

## Chapter 12 Climate-Ecosystem Dynamics

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## 12.1 Introduction

The traditional ecological view of terrestrial vegetation is one in which community composition and ecosystem structure are determined by climate. Changes in climate alter competitive relationships among species, ecosystem processes such as net primary production, decomposition, and nutrient mineralization, and thus alter the structure and biogeography of ecosystems. However, this represents only part of the interaction of ecosystems with climate. Terrestrial ecosystems affect climate through exchanges of energy, water, momentum, CO<sub>2</sub>, and other radiatively important atmospheric gases. Changes in community composition and ecosystem structure alter surface properties such as albedo, roughness, stomatal physiology, leaf area index, rooting depth, and nutrient availability and in doing so alter surface energy fluxes, the hydrologic cycle, and biogeochemical cycles. As a result, changes in ecosystem structure and function and the replacement of one ecosystem with another in response to climate change feed back to influence climate.

The coupling of ecosystems and climate occurs over a continuum of timescales from minutes to seasons to thousands of years (Table 12.1). At short timescales, the seasonal emergence and senescence of leaves alters the absorption of radiation, the dissipation of energy into latent and sensible heat, and CO<sub>2</sub> uptake. The effect of these changes can be seen in air temperature, humidity, and the seasonal drawdown of CO<sub>2</sub> in the atmosphere. Interannual variability in temperature and precipitation alter ecosystem metabolism, which is again evident in the concentration of CO<sub>2</sub> in the atmosphere. At longer timescales of decades to centuries, successional changes in response to recurring disturbances alter surface energy fluxes and carbon storage. Coupled climate-ecosystem dynamics are particularly evident over periods of centuries to millennia when broad changes in ecosystem geography in response to climate change influence atmospheric CO<sub>2</sub> concentration and climate.

Figure 12.1 illustrates the coupling of climate and ecosystems over periods of decades to millennia. Successional changes in community composition and ecosystem structure in response to recurring disturbance initiate a natural cycle to ecosystem development in which, for example, a clearing is reforested. Climate change is superimposed on this successional backdrop so that changes in temperature, precipitation, and atmospheric CO<sub>2</sub> concentration alter ecosystem processes and might, for example, convert a grassland into a forest. Human activities also disturb the landscape, initiating vegetation change.

The introduction of invasive or non-native species can alter resource utilization and the competitive balance among species. Abandonment of farmland initiates the successional regrowth of trees and grasses.

This chapter examines how ecosystem processes at metabolic, successional, and biogeographical timescales affect climate. Human activities in terms of agroecosystems and urban ecosystems are discussed in Chapters 13 and 14.

## **12.2 Biogeophysics**

Changes in regional and global climate due to biogeophysical processes such as energy, water, and momentum fluxes are difficult to establish through observations because of interannual variability and confounding influences. While differences in energy fluxes are readily found when comparing vegetation types, the relationship between these differences and any possible difference in temperature is much more difficult to document. In some cases, such as with leaf phenology, careful examination of climatic data can reveal an ecological influence. More often, however, climate models with detailed representation of land surface processes are used to demonstrate the effects of vegetation on regional and global climate (Figure 8.23). Paired climate simulations, one serving as a control to compare against another simulation with altered surface properties, demonstrate the influence of vegetation on climate (Figure 8.24).

### **12.2.1 Phenology**

The seasonal emergence and senescence of leaves on deciduous trees alters sensible and latent heat fluxes and in doing so alters surface climate. In eastern United States, springtime air temperatures are distinctly different after leaves emerge (Schwartz and Karl 1990; Schwartz 1992, 1996). For example, a study of long-term air temperature observations in 13 locations in north central and northeast United States found daily maximum temperature increased at a rate of 0.17 °C per day well before springtime leaf emergence to 0.31 °C per day just prior to leaf emergence (Figure 12.2). After leaves emerged, the rate of temperature increase dropped to less than 0.07 °C per day. Consistent with this, a subsequent analysis found that diurnal temperature range increased for several weeks prior to leaf emergence, but was essentially unchanged for several weeks following leafing out (Figure 12.2). This temperature discontinuity over a period of less than a few weeks is related to increased transpiration upon leaf emergence that cools

and moistens air (Fitzjarrald *et al.* 2001). A similar distinct seasonal pattern to air temperature is seen in west central Canada (Hogg *et al.* 2000). Long-term mean daily temperatures for nine climate stations in the Canadian prairie provinces show that air temperatures in this region are 2-3 °C warmer than expected during April and October while summer temperatures are up to 2 °C cooler than expected (Figure 12.3). This distinct seasonal pattern coincides with the absence or presence of leaves on deciduous trees in the aspen forests of west central Canada. The spring and autumn warming is related to greater sensible heat flux when leaves are absent while the summer cooling is related to greater transpiration when leaves are present. A similar seasonal pattern does not occur in evergreen-dominated forests because of their low summer transpiration.

Because of the importance of foliage in regulating surface climate, improved representation of leaf area and phenology are being implemented in regional and global climate models. Several climate model studies have examined the sensitivity of climate to leaf area index (Chase *et al.* 1996; Bounoua *et al.* 2000; Buermann *et al.* 2001). In general, higher leaf area index increases evapotranspiration over vegetated regions in summer provided there is sufficient soil water. As a result, surface temperature cools and precipitation increases. Other studies used satellite observations to derive leaf area index and phenology (e.g., Figures 9.21, 9.22). In one such study, the satellite leaf area index was less than the climate model's prescribed leaf area (Buermann *et al.* 2001). This satellite data resulted in a warmer, drier climate that better matched observations.

Interactive models of leaf area index and phenology in which the amount of foliage and its phenology depend on temperature, precipitation, and plant productivity, which in turn depend on leaf area, are being included in the land models used with climate models. One such climate study with interactive leaves found increased air temperature and reduced evapotranspiration and precipitation over extratropical regions of the Northern Hemisphere in summer as result of lower leaf area (Dickinson *et al.* 1998). In the central Great Plains, interactive phenology for crops and grasses generally lowers leaf area compared with control simulations with prescribed leaf area and improves the simulated climate compared with observations (Lu *et al.* 2001; Tsvetsinskaya *et al.* 2001a,b). In particular, the phenology of crop growth has considerable effect on the warm season climate of the Great Plains (Tsvetsinskaya *et al.* 2001b). Lower leaf area early in the growing season warms surface air temperature by 1-4 °C in June and reduces atmospheric

moisture as a result of lower transpiration. Later in the growing season, during periods of drought, less leaf area as a result of stunted plant growth leads to more heating of the atmosphere, less water vapor, and less precipitation than with prescribed leaf area.

### 12.2.2 Stomatal physiology

In vegetated landscapes, the partitioning of net radiation into sensible and latent heat fluxes is regulated in part by canopy conductance. Studies of the physiological response of plants to short-term exposure to enhanced CO<sub>2</sub> concentrations routinely find reduced stomatal conductance and greater photosynthesis (Eamus and Jarvis 1989; Bazzaz 1990; Körner 1993b, 2000; Amthor 1995; McGuire *et al.* 1995; Curtis and Wang 1998; DeLucia *et al.* 1999; Gifford *et al.* 2000). The density of stomata declines with higher atmospheric CO<sub>2</sub> (Woodward 1987b, 1993b; Peñuelas and Matamala 1990; Beerling and Chaloner 1993; Beerling *et al.* 1998). For example, comparison of modern and historically preserved leaves reveals a decline in the density of stomata on leaf surfaces over the past 200 years (Figure 12.4) – a period in which atmospheric CO<sub>2</sub> increased greatly from pre-industrial values (Figure 4.18). A similar reduction in stomatal density has been observed over the past 30 000 years as atmospheric CO<sub>2</sub> increased from a glacial low (Van de Water *et al.* 1994). Such changes in stomatal density can be used to reconstruct past atmospheric CO<sub>2</sub> concentrations (McElwain *et al.* 1999; Wagner *et al.* 1999; Royer *et al.* 2001).

Climate model simulations in which stomatal conductance decreases with a doubling of atmospheric CO<sub>2</sub> routinely show a decrease in evapotranspiration, increase in sensible heat, and surface warming over large vegetated regions in summer (Henderson-Sellers *et al.* 1995; Pollard and Thompson 1995; Sellers *et al.* 1996a; Bounoua *et al.* 1999; Douville *et al.* 2000; Levis *et al.* 2000). The effects of increasing concentrations of atmospheric CO<sub>2</sub> on climate can be partitioned into radiative and physiological effects (Sellers *et al.* 1996a; Bounoua *et al.* 1999; Levis *et al.* 2000). Radiative effects consider only climate changes associated with altered atmospheric radiation (i.e., the greenhouse effect). Physiological effects are changes due to reduced stomatal conductance with higher atmospheric CO<sub>2</sub>. In general, the physiological effects of doubled CO<sub>2</sub> amplify the warming associated with the radiative effects of doubled CO<sub>2</sub> (Table 12.2). The radiative forcing generally increases evapotranspiration, warms surface temperature, and increases precipitation. The physiological forcing from reduced stomatal conductance reduces evapotranspiration and precipitation and further warms the surface.

### 12.2.3 Biogeography

Changes in ecosystem geography alter numerous surface properties such as albedo, roughness, stomatal physiology, leaf area index, and rooting depth and in doing so can alter climate. An extreme example of this is a study of the maximum effect of vegetation on global climate, assessed by comparing climate model simulations with a vegetated and bare planet (Betts 1999; Fraedrich *et al.* 1999; Kleidon *et al.* 2000). One study compared climate simulations with the extreme endpoints of land cover: a desert planet in the absence of vegetation and a green planet where all non-glaciated land is covered by forest (Fraedrich *et al.* 1999; Kleidon *et al.* 2000). The desert planet has no vegetation, high albedo, low surface roughness, and low soil water storage capacity. In contrast, the green planet is fully vegetated by trees with high leaf area index and has lower albedo, higher surface roughness, and greater soil water storage to sustain transpiration during dry periods. The hydrologic cycle over land is greatly intensified as a result of vegetation (Figure 12.5). Annual evapotranspiration in the green planet simulation more than triples compared with the desert planet while precipitation nearly doubles. This is a result of more absorbed radiation at the surface, which provides more energy for evapotranspiration, and large soil water storage, which sustains evapotranspiration throughout the year. Despite the increase in precipitation, annual runoff decreases by 25% because a greater portion is recycled as evapotranspiration and because of the greater soil water-holding capacity. Enhanced evapotranspiration over land reduces near-surface temperatures and moistens the atmosphere. The enhanced precipitation warms the middle and upper troposphere, which leads to associated changes in the intensity and position of the jet streams. The geographic extent of Köppen climate types shows the changes in climate arising from the desert and green planets. About one-quarter of the total land area has a different climate. The extent of tropical and arctic climates changes little. Most of the differences arise from a reduction in the area of arid climate and an increase in the area of temperate climate in the green planet compared with the desert planet. This indicates a change in climate from one that favors desert or grassland to one that favors forest.

More realistic vegetation changes occur regionally in response to gradients in soil water or temperature. In the tropics, the gradient from rainforest to deciduous forest to savanna to desert represents increasing aridity (Figures 10.38, 10.39). This gradient is not only a response to soil moisture but also feeds back to affect climate, especially precipitation. An example of this is in West Africa, where numerous

climate simulations have demonstrated that the expansion of grasses and shrubs into the Sahara Desert in response to increased rainfall feeds back to increase rainfall. Another example is the boreal forest-tundra ecotone. The transition from forest to tundra is related to cold temperature (Figures 10.38, 10.39). Numerous studies have found that the northward migration of trees in response to climate warming feeds back to accentuate the warming. These feedbacks are examined in more detail.

#### Boreal forest-tundra ecotone

A vast expanse of needleleaf evergreen, needleleaf deciduous, and broadleaf deciduous trees forms the boreal forest in interior Alaska, much of Canada, northern Europe, and Russia (Figure 10.29, color plate). The boreal forest is the northernmost forest, lying just south of the treeless tundra. Because of differences between boreal forest and tundra ecosystems in albedo, roughness, and the partitioning of energy into latent and sensible heat, the geographic extent of these ecosystems is an important regulator of global climate (Bonan *et al.* 1995; Chapin *et al.* 2000; Eugster *et al.* 2000).

One important difference among ecosystems is surface albedo when the ground is covered by snow (Leonard and Eschner 1968; Federer 1968, 1971; Robinson and Kukla 1984; McCaughey 1987; Kunkel *et al.* 1999b; Baldocchi *et al.* 2000). Fresh snow has a very high albedo, generally reflecting 80-90% of incident solar radiation (Table 8.1). Snow-covered ground reflects a lot of solar radiation and there is little energy to warm the surface. This is also true for short tundra vegetation, which is typically buried by snow. In contrast, trees protrude over the snow-covered ground. Foliage has a much lower albedo than snow, and dense canopies of leaves mask the high albedo of snow (Figure 8.17). Even deciduous trees absorb much of the incoming solar radiation because their twigs, branches, and stems have a lower albedo than the bright snow. This vegetation masking of snow albedo is seen locally in comparison of summer and winter albedos for various boreal ecosystems (Table 12.3). Treeless areas have a much higher albedo when snow is on the ground than do forests. Vegetation masking is also evident in satellite-derived maps of surface albedo during winter. Forested regions of northern Europe, Russia, and North America have a lower albedo, generally less than 0.4, than treeless regions to the north (Robinson and Kukla 1985).

Forest and tundra ecosystems differ not just in albedo. They also differ in how they partition net radiation into sensible and latent heat fluxes (Rouse 1984a,b,c; Lafleur *et al.* 1992, 1993, 1997; Lafleur and

Rouse 1995; Eugster *et al.* 2000). Throughout summer, tundra sites generally have higher latent heat flux and lower sensible heat flux compared with nearby forests. These differences are greatest when the ground is wet. The various types of ecosystems within the boreal landscape also differ in latent heat exchange (Table 12.4). Summertime evaporative fraction, expressed as a ratio of net radiation or available energy (net radiation minus soil heat flux) is largest over wetland and aspen forests where 61-76% of energy is dissipated as latent heat. Needleleaf forests, on the other hand, have evaporative fractions ranging from one-third to one-half of available energy. Needleleaf forests generally have low leaf area and narrow crowns, which allows more solar radiation to reach the ground where it drives heat exchange on the forest floor rather than in canopy. The low evaporative fraction is also related to the large canopy resistance of boreal needleleaf forests as a result of low leaf area, soil moisture deficit, or high vapor pressure deficit. In addition, low stomatal conductance due to low foliage nitrogen content and low photosynthetic capacity limits transpiration in boreal needleleaf forests (Sellers *et al.* 1997b; Baldocchi *et al.* 2000; Eugster *et al.* 2000). This is seen in the ratio of evapotranspiration to equilibrium evapotranspiration (Chapter 7), which declines as maximum canopy conductance decreases (Figure 12.6). Arctic and boreal ecosystems are generally drier than the peak value of 1.26 achieved for well-watered, closed canopy crops. Deciduous forest and tundra have latent heat fluxes comparable to equilibrium evapotranspiration, but needleleaf forests have a much lower ratio.

Because the boreal forest absorbs so much more solar radiation than tundra in winter and spring, it warms climate (Bonan *et al.* 1992; Thomas and Rowntree 1992; Chalita and Le Treut 1994; Douville and Royer 1996). Figure 12.7 shows results from one study that compared climate simulations with the boreal forest and with boreal forest replaced with tundra (Bonan *et al.* 1992). In January, temperatures for the region bounded by latitude 40° N and 70° N are 3-7 °C warmer in climate simulations with the boreal forest than without. The largest warming occurs in April, when the region between 50° N to 60° N is more than 11 °C warmer. The warming persists into summer (July) and autumn (October), when regions north of 45° N are 3-5 °C warmer with the boreal forest present than without. In these snow-free months, when there are much smaller differences in surface albedo, the warming reflects the influence of oceans. The warmer winter climate warms the Arctic and North Atlantic Oceans, which with their high heat capacity store the heat and distribute it throughout the year.

Such vegetation feedback on climate has been found at other periods in time. For example, climate was warmer than present during the late Cretaceous 66 million years ago when atmospheric CO<sub>2</sub> concentration was much higher than present (about 580 parts per million). Climate model simulations of the late Cretaceous show that the presence of high and middle latitude forests warm climate by reducing albedo compared with simulations without forests (Otto-Bliesner and Upchurch 1997). The warmer high latitude temperatures warm the adjacent ocean, delaying sea-ice formation, which further warms climate. Inclusion of northern forests results in a simulated climate that agrees better with reconstructions from fossil vegetation data, suggesting these forests were an important contributor to the warm climate of this period.

The forest-tundra ecotone may have played a role in the onset of glaciation (Gallimore and Kutzbach 1996; de Noblet *et al.* 1996). At the onset of the last glaciation 115 000 years ago, Northern Hemisphere summer solar radiation was reduced by 8% compared with modern values and atmospheric CO<sub>2</sub> was 267 ppm. Simulations with a climate model (Gallimore and Kutzbach 1996) show that the combination of these two climate forcings cool high latitude land temperatures by about 5 °C and increase the duration of snow cover by about one month compared with the modern climate (Table 12.5). This cooling reflects feedbacks among water vapor, clouds, snow, and sea ice as a result of the reduced solar radiation and atmospheric CO<sub>2</sub>. Observational evidence shows widespread changes in vegetation 115 000 years ago. High latitude forests died back and were replaced with tundra and cold grassland-like vegetation. Additional climate simulations examined the impact of increases in surface albedo associated with the expansion of tundra. Increases in surface albedo associated with a modest expansion of tundra cools climate by an additional 2.9 °C in North America and 2.8 °C in Eurasia and increases the duration of snow on the ground by 18 days. A more extensive tundra results in a catastrophic climate change, with summer temperatures cooling 17-18 °C and snow cover persisting almost 3 months longer compared with no changes in tundra. The longer snow cover arises from increased duration of winter snow pack and occurrence of snowfall in summer. Regions of permanent snow cover occur, indicating the onset of glaciation. These results suggest that expansion of tundra, and the associated higher albedo, was important to initiate the last ice age.

The location of the treeline separating forest and tundra changed over the past 18 000 years with the transition from glacial to interglacial (Figure 11.24, color plate). At the height of the last glaciation 18 000 to 21 000 years ago, much of the northern high latitudes was covered by glaciers and the treeline was several hundred kilometers south of its current location. Climate model simulations show the reduction in forest cover at middle to high latitudes exposed the high albedo of the winter and spring snow cover, reducing the absorption of solar radiation and reinforcing the cold climate (Crowley and Baum 1997; Kubatzki and Claussen 1998; Levis *et al.* 1999a). As climate warmed and the glaciers retreated northwards, the treeline migrated northwards. The decrease in surface albedo caused by the northward expansion of the boreal forest in response to the climate warming accentuated the warming. The period some 6000 years ago was a particularly noteworthy time (TEMPO 1996; Prentice *et al.* 2000b). Changes in Earth's orbital geometry resulted in more solar radiation than present during summer in the Northern Hemisphere (Figure 4.3), creating a warmer climate than present. Boreal forests extended north of the modern treeline in response to this warm climate. A climate model simulation shows that these changes in orbital geometry warm high latitude land between 60° N and 90° N by 1.8 °C in the annual mean (Foley *et al.* 1994). A positive snow-ice albedo feedback related to decreases in snow cover over land and Arctic sea ice contributes to this warming. An additional simulation shows that the northward expansion of forest gives an additional warming of 1.6 °C, which is comparable to that of the orbital forcing alone. This additional warming is larger in spring (4 °C) than in other seasons (1 °C).

These climate model simulations show amplification by vegetation of the climate response to changes in solar radiation or atmospheric CO<sub>2</sub>. Historically, ecologists have thought that climate determines the extent and nature of the boreal forest by affecting tree growth and reproduction (Larsen 1980; Bonan and Shugart 1989; Shugart *et al.* 1992). For example, the northern and southern boundaries of the boreal forest are correlated with the July 13 °C and 18 °C isotherms, respectively. However, these correlations likely reflect the outcome of coupled climate-ecosystem dynamics in which the geographic extent of the boreal forest affects and is affected by climate (Bonan *et al.* 1992). In addition, the northern and southern boundaries of the North American boreal forest are correlated with the mean summer and winter positions of the Arctic front (Bryson 1966). However, the forest-tundra ecotone may itself control the position of this front in summer due to the large contrast in albedo, roughness, and energy exchange, which results in

strong heating of the atmosphere over forest and weaker heating over tundra (Hare 1968; Pielke and Vidale 1995; Lynch *et al.* 2002). This creates a warm surface, dry near-surface air, and a deep planetary boundary layer during the course of a typical summer day. The deep boundary layer may feed back to limit evapotranspiration by entraining a large amount of dry air, which decreases stomatal conductance by increasing the vapor pressure deficit and forcing stomata to close (Sellers *et al.* 1997b; Baldocchi *et al.* 2000; Eugster *et al.* 2000).

#### Green Sahara Desert

The Sahara Desert in North Africa is another example of the importance of vegetation to climate. In the current climate, precipitation is sparse, the soil is dry, and desert is the dominant land cover. These conditions reinforce the dry climate (Charney 1975; Charney *et al.* 1975). Under desert conditions, more solar radiation is reflected to space because of the high soil albedo. The decreased net radiation at the surface cools the atmosphere, which promotes subsidence of the air aloft. Subsidence decreases cloud formation and convection, leading to less rainfall.

About 6000 years ago, this region received much more precipitation than it currently does. The wetter climate was caused by changes in Earth's orbit, which increased summer solar radiation, heated the land, and strengthened the African summer monsoon (Kutzbach and Otto-Bliesner 1982; Street-Perrott and Perrott 1993; Kutzbach and Liu 1997; Jolly *et al.* 1998a; Braconnot *et al.* 2000). As a result of the wetter climate, grasses and shrubs covered much of the modern Sahara Desert (Hoelzmann *et al.* 1998; Jolly *et al.* 1998a,b; Prentice *et al.* 2000b). Most climate model simulations of this period underestimate the climate change compared with paleoclimate reconstructions. This weak response to orbital forcing is attributed to ecosystem feedbacks. Climate model experiments show that expansion of grasses and shrubs into the desert in response to enhanced summer precipitation results in more precipitation (Kutzbach *et al.* 1996; Claussen and Gayler 1997; Texier *et al.* 1997; Broström *et al.* 1998; Ganopolski *et al.* 1998; Brovkin *et al.* 1998; Claussen *et al.* 1999; Joussaume *et al.* 1999; de Noblet-Ducoudré *et al.* 2000). The decreased surface albedo, increased soil water-holding capacity, and other changes as the desert soil was vegetated likely caused more water to be returned to the atmosphere during evapotranspiration, creating a cloudier, more humid, and wetter climate.

Climate model simulations shown in Table 12.6 illustrate the effects of altered solar radiation, vegetation, and soils on the climate of North Africa 6000 years ago (Kutzbach *et al.* 1996). A control simulation was performed for modern conditions. A second simulation utilized the orbital geometry of 6000 years ago but with modern desert vegetation. In a third simulation for 6000 years ago, vegetation between latitudes 15° N and 30° N was changed from desert to grassland. An additional simulation changed the desert soil to loam, increasing soil water-holding capacity and reducing soil albedo, to reflect a more organic grassland soil. The greater summer solar radiation due to orbital geometry increases precipitation between latitude 15° N and 22° N by 12% compared with the control simulation. Evapotranspiration increases because of more energy at the surface and because the soils are wetter. Replacement of desert with grassland vegetation and loamy soil enhances the summer monsoon, and the climatic response equals or exceeds that of the orbital forcing alone. Net radiation increases as a result of reduced albedo, latent heat increases, and the near-surface atmosphere moistens. Precipitation increases by 18% in the grassland simulation and by 28% in the grassland and soil simulation compared with the control simulation. The increase in precipitation reduces the area of the Sahara by 11% due to orbital forcing alone and by 20% due to feedback from vegetation and soil changes.

In this region, ecosystem feedbacks enhance the orbitally induced summer monsoon. Inclusion of vegetation changes in climate models results in a better match of simulated climate with paleodata, suggesting vegetation feedbacks are important in explaining the climate of this era. The consensus is that the climate of North Africa 6000 years ago cannot be realistically simulated without vegetation feedback on climate.

### **12.3 Carbon cycle**

Terrestrial ecosystems are coupled to climate through the carbon cycle (Figures 4.11, 10.47). The influence of terrestrial ecosystems on atmospheric CO<sub>2</sub> can be seen at several timescales: seasonal-to-interannual as a result of changes in ecosystem metabolism; decadal-to-century as a result of land use and forest stand dynamics; and centuries-to-millennia as a result of climate change and resulting changes in ecosystem geography.

### 12.3.1 Ecosystem metabolism

Metabolic activity by terrestrial ecosystems during the growing season is seen in the concentration of CO<sub>2</sub> in the atmosphere. Atmospheric CO<sub>2</sub> concentrations vary by several parts per million during the year (Figure 10.49). In the Northern Hemisphere, high concentrations occur in winter, when plants are seasonally dormant but carbon is still lost during autotrophic (plant) and heterotrophic (microbial) respiration. Low concentrations occur in summer, when photosynthetic uptake exceeds respiration loss. The annual amplitude of the atmospheric CO<sub>2</sub> cycle (i.e., the difference between maximum and minimum concentrations) is greatest in high latitudes of the Northern Hemisphere and declines with latitudes closer to the equator. In the Southern Hemisphere, where there is less land, oceans dominate atmospheric CO<sub>2</sub> exchange and there is little seasonal variation in atmospheric CO<sub>2</sub>.

Modeling studies of ecosystem CO<sub>2</sub> fluxes and atmospheric transport of CO<sub>2</sub> suggest that the annual amplitude in the Northern Hemisphere primarily reflects the seasonality of net ecosystem production by terrestrial ecosystems (D'Arrigo *et al.* 1987; Randerson *et al.* 1997). Randerson *et al.* (1997) found that north of the equator the contribution of terrestrial ecosystems to the annual amplitude ranges from 71% to 92%, with higher contributions at high latitudes (Figure 12.8). Tundra, boreal forest, mixed forest, and other northern ecosystems cause most of the seasonal variation in atmospheric CO<sub>2</sub> in the Northern Hemisphere (Figure 12.9). In these latitudes, the timing of photosynthesis and respiration is asynchronous, with photosynthesis restricted to a short growing season while respiration occurs year-round. Boreal forest has the greatest influence at high latitudes in the Northern Hemisphere. North of latitude 55° N, boreal forest accounts for 34-42% of the terrestrial ecosystem signal. Even at Mauna Loa, boreal forest contributes 24% of the terrestrial component. Grassland also has a large influence, becoming increasingly important in middle and tropical latitudes. Overall, croplands account for 20% of the terrestrial signal in middle latitudes of the Northern Hemisphere, with lowest contribution in northern latitudes. Deciduous forests generally contribute between 10% and 18% of the terrestrial component in middle to high latitudes. Tropical forests contribute minimally (less than 5%) to the terrestrial component of the annual amplitude at middle and high latitudes in the Northern Hemisphere. Their maximum contribution (18%) occurs in the tropics. In the tropics, decreased seasonality of ecosystem processes and a closer match between net primary production and decomposition reduce the annual amplitude.

Temporal changes in the amplitude and seasonality of the atmospheric CO<sub>2</sub> cycle, although also reflecting oceanic carbon exchange in relation to climate variability such as El Niño, are important indicators of changes in the metabolic activity of terrestrial ecosystems (Rayner and Law 1999; Holmén 2000; Houghton 2000a; Prentice *et al.* 2000a). For example, the annual amplitude of atmospheric CO<sub>2</sub> concentration has increased since the early 1960s by 20% at Mauna Loa, Hawaii, and 40% at Point Barrow, Alaska (Keeling *et al.* 1996). This reflects a stimulation of metabolic activity by terrestrial ecosystems with either greater CO<sub>2</sub> drawdown during the growing season or greater CO<sub>2</sub> efflux during the dormant season (or both). Northern ecosystems, because of their large role in the annual cycle of atmospheric CO<sub>2</sub>, are the likely region of such a change. Indeed, greater summertime uptake of CO<sub>2</sub> by northern ecosystems is consistent with the reported large middle to high latitude terrestrial carbon storage needed to balance the global carbon budget (Figure 4.11).

### 12.3.2 Terrestrial carbon storage

Currently, about 56% of the carbon emitted annually during the combustion of fossil fuels remains in the atmosphere. About 37% is taken up by oceans. Terrestrial ecosystems are thought to absorb the remaining 7%. This net terrestrial storage is a balance between carbon emission from changes in land use (equivalent to 33% of annual fossil fuel emission) and a residual carbon uptake (40% of fossil fuel emission). The magnitude, location, and causes of this terrestrial storage are uncertain, but it likely occurs in middle latitudes of the Northern Hemisphere. Several mechanisms can account for this increase in carbon storage (Houghton *et al.* 1998; Lloyd 1999; Prentice *et al.* 2000a). It may reflect changes in ecosystem metabolism as a result of climate variability or enhanced plant production due to stimulation of photosynthesis by rising concentrations of atmospheric CO<sub>2</sub> or due to deposition of nitrogen from industrial pollution. It may also be caused by regrowth of forests following the abandonment of farmland.

#### Ecosystem metabolism

Changes in carbon storage are a consequence of shifts in the balance of carbon uptake during gross primary production and carbon loss during autotrophic and heterotrophic respiration. These processes differ in their sensitivity to climate. Photosynthesis generally has a parabolic response to temperature, decreasing above and below some optimal temperature (Figure 9.6), while respiration increases with

warmer temperatures (Figures 6.21, 9.18). Global analyses of atmospheric CO<sub>2</sub>, temperature, and vegetation production (NDVI) show significant interrelationships, indicating modulation of atmospheric CO<sub>2</sub> by terrestrial ecosystems in response to climate variability (Braswell *et al.* 1997). Historical climate variability that favors net primary production over decomposition may lead to enhanced carbon storage by terrestrial ecosystems. Terrestrial ecosystem models have shown increased carbon accumulation when forced with the observed climate over the past several decades (Dai and Fung 1993; Post *et al.* 1997). Such storage can account for a substantial portion of the required Northern Hemisphere carbon uptake. Other studies also highlight the importance of climate variability in regulating the carbon cycle. For example, one study found tropical ecosystems in the Amazonian region of South America to be a source of carbon to the atmosphere during El Niño years, when hot, dry weather in the region reduces net primary production and increases decomposition (Tian *et al.* 1998). In other years, these ecosystems gain carbon. Another modeling study suggests reduced carbon storage in United States ecosystems as a result of climate variability (Tian *et al.* 1999). Dry periods during the 1930s and 1950s (Figures 3.4, 3.6) are largely responsible for less carbon storage. Another modeling study found terrestrial ecosystems in the conterminous United States to have a small net carbon gain over the period 1980 to 1993, but interannual climate variability switches them from net storage to net efflux from year to year (Schimel *et al.* 2000).

Greater carbon storage in Northern Hemisphere terrestrial ecosystems could also be due to changing climate that alters ecosystem processes. For example, a longer growing season as a result of warmer temperatures enhances carbon uptake, and modeling studies in temperate and boreal forests show greater net primary production over the past several decades as a result of a longer growing season. (White *et al.* 1999; Keyser *et al.* 2000). Modeling studies suggest increased net ecosystem production during spring and early summer is required to match the observed changes in the annual cycle of atmospheric CO<sub>2</sub> between 1980 and 1997 (Randerson *et al.* 1999). Satellite observations show the photosynthetic activity of terrestrial ecosystems between latitudes 45° N and 70° N increased from 1981 to 1991 in association with marked springtime warming over the same period that increased the growing season length by one to two weeks (Myneni *et al.* 1997).

Studies of the physiological response of plants to short-term exposure to enhanced CO<sub>2</sub> concentrations routinely find greater photosynthesis (Eamus and Jarvis 1989; Bazzaz 1990; Körner 1993b,

2000; Amthor 1995; McGuire *et al.* 1995; Curtis and Wang 1998; DeLucia *et al.* 1999; Gifford *et al.* 2000). This enhancement is greatest for plants with the C<sub>3</sub> photosynthetic pathway because of the low affinity of rubisco for CO<sub>2</sub> and high rates of photorespiration. Plants utilizing the C<sub>4</sub> photosynthetic pathway have less response to CO<sub>2</sub> because of their low rates of photorespiration. This short-term photosynthetic enhancement may decline over time as plants acclimate to higher CO<sub>2</sub>. Ecosystem models forced with higher CO<sub>2</sub> concentrations routinely show increased photosynthesis and carbon storage in response to CO<sub>2</sub> fertilization (Kohlmaier *et al.* 1987; Bonan 1992; Friedlingstein *et al.* 1995a; King *et al.* 1995; McGuire *et al.* 1997; Post *et al.* 1997; Cao and Woodward 1998a,b; Tian *et al.* 1998, 1999; Kicklighter *et al.* 1999b; Schimel *et al.* 2000; Gifford *et al.* 2000). This storage can account for a large portion of the required Northern Hemisphere carbon uptake. The potential for increased carbon storage as a result of higher atmospheric CO<sub>2</sub> is modulated by climate variability. Model studies show greater carbon uptake due to climate variability when CO<sub>2</sub> fertilization of photosynthesis is included (Post *et al.* 1997; Cao and Woodward 1998b; Tian *et al.* 1998, 1999; Schimel *et al.* 2000). For example, modeling studies of United States ecosystems indicate a gain of carbon between 1980 and 1993 as a result of CO<sub>2</sub> fertilization and climate variability (Schimel *et al.* 2000). The bulk of this increase is due to higher atmospheric CO<sub>2</sub>, with wide fluctuations from year to year of about 100% of the long-term mean due to climate variability. Although models show increased carbon storage from CO<sub>2</sub> fertilization, observations are less clear. For example, enrichment of atmospheric CO<sub>2</sub> concentrations by 200 ppm above ambient in loblolly pine forests in North Carolina reveals limited long-term net carbon sequestration in forest soils (Schlesinger and Lichter 2001). Much of the increased photosynthesis is allocated to foliage, which decomposes faster than wood. Low nitrogen availability also limits CO<sub>2</sub> fertilization in these forests (Oren *et al.* 2001).

In most terrestrial ecosystems, net primary production is limited by nitrogen availability. Nitrogen is deposited in terrestrial ecosystems through precipitation or dry deposition, and additional nitrogen inputs can enhance carbon storage by increasing net primary production. This storage is realized primarily in forest ecosystems as accumulation of either wood in living trees or soil organic matter from increased litterfall. Nitrogen is emitted to the atmosphere from industry, agriculture, and other human activities. For example, the burning of fossil fuels adds about  $20 \times 10^{12}$  g N per year when nitrogen in industrial and automotive emissions is deposited onto land through precipitation or dry deposition (Galloway *et al.* 1995;

Vitousek *et al.* 1997a). Greatest deposition occurs in industrialized regions such as eastern United States, Europe, and China (Holland *et al.* 1997). Widespread emission of nitrogen into the atmosphere and its subsequent deposition onto terrestrial ecosystems can reduce nitrogen limitation of net primary production and thus contribute to greater carbon storage (Peterson and Melillo 1985; Schindler and Bayley 1993; Hudson *et al.* 1994; Townsend *et al.* 1996; Holland *et al.* 1997; McGuire *et al.* 1997). Much of the evidence for this is related to the high C:N ratio of plant material, which indicates that large amounts of carbon can be assimilated per unit increase in nitrogen.

Ecosystem models confirm the potential for increased carbon storage as a result of nitrogen fertilization (Townsend *et al.* 1996; McGuire *et al.* 1997), but observational studies are less clear (Nadelhoffer *et al.* 1999). Nitrogen cycling does, however, play an important role in the response of forests to increased atmospheric CO<sub>2</sub> through complex interactions among leaf nitrogen concentration, plant growth, carbon allocation, and higher atmospheric CO<sub>2</sub> that alter decomposition and nitrogen mineralization (Schimel *et al.* 1994; McGuire *et al.* 1995, 1997; Curtis and Wang 1998; Körner 2000; Oren *et al.* 2001). For example, increased nitrogen availability favors allocation of carbon to aboveground biomass to capture more light and CO<sub>2</sub> while increased atmospheric CO<sub>2</sub> enhances belowground allocation. This influences decomposition because of the lower chemical quality of woody biomass litter compared with fine root litter. In addition, elevated CO<sub>2</sub> increases the C:N ratio in plant biomass, which then decomposes more slowly because of its poor litter quality.

#### Disturbance and succession

Disturbances from fires, insect attacks, windthrow and human uses of land play an important role in the global carbon cycle. Human uses of land such as the clearing of forest for agriculture are particularly important (Houghton *et al.* 1983, 1985, 1998, 2000a,b; Houghton 1991, 1995, 1999, 2000a,b; Houghton and Hackler 1999, 2000). Much of the carbon stored in trees and soils is released to the atmosphere when forests are cleared and land cultivated. Some of this carbon is released rapidly when plant debris is burned during land clearing. Some is released slowly as dead plant material decomposes. Between 1850 and 1990, changes in land use worldwide are thought to have added  $124 \times 10^{15}$  g of carbon to the atmosphere (Houghton 1999). This is about one-half as much as the carbon released during the combustion of fossil

fuels over the same period. Most of this release ( $108 \times 10^{15}$  g) occurred during clearing of forests for agriculture, with tropical forests accounting for two-thirds and the rest from temperate and boreal forests. Another  $16 \times 10^{15}$  g were released to the atmosphere as a result of cultivating middle latitude grassland soils. Over the period 1980 to 1995, clearing of forested lands for agriculture released  $2 \times 10^{15}$  g of carbon each year (Houghton 1999). Almost all of the emission of carbon attributable to land use change during this period was from tropical deforestation.

Conversely, the regrowth of forests following disturbance represents a withdrawal of carbon from the atmosphere and storage in woody biomass and soil. Changes in forest ecosystems in response to past land management and uses including timber harvesting, abandonment of agricultural land, and fire suppression are emerging as additional controls of Northern Hemisphere carbon uptake (Harmon *et al.* 1990; Kauppi *et al.* 1992; Dixon *et al.* 1994; Kurz *et al.* 1995; Phillips *et al.* 1998; Brown and Schroeder 1999; Kurz and Apps 1999; Houghton *et al.* 1999; Schulze *et al.* 1999; Marland 2000; Chen *et al.* 2000; Caspersen *et al.* 2000; Schimel *et al.* 2000). In particular, old-growth forests store much more carbon than young stands. Analyses of carbon storage based on forest inventory data suggest Canadian forest ecosystems absorbed about  $0.2 \times 10^{15}$  g carbon per year between 1920 and 1980 (Kurz *et al.* 1995; Kurz and Apps 1999). This was primarily a result of decreased fire frequency that shifted the age structure of Canadian forests to older stands. The magnitude of annual carbon uptake decreased in the 1980s when increased fires released carbon to the atmosphere during combustion and decreased average stand age. Another analysis partitioned the causes of the Canadian carbon storage into stimulated ecosystem metabolism from CO<sub>2</sub> fertilization, atmospheric nitrogen deposition, and climate variability and to regrowth following fire, insect-induced mortality, and harvesting (Chen *et al.* 2000). Forest regrowth of disturbed areas stored an amount of carbon that was comparable to non-disturbance factors and accounted for almost one-half of the carbon gain. Analyses of Siberian forests provide a similar conclusion (Schulze *et al.* 1999). Maintaining old-growth forests contributes more to net ecosystem carbon uptake than reforestation following fire or logging.

Interactions between disturbance and carbon storage are complex. In high latitudes, fires change ecosystem composition from dominance by evergreen plants to deciduous plants. Deciduous plants generally have higher productivity than evergreens, and their litter decomposes more readily. As a result,

recently disturbed ecosystems dominated by deciduous plants have enhanced summer carbon uptake and winter loss while undisturbed ecosystems dominated by evergreens have reduced seasonal variation. An increase in the frequency and extent of fires, as has been observed, may contribute to the increased annual amplitude of atmospheric CO<sub>2</sub> by creating a greater area of disturbed ecosystems in the landscape (Zimov *et al.* 1999).

In the conterminous United States, land use is likely to be a dominant factor governing the rate of carbon accumulation in terrestrial ecosystems (Brown and Schroeder 1999; Houghton *et al.* 1999; Caspersen *et al.* 2000; Schimel *et al.* 2000; Pacala *et al.* 2001). This is especially true in eastern United States, where there has been widespread reforestation of abandoned farmland during the 1900s. One analysis shows an overall net release of carbon to the atmosphere from United States ecosystems during the period 1700 to 1990 due to conversion of forest to agricultural land and cultivation of prairie soil (Houghton *et al.* 1999, 2000a; Houghton and Hackler 2000). However, United States ecosystems have accumulated carbon since 1945 largely as a result of fire suppression and forest regrowth on abandoned farmlands. During the 1980s, United States ecosystems accumulated carbon at a rate of 0.15 to  $0.35 \times 10^{15}$  g C per year. This is equivalent to 10-30% of United States fossil fuel emissions over the same period. Another analysis found larger carbon uptake by United States ecosystems in the 1980s ( $0.30$  to  $0.58 \times 10^{15}$  g C yr<sup>-1</sup>), in part by including carbon accumulation outside the forest sector which amounts to about one-half of the total (Pacala *et al.* 2001).

### 12.3.3 Biogeography

Over long periods of centuries to millennia, climate change affects the global carbon cycle as a result of changing ecosystem structure and geography. Terrestrial ecosystems store large amounts of carbon in plant biomass and as soil organic matter (Tables 10.3, 10.4). Temperature and precipitation are important determinants of ecosystem geography (Figures 10.38, 10.39) and long-term climate changes alter the geographic extent of various ecosystems. These changes in ecosystem geography are likely to alter the storage of carbon by terrestrial ecosystems. For example, tropical rainforests store  $25\ 400$  g C m<sup>-2</sup> in plant biomass and soil while tropical savannas store only  $5700$  g C m<sup>-2</sup>. A drier climate that replaces tropical forests with savanna results in an efflux of carbon to the atmosphere.

Studies of the last glacial maximum show arid ecosystems such as desert, desert scrub, and grassland were much more extensive 18 000 years ago than now (Adams *et al.* 1990; Prentice and Fung 1990; Friedlingstein *et al.* 1992, 1995b; Prentice *et al.* 1993). Boreal and temperate forests were less extensive. Dry woodlands, savanna, and tropical montane forests encroached into present day tropical rainforests. Ecosystems that prevailed under the cooler, drier climate of the last glacial maximum have low carbon storage per unit area. As a result, terrestrial ecosystems stored less carbon at this time than at present. For example, one study (Prentice *et al.* 1993) estimated that terrestrial carbon storage was  $300 \times 10^{15}$  g C less than present (Table 12.7). Large carbon losses occurred with a 5 million km<sup>2</sup> reduction in the area of temperate forests and 11 million km<sup>2</sup> loss of boreal forest.

Ecological models routinely show large changes in terrestrial ecosystems as a result of climate changes arising from a doubling of atmospheric CO<sub>2</sub> from pre-industrial levels (Emanuel *et al.* 1985; Solomon 1986; Pastor and Post 1988; Prentice *et al.* 1991b; T. Smith *et al.* 1992a,b; Neilson and Marks 1994; Parton *et al.* 1995; Starfield and Chapin 1996; Walker and Steffen 1996; Watson *et al.* 1996; Van Minnen *et al.* 2000; Coops and Waring 2001). Changes in community composition and ecosystem structure are particularly prominent along ecotones. Boreal forests expand into tundra with a warmer climate. Forests along the prairie-forest ecotone die back in a drier climate and are replaced with grasses. Tropical rainforests die back and tropical seasonal forests and savannas expand with a drier climate. With a wetter climate, forests expand into areas currently occupied by dry forests, grasslands, and savanna. Table 12.8 illustrates results from one such study that utilized the Holdridge life-form classification (Figure 10.39) to predict changes in ecosystem geography with four scenarios of climate change (T. Smith *et al.* 1992a). In this study, the geographic extent of tundra and desert decreases in all climate change scenarios. Grasslands and forest expand, though there is disagreement on the fate of mesic forests. As with the last glacial maximum, changes in carbon storage can be assessed by assigning each ecosystem an average carbon density. In this study, global carbon storage is estimated to increase by  $8-180 \times 10^{15}$  g C. The decline in tundra area is primarily a result of northward expansion of boreal forest in a warmer climate. This is associated with a large increase in aboveground carbon pools. The decline in desert area arises from a shift from polar desert to tundra with a warmer, wetter high latitude climate and from desert to grassland with a wetter temperate and tropical climate. This represents a net increase in carbon storage. Grasslands also

expand where forests die back as a result of a drier climate. This transition represents a source of carbon to the atmosphere as grasslands sequester less carbon than forests. Greater precipitation in grassland areas increases the extent of dry forest. However, the greatest gain in dry forests is in subtropical and tropical regions where decreased rainfall causes mesic forests to die back. Carbon storage decreases with the transition from mesic to dry forest. The major gain in mesic forest area is due to expansion of boreal forest into tundra. In some climate changes, this gain is more than offset by loss of mesic forest in the subtropics and tropics.

In contrast to this simple model of potential carbon storage, sophisticated models of ecosystem processes have been used to study changes in terrestrial carbon storage with a warmer climate (Schimel *et al.* 1990; Melillo *et al.* 1993; VEMAP 1995; Cao and Woodward 1998a,b; McGuire *et al.* 2000; Friedlingstein *et al.* 2001). In these models, net ecosystem carbon storage is a balance between carbon uptake during net primary production and carbon loss during decomposition. These two ecosystem functions have different sensitivity to climate. For example, it is widely expected that rates of decomposition will increase with a warmer climate, leading to less carbon storage. Indeed, the sensitivity of soil carbon, which is a large component of the global terrestrial carbon stores, to climate is an important determinant of terrestrial feedback on the carbon cycle (Schlesinger *et al.* 2000). It is estimated that warming reduces soil carbon storage by about  $3 \times 10^{15}$  g C per degree in the tropics and  $8 \times 10^{15}$  g °C<sup>-1</sup> in middle to high latitudes for a global loss of  $11 \times 10^{15}$  g °C<sup>-1</sup> excluding arid and peat soils (Schimel *et al.* 1994). These losses occur over a period of tens of years in the tropics to more than 100 years in high latitudes. However, net primary production is likely to increase with a warmer, wetter climate and due to CO<sub>2</sub> fertilization. Increased litterfall as a result of greater vegetation production is likely to increase the storage of carbon in soil (Janssens *et al.* 2001). Moreover, increasing atmospheric CO<sub>2</sub> reduces the effect of warming on soil carbon loss because CO<sub>2</sub> fertilization increases the C:N ratio of plant biomass, retarding decomposition (Schimel *et al.* 1994). As a result, carbon storage may increase with global warming. However, terrestrial ecosystems may initially be a transient source of carbon to the atmosphere for several decades. Net release as a result of dieback and fires may initially offset carbon gains (Smith and Shugart 1993; Van Minnen *et al.* 2000). Indeed, the rate at which climate changes relative to the rate at which new species can colonize an area is likely to be a key determinant of vegetation change and carbon storage.

In addition to altered temperature and precipitation as a result of the radiative effects on climate, atmospheric CO<sub>2</sub> alters plant physiology and the competitive balance among plants. Although laboratory studies show that photosynthesis increases with higher CO<sub>2</sub> concentrations, less is known about the long-term acclimation of plants to higher CO<sub>2</sub> levels, how CO<sub>2</sub> affects carbon allocation, nutrient availability, and nutrient use efficiency, how physiological changes affect stand structure and composition, and whether growth increases will be realized in the field where temperature, soil water, and nutrients limit plant growth (Eamus and Jarvis 1989; Bazzaz 1990, 1996; Körner 1993b, 2000; Amthor 1995; McGuire *et al.* 1995; Curtis and Wang 1998; DeLucia *et al.* 1999; Gifford *et al.* 2000). Even seed production and seedling recruitment may change with higher CO<sub>2</sub> levels. A study of a loblolly pine plantation growing under enriched atmospheric CO<sub>2</sub> found that after four years trees were twice as likely to be reproductively mature and produced three times more cones and seeds as trees growing under ambient CO<sub>2</sub> concentration (LaDeau and Clark 2001). This increased fecundity arises from earlier reproductive maturation and higher proportionate allocation to reproduction.

Evidence suggests that the historical changes in the concentration of CO<sub>2</sub> in the atmosphere has altered ecosystem geography by changing the competitive balance among C<sub>3</sub> and C<sub>4</sub> plants. Photosynthesis in C<sub>3</sub> plants is greatly inhibited at low CO<sub>2</sub> concentrations, but increases along with water-use efficiency with higher CO<sub>2</sub>. In contrast, the C<sub>4</sub> photosynthetic pathway, with the high affinity of PEP carboxylase for CO<sub>2</sub>, low photorespiration, and spatial separation of mesophyll and bundle-sheath cells, is advantageous at low atmospheric CO<sub>2</sub> but is more expensive energetically compared with the less efficient C<sub>3</sub> metabolism at high CO<sub>2</sub> levels. Paleocological data from the last glacial maximum suggest that the low atmospheric CO<sub>2</sub> at this time favored C<sub>4</sub> grasses in the tropics at the expense of C<sub>3</sub> trees (Street-Perrott *et al.* 1997; Jolly and Haxeltine 1997). Higher atmospheric CO<sub>2</sub> levels since then have allowed trees to gain dominance at the expense of C<sub>4</sub> grasses.

The addition of nitrogen can also change the competitive balance among species. A 12-year study in temperate grasslands found that nitrogen fertilization greatly alters community composition and ecosystem functions (Tilman 1987, 1996; Inouye and Tilman 1988, 1995; Wedin and Tilman 1996). Native C<sub>4</sub> grasses decline in abundance with additional nitrogen while weedy C<sub>3</sub> grasses gain dominance (Figure 12.10). While nitrogen fertilization enhances net primary production, ecosystem carbon storage decreases

with additional nitrogen. The shift in community composition from  $C_4$  species to  $C_3$  decreases the C:N ratio of plant material. Detritus decomposes rapidly because of its better chemical quality so that the overall ability to sequester carbon diminishes. This study shows that nitrogen-induced shifts in species composition limit the ability of temperate grasslands to serve as significant long-term carbon stores.

## 12.4 Mineral dust

An estimated  $1500 \times 10^{12}$  g of mineral dust are mobilized by winds each year, mostly in arid regions (Table 4.4). Substantial amounts of this dust are carried over great distances in the atmosphere (Figure 6.10). The Sahara Desert is the single largest source of dust to the atmosphere. Large quantities of dust are carried north across the Mediterranean Sea to Europe and west across the North Atlantic Ocean (Figure 12.11). Annually, about  $170 \times 10^{12}$  and  $25 \times 10^{12}$  g of Saharan dust are deposited to the North Atlantic Ocean and Mediterranean, respectively. Trans-Atlantic transport of dust from North Africa to South America, the Caribbean, and southeastern United States by the northeasterly trade winds in plumes extending over several hundred kilometers in latitude at altitudes up to 5-7 km is common (Prospero *et al.* 1981, 1987, 1996; Prospero and Nees 1986; Prospero 1996, 1999). Some  $5 \times 10^{12}$  g of dust are transported across the Atlantic to the Caribbean in this manner (Figure 12.11). Asia, especially the deserts of Mongolia and China, is another large source region of dust. These deserts contribute significantly to the dust found in Greenland and throughout the Arctic because they are the most northerly major arid areas, their high altitude facilitates uplifting of dust into long-range transport winds, and they are located in a system of prevailing westerly winds (Svensson *et al.* 2000).

Mineral dust aerosols influence climate through a variety of radiative and biogeochemical feedbacks. Dust aerosols reduce surface net radiation by absorbing and reflecting solar radiation, but also contribute to warming by trapping in the atmosphere longwave radiation emitted from the surface (Overpeck *et al.* 1996; Tegen *et al.* 1996; Miller and Tegen 1998, 1999). Dust aerosols are an important climate forcing over the tropical and subtropical North Atlantic, where the concentration of mineral dust from the Sahara is high (Li *et al.* 1996). Over snow- and ice-covered surfaces, dust reduces the backscattering of solar radiation compared with the high albedo of snow and ice and may warm climate (Overpeck *et al.* 1996). Mineral dust aerosols also carry nutrients. Some of the nutrients deposited into the

North Pacific are derived from dust from desert regions of Asia (Duce *et al.* 1980; Prospero and Savoie 1989). About  $6 \times 10^{12}$  g of iron (Fe) and  $0.2 \times 10^{12}$  g of phosphorus (P) are deposited annually to the North Atlantic from Saharan dust, assuming a composition of 3.5% Fe and 0.105% P (Prospero 1996; Prospero *et al.* 1996). Deposition of dust to oceans supplies micronutrients, especially iron, to ocean ecosystems, which may stimulate carbon uptake by phytoplankton (Duce *et al.* 1991; Falkowski *et al.* 1998; Fung *et al.* 2000). In doing so, the net primary production of oceans is linked to the biogeochemistry of terrestrial ecosystems.

Trans-Atlantic transport of dust from North Africa to the Caribbean and South America influences soil biogeochemistry. Saharan dust has contributed significant amounts of silicate clay and other minerals to soils of the Caribbean and eastern United States seaboard (Herwitz *et al.* 1996). Parts of the Amazonian rainforest are dependent on nutrients carried in soil dust across the Atlantic Ocean from sub-Saharan West Africa (Swap *et al.* 1992). In these nutrient-poor soils, critical nutrients such as phosphorus and potassium are delivered in trace amounts by intermittent pulses of dust deposited during rainstorms. Thus, the productivity of parts of the rainforest is critically linked to events in sub-Saharan West Africa some 5000 km distant. In particular, the concentration of dust in these regions (e.g., Barbados) is correlated with drought in sub-Saharan Africa (Middleton 1985; Prospero *et al.* 1996; Prospero and Nees 1977, 1986; Prospero 1996).

Over longer timescales, changing ecosystem geography affects the amount of mineral dust in the atmosphere. For example, dust concentrations were higher during glacial periods than in interglacials (Petit *et al.* 1990; Jouzel *et al.* 1993; Overpeck *et al.* 1996; Andersen *et al.* 1998; Mahowald *et al.* 1999; Svensson *et al.* 2000). During the last glacial maximum, this was likely due to expansion of unvegetated areas in high latitudes and central Asia as a result of increased aridity and lower atmospheric CO<sub>2</sub> concentrations (Mahowald *et al.* 1999).

## 12.5 Coupled climate-ecosystem models

Dynamic global vegetation models have been developed to allow interactive coupling of climate and terrestrial ecosystems. Most studies of coupled climate-ecosystem dynamics have focused on physical climate. In these models, vegetation growth and biogeography is influenced by temperature, precipitation, and other climatic variables. In turn, vegetation height, leaf area, rooting depth, and composition influence

albedo, radiative exchange, turbulent fluxes, and hydrology and in doing so influence climate. The initial emphasis on biogeophysical feedbacks is now being expanded to include biogeochemical feedbacks, especially the role of terrestrial ecosystems in the carbon cycle.

### 12.5.1 Daisyworld

The simplest depiction of coupled climate-vegetation dynamics is Daisyworld (Watson and Lovelock 1983). Daisyworld is a mathematical model of a planet with two species of daisies of different colors. One species is black, has a low albedo, and reflects less solar radiation than bare ground. The other is white, has a high albedo, and reflects more solar radiation than bare ground. The growth of daisies over time is a parabolic function of local temperature scaled to equal zero with temperatures of 5 °C and 40 °C and equal one (i.e., optimum) with a temperature of 22.5 °C. The local temperature is related to the effective planetary temperature based on the deviation from the planetary albedo. Black daisies, with their lower albedo, absorb more solar radiation and are locally hotter than white daisies.

In Daisyworld, the extent of daisy coverage affects temperature, which feeds back to affect daisy growth and coverage. Black daisies are warmer than white daisies and dominate in cold climates. However, an increase in the area of black daisies, by lowering planetary albedo, warms climate, creating conditions in which white daisies are favored. White daisies have the opposite effect. Decreased coverage of white daisies leads to a lower albedo which leads to warmer temperature. Figure 12.12 shows steady state values of planetary temperature and areas of black and white daisies as solar luminosity is increased. Below a luminosity of 0.7, planetary temperature is too cold to support daisies. With warmer temperature, black daisies are favored in the cold climates of low luminosity because they warm the planet and quickly gain dominance. White daisies are at a disadvantage because they create locally colder temperature. As the black daisies spread across the planet, they warm temperature. Their growth declines in the warm climate above 22.5 °C while that of white daisies increases.

Daisyworld has generated much scientific controversy because it illustrates the regulation of climate by life. Across a wide range of luminosity, planetary temperature is close to optimum. Only at high (low) luminosity is temperature is too warm (cold) for any life. Daisyworld and the concept of the

regulation of climate by life that it generated still attract scientific attention (Zeng *et al.* 1990; Schneider and Boston 1991; Nevison *et al.* 1999).

### 12.5.2 Asynchronous equilibrium coupling

In contrast to Daisyworld, which is a toy model of climate-vegetation dynamics, sophisticated models of ecosystem processes and vegetation dynamics have been coupled to global climate models to understand the role of terrestrial ecosystems in the climate system. There are several approaches to examine climate-vegetation interactions. Vegetation can be treated as a prescribed surface boundary condition. Climate model simulations examine the sensitivity of climate to different prescriptions of vegetation cover such as a desert planet or green planet (Figure 12.5), boreal forest or tundra (Figure 12.7, Table 12.5), and desert or grassland (Table 12.6). Such studies raise the possibility of coupled climate-vegetation dynamics, but they do not address whether the resulting climate change maintains the imposed vegetation change.

Interactive vegetation coupling allows vegetation to change over time and affect climate (Figure 12.13). One approach, known as asynchronous equilibrium coupling, takes advantage of the relationships between climate and biogeography to interactively change vegetation cover. Climate is simulated with an initial vegetation cover. This climate is then used in a biogeography model to simulate the geographic distribution of vegetation. This map is then used as input to the climate model to obtain a new climate. Climate is iterated in this manner several times until a stable solution is obtained. One of the first such couplings used the Holdridge vegetation model shown in Figure 10.39 (Henderson-Sellers 1993; Henderson-Sellers and McGuffie 1995). More commonly, the biome model of Prentice *et al.* (1992) and Haxeltine and Prentice (1996), which is based on the physiological response of plant functional types to soil water, growing degree-days, minimum winter temperature, and other climatic variables, is used (Claussen 1994, 1996, 1997, 1998; de Noblet *et al.* 1996; Claussen and Gayler 1997; Texier *et al.* 1997; Kubatzki and Claussen 1998; Claussen *et al.* 1998; Kubatzki and Claussen 1998; de Noblet-Ducoudré *et al.* 2000).

Studies utilizing this type of climate-vegetation coupling show that interactive vegetation amplifies the climate response to changes in forcings such as solar radiation or atmospheric CO<sub>2</sub>. For example, the colder climate as a result of reduced solar radiation and lower atmospheric CO<sub>2</sub> some 115 000 years ago is not in itself enough to initiate an ice age. However, the associated reduction in the geographic

extent of the boreal forest and the expansion of tundra due to the cold climate produces additional cooling that is sufficient to initiate an ice age (de Noblet *et al.* 1996). Coupled climate-vegetation models highlight the importance of the treeline in reinforcing the cold high latitude climate of the last glacial maximum some 21 000 years ago and the high latitude warming 6000 years ago (Texier *et al.* 1997; Kubatzki and Claussen 1998).

These coupled models also show that changes in the geographic extent of vegetation enhance the orbitally induced summer monsoon of 6000 years ago in North Africa (Claussen and Gayler 1997; Texier *et al.* 1997; de Noblet-Ducoudré *et al.* 2000). Figure 12.14 shows changes in vegetation cover during one such climate-vegetation simulation, when the model is given the solar radiation of 6000 years ago (Claussen and Gayler 1997). From an initial condition of extensive desert and sparse savanna, interactive vegetation causes climate changes such that desert shrinks while savanna, woodland, and grassland expand. The climate-vegetation model converges on an equilibrium solution in which desert is reduced by 50% from its initial extent. This represents a northward shift of savanna of some 600 km in the western region of the Sahara. The northward shift of savanna amplifies the climate response to changes in Earth's orbit (Table 12.9). With interactive vegetation, the surface temperature cools by 3.1 °C and precipitation quadruples. Evapotranspiration also increases because of wetter soils, but net water gain (P - E) increases from 8 mm to 44 mm per month. The cooler, wetter climate reflects a change in net radiation at the surface and the partitioning of this energy into latent and sensible heat. Net solar radiation at the surface is unchanged. Incident radiation decreases with interactive vegetation due to more cloud cover, but this is compensated by a reduction in albedo from 0.34 to 0.22. Net loss of longwave radiation decreases with interactive vegetation due to the colder surface, which reduces upward longwave emission. In total, the vegetated surface receives  $30 \text{ W m}^{-2}$  more net radiation than the desert. This energy is used to evaporate water. The Bowen ratio (i.e., the ratio of sensible to latent heat) decreases from 3 to about 0.6 with interactive vegetation. The simulated climate and vegetation geography is in better agreement with interactive vegetation than without.

Other asynchronously coupled climate-vegetation model studies show that the choice of initial vegetation cover of desert or forest can lead to different climates in the western region of the Sahara Desert (Claussen 1994, 1997, 1998; Claussen *et al.* 1998; Kubatzki and Claussen 1998). Under present-day orbital

forcing, simulations when the model is initialized with the modern geographic extent of desert result in the present-day climate and distribution of vegetation. However, simulations in which land is initially vegetated instead of desert result in a wetter climate that supports a northward extension of savanna and shrubland from their modern distributions. This suggests the existence of two stable climate-vegetation regimes in West Africa. A similar dichotomy of two stable climate-vegetation equilibria are possible 21 000 years ago at the last glacial maximum but not for 6000 years ago, when a green Sahara is the only model solution. Six thousand years ago, increased summer solar radiation strengthened the monsoon and created a climate that was wet enough to maintain vegetation regardless of vegetation feedback. In contrast, the drier climate of today and at the last glacial maximum due to reduced summer solar radiation is quite sensitive to vegetation feedback.

Asynchronous equilibrium coupling demonstrates the importance of including dynamic vegetation cover in climate models. However, this type of coupling is limited in scope (Foley *et al.* 1998, 2000). It does not recognize the timescales at which vegetation changes. Biogeography models are equilibrium models. They are based on the assumption that climate alone controls the geographic distribution of vegetation. While this is true at long timescales of centuries to millenia, it is not true at shorter timescales of decades to centuries where succession and the response of plants to disturbances control vegetation dynamics. Hence, models coupled in this manner can only consider the equilibrium state of the climate system, not transient behavior. Moreover, the vegetation model is not always ecologically and hydrologically consistent with the climate model (Bonan 1993c, 1995b; Foley *et al.* 1998, 2000). For example, due to the importance of evapotranspiration to climate and biogeography, both models simulate evapotranspiration. However, they are likely to differ in the representation of this process. Climate models typically use a detailed parameterization of surface energy fluxes controlled by available energy, turbulent transfer, vapor pressure deficit, and stomatal physiology. Vegetation models might use a less mechanistic parameterization with a daily or monthly timescale. The two models might also differ in soil water, with the climate model using multilayer soil water transfer based on soil hydraulics while the vegetation model might use a simple bucket model. Finally, biogeography models only simulate the geographic distribution of vegetation. They do not include vegetation structure and changes in leaf area index or height. These must still be ascertained from biome type.

### 12.5.3 Integrated synchronous coupling

An alternative type of coupling integrates the longer timescales of vegetation dynamics with the short timescale processes (Figure 12.13). This type of model, known as an integrated synchronously coupled climate-ecosystem model, integrates the traditional focus on biogeophysics and hydrology found in land models used with climate models (Figure 8.23) with ecosystem and vegetation dynamics models (Figure 10.50) to simulate the growth and development of various plant functional types in response to climate and soil (Foley *et al.* 1996, 1998, 2000; Delire and Foley 1999; Levis *et al.* 1999a,b,c, 2000; Kucharik *et al.* 2000; Doherty *et al.* 2000). Figure 11.28 illustrates the scope of such a model. Climate determines energy exchange, water availability, and the productivity and geography of terrestrial ecosystems. In turn, the types of plants, biomass, and leaf area influence exchanges of energy, water, momentum, CO<sub>2</sub>, dust, and trace gases with the atmosphere and in doing so alter climate.

Climate simulations with synchronously coupled, integrated climate-ecosystem models reveal similar feedbacks and insights as asynchronous equilibrium models. For example, studies of climate at the last glacial maximum 21 000 years ago illustrate the importance of vegetation feedbacks (Crowley and Baum 1997; Kubatzki and Claussen 1998; Levis *et al.* 1999a). One such study (Levis *et al.* 1999a) found that the cold, dry climate reduces forest cover in the tropics and northern latitudes (Figure 1.5, color plate). Instead, tundra dominates much of the middle to high latitudes while grasslands cover the tropics and subtropics. These changes in biogeography are consistent with fossilized plant remains, which show more extensive tundra and grasses in middle to high latitudes and forest dieback and replacement by grasses in the tropics. The simulated climate is quite different when vegetation is allowed to respond to this climate change than with prescribed vegetation. With interactive vegetation, temperatures cool compared with prescribed vegetation over much of Eurasia, where tree cover decreases and albedo increases in winter and spring. Temperatures warm in the tropics and subtropics where grasses replace trees and evapotranspiration is reduced in a drier climate. Other climate simulations show the orbitally induced precipitation increase in North Africa 6000 years ago is sufficient to sustain a northward encroachment of plants into desert and that this greening of the desert enhances precipitation (Doherty *et al.* 2000).

The doubling of atmospheric CO<sub>2</sub> from pre-industrial levels is likely to result in changes in ecosystem structure and function in response to altered temperature, precipitation, and CO<sub>2</sub> fertilization.

Climate simulations with coupled climate-ecosystem models show large changes in climate as a result of vegetation changes (Betts *et al.* 1997, 2000; Levis *et al.* 2000). Table 12.2 shows results from one such study (Levis *et al.* 2000). The radiative effect of increased atmospheric CO<sub>2</sub> is overall surface warming and intensification of the hydrologic cycle with increased precipitation and evapotranspiration. The reduction in stomatal conductance with higher atmospheric CO<sub>2</sub> reinforces the warming, but decreases precipitation and evapotranspiration in middle to low latitudes. With interactive vegetation, leaf area index generally increases due to expansion of forests at the expense of grasses as a result of changes in temperature, precipitation, and the different impact of CO<sub>2</sub> fertilization on C<sub>3</sub> plants (trees, cool grasses) and C<sub>4</sub> plants (tropical grasses). Vegetation changes generally mitigate the physiological effects of increased CO<sub>2</sub> in many regions. In northern latitudes, the greening of vegetation enhances the spring and summer radiative warming due to a decrease in surface albedo (Figure 12.15, color plate), but reduces winter warming due to decreased net radiation in regions of increased forest cover (Levis *et al.* 1999b). Without vegetation feedbacks, doubling atmospheric CO<sub>2</sub> warms temperatures over ice-free land north of latitude 45° N by 1.7-5.6 °C depending on the season. Vegetation feedbacks enhance this warming by 1.6 °C in spring, when the albedo feedback is greatest, and by 0.4 °C in summer and autumn, when the albedo feedback diminishes but warming persists due to the thermal inertia of the Arctic Ocean (Levis *et al.* 1999b). Growth of temperate deciduous trees and grasses leads to summer cooling in middle latitudes compared with the physiological effects as a result of greater leaf area and evapotranspiration. Spring and autumn temperatures warm due to reduced albedo as vegetation cover increases. Annual precipitation and evapotranspiration increase. In the tropics, evergreen and deciduous trees expand at the expense of grasses. This change offsets the reduction in precipitation and evapotranspiration due to physiological effects so that the combined vegetation forcing has greater precipitation and evapotranspiration compared with the radiative forcing.

Despite the importance of vegetation feedbacks to the high latitude climate, multiple climate equilibria apparently do not exist with present-day solar radiation and atmospheric CO<sub>2</sub> as they do in North Africa (Levis *et al.* 1999c). Simulations with a synchronously coupled, integrated climate-ecosystem model show that extension of evergreen boreal forest to the Arctic coast does not result in sufficient warming to support the expanded boreal forest (Figure 12.16). A control simulation with modern vegetation cover and

another simulation with expanded forest both converge on a solution of cold temperature and low leaf area index. In the extended forest simulation, the initial reduction in leaf area index does not cool climate. However, below a leaf area index of about  $2 \text{ m}^2 \text{ m}^{-2}$ , tundra replaces forest and climate cools rapidly. The simulation with modern vegetation cover attains equilibrium more rapidly because it is initialized closer to the final state.

The complexity of atmospheric, ecological, and hydrological processes in synchronously coupled, integrated climate-ecosystem models and the numerous interactions among these processes are computationally demanding and difficult to understand fully. As a result, climate-vegetation models of intermediate complexity have been developed to investigate vegetation feedbacks (Ganopolski *et al.* 1998; Claussen *et al.* 1999; Zeng *et al.* 1999; Wang and Eltahir 2000a,b,c,d; Zeng and Neelin 2000; Kubatzki *et al.* 2000). The Sahel region of West Africa – the extensive dry grasslands and shrublands located between the Sahara desert to the north and tropical rainforest to the south – has been the focus of several such studies. The existence of two stable climate-vegetation equilibria (wet-green, dry-desert) in asynchronously coupled models suggests that vegetation feedbacks play an important role in the climate of this region.

Rainfall in the Sahel decreased from the 1950s to the early 1990s. Oceanic heat exchange influences atmospheric circulation over West Africa and interannual variability in sea surface temperatures contributes to precipitation variability (Folland *et al.* 1986; Nicholson and Entekhabi 1987; Rowell *et al.* 1995; Janicot *et al.* 1996; Nicholson and Kim 1997; Nicholson 2000). However, several studies with coupled atmosphere-vegetation models of intermediate complexity suggest that natural vegetation feedbacks enhance precipitation variability (Zeng *et al.* 1999; Wang and Eltahir 2000a,b,c,d). For example, one study (Zeng *et al.* 1999) compared oceanic and terrestrial influences on precipitation variability (Figure 12.17). A simulation with interannually varying sea surface temperatures and prescribed soil moisture and vegetation cover shows weak interannual variation and drying compared with the observations. Allowing soil water to respond to changes in precipitation increases the drying trend and provides a better match with observations, but the best fit with observations occurs when vegetation also responds to precipitation. The wet period in the 1950s and early 1960s and the dry periods of the 1970s and 1980s stand out and are similar to observations. Interactive vegetation influences precipitation through a positive feedback loop. Decreased rainfall leads to drier soils and reduced vegetation cover, which in turn leads to higher surface

albedo and reduced transpiration. This weakens atmospheric circulation by reducing the energy and water flux in the atmosphere, resulting in less rainfall. Similar to asynchronously coupled models, another study (Wang and Eltahir 2000b) found that the simulated climate-vegetation equilibrium has two stable regimes depending on initial conditions (Figure 12.18). An initial forest cover results in a climate-vegetation equilibrium with large annual rainfall and extensive forest vegetation over much of West Africa. Desert initial conditions result in substantially less rainfall, an absence of forest, and a wide distribution of grasses and desert. This raises the possibility that the persistence of the long drought represents a change from one equilibrium to another brought about by vegetation feedbacks triggered by external forcings.

An additional study demonstrated the importance of interannual precipitation variability in shaping the African savanna (Zeng and Neelin 2000). Simulations compared the vegetation cover resulting from forest or desert initial conditions using climatological or interannually varying sea surface temperatures (Figure 12.19). Simulations with climatological sea surface temperatures and initial forest or desert conditions result in largely forest or desert with high or low vegetation cover, respectively. Interannual variation in sea surface temperatures creates interannual variability in precipitation. Annual rainfall and vegetation cover decreases in wet regions and increases in drier regions. This results in a smoother desert-forest transition. The interannually forced simulations have an equilibrium solution that is intermediate between the forest or desert extremes regardless of whether the model is initialized with forest or desert. These results show that without climate variability positive feedback from vegetation enhances desert and forest regions at the expense of savanna. Interannual climate variability, through its non-linear effects on the land-atmosphere system, smooths the transition between forest and desert, contributing to the maintenance of savanna.

Studies of coupled climate-ecosystem dynamics have focused on the biogeophysical effects of changing ecosystem structure and geography on climate. However, large changes in terrestrial carbon storage as a result of climate change are likely to affect climate change. For example, the northward expansion of boreal forest into tundra decreases surface albedo and removes carbon from the atmosphere. The climate cooling resulting from increased carbon storage and lower atmospheric CO<sub>2</sub> concentration may offset the warming from the lower surface albedo (Betts 2000). Climate model simulations with an interactive carbon cycle, which includes oceanic and terrestrial carbon fluxes and their effect on

atmospheric CO<sub>2</sub>, highlight the potential for large terrestrial ecosystem feedbacks on climate change. One study with a model of intermediate complexity (Claussen *et al.* 2001) contrasted the biogeophysical and biogeochemical effects of boreal and tropical deforestation (Table 12.10). Simulations included only changes in surface energy, moisture, and momentum fluxes (i.e., biogeophysical feedbacks) as a result of deforestation, only changes in carbon pools and fluxes (biogeochemical feedbacks), and both feedbacks. The biogeophysical effect of boreal deforestation cools climate as a result of the snow-vegetation albedo feedback. Release of carbon with deforestation warms climate through the greenhouse effect, but not enough to compensate for the biogeophysical cooling. Tropical deforestation warms climate regionally due to reduction in evapotranspiration, but produces a slight global cooling because of less moisture in the atmosphere. Deforestation releases carbon to the atmosphere, resulting in warming that exceeds that from biogeophysical processes. Another study coupled models of vegetation dynamics, terrestrial carbon fluxes, and oceanic carbon fluxes to a global climate model to examine carbon feedbacks with climate change (Cox *et al.* 2000). In climate simulations for the period 1860 to 2100, during which anthropogenic emissions increase atmospheric CO<sub>2</sub>, terrestrial ecosystems change from net global uptake of carbon to a net source as a result of climate warming. Most of this loss of terrestrial carbon is due to dieback of tropical rainforests. The release of carbon increases atmospheric CO<sub>2</sub> and reinforces the warming.

Coupled climate-ecosystem models are abstractions of a complex climate system. Many ecological and hydrological processes are represented in detail, but nature continually surprises us. For example, a warmer, drier climate has altered the long-term sequestration of carbon in Alaskan arctic tundra ecosystems, resulting in substantial loss of carbon to the atmosphere. This prompted concern about a positive climate feedback, but despite continued warming and drying the loss of carbon has slowed as a result of greater summertime carbon uptake (Oechel *et al.* 2000). This suggests an ability of these ecosystems to adjust metabolically to long-term changes in climate through changes in nutrient cycling, physiological acclimation, and community reorganization. It will be many years, if ever, before the complexity of nature and all the possible feedbacks are included in climate models. However, the picture emerging now is one of terrestrial ecosystems as an important regulator of climate. Whether changes in terrestrial ecosystems as a result of climate change enhance or mitigate climate change we cannot say with accuracy. We can, however, say that climate will change as a result of ecosystem feedbacks.

## 12.6 Tables

Table 12.1. *Timescales of vegetation change*

Type of change	Timescale	Environmental signal	Controlling processes
<i>Natural processes</i>			
Ecosystem metabolism	Seasonal to interannual	CO <sub>2</sub> drawdown Albedo Latent heat Sensible heat Temperature Humidity	Leaf phenology Air temperature Soil water Humidity Solar radiation Atmospheric CO <sub>2</sub>
Succession	Decadal to century	Carbon storage Woody biomass Soil organic matter Leaf area Species composition Nutrient availability Surface energy fluxes	Carbon allocation Litterfall Litter quality Soil water Soil nutrients Stand age Life history patterns Disturbance
Biogeography	Centuries to millennia	Ecosystem structure Species composition Carbon storage Surface energy fluxes Temperature Precipitation	Climate Succession Life history patterns
<i>Human-mediated change</i>			
Agroecosystems	Decadal	Temperature Precipitation Carbon storage Nutrient availability Biodiversity	People
Farm abandonment	Decadal	Temperature Precipitation Carbon storage Ecosystem structure Species composition	People, then succession
Urbanization	Decadal	Warmer temperature Greater runoff Increased pollution Altered biodiversity	People

Table 12.2. *Effect of doubled atmospheric CO<sub>2</sub> concentration on mean annual climate as determined from four climate model simulations*

	Control (C)	Radiative forcing (R-C)	Vegetation forcing	
			Physiological (RP-R)	Physiological and vegetation cover (RPV-R)
<i>Ice-free northern high latitude continents (60°N-90°N)</i>				
Temperature (°C)	-6.7	3.9	0.6	0.6
Precipitation (mm day <sup>-1</sup> )	0.76	0.15	0.02	0.04
Evapotranspiration (mm day <sup>-1</sup> )	0.35	0.09	0.00	0.05
Canopy conductance (mm s <sup>-1</sup> )	0.28	0.02	-0.06	0.12
Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	2.5	0.0	0.0	3.0
Albedo	0.38	-0.03	0.00	-0.06
<i>Middle latitude continents (30°N-60°N)</i>				
Temperature (°C)	6.9	2.7	0.3	0.3
Precipitation (mm day <sup>-1</sup> )	1.51	0.19	-0.07	-0.02
Evapotranspiration (mm day <sup>-1</sup> )	1.16	0.14	-0.03	0.04
Canopy conductance (mm s <sup>-1</sup> )	0.57	0.03	-0.09	0.09
Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	5.0	0.0	0.0	2.4
Albedo	0.17	-0.01	0.00	-0.01
<i>Tropical continents (15°S-15°N)</i>				
Temperature (°C)	26.6	2.1	0.1	0.0
Precipitation (mm day <sup>-1</sup> )	5.22	0.12	-0.17	0.03
Evapotranspiration (mm day <sup>-1</sup> )	3.50	0.17	-0.02	0.15
Canopy conductance (mm s <sup>-1</sup> )	1.04	-0.06	-0.09	0.15
Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	5.2	0.0	0.0	2.2

*Note:* C, control simulation with modern CO<sub>2</sub> (345 ppm) and vegetation. R, doubled CO<sub>2</sub> (690 ppm) without changes in vegetation. RP, doubled CO<sub>2</sub> with changes in stomatal physiology. RPV, doubled CO<sub>2</sub> with changes in stomatal physiology and vegetation cover. Radiative forcing is the difference between the radiative and control simulations. Vegetation forcings are the climate change in addition to the radiative forcing.

*Source:* Data from Levis *et al.* (2000).

Table 12.3. *Daily averaged broadband albedo during summer and with snow for elements of the boreal landscape*

	Summer	Snow-covered
<i>Treeless</i>		
Grassland	0.20	0.75
Wetland	0.16-0.18	0.70
<i>Forest</i>		
Quaking aspen	0.11	0.21
Jack pine	0.09-0.14	0.12-0.15
Spruce	0.08-0.09	0.11

*Source:* Data from Baldocchi *et al.* (2000).

Table 12.4. *Mid-growing season latent heat ( $\lambda E$ ) normalized by net radiation ( $R_n$ ) or available energy ( $R_n - G$ ) for various elements of the boreal landscape*

Vegetation	Normalized latent heat	
<i>Wetland</i>		
Manitoba, Canada	$\lambda E / (R_n - G)$	0.76
<i>Quaking aspen forest</i>		
Saskatchewan, Canada	$\lambda E / R_n$	0.61
<i>Jack pine forest</i>		
Saskatchewan, Canada	$\lambda E / R_n$	0.39
Manitoba, Canada	$\lambda E / (R_n - G)$	0.34
<i>Scots pine forest</i>		
Russia	$\lambda E / (R_n - G)$	0.48
Sweden	$\lambda E / R_n$	0.59
Sweden (with Norway spruce)	$\lambda E / (R_n - G)$	0.38
<i>Black spruce forest</i>		
Ontario, Canada	$\lambda E / (R_n - G)$	0.49
Saskatchewan, Canada	$\lambda E / (R_n - G)$	0.38
Quebec, Canada (with white spruce)	$\lambda E / (R_n - G)$	0.35
<i>Siberian larch forest</i>		
Russia	$\lambda E / (R_n - G)$	0.44

Source: Data from Baldocchi *et al.* (2000).

Table 12.5. *Climate at the onset of glaciation 115 000 years ago as determined from four climate model simulations*

	Control (C)	Radiative forcing (R-C)	Vegetation forcing	
			Modest tundra expansion (RV-R)	Large tundra expansion (REV-R)
<i>North America</i>				
Summer temperature (°C)	12.6	-5.1	-2.9	-18.0
Snow cover (days)	237	32	18	85
<i>Europe and Asia</i>				
Summer temperature (°C)	14.3	-5.2	-2.8	-17.1
Snow cover (days)	240	24	18	84

*Note:* C, control simulation with modern solar radiation and atmospheric CO<sub>2</sub>. R, orbital geometry and atmospheric CO<sub>2</sub> of 115 000 years ago. RV, orbital geometry and atmospheric CO<sub>2</sub> of 115 000 years ago and modest expansion of tundra. REV, as in simulation RV but extensive tundra expansion. Data are averaged over land between latitudes 60° N to 90° N. Radiative forcing is the difference between the radiative and control simulations. Vegetation forcings are the climate change in addition to the radiative forcing.

*Source:* Data from Gallimore and Kutzbach (1996).

Table 12.6. *Effect of vegetation on the mean annual climate of North Africa 6000 years ago as determined from four climate model simulations*

	Surface forcing			
	Control	Radiative forcing	Vegetation	
			Vegetation	and soil
(C)	(R-C)	(RV-R)	(RVS-R)	
Net radiation ( $\text{W m}^{-2}$ )	94	1	3	9
Sensible heat ( $\text{W m}^{-2}$ )	56	-3	1	4
Latent heat ( $\text{W m}^{-2}$ )	38	4	2	5
Precipitation ( $\text{mm day}^{-1}$ )	1.28	0.15	0.08	0.20
Near-surface specific humidity ( $\text{g kg}^{-1}$ )	6.2	0.6	0.3	0.6

*Note:* C, control simulation with modern solar radiation and vegetation. R, orbital geometry of 6000 years ago and modern vegetation. RV, orbital geometry and vegetation of 6000 years ago. RVS, orbital geometry, vegetation, and soil of 6000 years ago. Radiative forcing is the difference between the radiative and control simulations. Surface forcings are the climate change in addition to the radiative forcing. Data are averaged between latitude 15-22° N and longitude 0-50° E.

*Source:* Data from Kutzbach *et al.* (1996).

Table 12.7. *Geographic area and carbon storage of major biomes at the last glacial maximum (LGM) and present*

	Area ( $10^6$ km <sup>2</sup> )		Carbon ( $10^{15}$ g)	
	LGM	Present	LGM	Present
Tropical rainforest	8.8	8.2	269	249
Tropical dry forest/savanna	25.9	24.5	402	381
Temperate and cool forest	14.7	19.9	354	499
Boreal and cold forest	5.7	17.0	131	403
Woodland/shrubland	13.5	11.3	154	129
Grassland	15.1	15.7	175	177
Tundra	10.2	9.7	192	184
Desert	36.9	27.2	134	102

*Source:* Data from Prentice *et al.* (1993).

Table 12.8. *Change from current values in the geographic area of five major biomes and global carbon storage with four projections of climate change*

	Climate change				
	Current	T: 2.8 °C	T: 4.0 °C	T: 4.2 °C	T: 5.2 °C
		P: 8%	P: 9%	P: 11%	P: 15%
<i>Geographic area (10<sup>6</sup> km<sup>2</sup>)</i>					
Tundra	9.4	-3.0	-5.2	-3.1	-5.7
Desert	37.0	-6.2	-6.3	-9.6	-9.8
Grassland	19.2	3.8	9.7	6.9	8.1
Dry forest	18.2	0.0	6.1	4.9	13.0
Mesic forest	51.7	5.6	-4.0	1.2	-5.2
<i>Global carbon (10<sup>15</sup> g)</i>					
Aboveground	737	123	45	92	28
Soil	1158	57	-7	54	-20
Ecosystem	1896	180	38	147	8

*Note:* T, change in global mean temperature. P, percent increase in global annual precipitation.

*Source:* Data from T. Smith *et al.* (1992a).

Table 12.9. *Summer climate (June, July, August) for the Sahara (latitude 15°N-30°N, longitude 10°W-30°E) 6000 years ago for climate simulations with prescribed modern desert vegetation and for interactive, asynchronously coupled vegetation*

	Prescribed vegetation	Interactive vegetation
Surface temperature (°C)	34.6	31.5
<i>Hydrologic cycle</i>		
Precipitation, P (mm month <sup>-1</sup> )	30	129
Evapotranspiration, E (mm month <sup>-1</sup> )	22	85
P - E (mm month <sup>-1</sup> )	8	44
<i>Radiative fluxes</i>		
Incident solar radiation (W m <sup>-2</sup> )	339	284
Reflected solar radiation (W m <sup>-2</sup> )	117	62
Net solar radiation (W m <sup>-2</sup> )	222	222
Albedo	0.34	0.22
Net longwave radiation (W m <sup>-2</sup> )	-120	-90
Net radiation (W m <sup>-2</sup> )	102	132
<i>Turbulent surface fluxes</i>		
Sensible heat (W m <sup>-2</sup> )	62	47
Latent heat (W m <sup>-2</sup> )	21	82
Bowen ratio	2.95	0.57

Source: Data from Claussen and Gayler (1997).

Table 12.10. *Contribution of biogeophysical and biogeochemical processes to changes in near-surface air temperature (annual mean) as a result of boreal and tropical deforestation*

	Boreal deforestation (50° N-60° N)		Tropical deforestation (0°-10° S)	
	Global	Region	Global	Region
Biogeophysical only	-0.23	-0.82	-0.04	+0.13
Biogeochemical only	+0.09	+0.12	+0.19	+0.15
Both processes	-0.11	-0.67	+0.16	+0.29

*Note:* Temperatures are the difference from a control simulation without changes in land cover.

*Source:* Data from Claussen *et al.* (2001).

## 12.7 Figure Legends

*Figure 12.1.* Climate-ecosystem dynamics showing the cycles of vegetation change due to climate change, succession, and human intervention.

*Figure 12.2.* Influence of springtime leaf emergence on air temperature in eastern United States. Top: Increase in daily maximum temperature in relation to leaf emergence. Adapted from Schwartz and Karl (1990). Bottom: Diurnal temperature range in relation to leaf emergence. Adapted from Schwartz (1996).

*Figure 12.3.* Influence of leaf emergence on daily air temperature in west central Canada. The two thin lines show observed and expected temperature (left axis). Expected temperature is from a sinusoidal curve fit to the observations. The thick line shows the difference between observed and expected temperatures (right axis). The typical period in which leaves are present is also shown. Data from Hogg *et al.* (2000).

*Figure 12.4.* Relative change in stomatal density in herbarium specimens of seven species of temperate trees and one species of shrub over the past 200 years. Adapted from Woodward (1987b).

*Figure 12.5.* Difference in climate between a desert planet and a green planet. Top: Surface boundary conditions. Middle: Annual hydrologic cycle showing precipitation, evaporation, and runoff in cubic kilometers per year. Bottom: Geographic extent of Köppen climate types over land. Data from Fraedrich *et al.* (1999) and Kleidon *et al.* (2000).

*Figure 12.6.* Ratio of evapotranspiration to equilibrium evapotranspiration as a function of maximum canopy conductance for Arctic and boreal ecosystems. Data from Eugster *et al.* (2000) and Baldocchi *et al.* (2000).

*Figure 12.7.* Difference in air temperature between a climate simulation with the boreal forest present and one in which the boreal forest is replaced with tundra. Data show January, April, July, and October mean

monthly land temperature as a function of latitude from the equator ( $0^{\circ}$  N) to  $70^{\circ}$  N. Adapted from Bonan *et al.* (1992).

*Figure 12.8.* Contribution of terrestrial ecosystems to the seasonal amplitude in atmospheric  $\text{CO}_2$ . Data from Randerson *et al.* (1997).

*Figure 12.9.* Contribution of different terrestrial ecosystems to the terrestrial component of the  $\text{CO}_2$  amplitude. Data from Randerson *et al.* (1997).

*Figure 12.10.* Grassland response to 12 years of nitrogen addition. Data are mean values for several replicate plots in two old fields initially dominated by  $\text{C}_4$  grasses. Left: Biomass of  $\text{C}_4$  plants as a percent of total aboveground biomass. Middle: C:N ratio of litter. Right: Net carbon storage per unit added nitrogen. Adapted from Wedin and Tilman (1996).

*Figure 12.11.* Annual mineral dust deposition in the North Atlantic Ocean, Mediterranean Sea, and Caribbean Sea for  $10^{\circ}$  longitude by  $10^{\circ}$  latitude grid boxes. Data from Prospero (1996) and Prospero *et al.* (1996).

*Figure 12.12.* Steady state response of Daisyworld to solar luminosity. Luminosity is the fractional change in solar constant. Top: Area of black and white daisies. Bottom: Planetary temperature. The dashed line shows planetary temperature without daisies. Adapted from Watson and Lovelock (1983).

*Figure 12.13.* Methods of coupling atmospheric and land models. Top: Asynchronous equilibrium coupling. Bottom: Integrated synchronous coupling. Adapted from Foley *et al.* (1998).

*Figure 12.14.* Area of vegetation types in North Africa (latitude  $8.5^{\circ}$  N- $36.6^{\circ}$  N, longitude  $15.5^{\circ}$  W- $52.0^{\circ}$  E) 6000 years ago in relation to iteration for an asynchronously coupled climate-vegetation model. Adapted from Claussen and Gayler (1997).

**Figure 12.15.** Effect of vegetation feedback with a doubling of atmospheric  $\text{CO}_2$  on spring temperatures. Vegetation feedback is the difference between a climate model simulation that doubled  $\text{CO}_2$  with changes in stomatal physiology and vegetation cover (RPV) and one that doubled  $\text{CO}_2$  without changes in

vegetation (R). Dashed lines denote regions with statistically significant temperature differences. From climate simulations described by Levis *et al.* (2000).

*Figure 12.16.* Relationship between growing degree-days above 0 °C and leaf area index of boreal evergreen trees in a region of central Siberia. Data are 20-year averages for a 120-year control simulation with modern vegetation cover and a second simulation with the circumpolar boreal forest extended to the Arctic coast. Numbers next to data points indicate the 20-year interval. Adapted from Levis *et al.* (1999c).

*Figure 12.17.* Precipitation variability and vegetation feedback in the West African Sahel (latitude 13° N-20° N, 15° W-20° E). Observed: Observed annual precipitation anomaly. Atmosphere-Ocean: Simulated annual precipitation anomaly with sea surface temperatures only. Atmosphere-Ocean-Land: Simulated annual precipitation anomaly with the addition of interactive soil water. Atmosphere-Ocean-Land-Vegetation: Simulated annual precipitation anomaly with the addition of vegetation feedback. Adapted from Zeng *et al.* (1999).

*Figure 12.18.* Equilibrium climate and vegetation in West Africa in relation to latitude. Top: Forest initial conditions. Bottom: Desert initial conditions. Adapted from Wang and Eltahir (2000b).

*Figure 12.19.* Fractional vegetation cover in the West African Sahel (latitude 10° N-20° N, 15° W-20° E) as a function of time in four climate model simulations using forest or desert initial conditions and climatological or interannually varying sea surface temperatures. Adapted from Zeng and Neelin (2000).