

PATTERNS AND MECHANISMS OF THE FOREST CARBON CYCLE¹

Stith T. Gower

Department of Forest Ecology and Management, University of Wisconsin, Madison, Wisconsin 53706; email: stgower@wisc.edu

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■ **Abstract** Forests are an important source for fiber and fuel for humans and contain the majority of the total terrestrial carbon (C). The amount of C stored in the vegetation and soil are strongly influenced by environmental constraints on annual C uptake and decomposition and time since disturbance. Increasing concentrations of atmospheric carbon dioxide (CO₂), nitrogen deposition, and climate warming induced by greater greenhouse gas (GHG) concentrations in the atmosphere influence C accumulation rates of forests, but their effects will likely differ in direction and magnitude among forest ecosystems. The net interactive effect of global change on the forest C cycle is poorly understood. The growing demand for wood fiber and fuel by humans and the ongoing anthropogenic perturbations of the climate have changed the natural disturbance regimes (i.e., frequency and intensity); these changes influence the net exchange of CO₂ between forests and the atmosphere. To date, the role of forest products in the global C cycle have largely been ignored, and important emissions associated with the production, transport, and utilization of the forest products have been excluded, leading to erroneous conclusions about net C storage in forest products.

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¹Abbreviations used include: P_{vi}, biomass production of the ith tissue and vth vegetation strata; C, carbon; CO₂, carbon dioxide; D, detritus; FACE, free-air CO₂ exchange; GHG, greenhouse gas; GPP, gross primary production; H, herbivory; IGBP, International Geosphere-Biosphere Program; LAI, leaf area index; NBP, net biome production; NEP, net ecosystem production; NPP, net primary production; NPP_A, net primary production above-ground; PAR, photosynthetic active radiation; R_A, autotrophic respiration; R_H, heterotrophic respiration; S, soil surface CO₂ flux.

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THE FOREST C CYCLE AND GLOBAL CHANGE

The forest carbon (C) cycle is characterized by a biological (forest ecosystem) and industrial (forest products) cycle (Figure 1). The vast majority of forest C cycle research has focused on the biological C cycle, for good reason. Forests cover 65% of the total land surface, they contain 90% of the total vegetation C in terrestrial ecosystems, they contain 80% of the total soil C in terrestrial ecosystems, and they assimilate 67% of the total CO₂ removed from the atmosphere by all terrestrial ecosystems (1). However, it is increasingly important to consider the industrial C cycle because humans harvest the forests and transport the wood fiber to production facilities where the C is stored in wood and paper products; eventually these products are incinerated, recycled, or landfilled as waste (2).

The most dramatic changes to the forest C cycle are society's increased reliance on forests for fiber and fuel and its conversion of forests to cropland and pasture (3, 4). Deforestation to develop cropland and pasture was the dominant land use change in temperate regions in the past and is now the dominant land use change in tropical regions (5). Other disturbances, such as wildfire and insect outbreaks, are natural processes in forest ecosystems, but there is growing evidence that the frequency and severity of these disturbances are increasing as an indirect result of human activities (6, 7).

Land use and human-modified rates of natural disturbance have directly and indirectly altered the exchange of carbon dioxide (CO₂) between forests and the atmosphere. The atmospheric concentration of CO₂, a greenhouse gas (GHG), has increased by 30% since the preindustrial era. Most scientists agree that increased concentrations of CO₂ and other GHG are responsible for climate warming (8). Multi-model simulation ensembles suggest that the average change in global surface air temperature from the 1961–1990 period to the 2071–2100 period will be +3°C (with a range of 1.3 to 4.5°C) with the greater warming in high versus low

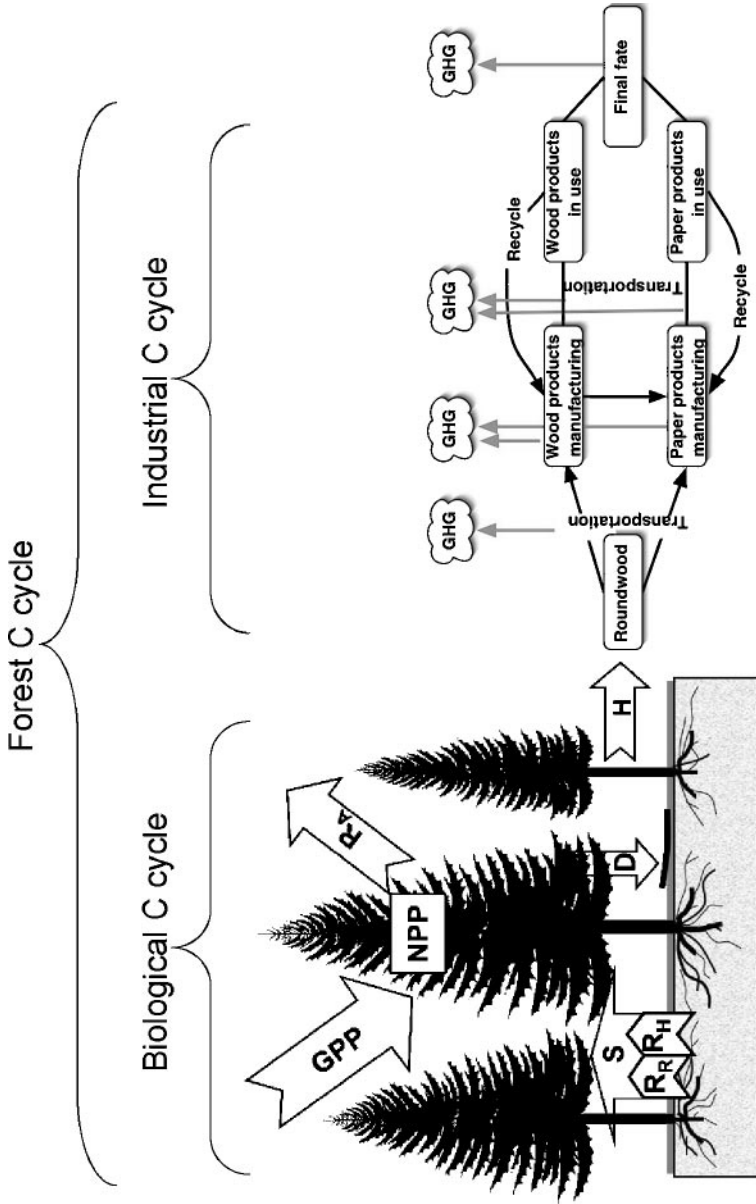


Figure 1 Conceptual diagram of the forest C cycle. The forest C cycle is comprised of a biological cycle (i.e., forest ecosystem) and an industrial cycle (i.e., forest products).

latitude zones (8). The effect of warming on the C budget of boreal forests is of particular interest because it is the second largest forest biome (9), and the soil C density is greater for boreal forest and peatland soils than for soils of other forest biomes.

The concentrations of other pollutants are also changing regionally, and forests will experience different exposures to these other pollutants, relative to the uniform increase in CO₂, depending upon their location to regional sources of ozone, nitrogen (N) deposition, and other pollutants. Chronic N deposition is a growing concern in highly industrialized regions of the world, and its effect on forest C cycle will change as total deposition increases (10). Ozone, a strong oxidant that adversely affects forest productivity (11, 12), now frequently exceeds critical threshold values in many forests near large industrial areas (13, 14).

In stark contrast to the myriad of studies that have quantified one or more of the major C fluxes of forest ecosystems, few studies have quantified the C content and emissions of the wood and paper products chains (2, 15). Yet, C storage in wood and paper products and their waste is increasing, and the production of some forest products requires large quantities of energy. For example, total world annual consumption of paper is approximately 270 million metric tons (16), and the pulp and paper industry is the fifth largest consumer of energy in the world (17).

The objective of this review is to summarize the major components of the forest C cycle and examine how global changes may affect the exchange of C between forests and the atmosphere. The first section of the paper briefly reviews the forest resource and the biological, or forest ecosystem, C cycle and its major components. The second section examines the environmental controls on (a) net primary production (NPP), (b) soil surface CO₂ flux (S), and (c) net ecosystem production (NEP). Comparisons of NPP, S, and NEP are provided to illustrate the general magnitudes of difference among forest ecosystems. The third section summarizes the effects of disturbance on forest ecosystem C cycle. The review includes initial changes in C pools directly caused by the disturbances and changes to the components of the forest C cycle during forest succession. The fourth major section reviews the effects of (a) climate warming, (b) elevated atmospheric CO₂ concentration, and (c) nitrogen deposition on forest ecosystem C cycle. The effects of multiple pollutants are briefly discussed. The fifth and last major section of the paper examines the role of forests in the GHG management schemes such as the Kyoto Protocol. The section begins by reviewing potential roles of forest ecosystems in meeting the Kyoto Protocol, which defines the first steps toward reducing the net emissions of GHG from terrestrial ecosystems. To date, most research on forest C cycle has focused on forest ecosystems but ignored the industrial C cycle. Important goals of this paper are to increase the readers' awareness of the important role forest products play in the forest C cycle and to demonstrate the great need for more rigorous analyses of this component of the forest C cycle. The paper concludes with a summary of critical issues that need to be resolved to reduce uncertainties of the forest C budget.

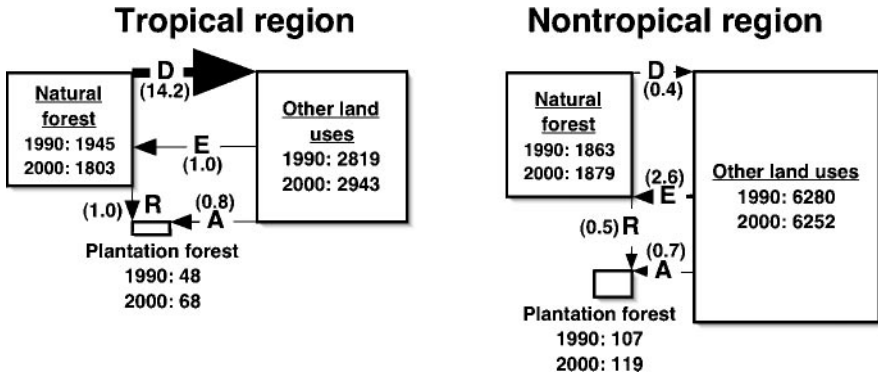


Figure 3 Forest land use change dynamics for tropical and nontropical regions. All data are averages for 1990–2000, and the units are million (10^6) hectares. Pools (*squares*) and fluxes (*arrows*) are drawn approximately to scale. Abbreviations for fluxes are D, deforestation; E, expansion of natural forests; R, reforestation; and A, afforestation. Redrawn from (3).

THE FOREST RESOURCE

Figure 2 illustrates the distribution of the major forest biomes of the world based on the International Geosphere Biosphere Program (IGBP) land cover classification scheme and 2000–2001 remotely sensed imagery from the moderate infrared spectrophotometer (MODIS). Scientists use different classification schemes to characterize global forest attributes such as land cover, soil and vegetation C content, and S because a universally applicable classification scheme does not exist. As a result, several vegetation classification schemes were used in this review. The lack of a universal scheme is partly historic and should be resolved with the widespread acceptance of the IGBP land cover classification scheme.

There are basic differences in the land use change dynamics between tropical and nontropical (temperate and boreal) regions (Figure 3). In 2000, natural forests comprised 38% and 23%, respectively, of the total land area in tropical and nontropical regions. During the 1990s deforestation was the dominant land use change process in tropical regions and occurred at a rate 14 times greater than each of the other land use changes (i.e., reforestation, afforestation, and natural forest expansion). The net loss of 7% of natural tropical forests annually during the 1990s differs greatly from the 1% increase in area of nontropical natural forests during the same time period. Natural expansion of forests was the dominant land use change process for nontropical forests during the 1990s and occurred at a rate 6.5 times greater than deforestation.

Natural forests cover approximately 4165×10^6 hectares, or approximately 65% of the Earth's land surface. Forest plantations cover an additional 112 to 187×10^6 hectares of the Earth's land surface (5, 18, 19). Low latitude tropical forests, including both evergreen and deciduous forests, cover 1755×10^6 hectares,

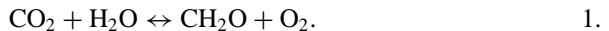
or approximately 42% of all forested area (Figure 4a). Over half of the low latitude tropical forests occur in Central and South America. Area estimates for boreal forests range from 900 to 2110×10^6 hectares (9). Dixon et al. reported high latitude forests cover 1560×10^6 hectares, making these forests the second largest biome. Midlatitude or temperate forests comprise 25% of the total global forest area (18).

Early estimates of forest C content were based on values from isolated studies reported in the literature that were never intended to be representative of the different types and age classes of forest ecosystems. The use of national forest inventory data and remotely sensed estimates of land use change have improved the accuracy of estimates of C content of world forests. Dixon et al. (18) estimated that the forest vegetation and soil contain 359 and 787 Pg C, respectively (Figure 4b). The boreal forest contains a greater amount of C than low latitude forests, although the latter is larger in area (Figure 4a). The C density, defined as the C content per unit area, of vegetation averages 127, 63, and 50 MgC ha⁻¹, respectively, for tropical, temperate, and boreal forests, but there is substantial variation among geographic regions within the same zone (Figure 4c). Despite the twofold greater C density of vegetation in tropical than boreal forests, the total (vegetation + soil) C density is almost 50% greater for the boreal than tropical forests.

Although tropical and temperate forest have four to five and two to three times more fine litterfall than boreal forests, the cold climate and poorly drained soils of the boreal forests severely restrict decomposition of detritus (D), resulting in large accumulations of C in the soil, much of it frozen in the permafrost (20, 21). The fraction of total C content (density \times area) contained in the soil generally decreases from high to low latitude forests, with boreal forest soils containing almost 60% of the total C content of boreal forests. The midlatitude forests account for the smallest percentage of the total forest C pool because temperate forests comprise a smaller percentage of the global forests and because the C density is lower for temperate forests than boreal and tropical forests (18). However, the midlatitude forests are young and increasing in area (Figure 3) and will accumulate C (see disturbance section below).

THE FOREST ECOSYSTEM C CYCLE

The net exchange of C between the forest and atmosphere is described by Equation 1.



Photosynthesis is the assimilation of CO₂ from the atmosphere by plants and the conversion to carbohydrates (CH₂O) that plants use to build organic matter. Respiration is the oxidation of carbohydrates and release of CO₂ to the atmosphere. The net difference between the two processes over time determines the net accumulation of C, assuming the C is not removed by disturbance (see below).

Gross primary production (GPP) is the total amount of CO₂ assimilated by all vegetation strata (i.e., overstory, shrub, herbs, and bryophytes) (Figure 1). Approximately 50% of the CO₂ assimilated by vegetation is used to construct

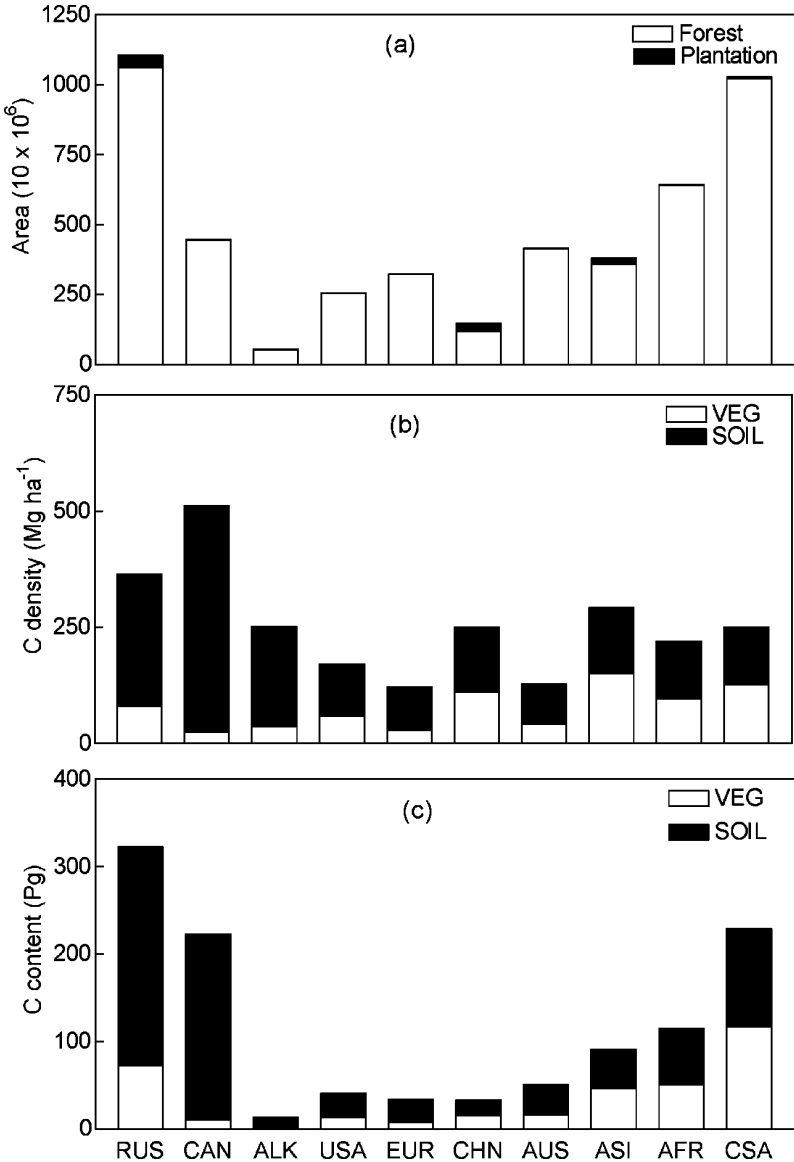


Figure 4 World forest summary estimates for (a) area in hectares, (b) carbon content, and (c) average carbon density. World forests were classified into low (0° to 25°), mid (25° to 50°), and high (50° to 75°) latitudinal zones that roughly correspond to tropical, temperate, and boreal forests, respectively. Abbreviations used are: RUS, Russia; CAN, Canada; ALK, Alaska; USA, United States; EUR, Europe; CHN, China; AUS, Australia; ASI, Asia; AFR, Africa; and CSA, Central and South America. Adapted from (18).

new tissue (growth respiration) and repair and maintain existing tissues (maintenance respiration). The sum of maintenance and growth respiration is referred to as autotrophic respiration (R_A) and results in a loss of CO_2 from the vegetation to the atmosphere (Figure 1).

NPP (Figure 1) is the balance between GPP and R_A (Equation 2).

$$\text{NPP} = \text{GPP} - R_A. \quad 2.$$

NPP is expressed on a dry organic matter or C basis, per unit area per year. Dry mass values can be converted to a C basis by assuming C: organic matter ratios of 0.45 for foliage, herbaceous vegetation, and fine roots and 0.50 for woody tissues such as stem wood, bark, branches, and coarse roots (22). GPP is difficult to measure directly; instead it is commonly simulated using an ecosystem process model or indirectly estimated from net ecosystem CO_2 flux data. NPP is calculated as the sum of the annual production (P) of all tissues (i) for all vegetation strata (j) (Equation 3).

$$\text{NPP} = \sum (P_{ij}) + H. \quad 3.$$

All tissues (e.g., stem, branch, foliage, coarse roots, fine roots, and mycorrhizae, reproduction) for all vegetation strata (overstory, understory, and ground cover) should be included. Fine root and mycorrhizae are the tissues that are most often excluded (22). Vogt et al. estimated mycorrhizae NPP comprised 15% of NPP in a cold temperate conifer forest, but it is not known if mycorrhizae comprise a similar fraction of total NPP in other forest ecosystems (23). A second bias is the exclusion of herbivory (H). The few studies that have quantified this loss of NPP have concluded that less than 10% of NPP of forests is consumed, except during insect outbreaks in some tropical forests (1, 24).

NEP is the annual net exchange of C, in the form of CO_2 between the atmosphere and terrestrial ecosystems, including the vegetation and soil (Figure 1). NEP is the difference between NPP and heterotrophic respiration (R_H). The sign convention for NEP used throughout this paper is $\text{NEP} > 0$, which implies a net transfer of C from the atmosphere to the forest ecosystem (C sink), and $\text{NEP} < 0$ implies a net transfer of C from the forest ecosystem to the atmosphere (C source). The efflux of CO_2 from the soil surface (S) results from the oxidation of soil organic matter by heterotrophic organisms (R_H) and root respiration (R_R) (Figure 1). The net exchange of C from the soil (S) is the difference between detritus (D) inputs (i.e., foliage, fine and coarse woody D production, and fine root turnover) and R_H . The loss of C via erosion and leached dissolved organic C should also be included (25). Net biome production (NBP) is the sum of NEP for all terrestrial ecosystems comprising a landscape, and accounts for C losses from disturbances.

Net Primary Production

Most plants are photoautotrophs, which acquire energy from solar radiation. Photosynthesis by leaves is proportional to absorbed visible quanta—or photosynthetic active radiation (PAR) (26). Although the light-photosynthesis relationship is

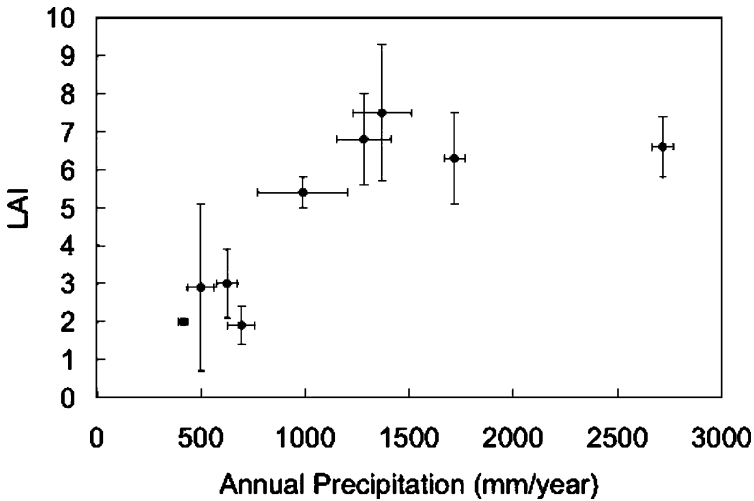


Figure 5 Average leaf area index (LAI) for the dominant forest and woodland biomes and its relationship to annual precipitation. Adapted from (32).

nonlinear for individual leaves, it is linear for most canopies (27–30), reducing the stand-level canopy photosynthesis to three primary factors: incident PAR, leaf area index (LAI), and environmental constraints on stomatal conductance. Incident PAR is strongly influenced by latitude, aspect, and cloud cover (31). The fraction of absorbed PAR that is usable by plants is strongly influenced by environmental constraints on stomatal conductance. Extreme cold temperatures, high vapor pressure deficits, inadequate soil moisture, and nutrient deficiencies restrict canopy conductance (28).

Average LAI varies fourfold among woodland and forest biomes, ranging from 1.9 for woodlands to 7.5 for tropical deciduous broadleaf forests (Figure 5). These biome-wide averages are based on literature reviews that may not be representative for all biomes. At the biome scale LAI is positively correlated to annual precipitation (Figure 5). Grier & Running first demonstrated the strong positive relationship between site water balance and LAI for terrestrial biomes (e.g., coniferous forests, woodland, and shrubland) occurring across a broad precipitation gradient in Oregon (33). This relationship is much weaker at the smaller forest ecosystem scale; instead LAI is positively correlated to soil water holding capacity (34).

The strong positive relationship between LAI and water availability results from the optimization of NPP. The simultaneous processes of photosynthesis and transpiration couple the C and water budgets of forests. Plants do not support a large LAI in drier environments because the soil moisture deficit and vapor pressure deficit severely restrict stomatal conductance and preclude CO₂ uptake, while constant foliage respiration costs reduce the net C uptake. The allocation of C to LAI appears to be in quasi-equilibrium with the environment in which they occur (35).

The availability of nutrients also influences the allocation of NPP to biomass components (1). Foliage has the highest nutrient concentrations of any major plant tissues (stem, branch, and roots), and large amounts of nutrients are required to construct a canopy. Evergreen forests have partially reduced the nutritional constraint on annual leaf production by retaining needles for several years, but the trade-off is that an evergreen canopy has a lower average photosynthetic rate than deciduous canopy (36). There is increasing evidence that plants optimize C allocation to equalize multiple resource limitations, thereby maximizing C gain. To optimize C uptake, trees allocate less biomass to foliage production and more to fine roots and mycorrhizae production to increase nutrient acquisition on infertile soils and *visa versa* on fertile soils (37, 38).

The ratio of NPP per unit of absorbed PAR is referred to as light use efficiency (LUE) or epsilon (ϵ). The lack of a universal acceptance of units for NPP (i.e., dry mass or C) and solar quanta [i.e., intercepted PAR, absorbed PAR, intercepted solar radiation (SR), and absorbed (SR)] has caused unnecessary variation in LUE values reported in the literature. Gower et al. standardized LUE coefficients reported in the literature to common units for the major terrestrial biomes and found the values were similar among forest biomes, although LUE was consistently greater for deciduous than evergreen forests for a given biome (22). If there really are no large differences in LUE among forest biomes, then the observed differences in NPP are largely the result of environmental controls on LAI. LUE coefficients based on GPP may vary greatly among biomes because many of the environmental constraints lie in controls on R_A resulting from varying C allocation patterns.

Average NPP values for the major forest biomes range from a low of 330 $\text{gC m}^{-2} \text{yr}^{-1}$ for boreal forests to highs of 820 and 1000 $\text{gC m}^{-2} \text{yr}^{-1}$, respectively, for tropical broadleaf evergreen and temperate broadleaf evergreen forests (Figure 6).

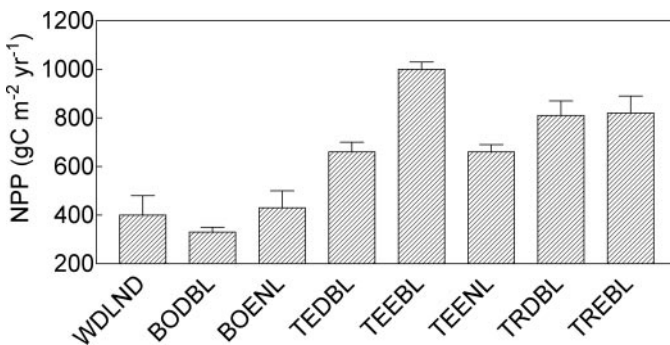


Figure 6 Average total net primary production (NPP) for the major forest biomes and woodlands of the world. Forest biome nomenclature used throughout this paper is as follows: WDLND, woodlands; BODBL, boreal deciduous broadleaf; BOENL, boreal evergreen needleleaf; TEDBL, temperate deciduous broadleaf; TEEBL, temperate evergreen broadleaf; TEENL, temperate evergreen needleleaf; TRDBL, tropical deciduous broadleaf; and TREBL, tropical evergreen broadleaf. Modified from (22).

The short growing season, caused by frozen soils in the spring and cold nighttime air temperatures in the fall, and infertile soils are the primary constraints on NPP of boreal forests. Interannual coefficients of variation for aboveground NPP (NPP_A) are several fold greater for nonforests than forests (39). Because the distribution, structure, and NPP of forest biomes are controlled by different environmental constraints, it is unlikely that the effect of climate change on NPP will be of similar magnitude or direction (40, 41). The physiologically-based interrelationships among water availability, LAI, and NPP suggest that changes in water balance, caused by changes in precipitation, temperature, or evaporative demand, will influence the structure and NPP of forest ecosystems differently depending upon the relative limitation of water versus nutrient(s), temperature, and light on NPP (42). Climate-induced changes in disturbance regimes could have greater effects than physiological responses (see the Disturbance section below).

Soil Surface CO_2 Flux

Forest soil scientists have long recognized the importance of soil organic matter because of its beneficial physical, chemical, and hydrological attributes to tree growth. Soil C is included in the organic layers composed of fine and coarse woody D and the mineral soil, with most of the C contained in the mineral soil. The notable exception is poorly drained boreal forest soils that contain as much as 90% of the C in peat. Forest soils are an important component of the global C cycle because of the large amount of C contained in the soil (Figure 4*b,c*).

Soil surface CO_2 flux, the sum of R_H and root respiration, is positively correlated to near-surface soil temperature and is most commonly modeled using a simple Q_{10} or Arrhenius function (43). These simple empirical models commonly explain 70%–90% of the variation in instantaneous chamber-based flux measurements during the year(s); however these same model forms explain only 34% to 50% of the variation among major terrestrial biomes of the world (44). Methodological differences may be responsible for some of the variation (45). Other important factors that influence S are (a) moisture (46, 47), (b) substrate quality (48), (c) fine root dynamics (49, 50), and (d) population and community dynamics of soil microbes (51, 52).

Average annual S ranges from $360 \text{ gC m}^{-2} \text{ yr}^{-1}$ for boreal evergreen needle-leaf forests to 1540 for tropical evergreen broadleaf forests (Figure 7). The almost twofold difference in S between boreal deciduous and evergreen is based on four studies; two values range from 430 to 450 and two values range from 860 to $870 \text{ gC m}^{-2} \text{ yr}^{-1}$. Interannual variation in S varied by 34%–55% and exceeded the interannual variation of NEP for an eastern deciduous forest (55). The importance of temperature and moisture control on S varies seasonally and with soil drainage; this suggests that climate change will not have a uniform effect on S for all forests.

Raich et al. used a simple temperature model to estimate S from satellite-derived estimates of temperature (56). The annual average for a fifteen year period was 80.4 PgC , of which forests and woodlands comprise 57% of the total. The

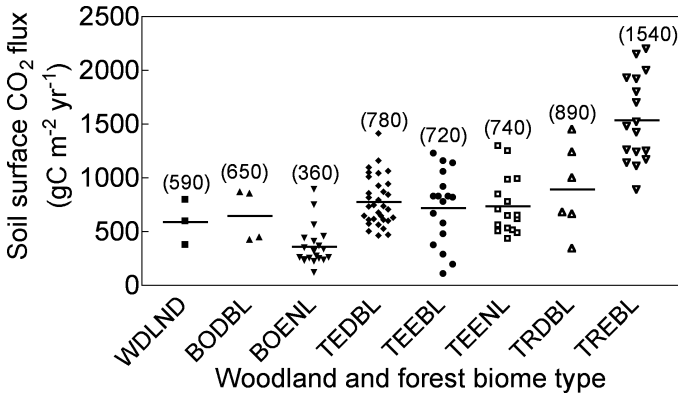


Figure 7 Average annual soil surface CO₂ (S) for major forest biomes and woodlands. Values were excluded if they were not for a full year or were for a treated (i.e., fertilized, drained, recently burned, or harvested) forest. See Figure 6 for forest biome nomenclature. Data sources were (44, 53, 54).

authors did not separate forest biomes by climate zone, but evergreen broadleaf forests contributed a greater fraction (0.30) of total biosphere S to the atmosphere than any other vegetation type. The modeled interannual variation in S suggested that precipitation explained the greatest amount of observed variation in S for seasonally dry biomes, but at the global scale interannual S variation was positively correlated ($r^2 = 0.78$) to mean annual temperature, as would be expected with the use of temperature relationships.

Partitioning S into heterotrophic (R_H) and autotrophic root respiration (R_R) is useful because the responses of the two fluxes to temperature differs (49). Also, R_H can be subtracted from NPP to estimate NEP, which provides a second independent approach that can be compared to the eddy covariance approach (57). R_H is commonly estimated using (a) independent estimates of litter, soil, and roots plus mycorrhizae, (b) flux measurements from soil plots with and without roots, or (c) natural abundance of stable isotopes (58). The contribution of root respiration to total S averages 0.54, 0.41, 0.56, 0.22, and 0.50 for boreal evergreen needleleaf, temperate deciduous broadleaf, temperate evergreen needleleaf, temperate evergreen broadleaf, and tropical evergreen broadleaf forests, respectively (Figure 8). The ratio of $R_R:S$ varies seasonally (50) and during stand development (53) as root biomass changes.

Net Ecosystem Production

NEP is commonly measured using a micrometeorological technique known as eddy covariance (57). During the last decade the number of eddy flux towers has increased dramatically, allowing comparison of NEP among major biomes, seasonal patterns of net CO₂ exchange for ecosystem, and even interannual variation

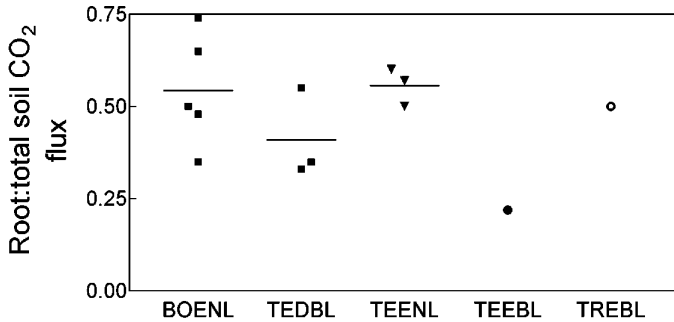


Figure 8 The contribution of root respiration to total soil surface CO₂ flux for forest biomes of the world. See Figure 6 for forest biome nomenclature. Data sources were (1, 53, 59).

of NEP. NEP and GPP generally increase from boreal to tropical forests, but there is sizable variation within a biome (Figure 9). Valentini et al. summarized the eddy covariance sites in Europe (EUROFLUX) and reported a significant inverse relationship between NEP and latitude (60); although this relationship did not hold when North American forest NEP data from the AMERIFLUX network were added. The lack of a simple relationship between NEP and latitude is not surprising

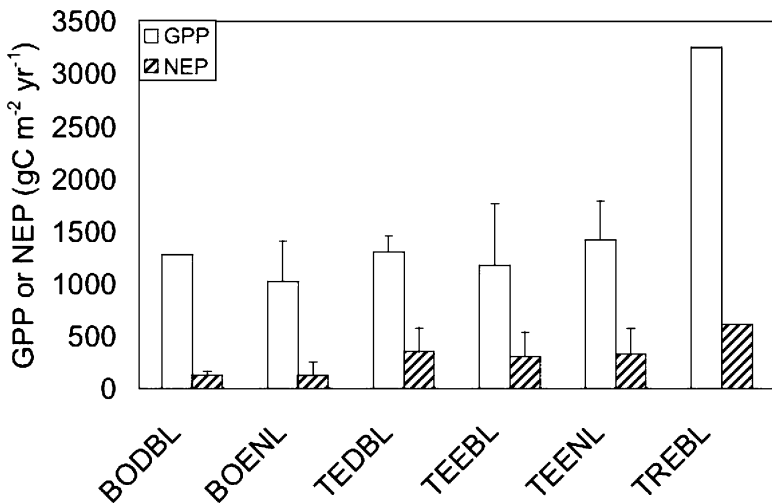


Figure 9 Summary of gross primary production (GPP, gC m⁻² yr⁻¹) and net ecosystem production (NEP, gC m⁻² yr⁻¹) for forest biomes of the world. Data sources (60–64). In some cases data originally published in Valentini et al. (60) were revised, as gap-filling approaches became more sophisticated, and republished by Falge et al. (61).

given the myriad of factors that influence NEP. Most, if not all, of the forests in Europe have a more maritime climate than the AMERIFLUX forests, which have a more continental climate. Differences in annual N deposition rates, stand age, soil edaphic, and management activity may also contribute to the large intrabiome variation in NEP. The metabolic activity of the plants (NPP) and microbes (R_H), which together determine NEP, are affected by both the phenology and quantity of a suite of environmental variables, and each will respond differently to interannual climate variation (65, 66).

Few sites have sufficient continuous eddy covariance measurements to examine interannual NEP variation, but those that do suggest that interannual variation of NEP can exceed observed variation in NEP among boreal and temperate forest biomes (Figure 10). For example, Arain et al. (62) reported NEP varied 3.5-fold (80 to 290 $\text{gC m}^{-2} \text{yr}^{-1}$) over a five year period for a boreal trembling aspen (*Populus tremuloides*) forest in central Saskatchewan, Canada, and Barford et al. (66) reported NEP varied two-fold (+120 to +250 $\text{gC m}^{-2} \text{yr}^{-1}$) over a nine year period for a mixed eastern deciduous forest in Massachusetts. Few of the scientists provided quantitative analysis of the source of the interannual NEP variation, but most suggested potential causes. Warm early springs appear to increase NEP of boreal forests (62, 67, 71). Other sources of interannual NEP variation were drought

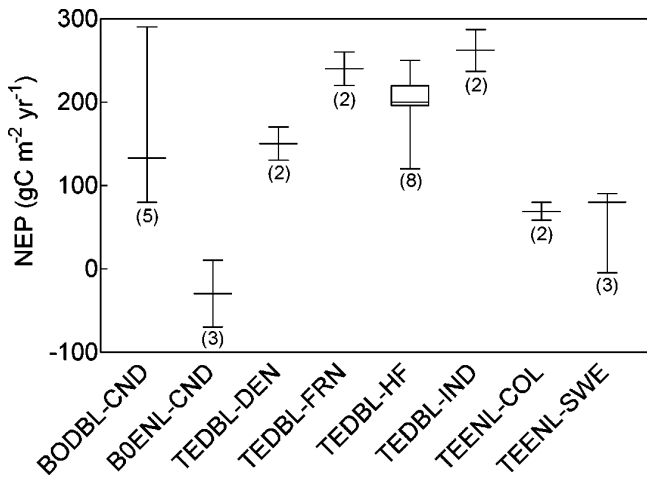


Figure 10 Interannual NEP variation for select forest biomes shown in box-and-whisker plots. The values in parentheses denote the number of years of measurements. The prefix for each observation describes the biome (see Figure 6 for forest biome nomenclature) and the last three letters depict the site location: BODBL-CND, Saskatchewan, Canada (62); BOENL-CND, Manitoba, Canada (67); TEDBL-DEN, Denmark [cited in (60)]; TEDBL-FRN, France (69); TEDBL-HF, Harvard Forest, Massachusetts (66, 72); TEDBL-IND, Indiana (68); TEENL-COL, Colorado (63); and TEENL-SWE, Sweden (70).

(63, 66, 67, 71), incident PAR and air humidity (68), winter snow cover (66), and fraction of incident diffuse:total PAR (63). Lagged ecosystem effects also influence interannual variation in NEP, so some year-to-year variation reflects environmental conditions of previous years (65). The magnitude and direction of the lagged effects differs among biomes depending upon whether the interannual variation in climate increased or decreased the environmental constraint(s) on C assimilation.

The importance of diffuse radiation C assimilation and net exchange of CO₂ between terrestrial ecosystems and the atmosphere is particularly relevant to global change because the increased fire frequency and cloud cover, products of global change, will increase the fraction of diffuse radiation. Diffuse radiation provides more uniform distribution of PAR over all foliage elements in the canopy than direct beam radiation that saturates the outer leaves but poorly illuminates shade foliage (22).

DISTURBANCES AND FOREST BIOLOGICAL C CYCLE

Disturbance is an important component of global change that influences forest ecosystem C budgets. Harvesting, fire, insects, pathogens, and wind are important disturbances, and the intensity of each varies greatly over time and space. For example, harvesting can range from single-tree removal to conventional harvesting that removes the stem wood up to a minimum top diameter, to whole-tree harvesting that removes the entire stem, branches, and sometimes foliage. While these disturbances are dramatic, they generally do not permanently change the vegetation composition and structure. For simplicity, it is convenient to categorize the effects of disturbance on the C cycle into two phases: initial disturbance effects on C pools and changes in C cycle processes during ecosystem recovery or succession. The phases are arbitrary, but they provide a useful framework to discuss the effects of disturbance on forest C cycles.

Initial Disturbance Effects on C Pools

The effects of land use change and forest management practices, especially harvesting, on soil C content is an important topic in global C cycles as more forests are harvested for the first time or are subject to more intense practices to meet the growing demand for fiber. Johnson & Curtis concluded that harvesting, on average, had little or no effect on the C content of the A horizon (73). They did note that whole-tree harvesting decreased C content of the A horizon by 6% while stem-only or conventional harvesting increased C content of the A horizon by 18%. Fertilization and planting N-fixing plants, two forest management practices to increase N availability, increased C content in the A horizon and in the total soil. The lack of standard sampling protocols and omission of certain components (i.e., fine and coarse woody D and deep soils) is a serious problem that prohibits a rigorous analysis of the effects of harvesting on total soil C content. In the future scientists need to quantify all soil and D pools; otherwise, it is impossible to

determine if a disturbance causes a net C loss or merely a redistribution of C into one or more unmeasured pools.

Fire consumes organic matter in the vegetation and D, and it is an important source of C emissions to the atmosphere (74, 75). Fire generally does not effect the C content of the upper mineral soil (73). Amiro et al. estimated that wildfires in Canadian boreal forests consumed 1.3 kgC m^{-2} (75) or roughly 15% of the forest floor. The effects of fires on soil C content differ from harvesting in several important ways. First, most fires consume a small fraction of the C contained in the woody biomass although harvesting removes 50%–80% of total aboveground woody biomass (76–78). Decomposition of standing dead stem is slow until the stem falls and makes contact with the soil, which facilitates colonization of the wood by heterotrophs and increases moisture in the woody tissue (79–81). Bond-Lamberty et al. reported a 50 t C input of coarse woody debris around year 12 after a stand-killing wildfire in a boreal black spruce forest (81). Processes that increase C accumulation in the soil are (a) incorporation of charcoal recolonization of early seres by nitrogen-fixing plants and (b) downward transport and deposition of hydrophobic organic compounds into the soil (82).

The effects of disturbance on soil C pools are highly variable for several reasons: (a) varying disturbance and management intensities and their effects on soil and detritus C pools (73, 83), (b) inconsistent treatment or exclusion of some detritus C pools, the most notorious being coarse woody debris (79), and (c) past land use and historic disturbance legacies (84). All of these factors make it extremely difficult, if not impossible, to detect small changes in the C content of the large and heterogeneous soil C pool (85).

Changes in the C Cycle During Succession

The rate of ecosystem recovery following a stand-killing disturbance depends on climate, edaphic soil conditions, and disturbance intensity, but the general ecosystem functional characteristics are thought to follow predictable patterns (86). Odum hypothesized that during forest succession (a) NPP and GPP would reach a maximum and decrease, (b) R_A would steadily increase, and (c) NEP would reach a maximum in synchrony with NPP and decline to a steady state near zero. Sufficient data have been compiled during the past several decades to begin to examine Odum's predictions.

Forest chronosequence studies reveal that NPP_A reaches a maximum during the early life of the stand, often corresponding to maximum LAI, and then declines (87, 88). Age-related NPP_A decline averages 37% across all forest biomes, but it is more pronounced (54%) in boreal forests (Figure 11). The age-related NPP decline often corresponds to a decrease in LAI (88). The physiological causes for this age-related NPP decline are not well understood, but it has been observed in almost every forest biome of the world (87). Kira & Shidei first hypothesized that the decline in NPP with stand age was due to an altered balance between respiring and photosynthetic tissue (92). This hypothesis persisted in the ecological literature for several decades before being tested and found not to be the primary cause

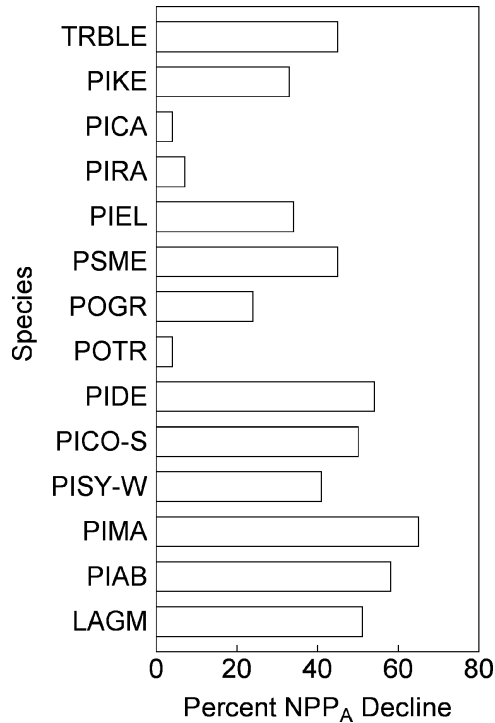


Figure 11 Summary of age-related aboveground net primary production decline for forest ecosystems in contrasting climates. Age-related NPP_A decline was calculated as (maximum NPP_A – minimum NPP_A, after maximum NPP_A occurred)/maximum NPP_A. The primary data source was (87), and additional data sources were (89–91). Species codes for boreal forests are; and TRBLE, tropical broadleaf evergreen mixed forest; PIKE, *Pinus keyisia*; PICA, *Pinus caribaea*; and PIRA, *Pinus radiata* for subtropical and tropical forests; PIEL, *Pinus elliottii*; PSME, *Pseudotsuga menziesii*; POGR, *Populus grandidentata*; POTR, *Populus tremuloides*; PIDE, *Pinus densiflora*; PICO-S, *Pinus contorta*; PISY-W, *Pinus sylvestris* for temperate forests; and PIMA, *Picea mariana*; PIAB, *Picea abies*; and LAGM, *Larix gmelinii* for boreal forests.

(87, 93, 94). The two most plausible explanations for the age-related decline in NPP are increased nutrient limitation and hydraulic constraint (87, 88), but other causes have been hypothesized (88).

More research is needed to elucidate the mechanism(s) responsible for the age-related NPP decline because NPP is a major component of NEP. Ongoing efforts to simulate global forest NPP must account for changes in NPP during succession. Ecosystem biogeochemical models need to incorporate the correct mechanism(s) that constrain NPP and C allocation because climate change, increased nitrogen deposition, and elevated CO₂ directly or indirectly affect water and nutrient

availability, two of the major factors thought to affect the magnitude and timing of the age-related NPP decline.

NEP, the net exchange of CO_2 between terrestrial ecosystems and the atmosphere, is the difference between two large fluxes of opposite effect on atmospheric CO_2 concentration. Results from a boreal forest wildfire chronosequence near Thompson, Manitoba, Canada provides the first comprehensive assessment of how NEP, and its major components, change during forest succession (Figure 12). NPP increased as the leaf area increased (96) and peaked 35 to 70 years after

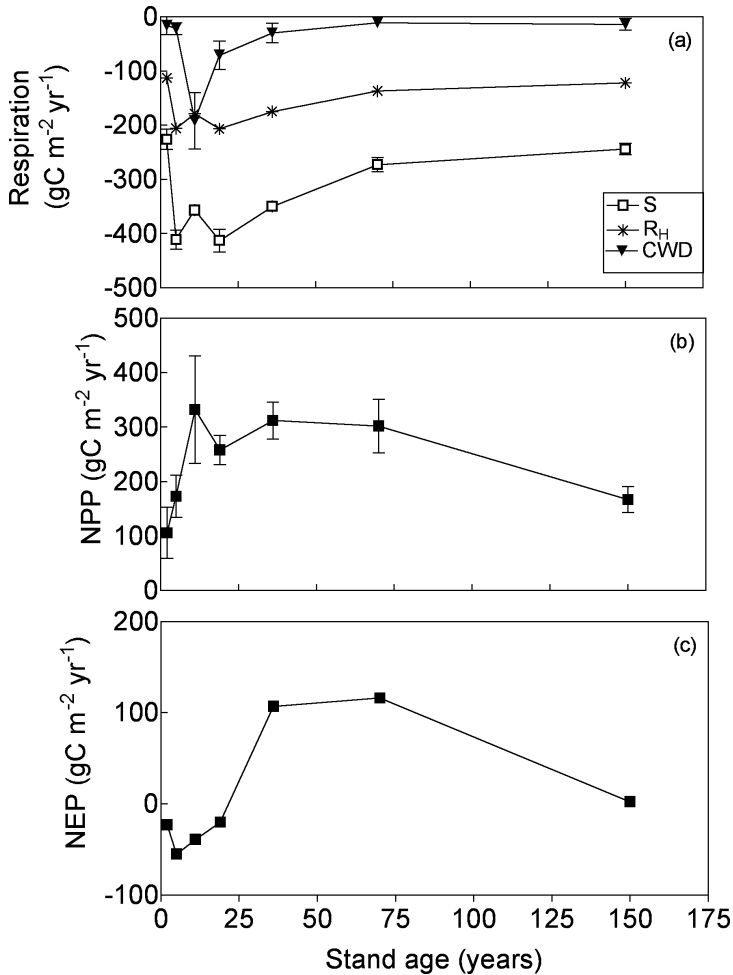


Figure 12 Comparison of (a) soil surface + coarse woody debris (CWD) CO_2 flux (b) NPP, (c) and NEP for a well-drained boreal black spruce chronosequence. Data sources were (53, 54, 89).

the stand-killing wildfire, and then it declined by 50%–60% depending upon soil drainage (89). During early succession, R_H from the soil and coarse woody debris were greater than NPP, causing NEP to be negative for several decades. Maximum NEP occurred at a similar stage in succession, and NPP and NEP both slowly declined with NEP approaching zero for the 150-year-old black spruce stand. The NBP was $48 \text{ gC m}^{-2} \text{ yr}^{-1}$ for the boreal forest landscape near Thompson, Manitoba, Canada (89). The observed patterns are very similar to the hypothesized patterns proposed over 40 years ago (86).

ATMOSPHERIC POLLUTANTS AND THE FOREST BIOLOGICAL C CYCLE

Humans have greatly altered atmospheric CO_2 concentrations, nitrogen deposition from the atmosphere, and tropospheric ozone concentrations (3). Much has been learned about the rates of increase of the various pollutants and their effects on forest ecosystems during the past several decades. A CO_2 enriched atmosphere and modest deposition of nitrogen may stimulate C uptake by forests temporarily, but the long-term effects may be negligible or possibly detrimental. Climate change is now well accepted by international scientists and policy makers (8, 40). Warming is the most publicized aspect of climate change, and there is now substantial evidence that increases in GHG in the atmosphere are responsible for the 0.3 to 0.6°C increase in air temperature over the last century (40, 97, 98). The effects of each of the pollutants and climate warming on the forest ecosystem C cycle are reviewed below.

Atmospheric N Deposition

Human activities have more than doubled the deposition of nitrogen (N) from the atmosphere to terrestrial ecosystems, with much of the annual deposition of 140 Tg yr^{-1} occurring in industrialized regions (99). Several excellent reviews on the effects of atmospheric N deposition and ecosystem responses have been published recently (100–103); therefore, the focus of this paper is on reported effects of atmospheric N deposition on forest C sequestration. The productivity of many temperate and boreal forest ecosystems are limited by nitrogen availability, and fertilization routinely increases annual C sequestration in the vegetation (1) and soils (73). Several experimental studies have shown that fertilization increased forest growth more than decomposition—implying N increased net C sequestration (104, 105). Estimates of the effects of N deposition on C sequestration by global forests ranges from 0.1 to 2.3 Pg C yr^{-1} (106–109).

However, not all evidence suggests that atmospheric N deposition enhances C sequestration. Results from modest ^{15}N additions in six European and three North American forests suggested that forest vegetation was a small sink (110). An even greater concern is that chronic N deposition will cause the terrestrial ecosystem to become nitrogen saturated and eventually lead to large nitrogen

leaching losses and decreased forest productivity (10, 100). In addition, because of the catalytic role of reactive nitrogen, atmospheric N deposition is often correlated to the deposition of other pollutants such as ozone (109). Long-term (1969–1990) fertilization studies of two Swedish forests added 1740 and 2160 kgN ha⁻¹ over a +20-year period and reported continued greater C accumulation in the vegetation and soil of the fertilized than control plots if nutrient imbalances were avoided by adding all plant-required elements (101). This study provides evidence that the N saturation threshold can be extremely high. The wide range of observed forest growth responses to atmospheric N deposition may be influenced by variations in such factors as the successional stage of development, forest type (evergreen versus deciduous), stand history, soil nitrogen accumulation, topography, and climate. All of these factors influence forest growth and most likely will help determine forest growth response to chronic atmospheric N deposition (100, 103). Understanding these determinants will be necessary in order to predict the effects of atmospheric N deposition on C sequestration in different forest types in the future.

Climate Warming

The sensitivity of terrestrial C cycles to climate warming is one of the most pressing scientific environmental problems. Views on the effect of climate change on the C cycling processes, especially respiration, have changed in recent years. The dominant paradigm once was that R_A and R_H were more positively temperature-dependent than GPP, which means that the R_A :GPP ratio would increase in a warmer climate (111, 112). However, comparative whole stand C budget studies have shown that the ratio of R_A :GPP for forests in contrasting climates is relatively stable, averaging around 0.50 (1). Adjustments in C allocation to various biomass components and physiological acclimation of respiration to temperature appear to be the most important mechanisms that maintain a stable proportion of GPP allocated to R_A (113). Dewar et al. (114), using a model, demonstrated that the short-term increase in respiration and long-term temperature acclimation of plants in response to warming could be explained by transient dynamics of nonstructural carbohydrate and protein pools. Results from experimental warming studies in greenhouses and growth chambers have further demonstrated that the acclimated R_A :GPP ratio is relatively insensitive to temperature (115–117).

The effect of climate warming on S is one of the most important and controversial topics related to global change and the C cycle. The issue is of great importance because soil contains twice as much C as the atmosphere (118), and small changes in S would have a pronounced effect on CO₂ concentrations in the atmosphere (119–121).

Numerous empirical studies have demonstrated a positive exponential relationship between S and soil temperature (see Soil Surface CO₂ Flux, above). Scientists have used these empirical models to predict S for a warmer climate and reported moderate to large losses of C to the atmosphere (119–121). Data from long-term eddy flux measurements have lead scientists to conclude that

warming causes terrestrial ecosystems to become a weaker C sink or even a C source (67, 122).

However, experimental data on the effects of climate warming on C sink strength of terrestrial ecosystems do not fully support modeling results. Peterjohn et al. reported little or no increase in S from an eastern deciduous forest soil that was heated 5°C above an adjacent unheated forest soil (123). Stromgren et al. (124) measured S in replicate irrigated-fertilized unheated and irrigated-fertilized heated Norway spruce stands in northern Sweden and reported a 17% greater S for the heated ($760 \text{ gC m}^{-2} \text{ yr}^{-1}$) than the control ($680 \text{ gC m}^{-2} \text{ yr}^{-1}$). Much of the greater C loss from the heated plots was attributed to the 12% increase in the length of the soil frost-free period. However, the modest increase in S in the heated stands was offset by a $280 \text{ gC m}^{-2} \text{ yr}^{-1}$ increase in NPP_A in the heated compared to the control (105). The results from the boreal warming experiment in northern Sweden are consistent with the meta-analysis results for warming experiments conducted in a variety of ecosystems using different artificial warming approaches. Rustad et al. (125) reported a similar, modest average increase in S (20%) and NPP_A (19%), providing little or no support for the hypothesis that warming will increase net C exchange to the atmosphere.

The discrepancy between the results from experimental studies and modeling is likely explained by the fact that most models use empirical zero-order temperature functions derived from quasi steady-state control ecosystems to predict S for ecosystems that are no longer at steady-state because of climate change and increased soil N mineralization (125–127). Over time periods greater than one year, S should be strongly correlated to D production, which is directly proportional to NPP. Annual S can be less than NPP over long time periods (i.e., decades to centuries), in which case the ecosystem accumulates C (128).

More problematic uncertainties of future global forest C budgets are the potential redistribution of ecosystem boundaries and its effect on C storage (129). Rapid changes in climate may cause large transient losses of C (130). In addition, large scale changes in the distribution of biomes may alter the structural characteristics (e.g., albedo and LAI) that produce climate feedback mechanisms, which can have positive or negative effects on climate change relative to the positive effect of radiative forcing (131). The magnitude and direction of the feedback are dependent the effects of elevated CO_2 and warming on vegetation growth and on the extent of vegetation-atmosphere coupling.

Elevated Atmospheric CO_2 Concentration

A central question related to global change and the C cycle is the response of terrestrial ecosystems to elevated atmospheric CO_2 concentration. Specifically, will elevated CO_2 stimulate NPP and result in greater C storage in long-lived tissues (i.e., wood) and humus, or alternatively, will stimulated NPP largely occur in short-lived tissues (i.e., foliage and fine roots) that decompose rapidly in the soil and contribute little to net C sequestration? This whole-ecosystem question is

being addressed with free-air CO₂ enrichment (FACE) experiments. The advantage of FACE studies is they have minimal effect on the microclimate, and they allow for feedbacks between vegetation and the soil (132).

CO₂ fertilization increased NPP by 21% and 25% during the first two years of enrichment at a warm temperate needleleaf evergreen (*Pinus taeda*) and broadleaf deciduous (*Liquidambar styraciflua*) forests (Figure 13). These short-term responses suggest only modest C accumulation in woody tissue and limited increase in C storage in the soil and litter (133, 134). However, the results from the two forest FACE experiments should be considered preliminary because it is unclear if the observed responses represent a new equilibrium or a transient response (135, 136). The measured growth response of the young stands to CO₂ enrichment may be the upper limit for forest C sequestration because the demand for nutrients may exceed nutrient mineralization rates in the soil. A decline in growth response to

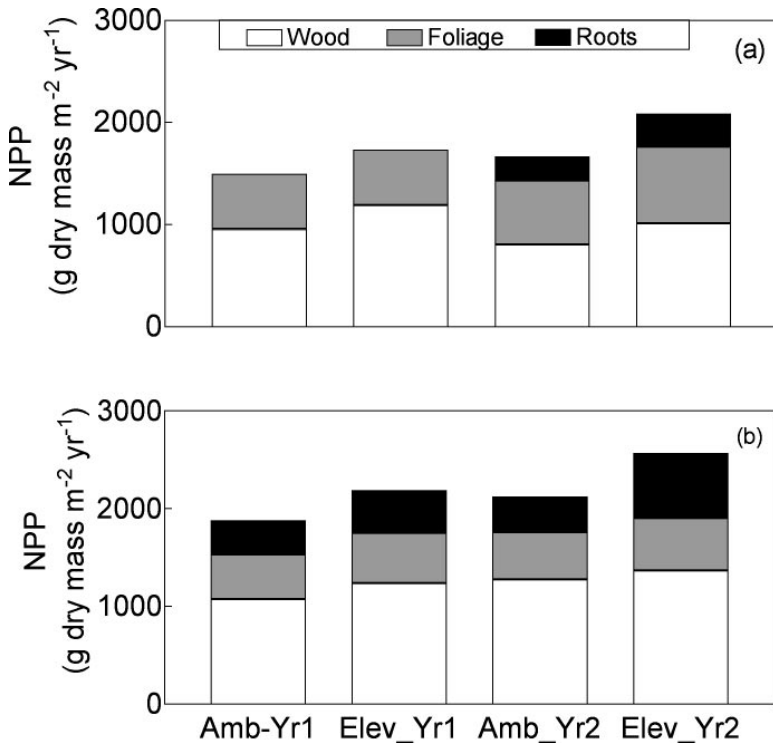


Figure 13 Comparison of NPP for (a) loblolly pine and (b) sweetgum grown in control and enriched atmospheric CO₂. The abbreviations are: Amb, ambient atmospheric CO₂ concentration; Elev, elevated atmospheric CO₂ concentration; Yr1, year 1 of treatment; and Yr2, year 2 of treatment. Data sources were (126, 127).

long-term CO_2 enrichment has been observed for individual trees grown in elevated CO_2 concentrations (137), *Quercus ilex* trees at a natural CO_2 spring (138), and *P. taeda* growth at the original, unreplicated FACE stand in North Carolina (139).

A pressing research need is the multiplicative effects of multiple atmospheric pollutants on the forest C cycle. Tropospheric ozone (O_3), a strong oxidant that is phytotoxic to many plants (11, 12), exceeds the deleterious threshold of 60 ppb in over 29% of all temperate and subboreal forests. Ozone concentrations are predicted to triple during the next 30 to 40 years and adversely affect over 50% of all temperate and subboreal forests by 2100 (13, 14, 140, 141). The increased concentrations of CO_2 and ozone have opposite effects on plant growth, but their interactive effect is poorly understood (140). In an ongoing study, NPP_A for aspen and mixed aspen + birch was greater (36%–62%) in elevated CO_2 than control FACE rings, less (2%–23%) in elevated O_3 than control FACE rings, and similar for $\text{CO}_2 + \text{O}_3$ and control FACE rings after three years of treatment (Figure 14).

Predicting the effect of atmospheric pollutants on forest ecosystem C budgets is complicated by the fact that stressed plants are more susceptible to insects and pathogens. Insect outbreaks, such as those by forest tent caterpillar, predispose the trees to disease and other environmental stresses that may result in large-scale dieback and increased fire susceptibility. Aspen trees exposed to ozone had lower concentration of phenolic glycoside, an antiherbivore defense compound, and greater growth of tent caterpillar pupae than aspen grown in ambient FACE rings (141). However, the adverse effects of ozone were ameliorated when aspen was grown in elevated $\text{CO}_2 + \text{O}_3$. The interactive effects of multiple atmospheric pollutants on forest C storage and cycling warrant greater attention, especially because it relates to increased susceptibility to stand-killing perturbations.

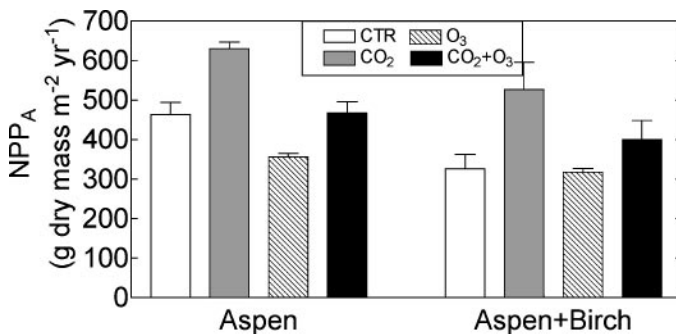


Figure 14 Comparison of NPP_A for mixed trembling aspen and birch trees grown in ambient or control atmospheric CO_2 concentration (CTR), enriched CO_2 , elevated ozone, and ozone + enriched CO_2 FACE rings. (Data were generously provided by E. Kruger, University of Wisconsin.)

GREENHOUSE GAS MANAGEMENT AND THE ROLE OF FORESTS

The Kyoto Protocol, an international treaty to decrease GHG concentrations in the atmosphere by reducing fossil fuel emissions, now awaits final ratification by individual nations (142). During the negotiation process, the focus shifted from reducing fossil fuel emissions toward implementation of biological sinks (8, 143). The final version of the Kyoto Protocol included afforestation, reforestation, and changes in the management of agriculture and forestry as allowable biological C sequestration activities. As the Kyoto Protocol is now written, the sum of the sequestered C resulting from the three practices cannot comprise more than 80% of the required 5% reduction in fossil fuel emissions below the base year (1990).

Forest landowners and associated forest product industries have three broad potential management options to offset rising CO₂ concentrations in the atmosphere: (a) C sequestration in forest vegetation and soil, (b) C sequestration in wood and paper products, and (c) offset fossil fuel emissions by substituting wood/paper material. The biological feasibility of each of these management opportunities is examined in the following sections. The socioeconomic and cultural constraints for the three management opportunities are not discussed in this review but are an integral part of a successful forest C sequestration management program (144, 145).

Carbon Sequestration Potential in Vegetation and Soil

Figure 6 summarizes average NPP rates for the dominant forest biomes of the world. Forest management activities can increase NPP, but few studies have quantified maximum C sequestration rates for different forest regions. Removing nutrient and water limitations are two obvious approaches, and there are several studies that have added sufficient water and nutrients to remove these constraints on NPP (146–148). The relative importance of water and nutrient limitations varied among forests. Irrigation and fertilization together (IF) increased NPP_A of radiata pine (*Pinus radiata*) in New South Wales, Australia; Scots pine (*Pinus sylvestris*) in southern Sweden; and loblolly pine (*Pines taeda*) in North Carolina, by 70%, 78%, and 154%, respectively. The effect of IF was additive for loblolly pine, but it was multiplicative for *P. radiata*.

Nutrient and water amendments clearly increased the gross C sequestration rates of the forests, and the rates appear promising from the point of view of C sequestration. However, gross C sequestration rates are misleading because they exclude GHG emissions required to manage the forest [GHG emitted from the production of fertilizers added to the forest (149)] and emissions produced via energy consumption during the production and transportation of the final products. For example, 0.58 mol of C is released as CO₂ per mol of N produced in fertilizer, and this factor increases to 1.4 if production, transport, and application of the fertilizer are included (150, 151). Future forest C sequestration management plans should be based on a complete accounting of all GHG emissions associated with

the management practices proposed to increased tree growth. The relationship between forest management intensity and net forest C sequestration is unknown and warrants investigation.

Land use changes such as afforestation, deforestation, and conversion of natural forests to plantation change the land cover compared to natural disturbances that often only reset the successional stage of the terrestrial ecosystem. The effects of land use change on soil C pools are of great importance to scientists and policy makers trying to reduce GHG emissions or enhance C sequestration, as mandated by the Framework Convention on Climate Change. Guo & Gifford (152) performed a meta-analysis on the effects of land use change on soil C stocks, and they found that conversion of forest to crops decreased soil C content by 42%, but afforestation of cropland increased soil C content by 53%. Conversion of natural forests to plantations decreased soil C content by 13%.

There are very few replicated afforestation studies that have quantified C accumulation rates and distribution for all major components (i.e., mineral soil, D, and vegetation) of a forest. The accumulation of C in D and mineral soil has a greater permanence than in vegetation, and it is therefore more desirable from a GHG management perspective. The pattern that emerges from a few studies is that 80%–90% of the total ecosystem carbon accumulation occurs in the forest vegetation, followed by forest floor and mineral soil (153, 154). C accumulation in mineral soil was extremely low after 40 years for both afforestation studies—a finding that corroborates earlier soil-only studies that concluded average C accumulation rates for a variety of forest ecosystems were near zero for most reforestation and modest for temperate and boreal afforestation activities (1). The general conclusion is that storing large amounts of C in the soil is not feasible, at least on a timescale of the life of a stand, and the focus should be of fate of the C contained in the trees.

Carbon Sequestration in Forest Products

Recently scientists have quantified the gross amount of C contained in paper and wood products in the United States (2, 155), Finland (156, 157), and in the major countries of the world (15). Since 1910, 2.7 Pg C, an amount that is equivalent to 20% of the total C contained in forest trees in the United States, has accumulated in wood and paper products that are currently in use or buried in landfills, and the annual C accumulation rate is projected to increase from present-day 61 Tg C yr⁻¹ to 74 Tg C yr⁻¹ by 2040 (2). The growing demand for wood and paper products and changed disposal practices are the primary factors responsible for the increased rate of gross C accumulation in forest products. Before 1986 wood and paper waste was disposed in dumps, where it was often burned; however, waste is now placed in landfills or recycled. The anaerobic conditions of landfills and high lignin concentration of wood and paper products make forest products extremely resistant to decay. On average, only 3%, 16%, 18%, and 38% of the total C contained in solid wood products, newsprint, coated paper (i.e., magazines), and office paper, respectively, are ever released back to the atmosphere when placed in landfills (2).

Côté et al. completed a C mass balance analysis for an integrated pulp mill in Texarkana, Texas, that produces bleached board and cupstock grades of paper (158). The rolls of product are transported to other locations where the paper is converted into milk and juice cartons. They concluded that the integrated mill and fiber basket (the forest that provides the fiber for the mill) were a net C sink. In other words, the C sequestered by their forests for that year exceeded the C released to produce the paper products by a factor of 1.4 to 2.8.

It is extremely important to note that almost all the forest product sequestration estimates are based on gross C accumulation. That is to say, GHG emissions from harvest, transportation of the roundwood or chips to processing plants (i.e., pulp and paper mills, saw mills), mill emissions, and transportation of the forest products to regional distributors and consumers are ignored (see Figure 1).

Industrial ecology is a rapidly emerging discipline that studies “technological ecosystems,” their consumption and recycling of resources, their potential impacts on the environment, and the ways in which the biological and technological ecosystems can be restructured to enable global sustainability (159). Life cycle analysis (LCA) is an important tool used in industrial ecology and can be used to quantify total GHG emissions for a forest product from cradle (i.e., forest establishment) to grave (i.e., final fate). The chain should include the entire life cycle of the product, process, or activity and encompass the extraction and processing of raw materials, manufacturing, transportation, distribution, use, reuse, maintenance, recycling, and final disposal, which includes the release of CO₂ and CH₄ from the landfills (160). LCA studies can be used to identify and quantify GHG emissions for all processes in the product chain. Such studies are greatly needed to identify potential management opportunities to reduce GHG emissions, increase biological C sequestration, and assess optimal disposal practices of end products. Scientists have yet to demonstrate that there is a net C storage in forest products if a complete LCA, from cradle to grave, is completed.

Offset Fossil Fuel Emissions by Substituting Wood/Paper Material

Many wood product and paper production mills generate some of their energy from wood waste (i.e., chips, bark, and sawdust) and paper waste recovered from the harvesting and manufacturing processes. The CO₂ emitted when wood and paper waste is burned is equivalent to the atmospheric CO₂ that was sequestered by the tree during growth and transformed into organic carbon compounds; hence there is no net contribution to the atmospheric CO₂ concentration, and the material is considered to be C neutral (161). The use of wood and paper waste as a biofuel is desirable because it is a C neutral energy source, and it decreases human dependency on non-C neutral fossil fuels. Row & Phelps (155) estimated that the use of wood and paper waste products as fuel in the United States prevented the release of 50×10^6 metric tons C from the combustion of fossil fuel annually.

Approximately 270×10^6 tons of paper are consumed annually worldwide (16), and the consumption of energy by the pulp and paper industry makes it the fifth largest consumer of energy in the world (17). The fiber used to produce paper is supplied by virgin fiber (e.g., wood) and recycled paper products. Different processes, which differ in energy requirements, material efficiencies, and paper characteristics (i.e., brightness, strength, and opacity), are used to manufacture wood into pulp—the primary material used to make paper. The kraft, or chemical, pulping process requires very little purchased power because almost all (>94%) of the required energy is derived from wood waste at the mill and black liquor (a by-product of the bleached kraft pulping of virgin fiber) that is produced in the kraft process. The carbon neutral wood waste and black liquors are burned to produce steam and electricity, which thus decreases the need for purchased energy that is commonly derived from fossil fuels. Mechanical pulping processes, the most prominent being stone-ground wood and thermomechanical, require large quantities of energy because mechanical pulping does not generate chemical by-products that can be burned to produce steam and electricity. However, the pulping yield coefficient (paper produced per ton of wood fiber consumed) is lower for kraft pulping (40% to 65%) than mechanical pulping (>80%) processes (16) because the kraft processes extract the lignin and other components. Many paper products are produced from a mixture of kraft and mechanical pulp to achieve (a) required paper characteristics (e.g., kraft pulp has greater strength and durability needed for printing, writing paper, packaging, and construction board products) and (b) desired characteristics by consumers. Policy decision makers, pulp and paper industry executives, and society are confronted with multiple goals of preserving forest biodiversity, fiber conservation, energy conservation, and the use of biomass for fossil fuel substitution. The trade-offs between the pulping processes (kraft versus mechanical) and virgin fiber versus recycled paper have numerous, complex implications on net energy consumption and warrant immediate study.

IMPORTANT ISSUES FOR FUTURE RESEARCH

Our knowledge of the factors controlling the carbon budgets of forests has increased dramatically during the past several decades and has helped focus new questions. Disturbance has a greater effect on NPP, R_H , and NEP than other aspects of global change such as warming or elevated CO_2 concentration. More process-based chronosequence studies for different types of disturbance regimes are warranted to elucidate physiological principles that need be incorporated into physiologically-based models. Rates of climate warming are predicted to differ among forest biomes, and the effects of warming on the structure and function of terrestrial ecosystems are likely to be complex and differ among ecosystems (162).

Important global change questions that remained unanswered include:

1. How will warming influence soil carbon dynamics and the net exchange of carbon between forests and the atmosphere?

2. What effect does past land use history have on current carbon budgets of forests?
3. How are disturbance regimes (i.e., frequency and intensity) for wildfire, harvesting, and insect outbreak changing? What effect will they have on carbon exchange between forests and the atmosphere?
4. What is the net effect of the multiple changes in atmospheric chemistry on forest carbon budgets?
5. What are the CO₂ and other GHG shadows for the major forest products? What are the near- and long-term opportunities to reduce GHG emissions for each chain? What intensity level of forest management maximizes net C sequestration?

The science questions outlined above will require the use of numerous research tools and approaches that can only be provided by interdisciplinary science teams. All the questions have direct implications to private, state, and federal forest managers, as well as policy makers. The forest C cycle is inextricably linked to the forest product industries that are very dependent upon fossil fuels for power to manufacture wood and paper products and that transport final wood fiber to the mills and final products to consumers. The interrelationships among the various industries provide many opportunities to reduce fossil fuel emissions. Forest product, energy, transportation, and waste management industries have the greatest understanding and insight into their respective components of forest product chains, and scientists must actively include these parties in future analyses and policy discussions.

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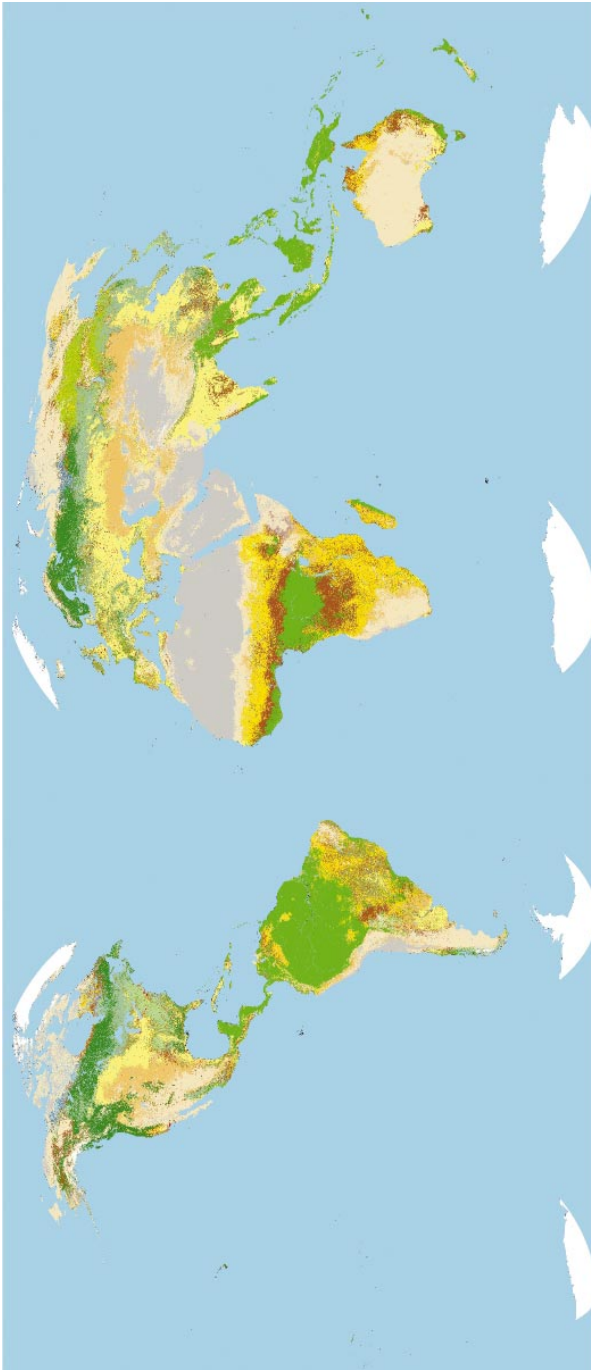
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|  | Water |  | Closed Shrublands |  | Croplands |
|  | Evergreen Needleleaf Forest |  | Open Shrublands |  | Urban |
|  | Evergreen Broadleaf Forest |  | Woody Savannas |  | Cropland/Natural Vegetation |
|  | Deciduous Needleleaf Forest |  | Savannas |  | Snow and Ice |
|  | Deciduous Broadleaf Forest |  | Grasslands |  | Barren or Sparsely Vegetated |
|  | Mixed Forest |  | Permanent Wetlands | | |

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Figure 2 Map of the major terrestrial ecosystems of the world based on MODIS 2000–2001 imagery and the IGBP land cover classification system. Source is Boston University <http://geography.bu.edu/landcover/userguidelc/intro.html>