CHAPTER 9

The Role of Forests in Global Ecology

I. INTRODUCTION

Forests cover approximately 30–40% of the vegetated area of Earth. If it were not for human and natural disturbances, forests might be expected to occupy most landscapes where annual precipitation exceeds about 25 cm, excepting polar regions where energy limitations constrain vegetation growth (Neilson, 1995). Global ecological studies frequently identify forests as major contributors to a host of important biospheric processes (Vitousek, 1994). Boreal forests are of particular interest because they are expected to undergo the greatest climatically induced change in the twenty-first century (Bonan *et al.*, 1992). Temperate forests are currently hypothesized to provide a major CO_2 sink that helps stabilize the global carbon balance (Tans *et al.*, 1990; Ciais *et al.*, 1995; Keeling *et al.*, 1995; Turner and Koerper, 1995). At present, tropical forests are believed to be undergoing the most rapid conversion to other land uses (Skole and Tucker, 1993; Houghton, 1994). Given this prominence of forests in many aspects of global science, one might expect that much detailed information would be available on their distribution and composition. The inherent physical magnitude of global scale questions, however, makes addressing even such obvious questions difficult.

To illustrate the challenge facing global scale assessments, scientists have yet to measure with accuracy the vegetated land surface of Earth; values range from 120 to 140 million km^2. Estimates of forest land cover are even more variable, ranging from 30 to 75 million km^2 (Townshend *et al.*, 1991). Some of this uncertainty results merely from disagreements among scientists on definitions of what is forested land, particularly along transitional zones where forests grade into grasslands in arid environments, or into tundra in boreal regions. Most of the uncertainty arises, however, from our inability to make accurate measurement over millions of square kilometers. Before the era of satellites, global estimates of forestland were derived from exhaustive compilations of national mapping surveys (Matthews, 1983; Olson *et al.*, 1983). Obtaining consistent, accurate mapping of global forests is only now becoming possible with new satellite systems. New models incorporate satellite and ancillary data sources to distinguish forests and other types of vegetation (Prentice *et al.*, 1992; Neilson, 1995; Woodward *et al.*, 1995) and to estimate regional and global scale biogeochemical activity (Melillo *et al.*, 1993; Schimel *et al.*, 1994; Field *et al.*, 1995; Hunt *et al.*, 1996).

This chapter summarizes current analyses of the distribution of global forests and their interactions with the biosphere. It also previews technical advances likely to increase our understanding of the role that forests play globally. To expand our analysis to a global perspective we continue on the logical path set in Chapters 7 and 8, where we seek further to simplify the kinds of questions asked, reduce the detail of data required, and select appropriate tools for the new endeavor. From a functional viewpoint, we emphasize the role of forests in global biogeochemistry and climate dynamics, but we will also consider the importance of forests in protecting global biodiversity and in sustaining a natural resource base for supporting cultural and economic goals.

II. GLOBAL FOREST DISTRIBUTION

A. Paleoecological Evidence of Past Forest Distributions

Paleoecological studies of tree pollen and fossilized wood in peat bog cores have documented that global forest cover changed dramatically as climate has changed, with particularly strong evidence from the last 20,000 years. Earth's climate has undergone a transition from glacial to interglacial conditions in the last 20,000 years that is as large as any climate fluctuation in the last 3,000,000 years (Webb and Bartlein, 1992). This recent and rapid climatic change has allowed pollen counts, dendrochronology, and carbon isotope analyses on ancient samples of wood to provide an accurate picture of the rate at which forests change in their distribution in response to climatic variations. From these paleoecological sources, for example, we know that the geographic distribution of tree species of the eastern North American forest has moved hundreds of kilometers in the last

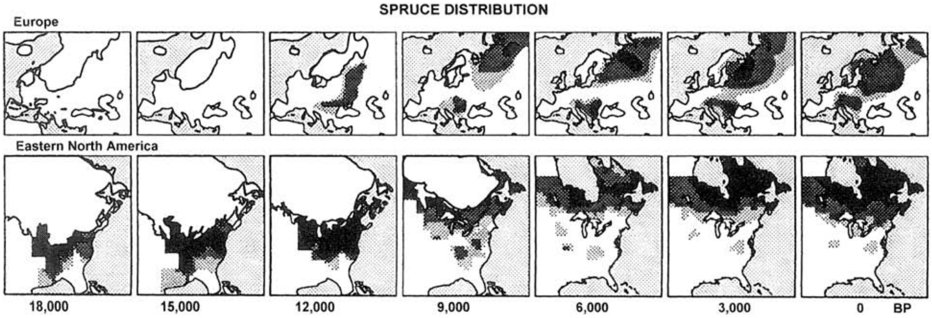


FIGURE 9.1. Changing distribution of spruce (*Picea*) during the past 18,000 years (BP, before present) in Europe and eastern North America. These maps are derived from radiocarbon-dated surface and fossil pollen records interpolated with climatic data and graphed to 100-km^2 cells. Shading refers to pollen abundance: black, >20%; medium, 5–20%; light, <5%. (Redrawn from Prentice *et al.,* 1991, and Webb and Bartlein, 1992.)

18,000 years as temperature and precipitation patterns changed. As the last major ice age ended, temperatures have warmed by at least 5°C and caused continental glaciers to melt, with species like spruce expanding their range slowly into areas once covered by ice (Fig. 9.1; Prentice *et al.,* 1991). Arctic timberline in northwestern Canada was 350 km further north during the warm mid-Holocene period 8500 to 5500 years ago relative to the current forest–tundra boundary (Ritchie *et al.,* 1983). However, there is a lag between the time of climatic change and the response of forest distribution because of the slow pace of tree mortality, seed dispersal, and regeneration. Gear and Huntley (1991) estimated a maximum migration rate of Scots pine in Scotland of about 0.5 km year^{-1} as Scots pine first moved north 70–80 km, then retreated back south during the last 4000 years in response to regional temperature changes. Prentice *et al.* (1991) estimated that it took 1000–1500 years for the distribution of spruce in Fig. 9.1 to equilibrate to a new climate.

Altitude acts as a surrogate for latitude in providing a climatic gradient for forests to move across. There is convincing evidence that alpine timberline in the Rocky Mountains and European Alps was 50–200 m higher during the mid-Holocene period than it is today. Movement of the timberline boundary is a complex response to both episodic trends and occasional extremes in a host of climate factors, making simple predictions of forest responses to future changes difficult (Graumlich and Brubaker, 1995).

These historical reconstructions give a sense of how climate controls the long-term distribution of forests over thousands of years, and they allow us to explore with models how responsive the terrestrial biosphere might be to future climatic change. Foley (1994) used a GCM (Global Circulation Model, often called a Global Climate Model) to simulate the mid-Holocene climate of 6000 years before present (BP) and then contrasted simulated global terrestrial carbon balances with present-day climate using a biospheric model. He concluded that a 20% decrease in carbon storage in boreal forests was offset by an increase of 20% in the area occupied by arid forest savanna, resulting in almost no change in total global terrestrial carbon storage (Fig. 9.2).

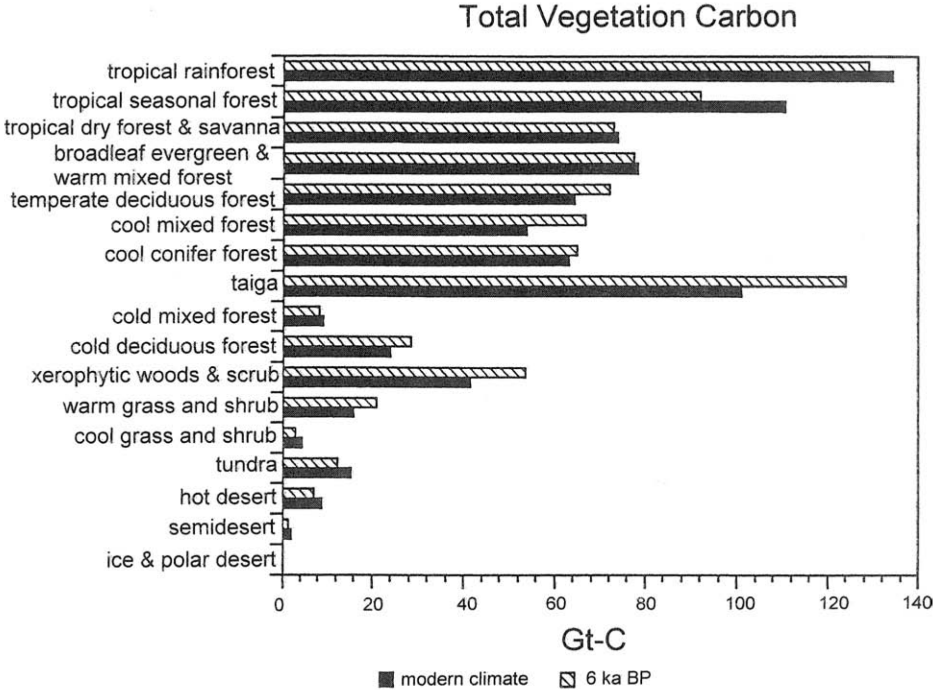


FIGURE 9.2. Simulation of global terrestrial carbon storage in the mid-Holocene (6000 BP) compared to the present. Comparative simulations were run with a global biosphere model using estimated 6000 BP climate and a present-day climate. Results suggest that tropical forests have gained carbon storage from 6000 BP to the present as continental monsoon rains strengthened. Temperate and boreal forests have lost carbon during the last 6000 years, primarily because the boreal forest boundary has retreated 300–500 km south of its northern limits in the mid-Holocene. (From J. A. Foley, *Global Biogeochemical Cycles* **8,** 505–525, 1994, published by the American Geophysical Union.)

B. Bioclimatic Definition of Potential Forest Distribution

Detailed analysis of specific climatic variables combined with additional knowledge of general tree physiology has allowed biogeography models to quantify the critical environmental limits for vegetation distribution. Trees, being perennial organisms must first endure the extremes of their environment in order to persist. Prentice *et al*. (1992) and Haxeltine and Prentice (1996) used absolute minimum air temperatures to discriminate boreal, temperate, and tropical forest ranges in their BIOME2 and BIOME3 biogeography models. Neilson (1995) used a combination of annual growing degree-days and monthly minimum temperatures to define boundaries between thermal zones (Tables 9.1 and 9.2). Woodward (1987) summarized the cellular mechanisms of cold tolerance physiology that are the basis for interpreting how minimum temperatures control global forest distribution, building on the original work of Sakai and Weiser (1973). Tropical trees are unable to withstand ice crystal formation within living cells. Temperate trees are able to withstand temperatures down to −45°C (where unbound water freezes spontaneously) by expelling

TABLE 9.1
Lethal Minimum Temperatures (°C) That Limit the Geographic Distribution of Various Woody Plant Forms[a]

Plant form	Lethal minimum temperature (°C)
Broad-leaved tropical deciduous (rain-sensitive)	0 to 10
Broad-leaved evergreen (frost-sensitive)	0
Broad-leaved evergreen (frost-resistant)	–15
Broad-leaved temperate deciduous	–40
Broad-leaved boreal deciduous (e.g., *Betula*, *Populus* spp.)	No limit
Needle-leaved evergreen (e.g., *Agathis*, *Araucaria*)	–15
Needle-leaved evergreen (temperate taxa)	–45
Needle-leaved evergreen (boreal taxa)	–60
Needle-leaved boreal deciduous	No limit

[a] From data summarized in Woodward (1987).

free water from cells during development of cold hardiness in autumn, and by binding the remaining water to cell walls during winter severe freezing conditions. Boreal species exhibit special protective mechanisms that allow them to withstand freezing in liquid nitrogen at –196°C when in their full cold hardened state, and to repair cellular damage in the spring, which are fascinating physiological feats (Havranek and Tranquillini, 1995).

Beyond adapting to different temperature limits, trees require a certain length of growing season to complete their morphological development and an adequate supply of water to support sufficient leaf area required to maintain a positive annual carbon balance. The summed number of growing degree-days above a minimum temperature level, usually 0°C, is used to quantify the overall "heat requirements" for tree development and, more significantly, to define the transition zone (*ecotone*) between tundra and boreal or alpine forests (Table 9.2). Although 25 cm is estimated as an approximate lower limit of annual precipitation required to support forests, a more precise definition is obtained by computing a water balance between precipitation and potential losses in evapotranspiration

TABLE 9.2
Definition of Global Biome Boundaries with a Combination of Limiting Minimum Temperatures and Temperature Thresholds for Morphological Development[a]

Boundary	Calibrated temperature threshold	Physiological interpretation
Tundra–taiga/tundra	735 growing degree-days	Short growing season (frost desiccation)
Taiga/tundra–boreal	1330 growing degree-days	Short growing season (no reproduction)
Boreal–temperate	–16°C (average monthly)	Supercooled freezing point (–45°C)
Temperate–subtropical	1.25°C (average monthly)	Annual hard frost (24 hr < 0°C)
Subtropical–tropical	13°C (average monthly)	No annual hard frost

[a] From Neilson (1995).

(Stephenson, 1990; Neilson, 1995). The transition from arid grasslands and shrubs to forest is often gradual; savannas support a variable mix of trees, grasses, and shrubs. An increase in the water availability favors more trees in savannas, but the seasonal distribution of precipitation and ET are also important. Haxeltine and Prentice (1996) were able to delineate savanna from grassland by defining which of the two types had the highest modeled NPP in a particular area. Once sufficient water is available to support some kind of forest, additional water provides greater development, particularly in the amount of leaves (LAI) and the duration of their seasonal display, as discussed in Chapter 2 (Grier and Running, 1977; Woodward, 1987).

It is important to recognize that climatic constraints alone only help to define *potential* forest cover. The actual distribution of forests is heavily influenced by both natural and human-induced disturbances. In Chapter 6 we considered that forest development over time rarely progresses to a hypothetical “steady-state” or “climax” condition because of frequent disturbances. These same mechanisms operate at continental scales to influence the geographic distribution of forests. The tall grass prairie of the North American Great Plains normally receives sufficient precipitation to support forests, yet periodic droughts, frequent fires, and historical grazing by bison herds maintained a grassland until European immigrants arrived and established what is now the wheat belt of the continent (Neilson *et al.,* 1992). Until the advent of satellites, of course, we had no means of obtaining a consistent measure of the *actual distribution* of vegetation on Earth.

C. Satellite Estimates of Current Forest Distribution

Since the launch of the Landsat series of satellites in the early 1970s, numerous remote sensing studies have quantified local land cover and provided quantitative estimates of the conversion of forestland to other uses (Peterson and Running, 1989; Loveland *et al.*, 1991). D. P. Turner *et al.* (1993) calculated that 45% of the potential forest cover of the continental United States has been converted to other land cover types. There has been much interest in defining tropical deforestation rates by satellite (Skole and Tucker, 1993; Skole *et al.*, 1994) to compare with temperate forest cutting rates (Chapter 8). Such analyses have to date been largely restricted, however, because of the difficulties in dealing with the huge volume of data required and the lack of an accurate means to distinguish forest cutting from large-scale disturbances such as fire or the conversion of forestland to other uses. Nemani and Running (1995) produced a satellite-derived estimate of present global forest cover, 52.6 million km^2, which lies near the middle of the range of 30–75 million km^2 cited by Townshend *et al.* (1991). Their analysis of global forest distribution was 49% tropical, 29% temperate, and 22% boreal (see Plate 12).

New processing of AVHRR data using visible, near-infrared, and thermal channels has also allowed the first mapping of global land cover *change*. The vast majority of global land cover change has been attributed predominantly to forest conversion to agricultural fields, pastures, and urban areas (Meyer and Turner, 1994). Nemani and Running (1995) first computed the potential land cover from climatic data with a simple biogeography model based on principles similar to those in models developed by Prentice *et al.* (1992) and Neilson (1995). Next, an annual sequence of biweekly AVHRR data was processed to define existing global land cover based on procedures outlined in Running *et al*. (1995).

By comparing the two maps a third could be derived that distinguished potential distribution of vegetation from the existing pattern, which emphasized regions of major land cover conversion (see Plate 13).

The surprising results were that only 26% of potential tropical forests have been deforested, substantially less than the estimates of nearly 50% given by Myers (1993). The analysis in Fig. 9.3 suggests that 40% of temperate forests have been altered, which is close to the 45% estimated by Turner and Koerper (1995) for U.S. forestlands. In boreal forests, the estimated reduction in area from the potential was only 20%, which probably reflects the remoteness and generally low adaptation of these ecosystems for other uses. In contrast, much of the once vast forests of Europe have been converted to agriculture and urban use. In this analysis, young, regenerating forests also are interpreted by the satellite as a land cover change, even if the change is temporary, which illustrates the importance of repeating land cover change analyses at regular intervals. The most concentrated regional change has occurred in Southeast Asia and India, where dense tropical and subtropical forests have been cleared for extensive agriculture, a conclusion verified by Dale (1994) from ground-based data. New EOS satellites launched in 2000 provide more precise and regular mapping of global forest land cover (Plate 14).

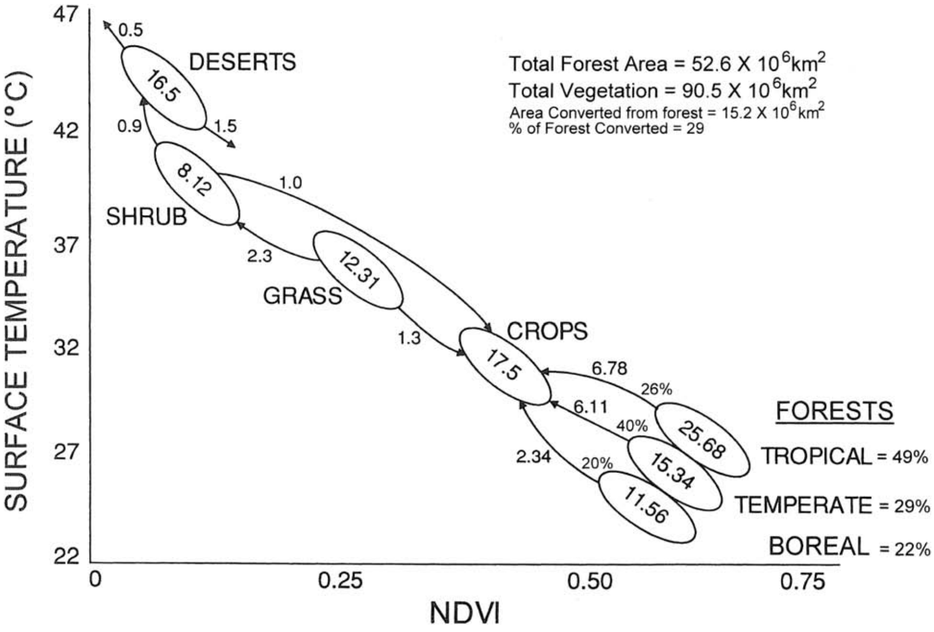


FIGURE 9.3. Areal changes in land surface area for each biome type from the land cover change map in Plate 13. The change trajectory is plotted on the NDVI versus surface temperature axes used by Nemani and Running (1995) to define biome types with satellite data. The numbers indicate areas in $10^6\,km^2$, except where percentages are noted. Numbers in the ovals are current land area in each biome type, and labeled arrows are the change in biome area from the maximum potential.

D. Future Forest Responses to Climate Change

The future distribution and activity of forests will be controlled predominantly by changes in climate, forest response to elevated CO_2, and land cover changes associated directly with human activities. Although changes in forest land cover are controlled substantially by socioeconomic factors that cannot be easily predicted, forest responses to potential climate change and CO_2 concentration can be assessed with various computer simulation models. As we covered in Chapter 3, the first response of increasing atmospheric (CO_2) will be increased photosynthetic rates and partial closing of stomata producing higher water use efficiency. An extensive literature review by Ceulemans and Mousseau (1994) of studies done with exposures of less than 2 years found that a doubling of CO_2 from 340 to 680 ppm enhanced photosynthesis rates by 40% in conifers and by 61% in broadleaf trees; however, the range of responses is large. The mean estimated increase in growth was 38% for conifers and 63% for broadleaf trees.

Evidence suggests that the long-term response of trees to rising CO_2 may not be nearly so large as the short-term response. In the last 200 years, atmospheric CO_2 concentrations have risen from about 280 to >360 ppm (Keeling *et al.*, 1995) as a result of land clearing and combustion of fossil fuels. The isotopic composition of C in the atmosphere has changed over recent decades and continues to change. Lloyd and Farquhar (1994) estimate $\delta^{13}C$ discrimination of photosynthesis to be 17.8‰ for C_3 plants that produce 79% of global terrestrial photosynthesis. Plant tissues, with $\delta^{13}C$ values predominantly between −27‰ and −32.5‰, have lowered the $\delta^{13}C$ of the atmosphere from about −6‰ to −8‰ in the twentieth century. Physiological and anatomical adjustments in the concentration of carboxylation enzymes and chlorophyll pigments, coupled with anatomical adjustments of the number of stomata, have allowed plants to maintain a relatively stable c_i/c_a ratio over eons of changing atmospheric CO_2 (Van de Water *et al.*, 1994). The historical evidence of the maintenance of a stable gradient in CO_2 suggests that future increases in net photosynthesis caused by increasing CO_2 may be much more modest than that inferred from short-term experiments (Gifford, 1994).

The longer term ecosystem-level responses of forests, such as changes in leaf area, carbon allocation, and regeneration, senescence, and mortality rates, cannot be as easily studied experimentally, so again we turn to computer simulation models (Bazzaz, 1990; McMurtrie *et al.*, 1992; Woodward, 1992; Neilson and Running, 1996). Initial modeling studies explored the possible changes in geographical range of forests on the basis of climatic changes alone. Smith *et al*. (1992) projected an overall increase in global forest cover associated with increased temperatures and precipitation, with an extension of boreal forests into present tundra and a decrease in the area of dry forests as drought causes conversion to more grasslands. More mechanistic biogeographic models now include the physiology of CO_2 enhancement and climate change in the biome redistribution. When Neilson and Marks (1994) added enhanced water use efficiency to their model analysis, forest LAI was projected to increase 14% compared to current climate conditions. McGuire *et al.* (1993) also illustrated that forest response to climatic changes may be highly variable in different parts of the world. High latitude forests, where development is limited by incident radiation, day length, and temperature, may accelerate in growth, while tropical forests may endure higher water stress and respiration losses.

Longer term simulations typically combine both direct CO_2 effects on tree physiology with climatic change scenarios from GCMs. A more comprehensive model analysis by VEMAP (Vegetation/Ecosystem Modeling and Analysis Project) developed climate chance scenarios from GCM simulations that were coupled with biogeographical models to compute shifts in biome distribution, which then were used in biogeochemical models to project final changes in NPP (VEMAP, 1995). Forest cover in the United States under the present climate was simulated with three biogeographic models to fall within a uniform range of 42–46% of the total land area. Simulations of future forest cover were much more variable, however, ranging from a reduction to 38% of the present area to an increase up to 53% of the area (see Plate 15). Likewise, although current NPP of the United States was calculated to be between 3.1 and 3.8 Pg year^{-1} with the three biogeochemical models, when simulations were made that incorporated changed climate, CO_2, and biome redistribution, predictions of increases in NPP ranged from 2 to 35% (Plate 15). These differences in model predictions primarily result from our inadequate understanding of the balance between water and nitrogen limitations in controlling carbon allocation.

Although the predictions from the VEMAP analysis should be interpreted cautiously, there were some important general conclusions derived from the project. First, the levels of uncertainty regarding future climates, future biome distribution, and future ecosystem biogeochemistry were roughly equal, suggesting the scientific understanding of each of these subjects is similar. This analysis probably brackets the possibilities of change in NPP, and all model combinations suggest at least a modest increase, although less than the NPP enhancements derived from short-term physiological experiments. Finally, because NPP is a conservative ecosystem property, important alterations in forest composition may still occur and not be noticed until all representatives of a functional group are lost.

The replacement of one species with one better adapted to a changed climate has historically taken many centuries, and, in the process, an increase in wildfires and insect outbreaks may cause much damage to surviving forests (Clark, 1988; Cannell *et al*., 1989). Flannigan and Van Wagner (1991) projected that the area of Canadian boreal forest burned annually may increase 40% based on current GCM projections of climatic change. Price and Rind (1994) used GCM results to estimate that the number of lightning-caused fires could increase by 44% and the area burned could increase by 78% for the United States in a doubled CO_2 climate. Overpeck *et al*. (1991) projected that plant distribution could shift by 500–1000 km in the next 200–500 years based on current GCM projections of the magnitude and rapidity of changing climate. Overpeck *et al*. (1990) hypothesized that these increases in disturbance frequency could provide opportunities for accelerated movement of forest distributions in a highly unpredictable way.

E. Monitoring Future Changes in Forest Dynamics

The impact of global change on forests, whether induced by climatic or sociopolitical forces, will require an accurate, regular monitoring of forest cover and productivity. Because forest redistribution is so hard to predict and will take many centuries, possibly the earliest evidence of change may come from following the interannual variability in phenology, the seasonal timing of leaf emergence in the spring and senescence in the autumn. Spring leaf onset of native trees was observed to vary by more than 90 days in a unique natural history record from England that spans 211 years (Sparks and Carey, 1995). In temperate forests, cold, rainy springs result in delayed budburst in trees relative to sunny, warm spring conditions, and interannual variability of 30–40 days is common (Lechowicz, 1995). Phenological observations were commonly recorded at field research stations earlier in the twentieth century, but most reports were discontinued in the 1960s and 1970s in favor of different types of research, interrupting what could have been a priceless record of global change (Hari and Hakkinen, 1991). In the future, both spring and autumn phenology of forest canopies will be monitored by combining satellite and surface meteorological data to produce maps that cover each continent (see Plate 16). Any trend toward earlier spring leaf emergence and/or later autumn senescence will provide sound evidence of warming climates at mid- to high latitudes.

New satellite systems will allow accurate regular mapping of global forest cover at 1 km scales (Nemani and Running, 1996). Documenting changes in observable ecotones, such as alpine timberline, forest—grassland, and boreal forest—tundra borders, should provide a sensitive measure of climatic influence on the distribution of various types of forests over the coming decades. More locally, tree-ring dendrochronology will continue to offer a valuable index of tree-growth responses to climate fluctuations (Jacoby and D'Arrigo, 1995). Where CO_2 and H_2O flux networks are permanently established, continuous measures of forest ecosystem gas exchange provide detailed insights into how net ecosystem carbon balances and other ecosystem properties respond to changing climate (Baldocchi *et al*., 1996).

In all of these cases, systematic measurements following standard procedures must be sustained over decades to provide adequate documentation of the effects of global change on forest distribution and function. Global scale monitoring will provide the best assessment of changes in forest cover. Regional scale monitoring will best define shifts in phenology and the displacement of ecotonal boundaries. Local monitoring will provide insights into shifts in carbon balance between photosynthesis, changes in biodiversity, and other important properties. There should, however, also be modifications in climate-forecasting models so that they better represent the actual distributions of vegetation and incorporate the interactions associated with changes in phenology (Henderson-Sellers and McGuffie, 1995; Chase *et al*., 1996).

III. FOREST–CLIMATE INTERACTIONS

A. Evidence of Climatic Warming

Although projections based on GCM simulations forecast rising global temperatures of around 2°–4°C as atmospheric CO_2 concentrations double in the coming centuries, the measured changes in air temperatures seem to bear out only a modest warming trend to date (IPCC, 1996). Pollution-producing aerosols cause haze to develop over urban areas, reducing incident solar radiation, cooling the land surface, and partially offsetting greenhouse gas-induced warming (Mitchell *et al*., 1995). Air temperatures are inherently highly variable on daily, seasonal, and interannual basis. In addition, lack of standards in instruments, sensor calibration, and shifts in weather station locations and reporting times contribute to inconsistencies in the global climate database (Karl *et al*., 1995). Intensive analyses in selected regions of air temperature extremes and their seasonal variations, however, show clear evidence of regional climate warming trends (Oechel *et al*., 1993). For example, Karl *et al*. (1993) report that the winter minimum temperatures in Alaska have increased 3.5°C since 1951, although the annual average temperatures have changed only slightly. Groisman *et al*. (1994) estimate that the maximum extent of seasonal snow cover in the northern hemisphere has retreated 10% from 1972 to 1992.

There is some clear evidence of warming at high latitudes based on simple but important observations that date back well over a century. Oerlemans (1994) plotted the long-term change in length of 48 glaciers worldwide, some with records going back to 1850 (Fig. 9.4). Every glacier in the study has retreated, and for the period 1884–1978 the average

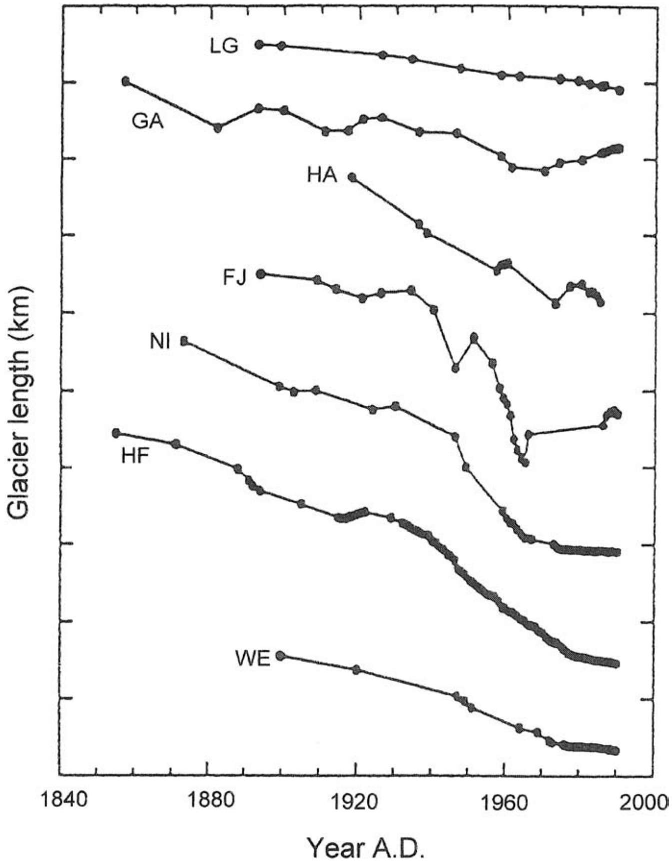


FIGURE 9.4. Fluctuation in length of glaciers distributed globally that have been monitored for at least 100 years. The locations of glaciers shown are as follows: LG, Kenya; GA, France; HA, Spitzbergen; FJ, New Zealand; NI, Norway; HF, Austria; WE, Canada. All 48 glaciers in the survey have retreated, on average more than 1.2 km, a significant indication of global warming. (Reprinted with permission from J. Oerlemans, “Quantifying global warming from the retreat of glaciers,” *Science* **264,** 243–245. Copyright 1994 American Association for the Advancement of Science.)

retreat was 1.23 km, correlated with a 0.62°C increase in temperatures through this period. Walsh (1995) reported data of Kuusisto (1993) showing that duration of ice cover in three lakes in Finland has decreased by 3 weeks since records began in 1830. A record of budburst dates from 1907 to 1950 for birch in central Finland suggests that leaf onset now averages about 1 week earlier than at the turn of the twentieth century (Hari and Hakkinen, 1991). Jacoby *et al*. (1996) analyzed 450-year tree-ring chronologies for Siberian pine at timberline (2450 m) at 48°N latitude in Mongolia. Cores averaged from 25 trees showed an extended period of enhanced growth since 1940 that corresponded with warmer regional temperatures (Fig. 9.5). In this severely energy-limited environment, warmer temperatures in conjunction with increased atmospheric CO_2 should result in longer growing seasons, higher photosynthetic rates, and increased primary production, decomposition, and mineral cycling rates.

An important conclusion is that the annual mean air temperature of Earth is among the least sensitive indicators of global climate change. Scientists now are placing more attention on evaluating the frequency of extreme events, trends in regional phenology, and related hydrologic variables to detect climatic changes (Chapman and Walsh, 1993).

B. Interactions of Forests with Climate

The pervasive influence of climate on vegetation is obvious, but vegetation also exerts influences back on local and regional climate (see also Fig. 8.5). Understanding the role

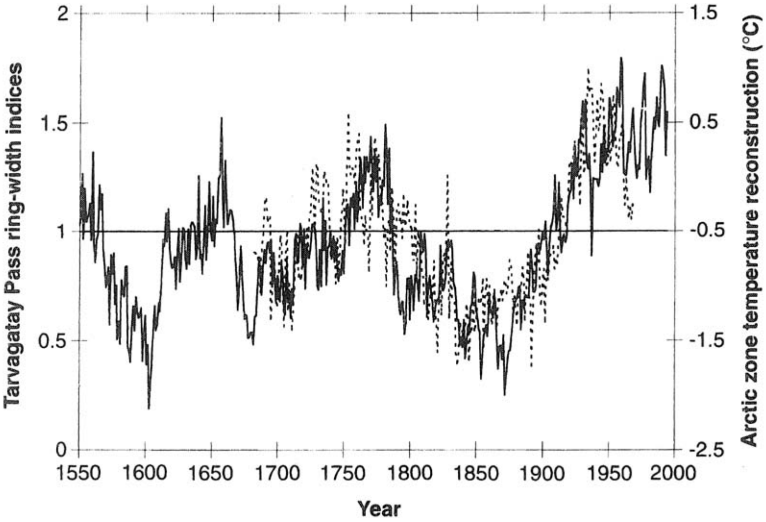


FIGURE 9.5. Chronology of tree-ring width indices for 300- to 500-year-old Siberian pine in Mongolia. The dashed line represents a reconstruction of annual air temperature departures from average for the region. Although isolated years early in the record showed high growth, the 10 widest annual growth rings have all been produced since 1920. Climate models predict that the greatest warming and biospheric models predict that the greatest increases in growth will occur at high latitudes. (Reprinted with permission from G. C. Jacoby, R. D. D'Arrigo, and T. Davaajamts, "Mongolian tree rings and 20th-century warming," *Science* **273,** 771–773. Copyright 1996 American Association for the Advancement of Science.)

of forests in directly influencing climate began with simple sensitivity studies of global climate models. Dickinson and Henderson-Sellers (1988) first ran their GCM with a standard vegetation, then replaced all of the tropical forests of the Amazon basin with a degraded grassland and concluded that evapotranspiration would be reduced substantially and result in an increase in surface temperature of 3°–5°C. A more accurate analysis used the satellite-derived estimates of partial Amazon deforestation reported by Skole and Tucker (1993) and found that evapotranspiration was reduced by 18%, leading to a decrease of precipitation in the basin of 8%, roughly 1.2 mm/day (Walker *et al*., 1995).

Bonan *et al.* (1992, 1995) simulated the influence of a major deforestation in the boreal forest zone on climate and concluded that removal of forest cover would expose the snowpack, increasing the surface albedo from January through April, and result in a predicted temperature *decrease* of 2°–5°C at high latitudes. Sellers *et al.* (1996b) reported that differences in the assumptions regarding stomatal response also affect the climate predicted over a continent. When more realistic stomatal regulation by humidity deficits and CO_2 was added to a GCM, canopy conductance was reduced by 34%. The associated reduction in transpiration increased sensible heat exchange and resulted in a predicted air temperature increase of 2.6°C above the original simulations (Sellers *et al*., 1996b). Schwartz and Karl (1990) showed dramatic and direct evidence of the control vegetation produces on current local climates. They documented that the regular increase in surface air temperatures during springtime is interrupted temporarily when leaves emerge on vegetation, in response to the cooling effects of additional transpiration (Fig. 9.6).

IV. FORESTS IN THE GLOBAL CARBON CYCLE

A. Elements of the Global Carbon Cycle

There are two important reasons for us to be concerned about the global carbon cycle. First, the CO_2 exchange from the terrestrial surface modulates the atmospheric CO_2 balance, with significant consequences on the climate. Second, and ultimately of more immediate importance, net primary production of vegetation is the renewable source of food, fuel, and fiber that supports our daily lives.

A simple box model shows the major components of the global carbon cycle (Fig. 9.7). Terrestrial vegetation contains about 550 Pg of carbon, soils 1200 Pg, the oceans 36,000 Pg, and the atmosphere 755 Pg. The fluxes of carbon (primarily as CO_2) between the terrestrial surface and the atmosphere are estimated as follows: gross photosynthesis, 110 Pg; autotrophic respiration of plants, 50 Pg; and soil respiration, 60 Pg (Moore and Braswell, 1994). Scientists face a challenge in determining the exchange rates among carbon pools because the annual fluxes are only a fraction of the total pool sizes. The most easily measured flux of carbon is reflected in changes of annual atmospheric CO_2 concentration. The interannual dynamics of atmospheric CO_2 concentrations have been monitored carefully since 1957 (Keeling, 1958), and longer term changes can be inferred from gases trapped in ice-core bubbles since before A.D. 1700 (Moore and Braswell, 1994). Fossil fuel emissions are also known fairly accurately and currently add 5.5 Pg C $year^{-1}$ of CO_2 to the atmosphere. The

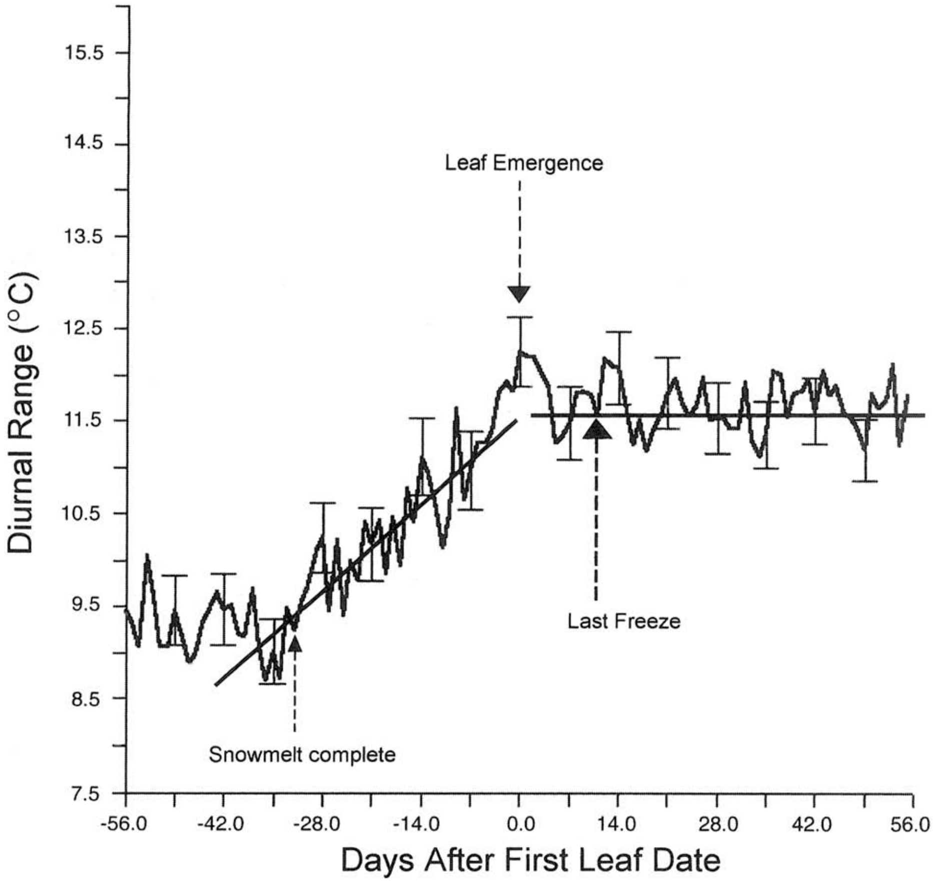


FIGURE 9.6. Average daily surface temperature amplitude (maximum – minimum), measured before and after spring leaf emergence of local vegetation, for 12 sites across the north-central United States. The rapidly warming spring temperatures generate progressively larger temperature amplitudes during the 2–3 weeks prior to leafing out, which are, however, interrupted by leaf emergence as the partitioning of incoming solar energy is shifted from sensible to latent heat in response to transpiring foliage. This is one of the most obvious illustrations of how forests directly influence climate (Schwartz and Karl, 1990). (From Schwartz, 1996.)

oceans are thought to absorb 2.0 Pg C year^{-1} of CO_2 from the atmosphere, and from the annual increase in atmospheric CO_2 we can compute an increase of 3.2 Pg C year^{-1} in the atmospheric carbon pool size (Schimel, 1995). The remainder, the terrestrial net CO_2 flux, amounts to only 0.3 Pg year^{-1} of carbon uptake from the atmosphere, a very small sink.

Determining the role of forests in the global carbon cycle is even more difficult. Studies estimate that forest ecosystems contain about 80% of all global aboveground carbon. The amount of carbon sequestered in forest biomass is not well established. Estimates range from 380 Pg in biomass, with 770 Pg in forest soils (Dixon *et al.*, 1994), to 458 Pg in biomass and 1200 Pg in the soil (Hunt *et al.*, 1996).

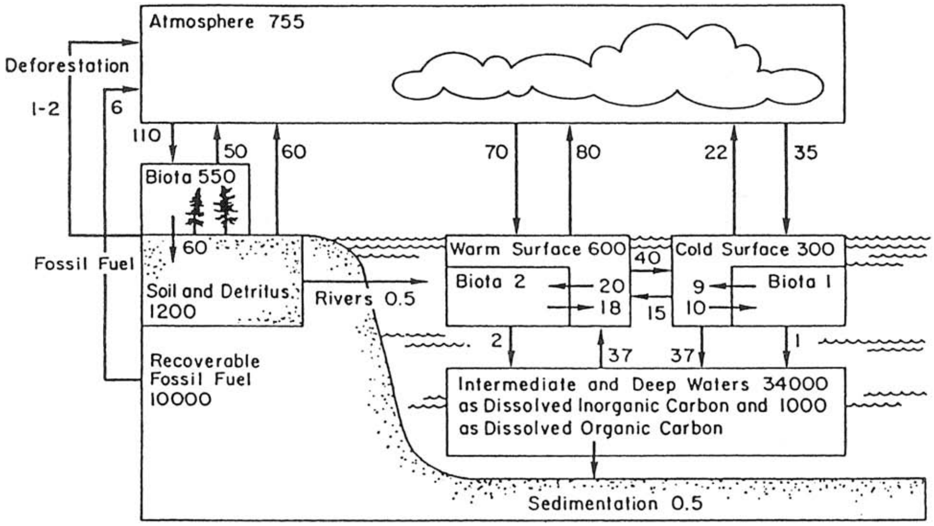


FIGURE 9.7. The global carbon cycle in units of petagrams (1 Pg = 10^{15} g). The annual fluxes of carbon, primarily as CO_2, are a very small percentage of the total carbon in each compartment. (From Moore and Braswell, *Global Biogeochemical Cycles* **8,** 23–28, 1994, copyright by the American Geophysical Union.)

B. Source/Sink Dynamics of the Global Carbon Cycle

An additional complication arises in that some forested regions such as the tropics are thought to be net sources of CO_2, while others, notably temperate forests, are thought to be net sinks (Grace *et al.*, 1995). Field *et al.* (1992) suggested three possible ecosystem mechanisms that could account for net accumulation of carbon in the terrestrial biosphere (Fig. 9.8). Dixon *et al.* (1994) estimated from ground-survey data that mid- and high latitude forests sequestered a net of 0.7 Pg of carbon annually, while deforestation in tropical forests transferred a net of 1.6 Pg of carbon to the atmosphere. Carbon isotope analyses of atmospheres over oceanic and terrestrial stations by Tans *et al.* (1990) projected that temperate, northern hemisphere forests were important sinks, absorbing more carbon in photosynthesis than they release through respiration. In contrast, the isotope analyses support the contention that tropical forests are net contributors of CO_2 to the atmosphere. One interpretation of these data is that temperate forests are regrowing after extensive harvesting in earlier decades, while tropical forests are now being harvested at accelerating rates. Ciais *et al.* (1995) used $^{13}C/^{12}C$ ratios in atmospheric samples from 43 globally distributed sites to estimate that half of the CO_2 produced annually by fossil fuel combustion is currently absorbed by northern temperate forests (3.5 Pg). These isotopic analyses, however, give only approximations of carbon cycling rates at the global scale. Some of the uncertainty in the global carbon budget estimates is reflected in the differences obtained from isotopic studies and the values presented in Fig. 9.7.

Studying subtle details of the seasonal changes in atmospheric CO_2 from stations around the world allows a more refined measure of the balance between terrestrial photosynthesis and respiration. Natural variability in global climate can change the annual terrestrial

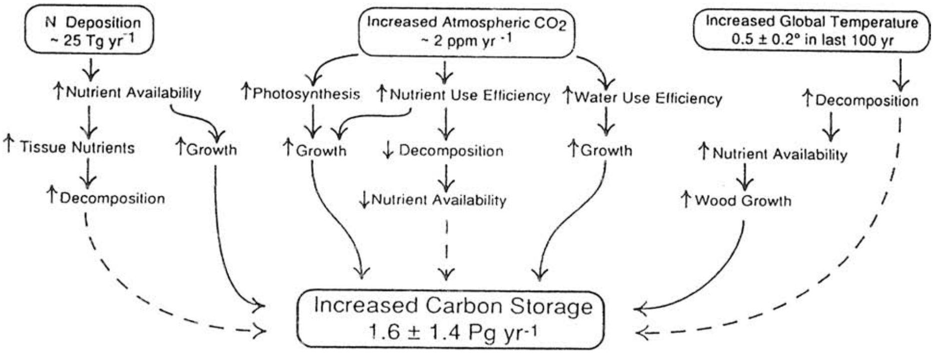


FIGURE 9.8. Schematic of three ecosystem mechanisms that may produce a terrestrial biospheric carbon sink. Solid arrows depict processes that increase carbon storage, and dashed arrows indicate the reverse. Increased atmospheric CO_2, air temperatures, and nitrogen deposition all have the potential to increase terrestrial carbon storage. The extent of these interactive responses varies with climate and biome type. (From Field *et al.*, 1992. With permission, from the *Annual Review of Ecology and Systematics*, Volume 23, © 1992, by Annual Reviews Inc.)

biospheric exchange by 10 Pg as documented by the atmospheric CO_2 monitoring network (Fig. 9.9; Keeling *et al.*, 1995). For example, periodic disruptions of the global climate, such as the eruption of Mt. Pinatubo in 1991, increased stratospheric aerosols and lowered the global average air temperature slightly for the following 2–3 years. The biosphere quickly responded to this rapid climatic variation as evidenced by a reduced rate in the expected annual increase in atmospheric CO_2. Scientists hypothesize that the slightly lower temperatures generally enhanced photosynthesis in water-limited regions and reduced autotrophic and heterotrophic respiration (Keeling *et al.*, 1995, 1996). The seasonal variation in atmospheric CO_2 concentrations at higher latitudes provides a regional scale impression of the seasonal shift in photosynthetic activity (Fig. 9.10; Hunt *et al.*, 1996).

C. Global Net Primary Production and the Contribution of Forests

The first geographically explicit estimates of global net primary production were based on correlations established between field measurements of NPP and simple climatic indices, because daily surface meteorology was the first accessible global database available to ecologists. Leith (1975) correlated NPP against an estimate of evapotranspiration derived from temperature and precipitation data. However, NPP is controlled by more than evapotranspiration, and climatic indices do not well represent existing biome distributions or actual vegetation cover. Biospheric process models now define the distribution of global biomes, represent biome-specific physiological processes, and incorporate global climate databases to produce considerably improved estimates of global NPP. Melillo *et al.* (1993) produced the first estimates of global NPP derived with an ecosystem model of 53.2 Pg C, 75% coming from forested areas. These global models represent ecosystem processes similarly to the regional simulations presented in Chapter 8 with the RHESSys modeling package. The underlying consistency in logic from regional to global scales provides some confidence that validations confirmed at a smaller scale support extrapolations at the next larger scale.

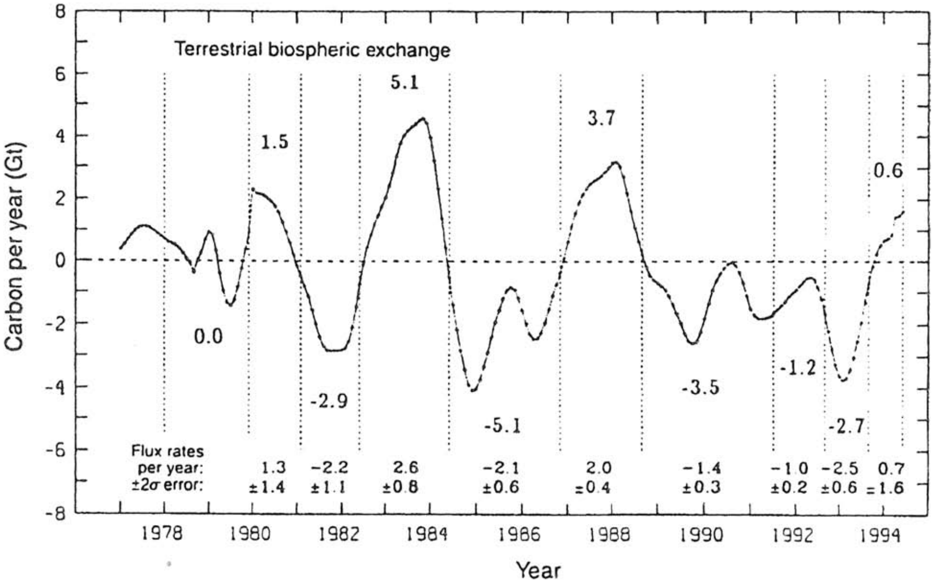


FIGURE 9.9. Interannual variability in terrestrial biospheric net CO_2 exchange, in gigatons (1 Gt = 1 Pg = 10^{15} g). Vertical lines separate periods of persistent positive (CO_2 loss) or negative (CO_2 uptake) fluxes that correspond to warm and cold phase of El Niño events. Annual flux rates are shown with standard errors. In arid areas, cooler temperatures are thought to alleviate water stress, favor photosynthesis, and reduce decomposition rates, leading to a net gain in ecosystem carbon uptake. (From Keeling *et al.*, 1995. Reprinted with permission from *Nature.* Copyright 1995 Macmillan Magazines Limited.)

These biospheric models represent the global land surface rather coarsely, at best currently with about sixty thousand 50 × 50 km cells. The basic principles summarized in Chapters 2–4 for water, carbon, and nutrient cycling are incorporated in these global models, although in less detail than in the stand models described in Chapter 5. As was true with regional modeling, biospheric models are limited mainly by a lack of global data necessary to provide the critical initializing variables. Variables that can be remotely sensed, such as LAI, can be incorporated into a global database with some confidence of the error in estimates involved (see Plate 17). Other variables, such as soil depth, however, cannot be directly estimated and must be inferred from geomorphic relationships. In spite of the obvious limitations, these global simulation models allow scientists to obtain the first estimates of the magnitude and spatial distribution of belowground processes such as decomposition and nitrogen mineralization (see Plate 18). As a result of the coarse spatial resolution, however, the primary value of these model predictions remains at the global scale for studies of biogeochemistry, climate forecasting, and broad policy analyses of natural resources.

For more practical applications, satellite-driven models can now be executed at a 1 km^2 scale resolution if desired over the entire land surface (150,000,000 km^2). Global NPP, for example, can be computed with Light Use Efficiency (LUE) models similar in structure to that presented for stand-level analyses in Table 3.5. Sellers (1985, 1987) demonstrated the nearly linear relation between FPAR and satellite-derived NDVI values. By combining

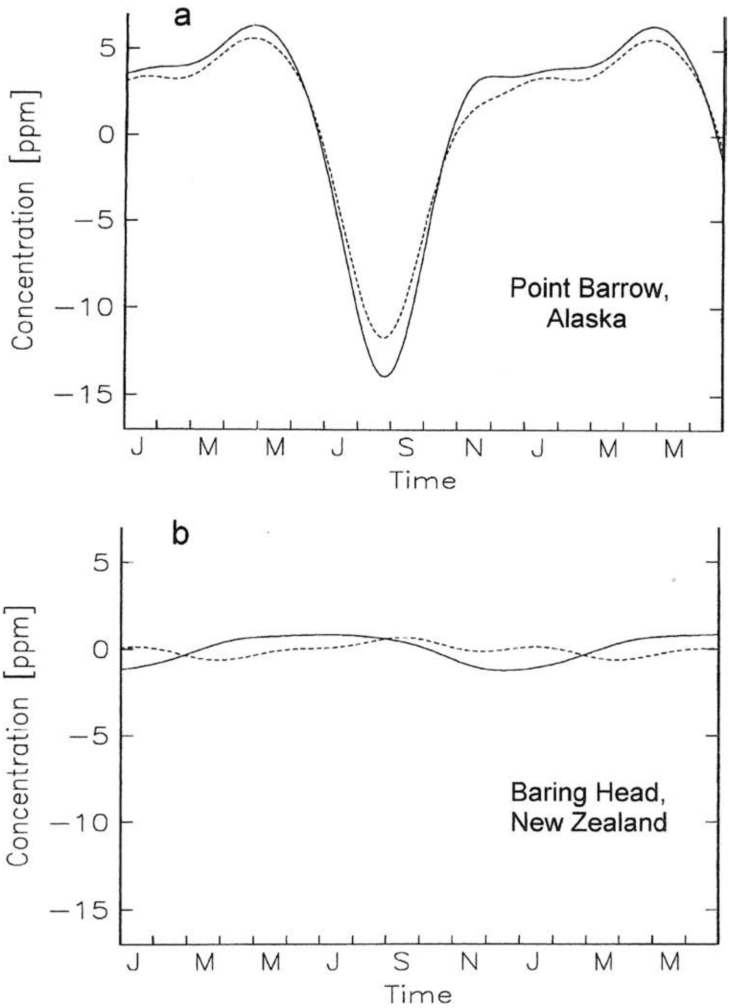


FIGURE 9.10. Seasonal variability of atmospheric CO_2 concentration that contrasts a boreal location with large seasonal differences in photosynthesis with a more maritime, low latitude site with less seasonal variation in the rates of processes affecting the carbon balance. BIOME-BGC simulations of daily terrestrial net CO_2 flux were entered into an atmospheric transport model to predict atmospheric concentrations, which were compared against measurements from the global sampling network of C. D. Keeling (Law *et al.*, 1996; Piper and Stewart, 1996). The difference in seasonal amplitude of [CO_2], 20 ppm at Point Barrow, Alaska, but only 2 ppm at Baring Head, New Zealand, reflects differences in the magnitude of winter–summer ecosystem processes, which are extreme at high latitudes. Photosynthetic activity draws [CO_2] down in the midsummer at the height of the growing season, but respiration and decomposition produce a net release of CO_2 during the leafless winter season. (From Hunt *et al., Global Biogeochemical Cycles* **10,** 431–456, 1996, copyright by the American Geophysical Union.)

estimates of monthly incoming PAR with FPAR, the upper limits to photosynthesis were established throughout the year. On the basis of climatic restrictions in life forms, a conversion efficiency specific to each biome has been applied to convert APAR to NPP (see Plate 19; Ruimy *et al.*, 1994; Field *et al.*, 1995; Prince and Goward, 1995). Because light conversion efficiency changes with climate and with the relative age and structure of forests, as discussed in Chapter 3, appropriate light use conversion factors (ε) for global scale extrapolations are generally attained from more detailed stand/seasonal level simulation models and then incorporated into global scale biospheric projections (Plate 20).

Validating any global estimate of ecosystem behavior is improbable, but wide scale sampling within regions of some variables such as aboveground forest growth shows good agreement with model predictions derived from satellite and weather station data (Coops *et al.*, 1998). These satellite-based estimates of NPP, however, are seriously limited by continuous cloud cover in some tropical areas, and by the effects of low sun angles on remote sensing at higher latitudes (Prince and Goward, 1995). Still, a quantitative assessment of regional and interannual variability of terrestrial productivity is possible within regions with particularly strong seasonal dynamics (Myneni *et al.*, 1995). Myneni *et al.* (1997b) showed from a record of AVHRR NDVI data for 1979–1990 that the growing season of boreal forests in Canada has increased by 12 days, an estimate consistent with the atmospheric CO_2 record from Keeling *et al.* (1996) for that region. As yet, unfortunately, no other important ecosystem processes have theoretical logic similar to the LUE–NPP relationship, allowing global extrapolation.

D. Other Trace Gas Emissions from Forests

In addition to CO_2, forests exchange other chemical compounds with the atmosphere that contribute to the global carbon cycle, primarily methane and a group of non-methane hydrocarbons such as isoprenes and terpenes. The atmospheric concentration of methane is only 1.7 ppm; however, it is increasing at 1% per year, and each CH_4 molecule is 20 times more active than CO_2 as a greenhouse gas. Fung *el al.* (1991) found intact forests to be a minor contributor to global methane sources compared to wetlands and rice fields. However, biomass burning may contribute 10% to the global atmospheric methane budget. Isoprenes and terpenes are chemicals trees emit when under stress, predominantly during the daytime in conjunction with photosynthesis, as discussed in Chapter 6. These chemicals are rapidly oxidized to carbon monoxide, so are never at high concentrations in the troposphere (Muller and Brasseur, 1995). Some regions, such as the Great Smoky Mountains of the eastern United States and the Amazon tropical forests, are high isoprene/terpene sources (Muller, 1992). Guenther *et al.* (1995) estimated that tropical woodlands at present contribute 50% of global natural nonmethane hydrocarbon emissions. Nonmethane hydrocarbons are thought to contribute 10% of the global CO production annually, although uncertainty in global estimates is large (Muller, 1992).

Forests produce only minor amounts of other atmospherically important gases. Gaseous sulfur in various forms is primarily produced by human industrial pollution, oceanic aerosols, and volcanic emissions. The biotic sources are mostly derived from microbial activity in anaerobic wetlands and from the release of gases during biomass burning, which together may contribute 20% of the annual global atmospheric loading (Schlesinger, 1991, 1997). Nitrous oxide is a trace constituent of only 0.3 ppm atmospheric concentration. However, each N_2O molecule has 200 times the greenhouse effect of a CO_2 molecule in the atmosphere, and because N_2O is increasing 0.3% per year, it may exert a climate warming potential similar to CO_2. As with methane, nitrous oxides are emitted during forest fires (Schlesinger, 1991, 1997; Muller and Brasseur, 1995).

V. FORESTS AND BIODIVERSITY

A. Measures of Biodiversity

The loss of global biodiversity is one of the ecological themes most commonly discussed in the popular press. The finality and irreversibility of a species becoming extinct are discomforting to any biologist. While on a conceptual level most people agree that biodiversity is generally desirable, building a firm quantitative basis for analysis of biodiversity has proved illusive. Various definitions of biodiversity have evolved and now include genetic, species, and ecosystem measures (WCMC, 1992). *Genetic diversity* represents the variability within a species of biochemical attributes, many of which are not externally expressed. Genetic diversity may explain why some tree species have much broader geographic ranges than others, or superior disease resistance.

Species diversity is the most common level of analysis because simple field observations are the only required data source. *Alpha species diversity*, or species richness, is a simple count of the number of species identified in a unit area. The highest published alpha species diversity was found in Amazonian Ecuador, where a single hectare of forest supported 473 tree species (Valencia *et al.*, 1994). The plot-to-plot difference in species count in a local area is defined by the *beta diversity*. Endemism is a term used to describe a species that is restricted to a limited geographic area or ecological habitat. Finally, *gamma species diversity* quantifies variation in the species list found across the landscape, so is a reflection of landscape and microclimate variability as well as evolutionary limitations. For example, the entire 420 million ha northern hemisphere temperate forests contain only 1166 tree species, illustrating rather low gamma diversity (Latham and Ricklefs, 1993).

Ecosystem biodiversity represents changes in the temporal, structural, and functional activity of forests. *Temporal biodiversity* is primarily the species dynamics observed in forest development and replacement over time, and it has a long history of study (Chapter 5). *Structural diversity* is an analysis of the spatial heterogeneity of age, height, and density of forest stands across a landscape. Bird habitat studies illustrated in Chapter 8 evaluated landscape structural patterns and arrangement.

B. Functional Attributes Related to Biodiversity

Functional biodiversity evaluates the role of each species in ecosystem biogeochemical cycles, as well as the redundancy present in the system to assure “normal” rates of carbon and nutrient cycling. In regard to biogeochemical cycles covered in Chapters 2–4, the loss of any one species probably has little effect on the basic carbon cycle of a forest, because another species rapidly fills the void in space and resource utilization (Shaver *et al.*, 1997). In this sense, the basic biogeochemical cycles are conservative properties of ecosystems that proceed in a fairly predictable way with a wide variety of species mixtures. In fact this simplifying assumption is essential in calculating global carbon cycle processes independently of species compositions (Plates 17 and 18). Indeed, critical physiological attributes such as maximum leaf conductance show very little interspecies variability. Kelliher *et al.* (1995) and Körner (1994) found high consistency in reported maximum leaf conductances for a wide variety of global forest types (Table 9.3). However, other ecosystem functions may be much more species sensitive. A critical life cycle activity such as pollination could be disrupted if an insect host were lost from the ecosystem. Susceptibility of trees to insect/disease attack is clearly species specific. These species-specific factors may determine which individuals are present to perform the conservative bigeochemical processes in the forest.

It is not completely clear what biophysical and ecosystem attributes provide optimum opportunities for biodiversity. Suggestions include high topographic and microclimate diversity, high vegetation structural diversity, high primary productivity, and low disturbance frequency (Johnson *et al.*, 1996). Various hypotheses have been advanced to relate species richness to ecosystem stability. Tilman (1996) in an 11-year study of grasslands in Minnesota measured year-to-year variability in total biomass of grasses and found that it was lower in plots with higher species richness. High numbers of species present in a single plot led to increased competition and eventual exclusion of some species. Tilman concluded that the underlying processes controlling biomass production were conservative, and that the dominance of individual species can fluctuate greatly without affecting the overall accumulation of biomass.

At global scales, species richness appears to be related to general rates of biogeochemical activity in association with climatic factors (Fig. 9.11). Ecosystems with favorable climates throughout the year, such as tropical wet forests, support greater numbers of species than seasonally unfavorable boreal or desert environments. At a continental scale, Adams and Woodward (1989) found a high correlation between annual NPP and species

TABLE 9.3
Global Average Maximum Leaf Conductance (g_{smax}) and Maximum Canopy Conductance (G_{smax}) to H_2O[a]

Superclass	Vegetation type	g_{smax} (mm s^{-1})	G_{smax} (mm s^{-1})
Natural herbaceous	Temperate grassland	8.0 ± 4.0	17.0 ± 4.7
Woody	Conifer forest	5.7 ± 2.4	21.2 ± 7.1
Woody	Eucalypt forest	5.3 ± 3.0	17.0
Woody	Temperate deciduous forest	4.6 ± 1.7	20.7 ± 6.5
Woody	Tropical rain forest	6.1 ± 3.2	13.0
Agricultural crop	Cereals	11.0	32.5 ± 10.9
Agricultural crop	Broad-leaved herbaceous crops	12.2	30.8 ± 10.2

[a] This summary suggests that canopy gas exchange processes, and more generally biogeochemical cycling, are conservative properties of an ecosystem with limited species differentiation. After *Agricultural and Forest Meteorology*, Volume 73, F. M. Kelliher, R. Leuning, M. R. Raupach, and E. D. Schulze, "Maximum conductances for evaporation from global vegetation types," pp. 1–16, 1995, with kind permission of Elsevier Science–NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

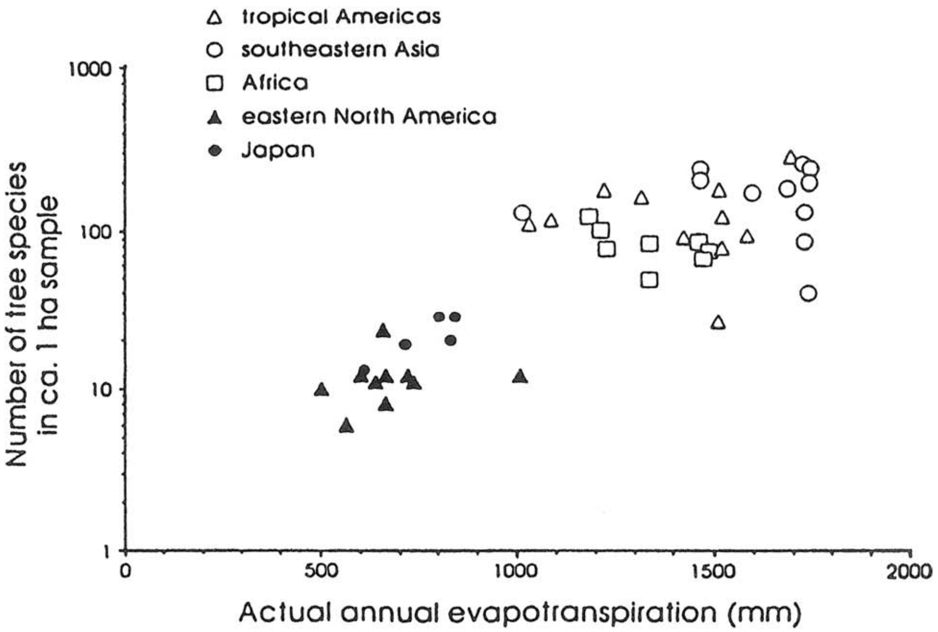


FIGURE 9.11. Relationship of tree species diversity in a globally distributed set of small forest plots and actual ET. A general trend is for warmer, wetter climates to support more species. (From Latham and Ricklefs, 1993. © 1993 *Oikos*.)

richness of northern hemisphere forests (Fig. 9.12). This suggests that NPP as we have presented at local (Plate 8), regional (Plate 10), and global (Plate 18) scales may provide a general index of biodiversity. Climate maps, as presented in Chapter 7 (see Plate 3), may also be useful for assessing biodiversity. Analysis of climate variability may be more valuable than the analysis of long-term mean conditions. The environment today, of course, may not reflect earlier conditions, so historical environmental and floristic (and zoological) analyses are warranted in areas where species richness differs significantly from general model predictions.

At present, climatic and NPP maps obtained from satellite-derived data offer a first approximation of spatial variation in biodiversity at the global scale. Estimates of future changes in biodiversity over large areas may be made by relating species richness to more observable biophysical characteristics, and by quantifying land cover changes over time. Tuomisto *et al.* (1995) used Landsat TM imagery to extrapolate their estimates of biodiversity of the 500,000-km^2 Peruvian lowland of Amazonia. Satellite imagery played an important initial role by providing an assessment of landscape-level heterogeneity for the establishment of field transects. Sisk *et al.* (1994) located areas with threatened loss of biodiversity by assessing the rates of land cover change in a region with large-scale AVHRR data sets. The satellite-based analysis indicated that 18.1 million km^2 of native vegetation has been converted since the mid-1980s to agriculture, the land cover type assumed to have the lowest species diversity. Our estimate from Fig. 9.3 of 17.5 million

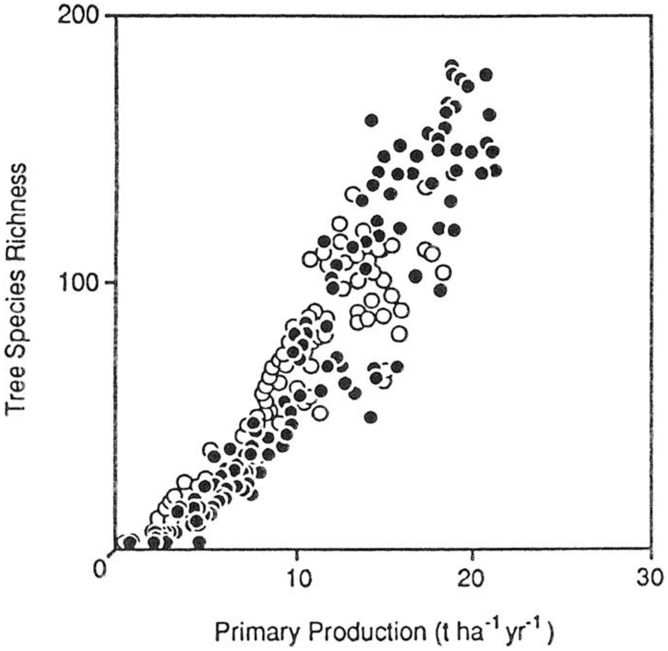


FIGURE 9.12. Relationship between tree species richness in European and North American forests and NPP. Figures 9.11 and 9.12 suggest that more productive sites exhibit higher species diversity. Harsher boreal and temperate or arid regions (○) support lower species richness than do tropical rain forests (●). (From Adams and Woodward, 1989. Reprinted with permission from *Nature*. Copyright 1989 Macmillan Magazines Limited.)

km^2 of forestland converted to cropland illustrates the improvement in precision that satellite-based estimates have brought to the land cover calculations that underlie the assessment of global biodiversity.

Related to biodiversity are questions of how forest ecosystems can be maintained through time. What are the critical components and functional activities of a forest ecosystem? As we know, maintaining a certain species composition is much more difficult than maintaining the rates of many conservative processes. Sustaining basic productivity of a forest is probably the easiest task, as many species can fulfill this role, although they will have different commercial value. Exotic species often show higher primary productivity than natives, which is the reason why many of the *Eucalyptus* forests of Australia and *Nothofagus* forests of New Zealand have been replaced with radiata pine (Benson *et al.*, 1992). In some cases, the introduced species have adaptations the native flora lack, and they may also be immune, at least temporarily, to local pathogens and insects. The reduction in native vegetation, of course, has a major impact on the dependent animal populations. Also, if some elements in the flora provided special adaptations to accessing water, fixing nitrogen, or withstanding fire, wind, floods, or other disturbances, their loss may not be immediately appreciated but will have long-term implications.

VI. SUSTAINABILITY OF GLOBAL FORESTS

A. Sustainability and Future Global Wood Supply

It is informative to compare the global forest carbon balance as computed by ecologists and economists. Melillo *et al.* (1993) computed an annual global NPP for all biomes of 53.2 Pg of carbon, an estimate constrained by the atmospheric CO_2 data (Ciais *el al.*, 1995). Of this 53.2 Pg, Melillo *et al.* calculate that 75% is associated with forested land; however, this estimate assumed potential, not existing vegetation. The satellite-based analysis of Nemani and Running (1996) showed that 29% of all global forestland has already been converted to other uses (Fig. 9.3). Reducing simulated NPP of forests (53.2×0.75) by the 29% of land cover lost provides an estimate of total forest NPP of 28.3 Pg year^{-1}. If we next convert total NPP (which includes roots and leaves) to usable fiber, based on the carbon allocation logic described in Chapter 3, we consider that as much as 70% of the total NPP could be allocated to roots, branches, and foliage. As a result of these assumptions, we arrive at a global estimate of stem wood production of 8.5 Pg C year^{-1}.

Let us compare this theoretical estimate of wood production derived from a biospheric model with the production data reported by economists. Mather (1990) estimated the total forested area to be 4100×10^6 ha worldwide, although he cites other published estimates ranging from 2800×10^6 to 6050×10^6 ha (recall that the satellite estimate in Fig. 9.3 is 5260×10^6 ha). Mather (1990) reported global wood production of 3.2×10^9 m^3 year^{-1} for 1986. Sharma *et al*. (1992) reported that combined fuelwood and industrial wood production was 4.3×10^9 m^3 year^{-1} harvested from growing stock with a standing live timber volume of 340×10^9 m^3. Using an average specific gravity for wood of 500 kg m^{-3}, and assuming that biomass is 50% carbon, gives global wood production of 1.1 Pg C year^{-1}, comparable to the estimates given by Vitousek *et al*. (1986) and Dixon *et al*. (1994). Sharma *et al.* (1992) forecasts future wood fiber demand of 1.8 Pg C year^{-1} by the year 2025.

It appears from this simple analysis that current global wood consumption is <15% of annual forest stem wood production and that opportunities could exist for a considerable increase in the rate of harvesting. This conclusion, however, ignores some important facts. First, Houghton (1994) estimated that tropical forests are being harvested at a rate of more than 3% year^{-1}. If this land is not soon returned to forest production, within less than a century the growing global demand for wood will certainly exceed the shrinking land base for production. Second, much of the world’s forests is inaccessible and/or serves other critical functions, including protection of watersheds, recreation, and cultural values. Third, even with present rates of wood production, regional shortages have developed that require imports or substitutions of other products. Viewed with these constraints, there is ample reason to support efforts to reduce the rate of forest conversion to other uses, to return degraded lands to production, and to support intensive management of plantations in some regions to offset pressures on native forestlands. As recognized by Vitousek *et al*. (1986), maintaining the production of forests will be a major challenge as population levels and standards of living continue to rise, and the demand for forest products with competition for food and living space further limit our options. For better, or for worse, the extent that future generations succeed in balancing demand for resources with the capacity of the landscape to maintain its functional integrity will be documented in changes in the distribution of forests and estimates of their performance derived from global satellite observations.

B. Forests Planting for Climate Stabilization and Fuel Replacement

It has been suggested that much of the potential for global climate warming could be averted by planting millions of hectares of new forests to sequester more of the 5.5 Pg of C annually transferred by combustion of fossil fuels into the atmosphere (Dixon *et al.*, 1994). Careful analysis of these optimistic scenarios points out two major problems. First, Sedjo (1989) estimated that to sequester just 1.8 Pg of atmospheric carbon annually in forest biomass would be equivalent to (1) planting over 400 million ha of fast growing plantations, which would cost at least $300 billion (US$), (2) increasing the annual production of current forests by about 70%, or (3) expanding the boreal forests northward to cover an additional 3 billion ha. The most productive areas, which provide a good investment, already support forests. Planting forests in marginal areas will not sequester much carbon nor provide as large of an economic return on the investment (Sedjo, 1992). Moreover, as we have discussed, current global trends show a net *loss* in forestland. Second, forests do not permanently sequester carbon, because as the forest is harvested, or dies naturally, the biomass is eventually decomposed or combusted and most of the carbon released back to the atmosphere (Harmon *et al.*, 1990). Although we support the establishment of forests for a myriad of benefits, it is unrealistic to view massive forest planting as a serious alternative to reducing the combustion of fossil fuels.

Wood fiber has also been suggested as an alternative to fossil fuels for energy production. Graham *et al*. (1992) estimated that, if short rotation woody crops were planted on 14 million ha of land in the United States and harvested for commercial electric power production, 10% of national electrical power needs could be supplied. The present cost of fossil fuels, however, makes this option uneconomical; crops with higher values can be grown on the most productive agricultural land, and marginal land cannot produce enough biomass to meet national needs. As costs of fossil fuels rise significantly, however, biomass farms may have a more significant role as a national energy supply, and wood will also be an important local fuel source in many regions.

VII. SUMMARY

According to satellite monitoring, forests currently cover about 53 million km^2 of Earth's surface. In comparison to the area to which they are climatically suited, tropical, temperate, and boreal forests have been reduced through human activities to about 26, 40, and 20%, respectively, of their potential distributions. The geographic distribution of forests has changed continuously over the last few million years. Future changes in forest distribution are difficult to predict without better projections of the rate at which forests are converted to other land uses and the extent to which projected changes in climate occur. Although the general influence of climate on forest distribution and productivity is well established, increasing evidence shows that, on regional scales, the presence of forests also alters the climate through modifications in the rates at which water and heat are exchanged from terrestrial surfaces. At higher latitudes, seasonal and interannual dynamics of atmospheric CO_2 mirror the net metabolic activities of forests in a very direct way. Forests are thought to account for about 28 Pg C year^{-1} of terrestrial NPP, of which we estimate 8.5 Pg year^{-1} is in the form of stem wood biomass. Current global wood consumption is approximately 1.1 Pg year^{-1}, implying that global forest production should be sustainable, although much is inaccessible to direct utilization. The most fundamental concern is the rate at which forestland continues to be converted to other uses. Planting additional land into forests may offset some atmospheric CO_2 increases and replace some fossil fuel uses, but it should not be considered a major alternative to reducing dependence on fossil fuels.

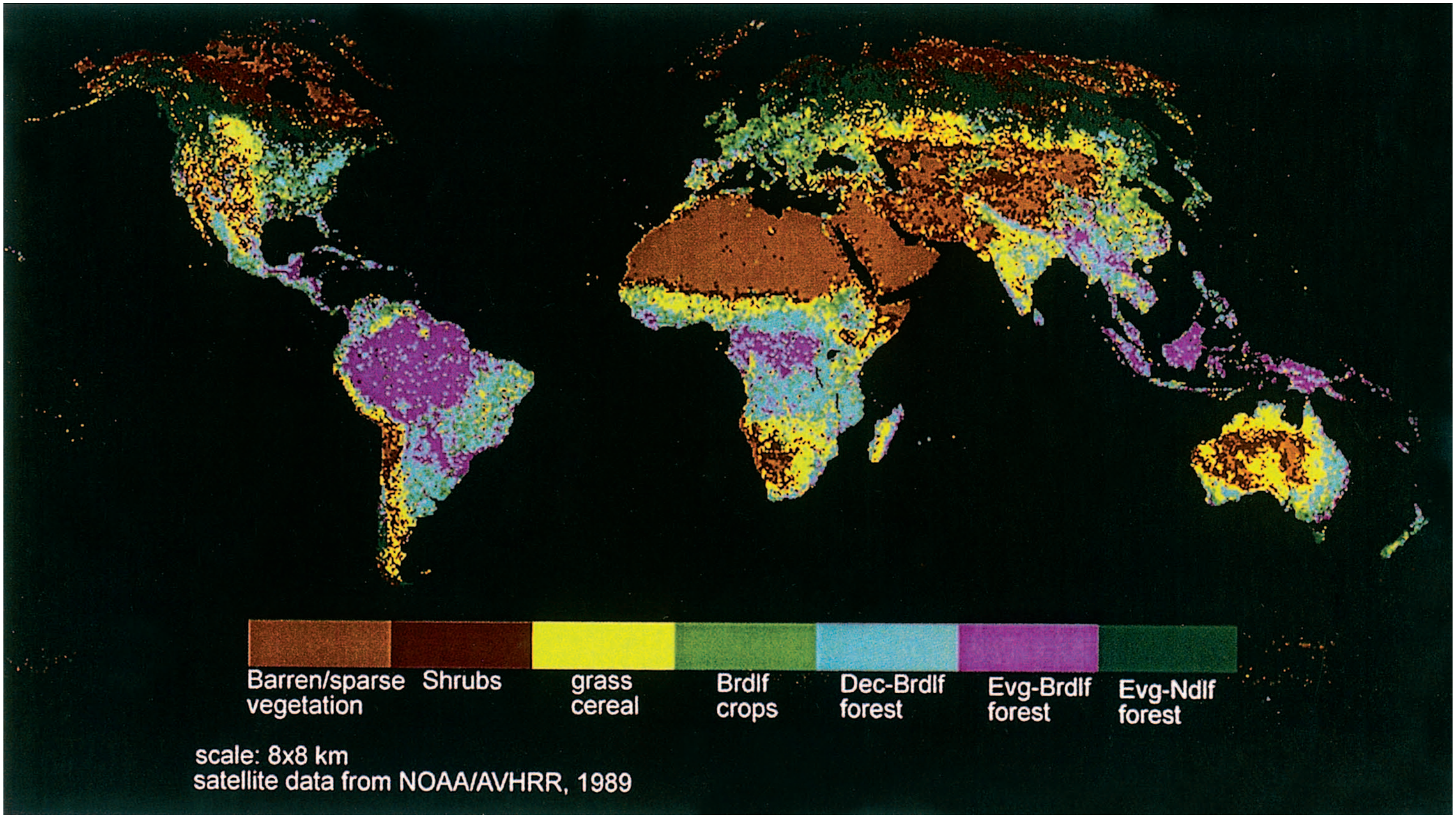


PLATE 12. From 8 × 8 km AVHRR satellite data acquired in 1989, a total of seven major land cover types could be recognized and mapped, which included shrubs, grass/cereal, broadleaf (Brdlf) crops, and three types of forests: deciduous broadleaf (Dec-Brdlf), evergreen broadleaf (evergreen broadleaf (Evg-Brdlf) and evergreen needleleaf (Evg-Ndlf). These types were distinguished with a combination of threshold limits and seasonal amplitude of NDVI, plus maximum temperature estimates acquired from the satellite throughout the year. (From Nemani and Running, 1995).

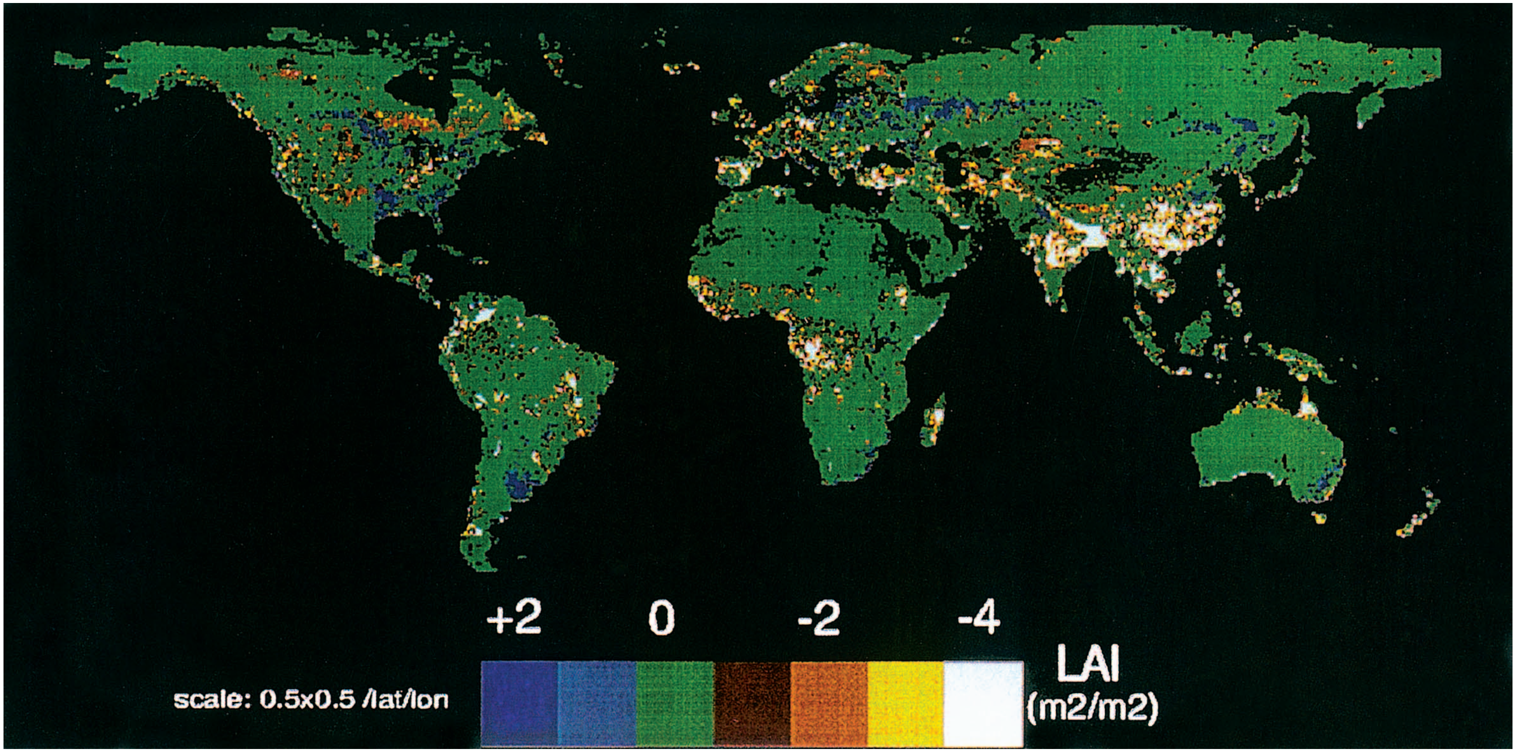


PLATE 13. Global land cover change analysis determined by comparing leaf area index from the satellite-derived existing land cover in Plate 12 with LAI from an ecosystem model that computes potential land cover from bioclimatic principles. (From Nemani *et al.*, 1996).

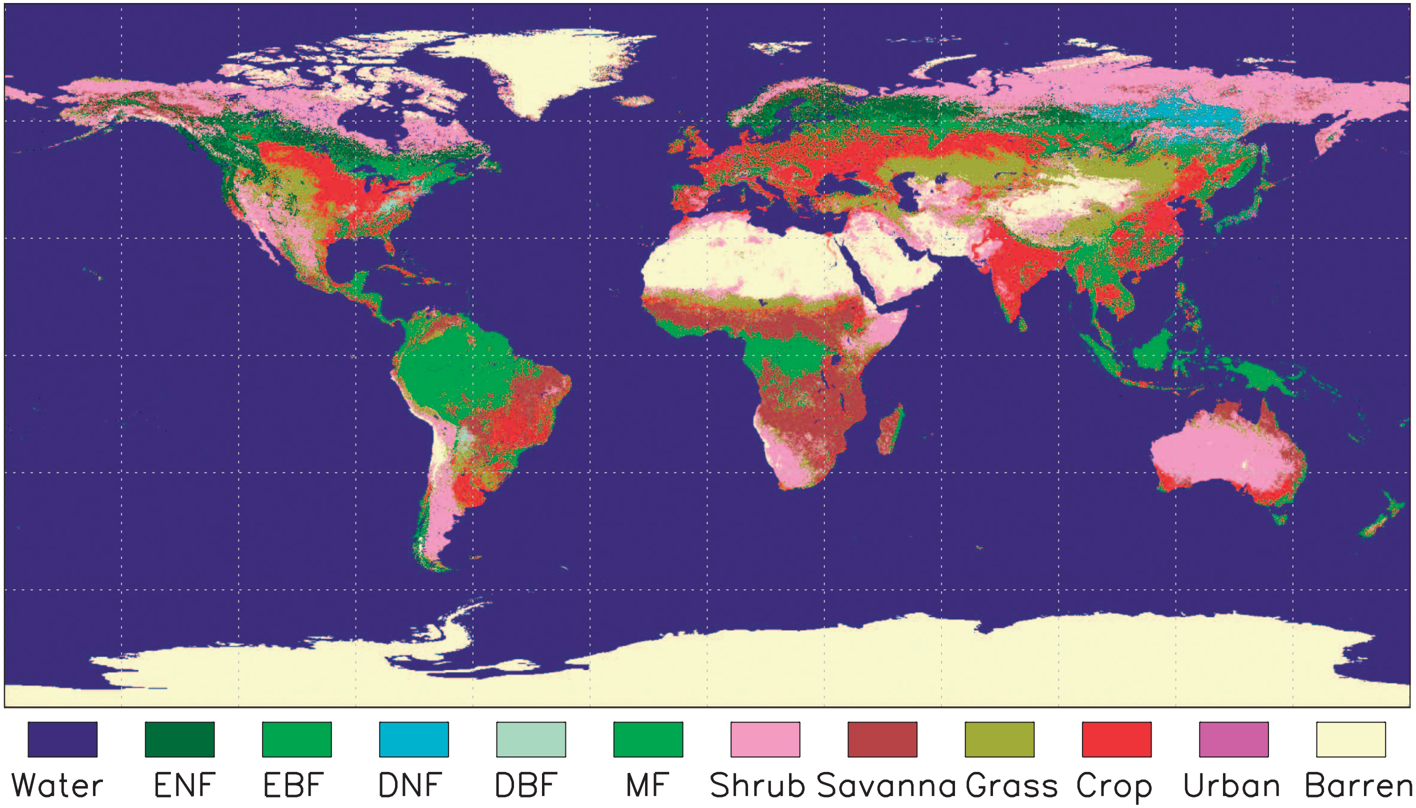
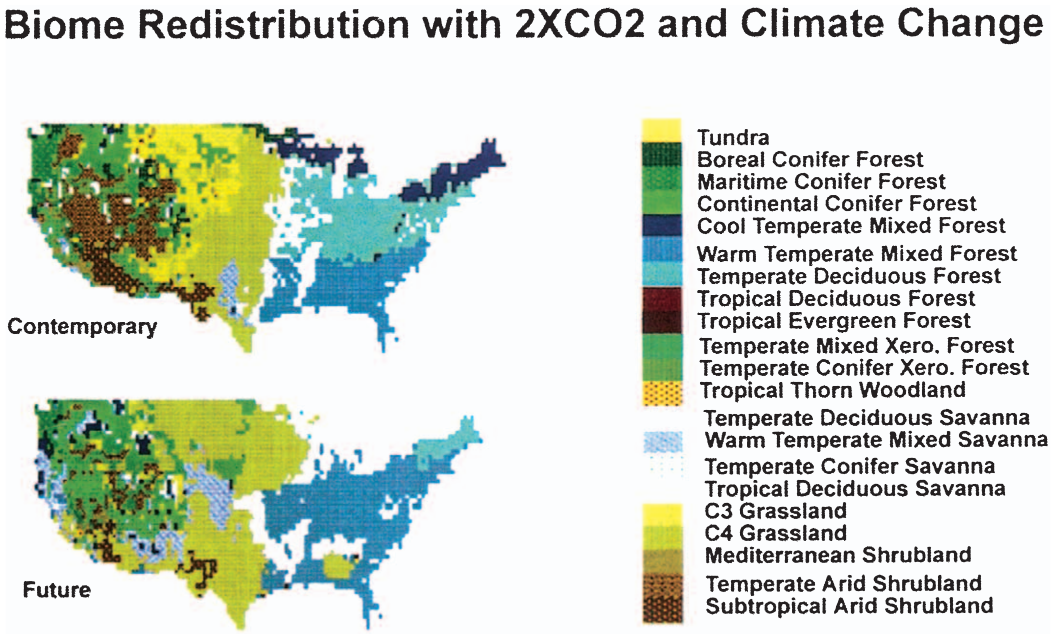


PLATE 14. From 1 × 1 km MODIS satellite data acquired since 2000, the number of definable cover types increased to twelve. Abbreviations: ENF (evergreen needle-leafed forest), EBF (evergreen broad-leafed forest), DNF (deciduous needle-leafed forest), DBF (deciduous broad-leafed forest), MF (Mixed forest). (Figure provided by Numerical Terradynamic Simulation Group, University of Montana).



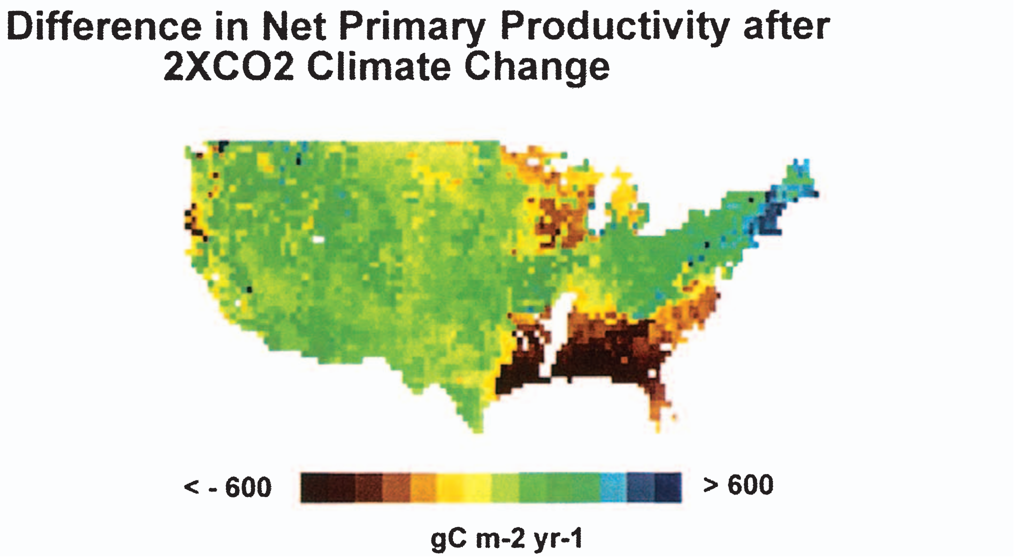


PLATE 15. The MAPSS biogeography model of Neilson (1995) evaluated the interactions of increased CO_2 on vegetation water use efficiency and projected climate warming scenarios on the future geographic distribution of forests in the United States. Biogeographic models incorporate various complex measures of temperature limits (Tables 9.1 and 9.2) and water balance controls to define the distribution of biomes. Climate warming scenarios tend to result in expanded grasslands in water-limited regions and expansion northward of boreal forests (VEMAP, 1995). The response of forest NPP to climatic warming is uneven. These BIOME-BGC simulations suggest that climatic warming could result in reduced NPP in tropical forests as a result of higher than normal respiration. However, NPP is projected to increase in semiarid forests associated with enhanced water use efficiency and in boreal forests as the growing season is lengthened and decomposition releases more nitrogen (VEMAP, 1995).

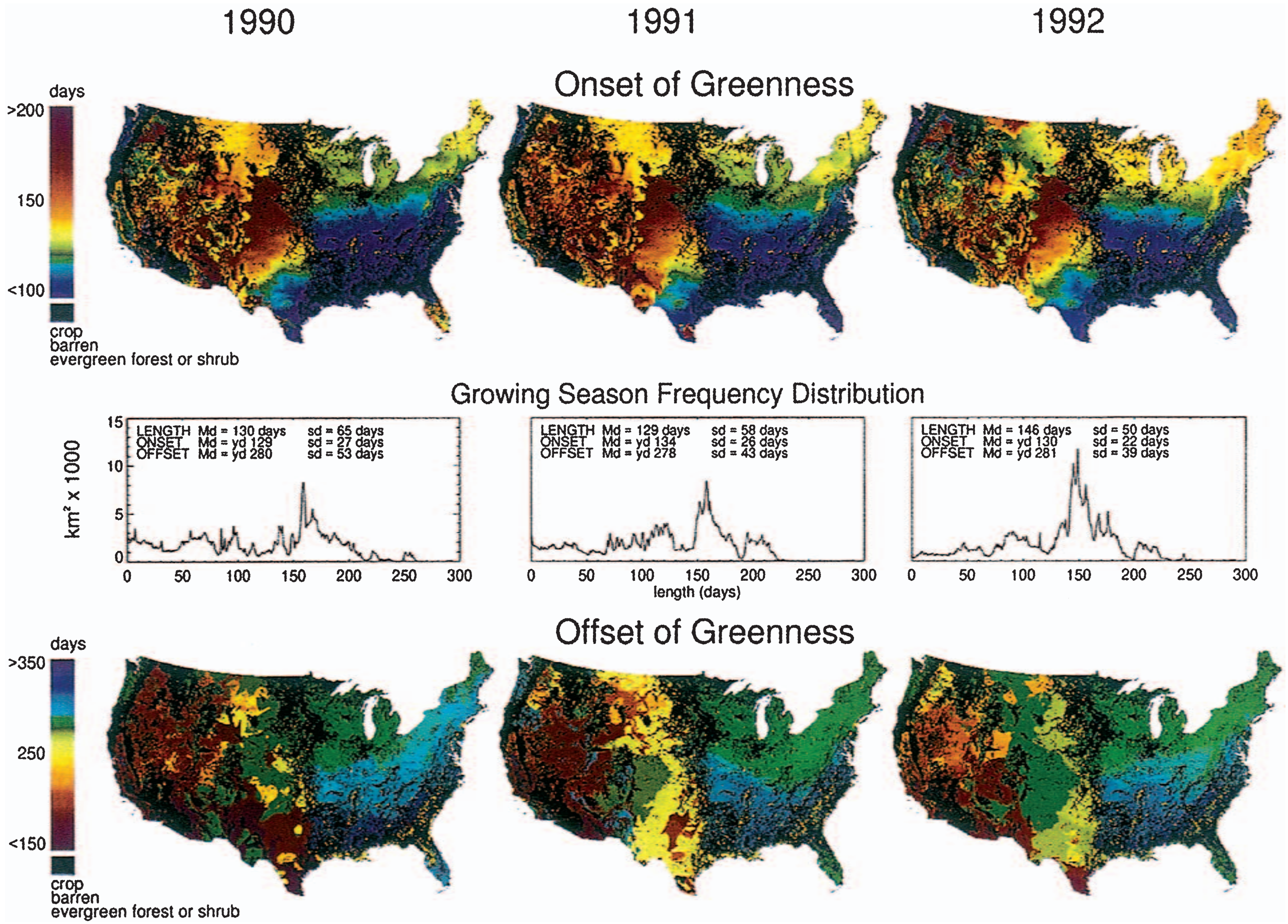


PLATE 16. Interannual variability of spring leaf emergence and autumn leaf senescence for natural deciduous forests and grasslands of the United States for 1990–1992. Traces in the boxes show the aggregate land area with the length of growing season indicated. This continental scale phenological analysis used a combination of daily AVHRR NDVI data and surface meteorological records of air temperature and precipitation. Consistent phenological monitoring provides an important means of quantifying the biospheric response to climate change. (From M. A. White *et al.*, *Global Biogeochemical Cycles* **11,** 217–234, 1998, copyright by the American Geophysical Union.)

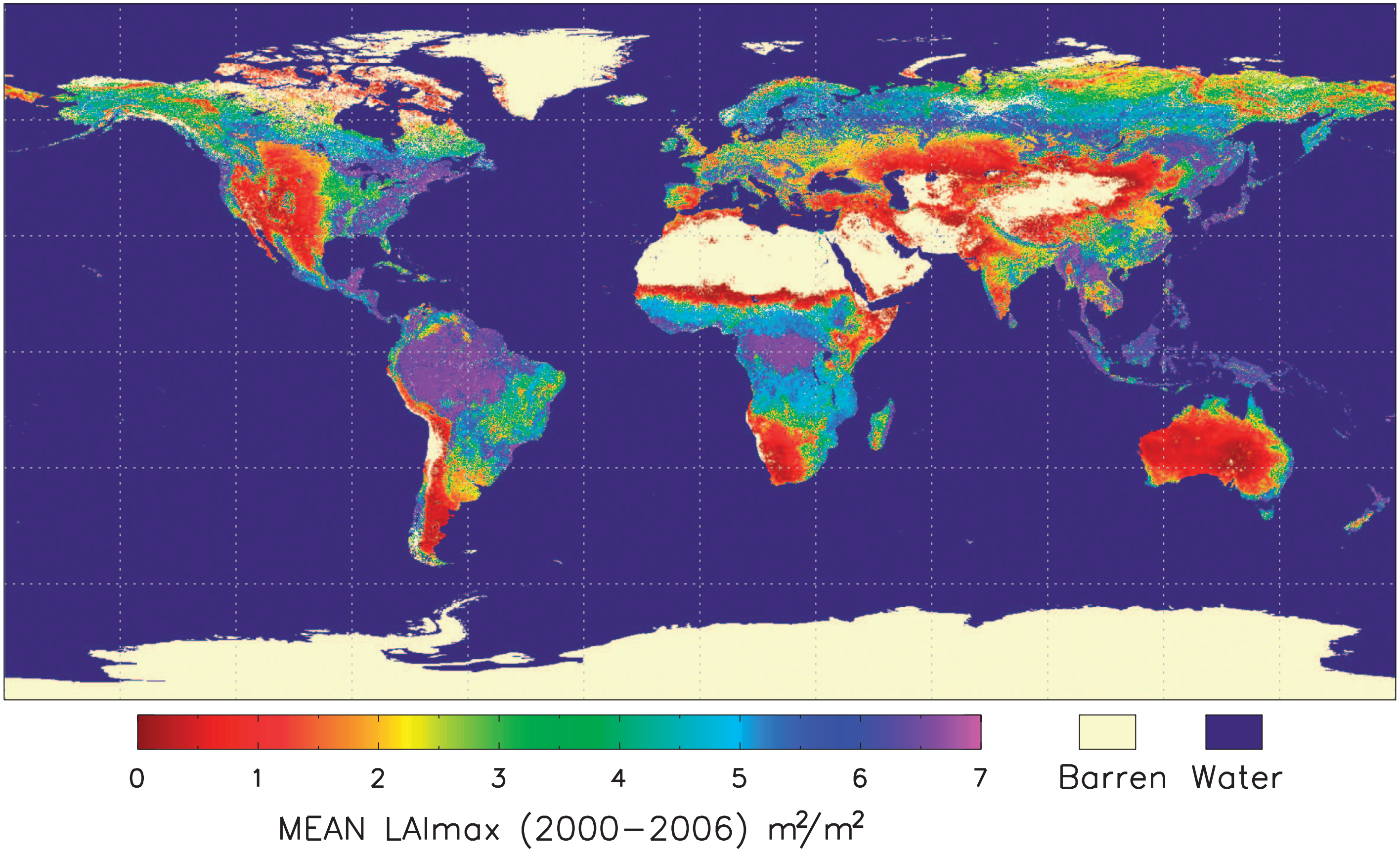


PLATE 17. The annual maximum leaf area index at 1 × 1 km spatial resolution from MODIS data averaged for 2000–2006, with improved spectral and radiometric resolution over the AVHRR sensor. (Figure provided by Numerical Terradynamic Simulation Group, University of Montana).

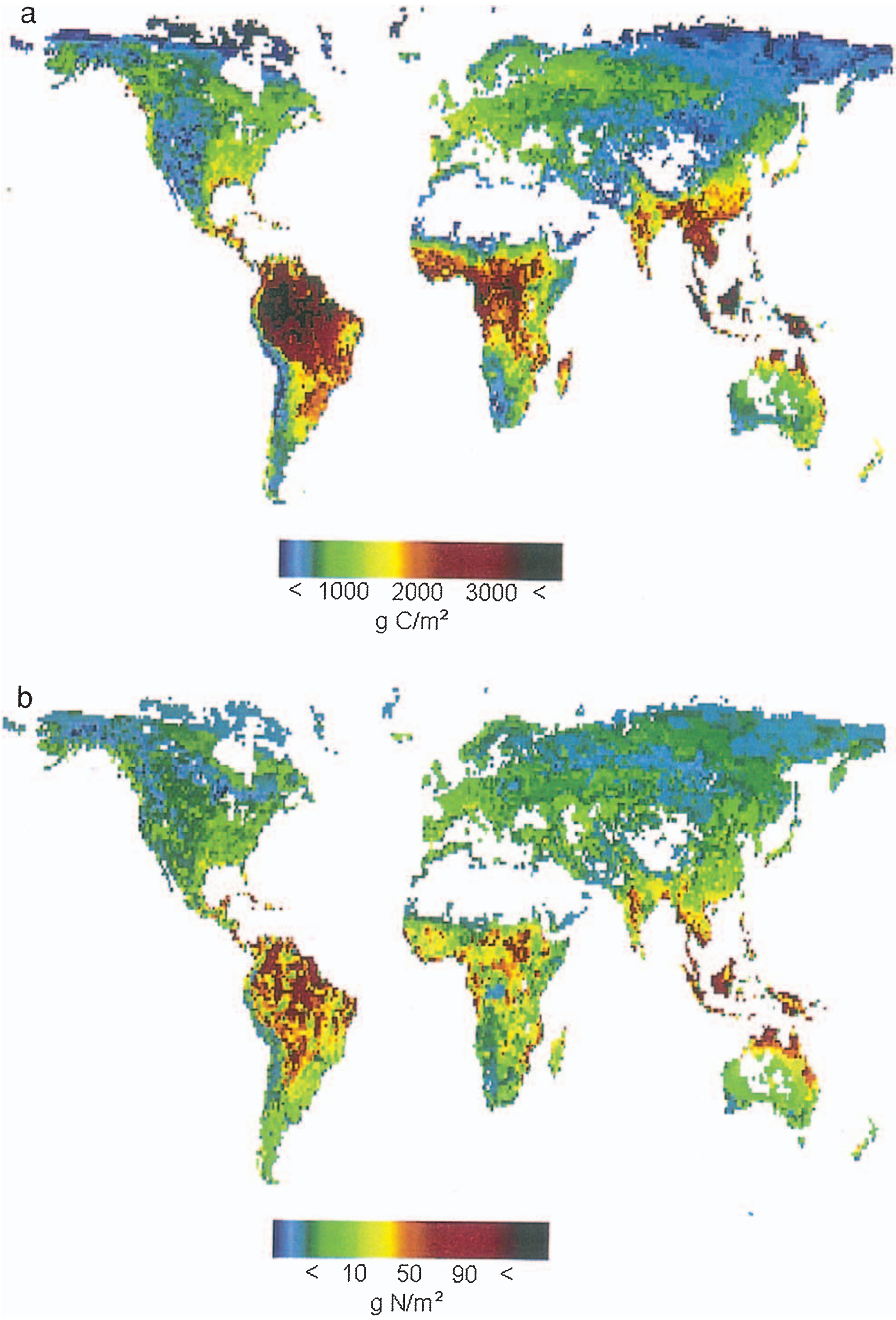


PLATE 18. Global annual (a) decomposition and (b) N mineralization computed by BIOME-BGC operating within the GESSys (Global Ecosystem Simulation System), a global version of the RHESSys model discussed in Chapters 7 and 8. A 1-year simulation was done with 1989 AVHRR data to define biome cover and LAI, with daily climatic data acquired from Piper and Stewart (1996). (From Galina Churkina, University of Montana, unpublished, 1997.)

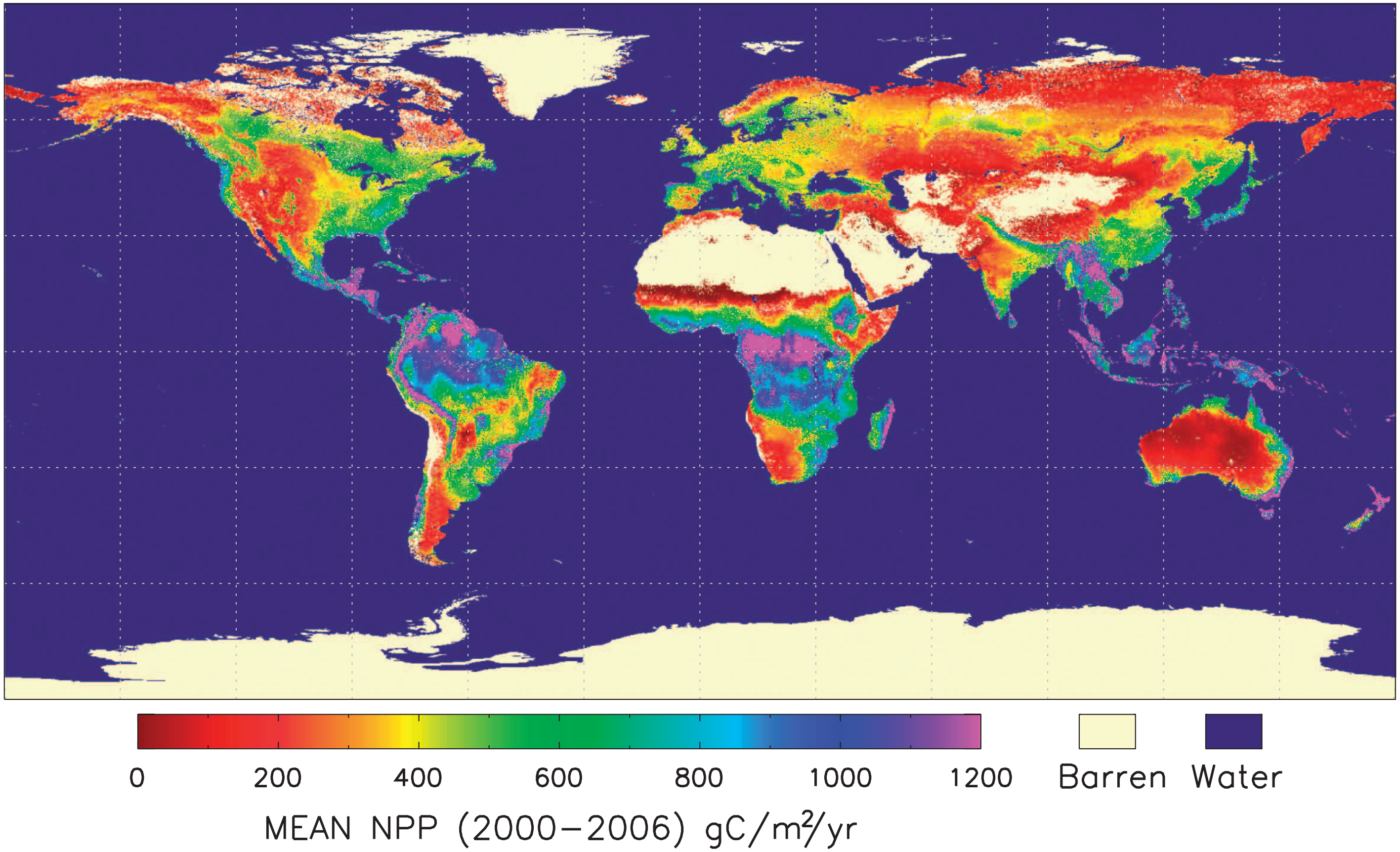


PLATE 19. Global annual net primary production for all vegetated land area, 110 million km^2 computed from MODIS 1 km data averaged for 2000–2006. Total annual global NPP averaged 821 gC/m^2/yr. Total annual global NPP averaged 51.9 Peta grams of carbon, of which 47% was from forests. See Running *et al*. 2004 (Figure provided by Numerical Terradynamic Simulation Group at the University of Montana).

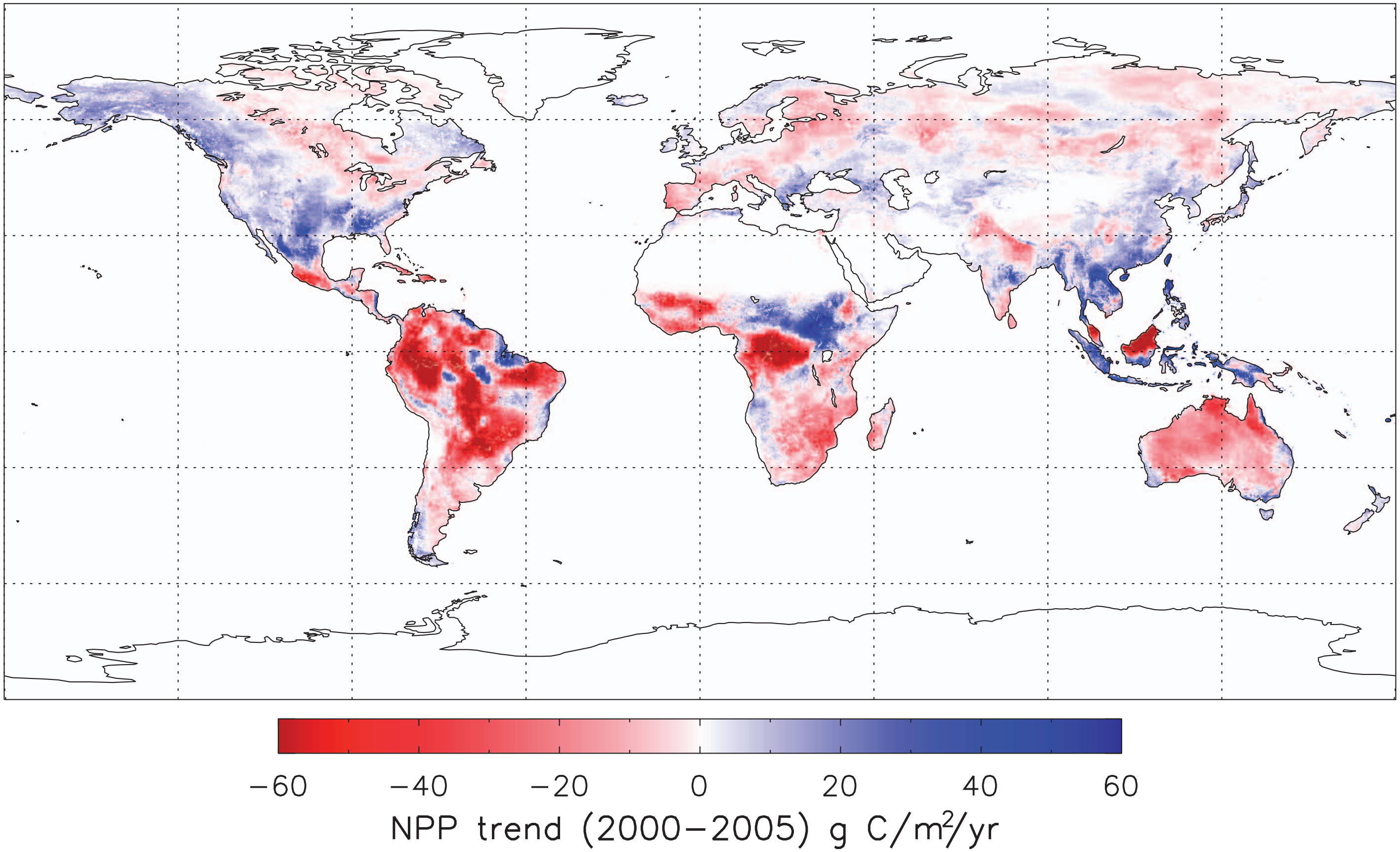


PLATE 20. The trend of annual NPP found from 2000–2005 in the MODIS dataset from Plate 19. Anomalies, or departures from some defined mean value, can be mapped from varying timescales, as an annual departure from a multi-year average productivity, or monthly as a departure from normal growing season seasonality. (After Running *et al*., 2004).