Solomon *et al.,* 1980; Delcourt and Delcourt, 1985; Foster and Zebryk, 1993). These bog and lake deposits, while extremely valuable in recording climatic changes and species migration rates (Chapter 9), usually cannot provide information that describes variation within individual stands over time.

The ability of tree species to survive over a range in climatic variation is of particular concern with rising atmospheric CO_2 levels and projected climatic warming. Variations in the abundance of stable isotopes of carbon, oxygen, and hydrogen bound in the rings of trees of known ages provide a basis for the assessment of climatic variation and growth responses. For example, Edwards and Fritz (1986) inferred from analysis of δD and δ^{18}O extracted from the stems of carbon-14-dated spruce trees buried in a single bog that mean annual temperatures have varied by more than 10°C, and growing season relative humidity by more than 40% over the past 11,500 years (Fig. 5.8). The isotopic ratios ^{18}O/^{16}O and ^{2}H (D)/^{1}H in cellulose, as explained in Chapter 2, are closely correlated to that in precipitation, and so provide an integrated signal of mean annual temperature. Differences in the ratios of these two sets of stable isotopes reflect changes in fractionation during transpiration and serve as a surrogate for estimation of atmospheric humidity during the growing season.

B. Dendrochronology

Annual rings in trees also reflect climatic variation in more recent years, as a result of changes in the amount and pattern of carbon allocation to stem increment (Chapter 3). Tree-ring data must be subjected to careful scrutiny in collection and analysis (Fritts and

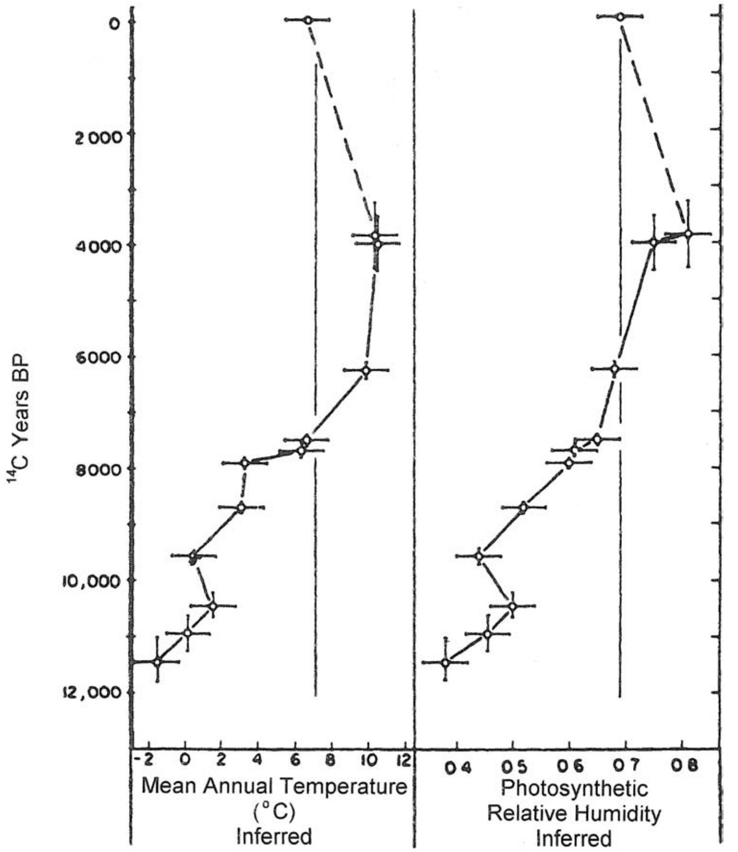

FIGURE 5.8. The abundance of heavier and lighter forms of hydrogen and oxygen isotopes in cellulose from current and fossil wood samples from a bog in Canada indicate that major changes occurred in climate over the last 11,500 years. (Modified from *Applied Geochemistry,* Volume 1, T. W. D. Edwards and P. Fritz, "Assessing meteoric water composition and relative humidity from δ^{18}O and δ^{2}H in wood cellulose: Paleoclimatic implications for southern Ontario, Canada," pp. 715–723. Copyright 1986, with kind permission from Elsevier Science Ltd, The Boulevard, Langford Lane, Kidlington OX5 1GB, UK.)

Swetnam, 1989). Ideal trees for analysis grow in exposed situations, often on infertile soils, where they lack competition with other trees and therefore show a more direct growth response to climatic variation. If conditions become too harsh, however, false and missing rings may occur; these must be recognized by analysis of replicate cores or cross sections. Finally, an adjustment must be made to account for the reduction in ring width as trees increase in girth. Once these corrections are made, recent variations in ring widths are correlated with recent climatic measurements, and inferences are made by extrapolation of older ring chronologies to climatic variation in the distant past (Fig. 5.9).

Cook *et al.* (1991) applied dendrochronological techniques to estimate climatic changes from a 1000-year tree-ring chronology on huon pine (*Lagarostrobus franklinii*) in Tasmania. The analyses suggested that during the twentieth century warming has exceeded

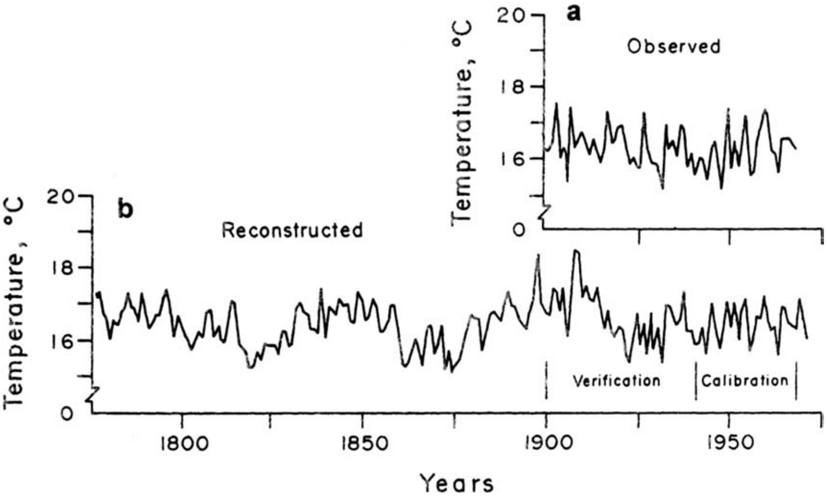

FIGURE 5.9. Correlations between tree-ring width and temperature obtained for the period 1940 to 1970, validated using the data from 1900 to 1940, were used to extrapolate the climate in Tasmania in the interval 1780 to 1900. (From LaMarche and Pittock, in *Climate from Tree Rings,* 1982, courtesy of Cambridge University Press.)

any recorded in the last millennium. Graumlich *et al.* (1989) attempted to extend tree-ring analyses to whole forests of Douglas-fir in the Pacific Northwest and concluded that, once climatic variation was accounted for, no additional response could be found in relation to rising atmospheric CO_2 concentrations during the twentieth century. Hunt *et al.* (1991) demonstrated the ability of a process model, FOREST-BGC, to achieve improved accuracy over conventional statistical analyses by predicting annual variation in growth recorded in a 50-year dendrochronological record extracted from pine trees in Montana (Fig. 5.10). To take account of likely continual changes in atmospheric composition, it is almost a requirement that more sophisticated analyses be developed to interpret dendrochronological records.

Assessments of the effect of rising CO_2 concentrations on tree growth have been inferred from comparisons of carbon-13 and carbon-12 deposited in the cellulose of annual rings. As discussed in Chapter 3, the stable isotope ^{13}C is discriminated against in photosynthesis and, as Farquhar *et al.* (1982) have shown, is quantitatively related to variation in the ratio of CO_2 within the leaf to that in ambient air. Because the $\delta^{13}C$ composition of the atmosphere has been diluted with carbon enriched in ^{12}C from fossil fuel consumption, adjustments must be made to account for these changes, which are derived from analyses of CO_2 trapped in gas bubbles of glacial ice (Polley *et al.,* 1993). Marshall and Monserud (1996) analyzed $\delta^{13}C$ from the annual rings of three species of conifers growing in Idaho and found that the calculated ratio of intercellular CO_2 to ambient CO_2 remained constant at 0.75 for the last 80 years. This implies that stomatal conductance has been reduced and that net photosynthesis has increased by 30%, in proportion to the rise in atmospheric CO_2. Similar responses have been reported for other gymnosperms in the western United States (Leavitt and Long, 1989; Stuiver and Braziunas, 1987) and in Europe (Freyer and Belacy,

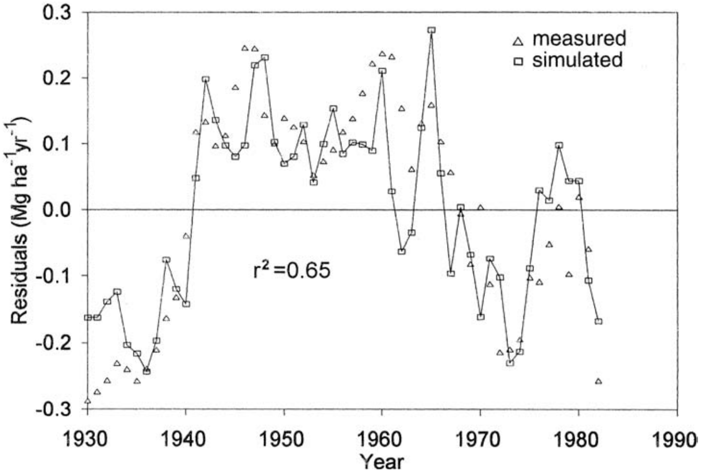

FIGURE 5.10. Detrended residuals of interannual stem biomass growth for a 52-year simulation of a ponderosa pine stand in Montana using FOREST-BGC show that process simulation models link growth with climate more closely than do more empirical dendrochronology models. (After Hunt *et al.,* 1991.)

1983), but not in Tasmania where huon pine appears to have maintained a constant intercellular CO_2 as atmospheric CO_2 levels have risen (Francy, 1981).

Walcroft *et al.* (1997) analyzed variation in the $\delta^{13}C$ within annual rings from *Pinus radiata* trees in New Zealand and showed that it is possible to discern seasonal variations in drought. It is sometimes difficult, however, to isolate CO_2 effects with $\delta^{13}C$ analyses alone because the discrimination of ^{13}C is controlled both by stomata and by the N status of leaves (Chapter 3). Nitrogen could become less available as carbon-rich substrates accumulate in litter and cause mineralization rates to decrease. On the basis of allocation models described in Chapter 3, more carbon resources would be shifted toward roots, as has been documented in at least one CO_2-enrichment experiment (Tissue *et al.,* 1993). On the other hand, atmospheric deposition of nitrogen associated with anthropogenic activities might compensate for deficiencies in N, if not other minerals (Chapter 6). No general rules are yet available to predict which species would benefit most, or how changes in C:N ratios might affect herbivory on trees, although important trends have been identified (Bazzaz, 1990; Woodward, 1991; Field *et al.,* 1992).

Norby (1996) showed the potential value of obtaining a retrospective estimate of leaf area to normalize the reported stem growth observed in eight CO_2-enrichment experiments. Coyea *et al.* (1990) demonstrated that in at least one species, *Abies balsamea,* retrospective estimates of leaf area could be made because sapwood, with a known correlation to leaf area, converted to heartwood after a fixed number of years (Fig. 5.11). The discovery that sapwood converts to heartwood after a fixed number of years allows a retrospective analysis of tree leaf area, which together with stem diameter growth provides a reconstruction of individual tree and stand growth efficiencies backward in time. The technique has important implications for interpreting the periodicity of outbreaks of insects, fire, and other agents of disturbance (Coyea and Margolis, 1994; Chapter 6).

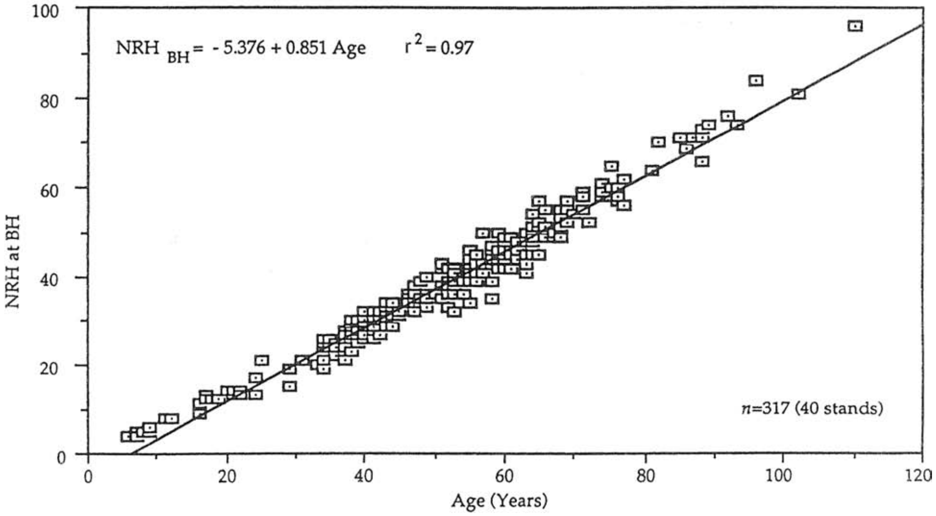

FIGURE 5.11. In balsam fir (*Abies balsamea*) the number of annual rings in heartwood at breast height (NRH_{BH}) is a linear function of tree age. The sapwood rings represent the outer 6.0 years of growth (equivalent to the intercept). By determining the sapwood area and diameter growth at any given age, historical reconstruction of stand LAI and tree growth efficiency is possible. (After Coyea and Margolis, 1994.)

C. Pedology

Most of the carbon in ecosystems is incorporated into soils. Conventional analyses of soil carbon are not sufficiently accurate to assess important changes in turnover rates or whether undisturbed ecosystems are truly in steady state. Isotopic analyses of soil organic fractions have much to contribute in answering these questions and can serve as a baseline against which to measure future changes.

As a result of thermonuclear weapons testing from 1955 to 1963, the amount of ^{14}C in the atmosphere was approximately doubled. As plants incorporated the radioactive carbon into biomass, and that biomass became litter, the bulk soil organic matter increased in ^{14}C in proportion to the rate of turnover of older carbon substrates. Trumbore *et al.* (1996) compared organic matter ^{14}C in present and in archived (pre-1963) soils collected across an elevational transect in the Sierra Mountains of California. On the basis of these analyses, they calculated the turnover time for three increasingly recalcitrant extracts of soil organic matter in six "steady-state" forest ecosystems. Only two fractions showed significant change over the 30 years. Turnover rates of these two less recalcitrant fractions varied from <10 to >200 years across the elevational gradient. When the rates were plotted against mean annual temperature, a general relation was derived that also applied to data from Brazil and Hawaii (Fig. 5.12). From these relationships Trumbore *et al.* (1996) estimated that organic matter turnover rates increase under warming climatic conditions. Calculating the net gain or loss of soil carbon, however, requires that primary production as well as decomposition be accounted for. There are obvious advantages in combining dendrochro-

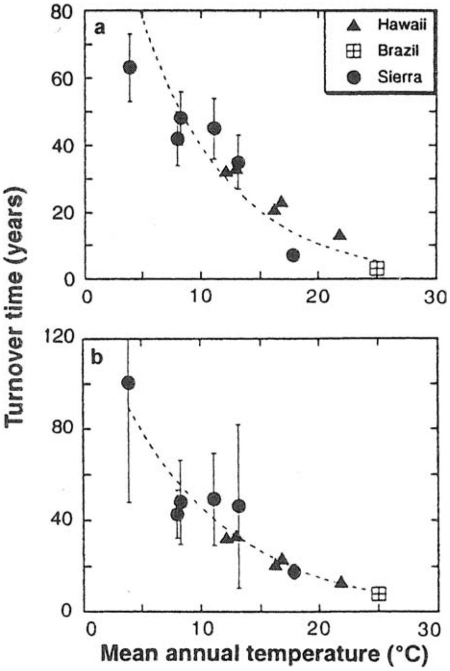

FIGURE 5.12. (a) Turnover times for fast-cycling fractions of soil organic matter in soils from transects in the Sierra Mountains of California, in Hawaii, and in the Amazon. The exponential curve with mean annual temperature is $Y = 151 \exp(-0.134T)$, where T is in °C. (b) Combined turnover times for the fast- and moderate-cycling fractions of soil organic matter described above; $Y = 138 \exp(-0.110T)$. (Modified with permission from S. E. Trumbore, O. A. Chadwick, and R. Amundson, 1996, "Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change." *Science,* Volume 272, pp. 393–395. Copyright 1996 American Association for the Advancement of Science.)

nological and soil carbon analyses with ecosystem modeling and analysis in future studies.

Conversion of tropical forest to pasture in Hawaii provided Townsend *et al.* (1995) with a chance to extend carbon isotope analyses to disturbed situations and to compare estimates of soil carbon turnover derived from ^{14}C measurements with those obtained from $^{13}C/^{12}C$ analyses. The latter comparison was possible because tropical trees and pasture grasses differ in their photosynthetic pathways; trees discriminate twice as much against the heavier ^{13}C isotope than do grasses. With the dates of forest conversion to pasture known, the turnover rates could be calculated on the basis of the degree of ^{13}C enrichment observed in three organic fractions for which the potential turnover rates were different by orders of magnitude. Predictions made with the two isotopic techniques agreed closely with turnover rates predicted with the CENTURY ecosystem simulation model (Parton *et al.,* 1987), and they confirmed that in order to estimate the residence time of soil carbon it is necessary to separate organic matter fractions into at least three major components (Townsend *et al.,* 1995).

Isotopic analyses of sulfur, nitrogen, and strontium (a surrogate for calcium and other cations) in soils provide the means to assess variation in sources and rates of atmospheric deposition on forests (Winner *et al.,* 1978; Peterson and Fry, 1987; Miller *et al.,* 1993; Durka *et al.,* 1994; Hedin and Likens, 1996). All of the techniques discussed in this section permit retrospective testing of models. In addition, they represent a long-term, widely dispersed source of data that, if properly dated, can serve as a continuous benchmark against which to measure change and compare model predictions of soil chemistry and elemental cycling through ecosystems (Chapter 4).

V. ECOSYSTEM MODELS, PROJECTIONS FORWARD IN TIME

Two classes of forest ecosystem models have been well developed, those that focus on the physiology and biogeochemistry of the ecosystem, such as FOREST-BGC, and those that concentrate on the life cycle dynamics of trees in the ecosystem, best exemplified by the family of canopy gap models (Bossel, 1991; Huston, 1991; Dale and Rauscher, 1994). Both classes are process models; the biogeochemical models compute growth from the seasonal dynamics of canopy carbon balances, while the gap models emphasize disturbance, recruitment, and mortality processes that affect individual trees. Ideally, both types of models should be used together to interpret and predict future changes in stand structure, composition, and function.

A. Biogeochemistry Models

The most direct initial test of a biogeochemical model is accurate simulation of an observable quantity such as stem growth over a short time. Successful simulation of stem growth requires that photosynthesis, respiration, carbon allocation, and tissue turnover all be balanced realistically. A number of models have illustrated the capability to simulate 1- to 5-year stem growth aggregated for a stand (Korol *et al.,* 1991; Aber and Federer, 1992; McMurtrie and Landsberg, 1992; Cropper and Gholz, 1993; Running, 1994).

Korol *et al.* (1991) simulated the 5-year growth for 176 Douglas-fir trees with different levels of canopy dominance growing in stands that contained trees of mixed age classes between 30 and 80 years. The trees were distributed across five sites that encompassed a productivity gradient in the dry interior forests of British Columbia. Individual tree stem growth increments, measured by stem analysis, were in close agreement with those modeled by FOREST-BGC (Fig. 5.13). Aber and Federer (1992) simulated the aboveground NPP for forests at ten sites across a broad climatic range of North America with the PnET model (Fig. 5.14). The high correlation shown between predicted and observed NPP is particularly impressive because PnET does not purport to be a comprehensive ecosystem analysis, but concentrates on a critical synthesis of the relationship between leaf nitrogen content, photosynthetic capacity, stomatal conductance, and leaf longevity, as discussed in Chapter 3. These models illustrate the important philosophical point that the most useful models are not the most complex but are the ones that cleanly and efficiently represent only the most critical processes and interactions operating in forest ecosystems.

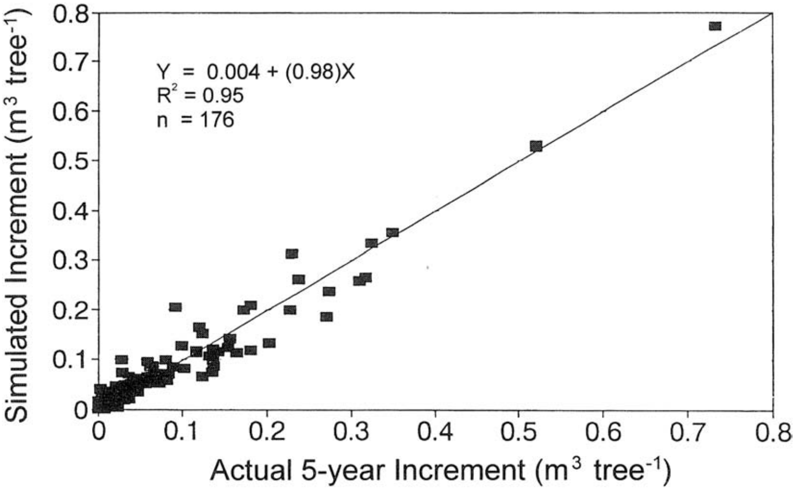

FIGURE 5.13. Comparison of measured 5-year growth increment with FOREST-BGC simulated growth for Douglas-fir trees 35–85 years of age in British Columbia. In this application, FOREST-BGC was defined for individual trees, and intertree competition for radiation and precipitation was added, based on canopy dominance. All other model parameters (Table II.1) represented stand-level conditions normally used by the model. (After Korol *et al.,* 1991.)

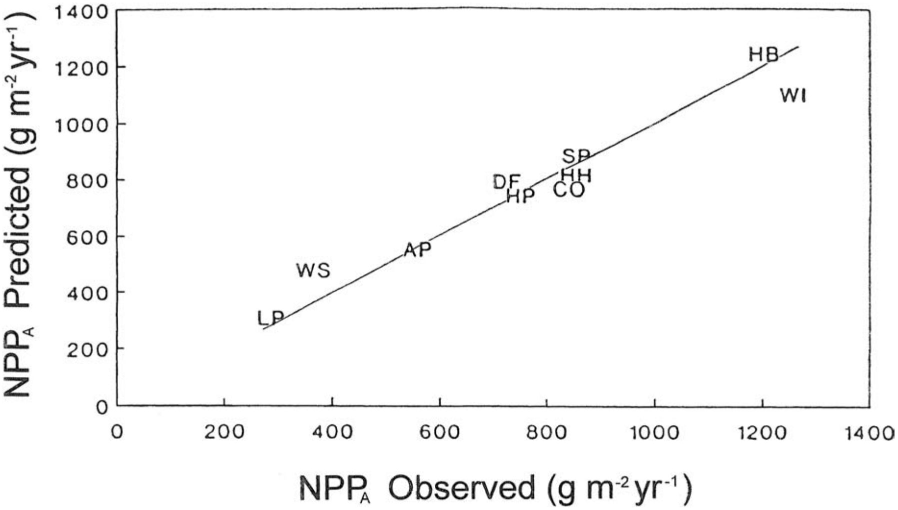

FIGURE 5.14. Comparison of observed aboveground net primary production (NPP_A) and simulated NPP_A with the PnET ecosystem model for ten forest ecosystems around the United States. LP, Wyoming; WS, Alaska spruce; AP, Alaska aspen; DF, Oregon; HP, Massachusetts pine; CO, North Carolina; HH, Massachusetts hardwood; SP, Florida; HB, New Hampshire; WI, Wisconsin. (From *Oecologia,* "A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems," J. D. Aber and A. Federer, Volume 92, p. 496, Fig. 2, 1992, © 1992 by Springer-Verlag.)

The next step in temporal analysis is to simulate stand biomass development over a longer period, a century or more. This is usually done retrospectively by defining the development of a current stand from its origin forward to its present age when measurements are available for comparison. Running (1994) simulated the annual NPP and accumulation of stem biomass over a century for mature forests on seven sites across the Oregon transect. This strong climatic gradient produced a range of measured stem biomass from about 10 to 700 Mg ha^{-1}, and FOREST-BGC replicated this range in production well (Fig. 5.15). A short-lived deciduous alder stand tested the ability of FOREST-BGC to quantify accurately the annual canopy turnover of deciduous trees, and the differing respiration and carbon allocation dynamics of short-lived species. Predictions of NPP$_A$ were >50% above that measured for alder, which suggests the need to confirm whether photosynthetic capacity actually increases with foliar N concentration, as assumed in the model. Another possibility is that symbiotic nitrogen fixation, which requires about 6 kg C per kilogram N fixed, was underestimated in the simulation when set at 50 kg N ha^{-1} year^{-1}.

A greater challenge for biogeochemical models is to simulate stand responses after various treatments that influence tree growth. McMurtrie and Landsberg (1992) used the BIOMASS model to analyze the variable growth response of *Pinus radiata* stands in Australia after irrigation, fertilization, and a combination of both treatments over a 5-year period. Foliage mass and stem growth responded to both water and nutrients and increased by 20–40% relative to untreated stands, and the BIOMASS biogeochemical model was able to replicate the responses (Fig. 5.16). Cropper and Gholz (1993) simulated the carbon dynamics of a slash pine stand, with special emphasis on the possible importance of a labile carbon pool. Field measurements illustrated that increased stem growth after fertilization could be attributed entirely to an increase in foliage mass as a result of reduced allocation to roots. No change in photosynthetic capacity or labile carbon was required to account for the measured growth response.

Site quality is a term used by foresters to represent the potential productivity of forested land, usually for wood production (Tesch, 1981a). Site quality is commonly estimated by *site index* (SI), defined as the height achieved by dominant trees at a specified age which have grown in even-aged stands. An SI(50) = 25 signifies that dominant trees will be 25 m tall at 50 years of age. The site index measurement suffers from the same shortcomings as forest growth models based on inventory data, namely, reliance on historical growth of established stands, with no way of adjusting estimates to new site or stand conditions. Additionally, where disturbance or past harvesting have eliminated stands, site index cannot be determined directly from tree measurements. Simulations of annual stand growth or photosynthesis at canopy closure offer a more biophysically sound estimate of site quality that does not require direct knowledge of current stand age or condition. McLeod and Running (1988) showed that annual estimates of net photosynthesis for a range of ponderosa pine forests correlated well with measured site indices ($r^2 = 0.96$). Milner *et al.* (1996) modeled the annual net photosynthesis of the forested area in the state of Montana.

B. Gap Models of Forest Dynamics

Much of the discussion in the previous sections has been concerned with changes in the biogeochemistry of forest stands through their life cycles. To simplify the treatment and

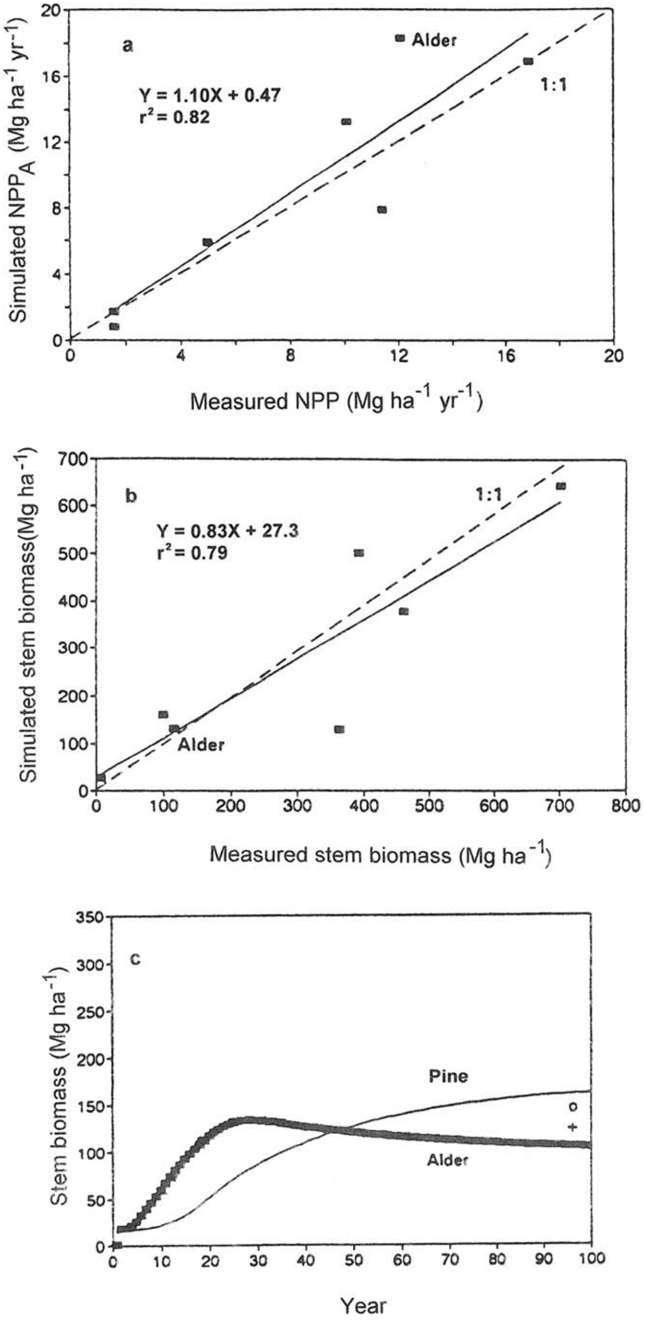

FIGURE 5.15. Observations and FOREST-BGC simulations from the Oregon transect study for (a) annual aboveground NPP_A, (b) stem biomass dynamics for a deciduous stand of alder and a fully stocked stand of ponderosa pine, and (c) stem biomass accumulation over 100 years. (From Running, 1994.)

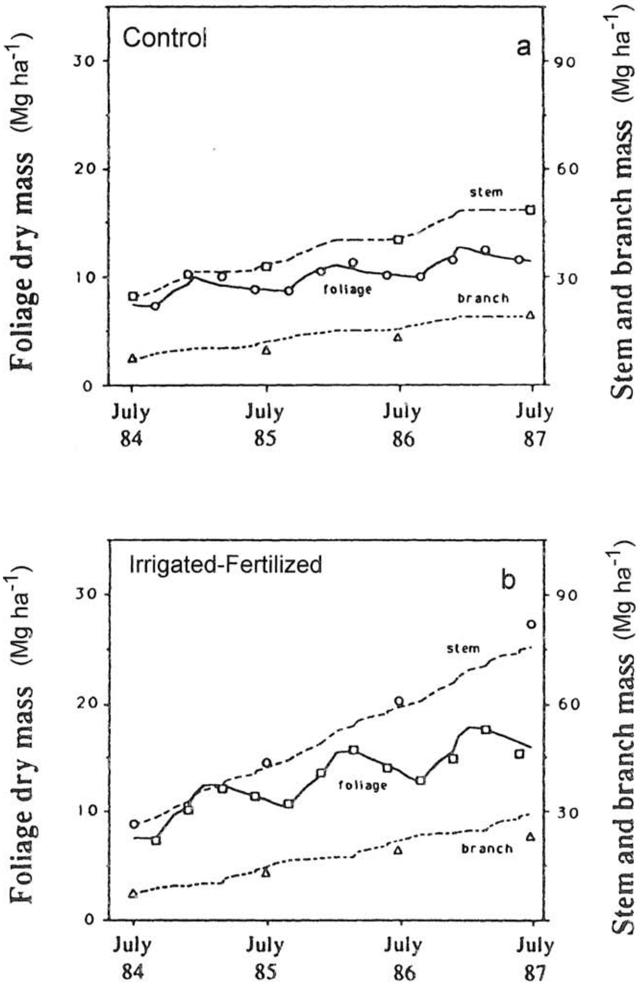

FIGURE 5.16. A 3-year time course of foliage, stem, and branch production measured and simulated with the BIOMASS ecosystem model for *Pinus radiata* stands growing in Australia that were provided irrigation and fertilizer throughout the experiment or left untreated (control). (Reprinted from *Forest Ecology and Management,* Volume 52, R. E. McMurtrie and J. J. Landsberg. "Using a simulation model to evaluate the effects of water and nutrients on the growth and carbon partitioning of *Pinus radiata,*" pp. 243–260, 1992, with kind permission of Elsevier Science–NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.)

explain the importance of quantitative analyses we have paid little attention to individual trees or species. Some of the earliest and most popular forest ecosystem models, however, were based on theories that included the dynamics of individual trees. Determining the number of tree seedlings that are present in the stand initiation stage is difficult because the type of disturbance that precedes the establishment of a new population has an enormous effect.

Historically, forests in arid climates, such as those in the western United States, Mediterranean countries, and Australia, have been periodically replaced by large-scale wildfires, often preceded by major insect epidemics which killed trees and made stands more inflammable. These wildfires produced extremely large areas of bare ground from which new forests arose. Major windstorms, such as hurricanes, do not clear the forest but may cause excessive mortality. In wetter climates, where only a small percentage of mature trees die in a year, the death of a single tree may create a gap in the canopy, below which seedlings have an opportunity to become established. This latter type of mortality which creates "gaps" gave inspiration for a wide variety of models designed to predict forest dynamics over long time spans.

D. Botkin, who produced the JABOWA model (Botkin *et al.,* 1972), provided the first example of a gap model which simulated vegetation dynamics. This has since been widely expanded through the efforts of H. Shugart and associates (Shugart, 1984; Shugart *et al.,* 1992). The central components of all gap models are (1) definition of site variables, which includes climate, (2) definition of stand variables, which includes species lists and maximum tree sizes, (3) a growth submodel that computes annual increments of diameter and height growth of each tree in a small (often 0.1 ha) simulation plot, (4) a recruitment submodel that calculates entry of new young trees into the simulation, (5) a mortality model that kills trees, and (6) a resource submodel that calculates the growth-limiting potential of various resources, expressed as growth multipliers that range from 0 to 1 (Fig. 5.17).

1. Recruitment

Whether the initial site is bare, burned, flooded, or covered with detritus after disturbance is important in determining the potential for establishment of various species. Information about the reproductive behavior of species must be stored in the model, for example, which species produce seeds or sprout from roots, how far and by what agent seeds disperse, and how long the propagules remain viable. When conditions are deemed suitable for establishment of certain groups of species, their presence on the imaginary plots is a matter of statistical probability. In early gap models, new seedling recruitment was computed as a simple random probability from an initial tree list with no seed dispersal constraints, even though some species might not be present at that time in the simulation. Newer gap models connect seedling recruitment with tree occupancy, represent seed dispersal surrounding a mother tree, compute herbivory losses, and make success of seedling germination a function of climate, so that, for example, seedling recruitment can be higher in a wet year than during a drought year (Pacala *et al.,* 1993, 1996).

2. Growth Submodel

Once a tree is established, its growth is then predicted, making allowances for limitations on light intercepted by adjacent trees and site-related variables (moisture, temperature, fertility). Plants are grouped with regard to their sensitivity to temperature, light, moisture, browsing, pollution, and other stresses. These groupings are broad; for example, most species are considered to be either shade tolerant or intolerant. Sensitivity to temperature is often inferred from the present distributional patterns in latitude and elevation.

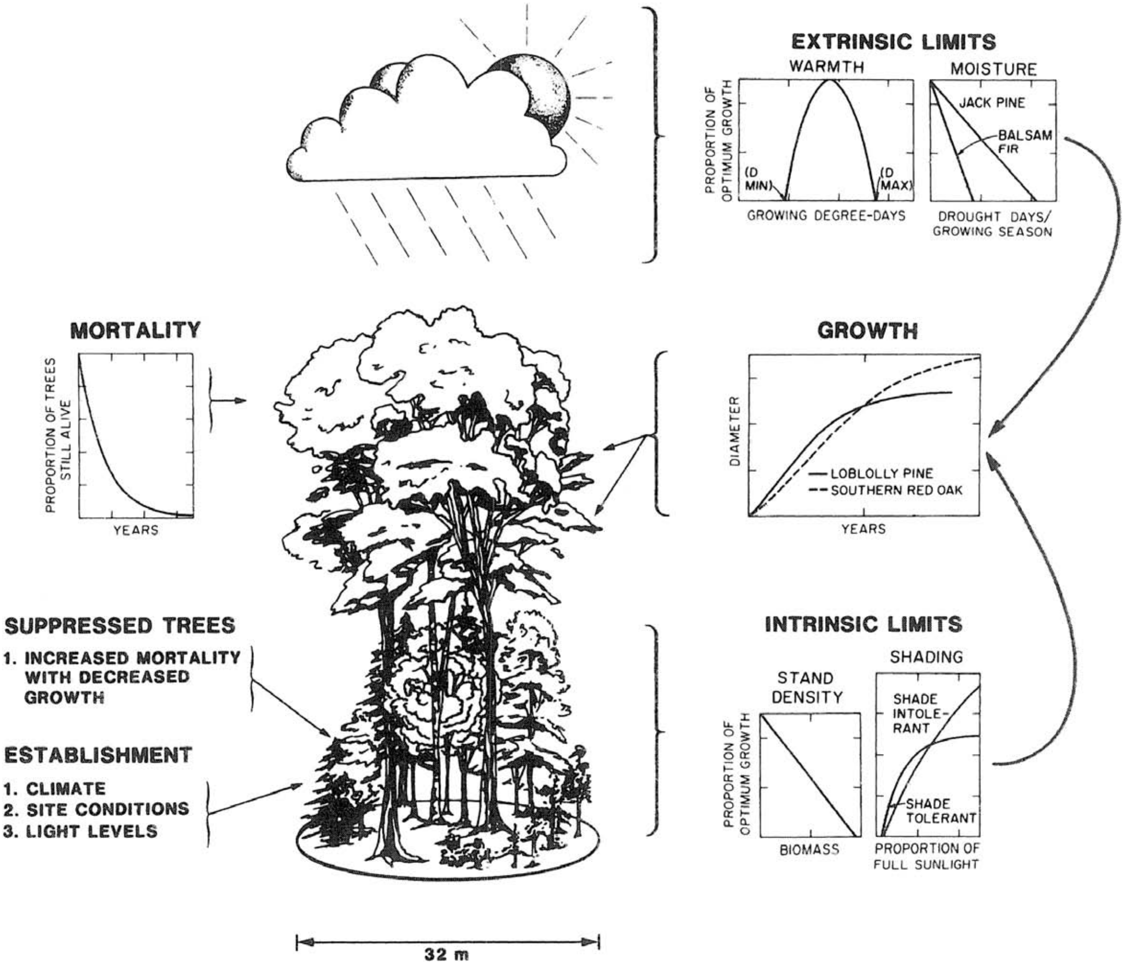

FIGURE 5.17. Summary diagram of the logic and main components of a forest succession or gap model. (From Solomon and Bartlein, 1992.)

The original gap models used a number of species-specific variables that mimic physiological processes, such as temperature and light controls on the growth equation, rather than a specific photosynthesis equation. Standard forest inventory data, which include stem diameters, tree heights, and growth increments by individual and species, are used to initialize the gap model. At the center of all gap models is a diameter-growth equation that quantifies the influence of climate on growth of each tree on the plot. There are many variations, but the equation generally includes a normalized height and diameter term and a series of empirical multipliers defining the effects of light, temperature, soil water, and nutrient availability. Height growth is also computed as a polynomial function of increases in stem diameter for each species (Dale *et al.,* 1985). In the earlier gap models, many of the variables were difficult to quantify; newer models have been modified so that they can be initialized with relatively easily collected field data (Paccala *et al.,* 1993, 1996).

Simple annual climate statistics are used to compute the growth multiplier factors, which relate growth to the maximum recorded within the range of the species. Species differences are reflected in the growth multipliers; thus, the minimum temperature limits of a subalpine tree are lower than for a coastal valley tree. In the moist hardwood forests of the eastern United States where this model was developed, light availability in the gap was the primary climatic determinate of initial seedling germination success. Hence, these early models tended to have rather complicated canopy light penetration and shading subroutines, where the vertical position of each individual tree crown in the stand was carefully followed to determine its competitive success for light. Soil fertility multipliers were added later to define nutritional limitations on tree growth. Growth multipliers to approximate enhancements of photosynthesis associated with higher levels of atmospheric CO_2 have also been added more recently (Solomon and Bartlein, 1992).

3. Mortality

Depending on the environment, some groups of trees are predicted to grow rapidly while others lag behind. Once trees are overtopped, light becomes limiting to their growth and the probability of death increases markedly. Death of a tree may be a simple function of age, sensitivity to fire, wind, snow breakage, insects, diseases, or specified activities of humans. The last point is important; these gap-phase models differ from most previous ecological schemes by incorporating both natural and human effects. When a tree dies, its fate is often critical in determining the future composition and growth rates of the stand. If left on the site, a tree may serve as shade, as a nesting site for birds that disseminate seeds, as a substrate for germinating seedlings, and eventually as a component of soil humus. When trees are harvested, on the other hand, minerals and organic resources are lost from the ecosystem. Whether foliage and branches are removed is often more critical to the assessment than the amount of bole wood because of the difference in nutrient content and resistance to decay (Chapter 4).

Mortality was initially computed as a random event whose likelihood increased as a tree reached its defined maximum size, or slowed in growth rate as a result of competition. Later models have incorporated stochastic disturbances such as fires, hurricanes, windthrow, and floods as mortality factors by adding the probability of these occurrences to the mortality probability of each tree (Shugart *et al.,* 1992).

Gap models are well suited for the evaluation of stand life cycle dynamics, specifically the recruitment, germination, and mortality of trees that define the vegetation dynamics of a stand, although it is necessary to remember that the predictions of gap models cannot be compared with individual stands because they generate averages from hundreds of hypothetical plots. The combination of multifactor growth multipliers and variable disturbance sensitivities allows the models to predict substantial variation in composition by accounting for dynamics and interspecies competition. Bonan (1989), using a gap model, successfully replicated the microclimate and topographically induced pattern of black spruce, white spruce, aspen, and birch in the North American boreal forest. His model incorporated two key controlling variables in that region: soil moisture content and depth of permafrost. White spruce, birch, and aspen occupy well-drained, south-facing slopes, whereas black spruce grows in saturated soils where the depth of thaw is very shallow (Fig. 5.18). Solomon and Bartlein (1992) simulated a diverse forest community in Michigan, which included a total of 19 deciduous and evergreen tree species. One thousand-year simulations run with multiple scenarios of CO_2 and climate change predicted substantial changes in species composition (Fig. 5.19).

Cattelino *et al.* (1979) offered a different set of principles on which to base models of vegetation dynamics. Their approach defined each species in relation to three critical attributes: (1) the persistence or viability of seeds, (2) the conditions required for seedling

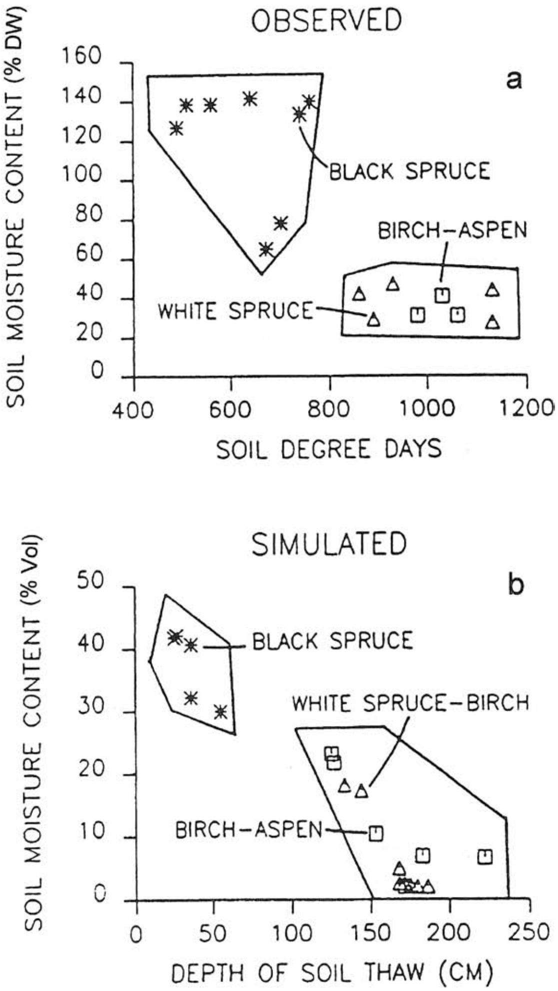

FIGURE 5.18. Observed distribution of upland forest types in interior Alaska in relation to soil moisture and temperature and distribution of forest types simulated with a gap succession model. (From Bonan, 1989.)

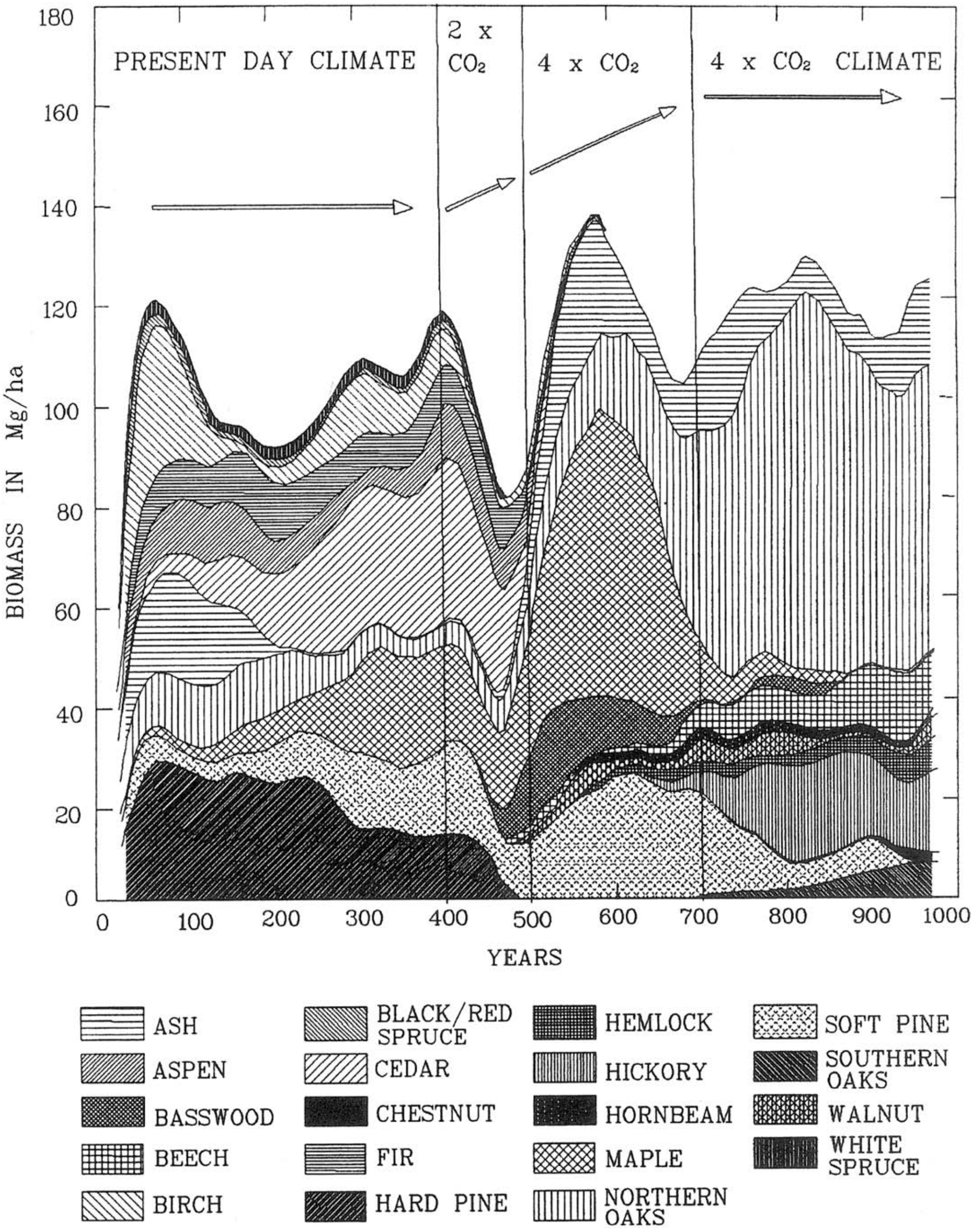

FIGURE 5.19. A one thousand-year simulation of a gap model (FORENA) illustrating dynamics of the species interaction and the response predicted by enhanced CO_2 and climatic change for a mixed Michigan forest. (From Solomon and Bartlein, 1992.)

establishment, and (3) the life history of the species, such as the age to seed-bearing maturity. Combinations of these “vital attributes” allowed Cattelino *et al.* to describe many variable pathways of forest compositional change observed in Glacier National Park, Montana, based on the sequence and timing of disturbances (Fig. 5.20). For example, a single wildfire in a mature spruce/fir stand establishes conditions favorable for aspen and lodgepole pine regeneration, but a second fire within 20 years kills pine saplings before they produce seed, while aspen reproduces from sprouting. Roberts (1996a,b) used vital attributes with fuzzy systems theory to simulate community dynamics of a mixed conifer

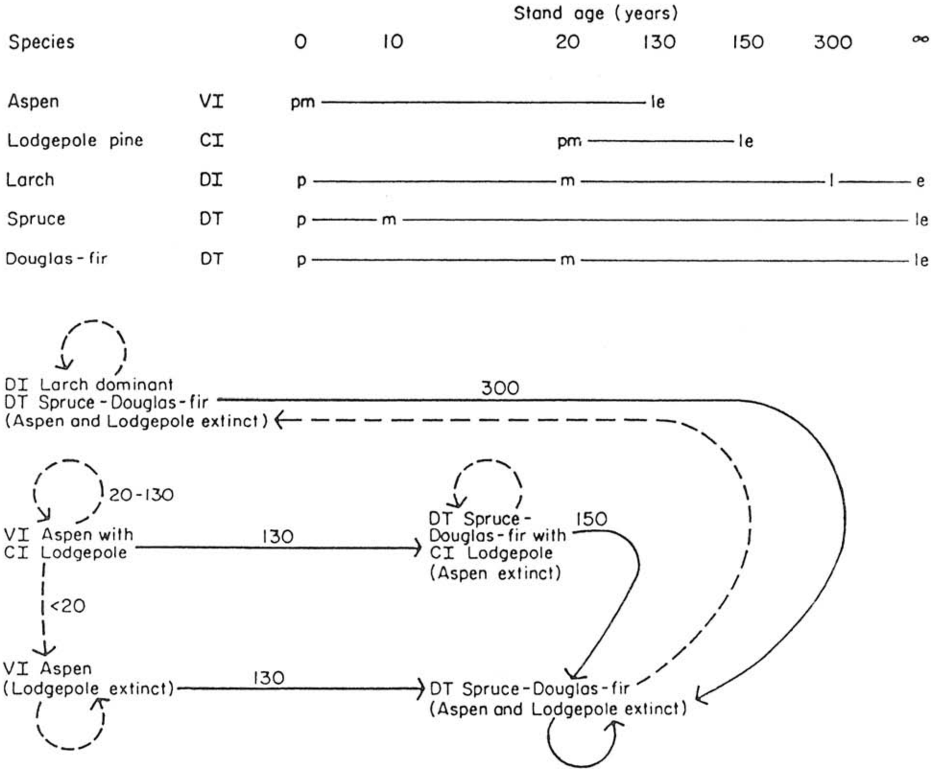

FIGURE 5.20. Life history characteristics and species replacement sequences for aspen, lodgepole pine, and western larch in Montana forests. Certain species attributes determine differential responses to disturbance events. The first attribute is seed persistence: D, widely dispersed, always available after a disturbance; S, stored, with long viability in the soil; C, canopy, with short viability; and V, vegetative propagation. The second attribute defines necessary conditions for establishment: T, tolerant of competition; or I, intolerant of competition. The third attribute specifies critical times in the life history: p, propagules available for regeneration; m, time to maturity when a species begins seed production; l, loss of the species from senescence and mortality; and e, extinction from the community. Each species has a defined life history incorporating relevant attributes. The collective development of the ecosystem then depends on the timing and magnitude of disturbances producing varying forest successional pathways as influenced by the available species, which change over time. Solid lines indicate pathways with large changes in forest composition over time; dashed lines indicate pathways that lead to repetition of one type of forest community. (From Cattelino *et al.,* 1979.)

forest in Utah under different fire frequencies. He found species diversity to be highest with a fire return interval of 250 years in these forests, and lowest with complete fire exclusion.

An important insight derived from analyses with gap models is the realization that tree species, and often other life forms, can be assigned to similar functional groups (or guilds). Model analyses further suggest that, as a consequence, ecosystem operation continues in a highly predictable manner in terms of the accumulation of biomass and leaf area as long as at least one representative from each major guild is present (Tilman, 1996). The removal of all representatives of a given functional group is therefore a signal that ecosystem and community composition could change significantly in the future.

C. Hybrid Models

Beginning in 1990, a number of groups began developing a new generation of forest ecosystem models that incorporated the best features of both biogeochemistry and gap succession models (Bossel, 1991; Huston, 1991). Models like FOREST-BGC compute carbon and water balances from physiological principles but do not grow individual trees, so they are unable to simulate a real forest stand. Gap models simulate individual tree and life cycle dynamics but do not represent growth allocation mechanistically. Use of annual climate statistics and simple growth multipliers precludes gap models from explicitly representing seasonal carbon balance physiology.

The combined models use a daily biogeochemistry model to simulate canopy processes like photosynthesis and respiration with fairly realistic physiology, then transfer the amount of photosynthate fixed annually to a dynamic vegetation model where carbon allocations are computed and growth increments (or mortality) distributed to individuals on the basis of the sum of carbon resource available and specified differences in the light environment (Friend *et al.,* 1993; Korol *et al.,* 1995; Keane *et al.,* 1996b).

Korol *et al.* (1996) applied the hybrid modeling approach with TREE-BGC and successfully predicted the distribution of basal area and volume growth on nearly 1000 trees in 24 stands across British Columbia. Plot-level measurements of basal area and volume growth were highly correlated (r^2 of 0.94 and 0.96, respectively) with TREE-BGC simulations for a 20-year growth period. In another analysis, Korol *et al.* (1995) demonstrated how thinning a stand from 2100 to 553 trees ha^{-1} reduced LAI from 3.3 to 2.6 and GPP from 19.5 to 16.1 Mg C ha^{-1} $year^{-1}$. Net primary production, however, was only reduced from 6.3 to 6.2 Mg C ha^{-1} $year^{-1}$ because maintenance respiration of foliage and other aboveground living tissue was reduced by one-third following thinning (Table 5.1). Over the following 5 years, the relative growth efficiency (annual photosynthesis per unit leaf area) increased for trees in the thinned stand and decreased for those in the unthinned stand (Fig. 5.21a). With the hybrid model Korol *et al.* also were able to calculate carbon allocation patterns for trees in relation to their exposure to sunlight (classified as dominant, intermediate, understory regeneration, and overtopped suppressed individuals). More dominant individuals with large crowns acquired more photosynthate than individuals with smaller crowns and less direct exposure to sunlight. The ratio of growth to maintenance respiration, however, was higher for intermediate and understory regeneration than for dominant trees in the stands (Fig. 5.21b).

TABLE 5.1
Allocation of Simulated Stand Carbon in Year 5 for the Stands in Fig. 5.21[a]

		Carbon (Mg C ha^{-1} year^{-1})			
Plot	LAI	GPP	R_m	R_s	Growth
Open (thinned, 553 trees ha^{-1})	2.6	16.1	7.2	2.7	6.2
Dense (unthinned, 2100 trees ha^{-1})	3.3	19.5	10.7	2.5	6.3

[a] From Korol *et al.* (1995).

Bossel (1996) captured the essential dynamics of forest stand growth in a model of 14 ordinary differential equations describing tree growth and soil processes. The model, TREEDYN3, does not require explicit daily climatic data, yet is still able to represent diurnal and seasonal physiological dynamics and multiyear tree growth. Luan *et al.* (1996) developed a forest ecosystem simulation that is hierarchical in both space and time. Their FORDYN model represents forest ecosystem dynamics at four space/time levels. The first level treats cellular CO_2 assimilation on time steps of seconds, the second level computes hourly leaf photosynthesis, respiration, and transpiration, the third computes soil carbon and nitrogen processes and carbon allocation, and the final level computes tree establishment, growth, and mortality. These examples show the continuous innovations in modeling forest stands integrating progressively more ecosystem processes.

VI. SUMMARY

In this chapter we have demonstrated that significant changes in ecosystem function occur as forests develop, even in stands composed of a single species. Four idealized stages in stand structure, which relate to changes in function, can be identified: initiation, stem exclusion, understory reinitiation, and old-growth. A unifying principle derived from analysis of stand development is that the total canopy LAI remains relatively stable in a given environment while the overstory LAI varies. Another scaling principle emerges from the recognition that species may be classified into broad functional groups, and that ecosystem operation may not be adversely affected until most, if not all, of the representatives of a guild are lost from the system. Because animals play such an important role at the initiation stage of forests, studies of their population dynamics might beneficially be concentrated on this stage to identify potentially dangerous trends in local extinction of plants and animals. On the longer term, changes in the regional flora and fauna must also be incorporated in the analyses.

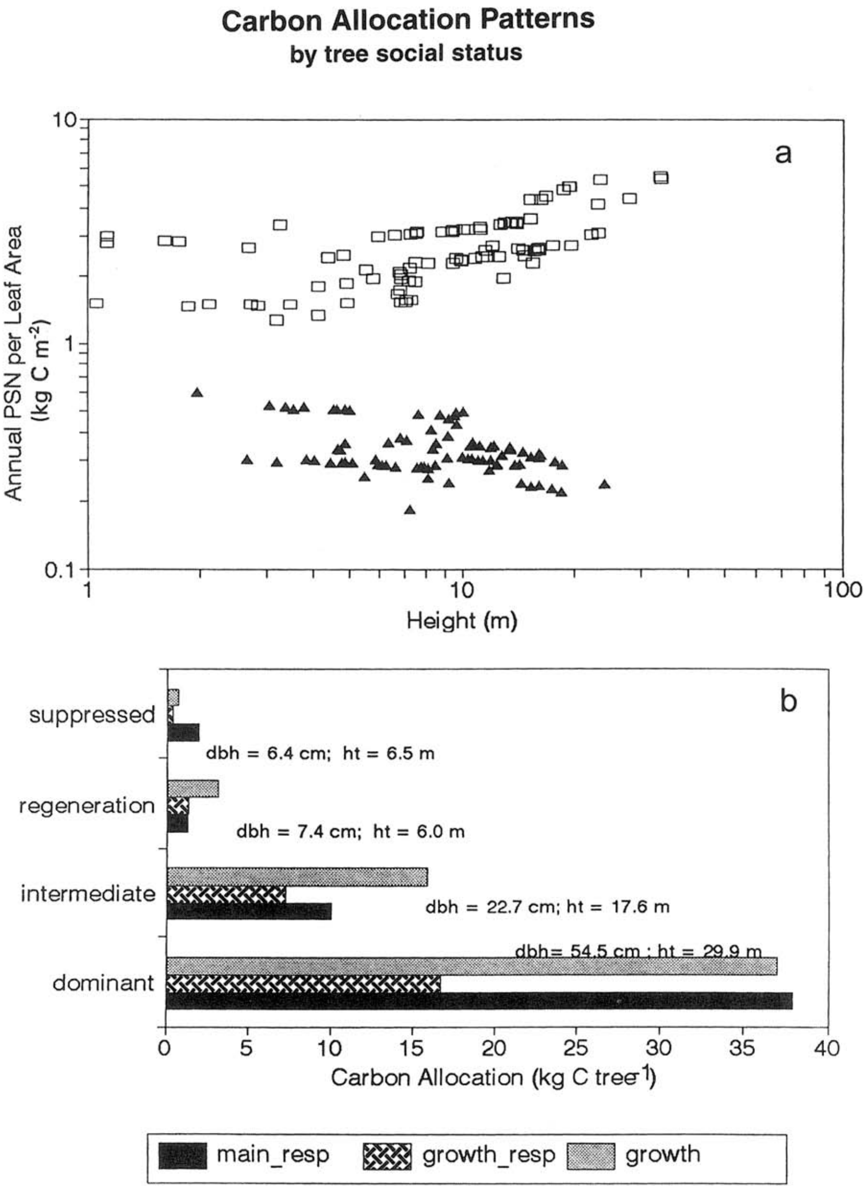

FIGURE 5.21. A hybrid model, TREE-BGC, contains a biogeochemical subroutine which calculates carbon uptake by thinned and unthinned stands (as described in Table 5.1). (a) A tree growth subroutine allocates the carbon generated by the biogeochemical model and distributes it differentially to dominant, intermediate, suppressed, and regenerating trees for 5 years following treatment. During this time, dominant (□) and suppressed (▲) trees showed opposite responses in terms of photosynthesis (PSN) per unit of leaf area. (b) The total photosynthate available for dominant and suppressed trees differed by 10-fold and was reflected in aboveground growth. Model calculations of growth/maintenance respiration ratios, which can be derived from the diagram, illustrate significant differences for dominant (~1.0), intermediate (~1.5), regeneration (~3.0), and suppressed (~0.5) trees. (From Korol *et al.,* 1995.)

From a historical perspective, a variety of techniques developed in paleobotany, dendrochronology, and pedology provide us with insights into the extent and frequency of changes in forest growth, species composition, soil organic matter dynamics, and atmospheric deposition. These historical interpretations, particularly those gained through isotopic analyses, offer a means of testing and calibrating models more widely than can be accomplished through long-term studies or experiments. Hybrid models able to integrate biogeochemistry and vegetation dynamics offer powerful tools to assess the implications of various forest policies and practices before they are put into operation. Because models provide the only means of evaluating options decades to centuries into the future, they deserve to be constructed with great care and to receive rigorous testing before being presented to decision makers.