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Productivity of America's Forests and Climate Change

Abstract

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This study assessed the impact of climatic change on the forestry sector and carbon storage on timberlands. Productivity changes reflected ecosystem sensitivities to temperature, precipitation, and nutrient availability. The largest increases in NPP occurred in the northerly ecosystems, and the least response to climate change occurred in timber management types in the southern regions. Increased timber inventories decreased prices, imports, and shifted production to low cost regions. In this analysis, only the most optimistic scenario shifts future forests from sources of carbon to a carbon sink. The strong demand for wood products in the future dampens any positive growth effects on forests, for all but the maximum scenario.

Keywords: timber supply and demand, productivity, climate models, carbon storage

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Productivity of America's Forests and Climate Change

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EXECUTIVE SUMMARY

Increasing levels of atmospheric carbon dioxide are expected to alter climate, with potential changes in forest productivity and timber supply. This study analyzes the impacts of elevated carbon dioxide and climate change on forested ecosystems, and the economic feedbacks on harvest patterns and vegetation change on private timberlands, in the United States. The analysis used a framework that linked general circulation model output, an ecosystem model (TEM), models of the forest sector (TAMM/ATLAS/NAPAP), and a carbon accounting model (FORCARB). Future climates were described with output from four different general circulation models (GCMs): one from the Oregon State University (OSU) model, one from the Goddard Institute of Space Sciences (GISS) model, and two from the Geophysical Fluid Dynamics Lab model (GFDL-1, and GFDL-Q). The four future climates encompass global temperature increases of 2.8°C to 4.2°C and precipitation increases from 7.8% to 11%.

The contemporary climate data and the four future climates were used as input for the Terrestrial Ecosystem Model (TEM) to estimate changes in net primary productivity (NPP) for temperate and boreal forests in the United States. The response to climate change was computed as the change in the NPP response between the future climate runs and the contemporary climate run. Three scenarios were developed: an average, a minimum, and a maximum productivity response for each timber management type, within each timber supply and demand region.

Under the IPCC Business-as-usual scenario, carbon dioxide doubles(625 ppm) in about 2065. The productivity responses were implemented gradually in the timber inventory model, the Aggregate Timberland Assessment System model (ATLAS); changes in productivity always were less than 1% per year. ATLAS is linked to the Timber Assessment

Market Model (TAMM), which provides projections of timber and wood product prices, consumption, and production trends. For the economic baseline, we used the 1993 Forest Service Assessment Update assumptions about population, economic activity, and income, technological and institutional changes, energy costs, capital availability, and public and private investments in forest management, utilization, and research. Carbon storage and flux from forest lands was estimated with FORCARB, which is tightly linked to the timber inventory model (ATLAS). Although FORCARB includes all forest ecosystem components, only carbon in trees is presented in the climate change scenarios. The projection period for this analysis is 50 years.

The effects of climate change in productivity varied by timber management type within each region. The largest increases in NPP occurred in the northerly ecosystems, and the least response to climate change occurred in timber management types in the southern regions. Because most of the productivity changes were positive, inventories increased for most of the scenarios. All softwood forest types show gains, while the hardwoods gain in all but the minimum scenario; growth declines for southern hardwoods under the minimum scenario. These inventory changes reflect not only the changes in productivity, but also changes in timberland area and changes in harvest.

The increased productivity impacts harvest towards the end of the projection period. Growth compounds quickly and, by the end of the projection, is 5% to 24% above the base (minimum and maximum projections). While the corresponding increase in inventory pushes stumpage prices lower (roughly 6% to 35%), harvest increases by only 1% to 3%. Consumption lags the growth and inventory for two reasons. First, early in the projection, most growth is on trees too young to harvest, and second, it takes

time to build processing capacity to take advantage of more abundant resources. But given this, the smaller gain in harvest is an indication that the primary determinants of timber demand are items other than wood costs.

With a change in available supplies of harvestable inventories, there is a redistribution of harvest across the United States, as demand in various regions adjusts to take advantage of lower cost raw materials. The change also is between softwood and hardwood fiber types, and between forest industry and the nonindustrial private ownerships. For example, as supply of softwood growing stock increases and prices decline, the amount of hardwoods used in the harvest mix declines. This increases the demand for softwood pulpwood while reducing demand for hardwood pulpwood. Increased softwood timber supplies also act to increase softwood sawtimber capacity, and lower softwood lumber prices result in some increases in lumber production in the South. Increased production also increases the amount of residues available for pulp, further lowering hardwood pulpwood harvest. Differences in resource management between the North and South also play a major role in the hardwood projections.

Between 1952 and 1992, carbon storage on forestland in the coterminous United States increased by 11.3 billion metric tons, an average of 281 millon metric tons/year, an amount that offset about one quarter of U.S. emissions of carbon for the period. Most of the historical increase in carbon storage has been on the private timberland analyzed in this study. Base projections for carbon storage on timberland through 2040 show a decline of 20 million metric tons per year on timberland at the end of the projection period. Responses with a minimum increase in productivity are similar to the baseline, but increase more than 40 million metric tons per year with a maximum increase in productivity.

This study presents a methodology to examine the effects of market forces on potential effects of climate on temperate and boreal forests in the United States, as well as the potential shifts in carbon storage in those same forests. In this analysis, only the most optimistic scenario shifts future forests from sources of carbon to a carbon sink. The strong demand for wood products in the future dampens any positive growth effects on forests, for all but the maximum scenario. Market factors need to be considered in any analysis of the use of forests for mitigating carbon emissions.

1. Climate and Climate Modeling

W. Massman[2]

INTRODUCTION

The possibility of climate change has been the subject of many discussions and speculations in the past few years. An awareness also has emerged that human activities may contribute to these changes, and that a continuation of these changes could drastically alter human social and natural environments (IPCC 1990). At present, it is not possible to accurately predict how climate will change or what future global environments will be. Nevertheless, some modeling tools (although imperfect) are available for developing climate scenarios that can be used to address issues concerning the impacts that climate change may have on ecosystems. This chapter provides a brief discussion of climate and some of the complexities of climate modeling, and provides a brief discussion of the four GCMs used in other chapters of this report.

Climate, as presently understood, is just one aspect of the total earth system. The earth's climate is driven primarily by solar radiation and the earth's rate of rotation, and results from the interactions between the five components of the earth system: the atmosphere, the hydrosphere, the cryosphere, the biosphere, and the land surface. Within this system, physical, chemical, and biological processes are coupled on virtually all temporal and spatial scales. Some of the complexity of this system is represented by figure 1.1, which shows a few of the processes that externally force the climate and that internally link the five earth system components. But figure 1.1 also indicates that our understanding of dynamics of the climate and of the earth system is still evolving. For example, the original diagram (GARP 1975) from which this figure is adapted does not specifically include methane (CH_4) or chlorofluorocarbons (CFCs) as important atmospheric trace gases. But, now we know that the combined effect of CH_4 and CFCs is nearly as important for global warming as is carbon dioxide (Rasmussen and Khalil 1981, IPCC

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1990). Consequently, other refinements to this figure can be expected as understanding of the earth system improves. In addition to representing climate and the earth system, this diagram also can be used to describe many smaller scale climate-driven ecosystems. On virtually all scales, the processes and couplings between all the major components of this system are the same, but the strength of these processes and couplings may vary significantly from one scale to another and from one ecosystem to another. The complexity or richness of climate derives from the enormous variety of linkages and feedbacks between these components and from the nonlinear nature of their interactions in time and space.

The science of climate modeling began with atmospheric general circulation models (AGCMs or GCMs). These models, originally developed for weather forecasting, are numerical representations of the atmospheric component of the climate system coupled with relatively simpler models for the hydrosphere, the cryosphere, the biosphere, and the land surface. Like the climate system, these models are also complex, nonlinear, and dynamic. Using equations representing the conservation of mass, energy, and momentum, GCMs attempt to predict the state of the global climate. They are used to simulate (at a discrete number of points distributed in the vertical and the horizontal) a variety of atmosphere-related climate variables. Some of these variables include wind speed and direction, the atmospheric temperature and pressure, cloudiness, precipitation, and the energy and water balance of the land surface. However, a GCM is only one type of climate model. More sophisticated climate models couple a GCM with a dynamic (and equally complex) ocean model that then can be used to simulate the ocean-related climate variables (i.e., the ocean surface temperatures, the salinity of the ocean, and position of the ocean currents). Ultimately a global climate model will require coupling detailed, complex and dynamic models of each of the earth system components (OIES 1992). However, regardless of

Changes in tidal or gravitational forces

Changes in solar radiation

SPACE

ATMOSPHERE

Terrestrial radiation

N_2, O_2, H_2O, CO_2, O_3, CH_4, CFCs, etc.

Aerosols

Clouds

Atmosphere land surface coupling

Atmosphere ocean biomass coupling

Atmosphere biomass coupling

Atmosphere ocean coupling

Atmosphere ice coupling

SNOW & ICE SHEETS

BIOMASS + SOILS

LAND

SEA-ICE

OCEAN

EARTH

Changes in atmospheric composition *

OCEAN BIOMASS

Ocean ice coupling

Changes in land features, orography, vegetation, albedo, biogeochemical cycling, etc. *
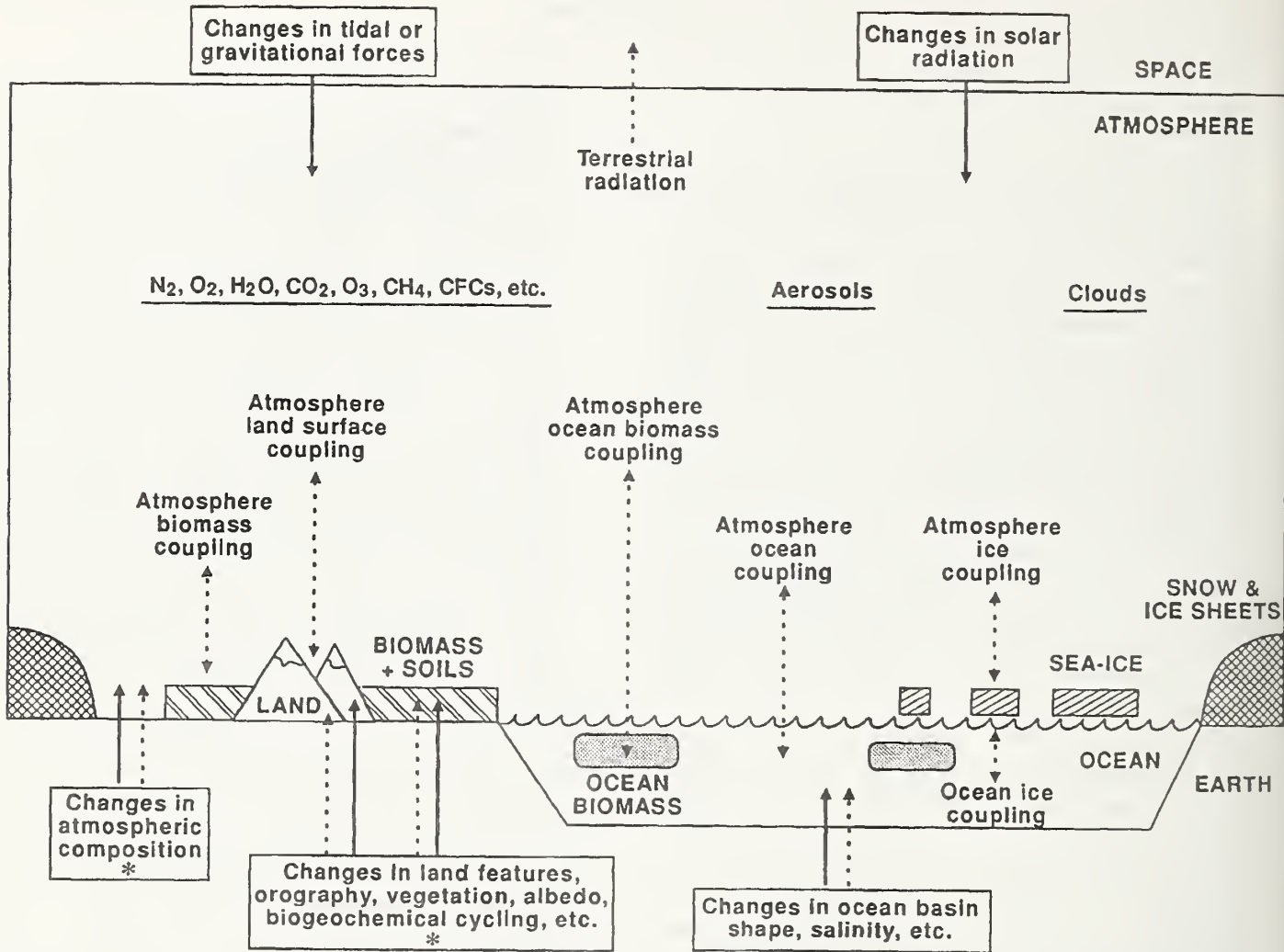
Changes in ocean basin shape, salinity, etc.

Figure 1.1—Schematic of earth system. Solid arrows indicate forcing by external processes. Dashed arrows indicate forcing by internal processes. Double arrows indicate internal coupling or two-way forcing. Processes most directly influenced by human activity are denoted by an asterisk (*).

their complexity and sophistication, climate models, like all mathematical models, will always be simplified versions of the full climate system.

However, the science of global climate modeling will continue to change and improve as understanding of the physical and numerical aspects of earth system modeling improve. To date, GCMs have shown to be extremely powerful tools for studying the earth's climate system. Furthermore, GCMs also may prove useful for distinguishing between alternate strategies for human response to climate change. But a fully integrated numerical model of the earth system has not been achieved. Several major hurdles must be overcome before any model can be used confidently for predicting ecosystem response to climate change. These hurdles include the limitations imposed by coarse spatial resolution, the inability to accurately model the effects of clouds, the inability to accurately model the global hydrologic cycle, the lack of an interactive biosphere model, the lack of an interactive human-climate model, the inherent complexity of the climate system, and the lack of knowledge of how to interactively couple several dynamic nonlinear models.

COARSE SPATIAL RESOLUTION

One critical impediment to climate modeling is spatial resolution. Coarse spatial resolution limits the ability to represent subgrid scale processes in a GCM. Physical processes associated with a dimensional scale smaller than 400 km × 400 km cannot be resolved in most GCMs, and in many GCMs the spatial resolution is even worse. Therefore, there is a need to include the effects these subgrid scale processes can have on the larger scales; however, the basic knowledge of how to accomplish this is incomplete. Furthermore, with such a coarse grid spacing GCMs cannot be used with confidence for regional climate simulations. However, finer resolution is possible with mesoscale models that have a grid spacing of about 60 km x 60 km and can be nested into a GCM. Although these high resolution models, like GCMs, are also limited by the problems associated with the subgrid scale effects, they offer some hope for improving regional climate predictions at least in regions where topographic effects are significant (IPCC 1992).

CLOUD EFFECTS

Another hurdle to the development of climate models is clouds. Clouds play a major role in regulating the radiative heating of the global climate system. Unfortunately, their interaction with radiation on a global scale is not well understood. Furthermore, most clouds are so small that they cannot be fully resolved within a GCM. Consequently, GCMs simulate clouds and cloud-climate interaction using approximations. Unfortunately, the climate is more likely to be sensitive to clouds than it is CO_2, CH_4, CFCs or any of the other radiatively active greenhouse gases (Ramanathan et al. 1989).

GLOBAL HYDROLOGIC CYCLE

Because the hydrologic cycle is not reliably modeled, it too is a problem in climate model development. For example, rainfall amounts and the spatial and temporal patterns of rainfall are not modeled consistently from one GCM to another nor do GCMs always produce large-scale rainfall patterns that resemble observed data (Boer et al. 1992). Therefore, the important connection between rainfall patterns and biospheric vegetation patterns cannot be reliably analyzed with current GCMs. Furthermore, because water (in all its forms) is the dominant internal factor controlling the earth system and the climate, climate predictions are likely to remain uncertain until such time as an adequate model of the hydrologic cycle is available (Chahine 1992).

LACK OF AN INTERACTIVE BIOSPHERE

A truly interactive biosphere model does not exist, partly because the biospheric feedbacks into the other components of the climate system are not understood. Although, there is little doubt that the biosphere will respond to climate change, current models of biospheric response (e.g., McGuire et al. 1992, Schimel et al. 1990) have yet to be coupled to a GCM. Nor is it understood how that response will affect the dynamic evolution of the climate system. Furthermore, in most GCMs, ecosystems are represented only in terms of their ability to exchange heat, moisture and some trace gases (e.g., Sellers et al. 1986), and these models often perform rather poorly when compared with surface meteorological and hydrological observations (e.g., Henderson-Sellers 1992). Consequently, present GCMs do not (and cannot) account for the dynamic distribution of plants and soil moisture characteristics of the land biosphere. However, even with their shortcomings, present-day biosphere models have improved GCMs' ability to simulate precipitation, evaporation, and the diurnal cycle of heat and moisture exchange of the land surface.

HUMAN INFLUENCES

No interactive human-climate model exists. Human activity, at least on a local scale, has had a significant impact on climate in the past century (Changnon 1992, Cotton and Pielke 1992). For example, urbanization, deforestation, desertification, damming rivers to create lakes, and cultivating the land surface are human activities that affect local climate. Humans also influence the global climate by burning fossil fuels, which increase the concentrations of atmospheric carbon dioxide, sulfur dioxide, and sulfate aerosols (IPCC 1990, Lelieveld and Heintzenberg 1992). But it is unclear how the global scale social and economic activities of humans, when

coupled with humanity's ability to radically and rapidly alter the land surface and the earth's biota, will feedback into the climate system. A better understanding of the climate system may not be possible without including some of the interactions and feedbacks between climate and humans.

COMPLEXITY OF THE EARTH SYSTEM

Both the earth system and GCMs are complex nonlinear systems that change over time. Therefore, their evolution can be sensitive to relatively minor changes in either the external forcing or the internal interactions between their components. They may exhibit relatively stable states for long periods of time before abruptly changing to a new (and sometimes very different) state (Gleick 1987). For example, regional multiyear drought/rainfall cycles may be a manifestation of this nonlinear (chaotic) phenomenon (Entekhabi et al. 1992). Furthermore, the climate system is continually subjected to random forcing, because volcanoes can inject large amounts of dust into the stratosphere, thereby significantly affecting global climate (Henderson-Sellers and McGuffie 1987, Brasseur and Granier 1992). However, including such events for use in a long-term GCM climate simulation is difficult. The inherently chaotic nature of the climate system makes reliable predictions even more difficult.

Table 1.2.—Model predictions.

Model	Predicted increase in global temperature	Predicted change in global precipitation
OSU	2.8°C	+7.8%
GISS	4.2°C	+11%
GFDL-1	4.0°C	+8.7%
GFDL-Q	4.0°C	+8.3%

INTERACTIVE COUPLING

Modeling the earth system in general is extremely complex, and although simulation models of the five components of the earth system exist, very little is known about their interactive coupling. Some critical areas of research include the interactive coupling of GCMs with models of (a) global surface hydrology, (b) global atmospheric chemistry, and (c) global ocean-sea ice. However, some of these issues cannot (and probably will not) be resolved without much more focused interdisciplinary efforts (Chahine 1992).

GENERAL SUMMARY - GCMS

As formidable as these hurdles are, GCMs are steadily improving. For example, new GCM simulations including a gradual CO_2 buildup and using a coupled atmosphere-ocean model have been per-

Table 1.1.—Model description.

model	Horizontal Spatial resolution (lat. x long.)	Number of vertical layers	Diel cycle[1]	Surface characteristics of horizontal grid box	Ocean Model	Incoming solar radiation at the top of the model atmosphere (Wm[-2])	Model atmospheric CO_2 concentration[5] (ppm)
OSU	4.00°x5.0°	2	no	Homogeneous[2]	1 layer ocean < 60m deep	1354	326
GISS	7.83°x10°	9	yes	Heterogeneous[3]	1 layer ocean < 65m deep	1367[6]	315[7]
GFDL-1	4.44°x7.5°	9	no	Homogeneous[2]	1 layer ocean < 68m deep	1443.7	300
GFDL-Q	4.44°x7.5°	9	no	Homogeneous[2]	1 layer ocean < 68m deep[4]	1443.7	300

[1]Related to temporal resolution.

[2]Permits only one category of land surface type (land, water, ice) for any grid box.

[3]Permits more than one category of land surface types (land, water, ice) for any grid box—determined as % areal coverage.

[4]The GFDL-Q model ocean is an "improved" version of the GFDL-1 model ocean.

[5]This parameter is adjusted or tuned so that the model produces the best simulation of the present climate.

[6]Agrees with satellite observations.

[7]The 1958 value.

formed (IPCC 1992, Manabe et al. 1992). Most of the previous GCM results used in assessment studies had an instantaneously doubled CO_2 concentration imposed on the atmosphere and did not include an ocean model. However, none of the recent improvements have significantly altered the expectations for a rise in global temperature (IPCC 1992). However, those GCM runs did not include possible opposing human-caused influences, including the effects from sulphate aerosols and stratospheric ozone depletion. Given the enormous complexity of both the climate system and GCMs, progress in understanding and modeling the climate system is likely to remain steady with major breakthroughs being very unlikely. However, GCMs (although imperfect) can provide physically plausible scenarios which can be used to evaluate the impact that climate change can have on ecosystems, because climate models explicitly model the physical constraints inherent to the climate system. Consequently, GCMs can be used to provide realistic bounds on the physically realizable states of the evolving climate.

Specific Summary and Comparison of GCMS Used in this Assessment

The four GCMs used in this study are the Oregon State University (OSU) model, the Goddard Institute of Space Sciences (GISS) model, and two versions of the Geophysical Fluid Dynamics Laboratory (GFDL) model. A short overview of these four models is given in table 1.1. It is adapted from Jenne (1992), who provides a much more detailed discussion of the models. Not all the issues discussed earlier in this chapter are included in table 1.1. This table is intended to parallel some of the points concerning simulating climate with GCMs that were outlined previously.

As table 1.1 and Jenne (1992) indicate, there are some significant differences between these four models. Consequently, the climates predicated by each model also can be expected to vary. Table 1.2 compares the models' predicted changes in the global annual mean temperature and global annual mean precipitation. All models predict an increase in temperature and precipitation, but the magnitudes differ significantly. Furthermore, the differences in predicted climate on a regional scale can be even more dramatic (not shown in this chapter) than they are on a

global scale. Regional rainfall patterns, storm tracks, and temperatures can vary much more than the globally averaged predictions. Because each of the model's predictions represent a possible climate scenario, we need a spectrum of possible climates to model possible forest response to a changing climate. Therefore, all four of these GCMs were used as a basis to examine the influences of climate on forest productivity.

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2. Responses of Net Primary Production to Changes in CO₂ and Climate

A.D. McGuire[3] and L.A. Joyce[4]

INTRODUCTION

Net primary production (NPP) is the net rate at which the vegetation in an ecosystem captures carbon from the atmosphere. Temperate forests, whose range covers 11% of the terrestrial biosphere, are potentially responsible for 17% of annual global terrestrial NPP (Melillo et al. 1993). As the atmospheric concentration of carbon dioxide (CO_2) continues to rise (Watson et al. 1992), the NPP of temperate forests may change in response to elevated CO_2, associated changes in climate, and other factors (Bazzaz 1990, Eamus and Jarvis 1989, Graham et al. 1990, Jarvis 1989, Joyce et al. 1990, Kramer 1981, Melillo et al. 1990, Mooney et al. 1991, Woodward et al. 1991). Assessing the sensitivity of NPP in temperate forests to global change is important, because humans rely on a portion of this production for fiber, fuel, and food.

The global atmospheric concentration of CO_2 has risen from pre-industrial levels of approximately 280 ppmv in the late 18th century to 355 ppmv in 1991 and continues to increase at the rate of 1.8 ppmv/yr (Watson et al. 1992). Much of this enrichment is attributable to emissions from the combustion of fossil fuels (Rotty and Marland 1986) and human land-use activities (Houghton and Skole 1990). Working Group I (1990) of the Intergovernmental Panel on Climate Change (IPCC) estimates that CO_2 concentrations will reach 500 ppmv by the year 2040 and 800 ppmv by the year 2100 if no steps are taken to limit CO_2 emissions. The atmospheric increase in CO_2 concentration has the potential to alter NPP directly by affecting plant physiology and indirectly by affecting climate.

The continued atmospheric enrichment of radiatively active gases such as CO_2, methane (CH_4),

nitrous oxide (N_2O), and chlorofluorocarbons (CFCs) (Watson et al. 1990) is predicted to increase the radiative forcing of climate (Shine et al. 1990). Equilibrium simulations of climate by general circulation models (GCMs) for doubled levels of atmospheric CO_2 predict a mean annual global warming of between 1.5° C and 4.5° C (Mitchell et al. 1990). Transient models of climate response to a CO_2 doubling time of between 60 and 100 years generally predict a global increase of approximately 0.3° C per decade (Gates et al. 1992). Equilibrium simulations also predict that global precipitation should increase between 3% and 15% (Mitchell et al. 1990) and that global cloud cover should decrease between 0% and 3% (Melillo et al. 1993).

In this chapter we first review the experimental literature to examine how NPP of forests may be affected by elevated CO_2 and changes in temperature, precipitation, and cloudiness. We focus on the functional response of NPP in existing regions of temperate forest, and do not consider how NPP is affected by the responses of disturbance and vegetation distributions to climate change. We attempt to use information primarily from studies that have examined the response of trees, and we clearly indicate when we reference studies that involve other plants. When we reference studies that involve both trees and other plants, we refer to them collectively as "plants." Because the literature suggests many different responses to potential changes in CO_2 and climate, we first try to identify the variability in the responses and then suggest possible explanations for the variability. Our approach in this review is to interpret responses in the context of ecosystem processes. Therefore, we examine major linkages between the carbon, nutrient, and water cycles in ecosystems before reviewing the experimental literature.

Next we evaluate potential implications of changes in CO_2 and climate for NPP of U.S. temperate forests (fig. 2.1). To accomplish this we first assess the appropriateness of using regression- and process-based approaches to modeling the NPP response of temperate forests. We then inves-

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Forest Vegetation

Boreal Forest
Boreal Forest - Wet
Temperate Mixed Forest
Temperate Conifer Forest
Temperate Deciduous Forest
Temperate Deciduous Forest - Wet
Temperate Broadleaf Evergreen Forest

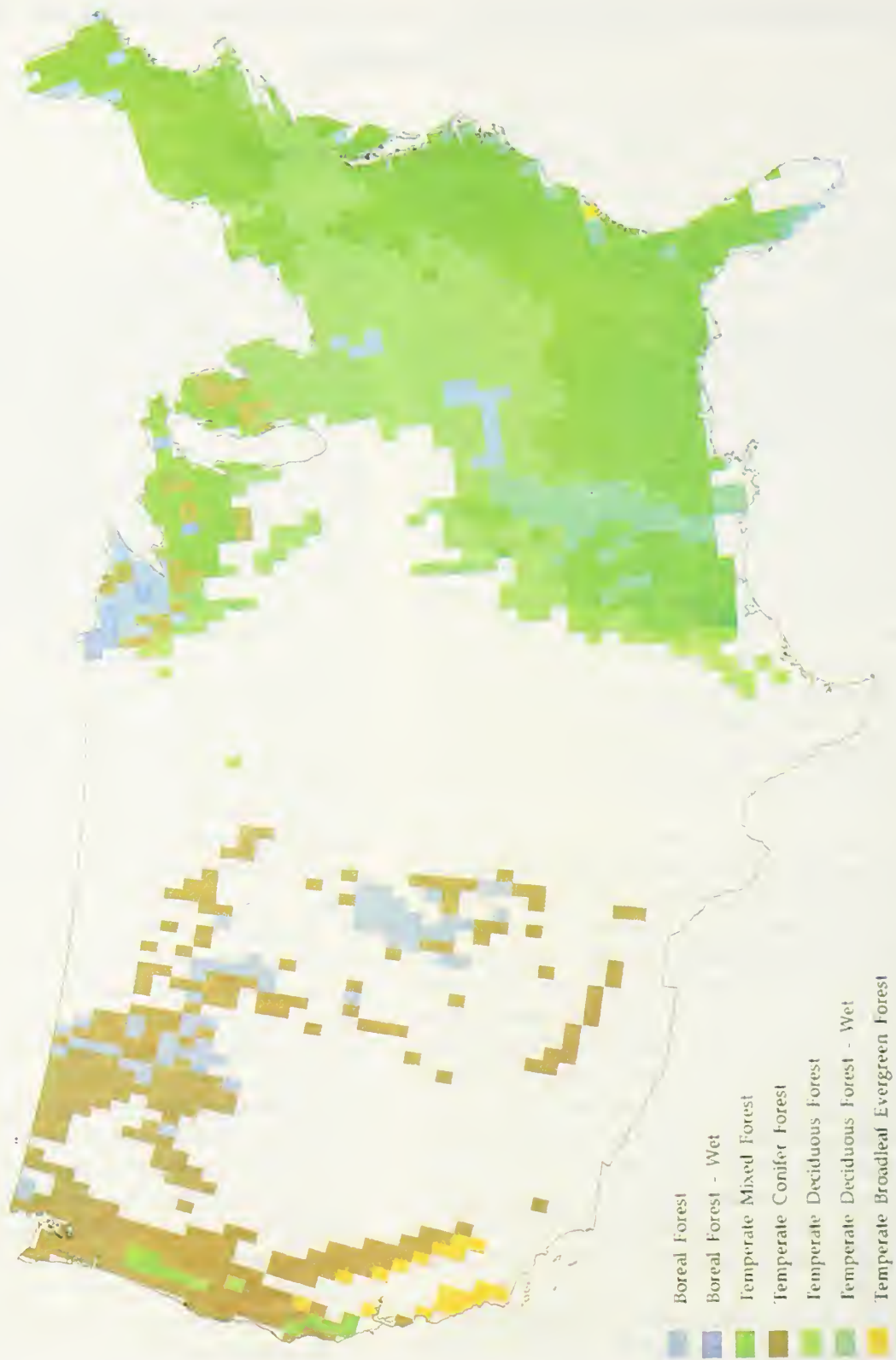Figure 2.1.—The vegetation used in this study to describe the historical range of temperate forests in the United States. The vegetation types are boreal forest, boreal forest wetland, temperate coniferous forest, temperate deciduous forest, temperate mixed forest, temperate broadleaf evergreen forest, and temperate forest wetland. We did not consider the boreal forests of Alaska in this study.
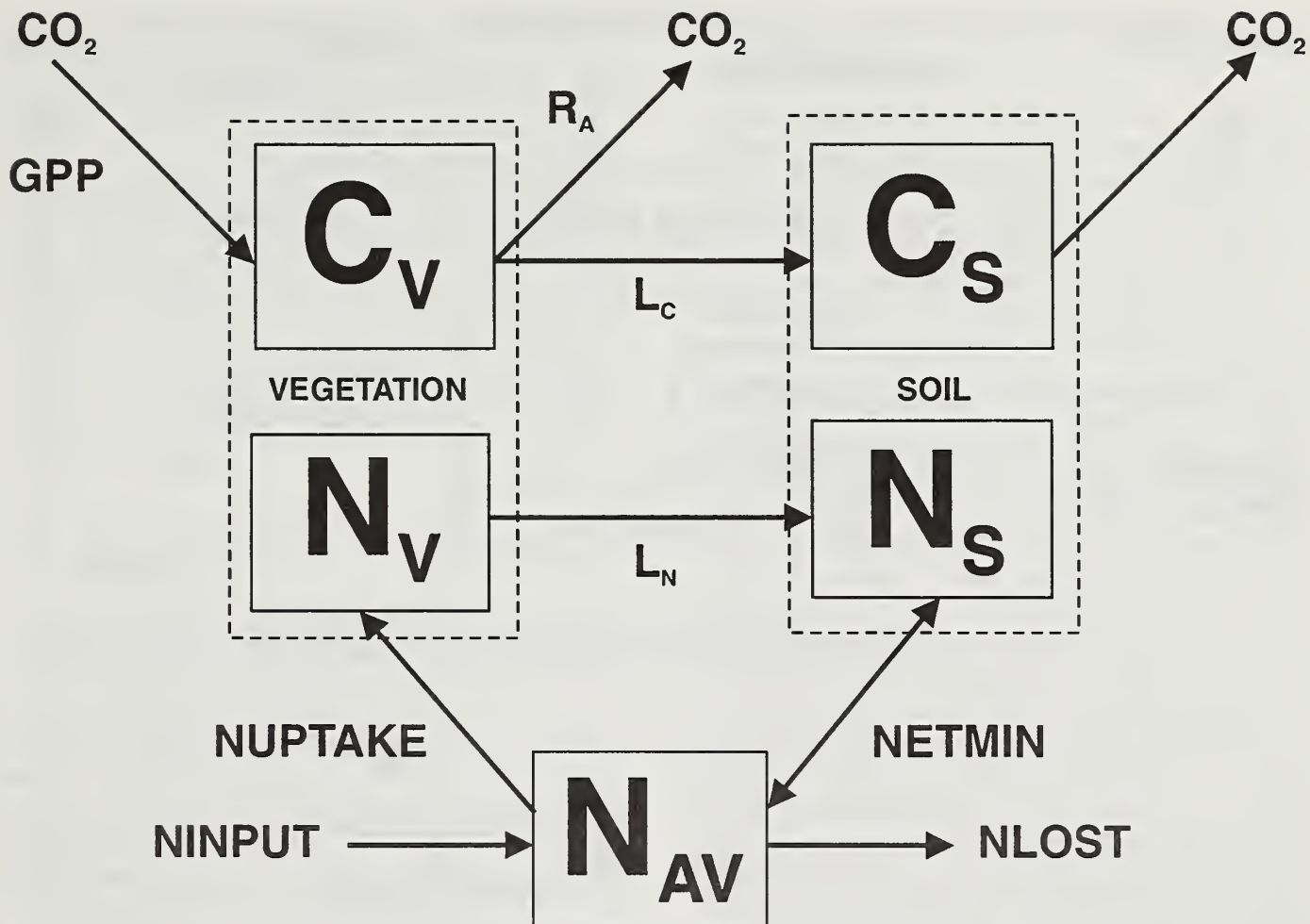
Figure 2.2.—A generalized depiction of carbon and nutrient cycles in terrestrial ecosystems. Carbon enters the vegetation pool (C_V) as gross primary production (GPP) and transfers either to the atmosphere as autotrophic (plant) respiration (R_A) or to the soil pool (C_S) as litter production (L_C); it leaves the soil pool as heterotrophic respiration (R_H). Nitrogen enters the vegetation pool (N_S) from the inorganic nitrogen pool of the soil (N_{AV}) as NUPTAKE. It transfers from the vegetation to the organic soil pool (N_S) in litter production as the flux L_N. Net nitrogen mineralization (NETNMIN) accounts for nitrogen exchanged between the organic and inorganic nitrogen pools of the soil. Nitrogen inputs from outside the ecosystem (NINPUT) enter the inorganic nitrogen pool; losses leave this pool as the flux NLOST.

tigate the implications of doubled CO_2 in a spatially explicit fashion by driving a process-based model, the Terrestrial Ecosystem Model (TEM), with the predictions of several global climate models to estimate the NPP response of temperate forests in the United States. We end the evaluation by addressing the limitations of using the predicted responses and identify the need for forest growth models of NPP response for making future progress.

In the final section of this chapter, we evaluate the use of different approaches to modeling forest growth in assessing the response of NPP to changes in CO_2 and climate. We then identify the issues that, in our opinion, must be addressed by forest growth models for them to properly constrain the response of NPP to change. Finally, we point out the need to evaluate different modeling approaches

and to integrate modeling studies with experimental studies of processes in growing forests.

REVIEW OF EXPERIMENTALLY DOCUMENTED RESPONSES

Major Linkages Between the Carbon, Nitrogen, and Water Cycles

Net primary production is the difference between the rate at which the vegetation acquires carbon from the atmosphere, i.e., gross primary production (GPP; fig. 2.2), and the rate at which it returns carbon to the atmosphere, i.e. plant respiration (R_A; fig. 2.2). GPP represents carbon captured through the process of
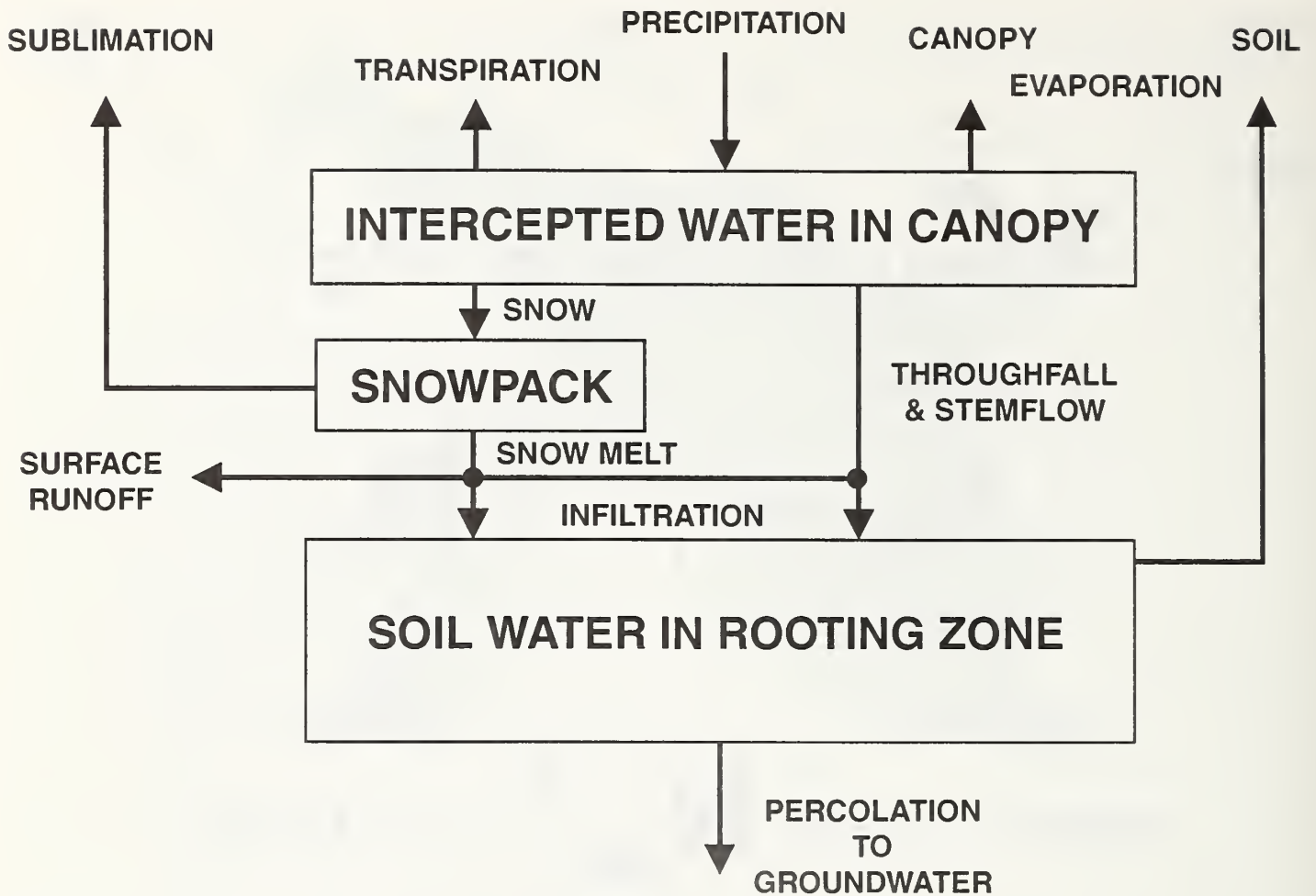
Figure 2.3.—A generalized depiction of the water cycle in terrestrial ecosystems. Water that enters the ecosystem in the form of precipitation may be intercepted by the canopy or reach the surface as snowfall or throughfall/stemflow. Infiltration into the soil depends on the portion of snowmelt and throughfall/stemflow that does not contribute to surface runoff. Some of the water that infiltrates the soil percolates to become groundwater. Moisture enters the atmosphere from the ecosystem as sublimation from snow, evaporated water from the soil and canopy surfaces, and transpired water from leaves of the canopy.

photosynthesis and R_A represents the carbon cost of constructing and maintaining tissue. The response of NPP to changes in CO_2 and climate depends on the responses of both GPP and R_A.

Changes in CO_2 and climate can directly or indirectly affect GPP and R_A. Direct effects may include, for example, the responses of photosynthesis to elevated CO_2 or of respiration to elevated temperature. Indirect effects may be caused by changes in the nutrient relations of vegetation. We use the representation of the nitrogen cycle in figure 2.2 to illustrate some linkages between carbon and nutrient cycling in ecosystems. Because the construction of new tissue requires nitrogen in addition to carbon, GPP may depend on the nitrogen status of vegetation. Nitrogen status is influenced by both the amount of nitrogen stored in vegetation (N_V) and the supply of

nitrogen to vegetation (NUPTAKE). The supply to vegetation depends on the amount of nitrogen available in the soil solution (N_{AV}), which is influenced by the net amount of nitrogen mineralized during the decomposition of soil organic matter (NETNMIN), inputs from the atmosphere (NINPUT), uptake by vegetation, and losses to both the atmosphere and ground water (NLOST). The response of NPP to changes in CO_2 and climate depends, in part, on how the processes that influence the availability of nitrogen and other nutrients respond to changes.

Changes in CO_2 and climate also may indirectly influence NPP by affecting the water relations of vegetation. The movement of carbon from the atmosphere into the vegetation (GPP) occurs through the stomata of leaves. This activity involves the loss of water (transpiration) from the vegetation (fig. 2.3). If

the availability of water in the soil is low, then the vegetation may close stomata to restrict moisture loss, which may reduce GPP. Conversely, GPP may increase if water availability rises. The amount of water available to vegetation depends on the balance of inputs and losses of water to and from the soil (fig. 2.3). Inputs that recharge the soil (infiltration) depend on precipitation, throughfall, stemflow, and snowmelt. Losses depend on transpiration, soil and canopy evaporation, sublimation, percolation to groundwater, and surface runoff. The response of NPP to changes in CO_2 and climate depends, in part, on how the processes that affect water availability respond to changes.

Responses to Elevated Carbon Dioxide

The effects of elevated CO_2 on NPP have been investigated at the leaf (tissue), plant, and ecosystem level. Studies at the leaf level have primarily focused on the response of net photosynthesis (P_n), which is GPP minus the leaf respiration that occurs simultaneous to measurements of P_n. Because P_n is an important component of NPP, we first review how it responds to elevated CO_2. Then we examine how respiration, an important component of both P_n and NPP, responds to elevated CO_2.

Next, we examine the responses of whole plants to elevated CO_2. In contrast to studies at the tissue level, those at the level of the individual plant have focused primarily on the response of growth, which is NPP minus biomass losses, such as herbivory and litter production (L_C in fig. 2.2). Because growth is essentially equivalent to NPP if biomass losses are negligible, it is generally a better integrative measure of NPP than P_n and respiration because of the difficulties in continually measuring both of these processes for entire plants.

Because the response of NPP to elevated CO_2 is most usefully understood in an ecosystem context, we finish our review of CO_2 responses by examining growth responses at the ecosystem level. Although studies of the growth response of whole plants to elevated CO_2 integrate the response of GPP and R_A for individual organisms, they do not necessarily represent the responses of communities. Studies at the ecosystem level primarily focus on how growth, expressed on an area basis, responds to elevated CO_2 in the context of the whole ecosystem.

Responses of Net Photosynthesis to Elevated Carbon Dioxide

The effects of elevated CO_2 on P_n may be different between plants that use the C_3 and C_4 photosynthetic pathways (Bazzaz 1990, Kramer 1981, Mooney et al. 1991, Woodward et al. 1991). Because temperate forest tree species primarily use the C_3 pathway (Eamus and Jarvis 1989), we will implicitly concentrate on how photosynthesis in C_3 plants is affected by elevated CO_2. P_n has been observed to increase in response to elevated CO_2 for several tree species (Bryan and Wright 1976, Conroy et al. 1986, Fetcher et al. 1988, Green and Wright 1977, Hollinger 1987, Idso and Kimball 1992, Jurik et al. 1984, Norby et al. 1992, Norby and O'Neill 1989, Regehr et al. 1975, Rogers et al. 1983a, 1983b, Teskey et al. 1986, Teskey and Shrestha 1985, Tolley and Strain 1985, Williams et al. 1986). However, the observation may be sensitive to the duration of exposure to elevated CO_2. Some studies that exposed trees to long-term elevated CO_2 found enhanced P_n persisting in leaves (Hollinger 1987, Idso and Kimball 1992, Norby et al. 1992, Norby and O'Neill 1989, Rogers et al. 1983a, 1983b, Tolley and Strain 1985, Williams et al. 1986), while others have not (Fetcher et al. 1988, Norby and O'Neill 1989, Oberhauer et al. 1985, Reekie and Bazzaz 1989, Silvola and Ahlholm 1992, Tolley and Strain 1985, Williams et al. 1986). The lack of persistence of enhanced P_n also has been observed in herbaceous species that have experienced long-term exposure to elevated CO_2 (Coleman and Bazzaz 1992, Larigauderie et al. 1988, Oberhauer et al. 1986, Oechel and Reichers 1986, Sage et al. 1989, Tissue and Oechel 1987, Wong 1979). To understand the response of P_n to elevated CO_2, it is important to consider the response of GPP.

Ribulose bisphosphate carboxylase (rubisco) is the enzyme in C_3 plants that is primarily responsible for capturing atmospheric carbon in the production of sugars. Rubisco may accept either CO_2 (carboxylation) or O_2 (oxygenation) as a substrate; oxygenation is responsible for photorespiration. Because CO_2 competes with O_2 for rubisco-binding sites, enhancement of GPP by elevated CO_2 is possible through increased carboxylation and decreased oxygenation (Gutteridge and Keys 1985, Lorimer 1981, Pearcy and Bjorkman 1983); reduced oxygenation results in decreased photorespiration. However, GPP also depends on both the concentration and activity of

rubisco. Decreased P_n at elevated CO_2 has been associated with lower concentrations of rubisco (Sage et al. 1989, Wong 1979) and reduced rubisco activity (Fetcher et al. 1988, Peet et al. 1986, Porter and Grodzinski 1984, Sage et al. 1989, Vu et al. 1983, Wong 1979), both of which may be related to nitrogen availability (Sage and Pearcy 1987a, 1987b, Wong 1979).

In general, nutrient availability affects photosynthesis (Chapin 1980, 1991a, Chapin et al. 1988, Clarkson 1985, Evans 1983, Lajtha and Whitford 1989, Sage and Pearcy 1987b, Silvola and Ahlholm 1992, Wong 1979). Because the availability of inorganic nitrogen often limits production in temperate forests (Aber et al. 1982, Auchmoody and Smith 1977, Binkley 1986, Burke et al. 1992, Ellis 1979, Gower et al. 1992, Miller 1981, Mitchell and Chandler 1939, Pastor et al. 1984, Peterson 1982, Proe et al. 1992, Safford and Filip 1974, Vitousek and Howarth 1991), the interaction of elevated CO_2 with nitrogen availability may affect the long-term response of P_n to elevated CO_2. The lower nitrogen concentrations of leaves that are often observed in plants exposed to long-term elevated CO_2 (Baker et al. 1992, Coleman and Bazzaz 1992, Curtis et al. 1990, Garbutt et al. 1990, Johnson and Lincoln 1990, Korner and Arnone 1992, Larigauderie et al. 1988, Norby et al. 1986a, 1992, Peet et al. 1986, Porter and Grodzinski 1984, Rochefort and Bazzaz 1992, Silvola and Ahlholm 1992, Williams et al. 1986, Wong 1979) may be symptomatic of a nitrogen supply that cannot keep pace with the increased availability of atmospheric carbon.

GPP also may be affected by how elevated CO_2 interacts with moisture availability. Elevated CO_2 generally decreases stomatal conductance in tree leaves (Curtis and Teeri 1992, Fetcher et al. 1988, Hollinger 1987, Jurik et al. 1984, Oberhauer et al. 1985, Reekie and Bazzaz 1989, Rogers et al. 1983a, 1983b, Surano et al. 1986, Tolley and Strain 1985, Williams et al. 1986), causing decreased transpiration rates (Norby and O'Neill 1989, Regehr et al. 1975, Tolley and Strain 1985). However, stomatal conductance and transpiration rates also may be unaffected by elevated CO_2 (Teskey and Shrestha 1985). If P_n does not decline in response to elevated CO_2, decreased stomatal conductance should lead to enhanced water use efficiency. The effect of enhanced water use efficiency in response to elevated CO_2 has been observed for many tree species (Hollinger 1987, Norby et al. 1986a, Norby and O'Neill 1989, Oberhauer

et al. 1985, Rogers et al. 1983a, 1983b, Teskey and Shrestha 1985), and has greater potential to enhance production in trees that are limited more by moisture availability than by nutrient availability (Conroy et al. 1986, Gifford 1979, Hollinger 1987, Idso 1989, Kimball and Idso 1983, McGuire et al. 1993, Polley et al. 1993, Sionit et al. 1980, Tolley and Strain 1984b, 1985).

Responses of Respiration to Elevated Carbon Dioxide

Respiration rates in plants that have received long-term exposure to elevated CO_2 have been observed to both decrease (Bunce 1990, 1992, Gifford et al. 1985, Idso and Kimball 1992, Norby et al. 1992, Reuveni and Gale 1985, Silsbury and Stevens 1984, Wullschleger et al. 1992, Wullschleger and Norby 1992) and to increase (Azcon-Bieto and Osmond 1983, Gifford et al. 1985, Nijs et al. 1989, Oechel and Strain 1985, Poorter et al. 1988). Although most of R_A in plants is generally maintenance respiration, construction respiration can represent a substantial portion of the total budget (Chung and Barnes 1977, Vertregt and Penning de Vries 1987, Williams et al. 1987). The effects of elevated CO_2 on construction respiration have not been studied extensively. Increased R_A in *Plantago major* has been suggested to be caused predominantly by enhanced construction respiration in roots when elevated CO_2 results in higher P_n (Poorter et al. 1988). Although construction respiration has been documented to decrease in white oak (*Quercus alba*) leaves at elevated CO_2 (Wullschleger and Norby 1992), root respiration was not investigated in the study. To make further progress in understanding the effects of elevated CO_2 on construction respiration, studies must attempt to quantify the cost of producing tissue in leaves, stems, and roots (Wullschleger and Norby 1992).

Elevated CO_2 may directly alter maintenance respiration by affecting the activity of respiratory enzymes (Amthor 1991). Increased activity of the cytochrome oxidase pathway and decreased activity of the cyanide-resistant pathway have been observed in sunflower and wheat roots, respectively (Gifford et al. 1985). However, higher levels of photosynthate that sometimes are associated with elevated CO_2 (Cave et al. 1981, Huber et al. 1984, Wulff and Strain

1982) are predicted to increase the activity of the cyanide-resistant pathway (Lambers 1982). Although increases in respiration generally are associated with higher levels of photosynthate (Amthor 1989, Azcon-Bieto and Osmond 1983), Silsbury and Stevens (1984) suggest that reduced costs of phloem loading at high CO_2 may decrease maintenance respiration.

Decreased maintenance respiration also may be related to decreased tissue nitrogen concentration (Amthor 1991, Ryan 1991), which often is observed in plants that have experienced long-term exposure to elevated CO_2. Lower leaf nitrogen concentration is generally associated with reduced respiration (Baker et al. 1992, Irving and Silsbury 1987, Jones et al. 1978, McCree 1983, Merino et al. 1982, Norby et al. 1992, Waring et al. 1985), which may result from reduced costs of producing and maintaining enzymes.

Responses to Elevated Carbon Dioxide at the Plant Level

Some dendrochronology studies indicate correlations between patterns in tree ring growth and the historical increase in atmospheric CO_2 for subalpine conifers in the western United States (Graybill 1986, LaMarche et al. 1984), for Scots pine (*Pinus sylvestris*) in Finland (Hari et al. 1984, Hari and Arovaara 1988), and for Douglas fir (*Pseudotsuga menziesii*) in British Columbia (Parker 1986). Although these studies suggest that the growth of mature trees may have responded to increasing CO_2, their conclusions have been challenged (Cooper 1986, Graumlich 1991, Kienast and Luxmoore 1988). Also, tree ring studies do not explain the causes of plant growth response to elevated CO_2. Contemporary studies at the plant level are better able to provide information on processes responsible for NPP responses to elevated CO_2; but for practical reasons the studies generally focus on the response of "potted" seedlings in growth chambers, greenhouses, and field chambers.

Enhanced growth of potted tree seedlings that have experienced long-term exposure to elevated CO_2 has been observed in many studies (Bazzaz et al. 1990, Brown and Higginbotham 1986, Canham and McCavish 1981, Conroy et al. 1986, Curtis and Teeri 1992, Higginbotham et al. 1985, Luxmoore et al. 1986, Norby et al. 1986a, Oberhauer et al. 1985, O'Neill et al. 1987, Purohit and Tregunna 1976, Rochefort and Bazzaz 1992, Rogers et al. 1983a, 1983b, Sionit et al.

1985, Surano et al. 1986, Tolley and Strain 1984a, 1984b). However, some of these studies also documented a decline in growth rate after an initial enhancement (Brown and Higginbotham 1986, Sionit et al. 1985, Tolley and Strain 1984a, 1984b). The absence of enhanced growth in response to elevated CO_2 also has been observed (Brown and Higginbotham 1986, Hollinger 1987, Reekie and Bazzaz 1989). Several factors may explain why enhanced growth in response to elevated CO_2 may not persist.

Some studies found that plant growth does not respond to elevated CO_2 under conditions of low nutrient availability (Brown and Higginbotham 1986, Goudriaan and de Ruiter 1983, Johnson and Lincoln 1991, Larigauderie et al. 1988, Marks and Clay 1990, Oberhauer et al. 1986, Wong 1979, Zangerl and Bazzaz 1984). The enhancement of nutrient availability increased the response of growth to elevated CO_2 for many species in these studies. Thus, lack of growth response to elevated CO_2 may be caused by nutrient limitation of photosynthesis. This explanation is consistent with the lower leaf nitrogen concentrations that often are observed in plants exposed to elevated CO_2.

Decreased nitrogen concentrations of stems (Norby et al. 1986a) and roots (Curtis et al. 1990, Norby et al. 1986a) also have been observed in plants exposed to elevated CO_2. Because changes in tissue quality may affect herbivory (Bryant et al. 1983), plant-fungal relationships (Cheplick et al. 1989), and decomposition (Melillo et al. 1982), they also may alter nutrient cycling rates in ecosystems. For example, elevated CO_2 could increase the ratio of lignin to nitrogen in litter (Melillo 1983), which should reduce rates of decomposition and net nitrogen mineralization (Melillo et al. 1982). The response of the lignin to nitrogen ratio of leaf litter to elevated CO_2 has been observed to both increase (Melillo 1983) and decrease (Norby et al. 1986b). Although it is not yet clear how CO_2-induced changes in litter quality will alter nutrient cycling rates, there is the potential for it to constrain the response of NPP to elevated CO_2.

The response of growth to elevated CO_2 also may be constrained by compromises in the allocation of biomass for the acquisition of carbon (i.e., allocation to leaves) and nutrients and water (i.e., allocation to fine roots). Elevated CO_2 may cause herbaceous plants to increase both leaf and root biomass relative to controls (Curtis et al. 1989, 1990, Fajer et al. 1991,

Johnson and Lincoln 1990, Marks and Clay 1990, Morison and Gifford 1984, Rogers et al. 1983a, Sionit et al. 1981), although there are cases in which it does not increase leaf biomass (Ackerly et al. 1992, Garbutt et al. 1990, Larigauderie et al. 1988, Marks and Clay 1990, Sionit et al. 1980, Wray and Strain 1986). In some experiments, elevated CO_2 may increase leaf biomass of tree seedlings compared to controls (Bazzaz et al. 1990, Brown and Higginbotham 1986, Curtis and Teeri 1992, Goudriaan and de Ruiter 1983, Higginbotham et al. 1985, Norby et al. 1986a, Oberhauer et al. 1985, O'Neill et al. 1987, Rochefort and Bazzaz 1992, Rogers et al. 1983a, Sionit et al. 1985). But for others, leaf biomass may not be enhanced (Bazzaz et al. 1990, Brown and Higginbotham 1986, Higginbotham et al. 1985, Norby and O'Neill 1989, Oberhauer et al. 1985, Reekie and Bazzaz 1989). Brown and Higginbotham (1986) observed that increased leaf biomass in white spruce (*Picea glauca*) occurred only at high nutrient availability. Similar to leaf biomass, root biomass of tree seedlings may increase in response to elevated CO_2 compared to controls in some cases (Brown and Higginbotham 1986, Curtis and Teeri 1992, Higginbotham et al. 1985, Luxmoore et al. 1986, Norby et al. 1986a, O'Neill et al. 1987, Rogers et al. 1983a, Sionit et al. 1985), but not in others (Brown and Higginbotham 1986, Norby and O'Neill 1989, Reekie and Bazzaz 1989). Brown and Higginbotham (1986) observed that increased root biomass in white spruce only occurred at low nutrient availability. Thus, the absolute response of leaf and root biomass to elevated CO_2 may be determined by compromises in allocation that are sensitive to nutrient availability.

Elevated CO_2 may result in the allocation of relatively more carbon to below- than to aboveground biomass in tree seedlings (Higginbotham et al. 1985, Norby et al. 1986a, O'Neill et al. 1987, Rochefort and Bazzaz 1992) although there are cases where it does not cause a shift (Bazzaz et al. 1990, Brown and Higginbotham 1986, Curtis and Teeri 1992, Hollinger 1987, Norby and O'Neill 1989, Oberhauer et al. 1985, Reekie and Bazzaz 1989, Sionit et al. 1985, Tolley and Strain 1984a, 1984b). Observed shifts in allocation to roots appear to be strongest in plants for which water or nutrients substantially limit growth (Brown and Higginbotham 1986, Johnson and Lincoln 1991, Larigauderie et al. 1988, Oberhauer et al. 1986, Sionit et al. 1981, 1982, Tolley and Strain 1984b). This is consistent with the hypothesis that resources are

allocated so that growth becomes equally limited by all resources, i.e., carbon, water, and nutrients (Bloom et al. 1985, Chapin et al. 1987).

Responses to Elevated Carbon Dioxide at the Ecosystem Level

Studies that use individual potted plants to evaluate the response of growth to elevated CO_2 have been criticized as potentially underestimating the response, because the rooting volume of plants may be restricted (Arp 1991, Idso 1991, Thomas and Strain 1991). Others have argued that this conclusion is premature and unsupported (McConnaughay et al. 1993). Whether or not the criticism is valid, studies of rooted plants in field chambers that control CO_2 concentration have the potential to better represent the integrated response of growth to elevated CO_2 in an ecosystem context than do plant-level studies. However, the results of only three field studies have been published for tree species; and each examines growth of immature trees. This section focuses on the results of these studies.

The impressive growth response in one of these studies, which found 180% increases between sour orange trees (*Citrus aurantium*) grown at ambient CO_2 and those grown at 300 ppmv above ambient (Idso and Kimball 1992), may be sensitive to supplemental watering and fertilization. In an experiment that provided yellow-poplar saplings (*Liriodendron tulipfera*) with no additional water or nutrients, there was no significant increase in growth between ambient CO_2 and 300 ppmv above ambient (Norby et al. 1992). Preliminary results from a study of loblolly pine (*Pinus taeda*) indicate a 33% growth increase between ambient CO_2 and 300 ppmv above ambient for only those plants provided with high levels of both nitrogen and phosphorus; growth in treatments receiving low levels of either nitrogen or phosphorus did not respond (Strain and Thomas 1992).

Both the sour orange and yellow-poplar studies documented enhanced photosynthetic rates and reduced leaf respiration rates at elevated CO_2. The sour orange study documented similar allocation of carbon to above- and belowground biomass between trees grown at ambient and elevated CO_2. This result is consistent with the application of water and fertilizer in sufficient quantities to prevent moisture and nutrient stress. In contrast, the yellow-poplar study

found enhanced fine root production and declines in leaf area at elevated CO_2. If nutrient supply did not keep pace with the increasing potential for carbon uptake in the yellow-poplar study, then a shift in allocation may have occurred to enhance the acquisition of nutrients. It is possible that growth did not increase in yellow-poplar because of the additional cost of constructing and maintaining fine roots (Poorter et al. 1988, Wullschleger and Norby 1992). In natural ecosystems, growth responses to elevated CO_2 may be constrained by nutrient availability.

Responses to Changes in Temperature and Precipitation

Changes in only temperature and precipitation may alter NPP by affecting GPP, R_A, leaf phenology, or allocation patterns. Given no change in nutrient or water relations, GPP generally approaches an asymptote as temperature increases (Fitter and Hay 1981, Kozlowski et al. 1991, Kramer and Kozlowski 1979, Larcher 1980) and does not decrease until temperatures are high enough to denature photosynthetic enzymes. However, changes in temperature may additionally influence GPP by affecting nutrient and water availability. Changes in precipitation also may affect nutrient and water availability.

Changes in temperature and precipitation may either increase or decrease GPP, depending on how they affect nutrient availability. Higher rates of decomposition in response to elevated temperature (Bunnell et al. 1977, Van Cleve et al. 1990) may enhance the release of inorganic nitrogen into the rooting zone of the vegetation (Van Cleve et al. 1990), which may increase P_n (Chapin 1980, 1991a, Chapin et al. 1988, Clarkson 1985, Evans 1983, Lajtha and Whitford 1989, Sage and Pearcy 1987b, Wong 1979). However, lower precipitation or the effects of elevated temperature in enhancing evapotranspiration (Monteith and Unsworth 1990, Sharma 1985) may decrease soil moisture. Lower soil moisture may reduce nitrogen availability by causing lower rates of decomposition (Bartholomew and Norman 1946, Bhaumik and Clark 1947, Carlyle and Than 1988, Miller and Johnson 1964, Orchard and Cook 1983, Sommers et al. 1981, Stott et al. 1986, Warembourg and Paul 1977) or slower diffusion of inorganic nitrogen in the soil (Chapin 1991b, Nye and Tinker 1977). Increased precipitation has the potential to enhance

nitrogen availability as long as decomposition rates rise with increasing soil moisture. Decomposition rates are maximum for soils that are 50% to 80% saturated with water, and decrease above the optimal level of soil moisture (Alexander 1977, Clark 1967); oxygen availability limits microbial decay as soils become more waterlogged (Stolp 1988).

If elevated temperature or decreased precipitation lower soil moisture, they also may decrease stomatal conductance (Bates and Hall 1981, Gollan et al. 1985, Morrow and Mooney 1974, Pereira et al. 1986, Zhang and Davies 1989). Reduced P_n of tree leaves may be associated with decreased stomatal conductance (Bacone et al. 1976, Kozlowski 1962, Kriedemann 1971, Lakso 1979, Pereira et al. 1986, Regehr et al. 1975, Teskey et al. 1986). Under conditions of severe water stress, P_n may be additionally decreased by factors other than stomatal conductance (Beadle and Jarvis 1977, DeLucia 1986, Scarascia-Mugnozza et al. 1986, Teskey et al. 1986).

Whereas R_A generally increases in response to elevated temperature (Amthor 1984, Butler and Landsberg 1981, Lawrence and Oechel 1983, Linder and Troeng 1981, Ryan 1990, 1991), it generally decreases in response to water stress (Bradford and Hsiao 1982, Hanson and Hitz 1982, Wilson et al. 1980) primarily because of reduced construction respiration (Hanson and Hitz 1982, Wilson et al. 1980). Maintenance respiration has been observed to both decrease (Wilson et al. 1980) and increase (Moldau and Rahi 1983) in response to water stress. The observed increases are probably attributable to tissue repair associated with damage that results from the rapid application of water stress (Ryan 1991). Because most of the effects of water stress on R_A are caused by altered construction respiration, it may be possible to ignore the effects of water stress on maintenance respiration (Ryan 1991).

Leaf emergence in temperate deciduous trees usually is predictable with population-specific cumulative thermal sums (Kramer and Kozlowski 1979, Lechowicz 1984, Lindsey 1963, Valentine 1983), although bud break in some species may be controlled by photoperiod (Romberger 1963, Wareing 1953). Leaf senescence may be triggered by reduced moisture availability as a means of avoiding severe water stress (Addicott 1982, Albertson and Weaver 1945, Griffin 1973, Kozlowski 1976, 1991, Landsberg and Jones 1981, Proebsting and Middleton 1980). This response may override other factors that usually

trigger senescence (Addicott 1982). Avoidance of cavitation of vessel elements in xylem is one explanation for patterns of leaf phenology that is generally consistent with anatomical considerations of wood, although protection of investment in leaves also may play a role (Lechowicz 1984). These explanations are consistent with a global model of canopy phenology, which indicates that the seasonal pattern of leaf area within an ecosystem is related to that of evapotranspiration (Raich et al. 1991). Because both temperature and precipitation affect leaf phenology, changes in these variables can affect NPP.

Changes in temperature and precipitation can alter NPP in temperate forests by affecting allocation to leaves and roots. Leaf area in mature conifer forest stands has been observed to be correlated with winter cold temperature indices (Gholz 1982), growing season precipitation (Grier and Running 1977), and indices of water balance (Gholz 1982, Grier and Running 1977). Leaf biomass in forest stands may be correlated with nitrogen availability (Covington and Aber 1980, Gholz et al. 1991, Gower et al. 1992, Myrold et al. 1989, Proe et al. 1992), which is largely controlled by patterns in temperature and precipitation (McGuire et al. 1992).

Root turnover in mature conifer forests has been observed to be positively correlated with a ratio involving precipitation and temperature (Vogt et al. 1986). However, Santantonio and Hermann (1985) observed that fine root production in three Douglas fir forests was inversely related to water availability. Fine root production has been observed to decrease in response to enhanced nitrogen availability in temperate conifer stands (Gower et al. 1992). Also, conifer stands on low quality sites have been observed to have greater fine root production than higher quality sites with the same climate (Keyes and Grier 1981). However, for conifer stands in Wisconsin, Nadelhoffer et al. (1985) reported that fine root production is positively correlated with nitrogen availability. It is not known whether nutrient availability controls fine root production differently in different climatic regimes, or if contradictory results are caused by the different methodologies used to estimate fine root production (Gower et al. 1992, Nadelhoffer and Raich 1992). Thus, it is not clear how changes in temperature and precipitation will qualitatively affect fine root production in conifer forests.

For deciduous forests, Vogt et al. (1986) found no significant correlations between root turnover and climatic variables. However, Nadelhoffer et al. (1985) found positive correlations between fine root production and nitrogen availability for mature deciduous stands in Wisconsin. Furthermore, Nadelhoffer and Raich (1992) found positive correlations between fine root production and litterfall for studies that use the "N Budget" method to estimate root production in forests. Litterfall in deciduous forests is largely determined by leaf production, which is sensitive to nutrient availability and therefore sensitive to changes in temperature and precipitation. If fine root production is related to litterfall, then it also should be sensitive to changes in temperature and precipitation.

Increased water availability has been observed to shift the allocation of biomass in favor of shoots in conifer stands (Gower et al. 1992, Megonigal and Day 1992) and conifer seedlings (Van Den Driessche 1992). Similarly, increased nitrogen availability has been observed to shift allocation in favor of shoots for conifer forest stands (Gower et al. 1992), tree seedlings (Burke et al. 1992, Van Den Driessche 1992), and evergreen shrubs (Aerts et al. 1991). These observations are consistent with the hypothesis that resources are allocated so that growth becomes equally limited by all resources. If this is the case, then relative allocation between leaves and fine roots should be sensitive to changes in temperature and precipitation. However, note that increased nitrogen availability was not observed to cause shifts in favor of shoots for forest stands in Wisconsin (Nadelhoffer et al. 1985).

Responses to Changes in Cloudiness

Changes in cloudiness may affect NPP by altering the amount and quality of radiation reaching both the canopy and the surface. Shortwave radiation plays an important role, because it drives both evaporation and transpiration (Monteith and Unsworth 1990, Sharma 1985); changes in evaporation and transpiration can alter soil moisture and water availability. As previously noted, water availability can affect plant production in a variety of ways. Thus, changes in cloudiness may affect NPP through effects on water balance.

Because the extinction of light through a continuous canopy often can be described with an exponential decay function (Kira et al. 1969, Landsberg 1986,

Monsi and Saeki 1953, Waring and Schlesinger 1985), the amount of photosynthetically active radiation (PAR) reaching individual leaves in a forest is likely to be affected by changes in cloudiness. Net photosynthesis, given adequate nutrients and water, is related to light intensity in a hyperbolic fashion (Kozlowski et al. 1991, Landsberg 1986). Therefore, increases in PAR reaching leaves have the potential to increase photosynthetic rates. However, the response of photosynthesis and growth to light availability may be constrained by the availability of nutrients (Chapin et al. 1987, Shaver et al. 1986, Shaver et al. 1992) and water (Kramer and Kozlowski 1979).

The availability of light also may affect allocation patterns in trees. If water availability does not substantially limit NPP, then the maximum leaf area of a tree can be altered by the availability of light. This can occur because the optimal leaf area for a tree should be that for which all leaves can still make a positive contribution to carbon gain (Mooney 1972). The physiological basis for this prediction is the existence of the light compensation point in leaves, which is the lowest irradiance at which GPP is greater than leaf respiration (Nobel 1991, Schoettle and Fahey 1995). However, nutrient availability may place additional constraints on the quantity of photosynthetic tissue (Chapin 1991a, Covington and Aber 1980, Gholz et al. 1991, Gower et al. 1992, Myrold et al. 1989, Proe et al. 1992).

MODELING NPP RESPONSES OF TEMPERATE FORESTS TO CHANGE IN CARBON DIOXIDE AND CLIMATE

Regression- vs. Process-based Approaches

Because of the complexity of interactions among biological processes that are affected by changes in CO_2 and climate, modeling the response of NPP in temperate forests to changes in CO_2 and climate requires the integration of ecosystem function. Because changes in climate can vary spatially (Mitchell et al. 1990), estimating the response of NPP will require using models that can make geographically referenced predictions. Both regression- and process-based models are available to assess the response of NPP in a geographically referenced fashion. Regression-based models use empirically derived relationships between climate and NPP to make

predictions (Agren et al. 1991). In contrast, process-based models describe how important ecosystem processes, such as photosynthesis, respiration, decomposition, and nutrient cycling, interact to affect NPP.

McGuire et al. (1993) compared the responses of NPP to elevated temperature and CO_2 for temperate forests in North America, using both a regression- and a process-based model. The regression-based model, called the Osnabruck Model (OBM) (Esser 1987, 1991), was found to have serious drawbacks. One problem with the predicted responses of OBM was that important feedbacks between temperature and ecosystem processes were not fully expressed. For example, the effect of elevated temperature in enhancing evapotranspiration to decrease water availability and reduce NPP could not be produced by OBM under any circumstances. Also, important interactions between temperature and elemental availability did not appropriately constrain the ability of the vegetation to incorporate elevated CO_2 into production.

Although the use of regression-based models in ascertaining the importance of terrestrial ecosystems in the global carbon cycle has been of enormous scientific value (Esser 1987, 1991, Gillette and Box 1986, Lieth 1973, 1975, Rosensweig 1968), McGuire et al. (1993) concluded that the application of the approach to address global change issues is undesirable. In particular, the regression-based approach may suffer the classic limitation of regression analysis, i.e., it may be inappropriate to extrapolate the regressions for conditions that are novel to ecosystems. For example, a mean annual increase of +5° C in the southeastern United States may create seasonal temperature distributions that are now found in the tropics; but the seasonal distributions of photosynthetically active radiation in this region will not be typical of the tropics. Global change has the potential to produce new combinations of environmental variables for some ecosystems.

McGuire et al. (1993) concluded that the process-based approach has the potential to overcome many of the drawbacks of the regression-based approach. The process-based model that was used in the comparison, called the Terrestrial Ecosystem Model (TEM) (McGuire et al. 1992, Raich et al. 1991), was able to simulate the effects of known feedbacks that occur between temperature and ecosystem processes and between temperature and elemental availability. It also was con-

cluded that the equations in process-based models, although not perfect, can be modified as understanding of ecosystem processes advances. Finally, the importance of considering feedbacks can be directly investigated by using a process-based model.

Potential Implications of Change for NPP of U.S. Temperate Forests

To investigate the potential implications of changes in CO_2 and climate for U.S. temperate forests, we drove TEM with the output of each of four General Circulation Models (GCMs) that were obtained from the National Center for Atmospheric Research (Jenne 1992). The simulations include: the Goddard Institute of Space Studies (GISS) GCM (Hansen et al. 1983, 1984); the Oregon State University (OSU) GCM (Schlesinger and Zhao 1989); and two GCM simulations from the Geophysical Fluid Dynamics Laboratory (GFDL 1 and GFDL Q) (Manabe and Wetherald 1987, Wetherald and Manabe 1988). The mean monthly temperature, monthly precipitation, and mean monthly percent cloud cover for both the current and $2XCO_2$ simulations of each GCM were organized by Melillo et al. (1993) at 0.5° latitude × 0.5° longitude resolution for the entire globe. For examining climate changes predicted for U.S. temperate forests we chose all 0.5° × 0.5° grid cells in the vegetation used by McGuire et al. (1992) that were classified as temperate coniferous forest in Alaska and in the continental United States as boreal forest, boreal forest wetland, temperate coniferous forest, temperate deciduous forest, temperate mixed forest, temperate broadleaf evergreen forest, and temperate forest wetland (fig. 2.1). We did not consider the boreal forests of Alaska in this study.

Boreal forest in our analysis may represent either true boreal forest, which occurs mostly in northern Minnesota, or subalpine forest in mountainous regions, which generally contain a mixture of spruce and fir species. Boreal forest wetland also occurs predominantly in northern Minnesota. Temperate coniferous forest occurs primarily in southeastern Alaska and the mountainous regions of the western United States. Much of the eastern United States is dominated by temperate mixed forest, except for the Ohio Valley, Middle Atlantic, and Appalachian Mountain regions, which are primarily classified as temperate deciduous forest. Temperate forest wetland occurs predominantly

Table 2.1.—Characteristics of the general circulation models (GCMs) used in this study for the spatial domain of temperate forests in the United States.[1,2]

GCM	GFDL 1	GFDL Q	GISS	OSU
Date of model run	1984-85	1987-88	1982	1984-85
Model resolution (lon° × lat°)	7.5×4.44	7.5×4.44	10.0×7.83	5.0×4.00
Baseline CO_2 (ppmv)	300	300	315	326
Mean change in mean annual temperature (C°) for $2XCO_2$	+5.2°	+4.3°	+4.4°	+3.2°
Maximum change in mean annual temperature (C°) for $2XCO_2$	+7.2°	+5.5°	+5.3°	+3.9°
Minimum change in mean annual temperature (C°) for $2XCO_2$	+3.2°	+3.4°	+3.1°	+1.9°
Mean change[3] in annual precipitation for $2XCO_2$	+1.2%	+5.0%	+6.7%	+4.4%
Maximum change[3] in annual precipitation for $2XCO_2$	+35.5%	+34.2%	+23.6%	+31.8%
Minimum change[3] in annual precipitation for $2XCO_2$	-17.2%	-14.4%	-7.1%	-12.9%
Mean change[3] in mean annual cloudiness for $2XCO_2$	-4.0%	-4.8%	-3.9%	-7.5%
Maximum change[3] in mean annual cloudiness for $2XCO_2$	+9.5%	+11.2%	+1.8%	+2.4%
Minimum change[3] in mean annual cloudiness for $2XCO_2$	-13.2%	-18.9%	-8.5%	-19.1%

[1]Defined as the 1443 grid cells (0.5° latitude by 0.5° longitude) in McGuire et al. (1992) classified as temperate coniferous forest in Alaska and in the continental United States as temperate coniferous forest, temperate deciduous forest, temperate mixed forest, temperate broadleaf evergreen forest, temperate forest wetland, boreal forest, and boreal forest wetland.

[2]Abbreviations for GCMs are as follows: GFLD 1, Geophysical Fluid Dynamics Laboratory 1; GFDL Q, Geophysical Fluid Dynamics Laboratory Q; GISS, Goddard Institute for Space Studies; and OSU, Oregon State University.

[3]Based on proportional differences.

in the floodplain of the southern Mississippi River, although there are some grid cells of this vegetation along the Atlantic Coast. Temperate broadleaf evergreen forest primarily represents evergreen oaks in California, except for one grid cell along the Atlantic coast in the southeastern United States.

The 1443 grid cells that describe potential temperate forests in the United States cover 3.41×10^6 km^2.

Among the GCMs, changes in mean annual temperature predicted for these grid cells vary between 1.9° C and 7.2° C, changes in annual precipitation vary between -17.2% and 35.5%, and changes in mean annual cloud cover (proportional differences) vary between -19.1% and 11.2% (table 2.1). Coupled with elevated CO_2, these climatic variations have the potential to alter the NPP of temperate forests in a variety of ways.

The Terrestrial Ecosystem Model

As concluded by McGuire et al. (1992, 1993), investigations of the response of NPP to changes in CO_2 and environmental variables require the use of process-based models that consider linkages between the carbon and nitrogen cycles. The TEM (fig. 2.4) is a process-based ecosystem simulation model that uses spatially referenced information on climate, elevation, soils, vegetation, and hydrology to make monthly estimates of
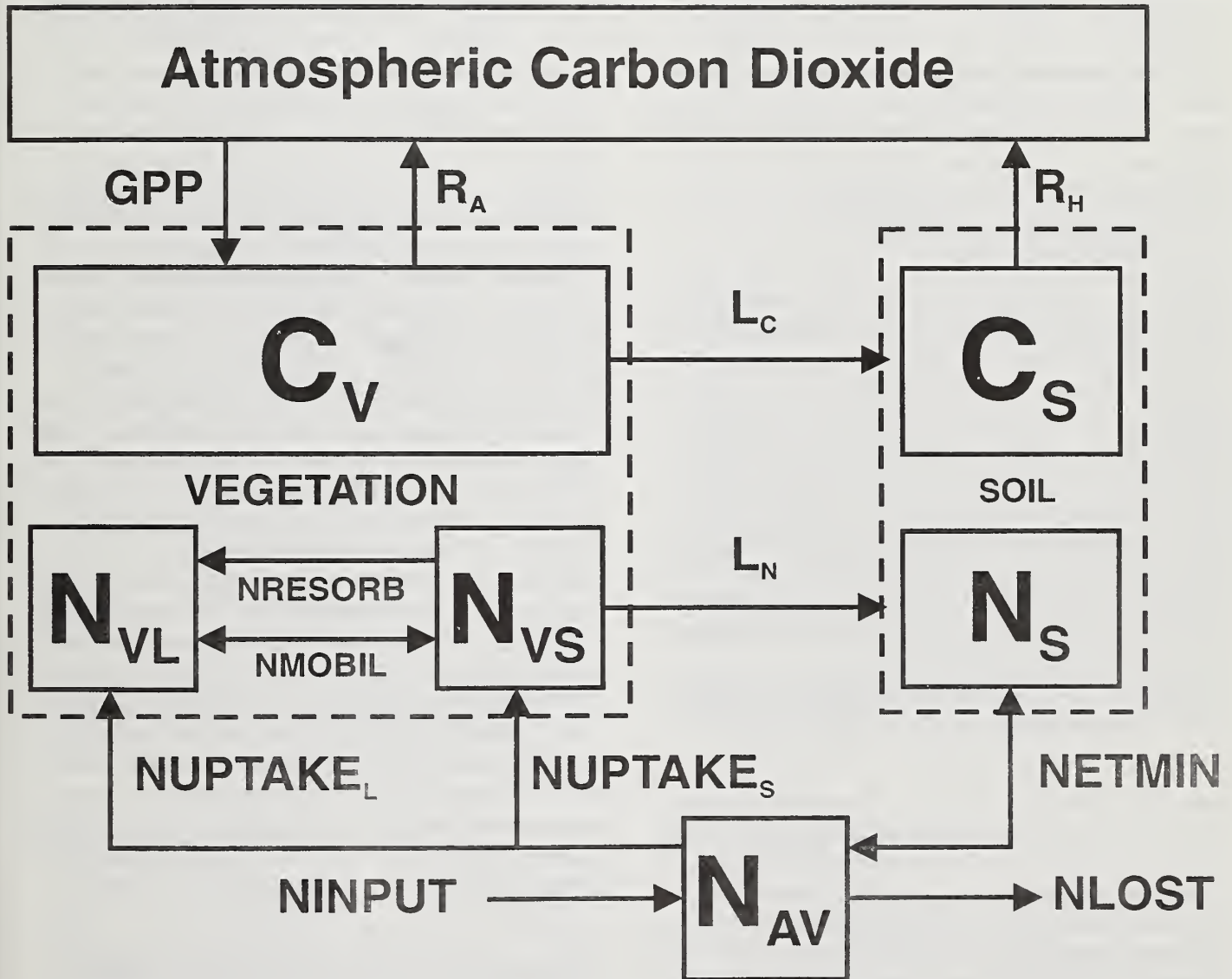
Figure 2.4.—The Terrestrial Ecosystem Model (TEM). The state variables are: carbon in the vegetation (C_V); structural nitrogen in the vegetation (N_{VS}); labile nitrogen in the vegetation (N_{VL}); organic carbon in soils and detritus (C_S); organic nitrogen in soils and detritus (N_S); and available soil inorganic nitrogen (N_{AV}). Arrows show carbon and nitrogen fluxes: GPP, gross primary productivity; R_A, autotrophic (plant) respiration; R_H, heterotrophic respiration; L_C, litterfall carbon; L_N, litterfall nitrogen; NUPTAKE$_S$, nitrogen uptake into the structural nitrogen pool of the vegetation; NUPTAKE$_L$, nitrogen uptake into the labile nitrogen pool of the vegetation; NRESORB, nitrogen resorption from dying tissue into the labile nitrogen pool of the vegetation; NMOBIL, nitrogen mobilized between the structural and labile nitrogen pools of the vegetation; NETNMIN, net nitrogen mineralization of soil organic nitrogen; NINPUT, nitrogen inputs from outside the ecosystem; and NLOST, nitrogen losses from the ecosystem.

important carbon and nitrogen fluxes and pool sizes (McGuire et al. 1992, 1993, Melillo et al. 1993, Raich et al. 1991). The model is grid-cell based, and extrapolation is accomplished by running the model to equilibrium for each of the 1443 grid cells that were earlier defined as describing temperate forests in the United States. Because we use TEM to make equilibrium predictions, its estimates of carbon and nitrogen dynamics apply only to undisturbed and mature (i.e., potential) vegetation; they do not include the effects of land use or other disturbances.

For each monthly time step in a model run, NPP in TEM is calculated as the difference between GPP and R_A. The calculation of R_A considers both maintenance respiration (McGuire et al. 1992, 1993) and construction respiration (Raich et al. 1991). The flux GPP considers the effects of several factors and is calculated at each time step as follows:

$$\text{GPP} = C_{max} \times f(\text{PAR}) \times f(\text{LEAF}) \times f(\text{T}) \times f(CO_2, H_2O) \times f(\text{NA})$$

where C_{max} is the maximum rate of C assimilation, PAR is photosynthetically active radiation, LEAF (i.e., leaf phenology) is leaf area relative to maximum annual leaf area, T is temperature, CO_2 is atmospheric carbon dioxide, H_2O is water availability, and NA is N availability. All of the functions in the GPP equation, as well as other mathematical expressions in the model, are well documented in previous studies with the model (McGuire et al. 1992, 1993, Raich et al. 1991). Here we review the descriptions of $f(CO_2, H2O)$ and $f(\text{NA})$, because of their importance in affecting the capacity of vegetation to incorporate elevated CO_2 into production.

The function $f(CO_2, H_2O)$ is described by the hyperbolic relationship (McGuire et al. 1993, Raich et al. 1991):

$$f(CO_2, H_2O) = C_i / (k_c + C_i)$$

where C_i is the concentration of CO_2 within leaves of the canopy and k_c is the half-saturation constant for CO_2 uptake by plants. The variable C_i is the product of ambient CO_2 and relative canopy conductance to CO_2, a variable which increases from 0 to 1 with increasing water availability (McGuire et al. 1992, Raich et al. 1991). The parameter k_c has been chosen to increase $f(CO_2, H_2O)$ by 37%, for a doubling of atmospheric CO_2 from 340 ppmv to 680 ppmv, with canopy conductance equal to 1 (McGuire et al. 1992, 1993). Among studies that have provided adequate water and nutrients to experimental plants, the range

in the response of plant growth to doubled CO_2 is between 24% and 50% (Gates 1985, Kimball 1975).

The function $f(\text{NA})$ models the limiting effects of plant nitrogen status on GPP (McGuire et al. 1992, 1993). It constrains C uptake when N supply, i.e., the combination of N uptake and vegetation labile N, limits NPP (McGuire et al. 1993). Information on the C to N ratio of production (P_{cn}), a quantity commonly measured in ecosystem studies, is used to determine when N supply limits NPP; $f(\text{NA})$ is adjusted so that production has a C to N ratio equal to P_{cn}. Thus, this implementation assumes that nitrogen use efficiency, i.e., the ratio of NPP to N in new production, is conservative within a vegetation type.

The data used to drive TEM were organized by Melillo et al. (1993) at a resolution of 0.5° latitude by 0.5° longitude. The sources for the global data sets on climate (air temperature, precipitation, and cloudiness), elevation, and soil texture are described in Raich et al. (1991). The climate data represent long-term averages (Hahn et al. 1988, Legates and Willmott 1990a, 1990b). Hydrologic inputs for TEM were determined by a water balance model (Vorosmarty et al. 1989) that uses the climate, elevation, soils, and vegetation data.

The application of TEM to a grid cell requires the use of monthly climatic and hydrologic data and soil- and vegetation-specific parameters appropriate to the grid cell. Although many of the vegetation-specific parameters in the model are defined from published information (McGuire et al. 1992, Raich et al. 1991), some are determined by calibrating the model to the fluxes and pool sizes of an intensively studied field site, the calibration site for the ecosystem type. Most of the data used to calibrate the model for the ecosystem types in this study are documented (McGuire et al. 1992). The temperate forest wetland and boreal forest wetland calibrations use parameters from the temperate deciduous forest and boreal forest calibrations, respectively. During extrapolation of these calibrations, they were run with soil moisture equal to field capacity and with estimated evapotranspiration equal to potential evapotranspiration.

Extrapolation of TEM for Contemporary Climate

To estimate carbon and nitrogen dynamics of potential vegetation for "contemporary" conditions, we applied TEM to the 1443 grid cells at 355 ppmv CO_2 using the long-term climate data. Under these conditions, TEM estimates the annual NPP for po-

Table 2.2.—Estimates by the Terrestrial Ecosystem Model (TEM) of annual net primary productivity (NPP) for temperate forests in the United States at an atmospheric concentration of 355 ppmv CO_2.[1]

Vegetation Type	Area 10^6 km^2	Cells	Total NPP 10^{15} g C yr^{-1}	Mean NPP	Max NPP	Min NPP
					-------- (g C m^{-2} yr^{-1}) --------	
Boreal forest	0.16	74	0.050	306.3	382.8	224.6
Boreal forest wetland	0.02	11	0.007	318.1	324.1	310.6
Temperate coniferous forest	0.76	352	0.325	427.4	585.5	253.9
Temperate deciduous forest	0.88	368	0.670	759.4	943.1	429.2
Temperate mixed forest	1.38	561	1.110	805.7	1044.6	464.1
Temperate broadleaf evergreen forest	0.05	19	0.023	487.5	925.3	321.8
Temperate forest wetland	0.15	58	0.138	926.7	1134.6	820.4
All U.S. temperate forests	3.41	1443	2.325	682.6	1134.6	224.6

[1]Vegetation-based estimates may not sum to totals because of the effects of rounding in reporting those estimates.

tential temperate forests in the United States to be 2.325 Pg (10^{15} g) C, or 682.6 g C m^{-2} yr^{-1} (table 2.2). The most productive ecosystem is temperate mixed forest, which accounts for 47.7% of NPP while comprising 40.5% of temperate forest land area in the United States (table 2.2). Mean NPP estimates for ecosystems range from 306.3 g C m^{-2} yr^{-1} for boreal forest to 926.7 g C m^{-2} yr^{-1} for temperate forest wetland (table 2.2). Estimates for individual grid cells range from 224.6 g C m^{-2} yr^{-1} in boreal forest to 1134.6 g C m^{-2} yr^{-1} in temperate forest wetland (table 2.2). The variability of NPP estimates by TEM, which reflects spatial heterogeneity in climate and soils, has been evaluated in previous applications of the model (McGuire et al. 1992, Melillo et al. 1993, Raich et al. 1991). In general, the NPP predictions of TEM compare well with field measurements of NPP in mature ecosystems (Melillo et al. 1993). Also, the accuracy of nitrogen cycling estimates by TEM compare well with field measurements (McGuire et al. 1992).

Future Climate Scenarios

Melillo et al. (1993) generated "GCM climates" for TEM by using the output variables of surface air temperature, precipitation, and total cloud cover for the current and $2XCO_2$ simulations of each GCM to modify the contemporary climate data for TEM. First, each of the output variables of each GCM were organized at 0.5° resolution with a spherical interpolation procedure (Willmott et al. 1985). Next, similar to the method of Adams et al. (1990), for each grid cell the ratio of the monthly output of the $2XCO_2$ simula-

tion to that of the $1XCO_2$ simulation was calculated for each of the three output variables; temperature was converted to Kelvin before calculating monthly temperature ratios. Each ratio then was multiplied by the corresponding variable in the data for contemporary climate to determine the input data for TEM that represent the $2XCO_2$ climate for each GCM. In comparison to contemporary climate, the mean changes for mean annual temperature, annual precipitation, and mean annual cloudiness are described for each vegetation type in tables 2.3 through 2.5.

To help separate the effects of changes in CO_2 concentration from those of the GCM climates on the estimates of NPP, we performed a factorial experiment with TEM involving two levels of CO_2 (355 ppmv and 625 ppmv) and five climate scenarios (contemporary and the four GCM climates). We chose the CO_2 level of 625 ppmv because it is an intermediate level of doubled CO_2 among the four GCMs (range 600 ppmv to 652 ppmv; table 2.1).

NPP Responses to Elevated CO_2

For elevated CO_2 with no climate change (contemporary climate at 625 ppmv CO_2), TEM predicts an NPP increase of 5.1% for temperate forests in the United States (table 2.6). Responses for individual grid cells range between 0% and 29.7% (fig. 2.5). The lowest ecosystem responses are predicted for the boreal forest ecosystems (less than 3%; table 2.6). The TEM predicts that NPP in these ecosystems is substantially limited by the availability of inorganic nitrogen (McGuire et al. 1992). Therefore, these veg-

Table 2.3.—Comparison of mean changes in mean annual temperature (C°) among vegetation types for potential temperate forests in the United States as predicted by different general circulation models for a doubling of atmospheric CO_2.

| | General Circulation Model | | | |
	GFDL 1	GFDL Q	GISS	OSU
Boreal forest	+5.8	+4.6	+4.7	+2.9
Boreal forest wetland	+7.0	+4.7	+4.5	+3.5
Temperate coniferous forest	+5.2	+4.3	+4.5	+2.6
Temperate deciduous forest	+5.4	+4.4	+4.6	+3.5
Temperate mixed forest	+5.1	+4.2	+4.2	+3.4
Temperate broadleaf evergreen forest	+4.2	+3.9	+4.4	+2.3
Temperate forest wetland	+4.4	+3.9	+4.6	+3.5
All U.S. temperate forests	+5.2	+4.3	+4.4	+3.2

Table 2.4.—Comparison of mean proportional changes in annual precipitation among vegetation types for potential temperate forests in the United States as predicted by different general circulation models for a doubling of atmospheric CO_2.

| | General Circulation Model | | | |
	GFDL 1	GFDL Q	GISS	OSU
Boreal forest	-0.8%	+7.1%	+13.4%	+5.5%
Boreal forest wetland	-5.6%	+28.4%	+10.4%	+6.5%
Temperate coniferous forest	+5.0%	+8.4%	+16.7%	+5.5%
Temperate deciduous forest	+4.3%	+3.2%	+3.6%	+3.1%
Temperate mixed forest	-2.8%	+3.2%	+2.3%	+5.1%
Temperate broadleaf evergreen forest	+0.0%	+4.1%	+2.9%	-2.7%
Temperate forest wetland	-1.4%	+5.0%	+1.2%	-0.6%
All U.S. temperate forests	+1.2%	+5.0%	+6.7%	+4.4%

Table 2.5.—Comparison of mean proportional changes in mean annual cloudiness among vegetation types for potential temperate forests in the United States as predicted by different general circulation models for a doubling of atmospheric CO_2.

| | General Circulation Model | | | |
	GFDL 1	GFDL Q	GISS	OSU
Boreal forest	-4.5%	-5.4%	-1.2%	-3.3%
Boreal forest wetland	-8.4%	+8.1%	-2.5%	-4.6%
Temperate coniferous forest	-2.1%	-3.9%	-0.5%	-3.7%
Temperate deciduous forest	-2.6%	-5.7%	-5.0%	-7.7%
Temperate mixed forest	-6.2%	-5.2%	-5.5%	-9.7%
Temperate broadleaf evergreen forest	-2.8%	-2.7%	-0.4%	-9.7%
Temperate forest wetland	-3.3%	-4.6%	-5.9%	-13.3%
All U.S. temperate forests	-4.0%	-4.8%	-3.9%	-7.5%

etation types have limited ability to incorporate elevated CO_2 into production (McGuire et al. 1993). The highest ecosystem response predicted by TEM is for temperate forest wetland (23.3%; table 2.6). This response occurs because nitrogen limitation of NPP for the grid cells of this ecosystem, which are not moisture limited, is predicted by TEM to be low in the vicinity of the southern Mississippi River (McGuire et al. 1993). These grid cells therefore substantially incorporate elevated CO_2 into production (McGuire et al. 1993). The range in the predicted response of NPP among temperate mixed, coniferous, and deciduous forests is between 3.1% and 5.8% (table 2.6). Although nitrogen limitation of NPP is not as strong in these systems as in boreal forests, it still is predicted to be substantial (McGuire et al. 1992). Thus, these systems demonstrate a modest capacity for incorporating elevated CO_2 into production.

NPP Responses to Changes in Climate

For no change in CO_2 concentration (355 ppmv CO_2), total NPP for temperate forests in the United States is predicted by TEM to decrease for the GFDL climates (-11.3% and -6.1% for GFDL 1 and Q) and increase for the GISS (+10.5%) and OSU (+5.7%) climates (table 2.6). The large decrease for the GFDL 1 climate may be caused by both the highest predicted temperature increase (table 2.3) and the lowest precipitation increase (table 2.4). Elevated temperature in the southeastern United States has the potential to decrease NPP by increasing respiration costs if NPP is not nitrogen limited (McGuire et al. 1993). The largest total NPP response, which is predicted for the GISS climate, is associated with the greatest increase in mean annual precipitation (table 2.4). The intermediate responses for the GFDL Q and OSU climates are associated with moderate temperature and precipitation increases. Note that for each GCM there is much variability in response among grid cells (fig. 2.5). The GFDL 1 climate, which has the most variability in response (fig. 2.5), also has the most variability for changes in mean annual temperature and annual precipitation (table 2.1).

For no change in CO_2, TEM predicts that NPP in boreal and coniferous forest ecosystems increases in response to all the GCM climates (table 2.6). Production may increase in nitrogen-limited ecosystems when elevated temperature enhances nitrogen avail-

Table 2.6.—Comparison of mean annual NPP (g C m^{-2} yr^{-1}) predicted by TEM, for vegetation types of potential temperate forests in the United States, in experiments involving two levels of atmospheric CO_2 and five levels of climate.[1]

	Climate									
	CON	GFDL1	GFDLQ	GISS	OSU	CON	GFDL1	GFDLQ	GISS	OSU
	----------- 355 ppmv CO_2 ------------					------------ 625 ppmv CO_2 ------------				
Boreal forest	306	353	358	381	354	313	424	412	416	381
Boreal forest wetland	318	341	334	381	372	322	442	401	412	400
Temperate coniferous forest	427	461	459	492	464	444	530	517	540	494
Temperate deciduous forest	759	587	648	901	803	803	752	791	1037	902
Temperate mixed forest	806	725	769	850	842	831	870	922	982	923
Temperate broadleaf evergreen forest	488	495	489	506	496	535	600	589	609	572
Temperate forest wetland	927	714	740	896	975	1143	926	960	1162	1250
All U.S. temperate forests	683	606	641	755	722	718	738	766	869	802

[1]Abbreviations for climates are as follows: CON, contemporary; GFDL1, Geophysical Fluid Dynamics Laboratory 1; GFDLQ, Geophysical Fluid Dynamics Laboratory Q; GISS, Goddard Institute for Space Studies; and OSU, Oregon State University.

ability (McGuire et al. 1992, 1993). Although moisture limitation may play an important role in affecting the NPP response of montane coniferous forests (McGuire et al. 1993, Running and Nemani 1991), increased precipitation predicted for temperate coniferous forests by the GCMs (table 2.4) may offset the tendency of elevated temperature to decrease soil moisture through enhanced evapotranspiration.
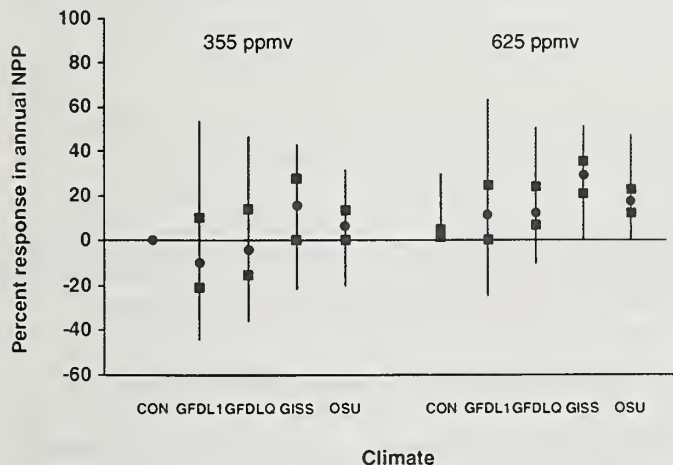

Figure 2.5.—The distributions of response of annual net primary production (NPP) between contemporary climate at 355 ppmv CO_2 and the various GCM climates at 355 ppmv CO_2 (left side of figure) and contemporary and GCM climates at 625 ppmv CO_2 (right side of figure) as predicted by the Terrestrial Ecosystem Model for the 1443 grid cells (0.5° latitude by 0.5° longitude) that describe the historical range of temperate forests in the United States (see fig. 2.1). Abbreviations for climates are as follows: CON, contemporary; GFDL1, Geophysical Fluid Dynamics Laboratory 1; GFDLQ, Geophysical Fluid Dynamics Laboratory Q; GISS, Goddard Institute for Space Studies; and OSU, Oregon State University. Circles identify the median and squares the 25th and 75th percentiles of the distributions. Solid lines delineate the range.

NPP Responses to Changes in CO_2 and Climate

Compared to the mean NPP of temperate forests in the United States for contemporary climate at 355 ppmv CO_2, the overall responses to changes in both CO_2 and climate are predicted by TEM to be positive for all of the GCM climates (table 2.6). Elevated CO_2 causes the distribution of responses for each GCM climate to shift in a positive direction (fig. 2.5). In moist regions, the effect of elevated temperature in enhancing nitrogen availability may allow the incorporation of elevated CO_2, which sufficiently offsets increased plant respiration (McGuire et al. 1993). In dry regions, the effect of elevated CO_2 in enhancing water-use efficiency may generally offset reductions that may be caused by reduced soil moisture and stomatal conductance (McGuire et al. 1993).

Although increases in NPP are predicted for all the GCM climates, there is substantial variation among the responses at smaller spatial scales (table 2.6, fig. 2.6). The response of boreal forest at elevated CO_2 (table 2.6) corresponds to mean increases in temperature (table 2.3). The highest response for temperate coniferous forest occurs for the GISS climate (table 2.6), which predicts the greatest increase in mean annual precipitation (table 2.4). The lowest response for temperate mixed forest (table 2.6), which occurs for the GFDL 1 climate, may be related to decreased precipitation (table 2.4) and to substantial respiration costs caused by high temperature increases (table 2.3).
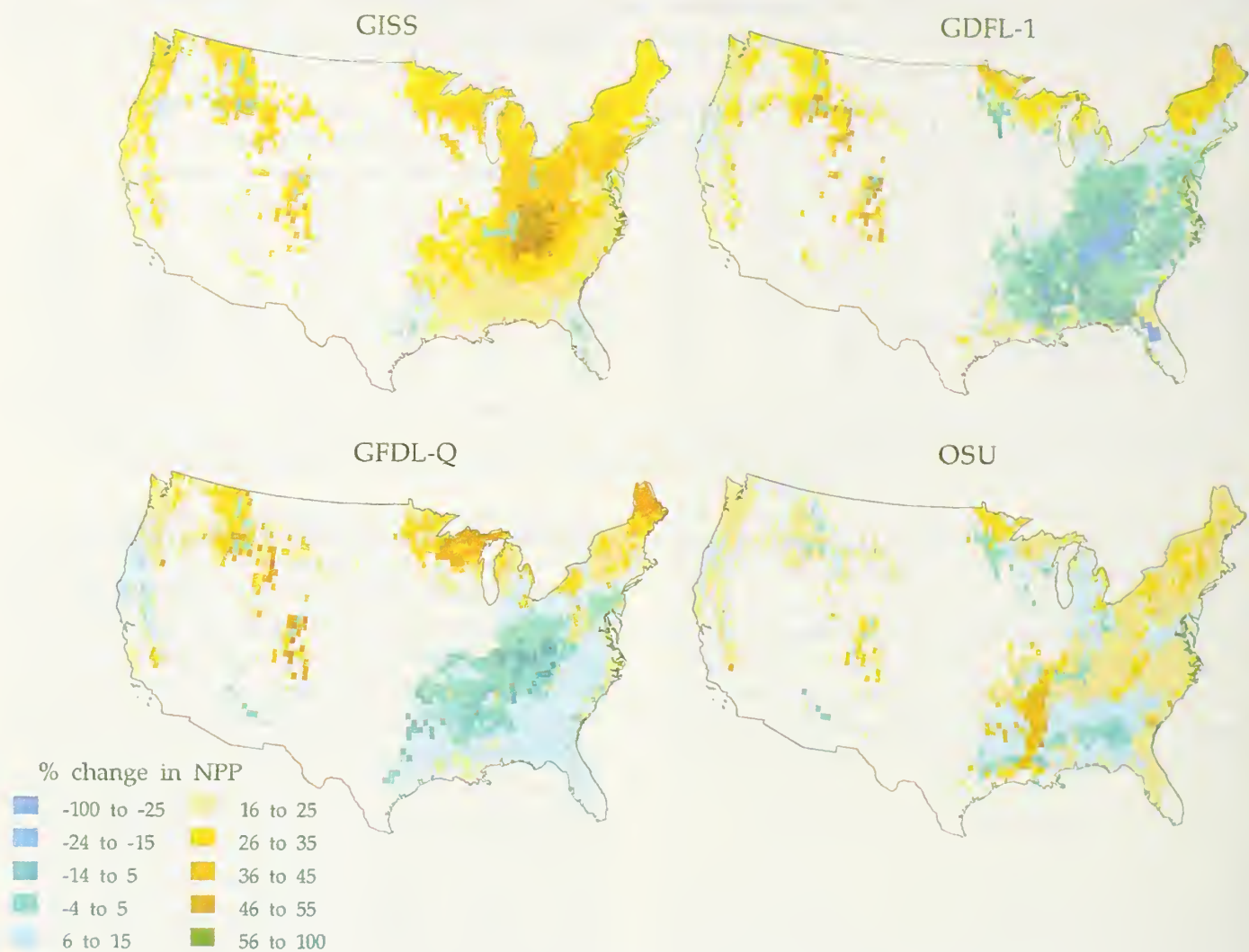
Figure 2.6.—Spatial comparison of the responses in annual net primary production (NPP) between contemporary climate at 355 ppmv CO_2 and the various GCM climates at 625 ppmv CO_2 as predicted by the Terrestrial Ecosystem Model for the 1443 grid cells (0.5° latitude by 0.5° longitude) that describe the historical range of temperate forests in the United States (see fig. 2.1).

Although the effects of changes in temperature and precipitation help explain much of the patterns in the NPP response of temperate forests, changes in cloudiness may be important in some cases. For example, the NPP response of temperate forest wetland (table 2.6), which is limited little by either moisture or nitrogen availability, corresponds to mean decreases in cloudiness (table 2.5). Decreases in cloudiness increase light availability, and light availability is correlated with predicted seasonal NPP in tropical evergreen forests (Raich et al. 1991), an ecosystem in which NPP is predicted by TEM to be limited little by soil moisture (Raich et al. 1991) or nitrogen availability (McGuire et al. 1992).

Limitations In Using the Responses Predicted By TEM

Because of the projected speed of global change, it is important to advance our ability to make predictions of how ecosystem function may respond to change. Using the outputs of atmospheric GCMs to drive process-based ecosystem models is an important step in this direction, because it provides the capability to explore the potential effects of climate change on forest production in a quantitative and geographically referenced manner. Although the results of this study represent our current understanding of how climate change will affect NPP of temperate forests, they are only a preliminary assess-

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ment of the potential effects of climate change on NPP of temperate forests. Because both GCMs and process-based models like TEM have recognized limitations, caution must be exercised in using the results of this study.

A critical concern in the prediction of GCMs is their inadequate treatment of clouds (Cess et al. 1989, Cubasch and Cess 1990, Gates et al. 1992, Ramanathan et al. 1989, Wetherald and Manabe 1988). Because the degree of cloudiness is important for determining the radiative forcing of climate (Ramanathan et al. 1989), predictions of temperature change are sensitive to how clouds are represented in GCMs (Cess et al. 1989, Schlesinger and Roeckner 1988). The degree of cloudiness also is important to ecological processes, because it affects evapotranspiration and the amount of photosynthetically active radiation available to plants. Other concerns in predicting future climates involve the representation in GCMs of surface albedo (Cess et al. 1991, Gates et al. 1992) and aerosols (Charlson et al. 1992, Gates et al. 1992).

Another limitation in applying GCM predictions is that the models operate at very large spatial scales, and predictions may not be very useful for regional interpretation of climate change (Cubasch and Cess 1990). We used the interpolated GCM results to drive TEM for the heuristic examination of potential implications at finer spatial scales, not to predict the future.

An additional limitation in the use of GCM results is that they are equilibrium solutions of climate that correspond to a radiative forcing caused by elevated CO_2. The actual response of climate to increasing levels of CO_2 is likely to lag that predicted for doubled CO_2 because of the thermal capacity of the oceans (Bretherton et al. 1990), although the effect of other radiatively active gases that are increasing may decrease the lag. The temporal response of NPP to changes in CO_2 and climate, i.e., the transient NPP response, also may be sensitive to the time-course of change (Schimel et al. 1990).

Finally, changes in the biosphere may affect the climate system (Melillo et al. 1990). Improved coupling of earth system models may be necessary to accurately predict both climate change and the effects of climate change on ecosystems. The atmospheric sciences community is actively addressing issues concerning the representation of feedbacks in GCMs, GCM spatial resolution, the transient response of climate, and model coupling (Gates et al. 1992).

Process-based models such as TEM also have limitations that affect their use as research and management tools. Although they do not use empirical relationships to directly predict NPP, some of the relationships that describe processes such as photosynthesis, respiration, decomposition, and nutrient cycling may, in part, be empirical. Also, calibration is an empirical procedure for determining some of the parameters in the relationships. The degree to which the relationships and the parameterization of the relationships are robust depends on how accurately they capture mechanisms of the processes they describe. Highly aggregated models such as TEM may need to be less aggregated to better represent the mechanisms of some processes. However, for global models such as TEM, incorporation of more mechanism and the disaggregation of processes should advance with understanding of ecosystem processes. Although the results of process-based models need to be treated with some caution, process-based models have the potential to accurately describe how processes interact to affect NPP.

One specific caution of the TEM results in this study pertains to those for temperate forest wetland that was treated as if it were a dryland ecosystem with no moisture limitation. Although decomposition in dryland ecosystems is appropriately modeled as an aerobic process, in wetland ecosystems, anaerobic processes may be more important. Therefore, the response of NPP in temperate forest wetland has the potential to be different from that predicted in this study. We consider the responses of this ecosystem to be primarily heuristic, and urge extreme caution in using the results.

Another limitation of the TEM results is that we did not consider how the response of vegetation distribution to climate change affects NPP. We also used the model to make equilibrium predictions, and we did not study the potential effects of elevated CO_2 and climate change on forest growth. Little of the temperate forest region is undisturbed; more than 90% of the forests of the United States have been affected by human land use activities (Klopatek et al. 1979, Waddell et al. 1989). It is not known if the equilibrium responses of temperate forest NPP are representative of NPP in growing forests. Furthermore, the transient response of growth may depend on the temporal pattern of changes in CO_2 and climate. Conversions of forest to agriculture, agriculture to forest, and forest harvest/regrowth also have

implications for carbon storage in temperate forests, that involve transient responses of ecosystem processes. To model transient NPP responses of forests requires a forest growth model of ecosystem function. Compared to an equilibrium model, there are additional issues that must be addressed in a forest growth model if it is to be useful to assess transient responses of NPP to changes in CO_2 and climate.

ISSUES IN THE MODELING OF TRANSIENT NPP RESPONSES

Approaches to Modeling Growth

The three major approaches to modeling forest growth are to be found in allometric models, community dynamics (or gap) models, and process-based models of forest growth. Compared to allometric and community dynamics models, the activity of developing process-based models of forest growth is more recent.

Allometric models of forest growth, which have been alternatively labelled forest growth models by Dale et al. (1985) and empirical models by Bruce (1990), traditionally have been used by silviculturists to estimate growth and yield in even-aged plantations (Bruce 1990, Dale et al. 1985). These models predict tree growth based on regressions with simple dependent variables that generally involve age, stand density, and site index (Bruce 1990, Pienaar and Turnbull 1973). Although allometric models reliably estimate yield for the range of the data used to calibrate the models, they do not perform well when extrapolated outside of the calibration range (Dale et al. 1985). Because these models usually are not driven by climatic variables, they cannot be used to predict the response of forest growth to changes in climate (Agren et al. 1991).

Community dynamics models of forest growth simulate the birth, growth, and death of individual trees in a forest. The death of trees in a forest stand creates gaps that provide the opportunity for the birth of trees. Thus, community dynamics models, hereafter referred to as gap models, are based on the premise that fine scale disturbances are the basis for landscape patterns in forest growth. The basic equation that describes diameter growth in trees usually depends on tree diameter, leaf area, tree height, and growth rate (Shugart 1984). Both leaf area and tree

height often are modeled as functions of tree diameter (Dale et al. 1985).

The growth rate of a tree in a gap model depends on a maximum growth rate that may be modified by the effects of light, temperature, moisture, nutrients, and competition (Shugart 1984). In general, the maximum growth rate for a species is empirically derived from diameter-age relationships for trees growing in a stand with a high site index (Shugart 1984). The effects of light depend on the amount of radiation reaching the crown of a tree and the degree to which the tree species is shade tolerant (Shugart 1984). The temperature effect usually is a parabolic function with an optimum that occurs between the maximum and minimum growing-season thermal sums that describe the range of the species (Shugart 1984); the temperature function is zero below and above the minimum and maximum thermal sums. The effects of moisture on diameter growth sometimes involve indices of drought that depend on available soil water calculated from evapotranspiration and rooting zone considerations (Shugart 1984). Gap models may consider the effects of nutrients implicitly or explicitly (Shugart 1984). Most older gap models implicitly implement nutrient limitation, similar to the approach used by Botkin et al. (1972), which assumes a maximum attainable biomass that is nutritionally dependent. Explicit consideration of nutrient availability involves modeling the release of nutrients in the soil through the process of decomposition; this was first done by Aber et al. (1979).

Because gap models consider the effects of temperature, moisture, and light on tree growth, they are potentially useful for investigating the response of forests to climate change (Shugart 1990). These models have been successfully applied to simulate species composition along altitudinal gradients (Botkin et al. 1972, Kercher and Axelrod 1984, Shugart and Noble 1981) and in climatically diverse locations (Bonan 1989, Pastor and Post 1986, Shugart 1984). Shugart and West (1977) used the FORET gap model to reproduce forest composition of Appalachian deciduous forests before the chestnut blight epidemic. Gap models also have reliably reconstructed species composition patterns to late Quaternary climate change (COHMAP members 1988, Solomon and Webb 1985). Studies have used gap models to investigate the potential consequences of CO_2-induced climate change on the species composition of forests (Bonan et al. 1990, Davis and Botkin 1985, Overpeck

et al. 1990, 1991, Pastor and Post 1988, Shugart et al. 1980, Solomon 1986).

Concerns about the use of gap models to predict the response of forests to changes in CO_2 and climate involve rates of species dispersal (Joyce et al. 1990, Overpeck et al. 1991), the quality of parameterization in the models (Cook and Cole 1991), the effects of elevated CO_2 on growth rates (Agren et al. 1991, Botkin 1977, Shugart 1990, Shugart and Emanuel 1985, Solomon 1986, Solomon and West 1986), and feedbacks between vegetation and soil processes (Pastor and Post 1986, 1988). Species in gap models are defined as being either present or absent (Pastor and Post 1986), and when present, migrate at the same rate as climate change. Because climate change during the next 200 to 500 years may exceed the maximum rate of change in the past 18,000 years by 2 to 5 times or more (Overpeck et al. 1991), species migration rates may not be able to keep pace with the rate of climate change (Davis 1981). Future vegetation is likely to be out of equilibrium with climate until the rate of climate change is slowed (Overpeck et al. 1991). The incorporation of species dispersal mechanisms into gap models is important for using these models to assess transient growth responses to the temporal pattern of global change.

Cook and Cole (1991) argue that the assumed climatic response of some species in gap models does not explain how the species presently respond to climate. They argue that dendrochronological data should be used to improve the parameterization of gap models. The use of maximum growth curves that are parameterized for contemporary climate also is a concern. Their use in global change studies may be subject to a similar limitation noted for regression-based models, in that it may not be appropriate to use the curves for conditions novel to ecosystems. In particular, because the curves were measured under conditions of approximately extant CO_2, they may not be appropriate for elevated CO_2.

The response of growth to elevated CO_2 is an important concern because of evidence of correlations between tree growth and the historical increase in atmospheric CO_2 (Graybill 1986, Hari et al. 1984, LaMarche et al. 1984, Parker 1986). Some simple formulations have been implemented in gap models to investigate the potential sensitivity of forest growth to elevated CO_2 (Botkin 1977, Shugart and Emanuel 1985, Solomon and West 1986). Shugart (1990) concluded that the results of these studies are conjec-

tural, and that more mechanistic implementations are required to investigate the effects of elevated CO_2 on forest growth.

Pastor and Post (1986) demonstrated the importance of considering interactions between the carbon, water, and nutrient dynamics of decomposition in gap models to predict the transient response of forest growth. Because the interaction of whole-ecosystem carbon, water, and nutrient dynamics is important to consider in the NPP response of equilibrium forests to changes in CO_2 and climate (McGuire et al. 1992, 1993), it also should be important in growing forests. As previously noted, the effects of elevated CO_2 in shifting allocation to belowground biomass in tree seedlings seems to be strongest for situations in which water or nutrients substantially limit NPP. If resources are allocated so that growth tends to become equally limited by the availability of carbon, water, and nutrients (Bloom et al. 1985, Chapin et al. 1987), then the response of growth should be sensitive to their relative availabilities.

The need to implement more mechanism in the response of growth to changes in CO_2, and the importance of considering linkages between vegetation and soil processes, suggest that gap models should evolve to be more process-based. For gap models, this means that individual trees in a stand should grow in a process-based fashion. However, because the pattern of species turnover in forests may reflect temporal patterns in resource availability (Pastor and Post 1986, Van Cleve et al. 1983, Van Cleve et al. 1991), process-based models of forest growth instead may model the growth of entire forest stands. If functional considerations, such as resource availability, control the death and birth of trees, it may be possible to implicitly account for the effects of these fine scale events on forest growth with a stand-level approach. The stand-level approach may be particularly useful in modeling the effects of large scale disturbances, such as harvest or fire, by determining the effects of disturbance on the pools of the model and restarting the model on the altered stand. Also, at large spatial scales, the stand-level approach has significant computational advantages compared to the individual-tree approach.

Regardless of whether a tree-based or stand-level approach is preferred, a critical challenge in developing process-based models of forest growth is to effectively model the allocation of biomass for the acquisition of carbon, water, and nutrients (Landsberg et

al. 1991). Allocation of biomass to leaves is critical in the harvesting of light and atmospheric carbon, and allocation of biomass to fine roots is important for acquiring water and nutrients. Branches, boles, and coarse roots, which can be broadly categorized as stem wood, are important both as storage organs and as conduits between leaves and fine roots.

Modeling Allocation in Process-based Models

Some process-based models of resource allocation have assumed constant allocation coefficients to partition biomass among plant organs (Makela and Hari 1986, McMurtrie and Wolf 1983, Running and Coughlan 1988), although others have implemented algorithms for flexible allocation. Thornley (1972) controlled the relative growth of roots and shoots with the concentrations of carbon and nitrogen in each of the organs; the transport of carbon from leaves to roots and of nitrogen from roots to leaves is determined by diffusion pipes between leaves and roots. The diffusion pipe approach recently was implemented by Rastetter et al. (1991) in a generalized ecosystem model. Running and Gower (1991) calculated a partitioning ratio that is sensitive to indices of water and nitrogen availability to determine relative allocation of available photosynthate between leaves and roots; allocation to stems is determined as a residual after satisfying leaf and root growth.

Another approach to flexible allocation is the principle of functional balance, in which shoot to root ratios are adjusted to maintain a constant carbon to nitrogen ratio in vegetation (Davidson 1969). This approach has been used in several models (Makela 1986, 1990, Reynolds and Thornley 1982). However, as trees get older, the carbon to nitrogen ratio generally increases because of increases in nitrogen-poor heartwood. Makela (1986, 1990) attempted to circumvent this problem by implementing a target carbon to nitrogen ratio of new growth. However, because leaves, sapwood, and fine roots have different carbon to nitrogen ratios, different allocation patterns should affect the target carbon to nitrogen ratio. Furthermore, the carbon to nitrogen ratios of these tissues may be environmentally sensitive (Ingestad 1979). This issue is particularly relevant because of the effect of elevated CO_2 in generally reducing leaf nitrogen concentrations, and perhaps in reducing whole plant nitrogen concentrations. If heartwood formation and the flexibility in tissue nitrogen concentrations can be modeled effectively, then the functional balance approach shows promise in the modeling of forest growth responses to changes in CO_2 and climate.

There are several constraints that assist in modeling allocation patterns. One is that a strong relationship often exists between leaf area and the cross-sectional area of sapwood (Bancalari et al. 1987, Benecke and Nordmeyer 1982, Blanche et al. 1985, Brix and Mitchell 1983, Coyea and Margolis 1992, Dean et al. 1988, Grier and Waring 1974, Hungerford 1987, Kaufmann and Troendle 1981, Keane and Weetman 1987, Kyker-Snowman and Wilson 1988, Long and Smith 1988, Magnussen et al. 1986, Marchand 1984, Paine et al. 1990, Robichaud and Methven 1992, Rogers and Hinkley 1979, Shinozaki et al. 1964a, 1964b, Snell and Brown 1978, Thompson 1989, Waring et al. 1977, 1982, Whitehead 1978, Whitehead et al. 1981, 1984). The explanation for this relationship, referred to as the pipe model theory (Shinozaki 1964a), is that the cross-sectional area of sapwood is indicative of the amount of vascular tissue that is necessary to support leaves on a tree. Therefore, heartwood represents unused pipes that once supported leaves (Shinozaki 1964a). Several process-based models of tree growth make use of the pipe model theory to model the diameter growth of trees (Ludlow et al. 1990, Makela 1986, 1990, Valentine 1985). However, it is important to note that the relationship between leaf area and sapwood area may be sensitive to a variety of factors including water stress, tree age, stand density, and site quality (Bancalari et al. 1987, Brix and Mitchell 1983, Coyea and Margolis 1992, Dean et al. 1988, Keane and Weetman 1987, Long and Smith 1988, Waring and Schlesinger 1985).

Although it may be possible to constrain sapwood area with leaf area, the problems of both height growth and heartwood formation must be solved to completely constrain diameter growth based on allocation to leaf area. There are empirical relationships between height and diameter of trees (Botkin et al. 1972, Ker and Smith 1955, Shugart 1984), although these may break down for old-growth forests in which diameter may continue to increase after height growth has ceased. Theoretical treatments of height growth in trees have been based on competition for light, and indicate upper limits to height growth that

depend on canopy closure (Iwasa et al. 1984, Makela 1985). Dynamic implementations of height growth have treated it as a calibrated function of changes in the growth of foliage biomass, for which height growth stops when canopy development ceases (Makela 1990, Valentine 1985). This latter approach seems most appropriate for implementation in process-based models of forest growth, although more data on mechanistic controls over tree height are needed (Makela 1990).

Understanding heartwood formation is important for several reasons. First, because heartwood is essentially metabolically inactive, it contributes little to whole plant respiration. Second, heartwood is nutrient-poor relative to sapwood. Therefore, the effective modeling of plant carbon budgets and of carbon-nutrient balance depend on understanding the relative formation of heartwood and sapwood. Finally, heartwood may represent a possible sink for carbon in mature forest ecosystems. Although tree height, leaf area, and sapwood area are known to plateau in mature forests (Carmean 1972, Waring and Schlesinger 1985, Yang and Hazenberg 1991a, 1991b, Yang and Murchison 1992), heartwood may continue to increase (Yang and Hazenberg 1991a, 1991b). Because sapwood plays an important role in the storage of carbon and nutrients (Gholz and Cropper 1991, Margolis et al. 1988, McLaughlin et al. 1980, Mooney 1972, Wargo 1979), it may be a source for carbon and nutrients in building new leaves. Old sapwood also may supply carbon and nutrients for new sapwood, which is needed for new leaves and which directly increases diameter growth. Thus, heartwood formation may be driven by the process of supplying carbon and nutrients from old sapwood to build new leaves and sapwood (Margolis et al. 1988).

Leaf area may plateau in older forests for several reasons. Water balance plays an important role in constraining leaf area (Gholz 1982, Grier and Running 1977). Nemani and Running (1989) formalized this constraint into the hydrologic equilibrium theory of leaf area. However, in areas where water availability does not substantially limit NPP, nutrient availability may constrain leaf area (Chapin 1991a, Covington and Aber 1980, Gholz et al. 1991, Gower et al. 1992, Myrold et al. 1989, Proe et al. 1992). Also, temperature may affect the canopy compensation point in conifers to constrain leaf area (Ryan et al. 1995). Finally, because light availability affects the carbon balance of leaves (Schoettle and Fahey 1995),

it also should play a role in limiting leaf area. In forests where leaf area has reached a maximum, leaf turnover, i.e., the rate of leaf shedding and production of new leaves, should drive the formation of new heartwood and sapwood. The mechanistic relationships among leaf area, sapwood cross-sectional area, tree height, and heartwood formation provide enough constraints to model the relative allocation between leaves and stems. However, modeling the relative allocation between leaves and fine roots is necessary to fully constrain the allocation problem.

There are several approaches to modeling the growth of fine roots, although only some are appropriate for modeling the response of fine root growth to global change (Santantonio 1990). Because the fixed partitioning approach (Makela and Hari 1986, McMurtrie and Wolf 1983, Running and Coughlan 1988) does not allow flexibility in allocation among different plant organs, it cannot be used to predict how fine root growth responds to change. Equilibrium approaches, such as the nitrogen budget method (Nadelhoffer et al. 1985), and indirect calculation methods (Briggs et al. 1986) also are not appropriate for predicting allocation responses of non-equilibrium forests. Thornley's (1972) substrate-control and diffusion-resistance approach may be appropriate for modeling the response of fine roots to global change (Santantonio 1990). Rastetter et al. (1991) used this approach to simulate fine root growth and allocation among leaves, stems, and fine roots in response to changes in CO_2, climate, and nitrogen deposition.

The functional balance approach of Davidson (1969) also is promising (Makela 1990), and has been suggested to be the most appropriate approach to modeling the growth of fine roots (Santantonio 1990). The approach may be implemented during any time step of a simulation by calculating carbon-nutrient balance and determining whether NPP is more limited by the availability of carbon or nutrients (McGuire et al. 1992). If NPP is more limited by carbon availability, then allocation should be in favor of leaves. Alternatively, if it is more limited by nutrients, then allocation should be in favor of fine roots. The importance of water availability in limiting NPP presents an interesting problem to this approach. The effect of low water availability is to cause NPP to be limited by carbon availability through increased stomatal resistance. The appropriate allocation response of a plant in this case may be to shift allocation in favor of fine

roots rather than leaves to gain access to more water. However, if the limiting effect of water availability on carbon-nutrient balance is detectable (McGuire et al. 1993), this problem can be resolved. Thus, it should be possible to implement the functional balance approach to constrain relative allocation between leaves and fine roots. By combining these constraints with those between leaf and stemwood production, it should be possible to implement allocation in process-based models of forest growth.

Although it may be possible to implement allocation in process-based models, the details of different solutions may result in different predicted growth responses to changes in CO_2 and climate. Also, different approaches to modeling decomposition and water relations in process-based models may affect predicted responses. Furthermore, the choice of tree-level or stand-level approaches to modeling forest growth creates potential for variability in predicted responses. Thus, there is a need to both develop and compare process-based models of forest growth that use different implementations and approaches. However, to effectively compare the responses of different models, data from experimental studies that are designed to test the modeling approaches are needed. At the first order, these experimental studies need to examine allocation and NPP responses during forest growth by manipulating single factors that may change: CO_2, temperature, precipitation, and light availability. If the models are used for predicting responses at large spatial scales, then these studies need to be replicated over a range of climates that occur in temperate forests. Because these studies need to provide data throughout the temporal sequence of forest growth, they must be long-term studies. The commitment to long-term integration between modeling and experimentation is important for generating confidence in the use of models to help define the implications of climate change for forest management and policy.

CONCLUSION

Much of the temperate forest region is disturbed by human land use activities (Klopatek et al. 1979, Waddell et al. 1989). Although process-based models of equilibrium ecosystem function can provide a preliminary assessment of the effect of changes in CO_2 and climate on forest production, models of

forest growth will be required to make predictions that forest managers and policy makers can use to prepare for change. Allometric models of forest growth are not appropriate for assessing production responses to climate change (Agren et al. 1991). Because of the complex interactions of CO_2 and environmental variables on plant and soil processes, gap models will need to implement more mechanistic processes to effectively model NPP responses (Pastor and Post 1986, 1988, Shugart 1990). Gap models need to become more process-based to address questions about the response of forest growth to changes in CO_2 and climate. The incorporation of process-based decomposition dynamics into a gap model by Pastor and Post (1986, 1988) demonstrated the value of this activity. Also, the absence of belowground biomass in most gap models makes them of little use in addressing questions concerning the use of forests to mitigate the atmospheric increase in CO_2; process-based models of forest growth must consider belowground processes to address questions about how whole-ecosystem carbon storage responds to global change. Allocation is a critical challenge in designing process-based models of forest growth that are capable of assessing responses to changes in CO_2 and climate. Observed constraints among the growth of leaf area, stemwood, and fine roots show promise in solving this problem. However, there is a need to both develop and compare process-based models of forest growth that use different implementations and approaches. Experimental studies that examine how changes in CO_2 and climate affect allocation and NPP during forest growth are needed to test different process-based models of forest growth. The commitment to long-term integration between modeling and experimentation is important for generating confidence in the use of models to help define the implications of change for forest management and policy. However, the use of geographically referenced responses from available process-based equilibrium models may help to explore those implications now.

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3. Influence of Climate Change on Supply and Demand for Timber

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This chapter examines the effect of increased atmospheric carbon dioxide on the timber situation in the United States. A doubling of carbon dioxide levels by the year 2065 is thought to be associated with widespread changes in forest productivity. Gains in productivity are expected from an increase in available carbon coupled with changes in precipitation and temperature (Chapter 2). This effect on forest productivity could be large enough to potentially make significant shifts in the supply and demand for wood products.

To assess the effect on timber markets, the TAMM/NAPAP/ATLAS forest sector model (TAMM, Adams and Haynes 1980; NAPAP, Ince 1994; ATLAS, Mills and Kincaid 1992) was run for three scenarios under which forest productivity was sensitive to climate change. The forest productivity data were derived from the Terrestrial Ecosystem Model (TEM, McGuire et al. 1992). The climate data input to TEM were derived from four general circulation models (GCMs) run under the assumption of doubled atmospheric carbon dioxide (Chapter 2.)

Powell et al. (1993) estimate there are 606 million acres of forest land in the conterminous U.S. The TAMM/NAPAP/ATLAS[6] solution represents the entire U.S. timber market, however, the changes in productivity presented here affect only private timberlands.[7] Excluded are public lands, reserved areas, sparsely stocked or arid lands, and urban areas.[8] The timberland share is significant in a market sense, however, because of the 490 million acres of timberland in the conterminous U.S., 73% are in private ownership. Most harvest comes from timberland and it was

estimated that 82% of the harvest in 1991 came from the private ownership (Powell et al. 1993). Harvest on public land is, however, included as exogenous input to the TAMM market solution.

THE TIMBER ASSESSMENT MARKET MODEL-TAMM

The TAMM system has become one of the best known examples of what are termed forest sector models.[9] Since its inception in the late 1970's, this system of models has undergone a number of extensions and revisions designed to improve the realism of its projections and the utility of its output to resource analysts and policy makers. Details about the various input assumptions used in TAMM are described briefly here, and in more detail in the 1989 RPA Timber Assessment (Haynes 1990).

TAMM provides an integrated structure for considering the behavior of regional prices, consumption, and production in both stumpage and product markets. Within this structure are a fuelwood model, a pulp and paper model, timber growth and yield models, and models that predict timberland area and forest type changes. They provide long-term projections of price, consumption, and trends in production. To a far greater extent than was possible in the past, the use of TAMM has focused attention on the effects of alternative forest policies and programs and the dependence of projections on (exogenous) input assumptions. In Forest Service assessments these assumptions concern the major determinants of the supply and the demand for various forest products.

The general structure of the modeling system is shown in figure 3.1. Exogenous inputs to TAMM include trade, fuelwood, and area change. Briefly, product demand, such as softwood lumber, is obtained by multiplying the ratio of product use per unit of activity (such as the number of housing starts) times the number of units and summing these results over all the various end uses for the product. Hard-

[5]Pacific Northwest Forest and Range Experiment Station, Portland, OR.

[6]Hereafter called TAMM

[7]Areas qualifying as timberland have the capability of producing in excess of 20 cubic feet per acre per year in natural stands and some may be inaccessible and/or inoperable. Further, these projections include only live trees of commercial species meeting specified standards of quality or vigor. When associated with volume, these net growing stock inventories include only trees 5.0-inches dbh and larger. Cull trees are excluded.

[8]Public timberland is not explicitly modeled, harvest on public lands is determined via formal land planning efforts (vs. markets), and detailed inventory data is not yet available for National Forest land in the West.

[9]A forest sector model, in general, combines activities related to the use of wood: forest growth and harvest; the manufacture of pulp, paper, and solid wood products; and international trade and intermediate and final consumption of these products (Kallio et al. 1987).
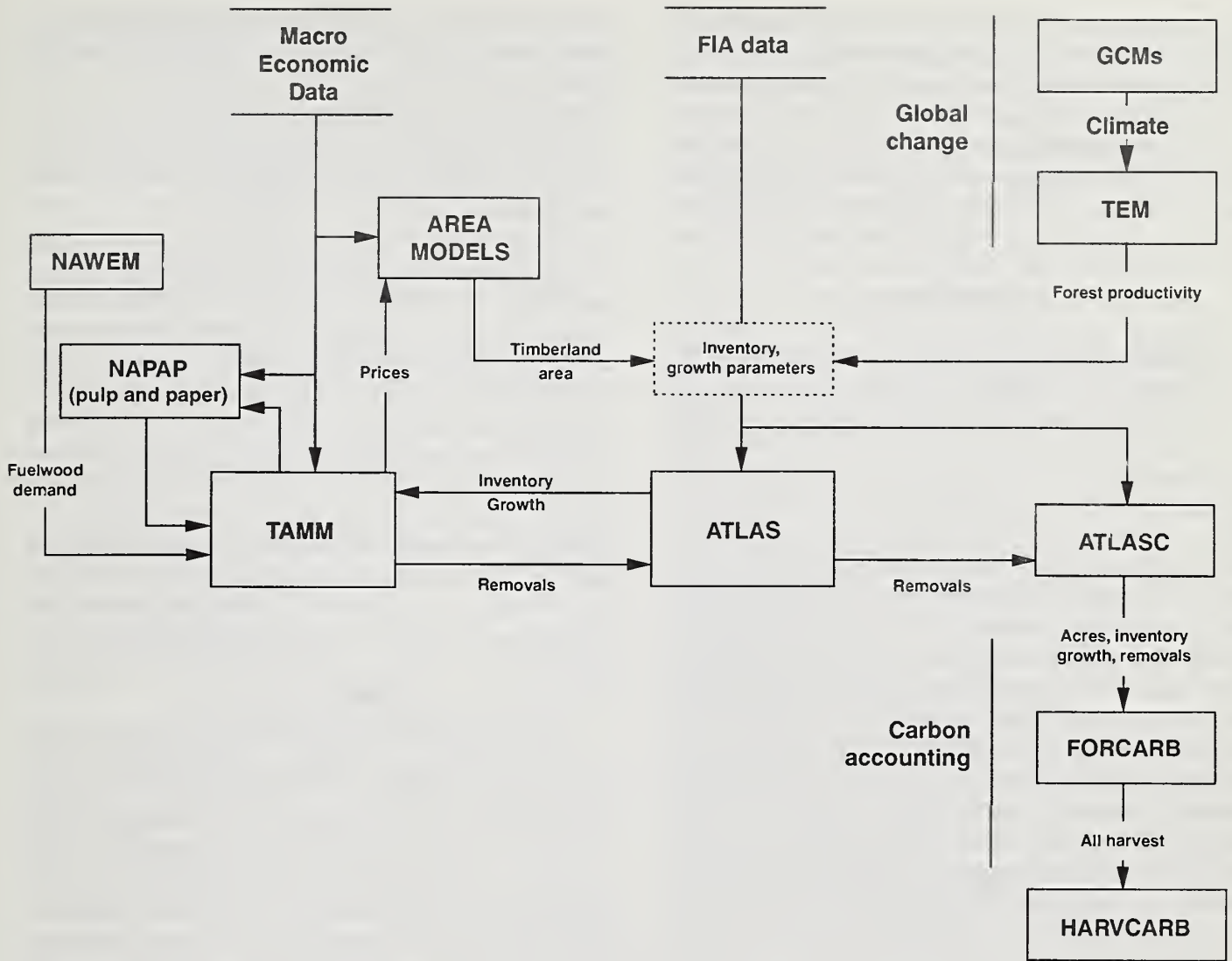
Figure 3.1.—The system of models used in the 1993 RPA Timber Assessment Update.

wood lumber is treated on the demand side in about the same end use detail as softwood lumber but consumption and production are set equal and price is determined as a function of softwood lumber prices. Hardwood sawtimber[10] stumpage prices are a function of hardwood lumber prices. Activity measures are exogenous and generally are taken from long-term macro forecasts prepared by Wharton Econometrics (WEFA 1987).

Each product supply function includes installed capacity as an independent variable. Shifts in in-

[10]Sawtimber stumpage includes live trees of commercial species containing at least one 12-foot sawlog or two noncontiguous 8-foot logs, and meeting regional specifications for freedom from defect. Softwood trees must be at least 9.0-inches dbh, and hardwood trees must be at least 11.0-inches dbh.

stalled capacity are modeled as a function of anticipated changes in relative regional profitability or rate of return. The basic economic representation of timber supply at any point in time is a function of the private timber inventory levels, stumpage prices, and the amount of public harvest available. Finally, the timber demand functions are derived from product market demand and supply functions. The pulp fiber requirements are determined by NAPAP's dynamic interaction with TAMM and ATLAS. Trade and fuelwood projections are also input variables.[11] The trade projections reflect a future where the U.S. remains a net importer of softwood forest resources.

The solution of TAMM represents a spatial equilibrium in the markets modeled for each year of the

projection period. These solutions do not represent, nor can the basic market solution algorithm[12] be readily used to find, intertemporal production or consumption strategies that are in some sense optimal. The production, consumption, and price time paths are only estimates of outcomes of contemporaneous interactions in freely competitive markets.

Pulp and Paper

TAMM produces the projections for the solid wood industries while NAPAP produces projections for the pulp and paper industry. The North American Pulp And Paper sector model (NAPAP) uses linear programming to solve for market equilibrium in spatially specific markets (Ince 1994). NAPAP shows how recovered paper and pulpwood markets are expected to respond to shifting demand and changing technology, and in turn how technology is expected to evolve in response to market conditions. The model includes regional supply functions for pulpwood and recovered paper (recycling), and a detailed representation of production capacity and supply for all principal grades of market pulp, paper, and paperboard, in five North American production regions. The model also includes demand functions for all end products, with separate demand functions for U.S. domestic demand, Canadian domestic demand, and demand from various trading regions for export from the U.S. and Canada.

Timber Supply Model

The remaining steps in the annual cycle of TAMM involve timber supply. The inventory projection system, ATLAS, was developed to model timber inventories at subregional, regional, and national scales.[13] The model was linked to TAMM for use in both the 1989 RPA Timber Assessment (Haynes 1990) and the 1993 Assessment Update (Haynes et al. 1995). In these assessments, ATLAS simulates growth, har-

vest, and the effects of timber management for approximately 339 million acres of private timberland in the conterminous U.S.

The projections are built on several assumptions, including: timberland data can be stratified by descriptive variables and then aggregated into bundles (or cells) without significant loss of growth and yield information; as we aggregate from the stand level to the regional (multi-state) scale, the even-age characterization of ATLAS gives way to a multi-age model as age classes represent broad mixes of actual conditions, age classes might be thought of as growth classes; the results of land area models developed for the 1989 Assessment could be input to work in the 1993 Update, though they are not integrated with the climate change models; a gross harvest request to supply industrial needs in TAMM could be converted via a set of factors into a net removal of hardwood or softwood growing stock from the ATLAS inventories; and timber management intensification practices that were assumed to both increase growth and lower the ages at which trees would be harvestable would actually take place.

In each simulation period, inventory change is the result of growth, area change, and harvest. The projection mechanism moves each starting cell along independent yield trajectories. The yield-tables and density change coefficients project cells by periods consistent with the inventory stand-age classes. The yield tables, density change coefficients, and stocking density coefficients required for growth models were derived from timberland inventory plot data collected by the various USDA Forest Service Forest Inventory and Analysis Units (FIA), and from previous studies (the inventory data inputs are summarized in Mills [1988, 1993]). Five-year age classes represented the South, and 10-year age classes represented all other regions. Thus, projections between 1990 and 2040 required 10 periods for the two Southern regions and 5 periods for the seven remaining regions.

For purposes of the RPA, the conterminous U.S. was divided into 9 timber supply regions. Within each region private timberland was stratified by 2 ownerships, up to 10 forest types, and up to 18 age classes. The South and the Pacific Northwest Douglas-fir subregion were further stratified by 3 site productivity classes and 5 management intensity classes.

Each unit of area identified by these attributes, a cell, is projected individually. The representation or weight of a cell is dependent on the area within a region

[12]A revised reactive programming algorithm is used (Brooks and Kincaid 1987). Briefly, reactive programming is a method for solving continuous demand and supply functions by successive adjustment of quantities produced and their distribution to demand regions so as to maximize producer profits net of transport costs in each supply region.

[13]The ATLAS system evolved from earlier work by Beuter, Johnson, and Scheurman (1976) and Tedder, LaMont, and Kincaid (1987).

identified with the same attributes. Cells range in size from several thousand acres, up to a million or more acres. In the following examples we will assume each cell can be identified by region, owner, forest type, site class, age class, and management intensity. Then periodic change in cell volume is represented by:

$$I_{t+1} = I_t + G_t - vL_t - H_t + vG_t \qquad (1)$$

where:

I_{t+1} is the inventory cell volume in period t+1,

G_t is the growth in period t,

vL_t is volume lost in period t due to area loss,

H_t is the harvest in period t, and

vG_t is volume gained in period t due to area gain.

Cell net growth in the period t is the sum of growth (net of mortality) from all possible activities that could affect the cell:

$$G_t = gI_t + gH_t + gG_t + gL_t, \qquad (2)$$

where:

gI_t is regular inventory growth in period t,

gH_t is the growth on harvest volume in period t,

gG_t is growth on area gained in period t, and

gL_t is growth on area lost in period t.

At the regional level, changes in inventories are simulated across a broad range of conditions. The initial conditions are derived from FIA plot data. Computations are made for treatments such as partial harvests, commercial thinning, final harvest, and losses and gains of timberland area. To represent improvements in forest practices, shifts in timber management regimes occur. Timberland area is adjusted each period for gains and losses as projected by area models. The area models were developed by modifying a version of the Southern Area Model (Alig 1985, Alig et al. 1990). Final-harvested acres can be regenerated into alternate forest types, placed in a nonstocked category, or lost from the timberland base to urban or farm use. The projection began with approximately 339 million acres, through a series of gains, shifts, and losses, the final area was 325 million acres, an overall net reduction of 4.4%.

Fiber type also plays a roll in aggregation. To interface with the markets in TAMM, forest types in ATLAS are grouped by fiber type, namely hardwoods and softwoods. Markets tend to categorize harvested trees by their major uses which often is dependent on whether timber is hardwood or softwood fiber. The market representation within TAMM is synonymous with this representation. Within each region ATLAS reports available stocks of timber by ownership class and fiber type, TAMM responds with a harvest for that class, e.g. Southern forest industry hardwoods. Though all forest types are modeled independently, ATLAS would allocate that harvest among the hardwood types. Reporting also is typically by ownership and fiber type; this chapter will be consistent with that format.

Scenarios

The TAMM/ATLAS scenarios resulted from several modeling steps. Initially, a baseline climate and 4 future climates[14] were derived. Globally, mean temperatures and mean precipitation increased, however regional climates may depart from these overall increases (Chapter 2). Using spatially-referenced data on climate, soils, and vegetation TEM produced projections of net primary productivity (NPP) for vegetation assumed in equilibrium with climate for both the baseline and the $2XCO_2$ projections. The change in NPP that occurred between the baseline and $2XCO_2$ projection was calculated for each of the 7 forest ecosystems examined within the U.S. The 7 ecosystems were then matched to the RPA forest types in ATLAS within the RPA timber supply regions. The GCMs produced different equilibrium climates (Chapter 1), and therefore TEM produced varying levels of NPP (Chapter 2). To represent this range of variability the differences in NPP between baseline and the $2XCO_2$ projections were grouped into three categories: minimum, mean, and maximum. The change in NPP for each category then was input into ATLAS and a TAMM/ATLAS projection was made for each category. The TAMM/ATLAS-TEM projections were compared to the RPA baseline (run 207). The RPA base projection can be considered to represent forest development under a continuation of

current or historical climate because the ATLAS growth and yield relationships are derived from either existing models or (historical) data collected from existing trees.

Climate Change and Forest Productivity

The change in NPP from TEM was associated with a change in forest productivity within ATLAS. A simple assumption was that changes in NPP were analogous to changes in net forest growth as calculated by ATLAS. The percent change in NPP represented the difference between current and equilibrium conditions at 2065, there was no specific information about the transient responses. For this analysis the assumption was made to use a linear rate of change between 1990 and 2065. The change in productivity was assumed to begin in the year 1990 and continue through the end of the projection. The TAMM/ATLAS projections were configured to end at the start of 2040, so we assumed TAMM/ATLAS total change in NPP to be two-thirds of the TEM value.

The ATLAS growth calculation was modified to allow for a factor to adjust growth. The following formula was used to derive the factor for linear periodic change:

$$PCP = (1 + (i/75)TCP)^{1/n} \qquad (3)$$

where PCP is the periodic change in NPP in factor form, i is the number of years in the projection (we assumed 50), TCP is the total change in NPP produced via TEM (expressed in decimal form), and n equals the number of projection periods.

In the ATLAS formulation, the change in productivity for each period is the sum of productivity change for the current period and all previous periods. When we assume equation [3], the factor for productivity for period t would equal PCP^t. So the factored growth (Fg) for projection period t would be calculated as:

$$Fg_t = g_t PCP_t, \qquad (4)$$

for all cases of g in equation [2].

RESULTS AND DISCUSSION

We assumed the change in NPP as projected by TEM to equate with a change both in the rate of growth and the amount of live biomass a site can sustain. This is a key assumption because if the site carrying capacity did not increase, net change would be smaller as gains from growth would be offset by losses to mortality. The changes in NPP cross-walked to ATLAS forest types were positive for all but five of 159 cases (table 3.1). Even in the minimum scenario increases in NPP far outweighed declines. On a percentage basis, high elevation forests or those in the North experienced significant gains. Hardwoods in the South experienced the largest productivity fluctuations between the minimum and maximum scenarios.

Projections of inventory are presented by softwood and hardwood forest types. Softwood and hardwood categories are associated with forest products and the market side of TAMM/ATLAS. Demand is aggregated by the dominant fiber type required in the production of various forest products, and harvest is applied to inventories based on their proportion of softwood or hardwood fiber. Though both fiber types are carried in each category, conifers are lumped into the softwood category and broadleaf deciduous species make up the hardwoods. Changes of inventory, growth, and harvest are all comparisons to the 1993 RPA baseline (run 207).

The minimum and maximum scenarios produced an inventory envelope that broadened with time (fig. 3.2). Past the year 2030, the RPA baseline inventory actually drops while the maximum scenario shows rather steep increases. In total, the maximum projections produced nearly 112 billion cubic feet of inventory above the base (table 3.2). The increase was split nearly equally between the fiber types, 24% for softwoods and a 21% for hardwoods.

The minimum scenario produced the lowest change in growth, and though softwood inventories increased, hardwoods dropped below the baseline. The gain in softwood was about 16 billion cubic feet (7%). Outside of the South, private hardwood inventories increased by 5% (8.8 billion cubic feet), but the 12% drop in Southern hardwood productivity was large enough to pull the U.S. hardwood total down by 2.6 billion cubic feet (1%).

Growth and Harvest

The resulting change in inventory volume is dependent on the rate of growth and amount of harvest

Table 3.1.—Fifty year cumulative percent change in net primary productivity by RPA region and forest type, by three projection scenarios.

Region and forest type	Minimum	Mean	Maximum	Region and forest type	Minimum	Mean	Maximum
Pacific Northwest Ponderosa Pine Subregion				**North Central**			
Ponderosa pine	9.7	13.1	16.8	Jack pine	7.8	14.1	19.7
Douglas-fir - western larch	9.3	13.2	14.9	Red pine	7.8	14.1	19.7
Fir - spruce	11.1	14.6	16.1	White pine	7.8	14.1	19.7
Lodgepole pine	9.2	13.8	15.7	Fir - spruce	16.5	19.4	23.7
Pacific Northwest Douglas-fir Subregion				Wetland conifer	17.2	20.1	26.1
Douglas-fir	10.3	14.0	19.8	Oak - hickory	4.0	11.1	22.9
Douglas-fir - mixed conifer	10.5	13.5	18.6	Lowland hardwood	6.9	14.3	21.8
Mixed conifer	9.3	11.7	13.6	Maple - beech	7.9	13.9	24.9
Western hemlock	11.2	14.6	19.9	Pines	6.9	12.7	18.1
Fir - spruce	11.7	15.0	18.8	**Northeast**			
Pines	6.7	12.3	16.8	White - red - jack pine	7.8	14.1	19.7
Red alder	10.3	14.0	19.8	Spruce - fir	16.9	22.3	26.0
Mixed hardwood	-0.3	6.9	17.9	Loblolly - shortleaf pine	6.7	9.6	11.7
Pacific Southwest				Oak - pine	5.7	9.1	11.5
Fir - spruce	9.6	13.6	17.8	Oak - hickory	2.9	11.5	24.0
Redwood	6.7	9.0	13.3	Elm - ash - red maple	9.0	16.3	26.0
Douglas-fir	5.5	8.3	14.3	Maple - beech - birch	14.8	16.8	21.8
Ponderosa pine	6.6	10.4	14.0	Aspen - birch	15.8	18.4	21.1
Mixed conifer	9.6	13.6	17.8	**South Central**			
Hardwood	8.3	11.4	16.4	Planted pine	2.4	7.1	12.7
Northern Rocky Mountain				Natural pine	2.4	7.1	12.7
Douglas-fir	10.0	16.8	20.3	Oak - pine	2.4	7.1	12.7
Ponderosa pine	10.5	15.3	19.2	Upland hardwood	-3.2	7.5	21.9
Fir - spruce	14.0	22.5	27.8	Lowland hardwood	-3.2	9.6	20.8
Southern Rocky Mountain				**Southeast**			
Douglas-fir	8.9	15.7	20.5	Planted pine	1.7	8.1	13.2
Ponderosa pine	8.5	11.9	15.1	Natural pine	1.5	8.3	13.5
Fir - spruce	16.0	23.5	27.0	Oak - pine	1.7	8.1	13.2
Lodgepole pine	13.1	20.6	24.5	Upland hardwood	-4.6	11.1	28.8
Hardwood	13.7	21.0	24.6	Lowland hardwood	-0.3	10.7	21.1

relative to growth. Assuming increases in carrying capacity, additions to growth increase the amount of live biomass. The consequence is a cumulative or compounding effect as additional inventory adds yet additional growth. Unless harvest or mortality increase proportionately, additions to inventory over time will be relatively larger than the percent change in productivity. Under lowered productivity we assume the opposite effect.

Much of the increase in growth does not impact harvest until the end of the projection. By 2040, the total increases of inventory ranged from 3% to 22% (minimum and maximum scenarios), while corresponding total annual harvest increased only 1% and 3%. Under the maximum scenario, harvest increased modestly for softwoods (6%) and actually declined for hardwoods (3%). This drop in hardwood harvest can be attributed to a greater abundance and lower prices for softwood fiber which offset a shift to hardwood fiber that was occurring in NAPAP for some

paper grades under the baseline projection. The reduction in hardwood harvest boosted the contribution of southern inventories to 57% of the total hardwood increase.

Harvest lags the increases in growth by several decades in these projections because harvest projections in TAMM and NAPAP are a function of available inventories (and prices). Increases in growth have to accumulate, leading to increases in the available timber inventories (those above minimum harvest ages) before harvests increase. Another factor is that these projections also show little consumer response, especially for lumber, to lower prices. Demand for solidwood products is derived from consumption of houses, other types of buildings, and a wide range of consumer and industrial products. Demand for paper is primarily influenced by overall economic growth. In both cases downward changes in wood (or fiber in the case of paper) represent only a small proportion of total production costs.

With a change in available supplies of harvestable inventories, there is a shift of harvest both among and within regions as TAMM and NAPAP adjust demand to take advantage of lower cost raw materials in some regions. Shifts occur between fiber types and between ownership classes. The competition between major timber producing regions causes harvest to shift toward regions with established capacity and lower production costs. Except for the North, all regions gain harvest under each of the three scenarios. The North experiences slight losses under the minimum and maximum TEM scenarios. Meanwhile, the harvest increase in the South is proportionally greater than that in the Pacific Coast. Though the shift is not large, it reflects the assumptions built into the models.

The projections show that as softwood inventories increase and softwood prices fall, demand shifts from hardwoods to softwoods. A large component of total hardwood harvest is pulpwood. As the supply of softwood growing stock increases and prices decline, NAPAP decreases the amount of hardwoods used in the fiber mix. This increases the demand for softwood pulpwood while reducing demand for hardwoods. The cheaper prices also act to increase softwood sawtimber capacity and the demand for softwood sawtimber. Increasing softwood sawtimber harvest also increases the amount of residues available for pulp.

Another shift within regions is between the two private ownership classes: the nonindustrial owners, and forest industry owners. On an aggregate basis, the nonindustrial ownership typically has a somewhat greater proportion of their inventories in older trees. It is assumed this ownership has a diverse set of objectives and is not as oriented toward growing timber for markets as are forest industry owners. However, as prices for stumpage increase, additional nonindustrial owners will enter the market but not to the same extent as industrial owners. Under the TEM scenarios we see a higher overall supply of softwoods and lower prices. Harvest then shifts toward the industry ownership. In most regions capacity increases and the harvest expands
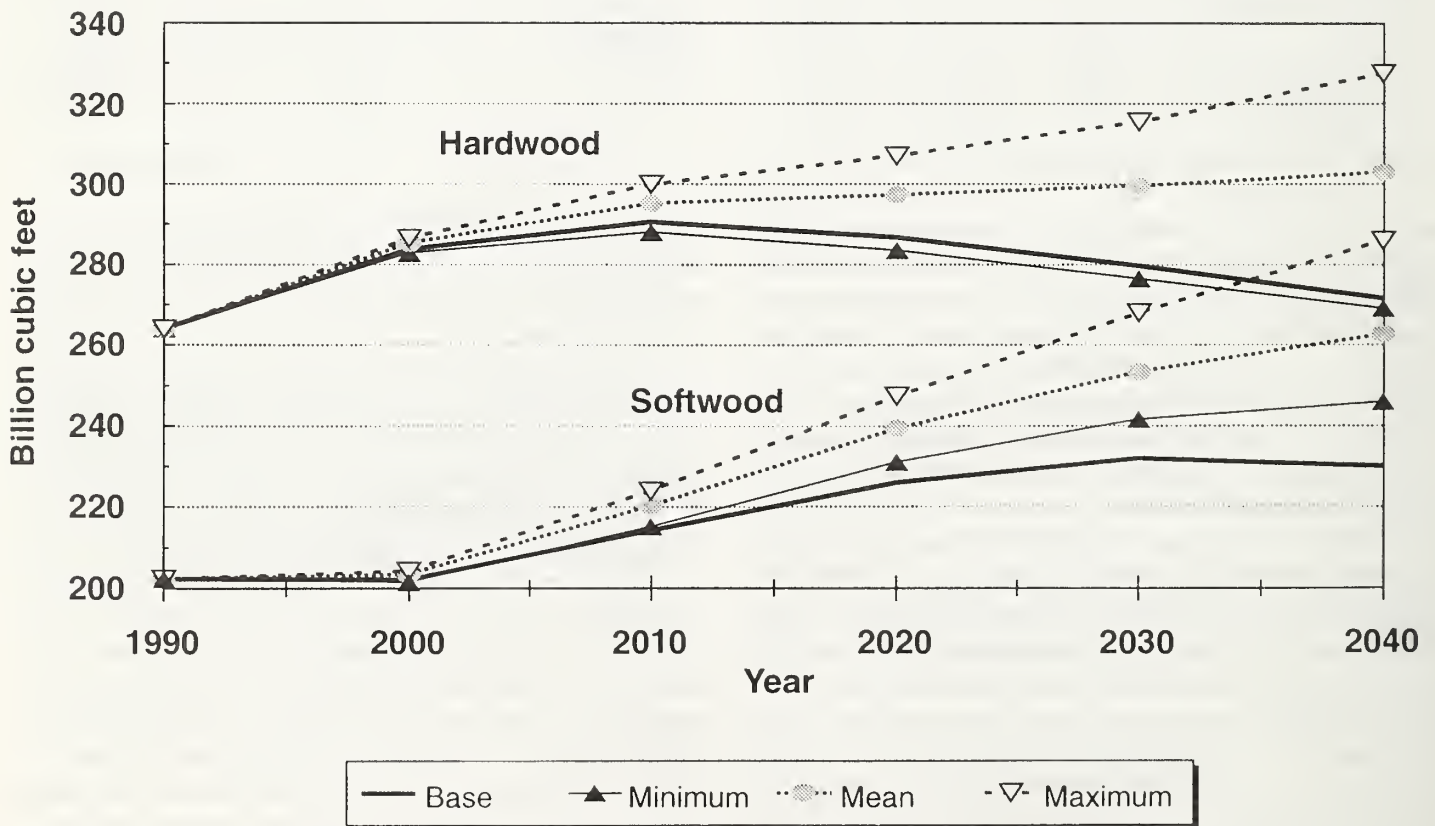

Figure 3.2.—Projections of net growing stock inventories on private timberland in the U.S. by fiber type. RPA base vs. three climate scenarios.

faster on industry land than it does on nonindustrial timberlands. In the Pacific Coast, the nonindustrial harvest declines under all three scenarios.

Prices

Softwood sawtimber stumpage prices in the RPA base projection (table 3.3) follow an upward sloping path to 2040. The mean and maximum scenarios show a leveling of prices by 2015 and then prices begin to decline and by 2040 drop below levels predicted for 1995.

These lower prices do two things. First, wood is more affordable as a raw material and the substitutes for wood become relatively more costly. Therefore, some additional demand occurs when wood is used instead of other materials (the reverse occurs with rising wood costs). And second, lower real prices reduce the price advantages enjoyed by Canada.

Table 3.2.—Volume of inventory, removals, and growth and percent change in volume resulting from the minimum and maximum scenarios for all private timberland in the U.S. (Growth and removals are annual averages for 10-year period beginning with reported year. Volumes are billion cubic feet, net growing stock.)

Fiber type and item	1990	2000	2010	2020	2030	2040
SOFTWOODS						
Inventory	202.4	202.1	214.3	226.0	232.0	230.1
Percent change						
Minimum	0	0	0	2	4	7
Maximum	0	1	5	10	16	24
Removals	8.6	9.1	9.7	10.6	11.5	
Percent change						
Minimum	2	1	-1	1	1	
Maximum	0	-1	1	4	6	
Growth	8.7	10.4	11.0	11.3	11.5	
Percent change						
Minimum	1	2	3	5	7	
Maximum	3	7	12	17	24	
HARDWOODS						
Inventory	264.1	283.9	290.7	286.8	279.8	271.7
Percent change						
Minimum	0	0	-1	-1	-1	-1
Maximum	0	1	3	7	13	21
Removals	5.5	6.6	7.3	7.4	7.5	
Percent change						
Minimum	2	3	2	2	2	
Maximum	0	-1	-2	-3	-3	
Growth	8.1	7.7	7.3	7.0	6.9	
Percent change						
Minimum	0	1	1	2	3	
Maximum	3	8	13	19	26	

Table 3.3.—Projected stumpage prices under the RPA Base vs. the minimum and maximum scenarios. (Prices are 5-year moving averages of 1982 U.S. dollars per thousand board feet, volume weighted by TAMM projection regions.)

Region and projection	1995	2000	2010	2020	2030	2040
SOFTWOODS						
Pacific Coast						
Base	254	234	256	280	274	271
Minimum	254	232	253	271	256	246
Maximum	252	230	243	249	205	171
Rockies						
Base	113	154	145	182	181	192
Minimum	113	153	148	181	176	182
Maximum	114	152	138	136	104	106
North						
Base	68	82	132	161	192	216
Minimum	68	82	128	152	178	197
Maximum	68	79	106	116	135	141
South						
Base	192	227	276	285	276	316
Minimum	193	228	269	279	269	303
Maximum	191	223	258	261	224	214
Canada						
Base	188	197	233	272	281	287
Minimum	188	197	233	270	275	279
Maximum	188	197	231	264	262	262

Without a change in market demand or a change in Canadian inventories, domestic harvest replaces Canadian harvest.

Canadian Imports

Softwood lumber imported from Canada is a significant part of the U.S. market (table 3.4). Since 1977, Canada has annually supplied between 20% and 30% of softwood lumber consumed in the U.S. In 1986 this amount peaked at 31%. The baseline projection shows Canadian imports increasing as a share of the U.S. market until about 2010, then as stumpage prices begin to plateau in the Pacific Coast and South, imports level near 30% and eventually decline to 23% of the market.

Under the scenarios, increasing domestic supply decreases U.S. stumpage prices make importing less profitable. Imports of Canadian lumber decrease both in total volume and as a percent of the market. By 2040 lumber imports from Canada are down by 18% and the Canadian share of the lumber market has dropped to 18%. Cheaper raw material has both increased lumber consumption and made the Cana-

dian lumber less competitive. Without explicitly modeling Canada's resource sector, it is difficult to say how a change in Canadian productivity would affect the level of U.S. imports. We would expect TEM to project a net positive change in Canadian forest productivity that would increase Canada's timber supply. It is plausible to assume this would boost Canada's ability to compete, but inventory alone might not influence competitiveness. Canada's pricing system is not based on the same market factors that operate in the U.S., trade barriers may exist, and transportation costs are a component that may not necessarily change.

Limitations

The study has several limitations, most are related to the scale of the analysis. Regions contain a broad range of habitats and species that were aggregated into forest types. Within regions, the TEM ecosystem types were loosely matched with forest types. Changes in growth did not recognize potential differences in productivity based on individual species, site, age, or forest management regimes. The change in forest productivity, and timber growth over time were assumed to be linear.

Though these models accounted for harvest and importation of wood products from Canada, they did not account for climate induced changes in Canadian inventories. We would expect the higher latitude forests to experience increases in productivity at least equal to those of the Northern U.S., leading to a higher import level than projected here.

To represent land use shifts associated with changing timber prices, an interactive area change model is needed. It is likely there would have been a greater shift to pine plantations under the decreased hardwood growth scenario, and as timber prices fell, an increase in acres moving from forest to agriculture and a decrease of acres to pine plantations.

Table 3.4.—Percent U.S. demand for softwood lumber supplied by Canada (5-year moving averages, RPA base run 207).

Projection	2000	2010	2020	2030	2040
Base	27	28	28	25	23
Minimum	27	28	28	24	22
Maximum	27	28	26	21	18

Despite its limitations, the study represents an important step to link a market model to a series of global change projections. Many of the limitations are being addressed. Aggregation has value at the regional scale because there currently is not enough data to independently project all timber resources. Plans call for the development of forestland and public timberland models for inclusion in the ATLAS system. Model refinements, stronger linkages, and broader coverage will increase our ability to examine the market and social effects associated with projected climates.

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4. Carbon Changes in U.S. Forests

R. A. Birdsey[15] and L. S. Heath[15]

INTRODUCTION

Global concern about increasing atmospheric concentrations of greenhouse gases, particularly carbon dioxide (CO_2), and the possible consequences of future climate changes, has generated interest in understanding and quantifying the role of terrestrial ecosystems in the global carbon cycle. Recent efforts to quantify the global carbon budget have revealed an unknown carbon sink of 2.0-3.4 billion metric tons/yr, of which some may be accounted for by changes in northern temperate forests (Tans et al. 1990). Estimates for European forests show a possible contribution of 5-9% of the "missing" carbon (Kauppi et al. 1992), and similar estimates for U.S. forests show a possible contribution of 12-21% of the unexplained flux since 1952 (Birdsey et al. 1993).

Forest ecosystems are capable of storing large quantities of carbon in solid wood and other organic matter. Forest disturbances such as fire or timber harvest may add to the pool of CO_2 in the atmosphere, while growing forests may reduce atmospheric CO_2 through increases in biomass and organic matter accumulation. Carbon in wood products may be effectively stored for long periods of time depending on the end use of the wood. By accounting for all of the forest changes and effects on carbon in each of the components of the system, it is possible to determine whether a land area containing forests is a net source or sink of CO_2.

As a consequence of expected increases in emissions of greenhouse gases, analysts have proposed various strategies to reduce emissions of CO_2 to the atmosphere, or to offset emissions by storing additional carbon in forests or other terrestrial carbon sinks (Intergovernmental Panel on Climate Change 1991). Carbon sinks are a likely component of any U.S. strategy for limiting national contributions to greenhouse gas concentrations in the atmosphere. Of particular interest in the U.S. are options for increased tree planting, increased recycling, changes

in harvesting and ecosystem management practices, and combinations of options, all within the context of the economic, demographic, and political assumptions that comprise the management and use of the Nation's forest resources.

To analyze these options, the Forest Service has developed a carbon accounting model that is linked with a socioeconomic model of the forest sector used for national assessments of forest resources. For the first time, the linked carbon accounting and forest sector models have been used with several climate change scenarios. This has been accomplished with a link between the Terrestrial Ecosystem Model (Raich et al. 1991, McGuire et al. 1992, 1993) and the forest sector model that allowed changes in forest productivity to alter projected timber supplies and affect the amount of carbon stored in U.S. forests. Although current models of global change effects on forests contain much uncertainty, analyses such as this give some indication of the magnitude of possible effects under different scenarios.

METHODS AND MODELS

Estimates of carbon storage for a base year (1992) were derived from national compilations of forest inventory statistics (Cost et al. 1990, Powell et al. 1993, Waddell et al. 1989), supplemented with information from ecosystem studies. These derived estimates provide a quantitative basis for calculating past carbon storage and projecting future changes. Estimates for the base year include all forest land classes and all 50 States. Past trends and projections focus on the conterminous U.S. where periodic inventories have been conducted over a long period of time, and where inventory projection models are well developed and linked with economic models. The general methods to calculate the past, current, and future estimates of carbon storage at periodic intervals are discussed in the following section. Additional details of the assumptions, estimation methods, and models can be found in Birdsey (1992a, 1992b) and Heath and Birdsey (1993).

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Carbon flux is estimated by calculating the change in carbon storage over a specified period of time. In the absence of harvesting or other disturbance, forests change relatively slowly and the changes are difficult to measure over a short time period. Statewide forest inventories are conducted in cycles of approximately 10 years which also is the average time period between major compilations of national forest statistics and the time period used in projections of forest inventories. To estimate the rate of carbon flux for a specified year, the total change in storage over the preceding and subsequent periods is divided by the total elapsed time, approximately 20 years. This method ties the rate of change closely to the reporting year, and avoids unrealistic changes in estimates between consecutive time periods.

Estimates for the Base Year

Carbon storage was estimated separately for several forest ecosystem components: trees, soil, forest floor, and understory vegetation. The definitions of these components are broad enough to include all sources of organic carbon in the forest ecosystem. The tree portion includes all above- and belowground portions of all live and dead trees, including the merchantable stem; limbs, tops, and cull sections; stump; foliage; bark and rootbark; and coarse tree roots (greater than 2 mm). The soil component includes all organic carbon in mineral horizons to a depth of one meter, excluding coarse tree roots. The forest floor includes all dead organic matter above the mineral soil horizons except standing dead trees: litter, humus, and other woody debris. Understory vegetation includes all live vegetation besides live trees.

Carbon storage was estimated in a four-stage process corresponding to the four major forest ecosystem components. Estimates of carbon storage in trees were based on periodic forest inventories designed to provide statistically valid estimates of timber volume, growth, removals and mortality (Waddell et al. 1989). Timber volume included merchantable live tree, 12.8 cm and larger at diameter breast height. Aboveground tree biomass was calculated by multiplying timber volume by conversion factors derived from the national biomass inventory (Cost et al. 1990). Belowground tree biomass was similarly calculated using conversion factors that range from 0.155 in northern hardwoods to 0.197 in southern hardwoods (Koch 1989).

Simple models were devised to estimate carbon storage in the forest floor and understory vegetation, based on the compilation by Vogt et al. (1986) and reviews of numerous intensive-site ecosystem studies (Birdsey 1992a). It was assumed that understory biomass peaked at age 5 and declined to between 1% or 2% of the tree carbon by age 50 in the South and age 55 elsewhere. Forest floor estimates from forest ecosystems studies were applied to related forest types. Soil carbon for individual States and forest types was related to mean annual temperature and precipitation using a model similar to Burke et al. (1989) with coefficients derived from data in Post et al. (1982). The estimation process accounted for forest disturbance and regrowth as described by average stand age. Estimates of carbon in the soil and forest floor components were calibrated with the projections for private timberland by equating current (1992) estimates with a base year from the projections (1990).

Historical Estimates

Estimates of past carbon storage in forests were derived from periodic assessments of forest resource conditions, each including a compilation of national inventory statistics (USDA Forest Service, 1958, 1965, 1974, 1982, Waddell et al. 1989). Generalized factors to convert growing stock volume to carbon for each ecosystem component were derived from current estimates and applied retroactively without adjustment to previous estimates of growing stock volume by region and species group (softwoods and hardwoods). Past estimates for carbon in the forest floor, soil, and understory vegetation vary proportionally to changes in tree carbon. Lack of detailed information about past age class distributions precluded the inclusion of age class effects in the historical estimates. The effects cause estimates of carbon flux to appear more variable than would be expected if the periodic inventory system were implemented continuously across the U.S.

Methods for Projections

Carbon in Forest Ecosystems

The projection model uses detailed information about current age class distributions to simulate the effects of harvesting on future age class distributions.

For private timberlands, profiles of average carbon storage by age of forest stands (carbon yield tables) were composed for each ecosystem component for forest classes defined by region, forest type, and land use history. The profiles were developed using methods similar to those used in estimating carbon storage in the base year. However, additional assumptions were required to estimate changes in soil and forest floor carbon over time. A search of the literature indicated that a major forest disturbance, such as a clearcut harvest, can increase coarse litter and oxidation of soil organic matter. The balance of these two processes can result in a net loss of 20% of the initial carbon over a 10-15 year period following harvest (Pastor and Post 1986, Woodwell et al. 1984), although a recent review suggested that the net effect may be less or even positive in many cases (Johnson 1992). There are indications that site preparation before replanting can cause a major loss of carbon in the southern U.S. (Johnson 1992). Recovery of carbon begins after an initial decline unless the harvest is followed by conversion to agricultural use, in which case loss could reach 60% under intensive cultivation (Anderson 1992, Johnson 1992).

Tree plantations established on agricultural land with depleted carbon stores can cause a substantial accumulation of soil organic matter, depending on species, soil characteristics, and climate (Johnson 1992). For example, *Populus* spp. established on sandy soils showed large increases in soil and forest floor carbon due to high litter production (Dewar and Cannell 1992). Expected changes in carbon storage for soil and forest floor components were derived by assuming a linear transition from average nonforest to average forest conditions.

After the initial 20% loss of soil carbon after harvest, it was assumed that soil carbon would return to pre-harvest levels by age 50 in the South and 55 elsewhere. If the forest land had reverted from agriculture, soil carbon was assumed to accumulate over time to levels similar to forest land that had never been cultivated. Then, after harvest, this forest land was treated the same as forest land that was never cultivated.

Carbon in Wood Products

The cumulative fates of carbon from projected harvests on private lands were estimated with a model based on the work of Row and Phelps (1991). The eventual disposal of all carbon removed from timberland since 1900 is included, based on data from detailed historical records of harvest volumes. There are four disposition categories: products, landfills, energy, and emissions. Products are goods manufactured or processed from wood including lumber and plywood for housing and furniture, and paper for packaging and newsprint. Landfills store carbon as discarded products that eventually decompose and are released as emissions. Emissions also include carbon from wood burned without generation of usable energy, or from decomposing wood. Energy is a separate category from emissions because wood used for energy may be a substitute for fossil fuels.

The Modeling System for Projections

Equations derived from carbon storage profiles form the basis of a forest carbon model, FORCARB (Plantinga and Birdsey 1993), which is linked with a forest sector model, TAMM/ATLAS (Adams and Haynes 1980, Alig 1985, Haynes and Adams 1985, Mills and Kincaid 1992). The forest sector model is linked with the Terrestrial Ecosystem Model (TEM - Raich et al. 1991, McGuire et al. 1992, 1993). The forest sector model provides an economic framework through which price, consumption, and production of timber and wood products are projected. Linkage with a forest sector model is critical for making valid projections because interactions with expected market responses will affect estimates of future forest harvest levels. Timber harvest on U.S. timberlands is currently the dominant cause of forest disturbance, accounting for 75% of the timber volume lost to all causes (Powell et al. 1993). Timber harvests from public lands are incorporated into the forest sector model as exogenous variables, because public lands are not managed to maximize economic return. The model ATLAS provides periodic estimates of area, inventory volume, growth, and removals by age class and management intensity for defined forest classes on private timberlands. The projected estimates of area, volume, growth, and removals for forest classes defined by region, owner, forest type, site class, stocking class, and age class are the basis for estimating carbon storage and fluxes in the four basic ecosystem components on private timberland using FORCARB.

TEM is an ecosystem-level process-based model that estimates potential changes in net primary productivity (NPP) for different ecosystem types as a function of atmospheric CO_2, climate, and other limiting factors such as nutrient and water resources. The values for each factor are set at current and future (doubled atmospheric CO_2 and associated climate changes) equilibrium levels. Transition levels are estimated as a linear interpolation between present and future levels. Actual changes in NPP during a transition to a new equilibrium would likely be quite different than the estimated changes based on the assumption of simple linear interpolation.

TEM was linked with the ATLAS portion of the forest sector model by altering volume growth functions for different forest types. Changes in volume were then reflected in the conversion of volume to carbon in FORCARB. Since FORCARB estimates carbon storage in all forest ecosystem components, the proportional changes in carbon storage are consistent with the change in net primary productivity projected with TEM.

For public lands, reserved timberland, and other forest land, projections of timber volume are made with simple growth and removal models based on expected harvest levels and growth rates, since the forest sector model TAMM/ATLAS is used for private timberland only. Projected forest inventories are converted to carbon estimates using volume-to-carbon conversion factors derived from the base year for each ecosystem component.

The effects of climate change are analyzed only for private timberland because of the lack of complete integration of all models for public forest land and other forest land. Furthermore, the link between TEM and FORCARB is not sufficiently well established at this time to allow FORCARB to account for prospective changes in carbon allocation between components of the ecosystem; yet this is a likely important consequence of changes in atmospheric CO_2. Therefore, when comparing the climate change scenarios to the base scenario, only carbon in trees is included in the results even though both FORCARB and TEM can project changes in other ecosystem components.

In estimating carbon for the reforestation scenarios, all land in the base scenario was accounted for in all scenarios even if that land was assumed to change from timberland to reserved status. This accounting avoided a sudden loss in carbon when there was only a classification change and not a true disturbance.

For additions to forest land through reforestation programs, the initial quantity of soil carbon was not added, to avoid the appearance of a pulse of carbon caused simply by reclassification. However, after a change in status, all increments of carbon in all components were accounted for in each scenario.

Uncertainty of the Estimates

Regional forest inventories are based on a statistical sample designed to represent the broad range of forest conditions actually present in the landscape. Therefore estimates of carbon storage in forest trees are representative of the true average values, subject to sampling errors, estimation errors, and errors in converting data from one reporting unit to another. Because of the complexity of making the estimates, the magnitude of the error in estimating tree carbon has not been estimated; but it is likely quite small, because the forest inventories used to derive the estimates have very small sampling errors over large areas.

Most regional estimates of carbon storage in the soil and forest floor are not based on a statistical sample but on compilations of the results of many separate ecological studies of specific ecosystems. Published estimates for soil carbon show wide variation for terrestrial ecosystems (Houghton et al. 1985). In an extensive literature review of the effects of forest management on soil carbon, Johnson (1992) highlighted the difficulties of aggregating estimates when sampling protocols and definitions generally are inconsistent among individual studies.

Problems with aggregation apply to this study because estimates of carbon storage in the soil, forest floor, and understory vegetation were developed through the use of models based on data from forest ecosystem studies. Uncertainty also is introduced into the estimation process by assuming that the results of specific ecosystem studies are representative of regional or national averages without being part of a statistical sample that represents a large geographical area. Therefore, estimates of carbon storage in the soil, forest floor, and understory vegetation are subject to the following errors: bias from applying data from past studies that do not represent all forest conditions, modelling errors (imperfect assumptions), and errors in converting estimates from one reporting unit to another. No attempt has been made to estimate the magnitude of these errors.

For the projections, all of the above uncertainties apply, and the errors are propagated through the model. To this basic uncertainty contained within FORCARB can be added the substantial uncertainty of projected forest inventories from TAMM/ATLAS, a function of uncertain economic, technological, and resource supply assumptions. Finally, uncertainties in projecting atmospheric greenhouse gas concentrations, associated climate changes, and forest ecosystem responses are quite high and therefore all results should be interpreted with great caution, as scenarios instead of predictions.

RESULTS

Base-year Estimates

Carbon Storage in the United States

Forest ecosystems in the United States contain approximately 54.6 billion metric tons of organic carbon above and below the ground (table 4.1). This is about 5% of all the carbon stored in the world's forests (Dixon et al. 1994). The area of U.S. forests is 298 million hectares, or 6% of the world's forest area.

Table 4.1.—Area of forest land and carbon storage by region, forest class, and forest ecosystem component, 1992.

Region	Forest Class	Area[1]	Soil	Forest Floor	Under-story	Trees	Total
		1000 ha	million metric tons				
Northeast	Timberland	32,153	4,348	562	53	2,041	7,004
	Reserved	1,841	315	44	4	163	526
	Other	559	68	8	1	35	113
	Total	34,554	4,731	615	59	2,239	7,643
North Central	Timberland	31,708	3,192	460	45	1,573	5,270
	Reserved	1,211	151	23	2	60	235
	Other	715	152	22	2	46	222
	Total	33,634	3,495	505	48	1,679	5,727
Southeast	Timberland	34,316	2,411	197	106	2,017	4,730
	Reserved	809	75	9	3	60	147
	Other	520	32	3	2	10	47
	Total	35,645	2,518	210	111	2,086	4,924
South Central	Timberland	46,344	3,044	230	155	2,691	6,121
	Reserved	425	42	4	2	33	81
	Other	3,316	205	17	13	102	337
	Total	50,085	3,292	251	170	2,825	6,539
Rocky Mountains	Timberland	25,346	2,164	452	29	1,415	4,060
	Reserved	4,971	479	86	7	328	901
	Other	26,233	1,248	185	30	970	2,432
	Total	56,549	3,891	723	65	2,713	7,393
Pacific Coast	Timberland	22,158	2,334	492	92	1,631	4,548
	Reserved	2,695	319	69	12	211	612
	Other	10,555	743	73	41	396	1,252
	Total	35,408	3,396	634	145	2,237	6,413
Alaska	Timberland	6,098	2,002	250	19	319	2,590
	Reserved	2,439	1,706	214	16	263	2,198
	Other	43,723	8,305	1,161	169	1,573	11,207
	Total	52,259	12,013	1,624	203	2,155	15,996
United States	Timberland	198,123	19,495	2,644	499	11,685	34,323
	Reserved	14,391	3,088	450	46	1,118	4,701
	Other	85,620	10,753	1,469	256	3,133	15,611
	Total	298,133	33,336	4,562	801	15,936	54,635

[1]From Powell et al. 1993. Estimates may differ slightly due to rounding.

The average forest in the United States contains 18.3 kg/m² of organic carbon. Trees, including tree roots, account for 29% of all forest ecosystem carbon (fig. 4.1). Live and standing dead trees contain 15.9 billion metric tons of carbon, or an average of 5.3 kg/m². Of this total, 50% is in live tree sections classified as growing stock, 30% is in other live solid wood above the ground, 17% is in the roots, 6% is in standing dead trees, and 3% is in the foliage.

The largest proportion of carbon in the average U.S. forest is found in the soil, which contains 61% of the carbon in the forest ecosystem, or approximately 11.2 kg/m². About 8% of all carbon is found in litter, humus, and coarse woody debris on the forest floor, and about 1% is found in the understory vegetation. By adding carbon in tree roots to the carbon in the soil, the average proportion of carbon below the ground in the United States is estimated to be 66%.

Carbon Storage by Region and Forest Class

Carbon storage and accumulation rates in a particular region or forest are influenced by many factors such as climate, solar radiation, disturbance, land use history, age of forest, species composition, site and soil characteristics. Even though all trees have similar physiological processes, there are significant differences in growth rates and wood density between species and individual organisms. The combination of species and site differences produces a wide variety of carbon densities across a landscape. Historical land use patterns and landscape attributes produce characteristic regional profiles of carbon storage.
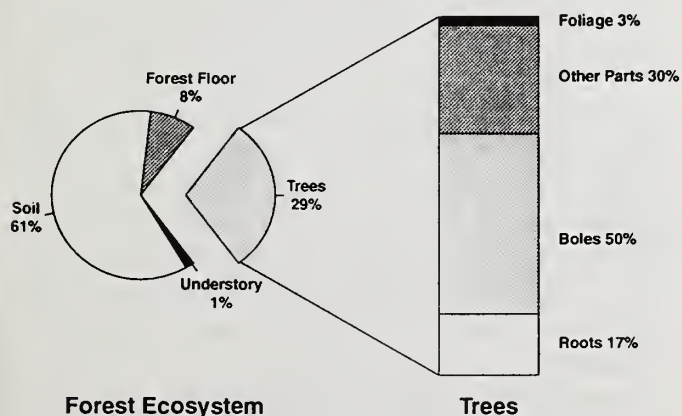
Figure 4.1.—Allocation of carbon in forest ecosystems and in trees, U.S. forests, 1992. Total storage in the U.S. is 54.6 billion metric tons.
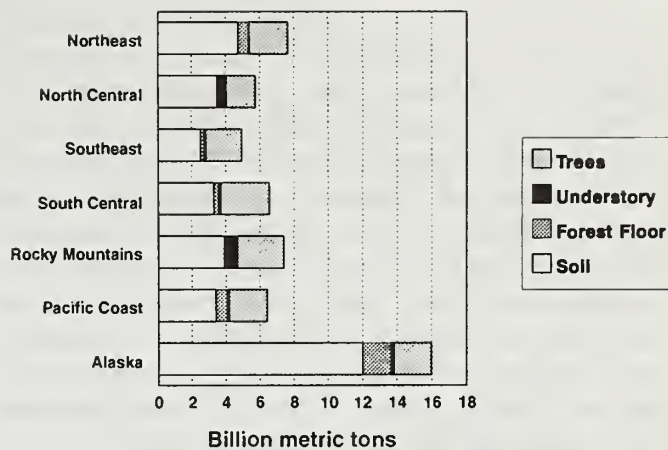
Figure 4.2.— Total carbon storage by region and ecosystem component, U.S. forests, 1992.

The proportion of carbon in the different ecosystem components varies considerably between regions (fig. 4.2). Alaska has the highest estimated amount of carbon in the soil, about 75% of the total carbon. The Southeast and South Central States each have about 50% of total carbon in the soil, but have a higher percentage in the trees. Soil carbon is closely related to temperature and precipitation, with higher amounts of soil carbon found in regions with cooler temperatures and higher precipitation. Cooler temperatures slow the oxidation of soil carbon, while higher rainfall tends to produce greater growth of vegetation, fine roots, and litter, which are the main sources of organic soil carbon. Carbon in the forest floor varies by region in a way similar to carbon in the soil. Western and Northern States contain the most carbon on the forest floor, and Southern States contain the least.

Two-thirds of all carbon in U.S. forests is on land classified as timberland. Most of the remainder is on land classified as other forest, primarily in the drier forests of the Western U.S. and the interior of Alaska.

Recent and Projected Trends in Carbon Storage and Flux

U.S. forests are constantly changing. The total area of forest land declined by 1.6 million hectares between 1977 and 1987 (Waddell et al. 1989) and increased by 2.4 million hectares between 1987 and 1992. These relatively small changes in the total area do not reflect the larger underlying gains and losses

that create a dynamic forest landscape. Each year forests are permanently lost to clearing for urban and suburban development, highways, and other rights-of-way. A larger area is typically cleared for agricultural use, but roughly balanced by agricultural land that was planted with trees or allowed to revert naturally to forest. In addition to land-use changes, each year about 1.6 million hectares of timberland are harvested for timber products and regenerated to forests, 1.6 million hectares are damaged by wildfire, and 1 million hectares are damaged by insects and diseases. And of course, all forests change continually as individual trees and other vegetation germinate, grow, and die.

Between 1952 and 1992, carbon stored on forest land in the conterminous U.S. has increased by an estimated 11.3 billion metric tons (table 4.2, fig. 4.3). This is an average of 281 million metric tons of carbon sequestered each year over the 40-year period, an amount that has offset about one fourth of U.S. emissions of carbon to the atmosphere (Boden et al. 1990). Most of the increase occurred in the Eastern and Central regions of the U.S., offsetting a much smaller decline in the West. Over the past 100 years or more, large areas of the East have reverted from agricultural use to forest. As these reverted forests have grown, biomass has increased substantially, and according to the assumptions described earlier, soil organic matter has increased proportionally.

In the South, increased harvesting and intensive forest management have significantly slowed the rate of increase in carbon storage. Northeastern and North Central forests have continued to accumulate carbon at a rapid rate since the mixed hardwood forests are less intensively utilized or managed for wood products. Although the West has not had the major land use shifts characteristic of the East, forest disturbance nonetheless has dominated the landscape as the original forests have been harvested and converted to second-growth forests. Declining carbon storage in the Pacific Coast region reflects the smaller amount of carbon contained in regenerating younger forests.

Projections through 2040 show an additional increase of 8.5 billion metric tons of carbon storage, or an average of 177 million metric tons per year (table 4.2, fig. 4.3). This projected trend reflects (1) a slow-down in the rate of accumulation in the North as the average forest has reached an age of slower growth relative to the past, and increases in soil carbon on

reverted land are less; (2) increasingly intensive use of forests for wood products in the South so that accumulation is balanced by removal; and (3) reduced harvest of public forests in the West coupled with a large area of younger, more vigorous and intensively managed forests on former old-growth forest land.

Estimates of carbon flux, in which a positive flux represents a net increase of carbon storage in forest ecosystems, highlight the relative contribution of forest floor and soil carbon to the estimated annual increases in carbon storage (table 4.3, fig. 4.4). Nationally, about 2/3 of the historical and projected positive flux is carbon buildup in the soil and forest floor. Despite the exaggerated variability in the past estimates, the trends over the whole period from 1952-1992 are representative of true changes in biomass, limited by assumptions about organic matter in the soil and forest floor.

Regionally, both the North and the South are expected to accumulate less carbon in forests, while Western forests will accumulate more carbon (fig. 4.4). The reasons for these changes, as discussed earlier, are related to changing levels of harvest and trends in land use.

Past and projected changes in forest carbon storage vary significantly by ownership group (table 4.3, fig. 4.5). Most of the historical increase in carbon storage has been on private timberland in the East. As these lands approach full stocking of relatively large trees with low rates of biomass accumulation (primarily in the North), or are more intensively used for timber products (primarily in the South), accumulation of carbon is expected to decline to near zero by 2040. Carbon storage on forest industry lands has increased slightly in the past, and is expected to remain relatively constant over the projection period. Carbon storage on National Forests has declined in the recent past, a consequence of harvesting old-growth stands in the far western U.S. High rates of harvest on National Forest lands appear as a negative carbon flux, mirroring the positive carbon flux evident on private lands during the same period (fig. 4.5). With restrictions on harvest levels, carbon storage on National Forests is expected to increase substantially, with an average annual addition to carbon storage of about 83 million metric tons per year between 2000 and 2040. Other public forests show similar but less pronounced changes.

Table 4.2.—Summary of historical estimates and projections of carbon storage and flux (in million metric tons) by geographic region and ecosystem component, conterminous U.S. forest land, 1952-2040.[1]

Region	Ecosystem component	1952	1962	1970	1977	1987	1992	2000	2010	2020	2030	2040
Northeast	Soils	2,438	2,961	3,418	3,901	4,349	4,731	5,016	5,278	5,532	5,786	6,033
	Forest Floor	317	385	442	507	567	615	661	686	704	716	727
	Understory	30	36	43	49	54	59	66	68	73	73	76
	Trees	1,133	1,380	1,582	1,814	2,054	2,239	2,512	2,686	2,811	2,912	2,986
	TOTAL STORAGE	3,918	4,762	5,484	6,270	7,024	7,643	8,255	8,717	9,119	9,487	9,821
	Annual Dead Flux[2]		61	71	62	63	58	34	28	27	26	
	Annual Live Flux[3]		26	30	28	29	36	25	15	12	9	
	TOTAL FLUX		87	101	91	92	95	60	43	38	35	
North Central	Soils	1,643	2,083	2,347	2,695	3,224	3,495	3,724	3,999	4,271	4,549	4,829
	Forest Floor	236	303	341	393	468	505	519	551	581	612	640
	Understory	24	29	32	38	46	48	57	61	62	66	67
	Trees	794	1,000	1,122	1,280	1,536	1,679	1,793	1,895	1,987	2,070	2,157
	TOTAL STORAGE	2,697	3,414	3,842	4,406	5,273	5,727	6,093	6,506	6,901	7,297	7,692

(continued)

North

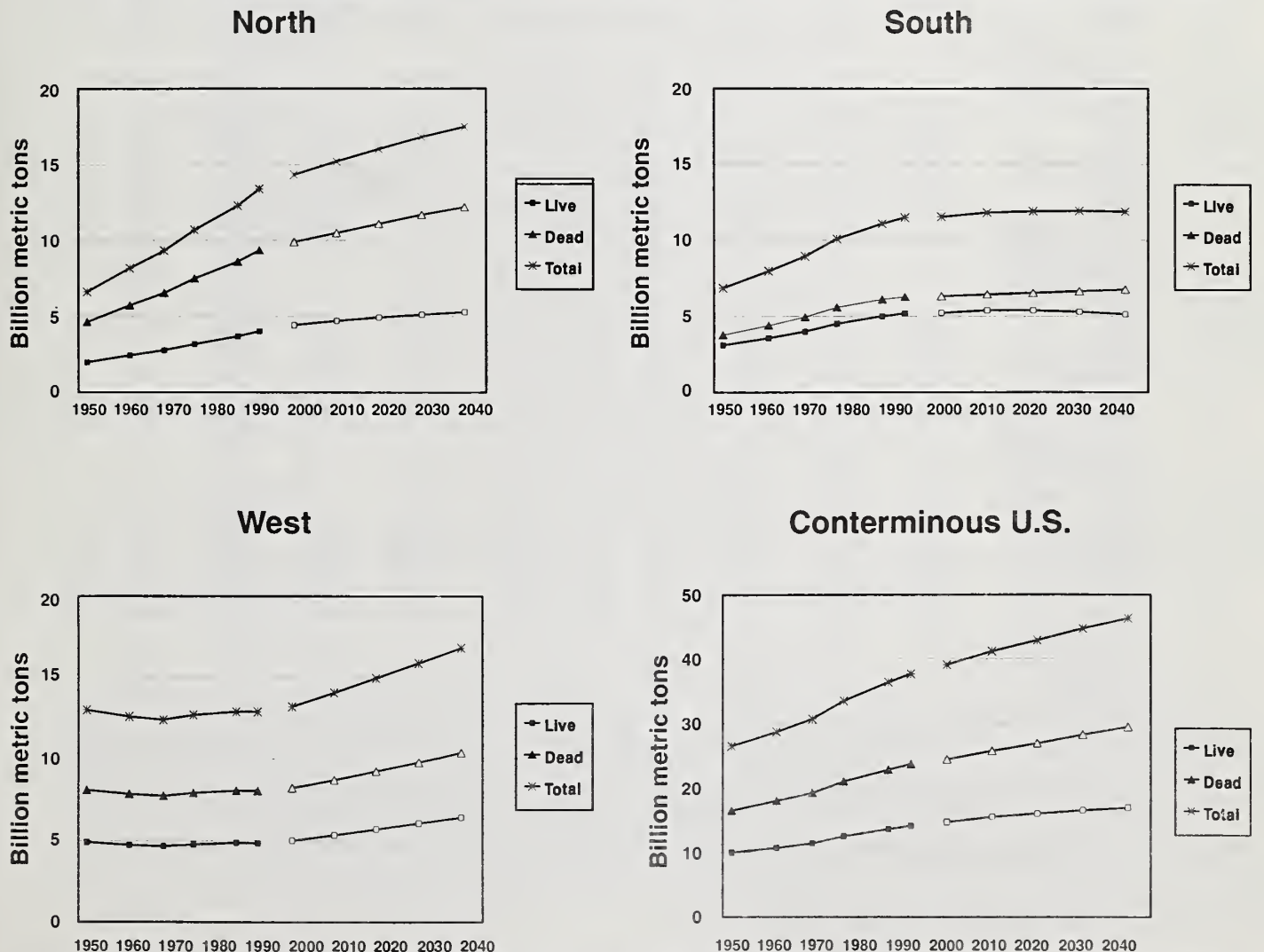## South

West

Conterminous U.S.

Figure 4.3.—Carbon storage in live (tree and understory) and dead (soil and forest floor) organic matter, conterminous U.S. forests, 1952-2040.

Table 4.2.—(continued).

Region	Ecosystem component	1952	1962	1970	1977	1987	1992	2000	2010	2020	2030	2040
	Annual Dead Flux		45	47	59	61	42	31	30	31	31	
	Annual Live Flux		19	19	25	27	21	13	10	9	9	
	TOTAL FLUX		64	66	84	88	63	43	40	40	40	
Southeast	Soils	1,602	1,810	2,039	2,314	2,514	2,518	2,532	2,566	2,590	2,625	2,671
	Forest Floor	130	147	166	190	209	210	198	195	192	191	195
	Understory	71	80	91	103	111	111	108	112	116	118	120
	Trees	1,299	1,469	1,664	1,895	2,079	2,086	2,059	2,005	1,904	1,830	1,776
	TOTAL STORAGE	3,102	3,507	3,960	4,503	4,912	4,924	4,897	4,878	4,802	4,764	4,762
	Annual Dead Flux		26	36	30	15	1	2	3	3	4	
	Annual Live Flux		21	30	26	13	(2)	(4)	(7)	(8)	(6)	
	TOTAL FLUX		48	66	56	28	(1)	(3)	(5)	(6)	(2)	
South Central	Soils	1,894	2,274	2,550	2,868	3,153	3,292	3,341	3,414	3,482	3,552	3,620
	Forest Floor	143	173	192	218	240	251	249	261	276	281	276
	Understory	99	118	133	148	164	170	158	162	169	172	177
	Trees	1,626	1,906	2,111	2,369	2,651	2,825	2,903	3,110	3,204	3,175	3,071
	TOTAL STORAGE	3,762	4,470	4,985	5,602	6,208	6,539	6,651	6,947	7,131	7,180	7,145
	Annual Dead Flux		39	43	38	31	15	7	8	8	7	
	Annual Live Flux		29	33	34	32	19	15	16	4	(6)	
	TOTAL FLUX		68	75	72	62	34	23	24	12	1	
Rocky Mtns.	Soils	3,623	3,507	3,510	3,708	3,898	3,891	3,983	4,242	4,514	4,788	5,071
	Forest Floor	650	641	645	679	711	723	747	794	845	896	946
	Understory	66	63	62	64	67	65	80	84	87	92	95
	Trees	2,571	2,469	2,463	2,606	2,735	2,713	2,737	2,931	3,129	3,329	3,528
	TOTAL STORAGE	6,911	6,679	6,680	7,057	7,410	7,393	7,547	8,051	8,574	9,105	9,639
	Annual Dead Flux		(7)	16	27	15	9	23	31	32	33	
	Annual Live Flux		(6)	9	16	7	1	13	20	20	20	
	TOTAL FLUX		(13)	25	43	22	11	37	51	53	53	
Pacific Coast	Soils	3,168	3,077	2,976	2,936	2,872	2,859	2,880	3,059	3,250	3,456	3,654
	Forest Floor	650	630	607	600	583	578	587	622	658	698	737
	Understory	129	125	121	119	117	117	111	116	122	128	135
	Trees	2,135	2,074	2,011	1,979	1,953	1,943	2,075	2,222	2,373	2,533	2,671
	TOTAL STORAGE	6,083	5,907	5,714	5,634	5,526	5,498	5,653	6,019	6,403	6,815	7,198
	Annual Dead Flux		(13)	(11)	(7)	(7)	1	14	22	24	24	
	Annual Live Flux		(7)	(7)	(4)	(3)	(9)	15	15	16	16	
	TOTAL FLUX		(20)	(18)	(11)	(9)	10	29	38	40	40	
TOTAL	Soils	14,368	15,711	16,840	18,422	20,009	20,785	21,475	22,557	23,638	24,757	25,878
	Forest Floor	2,126	2,279	2,394	2,585	2,778	2,882	2,960	3,109	3,256	3,393	3,521
	Understory	419	451	480	521	558	570	580	604	628	649	669
	Trees	9,560	10,298	10,953	11,943	13,009	13,487	14,079	14,849	15,407	15,849	16,188
	TOTAL STORAGE	26,473	28,738	30,666	33,471	36,353	37,724	39,094	41,119	42,930	44,647	46,257
	Annual Dead Flux		152	201	209	177	127	111	123	124	125	
	Annual Live Flux		81	114	126	106	84	78	69	52	41	
	TOTAL FLUX		233	316	335	284	211	189	192	176	166	

[1]Assumptions about forest land area used in projecting carbon storage and flux: (1) area of other forest land, reserved lands, and National Forest timberland are unchanged after 1992, (2) volume on reserved lands assumed to grow at the same rate as volume on similar unreserved lands, (3) area for private lands and other public lands are equal to projections from the 1993 RPA Assessment update, (4) for National Forest lands, harvest and growth rate projections are from National Forest plans and from previous RPA projections.

[2]Dead flux refers to average annual change in carbon in soils and the forest floor for the preceding and following periods. A positive flux indicates increasing carbon storage in dead organic matter.

[3]Live flux refers to average annual change in carbon in understory and trees for the preceding and following periods. A positive flux indicates increasing carbon storage in live organic matter.

Table 4.3.—Summary of historical estimates and projections of carbon storage and flux (in million metric tons) by ownership group and ecosystem component, U.S. timberland, 1952-2040.[1]

Owner	Ecosystem component	1952	1962	1970	1977	1987	1992	2000	2010	2020	2030	2040
National Forest	Soils	5,183	5,458	5,482	5,439	4,824	4,585	4,621	5,031	5,472	5,949	6,440
	Forest Floor	837	882	882	875	784	760	771	842	917	997	1,080
	Understory	101	108	109	109	99	99	101	112	123	135	145
	Trees	2,294	2,482	2,512	2,540	2,456	2,458	2,554	2,826	3,110	3,408	3,714
	TOTAL STORAGE	8,415	8,930	8,985	8,963	8,163	7,902	8,047	8,811	9,622	10,489	11,379
	Annual Dead Flux[2]		19	(2)	(44)	(65)	(17)	29	50	54	57	
	Annual Live Flux[3]		13	4	(4)	(6)	8	21	29	30	31	
	TOTAL FLUX		32	2	(48)	(71)	(9)	51	79	84	88	
Other Public	Soils	1,954	2,177	2,359	2,510	2,380	2,311	2,595	2,912	3,212	3,510	3,811
	Forest Floor	302	332	357	378	369	350	392	439	485	530	578
	Understory	36	39	42	44	48	46	51	56	63	68	74
	Trees	818	914	993	1,066	1,178	1,145	1,263	1,391	1,523	1,662	1,810
	TOTAL STORAGE	3,110	3,462	3,751	3,998	3,975	3,852	4,301	4,798	5,283	5,770	6,273
	Annual Dead Flux		26	25	2	(15)	18	38	36	34	35	
	Annual Live Flux		10	10	11	5	7	14	14	14	15	
	TOTAL FLUX		36	35	13	(10)	(25)	53	49	49	50	
Forest Industry	Soils	1,997	2,220	2,419	2,561	2,579	2,559	2,536	2,523	2,543	2,584	2,626
	Forest Floor	306	318	333	341	342	338	297	296	309	314	314
	Understory	62	68	70	75	76	73	88	87	87	86	87
	Trees	1,208	1,324	1,392	1,470	1,501	1,473	1,464	1,587	1,733	1,822	1,855
	TOTAL STORAGE	3,573	3,930	4,214	4,447	4,498	4,443	4,385	4,493	4,672	4,806	4,882
	Annual Dead Flux		25	24	10	0	(7)	(4)	1	4	4	
	Annual Live Flux		11	10	7	0	(2)	7	13	12	6	
	TOTAL FLUX		36	34	17	0	(9)	3	14	16	11	
Other Private	Soils	5,480	6,296	6,998	7,751	9,254	10,040	10,253	10,575	10,843	11,083	11,306
	Forest Floor	663	756	828	906	1,081	1,196	1,237	1,258	1,256	1,247	1,228
	Understory	165	186	210	232	265	281	265	273	275	277	279
	Trees	3,840	4,338	4,815	5,308	6,090	6,609	6,885	7,056	6,971	6,797	6,559
	TOTAL STORAGE	10,148	11,576	12,851	14,197	16,691	18,126	18,640	19,162	19,345	19,404	19,372
	Annual Dead Flux		94	107	148	172	89	33	30	25	22	
	Annual Live Flux		57	68	78	90	61	24	5	(13)	(20)	
	TOTAL FLUX		150	175	226	262	150	58	35	12	1	
TOTAL	Soils	14,614	16,151	17,258	18,261	19,037	19,495	20,005	21,041	22,070	23,126	24,183
	Forest Floor	2,108	2,288	2,400	2,500	2,576	2,644	2,697	2,835	2,967	3,088	3,200
	Understory	364	401	431	460	488	499	505	528	548	566	585
	Trees	8,160	9,058	9,712	10,384	11,225	11,685	12,166	12,860	13,337	13,689	13,938
	TOTAL STORAGE	25,246	27,898	29,801	31,605	33,327	34,323	35,373	37,264	38,922	40,469	41,906
	Annual Dead Flux		163	155	115	92	84	97	117	117	117	
	Annual Live Flux		90	92	92	89	74	67	61	43	32	
	TOTAL FLUX		253	247	207	181	157	163	177	160	149	

[1]Assumptions about forest land area used in projecting carbon storage and flux: (1) area of National Forest timberland are unchanged after 1992, (2) area for private lands and other public lands are equal to projections from the 1993 RPA Assessment update, (3) for National Forest lands, harvest and growth rate projections are from National Forest plans and from previous RPA projections.

[2]Dead flux refers to average annual change in carbon in soils and the forest floor for the preceding and following periods. A positive flux indicates increasing carbon storage in dead organic matter.

[3]Live flux refers to average annual change in carbon in understory and trees for the preceding and following periods. A positive flux indicates increasing carbon storage in live organic matter.

North

South
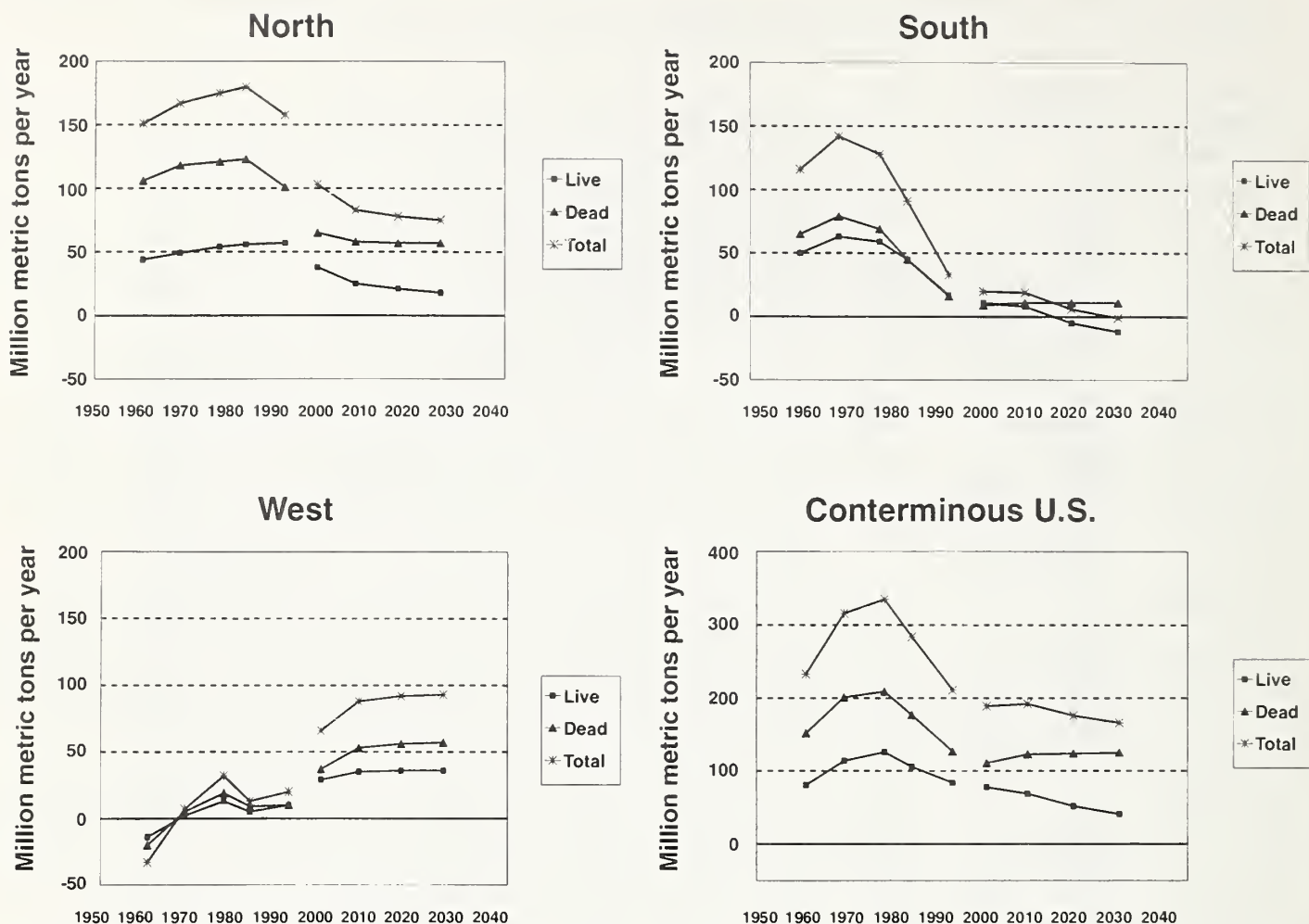

West

Conterminous U.S.

Figure 4.4.—Carbon flux in live (tree and understory) and dead (soil and forest floor) organic matter, conterminous U.S. forests, 1952-2040. A positive flux indicates increasing carbon storage in forest ecosystems.

Carbon in Harvested Wood Products

Harvested wood can represent a substantial carbon sink (Heath et al. 1995). Based on harvests for the period 1900-2040 on private timberland, an estimated 27-39 million metric tons per year of additional carbon may be added to physical storage in wood products and landfills (table 4.4). Larger amounts of the harvested carbon are used for energy or decomposition and returned to the atmosphere. These estimates are sensitive to assumptions about recycling, age of trees at harvest, and other factors that affect the amount of wood and the retention periods in various pools. A comprehensive analysis of alternative scenarios should account for harvested carbon; however, a lack of quantitative information about how this carbon will change under the different assumptions has precluded full use of this modeling capability.

Alternative Scenarios

The effects of increasing atmospheric CO_2 and prospective climate change on productivity could have a significant impact on carbon storage in forests (table 4.5). Responses range from minor with a minimum increase in productivity, to an increase over the base of 67 million metric tons per year by 2040 with a maximum increase in productivity. This amount is significant enough on private timberland to reverse the projected decline in carbon storage that would begin by 2020 under baseline conditions. The increase also is equivalent to that projected by 2040 under a massive reforestation program (table 4.6). The estimates for climate change scenarios represent only the increase in tree carbon. Based on the increases in productivity, there was a small increase in the amount of carbon stored in wood products and landfills as more timber was available for harvest.

One mitigation option favored for increasing carbon sinks is an increase in reforestation of marginal cropland and pasture. Several scenarios investigated in previous studies show the possibility of medium- to long-term gains in carbon storage, on the order of 5-10 million metric tons per year for a relatively low-cost program treating about 20 million acres of timberland that would also produce an economic return on investment (table 4.6). A more ambitious program treating all biologically suitable land in the U.S. could achieve substantially higher gains, on the order of those attainable under a major climate shift.

A moderate tree planting scenario affecting only the South Central region, and a separate recycling scenario, were run using the new base projections (table 4.7). Small gains were estimated from tree planting, appearing by 2030 when the trees were sufficiently grown to make some difference. Increased recycling produced a more immediate and larger gain; however, this analysis included only the effects on forest carbon storage, which may be partly increased or offset by changes in the carbon held in product pools.
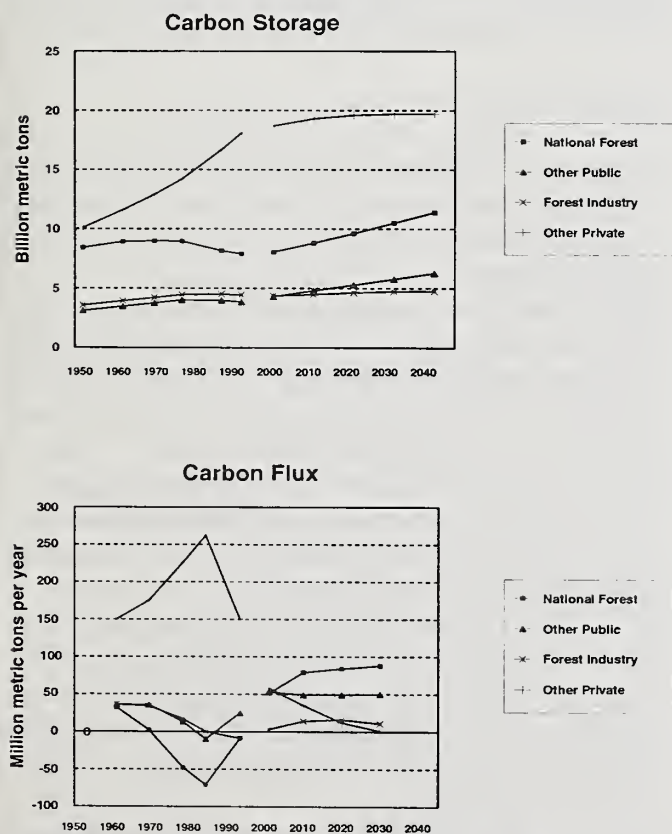
Carbon Storage

Carbon Flux

Figure 4.5.—Carbon storage and flux by owner, U.S. timberland, 1952-2040. A positive flux indicates increasing carbon storage in forest ecosystems

Table 4.4.—Cumulative disposition of carbon harvested from private timberland in the conterminous U.S., 1980-2040.[1]

Year/Period	Wood in use	Landfill	Used for energy	Emitted
	---------------- million metric tons ----------------			
Storage:				
1980	1,272	1,236	3,642	3,129
1990	1,407	1,374	4,129	3,598
2000	1,520	1,533	4,647	4,109
2010	1,662	1,734	5,269	4,683
2020	1,804	1,954	5,942	5,314
2030	1,948	2,185	6,656	5,911
2040	2,097	2,426	7,416	6,719
	---------- million metric tons per year ----------			
Flux:[2]				
1990	12	15	50	49
2000	13	18	57	54
2010	14	21	65	60
2020	14	23	69	65
2030	15	24	74	70

[1]Includes carbon removed from timberland after 1990.
[2]Calculated as average annual change over the preceding and following periods.

Table 4.5.—Comparison of carbon storage and flux for base run and climate change scenarios, trees only, private timberland in the conterminous U.S., 1990-2040.

Year/Period		Change in productivity		
	Base Run	Minimum	Average	Maximum
	---------------- million metric tons ----------------			
Storage:				
1990	7,838	7,838	7,838	7,838
2000	8,266	8,232	8,313	8,351
2010	8,554	8,501	8,728	8,876
2020	8,610	8,584	8,998	9,312
2030	8,516	8,533	9,202	9,732
2040	8,303	8,398	9,375	10,193
	---------- million metric tons per year ----------			
Flux:[1]				
1990-2000	43	39	48	51
2000-2010	29	27	42	53
2010-2020	6	8	27	44
2020-2030	(9)	(5)	20	42
2030-2040	(21)	(14)	17	46

[1]Positive flux indicates net transfer of carbon from atmosphere to trees.

CONCLUSIONS

This analysis has shown that U.S. forests have been a significant carbon sink since 1952, and that additional carbon sequestration will likely occur through 2040 but at a slower rate. Between 1952 and 1992, carbon stored on forest land in the conterminous U.S. increased by 11.3 billion metric tons, an average of 281 million metric tons for each year, and an amount that offset about one quarter of U.S. emissions of carbon for the period. Most of the historical increase in carbon storage has been on private timberland. Base projections through 2040 show an additional increase of 8.5 billion metric tons of carbon storage, and average accumulation of 177 million metric tons per year.

Most of the projected increase in carbon storage is expected on public forest land. The effects of global change and alternative forest management strategies could result in additional carbon storage through 2040. Carbon in harvested wood, the effects of increased CO_2 in the atmosphere, and large reforestation programs may all have a substantial effect on the rate of carbon sequestration.

Table 4.6.—Comparison of carbon storage and flux for previous base run and reforestation scenarios,[1] all ecosystem components, private timberland in the conterminous U.S., 1980 - 2040.

Year/Period	Base Run	Planting M/R	Planting AF-1	Planting AF-2
	---------------- million metric tons -----------------			
Storage:				
1980	20,308	20,308	20,308	20,308
1990	21,471	21,471	21,514	21,569
2000	22,102	22,135	22,198	22,467
2010	22,515	22,649	22,691	23,303
2020	22,715	23,042	22,860	23,982
2030	22,790	23,241	22,878	24,511
2040	22,839	23,342	23,161	25,332
	---------- million metric tons per year ----------			
Flux:				
1980-1990	116	116	121	126
1990-2000	63	66	68	90
2000-2010	41	51	49	84
2010-2020	20	39	17	68
2020-2030	8	20	2	53
2030-2040	5	10	28	82

[1] These scenarios were run on an earlier base prior to the 1993 RPA Update. M/R refers to a study by Moulton and Richards (1990) to estimate the amount of land and cost of reforestation for carbon storage. A $220 million investment level is assumed here. AF-1 refers to implementation of the "economic opportunities" described in Sampson and Hair (1992). AF-2 refers to implementation of the "biological opportunities" described in the same study.

Table 4.7.—Comparison of carbon storage and flux for current base run, reforestation and recycling scenarios,[1] all ecosystem components, private timberland in the conterminous U.S., 1990-2040.

Year/Period	Base Run	Planting M/R	Recycling
	----------------- million metric tons ----------------		
Storage:			
1990	21,621	21,621	21,621
2000	22,394	22,356	22,421
2010	22,964	22,913	23,108
2020	23,271	23,306	23,552
2030	23,401	23,468	23,795
2040	23,390	23,492	23,874
	--------- million metric tons per year ---------		
Flux:			
1990-2000	77	74	80
2000-2010	57	56	69
2010-2020	31	39	44
2020-2030	13	16	24
2030-2040	(1)	2	8

[1] M/R refers to a study by Moulton and Richards (1990) to estimate the amount of land and cost of reforestation for carbon storage. A $110 million investment level is assumed here. For the recycling run (described in the 1993 RPA Update), only changes in forest carbon are included. Changes in the disposition of harvested carbon, not simulated here, could offset some of the changes in forest carbon storage and flux.

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