EFFECTS OF GLOBAL WARMING ON FORESTS

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1. Introduction

Forests cover about 3454 million ha of the earth's surface, nearly 27% of the land area (excluding Greenland and Antarctica). Together with marine phytoplankton, they form the primary photosynthetic organ of the planet, and as such are responsible for the bulk of the free oxygen in the atmosphere, and for most of the fixing of carbon dioxide (CO_2)

and solar energy. As sedentary organisms with long life spans, individual trees are highly susceptible to climate change. Climate change is therefore expected to cause significant changes in forest distributions, and in the internal character of forests. This will in turn mean significant changes in the ecosystem and life support services provided by forests.

Forest margins are most often determined by a suite of environmental conditions, foremost among which is climate. At high latitudes, the tree line separating forest from tundra is a function of summer temperature, length of frost-free season, and winter snow depth. At more temperate latitudes, ecotones between forest and grassland or savanna regions are often determined by a combination of drought and frequent fires—themselves a function of climate, although human activity also plays a role. In mountain regions **(see also *Effects of Global Warming on Mountains*)**, upper tree lines are determined by much the same conditions that determine high latitude tree lines, while low elevation tree lines are similar to forest/grassland ecotones, determined largely by moisture conditions.

Climate change is expected to be more pronounced at higher latitudes, and it is therefore the boreal forest that is expected to be most affected. Boreal forests have experienced large climate swings in the past; the geologically recent ice ages covered almost the entire present range of the North American boreal forest, so that this forest has occupied its present range for only a few thousand years—in most of the glaciated areas, this may be only a few hundred generations of trees. Because of these large climate variations in the past, the boreal forest may be better able to adapt to a moderate range of climate changes than can the tropical forests, which experienced only minor climate fluctuations over the last several million years, and therefore may be less resilient to change. The future climate change, however, is expected to be stronger in high latitude regions.

Both simple and more complex models agree that the ranges of major forest types around the world are likely to shift dramatically with future global warming. The eventual stable ranges that might be achieved several hundred or thousand years from now have been projected by models using modern climate/range correlations; in many regions, the change is not simply from one forest type to another, but rather from forest to grassland or even desert, while other regions may shift from tundra to forest. The eventual stable ranges are, however, in many ways less of a concern than are the transitional responses. The projected climate change is more rapid than any that has occurred since the end of the last glaciation, and possibly more rapid than even that climatic event. The transitional state of the forest is therefore of grave concern: harder to predict than eventual stable ranges, the transitional state may include significant areas of essentially dead forest where the existing vegetation is not able to cope with changed climatic conditions, while the forest type that would be stable has not yet had time to migrate and establish itself in that area.

Any change in the forest implies a change in the ecosystem and life-support services provided by the forest. As a major carbon store and evapotranspirative organ, the forest plays a key role in the global climate. A significant loss of forest cover due to an excessively rapid climate change, even if temporary, could accelerate the climate change by reducing forest carbon reserves and hampering water cycle services **(see**

***Effects of Global Warming on Water Resources and Supplies*)**. At the same time, human activities will increasingly influence the state of the forest, and the forests' response to global warming.

Signs of climate change impact on the forest may already be discernible in some regions. Increases in forest fire activity in boreal North America and increasing growth at tree line in Scandinavia are both clear early warning signs. In other, more heavily populated regions, increased losses due to insects and disease and loss of forest at the grassland margin are more ambiguous, as human activity may be equally responsible for the change.

To prepare for these coming changes in the world's forests, we can implement a variety of policies. These may include intensive forest management in the form of short-rotation plantations, preemptive planting of trees outside their current range but within their projected future ranges, and preparation for increased disturbances such as fire and insect infestations.

2. Controls on Forest Distribution

Forest distribution is controlled largely by climate, either directly or indirectly. Direct climate controls include changes in the length of the growing season, winter temperature minima, or precipitation. Indirect climate control of vegetation is achieved through the effect of climate on fire and other natural disturbances, or on human activities. Many correlations between various aspects of climate and vegetation have been noted for individual species, communities, ecoregions, and plant functional types. In projecting the impact of future climate change on vegetation communities, these classifications can suggest likely future stable ecotype ranges; they cannot, however, address the important issue of transitional states between now and a possible future stable condition.

2.1. Major Direct Climatic Controls

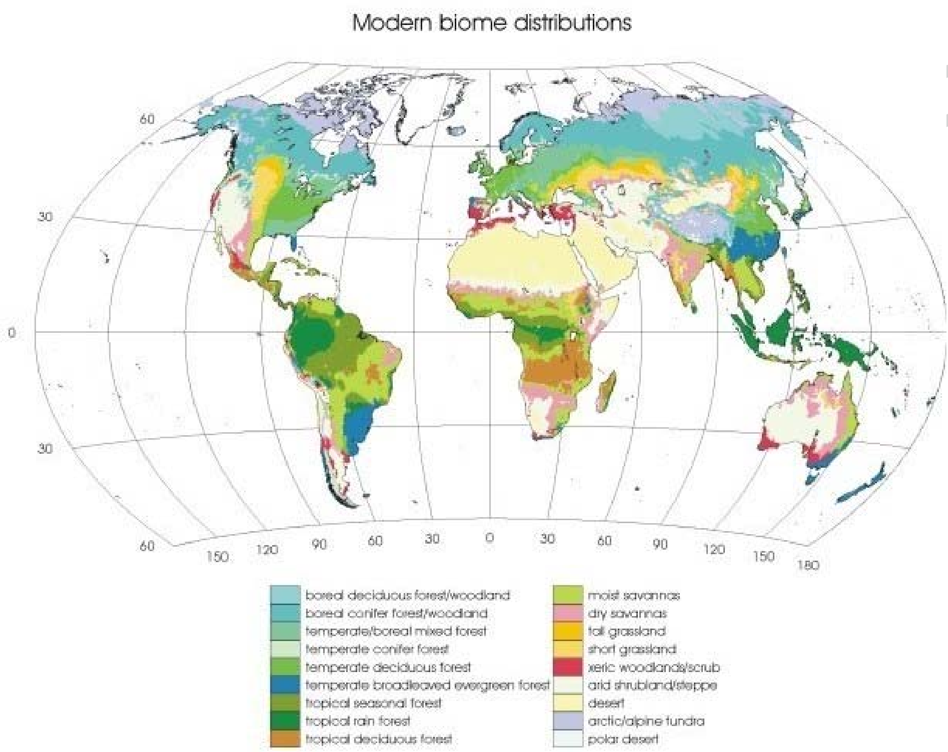
A number of direct climatic controls over vegetation distribution are well recognized. These include growing degree-days (the sum of degree-days above 5°C), the occurrence and timing of killing frosts, and mean annual precipitation. Models based on such coarse climatic parameters are reasonably successful at describing the present global vegetation distribution (Figure 1a). They have been used to project possible future vegetation distributions under various global warming scenarios.

Such models, however, cannot accurately predict the transient responses of vegetation to climate change; that would require more detailed process-based models that are currently only in early stages of development. They can, however, suggest regions that may be particularly vulnerable to climate change, and the direction in which the vegetation might develop. Such regions show as areas in which the projected future vegetation is markedly different from the present vegetation.

One such model, BIOME3, has been used extensively to investigate vegetation sensitivity at a global scale. A comparison of the results of a simulation using a 2xCO_2

climate (Figure 1b) with the present vegetation distribution (Figure 1a) shows the greatest vulnerability lies at high latitudes, as in Canada and northern Eurasia, and at high altitudes, as in the Himalayas. Tropical regions show relatively slight changes.

These model results must be taken in their proper context: they do not include a host of factors, such as extreme weather events and the effect of changing snow depth on soil temperatures. They also do not include a variety of potential competitive interactions that may occur, or the possible impacts of migrating species encountering new pests and diseases, or being limited by soils.



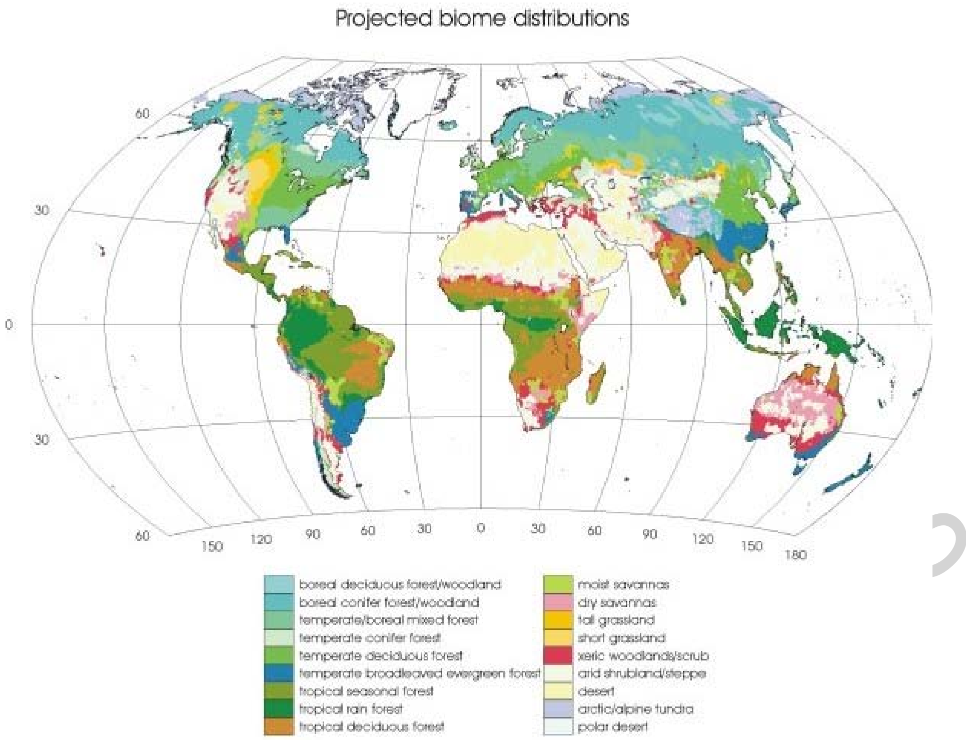


Figure 1. (a) Modern biome distributions; (b) Projected biome distributions (from A. Haxeltine and I.C. Prentice I.C., BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types, *Global Biogeochemical Cycles* **10** (1996), by permission of Prentice)

Perhaps their greatest limitation, however, is that they do not yet incorporate and predict the disruptions and disturbances that occur within an area whose gross forest type does not change. It may well be that trees growing on dry sites will be able to survive in the same area, but only on what are now wet sites. This could lead to widespread mortality or regeneration failure in areas climatically suited to the species currently found there, and early successional species could benefit from canopy openings during the transition period. This could result in a pulse of CO_2 release from forests in a state of transition, which would in turn exacerbate the warming trend.

2.2. Air Masses and Tree Lines

More detailed work has been done on relating air masses and mean front positions to major vegetation boundaries. This has been a particularly productive approach in North America, where the vegetation is broadly zonal. The position of the northern tree line in Canada, for instance, has been shown to be related to the mean summer position of the arctic front; the southern limit has been related to the mean winter position of the same front. The precise mechanisms for this observed correlation are still under debate with some arguing that the climate controls the tree line position and others arguing the tree line determines the frontal position. It is probable that the two phenomena are mutually reinforcing and resonant with polar circulation patterns of air masses.

While this approach is useful for some regions, it is more complicated in areas of mountainous terrain. It is also in a sense one step removed from climate: it is not the fact of the arctic air mass that affects vegetation, but rather the climatic conditions associated with that frontal air mass. Thus knowing that the position of the arctic front today correlates well with vegetation is interesting, but not very useful for projective purposes: while we can project the future position of the front, the properties of the air mass itself are likely to change, and thus the correlation observed today between the position of the front and the vegetation is likely to change as well.

2.3. Other Direct Climatic Controls

Other aspects of climate also directly affect vegetation distribution. For example, snow depth may be a determining factor in the distinction between forest and forest tundra. Winter temperature minima may partly explain the distribution of American beech, as that tree cannot survive temperatures below –40°C. In contrast, the tolerance of Siberian larch to very low temperatures is likely a major factor contributing to its widespread distribution in interior Siberia. The annual distribution of heat may also be important: some continental regions accumulate significant heat sums during a very short growing season, while more maritime regions may have a longer growing season but a lower temperature sum.

The annual distribution of precipitation is also critical in many regions. Large areas of savanna occur where there is sufficient annual precipitation to support closed-canopy forest, but where the precipitation is concentrated in only a few months of the year. In some regions, the annual precipitation is primarily in the form of snow during the winter and the accumulated snow pack acts as an important reservoir to provide spring moisture.

Extreme weather events also affect vegetation, although their effect on the distribution of forest types may be more subtle. Hurricanes are certainly a major factor in the growth and development of the vegetation along the east coast of the United States, but it is unclear whether or how the forest would be significantly different in the absence of hurricanes. Floods are important in riparian zones, and such rare extreme events as the eastern Canadian ice storm of 1998 or the western European windstorms of 1990 certainly affect the composition of the forest for some time after the event. Should such extreme events become frequent enough, it is conceivable that they will become significant factors in the forest composition. In some regions, such as Siberia, windstorms are so frequent a disturbance that they are considered to be partly responsible for the character of large parts of the boreal forest. Various other extreme weather phenomena, including spring droughts, winter thaws, and summer frosts may also affect vegetation distribution.

2.4. Climate Feedbacks

There are also feedbacks between the vegetation and global climate. Forests store carbon that would otherwise mostly be in the atmosphere; thus forests in effect cool the planet through carbon storage. Forests also have a significant effect on regional climate through their albedo (reflectivity): forests are much darker than grasslands or barren landscapes, and thus retain considerable heat that would otherwise be reflected or re-emitted back into space. Furthermore, forests are a major component of the global water cycle with evapotranspiration being responsible for much of the atmospheric humidity over large regions.

Climate feedbacks operate at all scales, from the microsite to the biome level. Mature trees provide a microclimate that may or may not be suitable for their own seedlings. Openings in the forest having different albedo and evapotranspirative properties than their surroundings can provide convection sources, thereby influencing local weather conditions. Changing patterns in the forest caused by indirect or direct climatic impacts can thus feed back to regional climatic conditions. Small-scale climatic effects such as these cannot be overlooked and are often studied, but their effects at broader scales has only recently begun with the fusion of complex models and large data sets made possible with recent advances in computing systems. This up-scaling problem remains one of the major challenges in climate change research.

2.5. Indirect Climate Controls

Climate also controls forest distribution indirectly, through its influence on major disturbances such as fire and insects, and through its effects on human activity, which may in turn affect forests. These indirect links between forests and climate frequently operate through complicated networks of feedback loops, and often the final result of a perturbation to one part of the system involves many complex interactions with other parts of the system—interactions that often have built-in time delays and phase shifts.
In many forests, the interactions between human activity and climate are likely to be the major indirect effects. Forest clearance for agriculture will occur independently of climate change. In a changing climate, however, there will likely be additional pressure for new land for agriculture, as currently productive agricultural regions become less suitable (e.g. too dry), and as regions that are presently too cold to support profitable agriculture become warm enough for crops. A further factor working in this direction is likely to be the development of hybrid and possibly genetically engineered crops capable of producing economically viable crops in colder regions. These indirect effects of climate change will not be easily distinguished from other pressures, including population growth and urbanization of prime agricultural land.

In natural responses to global warming, the greatest indirect effects on forest will probably be from changes in disturbance regimes. Fire and insect infestations are both known to be highly correlated with weather, and there is every reason to believe that global warming will cause significant shifts in natural disturbance patterns in all forests around the world. Exactly what these indirect effects will be—where and when the disturbances will occur—is difficult, if not impossible, to predict with current data and understanding, as well as requiring assumptions about the levels of future human interventions. The relationships between forest fire, climate, and vegetation in the North American boreal forest have been particularly well studied. The complex feedbacks by which vegetation influences fire and fire influences vegetation—and climate affects both—are expected to result in a net increase in early successional hardwoods. Where droughty conditions interfere with regeneration of trees, some localized reversion to savanna-like conditions may occur, a situation that is expected in parts of northwestern North America.

3. Impacts of Past Climate Changes

The complexities of forest ecology are such that past episodes of climate change have often been used as a guide to possible future forest responses. This approach has many weaknesses: the lack of past climate change episodes that are strictly analogous to the present and future warming, the increasing human effect on forest ecology, and the often imprecise nature of the data available on past forest responses to climate change are the chief shortfalls. Nevertheless, studies of past forest responses to climate provide empirical data on the limits of potential forest responses to changes in the global climate.

The Hypsithermal interval, which occurred some 6000–8000 years ago in most of the Northern Hemisphere, is often used as an analogue for a possible future forest in equilibrium with a warmer global climate. Potential migration rates are suggested by the observed spread northwards following deglaciation between 15 000 and 8000 years ago, and intervals of rapid climate change provide insights and data on forest stability and transient effects.

3.1. Postglacial Migration

During the last glacial period, much of North America and Europe were covered in ice, and global climate patterns were markedly different from today's. Species in the North American boreal forest migrated to their present ranges from full-glacial refugia that, in many cases, are no longer even in the present range of the species. Some of these migrations have involved distances of several thousand kilometers, and some, such as the range expansion of lodgepole pine in northwestern North America, may still be continuing today.

Migration of forest-dependent species such as birds and mammals is obviously limited by the migration rate of the trees upon which they depend. At the same time, many tree species have seeds dispersed by animals and birds. The boreal forest is unusual in this respect: most tree species in the boreal are not dependent on animals or birds for seed dispersal, and most are not even dependent on insects for pollen dispersal. Thus the boreal forest is composed mainly of tree species that are adapted to rapid migration across the landscape, and many are adapted to rapid colonization of the large clearings formed by large forest fires.

Despite this, even boreal forest tree species have limited migration rates. Table 1 shows selected postglacial migration rates estimated from paleoecological data, and selected potential migration rates estimated from seed dispersal studies. Clearly, the postglacial migration rates are in many cases more rapid than those estimated from seed dispersal studies, suggesting that rare dispersal events may be key in rapid migrations. At the same time, the future required migration rates may be as high as 20–50 km per generation, clearly exceeding the maximum rates estimated from either seed dispersal studies or from paleoecological data. In this context, it is worth noting that many studies suggest that forests in glaciated areas may have been in climatic disequilibrium for as much as several thousand years following deglaciation, due in large part to slow species migration.

Species	Postglacial estimate	Theoretical from seed dispersal studies
Pine	8	0.5
Beech	7	4.0
Hemlock	5	1.6
Maple	4	0.5

Table 1. Estimated migration rates of selected species (km/generation)

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Biographical Sketches

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