Forests in Flux

REVIEW

Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests

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The world’s forests influence climate through physical, chemical, and biological processes that affect planetary energetics, the hydrologic cycle, and atmospheric composition. These complex and nonlinear forest-atmosphere interactions can dampen or amplify anthropogenic climate change. Tropical, temperate, and boreal reforestation and afforestation attenuate global warming through carbon sequestration. Biogeophysical feedbacks can enhance or diminish this negative climate forcing. Tropical forests mitigate warming through evaporative cooling, but the low albedo of boreal forests is a positive climate forcing. The evaporative effect of temperate forests is unclear. The net climate forcing from these and other processes is not known. Forests are under tremendous pressure from global change. Interdisciplinary science that integrates knowledge of the many interacting climate services of forests with the impacts of global change is necessary to identify and understand as yet unexplored feedbacks in the Earth system and the potential of forests to mitigate climate change.

Forests cover ~42 million km² in tropical, temperate, and boreal lands, ~30% of the land surface (Fig. 1A). These forests provide ecological, economic, social, and aesthetic services to natural systems and humankind (1), including refuges for biodiversity, provision of food, medicinal, and forest products, regulation of the hydrologic cycle, protection of soil resources, recreational uses, spiritual needs, and aesthetic values. Additionally, forests influence climate through exchanges of energy, water, carbon dioxide, and other chemical species with the atmosphere.

Forests store ~45% of terrestrial carbon (Fig. 1B), contribute ~50% of terrestrial net primary production (2), and can sequester large amounts of carbon annually (Fig. 1C). Carbon uptake by forests contributed to a “residual" 2.6 Pg C year⁻¹ terrestrial carbon sink in the 1990s, ~33% of anthropogenic carbon emission from fossil fuel and land-use change (3). Forests have low surface albedo and can mask the high albedo of snow (Fig. 1D), which contributes to planetary warming through increased solar heating of land. Forests sustain the hydrologic cycle through evapotranspiration, which cools climate through feedbacks with clouds and precipitation. The ratio of evapotranspiration to available energy is generally low in forest compared with some crops and lower in conifer forest than in deciduous broadleaf forest (Fig. 1E).

That forests influence climate has long been postulated. From the onset of European settlement of North America, it was believed that clearing of forests for cultivation, wood products, and settlement altered climate (4). Today, scientists have a diverse array of methodologies, including eddy covariance flux towers, free-air CO₂ enrichment systems, satellite sensors, and mathematical models to investigate the coupling between forests and the atmosphere. It is now understood that forests and human uses of forests provide important climate forcings and feedbacks (3), that climate change may adversely affect ecosystem functions (5), and that forests can be managed to mitigate climate change (6). What is lacking, however, is science that integrates the many interacting climate services of forests with the impacts of global change to inform climate change mitigation policy.

Accordingly, this article reviews biosphere-atmosphere interactions in tropical, temperate, and boreal forests. Emphasis is placed on biogeochemical processes (albedo and evapotranspiration) (7), their comparison with biogeochemical processes (carbon cycle) (8), and alteration of forest-atmosphere coupling through biogeographical processes (land use and vegetation dynamics) (9).

The Ecology of Climate Models

The influence of forests on large-scale climate is difficult to establish directly through observations. Careful examination of climatic data can sometimes reveal an ecological influence, such as the effect of leaf emergence on springtime evapotranspiration and air temperature. Eddy covariance flux towers and field experiments provide local-scale insight to forest-atmosphere interactions, and advances in remote sensing science can aid extrapolation of this knowledge to larger spatial scales. More often, however, our understanding of how forests affect climate comes from atmospheric models and their numerical parameterizations of Earth’s land surface (10). Paired climate simulations, one serving as a control to compare against another simulation with altered vegetation, demonstrate an ecological influence on climate.

Atmospheric models require fluxes of energy, moisture, and momentum at the land surface as boundary conditions to solve numerical equations of atmospheric physics and dynamics. The first generation of land surface parameterizations developed in the late 1960s and 1970s used bulk aerodynamic formulations of energy exchange without explicitly representing vegetation [supporting online material (SOM)]. Soil water availability regulates latent heat flux, and the hydrologic cycle, when included, was simplified to a “bucket" model of soil water. In this approach, precipitation fills the soil column up to a specified water-holding capacity, beyond which rainfall runs off.

By the mid-1980s, the second generation of land surface parameterizations, included the hydrologic cycle and the effects of vegetation on energy and water fluxes. These models explicitly represent plant canopies, including radiative transfer, turbulent processes above and within the canopy, and the physical and biological controls of evapotranspiration (Fig. 2A). Snow cover, the soil water profile, and vegetation influences on the hydrologic cycle are also included (Fig. 2B). In the mid-1990s, plant physiological theory further advanced the incorporation of biological control of evapotranspiration in the third generation of models. Models now routinely link the biochemistry of photosynthesis with the biophysics of stomatal conductance. Leaf photosynthesis and conductance are scaled to the plant canopy based on the optimal allocation of nitrogen and photosynthetic capacity in relation to light availability. Simulations with these models have routinely demonstrated biogeophysical regulation of climate by vegetation through albedo, turbulent fluxes, and the hydrologic cycle (10).

The current generation of models has capability beyond hydrometeorology and incorporates ecological advances in biogeochemical and biogeographical modeling (10). Many models simulate the carbon cycle (Fig. 2C) and vegetation dynamics (Fig. 2D). In these models, the biosphere and atmosphere form a coupled system whereby climate influences ecosystem functions and biogeography, which feed back to affect climate. Much of the natural vegetation of the world has been cleared for agriculture (Fig. 3D), and some models also include land-use change.

Tropical Forests

Climate model simulations show that tropical forests maintain high rates of evapotranspiration, decrease surface air temperature, and increase precipitation compared with pastureland (SOM). The most studied region is Amazonia, where large-scale conversion of forest to pasture creates a warmer, drier climate. Surface warming arising from the low albedo of forests is offset by strong evapo-
The net balance among these processes is likely a positive benefit that mitigates global warming through evaporative cooling and carbon sequestration (8). Yet a more complete analysis of forest-atmosphere interactions is required. The biogeochemistry of tropical forests and biomass burning affects atmospheric chemistry and aerosols, which can alter clouds and rainfall (16). Interannual climate variability modulates forest-atmosphere coupling. There is net release of carbon from the biosphere to the atmosphere during warm, dry El Niño years, seen in high atmospheric CO2 growth rates (3), especially in the tropics (17). Drought makes tropical forests more susceptible to burning during land clearing (18). However, tropical forest productivity may be more resilient to drought than expected (14).

The future of tropical forests is at risk in a warmer, more populous 21st-century world. Tropical forests are vulnerable to a warmer, drier climate (19), which may exacerbate global warming through a positive feedback that decreases evaporative cooling, releases CO2, and initiates forest dieback (20). Loss of natural forests worldwide in the tropics during the 1990s was as high as 152,000 km2 year−1 (1), and Amazonian forests were cleared at a rate of ~25,000 km2 year−1 (19). Such land-use pressures are expected to continue in the future and may shift the Amazonian region to a permanently drier climate once a critical threshold of clearing is reached.

**Boreal Forests**

Climate model simulations show that the low surface albedo during the snow season, evident in local flux measurements (21) and satellite-derived surface albedo (Fig. 1D), warms climate compared to when there is an absence of trees (SOM). Consequently, the boreal forest has the greatest biogeophysical effect of all biomes on annual mean global temperature (7). Loss of boreal forest provides a positive feedback for glaciation (22), whereas forest expansion during the mid-Holocene 6000 years ago amplified warming (23).

Boreal forests differ in their partitioning of net radiation into sensible and latent heat fluxes. Conifer forests have low summertime evaporative fraction (defined as the ratio of latent heat flux to available energy) compared with deciduous broadleaf forests, producing high rates of sensible heat exchange and deep atmospheric boundary layers (21). Flux tower measurements illustrate the potential for changes in species composition, arising from change in the fire regime, to affect climate (24). Along an 80-year fire chronosequence in Alaska, annual net radiation declined by 31% at a 3-year-old postburn

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**Fig. 1.** Biogeochemical (carbon) and biogeophysical (albedo and evapotranspiration) processes by which terrestrial ecosystems affect climate (SOM). (A and B) Geographic extent and total (plant and soil) carbon stock of nonforest (green) and forest (blue) biomes (2). Individual forest biomes are also shown and sum to the forest total. (C) Net ecosystem production (NEP) for tropical, temperate, and boreal forest (47). Individual symbols shown mean NEP for humid evergreen tropical forest, three types of temperate forest, and three types of boreal forest. Vertical bars show NEP averaged across forest types. (D) Satellite-derived direct-beam albedo for snow-covered and snow-free nonforest (green) and forest (blue) biomes (48). Also shown are individual forest biomes. (E) Evapotranspiration normalized by its equilibrium rate in relation to canopy resistance for wheat, corn, temperate deciduous forest, boreal jack pine conifer forest, and oak savanna (49, 50). Shown are individual data points and the mean for each vegetation type.
site dominated by grasses and a 15-year-old aspen (Populus tremuloides) forest compared with an 80-year-old black spruce (Picea mariana) forest, primarily in spring and summer. Annual sensible heat flux decreased by more than 50% compared with the 80-year site, mostly in spring and summer. During summer, the aspen forest had the highest latent heat flux, lowest sensible heat flux, and lowest midday Bowen ratio (defined as the ratio of sensible heat flux to latent heat flux).

Boreal ecosystems store a large amount of carbon in soil, permafrost, and wetland (2) and contribute to the Northern Hemisphere terrestrial carbon sink (3), although mature forests have low annual carbon gain (Fig. 1C). The climate forcing from increased albedo may offset the forcing from carbon emission so that boreal deforestation cools climate (8). Similar conclusions are drawn from comprehensive analysis of the climate forcing of boreal fires (25). The long-term forcing is a balance between postfire increase in surface albedo and the radiative forcing from greenhouse gases emitted during combustion. Averaged over an 80-year fire cycle, the negative forcing from surface albedo exceeds the smaller positive biogeochemical forcing. Yet in the first year after fire, positive annual biogeochemical forcing from greenhouse gas emission, ozone, black carbon deposited on snow and ice, and aerosols exceeds the negative albedo forcing.

Boreal forests are vulnerable to global warming (5). Trees may expand into tundra, but die back...
along southern prairie ecotones. In the main boreal forest, there may be loss of evergreen trees and a shift toward deciduous trees. Siberian forests may collapse in some areas and become more evergreen in the north. Increased disturbance from fire or insect outbreaks will shift the forest to a younger age class. Climate forcing arising from younger stand age may be comparable to that arising from biome shifts (24).

Temperate Forests
Much of the temperate forests of the eastern United States, Europe, and eastern China have been cleared for agriculture (Fig. 3D). Croplands have a higher albedo than forests (Fig. 1D), and many climate model simulations find that trees warm surface air temperature relative to crops (SOM). Misting of snow albedo by trees is important in cool temperate climates with snow. Studies of eastern United States forests find that trees also maintain a warmer summer climate compared with crops because of their lower albedo, augmented by evaporative cooling from crops and feedbacks with the atmosphere that affect clouds and precipitation (26). The influence of crops on evapotranspiration is seen in flux tower measurements. Growing season evaporative cooling is greater over watered crops compared with forests, and these plants exert less evaporative resistance (Fig. 1E).

Although global climate models find that temperate forests in the eastern United States warm summer temperature (26), mesoscale model simulations of the July climate of the United States find that trees increase evapotranspiration and decrease surface air temperature compared with crops (27, 28). Atmospheric feedbacks that alter cloudiness affect the magnitude of the temperature response in these simulations. Flux tower analyses show that conifer and deciduous broadleaf forests in North Carolina have lower surface radiative temperature than grass fields because of greater aerodynamic conductance and evaporative cooling of trees compared with grasses (29), but the same may not pertain to cropland (Fig. 1E).

Interannual climate variability affects biosphere-atmosphere coupling. In western Europe, forest and agricultural land have comparable surface radiative temperature when soil is moist but respond differently to drought (30). Forest maintains green vegetation, as indicated by the normalized difference vegetation index, although surface temperature and sensible heat flux increase with drought. Vegetation greenness in cropland declines by ~50%, the surface warms 13°C more than in forest, and the drought enhancement in sensible heat flux is greater than for forest. The different response to drought arises from the deep roots of trees and their access to deeper reservoirs of soil water.

Temperate forests hold ~20% of the world’s plant biomass and ~10% of terrestrial carbon (Fig. 1B). Carbon sequestration rates of mature forests are high (Fig. 1C), but temperate forests in the United States historically have been carbon sources because of deforestation (31). Socioeconomic trends in reforestation and fire suppression have shifted these forests to a carbon sink. Similar trends are seen in Europe (3).

The net climate forcing of temperate forests is highly uncertain. Competing biogeochemical forcings from low albedo during winter and evapotranspiration during summer influence annual mean temperature (7). Higher albedo with loss of forest cover could offset carbon emission so that the net climatic effect of temperate deforestation is negligible (8), or reduced evapotranspiration with loss of trees could amplify biogeochemical warming.

The future of temperate forests and their climate services is highly uncertain. The present carbon sink in eastern United States forests is likely to decline as recovering forests mature (31), and these forests face uncertain pressure from climate change, atmospheric CO₂ increase, and anthropogenic nitrogen deposition (5). Change in the balance between deciduous and evergreen trees is likely in the future. Temperate forests are particularly vulnerable to human land use. The trend over the past several decades has been toward farm abandonment, reforestation, and woody encroachment from fire suppression, but meeting the needs of a growing global population could place greater pressures on these forests.

Carbon Cycle Feedbacks
The carbon cycle has long been recognized as important for understanding climate change. Climate models that include the terrestrial and oceanic carbon cycle simulate a positive feedback between the carbon cycle and climate warming that increases the air–sea CO₂ exchange (32). Terrestrial carbon models find that a ~50% increase in atmospheric CO₂ concentration reduces evapotranspiration and reinforces warming (SOM). More extensive tree cover may enhance warming in boreal forests by decreasing surface albedo. Reduced evapotranspiration in a drier climate may initiate a positive climate feedback leading to loss of tropical forest (20).

Land-Use Forcing
Although carbon emission from forest clearing has long been studied, only recently has the biogeochemical forcing of climate from land use been recognized. Vast tracts of forestland have been converted to agriculture (Fig. 3D), and climate warming over the industrial era may be smaller than that expected from rising atmospheric CO₂ alone, primarily from increased spring albedo with loss of extratropical forests (36).

Carbon emission from land use dampens biogeochemical cooling. The dominant competing signals from historical deforestation are an increase in surface albedo counteracted by carbon emission to the atmosphere. Biogeochemical cooling may outweigh biogeochemical warming at the global scale (37) or may only partially offset warming (38). The net effect of these competing processes is small globally but is large in temperate and high northern latitudes where the cooling due to an increase in surface albedo outweighs the warming due to land-use CO₂ emission.

Climate trends over the 21st century, too, should be driven by interactions among CO₂ emission, land use, and forest-atmosphere feedbacks. The biogeochemical land-use forcing of climate may in some regions be of similar magnitude to greenhouse gas climate change. The Intergovernmental Panel on Climate Change (IPCC) Special Report on Emission Scenarios (SRES) A2 narrative storyline has high CO₂ emission (SOM), and climate model simulations of Feddema et al. (39) produce 2°C warming of planetary temperature over the 21st century in the absence of land cover change. The A2 storyline describes widespread agricultural expansion with most land suitable for agriculture used for farming by 2100 to support a large global population (Fig. S1). Forest loss leads to additional warming in Ama-
zonia, but cooling that mitigates warming in mid-latitudes (39). The B1 narrative storyline is a low greenhouse gas emission scenario. Farm abandonment and reforestation yield loss of farmland by 2100 because of assumed increases in agricultural efficiency and declining population (fig. S1). The model simulates 1°C warming in the absence of land cover change and weaker land-use forcing.

When the carbon cycle is included, the different SRES storylines of fossil fuel emission and land use may yield similar 21st-century climates despite vastly different socioeconomic trajectories (9). Widespread expansion of agriculture in A2 leads to biogeophysical cooling. Biogeophysical processes lead to warming in B1, primarily because of temperate forest regrowth. In the A2 and B1 storylines, net carbon loss from deforestation causes biogeochemical warming, greatest in A2 because of extensive deforestation and weaker in B1 because of temperate reforestation and less tropical deforestation. Biogeochemical warming offsets biogeophysical cooling in A2 to provide net global warming. The B1 net warming is similar to A2 because moderate biogeophysical warming from temperate reforestation augments weak biogeochemical warming from tropical deforestation.

**Research Needs**

Through albedo, evapotranspiration, the carbon cycle, and other processes, forests can amplify or dampen climate change arising from anthropogenic greenhouse gas emission. Negative climate forcing in tropical forests from high rates of carbon accumulation augments strong evaporative cooling (Fig. 3A). The combined carbon cycle and biogeophysical effect of tropical forests may cool global climate, but their resilience to drought, their status as carbon sinks, interactions of fires, aerosols, and reactive gases with climate, and the effects of small-scale deforestation on clouds and precipitation are key unknowns. The climate forcing of boreal forests is less certain (Fig. 3C). Low surface albedo may outweigh carbon sequestration so that boreal forests warm global climate, but the net forcing from fire must also be considered, as well as effects of dis-
turbance and stand age on surface fluxes. The climate benefit of temperate forests is most uncertain (Fig. 3B). Reforestation and afforestation may sequester carbon, but the albedo and evaporative forcings are moderate compared with other forests and the evaporative influence is unclear.

Much of our knowledge of forest influences on climate, and our ability to inform climate change mitigation policy, comes from models. Models of climate and the biosphere are abstractions of complex physical, chemical, and biological processes in the Earth system. Extrapolation of process-level understanding of ecosystem functioning gained from laboratory experiments or site-specific field studies to large-scale climate models remains a daunting challenge. Biosphere models must be better constrained with observational data across a range of scales from in situ experimentation, flux tower measurements of ecosystem functioning, ecological syntheses of long-term ecosystem research, satellite monitoring of vegetation, and atmospheric monitoring of CO₂. Synthesis of flux tower data from a variety of boreal, temperate, and tropical regions in various stages of ecosystem development is essential to understand the functioning of forests across wide gradients of climate, soils, disturbance history, and plant functional types (40). Large-scale monitoring of Northern Hemisphere "greening" (41) or the response of vegetation to drought (42) provide essential tests of model response to perturbations. Global atmospheric CO₂ analyses provide key constraints to biospheric functioning to augment process-level model validation at specific locales (15).

Global models of the biosphere-atmosphere system are still in their infancy, and processes not yet included in the models may initiate unforeseen feedbacks. The effect of nitrogen on carbon uptake (43), physiological effects of high ozone concentration (44), photosynthetic enhancement by diffuse radiation (45), and disturbance (46) are poorly represented, if at all. Realistic depictions of vegetation dynamics, especially the time scales of vegetation response to disturbance, long a mainstay of forest ecosystem modeling, are barely considered in the current generation of models. Nor are fires, aerosols, and reactive chemistry well represented in the models.

The carbon cycle and its response to multiple interacting drivers of global change is a key aspect of the biospheric forcing of climate. So, too, are human uses of land and the socioeconomic trends and societal responses to a changing climate that drive land use. What are the greatest uncertainties in simulating the carbon cycle of the 21st century? The prevailing paradigm of current models is that CO₂ fertilization drives terrestrial carbon sinks, weakened by global warming (3, 32). This carbon cycle-climate feedback will almost certainly be refined with further studies that incorporate the nitrogen cycle. Accounting for disturbance from wildfires and insect outbreaks further weakens terrestrial carbon sequestration in Canadian forests (46). Trajectories of land use driven by socioeconomic needs and policy implementation will also come into play and have competing biogeochemical and biogeophysical impacts on climate (9).

As the climate benefits of forests become better understood, land-use policies can be crafted to mitigate climate change (6). It has been inferred, for example, that tropical afforestation is likely to "slow down" global warming, whereas temperate afforestation has "little to no" climate benefit and boreal afforestation is "counterproductive" (8). These policies must recognize the multitudes of forest influences, their competing effects on climate, their different spatial and temporal scales, and their long-term effectiveness and sustainability in a changing climate.

An integrated assessment of forest influences entails an evaluation beyond albedo, evapotranspiration, and carbon to include other greenhouse gases, biogenic aerosols, and reactive gases. The geographic impact of these processes varies, as do their time scale of climate forcing. Greenhouse gases are well mixed in the atmosphere and influence global climate; biogeochemical feedbacks have a regional impact. Biogeochemical processes influence climate more immediately than does the carbon cycle. Slow rates of carbon accumulation in boreal forest may in the short-term be offset by more rapid albedo effects. How forests attenuate or amplify climate change will vary with global warming. Vegetation masking of snow albedo becomes less important in a warmer world with less extensive snow cover. The evaporative cooling of forests decreases in a warmer world with less extensive snow cover. The evaporative influence is unclear.

Fig. 3B. Reforestation and afforestation may sequester carbon, but the albedo and evaporative forcings are moderate compared with other forests and the evaporative influence is unclear.

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