The factors that determine properties of both ecosystems and the climate system have changed more rapidly in the past 50 years than during the previous 10,000 years (Steffen et al. 2004; Figure 1). Our children will probably see even more profound changes during their lifetimes. Some of these, such as changes in climate and atmospheric composition, alter the dynamic interactions between land, ocean, and atmosphere and, therefore, future transformations in climate and the ecosystems on which society depends (IPCC 2007a). Development of policies that reduce rates of climate change, while sustaining the services provided by ecosystems, requires a clear understanding of these dynamics.

Changes in ecosystems influence the climate system through several processes (Figure 2), including (1) emission of greenhouse gases, which causes an imbalance in the Earth’s energy budget at the top of the atmosphere; (2) altered albedo (the proportion of solar radiation that the Earth’s surface reflects back to space), which influences the amount of heat transferred from ecosystems to the atmosphere; (3) altered evapotranspiration (evaporation from the Earth’s surface plus that from leaves), which cools the surface and provides moisture to form clouds and fuel atmospheric mixing; (4) altered long-wave radiation, which depends on surface temperature and cloudiness; (5) changes in production of aerosols (small particles that scatter and absorb light); and (6) changes in surface roughness, which determines the strength of coupling between the atmosphere and the surface and, therefore, the efficiency of water and energy exchange. For trace gases and aerosols, the impact of an individual constituent on climate depends on the magnitude of the instantaneous forcing and the turnover time of each constituent in the atmosphere (i.e., the total quantity divided by the average rate of input and loss; Table 1). In general, energy, water, and highly reactive compounds from fossil-fuel emissions (e.g., nitric oxide, sulfur dioxide) have such short atmospheric lifespans that they have strong local or regional effects, as well as global consequences. In contrast, the effects of greenhouse gases, such as carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O), are globally dispersed, so their impacts are averaged over the entire planet.

Discussions about, and efforts to reduce human impacts on, the climate system have generally focused on green-
Changing climate–biosphere feedbacks

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house-gas balance only, largely ignoring the multiple pathways by which ecosystems interact with the climate system (Field et al. 2007). The Kyoto Protocol, for example, addresses only CO₂ emissions and ignores the effects of altered ecosystem carbon storage on other pathways of ecosystem–atmosphere interaction. Here, we discuss four major ways in which human activities have altered multiple feedbacks to the climate system: (1) CO₂ emissions, (2) climate warming, (3) desertification, and (4) changing forest cover. We show that consideration of multiple feedbacks between ecosystems and the atmosphere raises important new scientific questions and suggests new policy directions that might reduce the overall human footprint on the climate system.

**Ecosystem effects of CO₂**

Fossil-fuel emissions of CO₂ are thought to be the largest direct human cause of recent climate warming (IPCC 2007a). However, terrestrial ecosystems fix through photosynthesis and release through respiration/burn about ten times more CO₂ than is released from combustion of fossil fuels and altered land use annually. Consequently, ecosystems have been viewed as one possible avenue for “solving the CO₂ problem” without reducing anthropogenic emissions. Over the past several decades, the land and oceans have indeed acted as a large negative feedback to climate warming (ie a feedback that slows climate warming) by absorbing and sequestering about 55–60% of the CO₂ released to the atmosphere by fossil-fuel emissions and land-use change (Canadell et al. 2007; Figure 3). The magnitude of this feedback depends on several processes in terrestrial ecosystems, including (1) the capacity of land plants to increase photosynthesis and carbon storage in response to rising atmospheric CO₂, and (2) the sensitivity of net primary production and heterotrophic respiration to increasing temperatures and shifting patterns of drought (Friedlingstein et al. 2006). Initial model simulations suggest that terrestrial ecosystem processes may play an important role in regulating these feedbacks over the 21st century. Over timescales of several centuries, ocean processes will probably become increasingly important, as terrestrial sinks saturate or become sources. Over this period, however, ocean sinks may also decrease in the quantity of CO₂ absorbed, as surface heating increases stratification and slows overturning.

The capacity of land and ocean sinks to remove anthropogenic carbon derived from fossil-fuel combustion and land-use change from the atmosphere has declined from about 60% to 55% of human emissions between 1960 and 2007 (Canadell et al. 2007). This proportion may continue to decline as the capacity of terrestrial ecosystems to sequester carbon saturates and forest cover decreases (Gitz and Ciais 2003). It is therefore unlikely that terrestrial ecosystems and oceans, as presently constituted, will “solve the CO₂ problem”, without substantial reductions in fossil-fuel emissions.

At the scale of a single leaf or plant, increasing atmospheric CO₂ above current ambient concentrations typically causes an increase in photosynthesis and/or a decrease in transpiration (Drake et al. 1997) – effects that also contribute to patterns observed at landscape-to-global scales (Field et al. 2007; Lobell and Field 2008). Although some of the global-scale trends in tree growth can be explained

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**Table 1. Turnover time and spatial scale of linkage between atmospheric constituents and the climate system**

<table>
<thead>
<tr>
<th>Constituent</th>
<th>Turnover time¹</th>
<th>Spatial scale</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO₂</td>
<td>3 years²</td>
<td>Global</td>
</tr>
<tr>
<td>CH₄</td>
<td>8.4 years</td>
<td>Global</td>
</tr>
<tr>
<td>N₂O</td>
<td>120 years</td>
<td>Global</td>
</tr>
<tr>
<td>H₂O</td>
<td>10 days</td>
<td>Sub-continental</td>
</tr>
<tr>
<td>Aerosols</td>
<td>Days to weeks</td>
<td>Regional to continental</td>
</tr>
<tr>
<td>NOₓ</td>
<td>&lt; 1 day</td>
<td>Regional</td>
</tr>
<tr>
<td>SO₂</td>
<td>&lt; 1 day</td>
<td>Regional</td>
</tr>
</tbody>
</table>

**Notes:** This represents the average time that each constituent remains in the atmosphere. The atmosphere mixes globally in about 1 year. Turnover time = atmospheric pool divided by the annual flux to the atmosphere. This is the mean residence time of CO₂ in the atmosphere with respect to exchange with terrestrial ecosystems (gross primary production) and air–sea fluxes. Note that injections of CO₂ into the atmosphere from fossil-fuel burning have a lifetime of hundreds to thousands of years, due to their effects on ocean chemistry. Ocean chemistry was in steady state with respect to atmospheric CO₂ levels prior to the Industrial Revolution; now, fossil-fuel CO₂ is consuming carbonate ions and lowering pH in the oceans, which in turn reduces their uptake capacity.

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**Figure 1.** Selected changes in ecosystems (land conversion and agricultural fertilizer use) and the climate system (atmospheric CO₂ and surface air temperature) since 1750 (Steffen et al. 2004). ppmv, parts per million by volume.
without invoking a CO₂ response (Caspersen et al. 2000), elevated CO₂ accounts for at least some of the observed growth enhancement, and probably some increment of carbon storage (Norby et al. 2005; Long et al. 2006).

Carbon sequestration by terrestrial ecosystems may also alter other feedbacks to the climate system. The stimulation of photosynthesis by rising CO₂, for example, may increase leaf area and forest cover, slightly darkening the Earth’s surface and increasing absorption of radiation. This could have a warming effect that partly offsets the negative feedback resulting from carbon sequestration (Matthews et al. 2007; Figure 3). In addition, the decrease in transpiration by individual leaves in response to elevated levels of CO₂ (Field et al. 1995) may warm the surface (Sellers et al. 1996), although other adjustments in ecosystem structure and species composition — including increases in leaf area and vegetation cover — may cancel this effect at regional scales. The net effect of ecosystems on carbon sequestration is least pronounced in old forests, especially those whose growth is strongly limited by nutrient availability (Körner et al. 2005).

In summary, ecosystems respond to increased atmospheric concentrations of CO₂ primarily by removing a fraction of it from the atmosphere (ie carbon sequestration). The resulting cooling effect on climate may be offset to a modest degree by changes in canopy cover that increase energy absorption. Furthermore, the net cooling effect on climate of carbon sequestration in land and ocean ecosystems is likely to decline as elevated CO₂ levels reduce the sensitivity of photosynthesis to additional changes, as tropical forest cover declines, and as ocean stratification and acidification intensifies. Thus, ecosystems are unlikely to solve the problem of rising atmospheric CO₂. Reduction in CO₂ emissions in those sectors and nations that produce the greatest quantity of emissions is likely to be the most effective long-term policy for reducing atmospheric CO₂ concentration.

II. Climate warming

Recent climate warming, resulting mainly from accumulation of greenhouse gases in the atmosphere, alters multiple feedbacks to the climate system, most of which amplify the rate of warming. As expected, these effects are most pronounced in cold climates, where warming has been most pronounced and physical and biological processes are particularly sensitive to temperature.

In the Arctic, warming has caused an increase in both photosynthesis and respiration, but the net effect on carbon balance has been variable regionally, with increased plant growth and net carbon accumulation in moist areas and net carbon loss in dry areas; the net effect has probably been a small amount of carbon sequestration (McGuire et al. 2000; Callaghan et al. 2004; Sitch et al. 2007), slowing climate warming.

However, changes in the surface energy budget in the Arctic have had a much larger and more consistent feedback to climate. In the northern oceans, the summer extent of sea ice has decreased; the resulting decline in albedo causes more absorption of radiation, which warms the air and water. Since the impacts of changes in energy balance are most pronounced at local to regional scales, this heating causes more melting of sea ice and, thus, further warming of the ocean and atmosphere. A similar process occurs on land, as warmer climate causes snow to melt earlier (by 1–2 days per decade), which reduces albedo, increases energy absorption, and amplifies the rate of local to regional warming (Chapin et al. 2005; Euskirchen et al.
Over the longer term, increases in shrub and tree cover will probably have an even stronger positive feedback to Arctic warming, by reducing both summer and winter albedo (Chapin et al. 2005). In contrast to a 30-year record of greening in the Arctic – presumably in response to climate warming, as documented by satellite records of vegetation greenness – boreal forest greenness increased until the 1990s and has since declined, as a result of some combination of increasing drought, insect outbreaks, and wildfire (Goetz et al. 2005). This suggests a decline in the capacity of boreal forests to sequester carbon. As in the Arctic, the feedbacks from a changing energy budget appear to predominate. Earlier snowmelt acts as a positive feedback to climate warming, just as in the Arctic.

Wildfire disturbances release carbon (a positive feedback to warming), but also replace an absorptive tree canopy with a reflective snow surface (increased albedo) during fall, winter, and spring. This reduces energy absorption and acts as a negative feedback to warming (Figure 4). The net effect of fire is probably a small negative feedback to warming at a global scale, but with much of the albedo-driven cooling concentrated over boreal land areas (Randerson et al. 2006). Future increases in boreal fires, however, may also increase the deposition of black carbon on sea ice and the Greenland ice sheet (Flanner et al. 2007; McConnell et al. 2007), with uncertain long-term consequences for ice-sheet dynamics and feedbacks to Arctic climate.

Carbon stored in permafrost constitutes another potentially large positive feedback to warming. There is at least as much carbon stored in permafrost as in the Earth’s entire atmosphere (Zimov et al. 2006), and thawing permafrost releases substantial CH₄ (a greenhouse gas with an effect that is 25 times more potent per molecule than CO₂) from enlarging thaw lakes (Walter et al. 2006). However, it is difficult to predict how quickly CO₂ and CH₄ might be released from thawing permafrost to the atmosphere.

In summary, observed temperature trends demonstrate that the net effect of climate warming at high latitudes is a positive regional feedback to climate warming. This occurs primarily because the reductions in sea-ice extent and seasonal snow cover cause a decline in albedo and, therefore, an increase in energy absorption and heat transfer to the atmosphere. Expected future changes in Arctic vegetation and thawing of permafrost will probably magnify high-latitude warming (a positive feedback), whereas changes in boreal forest cover associated with increases in fire and insect outbreaks may have the opposite effect (a negative feedback). Although the net effect of these high-latitude changes in plant functional types is uncertain, they are unlikely to negate the strong positive feedback from declining snow-ice albedo, resulting in continued high-latitude warming. The human activity that most strongly contributes to this warming is emission of greenhouse gases (IPCC 2007a), suggesting that reductions in these emissions would be the most effective way to reduce climate warming.

### Changing arid lands

Just as ecosystem feedbacks have amplified rates of climate warming at high latitudes, ecosystem changes may have amplified the magnitude and duration of regional droughts in dry areas. For example, in the Sahel, a dry region south of the Sahara Desert, a drought that extended through the final three decades of the 20th century appeared to be initiated either by changing sea-surface temperatures in the adjacent Atlantic Ocean, or by land degradation in the Sahel region due to overgrazing (Foley et al. 2003a). However, although patterns of ocean circulation or overgrazing appear to have triggered the drought, they cannot readily explain its 30-year duration (Foley et al. 2003a), which greatly exceeds the normal length of droughts in other parts of the world.

Millions of people died from drought-associated famine...
and disease over the 30-year duration of the drought – an example of the tragic societal consequences of changes in climate–ecosystem feedbacks. It is thought that the initial drought caused a substantial reduction in plant cover, extending beyond the lands already overgrazed by local herders. As Sahel vegetation declined, albedo increased and evaporative energy transfer to the atmosphere further reduced convective uplift and associated monsoon rains in the region (Zeng et al. 1999; Wang and Eltahir 2000; Foley et al. 2003a; Figure 3). Although the drought in the Sahel was probably triggered by changes in ocean circulation and/or land-use practices, ecosystem feedbacks apparently contributed to its magnitude and extended duration.

Even localized changes in land cover and albedo can trigger hydrologic changes. In Western Australia, for example, extensive areas of heathland were cleared for wheat. The native heathlands had a lower albedo and therefore greater convective uplift, causing movement of moist air from the wheatlands toward the heathlands. This generated a local pattern of air circulation similar to that described for the Sahel, with a 10% increase in precipitation over the heathlands and a 30% decrease in precipitation over the wheatlands (Chambers 1998; Figure 5). A more heterogeneous pattern of heath and wheat would probably have prevented this local change in precipitation.

In summary, local and regional droughts may be amplified by ecosystem feedbacks that decrease vegetation cover, energy absorption, and convective uplift. This is an important issue: desertification is now widespread in arid regions of the world, due to both climatic and social changes (Reynolds and Stafford Smith 2002; Safriel et al. 2005). To what extent might these human influences contribute to drought? Alternatively, to what extent might afforestation (the deliberate planting of new forest tracts) or other efforts to increase vegetation cover reduce the likelihood of continued drought? The apparent importance of ecosystem feedbacks suggests that appropriate management could potentially reduce the likelihood of extended droughts.

## Changing forest cover

Complex social and economic forces contribute to large-scale changes in forest cover throughout the world (Shvidenko et al. 2005). Forests are being cleared in the tropics and in boreal Canada and Siberia, but are regrowing on abandoned agricultural lands in Europe and temperate areas. The impacts of these changes on the climate system are complex and depend on the local conditions. For example, deforestation in the tropics can lead to increased albedo and decreased energy transfer to the atmosphere, while afforestation can have the opposite effects. The balance among these climate feedbacks is poorly known, although the albedo (cooling) effects are strongest at high latitudes, and the moisture and carbon-balance feedbacks (warming) are strongest in the tropics. Preventing deforestation or expanding forest cover would have the opposite effects: warming through reduced albedo (strongest at high latitudes) and cooling through increased transpiration and carbon sequestration (strongest in the tropics).
dominate in the tropics, where a combination of high solar input to evaporate water, high soil moisture availability, and a long photosynthetic season drives large water fluxes from ecosystems to the atmosphere. In the Amazon, for example, 20–30% of annual precipitation derives from water that is recycled by evapotranspiration (Costa and Foley 1999). Model simulations suggest that extensive deforestation could lead to a drier, more savanna-like climate that would be less suitable for reforestation (Shukla et al. 1990; Foley et al. 2003b). Warm temperatures in the tropics probably also cause more rapid loss of soil carbon after logging than at high latitudes, augmenting the warming impacts of tropical deforestation.

In summary, the net warming feedback to climate from deforestation is strongest in the tropics (Bala et al. 2007). Conversely, planting of new forests is progressively more effective in reducing the potential for climate warming as we move from cold to warmer, wetter climates (Figure 6). Thus, reducing rates of deforestation and fostering reforestation in the tropics may be particularly effective in mitigating climate warming (Gullison et al. 2007).

### Socially mediated feedbacks between ecosystems and climate

We have shown that ecosystem feedbacks play an important role in modulating the effects of ecosystem or land-use change on the climate system. However, ecosystem changes in the coming decades will probably involve an additional layer of interaction, as society responds to climate change by altering land use or land cover in ways that feed back to further influence climate. For example, as discussed earlier, droughts in semi-arid zones can interact with social changes to trigger desertification, which increases albedo, weakens moisture-bearing monsoons, and predisposes semi-arid climate systems to drought. Other important classes of socially mediated climate feedbacks include the sensitivity of tropical deforestation to changes in the hydrologic cycle, shifts in temperate and boreal agriculture in response to drought and warming, and changes in trade and fossil-fuel consumption caused by climate-induced changes in infectious disease, human migration, and civil strife.

The lengthening of the growing season in the southern boreal forest may be a stimulus for widespread, human-driven conversion of forest to grassland and cropland in southeastern Siberia. This loss of forest cover might counteract some warming, with large changes in albedo during spring and summer serving as a negative feedback to regional warming.

More generally, many classes of land use are sensitive to climate and are likely to have important consequences for the evolution of atmospheric CO₂, air temperature, and water cycling over the next several centuries. We are only now beginning to understand how the ecosystem/climate feedbacks discussed here may interact with climate feedback processes (Mölders and Kramm 2007). For example, we cannot yet identify thresholds at which these interac-

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**Figure 5.** Boundary between heathland and wheat croplands in southwestern Australia (Chambers 1998). The heathlands absorb more radiation (low albedo) and transmit a larger proportion of this energy to the atmosphere as sensible heat than does adjacent croplands. This causes air to rise over the heathland and draws in moist air laterally from the irrigated cropland, which causes subsidence of air over the cropland. Rising moist air forms clouds and increases precipitation by 10% over heathland, whereas subsiding dry air reduces precipitation by 30% over the cropland.
tions change dramatically, and we cannot calculate the probability that a regionally focused climate change in one place (for example, from albedo effects associated with deforestation) might have teleconnections to changes in temperature or precipitation in other places. Still, climate–ecosystem feedbacks are understood better than climate–land-use–ecosystem feedbacks. The latter are complicated not only by the expanded set of decisions they involve, but also by the prospect that the climate signal initiating some of these feedbacks will weaken or strengthen the motivation for action to mitigate climate change. These climate–land-use–ecosystem feedbacks are completely absent from state-of-the-art climate models and are represented only crudely or not at all in Earth-system and integrated-assessment models.

Representing socially mediated feedbacks in climate system models is challenging, in part because many of the elements are only weakly coupled. For example, other economic, social, and political factors are likely to be more important than climate in shaping future trajectories of land cover (Ellis and Ramankutty 2008). Nevertheless, the carbon losses, albedo changes, and aerosol impacts caused by the sensitivity of land-use change to climate could exceed the magnitude of all the direct climate–ecosystem linkages described above.

### Conclusions

Five major messages emerge from this paper:

1. Ecosystems influence climate through multiple pathways, so efforts to mitigate climate through consideration of only one of these pathways, as with carbon in the Kyoto Protocol, are incomplete. Consideration of multiple feedbacks could lead to climate-mitigation strategies that provide more consistent mitigation of climate change, but will require careful quantification of these feedbacks and their interactions.

2. There is no “one-size-fits-all” solution for mitigating warming through managing ecosystems. Practices that effectively mitigate climate warming in the tropics may prove less effective or counterproductive in other regions.

3. Industrial greenhouse-gas emissions that contribute to climate warming originate primarily from industrialized nations in the temperate zone (Raupach et al. 2007), but some of the most promising strategies for ecosystem-based mitigation involve reducing deforestation in tropical developing nations or reducing desertification of arid zones. Although there are many opportunities for reducing these emissions, some of the lowest cost, highest benefit options for mitigation of climate change (e.g., sustaining biodiversity) come from reducing tropical deforestation (IPCC 2007b). The challenge is to find an equitable approach for distributing the attendant social and economic costs among nations.

4. Climate change is a much broader issue than temperature. Associated changes in the hydrologic cycle often have even greater societal impacts through changes in precipitation, evapotranspiration, runoff, and water available for human use.

5. Although our understanding of the multiple feedbacks between climate and ecosystems is far from complete and requires careful quantification, it is clear that ecosystems cannot “solve the climate problem” by removing all the CO$_2$ produced by fossil-fuel emissions. The ultimate solution to this problem may require major reductions in emissions from fossil-fuel combustion. Given the highly non-linear nature of feedbacks between ecosystems and climate, the benefits of reduced emissions will probably be much greater if implemented soon rather than in the distant future.

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