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Climate Change Impacts on Forests

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EXECUTIVE SUMMARY

Forests are highly sensitive to climate change. This has been shown by observations from the past, experimental studies, and simulation models based on current ecophysiological and ecological understanding. In particular, the following was concluded:

- Sustained increases of as little as 1°C in mean annual air temperature can be sufficient to cause changes in the growth and regeneration capacity of many tree species. In several regions, this can significantly alter the function and composition of forests; in others, it can cause forest cover to disappear completely (Medium Confidence).
- Suitable habitats for many species or forest types are likely to shift faster with climate change than the maximum natural rate at which many species can migrate and establish. Consequently, slow-growing species, such as late successional species, or those with restricted seed dispersal will be replaced by faster-growing, highly adaptable or more mobile species (High Confidence).
- Forests are particularly vulnerable to extremes of water availability (either drought or waterlogging) and will decline rapidly if conditions move toward one of the extremes (High Confidence).
- Forced by a doubled carbon dioxide (2 x CO_2) climate, global models project that a substantial fraction of the existing forests will experience climatic conditions under which they do not currently exist; eventually, large forested areas will have to change from the current to new major vegetation types (High Confidence). Averaged over all zones, the models predict that 33% of the currently forested area could be affected by such changes; in the boreal zone, one model projects it to be as high as 65% (Medium Confidence). Yet it is currently not possible to predict transient forest responses at a regional to global scale.
- Although net primary productivity may increase, the standing biomass of forests may not increase because of more frequent outbreaks and extended ranges of pests and pathogens and increasing frequency and intensity of fires (Medium Confidence).
- Mature forests are a large store of terrestrial carbon. Because the maximum rate at which carbon can be lost is greater than the rate at which it can be gained, large amounts of carbon may be released transiently into the atmosphere as forests change in response to a changing climate and before new forests replace the former vegetation. The loss of aboveground carbon alone has been estimated to be 0.1–3.4 Gt yr^{-1} or a total of 10–240 Gt (Medium Confidence).

The following regional assessments were primarily based on transient climate-change scenarios for 2050 (Greco *et al.*, 1994).

Tropical Forests

- Tropical forests are likely to be more affected by changes in land use than by climate change as long as deforestation continues at its current high rate (High Confidence).
- Any degradation of tropical forests, whether it is caused by climate or land-use changes, will lead to an irreversible loss in biodiversity (High Confidence).
- CO_2 fertilization may have its greatest effect in the tropics and may lead to a gain in net carbon storage in undisturbed forests, especially in the absence of nutrient limitations (Medium Confidence).
- Tropical forests are likely to be more affected by changes in soil water availability (caused by the combined effects of changes in temperature and rainfall) than by changes in temperature *per se*. Decreases in soil moisture may accelerate forest loss in many areas where water availability is already marginal. In other areas, increasing precipitation may be more than adequate to meet increased evaporative demand and may even lead to erosion (Medium Confidence).

Temperate Forests

- Compared with other latitudinal zones, the potential area for temperate forests is projected to change the least; however, many existing forests will still undergo significant changes in their species composition (High Confidence).
- Water availability will change in many regions, and in some regions where water supply is already marginal, forests may be lost in response to increased summer droughts (Medium Confidence).
- While warming and elevated CO_2 are likely to increase net primary productivity of many forests, net carbon storage may not increase because of the associated stimulation of soil organic matter decomposition by soil warming (Medium Confidence).
- Temperate forests are currently a carbon sink, mainly because of regrowth that started in many regions in the 19th century. However, these forests could become a source if they degrade due to climate change or other causes such as air pollution (Medium Confidence).

- Most temperate forests are located in developed countries with resources to reduce the impacts of climate change on their forests through integrated fire, pest and disease management, and/or encouraging reforestation (Medium Confidence).

Boreal Forests

- Because warming is expected to be particularly large at high latitudes, and boreal forests are more strongly affected by temperature than forests in other latitudinal zones, climate change is likely to have its greatest impact on boreal forests (High Confidence).
- Northern treelines are likely to advance slowly into regions currently occupied by tundra. (High Confidence).
- Increased fire frequency and pest outbreaks are likely to decrease the average age, biomass, and carbon store, with greatest impact at the southern boundary where the boreal coniferous forest is likely to give way to temperate-zone pioneer species or grasslands (Medium Confidence).
- The net primary productivity of forests not limited by water availability is likely to increase in response to warming, partly mediated by increased nitrogen mineralization. However, there may be a net loss of carbon from the ecosystem because of associated increases in soil organic matter decomposition (Medium Confidence).

1.1. Introduction

Forests are among those ecosystems on Earth that remain the least disturbed by human influences. They are of great socioeconomic importance as a source of timber, pulpwood for paper making, fuel, and many non-wood products (see Chapter 15). Furthermore, forests provide the basis for a broad range of other economic and non-economic values, such as resources for tourism, habitat for wildlife, or the protection of water resources. Forests harbor the majority of the world's biodiversity (mainly in the tropics) and, as such, they represent indispensable, self-maintaining repositories of genetic resources. These are essential for improvements in crop and timber selection and in medicine. Finally, aside from special economic interests, forests are also of spiritual importance to many indigenous people.

Globally, forests in 1990 covered about one-fourth of the Earth's land surface (3.4 Gha: FAO, 1993b), although estimates differ due to the exact definition of forests (e.g., 4.1 Gha: Dixon *et al.*, 1994; or, in a very wide definition, 5.3 Gha: Sharma *et al.*, 1992). About 17% of high-latitude, 20% of mid-latitude, and 4% of low-latitude forests can be considered actively managed (see Chapter 24), but only about 100 Mha (~2%) consist of intensively managed plantations (Dixon *et al.*, 1994). The forest regions have been broadly subdivided into latitudinal zones (i.e., the tropical, temperate, and boreal zones).

Forests are ecosystems in which trees interact with each other, with other plants like shrubs and grasses, and with animals or other heterotrophic organisms such as insects or fungi. At a broad scale, forest structure is modified by processes ranging from almost continuous change due to the death of individual trees and the subsequent recruitment of seedlings, to catastrophic events such as fire, insects, wind-fall or logging that kill whole stands of trees simultaneously. At any given moment, a forest represents the outcome of long-lasting past processes, often covering many centuries.

As components of the global climatic system, forests play a major role in the present and projected future carbon budget, since they store about 80% of all aboveground and 40% of all belowground terrestrial organic carbon (e.g., Melillo *et al.*, 1990; Dixon *et al.*, 1994) and can act as sources through deforestation and degradation, as well as sinks through forestation and possibly enhanced growth (see Chapter 23 on the role of forests for mitigation of greenhouse gas emissions). Moreover, forests can directly affect the climate system from local up to continental scales: They influence ground temperatures, evapotranspiration, surface roughness, albedo, cloud formation, and precipitation (e.g., Henderson-Sellers *et al.*, 1988; Gash and Shuttleworth, 1991).

Forest ecosystems respond to environmental changes with time constants ranging from hours to decades and up to millennia (see Box 1-1); they are among the components of the biosphere that respond most slowly to climatic change. The role of forest dynamics in the global climatic system is likely to be long lasting, complex, and difficult to predict. Because of their longevity and because adaptive measures, such as replacement of species, are harder to implement than in agricultural systems, forests may be particularly vulnerable to climatic change.

Sections 1.2.1 and 1.2.2 present assessments of direct forest responses to climatic change, including possible secondary effects on forest pests, fire, and other issues, which may cause forests

Box 1-1. Scales and Equilibrium Assumptions

Climatic changes affect forests on spatial scales ranging from leaves to the canopy and on temporal scales from minutes to centuries; relevant climatic changes occur at all levels, from short-term weather fluctuations creating disturbances (such as frosts) to longer-term changes in average climatic conditions (such as moisture availability or the length of the growing season) or the frequency of extreme events (such as droughts, fires, or intense storms). Current climate models (GCMs) do not fully match these levels, since they are best at simulating average conditions at a relatively coarse spatial resolution and are usually not yet run for longer than a century. Changes in frequencies of extreme events are highly uncertain, as are local-scale climate changes, although both are of high relevance to forests.

Some of the limitations caused by this problem can be overcome in local analyses using downscaling techniques (e.g., Gyalistras *et al.*, 1994), but for global applications the implicit assumption must be made that the probability of extreme events will remain unchanged. Most transient changes in the structure of forests, such as the decline of certain tree species, are driven by a combination of climatic changes and are modified by local, biological interactions acting on temporal scales ranging from months to centuries. It is currently very difficult, therefore, to assess the likely rates of climate-driven, transient change in forests. However, possible future equilibrium conditions can be more adequately predicted.

Equilibrium projections of forest responses implicitly assume the climate to have stabilized at a new steady state, which is not likely to occur soon in reality. However, GCM-derived climate scenarios arbitrarily held constant (e.g., for 2050) allow an assessment of the direction and magnitude of the expected change. Equilibrium projections for future forests, therefore, represent conservative interpretations of minimal changes likely to occur sooner or later and hence include the potential of even greater biospheric changes than the ones currently simulated by the forest models.

Box 1-2. Temperature Thresholds

Trees have widely differing responses to temperature. Some tropical tree species suffer chilling injury at temperatures below +12°C (Lyons, 1973; Lyons *et al.*, 1979), whereas species of colder regions can survive -5°C without ice formation but are sterile at lower temperatures. Classic examples for this phenomenon are *Ilex* and *Hedera* (Iversen, 1944). Broad-leaved evergreen perennials can survive to a limit of about -15°C by supercooling, whereas broad-leaved deciduous trees can supercool to about -40°C (Arris and Eagleson, 1989). Evergreen needle-leaved trees can survive to about -60°C, below which only deciduous species survive. Apart from these killing temperatures, many species require certain minimum numbers of degree days to complete essential life-cycle processes such as bud initiation, pollen formation, flowering, or others (Stern and Roche, 1974). Others require particular sequences of cool temperatures to become frost-hardy at the optimum time and a minimum duration of chilling temperatures to break winter dormancy (Cannell, 1990). Insect pests and other biotic agents that affect forest health may have critical threshold subzero temperatures for winter survival and thermal times to complete a generation. Warming may have positive effects on the growth of many trees and their survival, but by being beneficial to insect pests it also may reduce tree survival or put cold-adapted species at a competitive disadvantage.

either to grow more vigorously or to decline[1] in a changing climate. These assessments are based on the current general understanding of the basic ecophysiological and ecological responses; the latter will be addressed on levels ranging from the stand to the globe. In the three remaining sections, we summarize more specific effects in the tropical, temperate and boreal forest zones.

1.2. Climate and Forests

1.2.1. Sensitivities to Expected Climate Change

Forests are highly dependent on climate in their function (e.g., growth) and structure (e.g., species composition). Forest distribution is generally limited by either water availability or temperature. The ratio of actual evapotranspiration (the amount allowed by available precipitation) to potential evapotranspiration (the amount the atmosphere would take up if soil moisture were not limiting) determines the maximum leaf area index that can be supported (Woodward, 1987). Forests are also usually absent where the mean temperature of the warmest month falls below 10°C (Köppen, 1936) or where the temperature sum above a 5°C threshold is less than 350 degree-days (Prentice *et al.*, 1992).

The survival of many species depends critically on temperature thresholds ranging from +12° to -60°C (e.g., Woodward, 1987; Prentice *et al.*, 1992; Box 1-2). Many species have narrow temperature niches for growth and reproduction. A sustained increase in mean annual temperature of 1°C may cause significant changes in the species composition of stands and hence the distribution of many tree species (Davis and Botkin, 1985; see also Section 1.3). Trees are also sensitive to changes in water availability during the growing season, and leaf area indices, volume growth, and the range boundaries of most tree species are strongly related to water availability (Holdridge, 1967; Hinckley *et al.*, 1981; Gholz, 1982; Austin *et al.*, 1990; Stephenson, 1990).

In addition to thresholds for growth, reproduction, and survival at a given site, there are limitations to the rate at which species can migrate unassisted. Current projected rates of climatic change may exceed these thresholds, as discussed in Section 1.3.5. Climatic warming and associated lower humidities and increase in the frequency and severity of droughts would increase the incidence and severity of wildfires, especially in the boreal region. Changes in fire or storm frequencies are likely to have major impacts on the composition, age-distribution, and biomass of forests (see Sections 1.5.4.5 and 1.6.4.4).

1.2.2. Expected Climatic Changes in Forested Areas

Future forest characteristics are likely to depend on a few specific aspects of the range of climatic changes that could occur. The most relevant are the following:

- Changes in the regional or seasonal pattern of climate, such as the temperature increases that are expected to be greatest at high latitudes, and there, greatest in winter (Greco *et al.*, 1994). Due to this, impacts on forests at high latitudes may be greater than elsewhere.
- Water shortages during the growing season. Decreasing summer precipitation together with increased evaporative demand would lead to decreases in soil water, especially in many mid-latitude regions where water is most critical for growth. It is important to note that water shortages can develop even with unchanged rainfall amounts, due to increasing temperatures causing increased evaporative demand. We expect significant regional variation, with water availability changing only marginally in some regions and improving in others, whereas in many other regions water availability may decrease drastically.

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[1] Decline is defined here as "an episodic event characterized by premature, progressive loss of tree and stand vigor and health over a given period without obvious evidence of a single clearly identifiable causal factor such as physical disturbance or attack by an aggressive disease or insect" (Ciesla and Donaubauer, 1994).

- Changes in climate forcing are expected to be one or two orders of magnitude faster than rates of climatic change experienced by forests during most of the past 100,000 to 200,000 years, except, perhaps, during the Younger Dryas Event 10,000 years ago (Dansgaard *et al*., 1989; Webb III and Bartlein, 1992; Gates, 1993). Such rapid climatic change would have particular impacts on forests. For example, there may be forest decline, interruption of tree life cycles, loss of slowly migrating species, and increasing abundance of more aggressive, early successional species.

1.3. Forests in a Changing Climate

For a detailed assessment of the effects of a changing climate on forest ecosystems, it is necessary to investigate this response to the simultaneous changes in several climatic variables (e.g., temperature, moisture availability, and ambient CO_2 concentrations). Current understanding of ecological relationships and ecophysiological mechanisms allows a comprehensive study of forests at three hierarchical levels of scale, connecting temporal and spatial resolution to the nature of the processes that are being considered (Table 1-1).

At the ecophysiological level, plant organs like stomata and leaves respond almost instantaneously to their environment. This mainly affects forest functions, such as net primary productivity. Some structural aspects, such as leaf area, may respond over a number of years, whereas others, such as species composition, may take centuries to respond to altered conditions. Typically, each species or plant functional type (PFT) is affected differently by climatic change: Some species or PFTs will remain unaffected, some will become more and others less competitive (Smith *et al*., 1993). Dynamic forest models can be used to simulate this transient behavior of forests (e.g., Shugart, 1984; Prentice *et al*., 1993). Landscape-scale processes such as the lateral interactions between neighboring patches (e.g., migration or fire) play an important role for possible changes in the local to regional pattern of many forest ecosystems. However, they become less relevant when aggregated to national or continental assessments. At the global level, it is currently possible to investigate only how climatic change might affect the potential geographic equilibrium distribution of biomes—i.e., biogeographic regions (e.g., Emanuel *et al*., 1985; Prentice *et al*., 1992)—or to study the major fluxes of trace gases into and out of these biomes (Melillo *et al*., 1993; Plöchl and Cramer, 1995), with research underway on dynamic modelling (see also Chapter 9, *Terrestrial Biotic Responses to Environmental Change and Feedbacks to Climate*, in the Working Group I volume).

The current models can be used with climatic inputs generated by general circulation models (GCMs) for future climate scenarios, including regionally differentiated, high-resolution scenarios (e.g., Gyalistras *et al*., 1994). However, current understanding of the physical and biological interactions between environment and organisms is still rather limited, so these techniques enable us only to project future responses as consequences of given assumptions and scenarios and not to make precise forecasts.

1.3.1. Ecophysiological Responses

1.3.1.1. Tree Responses to Temperature and Water Availability

When they are well supplied with water, trees of most temperate and boreal species respond to increased temperature (e.g., from year to year, or when planted at a slightly warmer location) by growing faster (e.g., Cannell *et al*., 1989; Beuker, 1994), and they reach their largest mass near the warmest boundaries of their geographic ranges (Korzukhin *et al*., 1989). Generally, there is a positive correlation between net primary productivity and temperature (Box, 1978; Kauppi and Posch, 1985; Kokorin *et al*., 1993; Morikawa, 1993) or between net primary productivity and actual evapotranspiration (Rosenzweig, 1968; Raich *et al*., 1991).

However, these potential growth responses to warming may be constrained by other factors. Increasing temperature increases evaporative demand; if rainfall does not increase, more severe water stress will result, which will adversely affect growth and may increase the risk of drought and fire. To what extent this can be compensated by increased water-use efficiency due to increasing CO_2 concentration is not yet known (see Section 1.3.1.2 and Chapter A). Photoperiodic limitations might also

Table 1-1: *Hierarchical levels at which it is currently possible to study and model the impact of climatic change on forest ecosystems. Note that transient responses of trees and forests can currently only be studied at the first two levels.*

		Time		Space	
Level	**Focus**	Resolution	Scope	Resolution	Scope
Ecophysiological Processes	Plant Metabolism	min..h	1..10 yr	0..100 m	locations
Individuals, Populations, Forest Stands	Ecosystem Dynamics	d..yr	1..10^3 yr	~100 m	regions to continents
Plant Functional Types, Vegetation, Vegetation Complexes, Biomes	Biospheric Equilibrium	–	≥10^3 yr	~10..10^3 km	globe

apply in areas where temperature becomes warm enough for tree growth (e.g., Heide, 1974, 1993), and increasing temperature might increase the range of insect pests, which could cause considerable damage.

GCMs suggest a globally averaged increase in precipitation of about 2.5% per degree warming (Mitchell *et al.*, 1990; Greco *et al.*, 1994), which may not be sufficient to meet the increased water requirements of forests. Most GCMs indicate significant declines in net soil moisture over continental areas during the growing season (e.g., Manabe and Weatherald, 1987; Greco *et al.*, 1994). There are likely to be considerable regional differences, however, with some regions likely to receive increased rainfall sufficient to meet increased evaporative demand and other regions receiving even less rainfall than at present. Because the present distribution of species and plant functional types is strongly determined by the total (Holdridge, 1967; Box, 1981; Hinckley *et al.*, 1981; Austin *et al.*, 1990) and seasonal availability of water (Stephenson, 1990; Prentice *et al.*, 1992), any changes in water availability are likely to greatly affect the distribution of species (see Section 1.3.2).

1.3.1.2. Tree Responses to Increased CO_2 Concentration

The importance of CO_2 fertilization continues to be controversial (e.g., Körner, 1993; Idso and Idso, 1994; see also Chapter A). While the response of photosynthesis to CO_2 concentration can be readily observed at the single-leaf or isolated plant level (Kimball, 1983; Cure and Acock, 1986; Mooney *et al.*, 1991; Luxmoore *et al.*, 1993; Wullschleger *et al.*, 1995), it has been argued that this initial benefit may be negated by the various feedbacks in the plant and soil (e.g., Bazzaz and Fajer, 1992; Diaz *et al.*, 1993; Körner, 1993). Quantification of some of these feedbacks has been attempted (e.g., Comins and McMurtrie, 1993; Kirschbaum *et al.*, 1994) but has not yet been possible for the great diversity of natural habitats, in which most of the feedback effects are still inadequately understood and poorly quantified. Experimental approaches have not yet resolved this controversy because of the enormous costs and technical difficulties involved. Only a small number of open-air CO_2 enrichment experiments have been conducted with mature natural populations—and none on forests.

Because atmospheric CO_2 has already increased from a preindustrial concentration of about 280 ppmv to about 360 ppmv at present, increased growth should be observable in the growth of plants under natural conditions. However, the evidence from tree-ring chronologies is unclear, and no generalizations can be made (Innes, 1991). Where growth increases have been observed, part or all of that probably could be explained by more favorable temperatures, water relations, successional age, or nitrogen fertilization by moderate levels of industrial pollution (Innes, 1991; Luxmoore *et al.*, 1993).

When plants have access to limiting amounts of water, growth is limited by the amount of CO_2 that can be obtained in the diffusive gas exchange during photosynthesis. Once the available water has been used up, tissue water potentials fall below threshold levels and growth ceases. Growth under these conditions is determined by the amount of available water multiplied by water use efficiency (WUE). Because WUE can be greatly enhanced by increased CO_2 concentration (Rogers *et al.*, 1983; Tolley and Strain, 1985; Morison, 1987; Eamus and Jarvis, 1989), relative plant responses to increases in ambient CO_2 should be most pronounced under water-limited conditions (e.g., Gifford, 1979; Allen, 1990). While increasing CO_2 concentration may be beneficial for plant growth, some researchers rank it of less importance than changes in temperature and/or precipitation, which can have large impacts when critical thresholds of drought, chilling, or degree-days are reached (e.g., Solomon, 1988).

1.3.1.3. Carbon Storage and Nutrient Availability

Although increasing temperature may lead to higher net primary productivity (NPP), net ecosystem productivity (NEP) may not increase, and may even become negative, because warmer temperatures also greatly stimulate soil organic matter decomposition (e.g., Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Kirschbaum, 1995; Chapter A). This could release large amounts of CO_2 to the atmosphere (e.g., Jenkinson *et al.*, 1991; Kirschbaum, 1993, 1995; Schimel *et al.*, 1995; Chapter 9, *Terrestrial Biotic Responses to Environmental Change and Feedbacks to Climate*, in the Working Group I volume). However, the direct effect of increasing CO_2 concentrations may partly offset or in some cases even reverse this effect and make NEP positive.

Enhanced decomposition of soil organic matter also should have the effect of mineralizing nutrients—especially nitrogen and phosphorus—that are held in soil organic matter and making them available for plant growth (e.g., Shaver *et al.*, 1992; Melillo *et al.*, 1993). This is likely to be of greatest importance in cool regions of the world, which are mostly nitrogen-limited and often contain large amounts of organic matter (Post *et al.*, 1982). This could sometimes lead to an increase in total carbon storage in systems if nutrients are redistributed from components with low C:N ratios (i.e., soil organic matter) to components with high C:N ratios (i.e., woody stems) (Rastetter *et al.*, 1992; Chapter 9, *Terrestrial Biotic Responses to Environmental Change and Feedbacks to Climate*, in the Working Group I volume). In industrialized regions, nitrogen deposition from the atmosphere may enhance NPP and NEP, leading to increased total carbon storage in forest ecosystems (Kauppi *et al.*, 1992), provided deposition has not reached levels that cause forest decline (Durka *et al.*, 1994).

1.3.2. Species Distributions

Species have responded individually to past environmental changes (Huntley and Birks, 1983; Davis and Zabinski, 1992; Solomon and Bartlein, 1992; Gates, 1993). The set of all possible environmental conditions in which a given species survives

Box 1-3. Ecological Niches and Climatic Change

Any species' survival is influenced by many factors, and the set of environmental conditions in which it can exist and reproduce is called its niche. A distinction must be made between a species' fundamental niche and its realized niche (Hutchinson, 1957; Malanson *et al.*, 1992). The fundamental niche encompasses all environmental conditions in which a species could potentially grow and reproduce with its specific physiological characteristics. The realized niche encompasses those conditions in which a species is actually found. The latter is usually a subset of the fundamental niche due to competition by other species (see Chapter A). Only rarely does the realized niche coincide with the fundamental one (Woodward, 1987; Booth *et al.*, 1988; Austin *et al.*, 1994). Examples of typical environmental factors that determine a species' niche are temperature and precipitation (see Figure 1-1).

Species with narrow niches are potentially very sensitive to climatic changes. A sustained temperature increase of only 1°C could have a major effect on the probability of occurrence of many species (e.g., Arolla pine, Figure 1-1), and in some instances a temperature increase of 2°C can be sufficient to change the environment for some species from very suitable to totally unsuitable (e.g., Whitehead *et al.*, 1993).

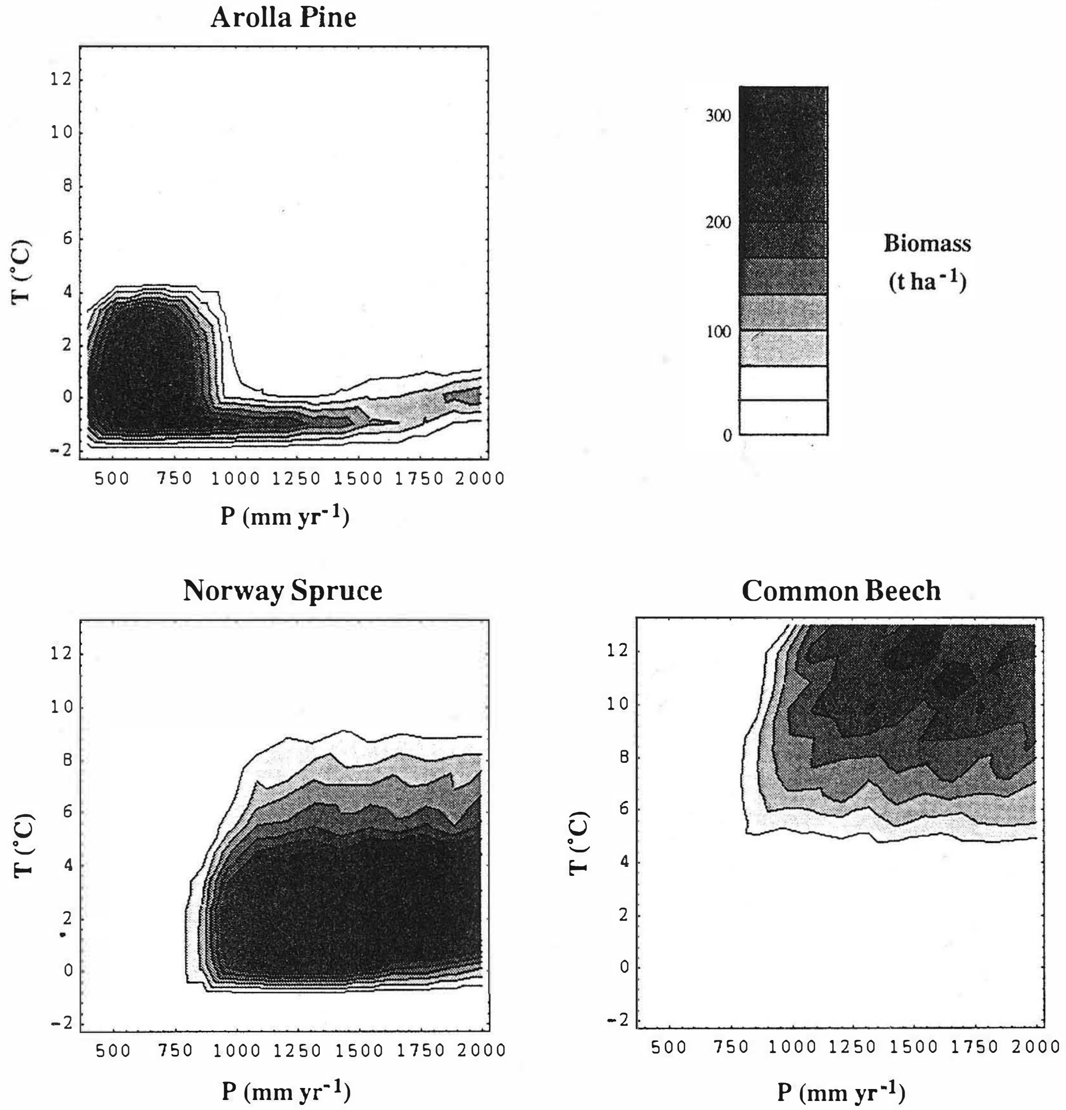

Figure 1-1: Simulated realized niches of three tree species [*Pinus cembra* L. (Arolla Pine), *Picea abies* (L.) KARST. (Norway Spruce), and *Fagus sylvatica* L. (Common Beech)] plotted as biomass versus annual means of temperature (T) and precipitation (P) (after Bugmann, 1994). The realized niches can be rather narrow (e.g., Arolla pine) and are usually smaller than the corresponding fundamental niches. For example, Norway spruce can easily be planted in climatic conditions where it naturally would be outcompeted by beech.

and reproduces (but without evolving—that is, changing its inherited characteristics such as physiological traits), is called its fundamental ecological niche (Hutchinson, 1957; Malanson *et al.*, 1992). In field conditions, species often survive only in a subset of the fundamental niche, the realized niche (Grubb, 1977; Booth *et al.*, 1988; Malanson *et al.*, 1992), owing especially to competitive interactions with other species (see Box 1-3).

With rapid climatic change, conditions may become unsuitable to complete one or more stages of the life cycle, especially if some climate variables were to change significantly more than other variables. For example, pollen and seed development require minimum heat sums and are sensitive to frosts (Stern and Roche, 1974). Seedlings are particularly vulnerable to short-term droughts, saplings to the presence or absence of sunlight, and mature trees to the availability of growing-season soil water. Populations could appear quite healthy while losing the ability to complete their life cycles.

Trees whose seedlings can now survive at a particular site will grow into adults in climates that may be unsuitable in 50–100 years; conversely, adults that could grow in an area in 50–100 years time must grow from seedlings that may be unable to survive current climatic conditions at those sites. A net ecosystem-level impact may be the loss of slow-growing species and the selection of species that complete their life cycles more quickly, such as early successional trees and shrubs. The ability to reach reproductive maturity in a short time favors early successional species that grow in full sun, whereas slower-growing species that begin their life cycles as understory species under closed canopies may be lost. Some model simulations have indicated that this opening of closed forests could result in the loss of three quarters of the trees and aboveground carbon in current temperate-zone forests (e.g., Solomon, 1986).

1.3.3. Transient Responses in Species Compositions

Concerns about the future of forest ecosystems relate not only to the geographic distribution of areas potentially suitable for forests and the performance of trees under different environmental conditions but also to the effect of climate change on the functioning and structure of ecosystems during the transient phase. For instance, it is well known that changing ambient conditions can reduce growth in forest ecosystems (e.g., Solomon and Webb III, 1985; Shugart *et al.*, 1986; Solomon, 1986; Woodwell, 1987; Prentice *et al.*, 1991b; Botkin and Nisbet, 1992; Davis and Zabinski, 1992). Moreover, the magnitude of climate change will subject many species assemblages, within a life cycle of their main species and in most of their distribution area, to climates that now occur outside their current ecological range (e.g., Solomon *et al.*, 1984; Roberts, 1989; Davis and Zabinski, 1992).

The transient response of species to such climatic changes can currently be assessed only with forest succession models (see Box 1-4). Despite some of their deficiencies (e.g., Moore, 1989; Bonan, 1993; Bugmann and Fischlin, 1994; Fischlin *et al.*, 1995), these models can be used to project transient changes in species composition of selected forest types for scenarios of climatic change in the past (Solomon *et al.*, 1981; Lotter and Kienast, 1992) or future (Pastor and Post, 1988; Kienast, 1991; Friend *et al.*, 1993; Bugmann, 1994; Bugmann and Fischlin, 1994; Smith *et al.*, 1994; see Box 1-4). These simulations suggest that climate change could cause widespread tree mortality within a few decades (Solomon *et al.*, 1984; Solomon, 1986; Solomon and West, 1987; Pastor and Post, 1988; Kienast, 1991; Prentice *et al.*, 1991b; Bugmann, 1994; Bugmann and Fischlin, 1994). Solomon and Bartlein (1992) and Pastor and Post (1993), for example, show how lags in population responses to climatic change could result in transient decreases in NPP before better-adapted species eventually replace the original vegetation and result in enhanced growth. It also should be noted that many simulations show species compositions that are not present in existing forests (Bugmann, 1994; Bugmann and Fischlin, 1994; Smith *et al.*, 1994).

Regrowth of better-adapted species or forest types requires many decades to centuries (Dobson *et al.*, 1989; Kienast and Kräuchi, 1991; Bugmann and Fischlin, 1994). Consequently, regions with forests in decline could release large amounts of carbon (e.g., Smith and Shugart, 1993), producing a large transient pulse of CO_2 into the atmosphere (e.g., Neilson, 1993; Chapter 9, *Terrestrial Biotic Responses to Environmental Change and Feedbacks to Climate*, in the Working Group I volume). Whereas some authors have estimated this carbon pulse from aboveground carbon alone to fall within a range of 0.1 to 3.4 Gt yr^{-1} for the annual flux, or 10 to 240 Gt for the accumulated pulse (King and Neilson, 1992), others have estimated a total carbon pulse from above and belowground C as high as 200 to 235 Gt, to be released to the atmosphere during a few decades to a century (see Section 1.3.4; Neilson, 1993; Smith and Shugart, 1993). Such responses, although debatable in their magnitude, are plausible because climatic changes also have been implicated in past episodes of forest and species decline (Cook *et al.*, 1987; Hamburg and Cogbill, 1988; Johnson *et al.*, 1988; Auclair *et al.*, 1992).

1.3.4. Potential Biome Distributions

Patch dynamics models cannot currently be used to simulate the transient behavior of forests in a changing climate on a global scale. This is because they require a large set of species-specific information that is not available from all regions of the world, especially not from the tropical zone. However, on the biospheric level (Table 1-1), several static global vegetation models have recently become available that enable us to make estimates of vegetation-climate equilibria (Box, 1981; Emanuel *et al.*, 1985; Prentice *et al.*, 1992; Smith *et al.*, 1992a; Cramer and Solomon, 1993; Leemans and Solomon, 1993; Monserud *et al.*, 1993b; Tchebakova *et al.*, 1993; Leemans and van den Born, 1994; Neilson *et al.*, 1994) based on earlier related studies (e.g., Köppen, 1936; Holdridge, 1947; Woodward, 1987).

Given any past or present climate, such vegetation models can be used to map the distribution of biomes (e.g., Prentice *et al.*,

Box 1-4. Forest Succession Models

Most forest succession models are based on the gap dynamics hypothesis (Watt, 1947; Bray, 1956; Shugart, 1984). They simulate the establishment, growth, and death of individual trees as a mixture of deterministic and stochastic processes within small—often $^1/_{12}$ ha—patches and average the actual forest succession at the ecosystem level from the successional patterns simulated for many individual plots (Shugart, 1984). Earlier work on the potential effects of climatic change on forests had to rely on spatial correlations between forest composition and climatic variables (e.g., Davis, 1986). Similarly, models that do not explicitly account for the differential effects of climatic change on different species may give optimistic projections of the effect of climatic change on ecosystem productivity. The more complex succession models that include the feedbacks between climate and ecosystem processes provide a more pessimistic outlook (see Figure 1–2).

On the other hand, most of these models do not include direct effects of increasing CO_2 concentration, which can ameliorate projected forest decline (e.g., Post *et al.*, 1992). Also, because of the limited availability of data on the fundamental niche of most species, these models are parameterized with information about the realized niche only (Austin, 1992). It has been argued that this might cause succession models to overestimate the extent of forest decline during the transient phase (e.g., Malanson *et al.*, 1992). Despite these caveats, patch models are the best tools currently available to study transient effects during climatic and other changes. Their simulations for current forests in response to past climatic changes provide fairly realistic assessments of likely future conditions (e.g., Solomon and Bartlein, 1992; Bugmann, 1994), although they cannot be interpreted as actual forecasts.

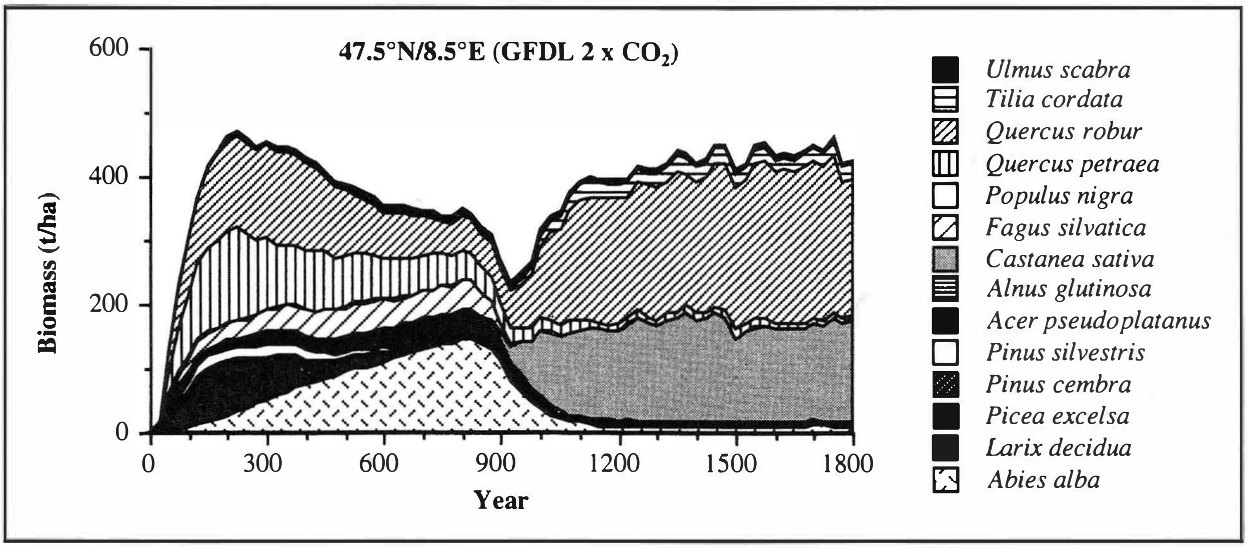

Figure 1-2: Transient response in species compositions simulated by the model FORCLIM-E/P (Bugmann, 1994; Fischlin *et al.*, 1995) at a site in Switzerland (47.5°N/8.5°E) under current climatic conditions (years 0–800) and under a scenario of climatic change derived from output of the GFDL GCM (years 900–1,800). A linear change of climatic parameters was assumed for the years 800–900. The graph shows the average cumulative biomass from 200 simulation runs (after Bugmann and Fischlin, 1996).

1992) or biospheric carbon storage (e.g., Solomon *et al.*, 1993) and to compare the simulated patterns with the present vegetation as provided by the few available global databases (Matthews, 1983; Olson *et al.*, 1983); see Figures 1-3, 1-5 (top), 1-6 (top), and 1-7 (top). Although these models are at an early stage of development (Leemans *et al.*, 1995), there is good statistical agreement between simulated and observed distributions of vegetation classes (e.g., Prentice *et al.*, 1992), except in areas where agriculture dominates. Although global models never can be strictly validated, their recent development toward inclusion of improved bioclimatic driving variables and mechanistic response functions offers increasing confidence in the magnitude of the results they generate. More about the nature and limitations of these models can also be found in Chapter 15.

The more recent models, such as BIOME (Prentice *et al.*, 1992), MAPSS (Neilson *et al.*, 1992), or TVM from IMAGE 2.0 (Leemans and van den Born, 1994), all attempt to simulate vegetation distribution considering ecophysiological traits and their relationship to particular climatic variables. This makes it possible to generate projections of vegetation distributions under past (Prentice, 1992; Prentice *et al.*, 1994; Figure 1-4), present [Prentice *et al.*, 1992; Neilson, 1993; Solomon *et al.*, 1993; Prentice and Sykes, 1995; Figures 1-5 (top), 1-6 (top), and 1-7 (top)], or future climates [Cramer and Solomon, 1993;

Leemans and Solomon, 1993; Neilson, 1993; Solomon *et al.*, 1993; Leemans *et al.*, 1995; Figures 1-5 (bottom), 1-6 (bottom), and 1-7 (middle)]. Apart from being used for climate-change impact assessment studies, they are now also used as a dynamic representation of the land surface for sensitivity studies of GCMs (see Claussen, 1994; Claussen and Esch, 1994; Chapter 9, *Terrestrial Biotic Responses to Environmental Change and Feedbacks to Climate*, in the Working Group I volume).

The models differ in their emphasis on particular processes and relationships (Leemans *et al.*, 1995). For example, BIOME (Prentice *et al.*, 1992) includes physiologically important aspects such as seasonality and moisture balance, and is based on PFTs, which to some extent simulate interspecific competition. MAPSS, on the other hand, couples the rate of transpiration to the conductance of the canopy by simulating maximum leaf-area index and stomatal conductance (Neilson *et al.*, 1994; Neilson and Marks, 1994). The latter makes it possible to incorporate ecophysiological responses such as CO_2 fertilization and WUE, but all species-specific information is lumped. These models use somewhat different vegetation classification schemes [e.g., compare Prentice *et al.* (1992) and Neilson (1993)], which usually makes direct comparisons possible only if some classes are aggregated (compare Figures 1-5 to 1-7 and Table 1-2 with Prentice *et al.*, 1992; Neilson, 1993; or Leemans and van den Born, 1994). Consequently, the vegetation distributions projected for a changed climate may differ substantially (Table 1-2).

One of these models, IMAGE 2.0, also has been used to incorporate the effect of climate change superimposed to the impacts of land-use changes (Alcamo, 1994; Figure 1-7). Its vegetation part (Leemans and van den Born, 1994) makes it possible to assess global forest distributions for the present [Figure 1-7 (top)] as well as the future [e.g., according to the conventional wisdom scenario of Figure 1-7 (middle and bottom)]. However, the potential natural vegetation is essentially modeled in a manner similar to BIOME (Prentice *et al.*, 1992).[2]

Although none of these models deals with transient forest responses, they offer the advantage of providing quantitative estimates for changes in a future climate on the scale of the distinguishable vegetation classes (Table 1-2; Figures 1-3 to 1-7). Due to the limited range of vegetation classes—BIOME and IMAGE, for instance, distinguish 20 (Prentice *et al.*, 1992; Leemans and van den Born, 1994; Prentice *et al.*, 1994); MAPSS distinguishes 33 (Neilson, 1993)—the projected changes (Table 1-2) tend to underestimate actual changes. Changes within a class remain by definition undetected and would have to be modeled by means of more detailed vegetation models.

The total area currently forested is likely to change significantly, if the changes occur according to any of the three models, from its present to a new vegetation class (Table 1-2, D). These estimates range from small changes [e.g., 7.5% (tropical rain forest)] to large ones [e.g., 65.1% (boreal forest)]—both estimated using the BIOME model. Net changes (Table 1-2, D*)—that is, the difference between the total forested area in the future versus the current climate—range from losses of 50.0% (IMAGE/TVM—tropical dry forest) to gains as large as 22.2% (MAPSS—tropical dry forest).

Except for MAPSS in the version shown here (i.e., without considering the partially compensating, increased WUE; Neilson and Marks, 1994), for the tropical zone models project a net

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[2] More information about this class of biosphere models can be found in Chapter 9, *Terrestrial Biotic Responses to Environmental Change and Feedbacks to Climate*, in the Working Group I volume, and in Chapters 15 and 24 of this volume.

Table 1-2: *Likely changes in forested areas (Mha) within four biogeographical zones according to three different vegetation models: BIOME (Prentice et al., 1992), MAPSS (Neilson, 1993), and terrestrial vegetation model (TVM) (Leemans and van den Born, 1994) from IMAGE 2.0 (Alcamo, 1994).*

	BIOME 2 x CO_2 (GFDL)			**MAPSS 2 x CO_2 (GFDL)**			**IMAGE-TVM 2050**			**Mean**	
Forest Type	D	s_o	D*	D	s_o	D*	D	s_o	D*	%D	%D*
Tropical Rain	57	706	19	281	1243	-234	129	296	-129	18.8	-14.4
Tropical Dry	153	640	-2	353	528	196	324	294	-309	37.2	-9.3
Temperate	346	1607	544	1007	1039	-155	388	583	-65	35.7	4.5
Boreal	952	511	-379	1231	1117	-529	42	1128	-33	40.4	-17.1

Notes: The first two models are used with a 2 x CO_2 equilibrium climate-change scenario generated by the GFDL GCM (Wetherald and Manabe, 1986). TVM from IMAGE 2.0 generated the changed climate internally, based on comparable assumptions (Conventional Wisdom Scenario) about greenhouse gas concentrations (Alcamo, 1994) and land-use changes as driven by population developments. All numbers relate to a potential forest vegetation in equilibrium with the climate, a steady state that is unlikely to be reached for many centuries. All figures were compiled by using the maximum number of vegetation classes as supported by the models (i.e., more than the 10 classes shown in Figures 1-3 to 1-7). D = Total forested area in transition from current type into a new one; s_o = Total forested area remaining within the same vegetation class; D* = Net change (data compiled by R. Leemans). The last two columns show means over all models as percentages of the currently forested area.

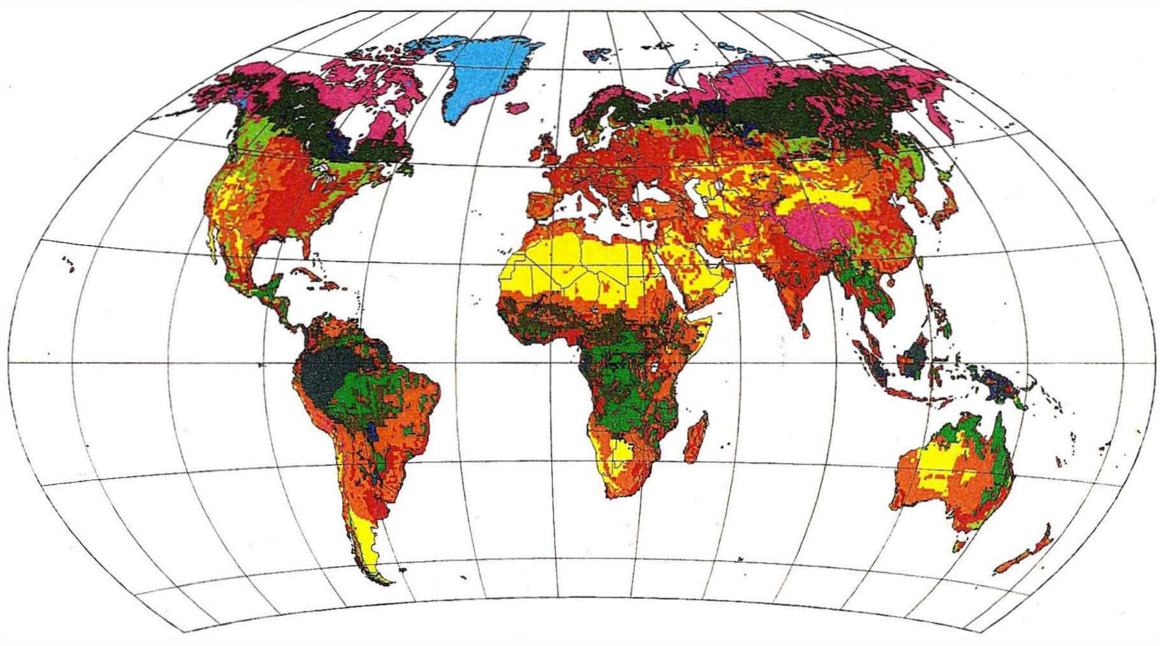


Figure 1-3: Present observed distribution of global vegetation complexes redrawn from the database compiled by Olson *et al.* (1983). For comparison, the vegetation classes have been aggregated to the same classification system as that used for all other model results shown here.

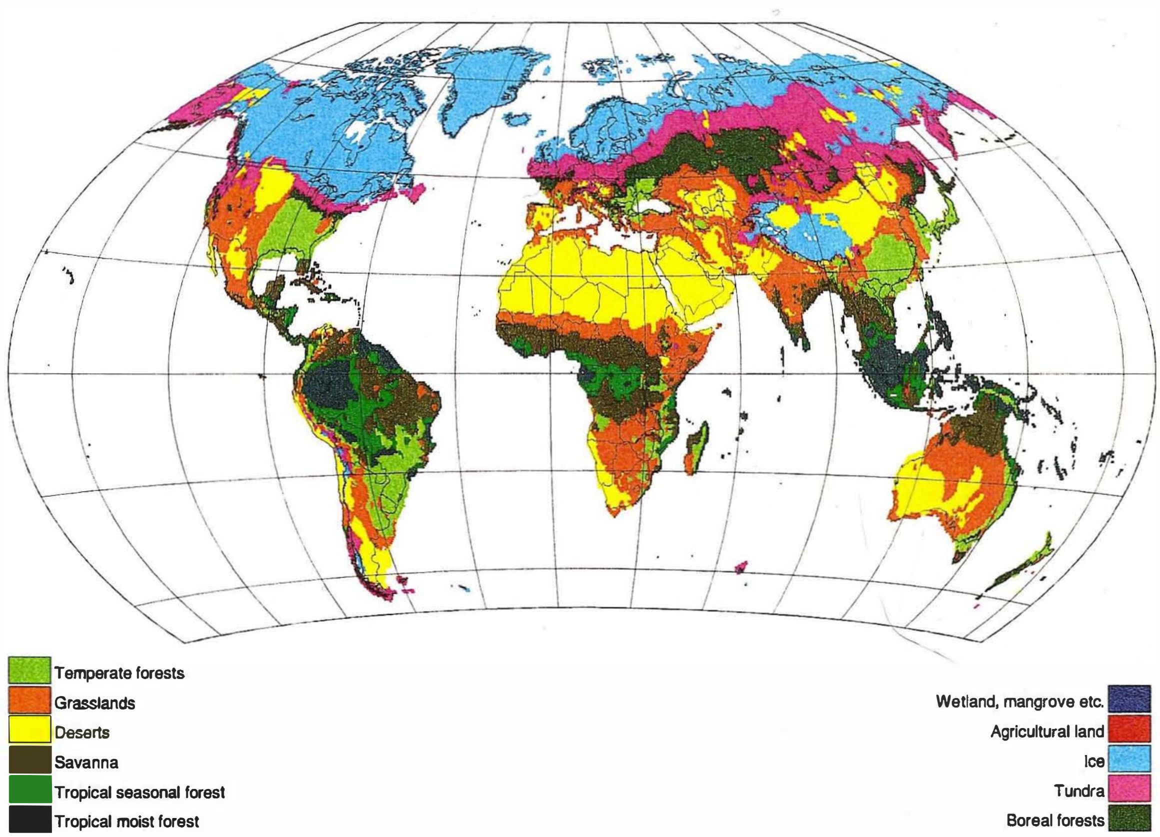


Figure 1-4: Past equilibrium vegetation according to BIOME (Prentice *et al.*, 1992) during the last glacial maximum [i.e., 18,000 years BP (Prentice *et al.*, 1994)]. The climate used for this simulation is derived from a GCM (not from paleoecological data, as this would lead to a circular argument). Note that according to this simulation, boreal forests cover only about 20% (Solomon *et al.*, 1993) of today's potential distribution (Prentice *et al.*, 1994).

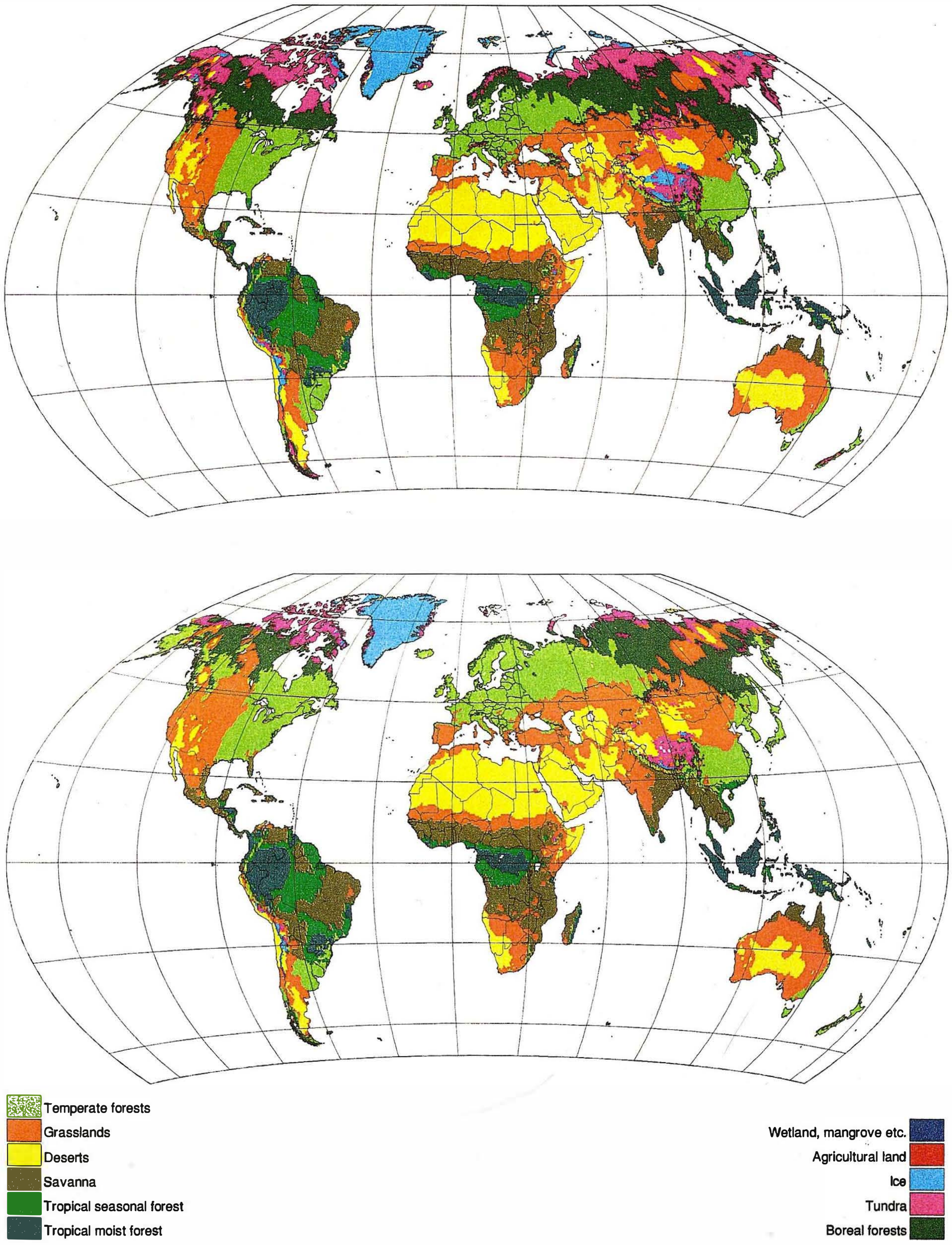


Figure 1-5: Present (top) and future (bottom) potential natural vegetation according to the BIOME model (Prentice *et al.*, 1992; Prentice *et al.*, 1994). The present climate is given by the IIASA climate database (Leemans and Cramer, 1991). The projected shifts in the boundaries of the vegetation classes are due to climatic changes as projected by the difference between a GFDL GCM control run and a 2 x CO_2 scenario (Wetherald and Manabe, 1986). They represent responses of plant functional types to cold tolerance, chilling requirements, and heat and water requirements of global vegetation (Solomon *et al.*, 1993; Prentice and Sykes, 1995).

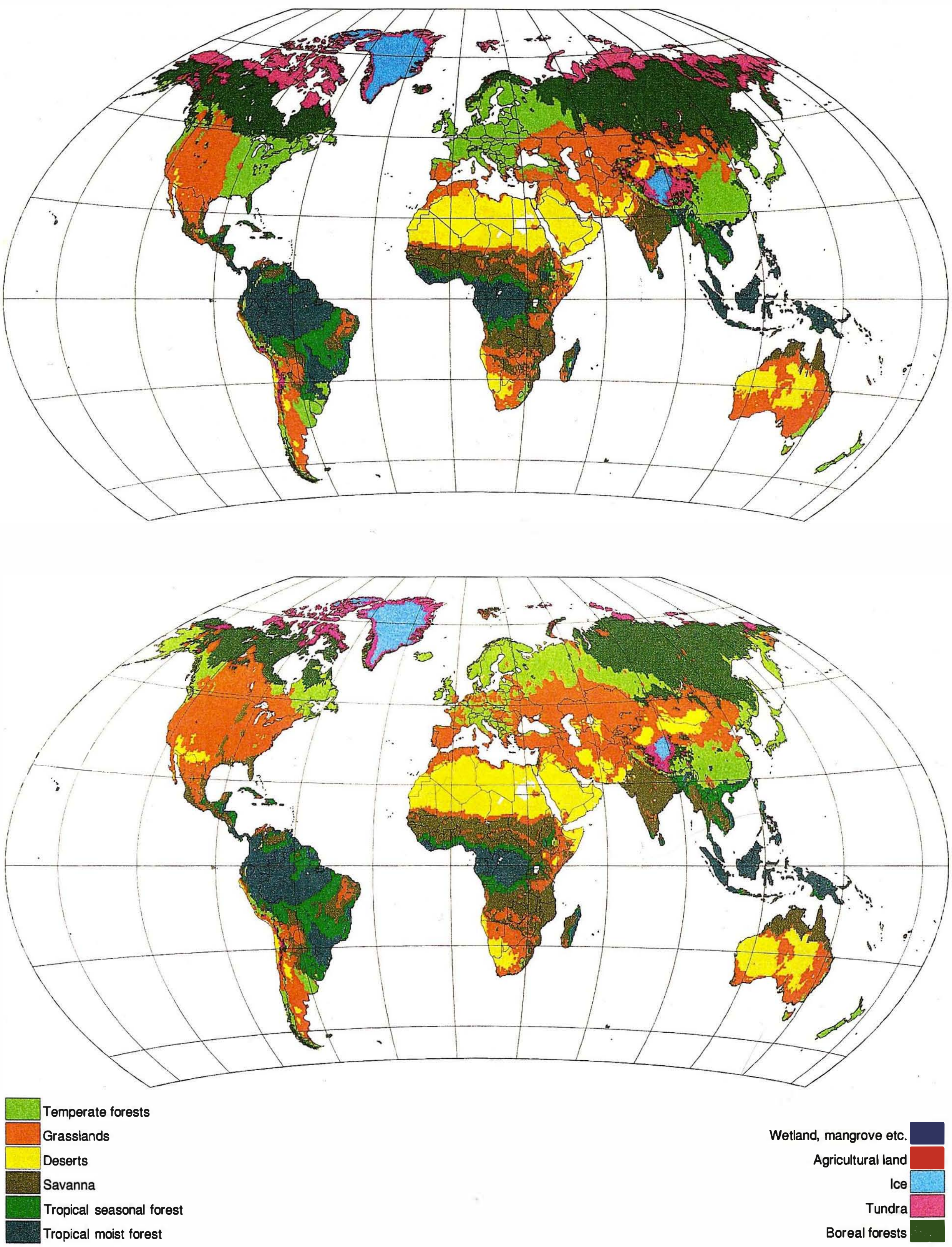
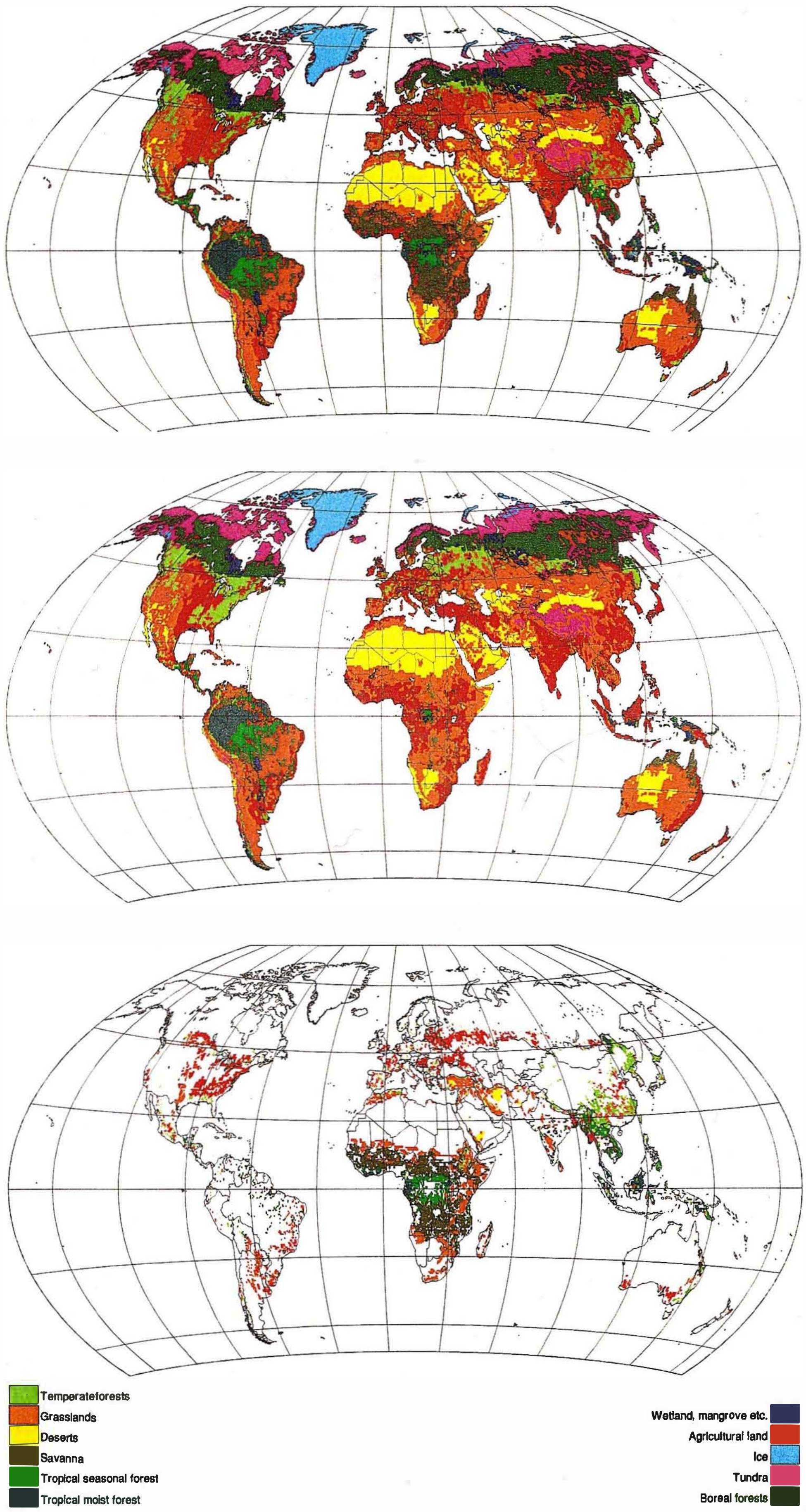


Figure 1-6: Present (top) and future (bottom) equilibrium potential natural vegetation according to the MAPSS model (Neilson, 1993). The present climate is given by the IIASA climate database (Leemans and Cramer, 1991). The projected shifts in the boundaries of the vegetation classes are due to climatic changes as projected by the difference between a GFDL GCM control run and a 2 x CO_2 scenario (Wetherald and Manabe, 1986). The model simulates climate responses due to a simulated steady-state leaf-area index, calculated from a site water and heat balance submodel (Neilson, 1993).


Temperateforests
Grasslands
Deserts
Savanna
Tropical seasonal forest
Tropical moist forest
Wetland, mangrove etc.
Agricultural land
Ice
Tundra
Boreal forests

gain in the potential area of forest distribution. Mainly IMAGE-TVM projects large net losses in the tropical rainforests. These losses are not due to climatic change, however, but are mainly caused by deforestation and other land-use changes (Zuidema *et al.*, 1994).

Although BIOME and MAPSS indicate relatively small net changes (Table 1-2, D*) in tropical dry forests, the actual changes encompass large gross losses (D), which are compensated by similarly large gross gains (not shown in Table 1-2). This is also partly true for the temperate zone, where MAPSS, for example, projects only relatively small net losses (D*); however, the associated gross losses (D) irrespective of gains (not shown) are more than six times larger. Mapped distributions indicate that temperate forests are likely to replace a large area of boreal forest, mainly due to the increase in winter temperatures (Figures 1-5 and 1-6). This allows temperate-zone vegetation to expand poleward into regions from which it is currently excluded by the -40°C threshold for the coldest month (Figures 1-5, 1-6, and 1-7).

The boreal regions, especially, are expected to undergo large vegetation shifts, with both MAPSS and BIOME projecting large changing areas (Table 1-2, D). Both models show large losses in area for current boreal forests, despite their encroachment into current tundra. Shrinkage in total area due to the geographically limited poleward shift leads to a net loss between 379 Mha (25.9%) and 529 Mha (22.5%).[3] The IMAGE model is an exception in this case; it projects much smaller losses of only 33 Mha (2.9%) (Figures 1-5, 1-6, and 1-7). This is mainly due to the structure of the model, in which vegetation change is primarily driven by human land use—which is not an important factor in the boreal zone.

In summary, all models suggest that the world's forests are likely to undergo major changes in the future, affecting more than a third of tropical dry (37.2%), temperate (35.7%), and boreal (40.4%) forests. Except in the temperate zone, the models suggest that there may be a net loss of forest area (Table 1-2, %D*). Averaged over all zones, this net loss amounts to 9.1% of the currently forested area. This is partly due to the fact that some regions are likely to lose forests for climatic reasons, while climatic gains in other regions might not be realized due to land-use pressures (IMAGE), and some models even predict a net loss (MAPSS). Averaged over all zones and all models, the projections indicate that 33% of the currently forested area is likely to change from the current vegetation class to a new one in response to climate forcing as generated by the GFDL 2 x CO_2 scenario. Compared with other GCMs, the latter represents a medium global warming scenario.

All models tend to underestimate potential changes, since they model only transitions among a limited number of vegetation classes. More importantly, as equilibrium models, none of them reflects the asymmetry between a temporary loss and the subsequent, much slower regrowth of forests in a new climate (see Section 1.3.3).

1.3.5. Past and Future Species Migration Rates

Shifts in the distribution of forest zones take place with significant time lags. The area occupied by different forest types has been quite plastic in the past 100,000 years, responding to changing environments with changes in species associations, structural properties of stands, and areas occupied (Solomon and Webb III, 1985; Webb III and Bartlein, 1992). Unlike the Pleistocene climatic changes, which occurred over thousands of years, future climatic changes of about the same magnitude are expected to take place over 100 years or less.

The change in annual mean temperature that occurs when one moves 100 km poleward may be as high as 0.7°C in mid- and high latitudes, but less at low latitudes. For summer temperatures and toward the interior of the continents, this value may be higher. With altitude, temperature changes of about 0.5–0.7°C per 100 m are also common (see also Chapter 5). With an expected warming between 0.1 and 0.35°C per decade, this means that species would have to migrate 1.5–5.5 km toward the poles per year or increase elevation by 1.5–5.5 m per year in order to remain within similar climatic conditions. Many studies of past changes have estimated natural rates of migrations of trees ranging from 40 to 500 m per year (Davis, 1976, 1981, 1986; Huntley and Birks, 1983; Solomon ***et al.***, 1984; Gear and Huntley, 1991; Torrii, 1991). Similarly, Gear and Huntley (1991) calculated from several sites in Britain migration rates for Scots pine of only 40–80 m yr^{-1}. However, for other species, such as white spruce, much faster dispersal rates of up to 1–2 km yr^{-1} also have been reported (e.g., Ritchie and MacDonald, 1986). It is not always clear whether the observed past rates were maximal rates of migration or whether they were limited by the rate at which the climate

≺ **Figure 1-7:** Present (top), future (middle), and differing (bottom) potential natural vegetation influenced by human land use as generated by the terrestrial vegetation module (TVM; Leemans and van den Born, 1994) from the integrated climate change assessment model IMAGE 2.0 (Alcamo, 1994). The areas shown represent a projection starting with the year 1970 (top) and the internal, dynamic changes calculated by IMAGE 2.0 by the year 2050 (middle). The bottom graphic shows the new class for all areas that are predicted to change from one to another vegetation class. The simulation results generated by IMAGE 2.0 incorporate the effect of land-use changes (e.g., deforestation) as driven by the dynamics of human populations and economic development. Note that IMAGE 2.0, unlike the other models, simulates climatic change independently from a GCM, since it generates its climate internally. The vegetational part (Leemans and van den Born, 1994) of the IMAGE model is similar to BIOME (Prentice *et al.*, 1992) and represents a mixture between a transient and a static response of vegetation to internally as well as externally generated changes.

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[3] The apparent lack of coincidence between relative and absolute changes is due to different definitions of the vegetation class "boreal forest." The MAPSS model has a greater area characterized as boreal forest than the BIOME model.

changed (Prentice *et al.*, 1991a; Prentice, 1992). Nevertheless, it is unlikely that future rates of species migration could match those required by the currently expected rates of climatic change in large areas. Pollen, on the other hand, may be dispersed much faster than seeds (e.g., Ennos, 1994), so the movement of genes of different ecotypes within a species might be able to match the speed of climatic change.

Migration of a tree species involves movement of propagules to new locations, establishment of seedlings, growth of individuals to reproductive maturity (which may take from years to decades), and production of new propagules. For long-distance migration, these stages need to be repeated. Several bottlenecks may be encountered: Strong competitors along the route may suppress the completion of full life cycles or specific, mandatory biological symbionts [e.g., the right species of mycorrhizal fungi (Perry *et al.*, 1987, 1990)], or specific pollinators for cross-fertilization may be absent at some point. Seed production, in particular, often depends on a phased sequence of development over at least 2 years, including many steps from floral bud differentiation to seed ripening (Fenner, 1991). Many stages in this sequence could be disrupted by unsuitable climatic conditions (Innes, 1994): With further warming, some species may fail to be chilled sufficiently to release dormancy (Murray *et al.*, 1989; Cannell, 1990), or dormancy may be released too early, which paradoxically could result under some circumstances in greater frost damage (Hänninen, 1991). Conversely, many trees flower profusely following hot, dry conditions (Stern and Roche, 1974). Hence, differential seed production by different species may limit rates of migration and drive substantial changes in species distributions.

Since each stage of a tree's life cycle requires specific environmental conditions, rapid climatic change is less likely to offer sufficiently favorable conditions to complete complex life cycles. This is especially true for some slow-growing species. More flexible species, such as those with wider seed dispersal, or a more invasive growth habit, may be able to move to more favorable habitats, whereas less mobile species are likely to be left behind and would be at a disadvantage as their former habitat becomes climatically unsuitable. Such a decoupling of climate determinants from species and community distributions probably has occurred already many times and at many places during the last millennia (Davis, 1986). The result has been a temporary absence of certain species for hundreds and thousands of years from regions in which they were previously capable of growing. Despite this, species diversity also could be transiently enhanced during a time of change because forests might form a richer mosaic of patches, consisting of some remaining old trees and a variety of invaders that are successful because of locally more favorable conditions.

In the future, human activities may to a certain extent enhance the migration of certain species, especially that of commercially important ones. On the other hand, natural migration of all other forest species will be further hampered by the fragmentation of natural habitats by human infrastructure, farmland, or exotic tree plantations, especially at mid-latitudes.

1.3.6. Biodiversity

To date, only about 1.4–1.7 million of an estimated total of 5–30 million species have been scientifically described (Wilson, 1985, 1992; May, 1990; Ehrlich and Wilson, 1991; Erwin, 1991; Gaston, 1991; Pimm *et al.*, 1995), and fewer than 100,000 are known well (e.g., Wilson, 1988; Pimm *et al.*, 1995). About 20% of the estimated total of 250,000 plant species are woody or tree species (e.g., Groombridge, 1992; Reid, 1992; Pimm *et al.*, 1995). There is poor understanding of the factors responsible for maintenance of high biodiversity (e.g., Grubb, 1977; Stork, 1988; Groombridge, 1992; Norton and Ulanowicz, 1992; Myers, 1995; Pimm *et al.*, 1995), but it is understood that biodiversity can only be managed indirectly through habitat and ecosystem management (e.g., Wilson, 1992). In this respect, forests are of paramount importance because they harbor about two-thirds of all species on Earth (Ehrlich and Wilson, 1991); tropical forests alone harbor at least half of all species (Raven, 1988; Ehrlich and Wilson, 1991; Webb, 1995). Species diversity generally increases strongly as one moves from colder to warmer sites (e.g., Groombridge, 1992), although the reasons for that trend are not well understood. When the size of an ecosystem is reduced to about 10% of its former size, about 50% of the species originally present generally will become extinct. Based on that relationship, it has been estimated, for instance, that a temperature rise of 2°C would cause 10–50% of the animals currently extant in the boreal Great Basin mountain ranges to be lost (Dobson *et al.*, 1989).

Climatic change can affect biodiversity either directly through altering the physiological responses of species or indirectly by altering interspecific relationships (e.g., Woodward, 1987; Tallis, 1990; Peters and Lovejoy, 1992). Whenever these changes lead to a habitat degradation, biodiversity will eventually be adversely affected (e.g., Peters and Lovejoy, 1992; Vitousek, 1994). Furthermore, biodiversity is affected not only by climate change but also by deforestation and other land-use changes that cause further habitat degradation and fragmentation (Janzen, 1988; Dobson *et al.*, 1989; Wilson, 1989; Ehrlich and Wilson, 1991; Myers, 1991, 1993; Postel, 1994; Daily, 1995; Pimm *et al.*, 1995). The combination of climate change with other pressures on ecosystems produces a particularly significant threat to biodiversity due to the following reasons:

- Climate change, together with other causes of habitat degradation, may locally decrease species diversity (Peters and Darling, 1985; Romme, 1991; Myers, 1992; Peters, 1992; Daily, 1995; Pimm *et al.*, 1995; Rind, 1995). Disturbance also may create opportunities for opportunistic or pioneer species, which will become more abundant (Myers, 1993) and, over time, replace many species that are slower growing and require more stable conditions. In some cases, this may lead to a temporary increase in species diversity (e.g., Lugo, 1988; Mooney, 1988; Vitousek, 1988).
- Species may become permanently extinct when local extinction cannot be reversed by reimmigration from

> surrounding areas. This problem would be most severe where the climate in a species' reserve changes from being favorable to being completely unsuitable (Peters, 1992), rendering "sanctuaries" into "traps" (Myers, 1993). Thus, an increasing fragmentation of habitats in combination with climate change may cause significant and irreversible species loss, a situation with which many of the current policies on reserves have large difficulties coping adequately (Ehrlich and Wilson, 1991; Botkin and Nisbet, 1992; Franklin *et al.*, 1992; Myers, 1992; Peters, 1992).

Although the effects of climatic change on biodiversity are still poorly understood, many authors anticipate a significant loss of species due to climatic change (e.g., Peters and Lovejoy, 1992; Reid, 1992; Myers, 1993; Vitousek, 1994). Due to its permanency, this must be considered as one of the most important impacts of climate change, not only in economic terms (e.g., Daily, 1995) but also in terms of all other utilitarian and spiritual values that have been attributed to species (e.g., Ehrlich and Wilson, 1991; Sharma *et al.*, 1992; Myers, 1993).

1.3.7. Adaptation

Forests themselves may to some extent acclimate or adapt to new climatic conditions, as evidenced by the ability of some species to thrive outside their natural ranges. Also, elevated CO_2 levels may enable plants to use water and nutrients more efficiently (e.g., Luo *et al.*, 1994). Nevertheless (see Sections 1.3.3 and 1.3.5), the speed and magnitude of climate change are likely to be too great to avoid some forest decline by the time of a CO_2 doubling.

Consideration may therefore be given to human actions that minimize undesirable impacts. Special attention may be given to poor dispersers, specialists, species with small populations, endemic species with a restricted range, peripheral species, those that are genetically impoverished, or those that have important ecosystem functions (Peters and Darling, 1985; Franklin, 1988; Davis and Zabinski, 1992; Franklin *et al.*, 1992). These species may be assisted for a time by providing natural migration corridors (e.g., by erecting reserves of a north–south orientation), but many may eventually require assisted migration to keep up with the speed with which their suitable habitats move with climate change. Some mature forests may be assisted by setting aside reserves at the poleward border of their range, especially if they encompass diverse altitudes, and water and nutrient regimes (Botkin and Nisbet, 1992; Peters, 1992; Myers, 1993), or by lessening pollutant stresses and land-use changes that result in forest degradation (e.g., Vitousek, 1994; Daily, 1995).

1.4. Tropical Forests

1.4.1. Characterization and Key Limitations

Tropical forests cover about 1,900 Mha (FAO, 1993a) and are found between 25°N and 25°S. They are distributed over five continents and are situated mainly in developing countries.

Box 1-5. Tropical Forests and Land-Use Changes

Tropical forests are endangered more by land-use practices than by gradual climatic change. Already at present much of the tropical forest is affected by deforestation due to land conversion and resource use (UNESCO, 1978; FAO, 1982; Brown *et al.*, 1993; Dixon *et al.*, 1994). Such anthropogenic tropical forest disturbances are expected to continue in response to economic development, population growth, and the associated need for agricultural land (DENR-ADB, 1990; Starke, 1994; Zuidema *et al.*, 1994).

Tropical rainforests have been cleared for agriculture since at least 3,000 BP in Africa and 7,000 BP in India and Papua New Guinea (Flenley, 1979). Africa has lost at least 50% of its rainforest, while tropical America and Asia have lost at least 40% (Mabberley, 1992). In addition to deforestation, large areas of previously undisturbed forest are being affected by removal of wood for timber and fuel (Brown *et al.*, 1993; Richards and Flint, 1994). Chapter 24 presents a detailed account of these deforestation trends in tropical forests.

The influence of tropical forests on local and regional climate may be as important as the effects of climate on forests (Lean and Warrilow, 1989). About 20% of the water flux to the atmosphere derives from evapotranspiration from the land, mostly from forested areas with high annual rainfall (Westall and Stumm, 1980; Lean and Warrilow, 1989). Deforestation can significantly reduce global evapotranspiration and increase runoff. This could affect the amount and distribution of precipitation over wide areas (Salati and Jose, 1984). For instance, in the Amazon basin, at least 50% of precipitation originates from evapotranspiration from within the basin (Salati *et al.*, 1979; Salati and Jose, 1984). Deforestation there will reduce evapotranspiration, which could reduce precipitation by about 20%—producing a seasonal dry period and increasing local surface temperatures by 2°C (Gash and Shuttleworth, 1991). This could result in a decline in the area of wet tropical rainforests and their permanent replacement by floristically poorer drought-deciduous or dry tropical forests or woodlands.

The forests consist of rainforests, drought-deciduous forests, and dry forests. In areas with prolonged dry seasons, especially where water limitations are intensified by edaphic conditions (Cole, 1986), there are savannas (Richards, 1966; Odum, 1971; Borota, 1991). Evergreen or partially deciduous forests occur in areas with a mean annual temperature greater than 24°C and with high regular rainfall throughout the year. Most of the closed tropical forests are found in the moist and wet zones, with precipitation to potential evapotranspiration ratios of 1–2 and greater than 2, respectively. The dry zone, with a ratio of precipitation to potential evapotranspiration of less than 1, covers about 40% of the total tropical region. In most of these forests, typical monthly temperatures fall between 24 and 28°C; daily extremes rarely exceed 38°C or fall below 10°C (Longman and Jenik, 1987).

Tropical forests represent about 40% of the world's forested area, containing about 60% of the global forest biomass and one-quarter of total soil carbon (210 Gt C in biomass and 220 Gt C in soils and litter) (FAO, 1982; Longman and Jenik, 1987; Brown *et al*., 1993; Dixon *et al*., 1994). Tropical forests cover only 6% of the world's surface but contain about half of all plant and animal species of the world (Bierregaard *et al*., 1992; Mabberley, 1992; Riede, 1993). Thousands of species in tropical forests are utilized by humans. It is of particular concern that tropical forests are currently being clear-cut, burned, or otherwise degraded by human activity (see Box 1-5).

An important characteristic of tropical forests is that they maintain a tightly closed nutrient cycle and often grow on a mass of very infertile soil, in which only the uppermost few centimeters have substantial amounts of plant-available nutrients. Phosphorus is generally the main limiting nutrient (Jordan, 1985). Therefore, any disturbance that results in loss of nutrients due to leaching, erosion, or timber harvesting can result in decreased growth rates, biomass, and diversity (Whitmore, 1984; Jordan, 1985; Vitousek and Sanford, 1986).

Fire significantly influences the structure, composition, and age diversity of tropical forests. In dry forests, fires tend to be frequent, which excludes fire-sensitive species. In tropical rainforest, fire is usually rare and does not usually spread over wide areas because there is insufficient dry and flammable plant material (Chandler *et al*., 1983a, 1983b). However, there have been instances in the past when thousands of hectares of tropical rainforest were burned following long dry periods (Goldammer and Seibert, 1990; Goldammer, 1992). Such fires are likely to significantly affect species diversity (Goldammer and Seibert, 1990) and may help prevent forest deterioration by promoting new growth and regrowth (Goldammer and Peñafiel, 1990).

Strong winds associated with tropical cyclones in tropical Asia, Central America, and northern Australia can profoundly influence the structure and floristic composition of forests (Whitmore, 1974; Hartshorn, 1978; Lugo *et al*., 1983; Longman and Jenik, 1987; DENR-ADB, 1990; Mabberley, 1992; O'Brien *et al*., 1992). Strong winds frequently damage tree canopies, create gaps in the forest, and modify the forest structure and micrometeorological environment. This may increase litter quality, allow more radiation to reach the forest floor, increase soil temperature, and make more soil water and nutrients available, which could promote the growth of new vegetation (Waring and Schlesinger, 1985).

1.4.2. *Projected Climatic Changes*

The climatic changes projected for the regions covered with tropical forest over the period 1990–2050 are increases in temperature of around 0.5–1.0°C, with no general change in seasonal amplitude; an increase in rainfall averaged over the region but with highly uncertain regional shifts in rainfall (differing greatly among GCMs), in the range -40% to +60%; and uncertain increases or decreases in soil water content (Greco *et al*., 1994). These projections imply the potential for an increased occurrence of droughts in some regions and floods in others.

We also must consider the possibility of changes in the frequency of ENSO (El Niño Southern Oscillation; see Glossary) events, which may increase rainfall seasonality in semi-tropical regions and could lead to a longer dry season in some areas and bring more rains in other places. Fire frequencies may increase in some areas in association with drought (Rind *et al*., 1990). Fires may further reduce local precipitation because fire-emitted aerosols increase the number of cloud condensation nuclei, producing smaller cloud droplets that are less likely to fall as rain (Andreae and Goldammer, 1992).

1.4.3. *Impacts of Climate and Land-Use Changes*

1.4.3.1. *Forest Area, Distribution, and Productivity*

All forests are expected to experience more frequent disturbance, with greater and possibly permanent impacts, such as increased soil erosion, and other forms of degradation and nutrient depletion. A study of 54 countries suggested that, between 1990 and 2050, a further 660 Mha are likely to be deforested, reducing the 1990 area by one-third and releasing 41–77 Gt C (Trexler and Haugen, 1995; see also Chapter 24). Rates of deforestation eventually must decrease as less and less of the original forest remains. There are, however, proposals to slow the loss of tropical forests (e.g., Deutscher Bundestag, 1990; UNCED, 1992), and many nations have large-scale plans for the protection or restoration of their forests (e.g., Brazil, India, and China: Winjum *et al*., 1993).

Global vegetation models do not agree on whether climatic change (in the absence of land-use change) will increase or decrease the total area of tropical forests (depending on the calculation of transpiration and vegetation properties; see Section 1.3.4), but any major shifts in rainfall pattern due to climate and land-use change are certain to change the present distribution of vegetation types within and among biomes (Neilson, 1993). Henderson-Sellers and McGuffie (1994) show that in an enhanced-CO_2 climatic regime, tropical evergreen broadleaf forests could readily re-establish after deforestation. In some areas, decreased rainfall may accelerate the loss of dry forests to savanna, while in others, increased rainfall and increased water-use efficiency with elevated CO_2 may favor the expansion of forests and agroforestry. In both cases, the outcome will be strongly influenced by human activities. Overall, shifts in rainfall patterns in the tropics could increase the rate of conversion of forests to agricultural land by increasing human migration from areas affected by droughts, erosion, or other forms of land degradation to non-degraded and more productive forest land.

The productivities of different areas of tropical forest are likely to increase or decrease in accordance with changes in rainfall, as indicated by simulation studies (Raich *et al.*, 1991). The overall effect of predicted changes in climate (excluding elevated CO_2) on the net primary productivity of tropical evergreen forests may be a decrease due to increased temperature and consequently increased respiration (in the absence of acclimation) and decreased photosynthesis due to increased cloudiness, but elevated CO_2 levels may cause an increase in productivity (in contrast to boreal regions) unless limited by phosphorus supply (Melillo *et al.*, 1993). CO_2 enhancement of photosynthesis and growth, particularly below ground (e.g., Norby *et al.*, 1986, 1992; Luxmoore *et al.*, 1993), is favored by high temperatures in species with C_3 photosynthesis (i.e., in trees) (Long, 1991; Kirschbaum, 1994) and possibly by vegetation disturbance and consequent fast nutrient cycling (Peterson and Melillo, 1985). This is also consistent with studies of the spatial distribution of CO_2 concentrations across the globe, which also suggest that the tropics constitute a biospheric sink that partially offsets the carbon release due to deforestation (Enting and Mansbridge, 1991; Schimel *et al.*, 1995). An alternative view is that elevated CO_2 levels will accelerate carbon and nutrient cycles in tropical ecosystems without increasing growth and biomass (Körner and Arnone, 1992). Researchers are agreed, however, that increased water-use efficiency by plants in response to elevated CO_2 is likely to enhance the productivity of vegetation in the drier tropical regions.

Land-use change is obviously the greatest threat to species diversity of tropical forests, but Cramer and Leemans (1993) speculate that climatic change alone could decrease the diversity of plant types at the boundaries of biomes, particularly in the tropics. Losses are likely to be greatest where the pressures of population and socioeconomic forces are greatest and least controlled (see also Section 1.3.6).

1.4.3.2. *Temperature*

In general, temperatures in non-montane tropical regions are already high enough for rapid growth year round, and a 2°–3°C increase in temperature alone will have a marginal effect on rates of photosynthesis, growth, decomposition, and nutrient cycling. However, if plants experience temperatures above 35°–40°C over extended periods, especially in combination with water shortage, tissue damage from desiccation and sunscald can occur (Fitter and Hay, 1987). In drier areas, the severity and duration of dry spells could be aggravated by increasing temperature. Also, some species sustain damage from temperatures below 10°–12°C or even below 15°–20°C, and there may be some limited future expansion of those species into regions from which they are currently excluded by cool temperatures (e.g., Smith *et al.*, 1992b).

1.4.3.3. *Water*

In the semi-arid tropical regions, climate-induced desertification will be a critical issue if precipitation decreases (Mitchell *et al.*, 1990; Greco *et al.*, 1994). Seasonally dry deciduous forests could burn more frequently and be permanently replaced with thorn scrub or savannah vegetation. It should be noted that changes in forest cover can have effects on groundwater supplies, surface runoff, sedimentation, and river flows (Brooks *et al.*, 1991), with potentially serious socioeconomic effects (see also Chapter 5). Also, hydrological changes that include shifts in atmospheric circulation could threaten the survival of cloud forests.

Some evergreen species of the humid forest clearly will be at a disadvantage in those areas that experience more severe and prolonged droughts. Significantly, drought affects the survival of individuals: Those without morphological or physiological adaptations to drought often die. In contrast, an abundance of moisture (in the absence of flooding) more often acts through changed competitive ability. Drought-adapted species are outcompeted by those that lack growth-limiting drought-adaptive traits. Species in moist tropical forests, including economically important hardwoods, are the least drought-adapted in the tropics, and their survival (with the attendant loss in diversity) in some areas must be considered at risk from climatic change.

1.4.3.4. *Soil Nutrients*

Climatic change (including elevated CO_2 levels) could enhance the supply of nutrients to plants in the tropics by, for instance, increasing root and mycorrhizal growth and thereby increasing access to soil phosphorus and enhancing nitrogen fixation by legumes, which are abundant in the tropics. On the other hand, the more important considerations are likely to be nutrient leaching and soil erosion wherever tree cover is lost (because of droughts or fire) or removed (by logging, clearing, or grazing)—especially where high-rainfall events occur in hilly areas—and immobilization of nutrients in soil organic matter in response to elevated CO_2.

1.4.3.5. *Pests and Pathogens*

Tropical rainforests contain large numbers of insects and pathogens that can cause serious damage to some plant species and may play a role in regulating species diversity (Coley, 1983). Many factors have been associated with the susceptibility of tropical plants to pests and diseases and with the virility of pests and pathogens. Some of these factors include suboptimal climate, availability of water and nutrients, and the presence of secondary metabolites that act as defensive compounds (Lambert and Turner, 1977; Levitt, 1980a, 1980b; Mattson, 1980; Mattson and Haack, 1987; Jones and Coleman, 1991). Drought stress can sometimes increase host plant suitability due to increases in soluble nitrogen and sucrose (White, 1974), whereas high temperatures and humidities (> 30°C and relative humidity of 50–90%) can decrease the growth rate, survival, and fecundity of some insects (Wilson *et al.*, 1982). Consequently, there is still great uncertainty as to whether the impacts of climate change on the relationship between host plants and pests and pathogens will lead to forest loss or gain.

However, the diversity of species in most tropical forests appears to confer some protection against widespread outbreaks of pests and diseases. The low population density of potential hosts prevents the rapid multiplication and spread of pests and pathogens (Longman and Jenik, 1987). Hence, most cases of debilitating outbreaks of pests and diseases—which can, for instance, affect entire stocks of some mahoganies—occur in plantations, agroforests, or stands that are dominated by one species (UNESCO, 1978).

1.4.3.6. Fire and Wind

It is clear from recent events that wherever there are more droughts, there will be more fires due to the accumulation of more combustible dry organic matter, with major potential economic costs in highly populated areas. In the extreme, recurrent fires will lead to the permanent loss of fire-prone species and the invasion and maintenance of fire-resistant species such as savanna vegetation. Fires, together with the action of wind—especially in regions where storms are frequent—will increase the dominance of pioneer species, including vines and herbs, preventing forests from developing to maturity.

1.5. Temperate Forests

1.5.1. Characterization

Temperate forests occur approximately from 25–50° N and S and are found primarily in developed countries in discontinuous blocks on five continents, sharing the landscape with agricultural land and urban areas. Closed forests originally covered about 1,400 Mha but have been reduced to about 700 Mha, 56% of which is in North America and 24% in Europe (see Chapter 15). Humans have had an impact on almost all of these forests; about 20% are managed for wood production or other uses, and many are being affected by pollutants, with both potentially positive and some obvious negative effects on growth (Innes, 1993).

These forests contain broadleaved and needle-leaved species that may be evergreen or deciduous. The most extensive types of temperate forests are the northern deciduous forests, commonly dominated by members of the *Fagaceae*, with leaf-shedding as an adaptation to winter frosts; the temperate coniferous forests of Europe, western and southeastern North America, and eastern Asia; warm evergreen forests in Australia dominated by *Eucalyptus* species; and other forests in the Southern Hemisphere dominated by *Nothofagus* species.

Temperate forests occur within a range of mean annual temperatures of 6–17°C, where average total precipitation exceeds 500 mm, with broad transition zones to boreal and subtropical forests. Within any region there are often steep gradients in forest types along climate gradients of rainfall and temperature, with change in altitude, and from oceanic to continental areas. At the low-rainfall margin, temperate forests change into savanna-type woodlands or Mediterranean shrublands. Temperate forests exist on a wide range of soils and have diverse ecological properties (Ellenberg, 1971; Bormann and Likens, 1979; Reichle, 1981; Edmonds, 1982).

The standing biomass and carbon content of temperate forests is currently increasing (at 0.2–0.5 Gt C yr^{-1}), largely due to reforestation (about 0.6 Mha yr^{-1}), underharvesting and regrowth after wood removal during the 19th and early 20th centuries (Armentano and Ralston, 1980; Heath *et al.*, 1993; Kurz and Apps, 1993; Sedjo, 1993; Sundquist, 1993; Dixon *et al.*, 1994; Galinski and Küppers, 1994; Kohlmaier *et al.*, 1995), and mainly fertilization effects of nitrogen deposition (Kauppi *et al.*, 1992). The temperate forests therefore are considered to be a carbon sink (Heath *et al.*, 1993). However, if the loss of carbon from decaying forest products and logging debris is taken into account, the net flux of carbon to the atmosphere from northern temperate forests is close to zero (Houghton, 1993) and, in the coming century, increased demand for wood may change the temperate forests to a net carbon source (Heath *et al.*, 1993).

Forest fires occur in most seasonally dry forests, despite control measures, and play an important role in ecosystem dynamics in these forests, especially in parts of North America, Australia, and Mediterranean Europe (Kozlowski and Ahlgren, 1974; Gill *et al.*, 1981; Goldammer and Jenkins, 1990). Fire affects species distribution by favoring fire-resistant species at the expense of those more sensitive to fire. Fire also creates conditions conducive to the establishment of new seedlings.

1.5.2. Key Limitations

The ranges and growth of temperate tree species in wetter, maritime, and high-latitude regions often can be related to the length of the growing season, measured in degree-days, and to absolute minimum temperatures in more continental areas. The temperature niches of individual species are often narrow (Figure 1-1) and are commonly determined by critical thermal requirements of the reproductive cycle (e.g., Pigott and Huntley, 1981).

In drier regions closer to the equator, the existence and growth of temperate forests are controlled largely by water availability. Variation in leaf-area indices and ring widths often is related to available water (Gholz, 1982). A minimum ratio of actual to potential evapotranspiration of approximately 0.65 is considered necessary to support the growth and regeneration of temperate-zone trees (Prentice *et al.*, 1992). Slight shifts to smaller ratios lead to open woodlands, savannahs, and grasslands. Soil water availability also strongly influences forest density, leaf area, growth, and standing biomass.

Seedling establishment is most vulnerable to shifts in precipitation patterns or amounts. Most temperate-zone seedlings can survive and become established only within narrow limits of soil moisture and sunlight. Slight changes in soil moisture can lead to the loss of a season's seedling crop, although losses in tree establishment cohorts may not lead to changes in forest structure for decades.

Like high-latitude populations experiencing low temperature, mid-latitude populations that are often subject to low soil water availability may be very plastic in their response to environmental variation. This plasticity enables temperate-zone trees to survive most weather variations that may be encountered only once every 200 years (Bugmann, 1994). Reproduction at these locations may be possible if conditions in rare years are favorable for the species' reproductive requirements (Pigott and Huntley, 1981).

1.5.3. Projected Climatic Changes

The climatic changes projected for most of the temperate forest region over the period 1990–2050 are increases in both summer and winter temperatures of 1–2°C; regional changes in precipitation in summer and winter, mostly in the ±20% range; and drier soils in summer (mostly with 2–8 mm less water) and, in winter, changes toward drier soils in some regions and wetter soils in others (Greco *et al.*, 1994). These projections imply longer and warmer growing seasons, less extreme subzero temperatures in winter, more frost-free winters in maritime areas, and more summer droughts, particularly in mid-continental regions (Manabe and Weatherald, 1987).

Possibly more important to temperate biotic communities than the magnitude of warming or precipitation change is the speed of climatic change (see Section 1.3.5). The projections imply that it will take less than a century for the summers to be warmer than now throughout the current geographic range of many temperate species.

1.5.4. Impacts of Climatic Change

1.5.4.1. Forest Area, Distribution, and Productivity

As long as the current agricultural surpluses in temperate regions persist, the temperate forest area is likely to be increased by afforestation. In Europe, the potential area for afforestation has been estimated as 44 Mha, and in the United States 100 Mha (Heath *et al.*, 1993).

Climatic change will enable the temperate forest to advance poleward, in many northern areas displacing boreal forest, and also potentially to expand in wet, maritime regions (Kellomäki and Kolström, 1992; Leemans, 1992; Morikawa, 1993). Early successional, pioneer species will be favored, and opportunities will exist for foresters to introduce species and ecotypes from warmer regions (Cannell *et al.*, 1989). However, in drier, continental regions, repeated summer droughts may lead to the loss of temperate forests. The rate of loss in biomass and carbon in these areas could exceed the rate of carbon gain in newly forested areas (Smith *et al.*, 1992a).

The net primary productivity of temperate ecosystems is predicted to increase in response to rising CO_2 concentrations, warming, and increased nitrogen mineralization rates; however, if drier areas, such as those west of the Appalachians, receive just 7% less rainfall, decreased productivity is predicted because of a decrease in the ratio of rainfall to potential evapotranspiration (Running and Nemani, 1991; Melillo *et al.*, 1993; Lüdeke *et al.*, 1995). Similarly, warming of 2°C and slightly decreased precipitation have been predicted to cause forest decline in Missouri (Bowes and Sedjo, 1993). Many experiments have confirmed that elevated CO_2 enhances the growth of young trees and that the effect is sustained over several years (Wullschleger *et al.*, 1995). However, it has proven difficult to detect CO_2-enhanced stem growth of mature trees over the last century (see Section 1.3.1.2 and Chapter A).

Forests that are not in decline may show little change in net carbon storage because, in temperate climates, increases in net primary productivity may be offset by increased soil respiration due to higher temperatures (Thornley *et al.*, 1991; Kirschbaum, 1993). That is, the net ecosystem productivity may not change, and may even decrease. Forests suffering from wildfire, pest outbreaks, or decline events will lose carbon and may become a major source of carbon (King and Neilson, 1992; Smith and Shugart, 1993).

1.5.4.2. Temperature and Water

Species in the temperate zone differ in their temperature optima for growth, their timing and degree of frost hardening and dehardening, their winter chilling requirements, and the number of degree-days needed to complete different stages in their reproductive development (Cannell, 1990). All of these differences are likely to be involved in driving changes in the distribution and productivities of species. Most studies predict substantial change during the next century, but confidence in our predictions is limited by knowledge of adaptive responses of species and the need to consider interactions among responses to temperature, CO_2, changed water relations, and pests and pathogens. Moderate temperature increases alone often can be beneficial, as evidenced by the faster growth and greater seed production of some commercial tree species when transferred to slightly warmer climates. But chilling requirements may not be met, and delayed budburst may limit the amount of light intercepted in the growing season while total respiration increases (LeBlanc and Foster, 1992). It also has been shown that frost hardiness can decrease in response to CO_2 enrichment (Barnes *et al.*, 1996), so that winter damage could even increase.

Species that are growing in regions where growth is limited by water shortages for at least part of the year may be adversely affected by intensification of summer soil water deficits (Greco *et al.*, 1994), as a result of decreases in the ratio of rainfall to potential evapotranspiration (e.g., Addison, 1991).

Warm winters will result in less precipitation falling as snow and reduced regional snow packs, resulting in less carry-over of water from the winter to the growing season (Mitchell *et al.*, 1990). Thus, less water will be available for vegetation in the following growing season, which may lead to drought-induced forest decline (King and Neilson, 1992).

1.5.4.3. Pests and Pathogens

Warming in winter may allow destructive insects and pathogenic fungi to survive at higher latitudes than at present, enabling subtropical or warm-temperate pests and pathogens to invade vegetation from which they are now excluded (Dobson and Carper, 1992). Some insects also will be able to complete more generations per year in warmer climates. Increased incidences of pests and diseases may further limit the growth of stands that are already declining from the effects of climate change or pollution. Summer droughts and other climatic stresses have been associated with outbreaks of bark beetles like the southern pine beetle (*Dendroctonus frontalis*) in southern parts of the United States, bark beetles in western Canada (Kimmins and Lavender, 1992), and bronze birch borers on paper birch in northern Michigan (Jones *et al.*, 1993). Elevated CO_2 can change the palatability of leaves and either promote or discourage insect herbivory (Overdieck *et al.*, 1988; Mueller-Dombois, 1992). In areas where forestry practice has led to the establishment of mono-specific stands, forests are particularly vulnerable to outbreaks of pests and diseases, especially where that combines with poor site quality or exposure to industrial pollutants.

1.5.4.4. Soil Nutrients

Nitrogen supply generally limits the productivity of many temperate forests (Tamm, 1991). Climatic warming will increase rates of turnover of soil nitrogen and carbon. In Europe and the United States, nitrogen fertility also may be improving through inputs from industrial and agricultural pollution. While a low level of nitrogen input may have a beneficial effect (Kauppi *et al.*, 1992), further inputs could reverse the initial gains through the development of nutrient imbalances and further acidification of the soil (Heath *et al.*, 1993).

1.5.4.5. Fire

The projected increase in the incidence of summer droughts in much of the temperate zone will increase the risk of forest fires and extend the hazard to areas that are not now affected, particularly where forests are defoliated or killed by drought, pests, or pathogens. Some species that are not adapted to withstand or regenerate after fire may be lost from fire-affected areas. However, large-scale fires may continue to be rare in the temperate zone and confined to drier parts of North America, Australia, and the Mediterranean region because temperate forests mostly occur in dissected landscapes in countries that can afford fire-control measures.

1.6. Boreal Forests

1.6.1. Characterization

The boreal forest covers approximately 17% of the world's land surface area in a circumpolar complex of forested and partially forested ecosystems in northern Eurasia and North America. It contains about 90 Gt C in living biomass and 470 Gt C in soils and detritus (Dixon *et al.*, 1994); the boreal region is estimated currently to be a sink of 0.4–0.6 Gt C yr^{-1} (Apps *et al.*, 1993; Dixon *et al.*, 1994).

The boreal forest consists primarily of evergreen and deciduous coniferous species and is floristically poor, being dominated by only about 15 tree species in both Eurasia and North America (Nikolov and Helmisaari, 1992). Many species have transcontinental distributions and are adapted to withstand extremes of climate and to regenerate after fire or insect attack. Three forest zones are often recognized (from south to north): closed-crown forest, open-crown forest (or lichen woodland), and forest-tundra. The closed-crown forest borders on steppe/prairie in continental areas, whereas in areas under maritime influence the boreal/temperate forest boundary consists of a relatively species-rich community—often in a mosaic of deciduous species on favorable soils and conifers at less favorable or colder sites (Apps *et al.*, 1993). Much of the boreal forest is embedded in a mosaic of wetlands and peatlands that may act as natural fire breaks. Mosses and lichens also play an important role in boreal ecosystem processes.

The northern limit of the boreal forest is largely determined by temperature (Garfinkel and Brubaker, 1980; Larsen, 1980, 1989; Arno, 1984), while both temperature and water supply determine the forest/steppe and forest/prairie boundaries. In general, the length of the vegetative period (related to the length of the frost-free period or July mean temperature) is of great importance in maritime regions. In more continental regions, drought or extreme subzero temperature may be more important—for instance, the apparent -40°C limit of sap supercooling of hardwood species (Arris and Eagleson, 1989) and the winter or drought tolerance of evergreen conifers. This tolerance may be exceeded in Siberia, which supports large areas of deciduous conifers (*Larix*) (Woodward, 1987). Drought is an important factor in interior Alaska and Siberia, where annual precipitation may be as low as 100–200 mm. Throughout the boreal region, droughts are generally necessary for the onset of fires. Some species, notably *Pinus sylvestris*, are drought-tolerant, whereas others such as *Picea abies* are dominant on wetter soils. A further factor determining the limits of species may be their winter chilling requirements.

The boreal forest consists of a patchwork of small to very large areas that are in various stages of recovery from fire or insect attack (van Cleve *et al.*, 1983a). Stands rarely reach maximum biomass or carbon content (Apps and Kurz, 1994), and many areas are dominated by one or a few species in a narrow age-class range. Also, it may be noted that the boreal forest is less than 12,000 years old and still may be expanding in some areas (Tallis, 1990), and even recovering from cool temperatures in the Little Ice Age (AD 1200–1850) (Campbell and McAndrews, 1993).

1.6.2. Key Limitations

Low air temperatures and small heat sums restrict growth and the production and germination of seed, which is a major factor limiting regeneration in the forest-tundra zone (Henttonen *et al.*, 1986). Unseasonal frosts can damage growth and reproductive cycles. Low soil temperature and permafrosts (in non-oceanic regions) have been demonstrated experimentally to limit growth and nutrient availability (van Cleve *et al.*, 1981, 1983b). Permafrost can restrict root growth and create an impervious layer that impedes soil drainage but can also be responsible for raised areas that permit drainage, producing islands where trees can grow within wetlands.

Low nutrient availability (except after fire) is characteristic of most boreal forests. Low soil temperatures limit the rate of litter decomposition and mineralization (Shaver *et al.*, 1992; Berg *et al.*, 1993; Kobak and Kondrasheva, 1993), and the litter of most coniferous boreal tree species is relatively resistant to decomposition because of its high lignin and low nutrient content. Nitrogen availability in boreal coniferous forests is generally in the range of 5–40 kg N ha^{-1} yr^{-1}, compared to 80–120 kg N ha^{-1} yr^{-1} in northern hardwood stands (Pastor and Mladenoff, 1992).

Natural wildfires are ubiquitous throughout the boreal region because of the buildup of large amounts of litter, much of which is not only resistant to decomposition but is also highly flammable. In the absence of fire-suppression measures, the interval between fires (the fire cycle) ranges from 50 to 200 years from south to north but may be over 1,000 years in wet northern ecosystems (Viereck, 1983; Payette *et al.*, 1989b; Payette, 1992). There are well-established relationships between fire-cycle length, species composition, age-class distribution, and carbon storage (Johnson and Larson, 1991; Kasischke *et al.*, 1995; Kurz *et al.*, 1995).

Boreal forests also are characterized by periodic outbreaks of insect pest populations. For many insect species, outbreaks have been clearly associated with climatic conditions and weather events (e.g., Martinat, 1987; Mattson and Haack, 1987; Volney, 1988), and outbreaks are often most common in the southernmost (warmest) part of the tree-host range (Kurz *et al.*, 1995). On sites where forests have remained unaffected by fire or insect damage for extended periods, they are characterized by multi-aged stands where tree-fall constitutes the most important disturbance. Tree falls create a variety of microenvironments that enhance diversity and affect regeneration patterns (Jonsson and Esseen, 1990; Liu and Hytteborn, 1991; Hofgaard, 1993).

The net primary productivity of boreal forests tends to be low—commonly 3–8 t (dry matter) ha^{-1} yr^{-1}, compared with 7–12 t ha^{-1} yr^{-1} for northern hardwoods (Cannell, 1982; Melillo *et al.*, 1993). Productivity is controlled in a complex way by interactions between various factors as discussed in Section 1.6.4 (Bonan and Shugart, 1989). As a boreal forest stand develops after fire, litter accumulates, more and more nutrients are immobilized in the litter, the depth of thaw is reduced because of the insulating properties of the litter, drainage may then be impaired by permafrost, and moss growth may impair regeneration from seed—some of which may be held within serotinous cones that release their seed only after fire (Bonan, 1992). Fire interrupts this process by burning litter on the forest floor, releasing mineral nutrients, leading to deeper thaw, improving drainage, and often removing the moss layer—all of which improves conditions for seed germination (Landhäusser and Wein, 1993).

1.6.3. Projected Climatic Changes

The climatic changes projected for most of the boreal region over the period 1900–2050 are increases in temperature of around 1–2°C in summer and 2–3°C in winter; regional changes in precipitation in summer and winter, mostly in the ±20% range; and drier soils in summer (averaging about 2–8 mm less water) (Greco *et al.*, 1994). These projections imply longer and warmer growing seasons, appreciably milder winters with the possibility of less extreme minimum temperatures, and less permafrost, which is related to annual mean temperatures.

Most importantly, the changes in temperature, soil water, and vapor pressure deficit may increase the frequency (shorten the return-time) of fires. Flannigan and van Wagner (1991) predict a 40–50% increase in the area burned each year in Canada in a 2 x CO_2 climate scenario, and others have predicted more frequent fires of higher intensity in the forest-tundra (Stocks, 1993; FIRESCAN Science Team, 1995). In Russia, an additional 7–12 million hectares of boreal forest are projected to burn annually within the next 50 years, affecting 30–50% of the land area (Dixon and Krankina, 1993).

1.6.4. Impacts of Climatic Change

There is a general consensus that climatic change will have greater impact on boreal forests than on tropical and perhaps temperate forests, and that more frequent or changed patterns of disturbance by fire and insect pests may be more important agents of change than elevated temperatures and CO_2 levels *per se* (Shugart *et al.*, 1992; Dixon and Krankina, 1993). Overall, the boreal forest is likely to decrease in area, biomass, and carbon stock, with a move toward younger age-classes and considerable disruption at its southern boundary (Neilson *et al.*, 1994; Kurz *et al.*, 1995). CO_2 enrichment itself may have less effect than in warmer climates. In Sections 1.6.4.1 through 1.6.4.4, we consider the likely changes in the distribution and composition of the forest and then elaborate on the factors driving change.

1.6.4.1. Forest Area, Distribution, and Productivity

On its southern border, the boreal forest may give way to northern deciduous forest (or agriculture) in areas with a maritime influence and to grassland or xerophytic steppe vegetation in midcontinental areas, and species shifts may occur in the mid-boreal region (Emanuel *et al.*, 1985; Kellomäki and Kolström, 1992; Rizzo and Wiken, 1992; Dixon and Krankina, 1993; Monserud *et al.*, 1993a; Tchebakova *et al.*, 1994; Prentice and Sykes, 1995). Near tree lines in many areas, there is potential for existing populations of suppressed individuals to grow taller and more vigorously, as has apparently happened in response to past climatic changes (Kullman, 1986; Payette *et al.*, 1989a; Hofgaard *et al.*, 1991).

Over the next century, the potential (or preferred) geographic ranges of species may shift approximately 300–500 km, implying changes in forest-based industries and considerable socioeconomic impacts. In the early Holocene (about 8,000 years ago), when the climate became warmer, fire-adapted hardwood species expanded northward to new sites after fire (Green, 1987). Where northern deciduous species, such as sugar maple, migrate northward, forest productivity may be increased on soils that retain adequate water, whereas productivity may decrease on dry soils where boreal forest may give way to oak-pine savanna (Pastor and Post, 1988).

There is concern that the maximum potential migration rates may be too slow to keep up with the rate of climatic change (see Sections 1.3.3 and 1.3.5)—in which case some researchers consider that there may be areas of transitory forest decline, especially if soils change slowly, are unfavorable for immigrating species, and lack necessary microbes and symbionts (Dixon and Turner, 1991; Davis and Zabinski, 1992; Solomon, 1992; Smith and Shugart, 1993), or where growth by more southern species is limited by photoperiodic constraints. The future of the transitory forest is likely to be determined by increasing occurrence of extended high-intensity wildfires until a new climate-vegetation-fire equilibrium is established (Crutzen and Goldammer, 1993). Other researchers suggest that there may be little forest decline. Intraspecific genetic diversity will buffer change, and species that are no longer in a favorable climate will simply grow and regenerate poorly and be overtaken by invading species either gradually or after disturbance (Malanson *et al.*, 1992; see also Section 1.3.3).

Increasing temperatures are likely to stimulate soil organic matter decomposition and increase nutrient (especially nitrogen) availability, leading to an increase in net primary productivity of non-stressed stands, averaging perhaps 10% in the boreal zone in a 2 x CO_2 climate (Melillo *et al.*, 1993). However, despite increasing productivity, there may be a net carbon loss from the ecosystem because a small temperature rise will greatly enhance decomposition rates (Jenkinson *et al.*, 1991), whereas CO_2 fertilization will be of low effectiveness because of low temperatures (Kirschbaum, 1993). Also, productivity may not increase in dry areas if water limitations were to increase due to increased evaporative demand. Hydrological and landscape changes in the patterns of bogs and forest also may be expected. In the north, melting of permafrost would favor the expansion of wetlands, while drier conditions in the south would lower the water tables (Apps *et al.*, 1993).

In the forest-tundra, rising temperatures are likely to enhance the development and germination of seeds of many species, increasing forest cover and enabling a northward migration to occur, probably after fire (Kullman, 1990; Kellomäki and Kolström, 1992; Landhäusser and Wein, 1993)—but again, hampered to some extent by slow changes in soil conditions (Rizzo and Wiken, 1992). There is clear evidence in the fossil pollen and macrofossil record of expansion and recession of boreal forest in both Eurasia and North America in response to temperature changes over the past 10,000 years (Ritchie, 1987). However, it will take more than 100 years for any new forest areas to mature in the forest-tundra, so the northward expansion of mature boreal forest is likely to be slower than the rate at which it is lost to grassland and temperate deciduous forest at its southern boundary (Rizzo and Wiken, 1992). The tundra itself is likely to become a carbon source in response to warming (Billings *et al.*, 1984; Oechel *et al.*, 1993).

1.6.4.2. Temperature

The productivity of boreal forests—except those at the warmer and drier edge of their species ranges—is likely to respond favorably to increases in temperature, as shown by long-term soil warming experiments and models (van Cleve *et al.*, 1990; Melillo *et al.*, 1993). It has long been known that trees in the boreal forest exhibit positive relationships between annual growth-ring widths and summer temperatures (Mikola, 1962) and between volume growth and number of degree-days (Kauppi and Posch, 1985; Worrell, 1987). Also, most provenance-transfer studies suggest that some southward movement of ecotypes to warmer climates promotes their volume growth (Beuker, 1994; Matyas, 1994). The magnitude of the growth response will depend on the effect of increased temperatures on nutrient availability, evapotranspiration, and the frequency of fires. Subtle interactions may be important. For instance, Bonan *et al.* (1990) and Bonan (1992) show how increased temperatures combined with increased evapotranspiration could result in a faster build-up of litter and a shallower permafrost zone, but an increased probability of fire. The net effect could be to reduce nutrient availability except after fires—whereas on the basis of temperature increases alone, nutrient availability would have been expected to increase (Shaver *et al.*, 1992).

Forest simulation models suggest large shifts in species composition in boreal forests (Shugart *et al.*, 1992). Large increases in temperature would cause annual heat sums to exceed the minimum thresholds for seed production, favoring the northward spread of species, especially in the forest-tundra zone. On the other hand, reduced winter chilling may disrupt both vegetative growth and reproductive processes of species at the southern edges of their ranges (Kimmins and Lavender, 1992).

1.6.4.3. Nutrients

Nitrogen is the nutrient that most limits the productivity of boreal forests (e.g., van Cleve *et al.*, 1983a, 1983b; Tamm, 1991). The critical factor is the rate at which nitrogen is recycled through the litter—which, as noted earlier, is a function of both temperature and litter quality (Berg *et al.*, 1993). Species differ in both their response to nitrogen and their litter quality. *Picea* sites in cold locations have forest floors with a high lignin content, little available nitrogen, and slow decomposition rates, whereas *Betula* or *Populus* sites, especially in warmer locations, have forest floors with less lignin. Thus, whereas small increases in temperature will increase rates of decomposition and nitrogen cycling, large or prolonged temperature increases also will lead to a shift from coniferous to deciduous tree species, and—because of the greater decomposability of deciduous litter—this may have a further positive effect on nitrogen availability, leading to increased productivity. On the other hand, increasing CO_2 concentration could increase the C:N ratio of litter, and the reduced litter quality might slow the rate of nutrient cycling (Taylor *et al.*, 1989; van de Geijn and van Veen, 1993).

1.6.4.4. Fire and Insects

In Canada over recent years, about 1 to 2 Mha have burned each year (Kurz and Apps, 1993), and in Russia, between 1.4 and 10 Mha burned each year between 1971 and 1991 (Dixon and Krankina, 1993). If fires occur very frequently, late successional species become unable to outcompete pioneer species, which will thereby become more common. A threefold increase in wildfire frequency in Canada between a high-fire year (1989) and a reference year (1986) resulted in an 86% reduction in the net ecosystem carbon sink (Kurz *et al.*, 1992). However, fires also have a beneficial effect on subsequent ecosystem function and facilitate regeneration (Landhäusser and Wein, 1993). Fires may have most impact in the forest-tundra zone; indeed, Payette and Gagnon (1985) conclude that the modern forest-tundra boundary of northeastern North America is the result of fires during the last 3,000 years, which were followed by lower temperatures that limited forest regeneration. If future fires were followed by higher temperatures, the fires could be catalysts for a return to coniferous forests that appear to have existed there 7,000–10,000 years ago.

Defoliating insects play an important role in boreal forests, and there are many instances where the proportion of different boreal tree species is related to the intensity of insect pest outbreaks. Pests usually are maintained at a low population equilibrium by a combination of host resistance, natural enemies, and weather conditions. Any one of these factors could be affected by climatic change, particularly tree resistance in response to environmental stress. Once an outbreak exceeds a certain patch size, it can become self-propagating and can spread largely independently of weather conditions. Following climatic warming, it seems very likely that insect outbreaks will expand northward and that new pest and pathogen problems will arise (Kurz and Apps, 1993).

1.7. Research and Monitoring Needs

Our capability to assess the likely fate of the world's forests under altered climatic conditions has been limited because the conceptual modeling framework for such an assessment is still in an early stage of development. It needs to be refined to improve the understanding of climate change impacts at the following three levels: (1) the ecophysiological responses of trees to changing climate and CO_2 concentrations, (2) the relationship between tree growth and transient forest dynamics, and (3) the influence of changing forest characteristics on the global carbon balance and hence their feedback to the greenhouse effect. The predictive power of current modeling approaches decreases from (1) to (3). A consistent research strategy to overcome these limitations needs to be accompanied by a monitoring program that can provide appropriate databases for initialization, calibration, validation, and application of the models. In particular, future work should address the following:

- *Ecophysiology*, specifically the influence of temperature, water availability, ambient CO_2 concentration, photoperiod, and nitrogen availability on the establishment, growth, water use efficiency, stomatal conductance, biomass allocation, and survival of trees under natural conditions. Urgently required also are studies of belowground plant and soil processes such as the decomposition of organic residues under changing environmental conditions. Most previous studies have been limited to short-term responses of young trees and therefore have ignored longer-term processes influenced by more than one factor, as well as the adaptive potential of plants. There is a need for more long-term studies that investigate simultaneously a well-defined set of key factors. The ecophysiological responses should be measured at experimental sites within a range of forest types, and those experiments should follow protocols that support modeling research.
- *Forest dynamics*. Studies should focus on the stability of natural and managed forests under different types of climatic (temperature, water availability) and

chemical (CO$_2$, nitrogen) regimes, including the influence of changing disturbance conditions (wind, drought, fire, pest frequencies). Because the direction and magnitude of possible climatic change is not known for all factors relevant to ecosystem dynamics, simulations and experimental studies should focus upon a broad range of such conditions. The potential rate of species migration (either assisted or unassisted) needs to be investigated further using appropriate models. A significant part of this activity should be devoted to further development of monitoring strategies that would allow the collection of data on realistic forest responses through all major forest regions.

- *Monitoring*. The development and application of forest models requires improved global databases on the present conditions of the world's forests, as well as their associated site characteristics. It is crucial that these data-gathering activities are intensified, both through the global network of ground observations that can be made in many research institutes worldwide and through the collection of data from spaceborne sensors. For ground-based data collection, standardization and worldwide availability are key issues, as is the continuation of already ongoing observational series. Satellite remote sensing is in a promising stage of development, with respect to both enhanced processing protocols of existing time series of satellite data (such as AVHRR) and the development of sensors with improved capacity to measure ecosystem properties at high spatial and temporal resolution.

To improve the overall modeling framework for the assessment of global forest response to climate change, and to provide an appropriate background for the synthesis of more detailed studies, there is a requirement for process-based terrestrial biosphere models of ecosystem dynamics. These models should build on knowledge from all other levels of model development. Specifically, they should involve a sufficiently high number of plant functional types and forest types to cover the wide range of forests occurring in different climate zones. Various initiatives for the development of such models are currently underway (e.g., Focus 2: Change in Ecosystem Structure, especially activity 2.3. in Steffen *et al.*, 1992; Landsberg *et al.*, 1995). To succeed, they need to be backed up by the research activities listed above.

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