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TERRESTRIAL ECOSYSTEM FEEDBACKS TO GLOBAL CLIMATE CHANGE

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ABSTRACT

Anthropogenic greenhouse gases are expected to induce changes in global climate that can alter ecosystems in ways that, in turn, may further affect climate. Such climate-ecosystem interactions can generate either positive or negative feedbacks to the climate system, thereby either enhancing or diminishing the magnitude of global climate change. Important terrestrial feedback mechanisms include CO_2 fertilization (negative feedbacks), carbon storage in vegetation and soils (positive and negative feedbacks), vegetation albedo (positive feedbacks), and peatland methane emissions (positive and negative feedbacks). While the processes involved are complex, not readily quantifiable, and demonstrate both positive and negative feedback potential, we conclude that the combined effect of the feedback mechanisms reviewed here will likely amplify climate change relative to current projections that have not yet adequately incorporated these mechanisms.

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INTRODUCTION

Predictions of global climate change resulting from the buildup of greenhouse gases (GHGs) in the atmosphere are based on models that largely ignore climate-ecosystem interactions. Nevertheless, such interactions have the potential to generate large positive or negative feedbacks to the climate system, thereby either enhancing or diminishing the magnitude of climate change. We review here the evidence that such feedback interactions exist and are relevant to global climate change.

Awareness that climate influences plants and animals must surely date back to prehistory, whereas recognition of ecosystem influences on climate is a more recent development. Interestingly, what are perhaps the first written speculations about how a major change in an ecosystem might have altered regional climate involved human-induced ecological changes. Christopher Columbus speculated that deforestation resulted in decreased fog and rain in the Canary Islands and the Azores (1). As if to presage current controversies over even the sign of some of the effects of ecosystem change on climate, a chronicler of late-sixteenth-century Southern France speculated that deforestation due to expanding fuel consumption at iron foundries led to more intense and frequent rain storms there (2).

Historically, the most significant human impacts on ecosystems undoubtedly have resulted from agriculture and deforestation (3, 4). Prior to the recent and historically unprecedented buildup of GHGs due to fossil-fuel burning, these land-use practices were also the cause of the most significant human impacts on climate (5–8). Indeed, much of our current understanding about mechanisms by which ecosystem degradation can alter climate stems from study of past land-use practices. Human enhancement of the greenhouse effect (referred to here as global warming or global climate change), however, introduces two unprecedented issues: alteration of natural, not just managed, ecosystems, and effects on a planetary, not just local, scale.

In a brief, pedagogic Background section, we give a broad overview of the major approaches to elucidating feedback effects between climate and ecosystems, we describe a mathematical formalism used to quantify feedback linkages, and we argue that not-yet-quantified (and possibly not-yet-identified) feedback effects are likely to play an important role in global warming science.

We have organized the review according to the category of mechanism by which altered ecosystems can alter climate. At the broadest level, we consider

effects of ecosystems on the exchange of materials and energy between the planetary surface and the atmosphere. Material exchanges include changes in net fluxes of gases that absorb outgoing infrared radiation (i.e. the most important GHGs: carbon dioxide and methane) and of materials that scatter and absorb sunlight (dust and aerosol-forming particles, which exert a significant net cooling effect).

We include in this review feedbacks resulting from direct ecosystem responses to increasing atmospheric levels of carbon dioxide (CO_2) as well as those mediated by ecosystem responses to the greenhouse gas-induced climate changes. Although our review focuses on feedbacks mediated by terrestrial, not marine, ecosystems, we do not suggest that marine feedbacks will be unimportant. Indeed, changes in the supply of nutrients to marine ecosystems could explain shifts in atmospheric CO_2 concentrations between glacial and interglacial periods (see below). Methane (CH_4) emissions from hydrates in marine sediments could also result in a significant positive feedback (9) that is not addressed here. Furthermore, large-scale shifts in ocean circulation could be triggered by climate change and would have profound implications both through direct physical effects and through altering terrestrial ecosystems. For a discussion of feedbacks mediated by marine ecosystems and for useful broad surveys of ecosystem/climate feedbacks, we refer readers to a recent edited volume of papers (10) and to chapters 9 and 10 of the 1995 IPCC Working Group I Assessment (11).

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BACKGROUND

To characterize and quantify ecosystem/climate feedbacks, knowledge of both ecosystem responses to climate changes and climate responses to ecosystem changes is needed. Advances in our understanding of ecosystem responses to climate change have resulted largely from empirical studies of how particular ecosystems respond to climate change. Such studies include laboratory measurements designed to unravel specific mechanisms by which ecosystem components respond to climate change, ecosystem manipulation experiments in which responses of whole ecosystems to artificially induced climate change are observed, measurement of patterns of ecosystem variation along natural climatic gradients in space, and measurement of patterns of ecosystem change over time intervals during which climate has varied naturally. Advantages and disadvantages of these empirical approaches have been reviewed (12). Mathematical models have also been used in studying ecosystem responses to climate change, with their major purpose being to integrate empirical findings and ultimately to provide predictive capability.

In contrast to the array of empirical approaches available for studying ecosystem responses to climate change, there are few methods for gaining direct

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empirical knowledge about climate responses to ecosystem change. Much of our knowledge of climate responses, therefore, has come from mathematical models that use physics-based knowledge of climate change to scale up experimental findings to a wider geographic region. For example, suppose that field studies indicate that climate change will likely induce a decrease in the amount of stored carbon per unit area of experimental ecosystem plots subjected to artificial warming, with the lost carbon passing to the atmosphere as CO_2. The amount of carbon passing to the atmosphere from experimental plots would not cause a detectable change in the atmospheric concentration, of course, and so no climate change signal resulting from the experimental warming will be detected. But if the effect of warming on stored carbon can be shown by ecologists to be applicable to a much larger area than just the experimental plots, then the feedback effect on climate could be analyzed with global climate models that incorporate the ecosystem-mediated CO_2 source terms, as well as sources from fossil fuel combustion.

A useful qualitative description of a feedback process, in diagrammatic form, consists of a set of labeled system components and connecting arrows that form one or more closed loops (see Figure 1). Each arrow is accompanied by a +, −, or 0, assigned according to the nature of the causal connection between components, as shown in Figure 1. In our review, we summarize each of the major feedbacks using such diagrams.

If an arrow extends from A to B and the increase in A causes an increase in B, then the sign is (+); if an increase in A causes a decrease in B, then the sign is (−); and if an increase in A has no effect on B, then the sign is (0). The feedback loop in Figure 1 indicates a process in which an increase in A causes a decrease

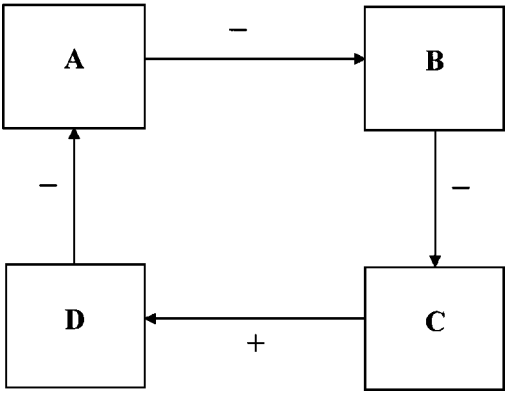


Figure 1 Qualitative description of feedback process.

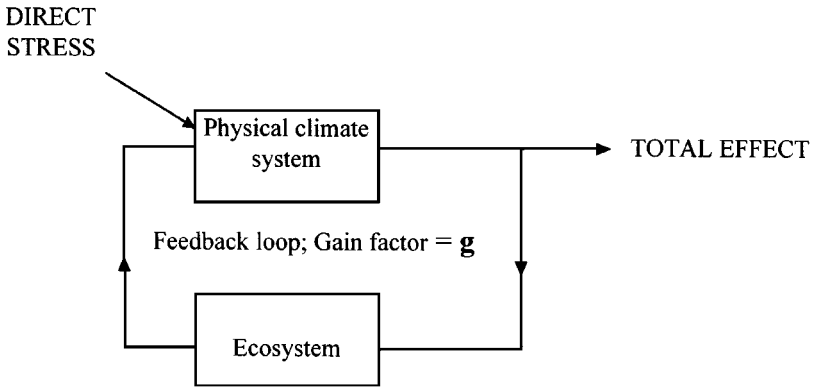


Figure 2 Quantification of feedback process.

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in B, an increase in B causes a decrease in C (or, equivalently, a decrease in B causes an increease in C), an increase in C causes an increase in D, and an increase in D causes a decrease in A. Because the product of $(-)(-)(+)(-)$ is $(-)$, this example describes a negative feedback (i.e. an initial increase in A triggers a sequence of events that reduces the original increase). Note that each of the signs is determined solely by the nature of the linkage between the two linked components and is independent of the other signs in the sequence. In this example, A might refer to surface temperature, B to soil moisture, C to area of desert, and D to surface albedo (i.e. reflectivity). If C was "area of nondesert," then the signs linking B to C and C to D would be reversed but the overall sign of the feedback would be unchanged.

A formalism for the quantification of such feedback effects is presented below and in Figure 2. This formalism achieves the goal of summing an infinite number of traverses around the feedback cycle: (climate change) $\rightarrow$ (ecosystem change) $\rightarrow$ (climate change) $\rightarrow \ldots$. However, it is valid only if the relationship between the state of the ecosystem and the state of the climate is linear or the perturbation is small in the sense that first-order Taylor series expansions of the state of the climate and of the ecosystem around the unperturbed state are valid. In more concrete terms, suppose that the climate variable of interest is globally averaged surface temperature, T_S, expressed on a Kelvin scale. The change in T_S is small in the sense above if the change in T_S is a small fraction of T_S itself. Practically speaking, the formalism would be generally considered useful if this fraction is ≤ 0.1, corresponding to a maximum temperature change of roughly 30 K.

As shown in Figure 2, the absence of a feedback loop means that

$$\text{TOTAL EFFECT} = \text{DIRECT EFFECT}.$$

But one pass around the feedback loop yields

$$\text{TOTAL EFFECT} = \text{DIRECT EFFECT} + (\text{g})(\text{DIRECT EFFECT}).$$

And infinitely many passes around the feedback loop results in

$$\begin{aligned}\text{TOTAL EFFECT} &= (\text{DIRECT EFFECT})(1 + g + g^2 + g^3 + \ldots) \\ &= (\text{DIRECT EFFECT})/(1 - \text{g}) \text{ if g} < 1. \end{aligned} \quad 1.$$

If $1 > g > 0$, then TOTAL EFFECT > DIRECT EFFECT, resulting in a positive feedback.
If $g < 0$, then TOTAL EFFECT < DIRECT EFFECT, resulting in a negative feedback.
If g > 1, then TOTAL EFFECT $= \infty$ (i.e. instability).

To calculate g, suppose the surface temperature, T_S, can be expressed as a function, F, of various factors, and that some of these factors themselves depend on T_S so that

$$T_S = \text{F}\,(p_1(T_S),\, p_2(T_S), \ldots)\,. \quad 2.$$

For example, $p_1(T_S)$ might equal the albedo of land surface, which may change if warming induces a change in the dominant vegetation. Then,

$$g = \sum_i (\partial \text{F}/\partial p_i)(\partial p_i/\partial T_S) = \sum_i g_i. \quad 3.$$

Consider the first term in this sum, with p_1 being surface albedo. The first partial derivative in this first product measures the effect of a change in surface albedo on global temperature. Estimation of that derivative could be carried out with a conventional (no ecosystem processes included) model such as a GCM (even if no closed form expression exists for the function F, the derivative could be evaluated numerically using the model with all other feedback processes turned off). Multiplying that derivative is the term $\partial p_1/\partial T_S$, which expresses the effect of temperature change on surface albedo. Evaluation of this term requires knowledge of the extent to which warming will induce a shift in vegetation cover and the effect of that shift on surface albedo. The former involves knowing about responses of plant species to climate change; the latter requires information about the optical characteristics of vegetation canopies. Note that if a model already incorporates $n - 1$ feedback processes, the effect on T of the introduction of an additional process will be influenced by the $n - 1$ processes already in the model. Then

$$\frac{(\Delta T_n - \Delta T_{n-1})}{\Delta T_n} = \frac{g_n}{\left(1 - \sum_{i=1}^{n-1} g_i\right)}, \quad 4.$$

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where ΔT_n is the effect of the direct stress with n feedbacks operating (and ΔT_{n-1} is the effect with only the first $n-1$ feedbacks operating).

Conventional general circulation models (GCMs) incorporate several important feedback mechanisms. One is the "ice-albedo feedback," in which warming induced by elevated atmospheric greenhouse gas concentrations results in the melting of ice and snow cover, which leads to a lower value of the earth's albedo. Because a lowered albedo enhances the original warming, this is a positive feedback. A second feedback involves water vapor. The amount of water vapor (itself a GHG) that the atmosphere can hold at constant relative humidity increases with rising atmospheric temperature. Combined with evidence that relative, not absolute, humidity is approximately invariant under warming, this leads to another positive feedback. A third feedback, of more uncertain magnitude and even sign, involves clouds. Clouds can warm Earth's climate by trapping outgoing radiated heat and outgoing sunlight reflected back to space from below the clouds. They can also cool the planetary surface by reflecting or absorbing incoming solar radiation. The net effect depends on the altitude and optical properties of the clouds and the albedo of Earth's surface below the clouds.

Together, these feedbacks to the direct effect on globally averaged surface temperature of increasing GHG concentrations result in a value of the gain, g, in the range of 0.4–0.78 (see Figure 2). Much of the spread in this range reflects the uncertainty in the cloud feedback. The direct effect of an increase in GHG levels to a level that is effectively equivalent to a doubling of the pre–Industrial Revolution CO_2 level (the "$2 \times CO_2$ scenario") is calculated to be roughly 1°C. Multiplying this by the factor $1/(1-g)$ from Figure 2, we find that the total effect of the GHG increase is an elevation of surface temperature by an amount ranging from $1°C/(1-0.4) = 1.6°C$ to $1°C/(1-0.78) = 4.5°C$. These estimates stand today as widely cited values for the effect of $2 \times CO_2$ on surface temperature. Inclusion of the climatic effects of aerosol results in somewhat lower estimates, however, because the direct effect of the sum of aerosol and $2 \times CO_2$ is less than the direct effect of $2 \times CO_2$ alone.

We note that the value of g is given by a sum over all the individual feedbacks that could possibly contribute to the Total Effect. Those individual feedbacks in the sum that are positive add to the value of g, while negative feedbacks reduce the value of g. At the upper limit of uncertainty of the combined effect of the ice-albedo, water vapor, and cloud feedbacks, where $g = 0.78$, it would take only a very small relative increase in g to exert a huge effect on the increase in surface temperature. For example, if one additional feedback process adds a term in the sum that raises the upper limit on g from 0.78 to 0.9, the effect would push the upper limit of warming up from 4.5°C to a value of $1°C/(1-0.9) = 10°C$. Yet, compared to the value of the other feedbacks, this is not a large additional process.

The above example shows that the climate system is very sensitive to the possible presence of additional feedbacks, and in particular could be strongly influenced by ecological processes that result in positive or negative feedback. As first pointed out by Lashof (13), a number of biogeochemical and other feedback effects not included in GCMs do indeed exist and could push up g to a value close to the point of instability ($g = 1$). It was true at the time of his analysis (1989) and is still largely true today that the uncertainties in our understanding of these feedbacks are considerable. Clearly it is important to better understand and quantify potential ecosystem-mediated feedbacks to climate warming. Table 1 provides a taxonomy of the feedbacks we review, along with their corresponding sign, as currently understood.

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MATERIAL EXCHANGES

Carbon Cycle Feedbacks

Terrestrial ecosystems contain three or four times more carbon (in the form of soil and plant organic matter) than is in the stock of atmospheric CO_2, and more than one eighth of atmospheric CO_2 is exchanged with ecosystems each year through the biological processes of photosynthesis and respiration. These natural biologically driven flows of CO_2 are more than ten times larger than the imbalance in flow from the anthropogenic additions expected to cause substantial global warming. Thus, based on magnitude considerations, ecosystem responses to rising CO_2 concentrations and climate change have the potential to introduce substantial climate feedbacks, since even small perturbations in natural carbon flows could cause large changes in atmospheric CO_2, and hence, climate.

This section reviews what is known about carbon cycle feedbacks and the biological and ecological mechanisms by which such feedbacks might come about. There is a spectrum of levels at which carbon feedbacks can be investigated, which might be characterized as ranging from top-down to bottom-up. Top-down approaches examine broad-scale patterns across space and time and then use these to impose constraints on integrated behavior of "the bottom." Bottom-up approaches focus on understanding the physiological and biochemical mechanisms that control the flow and storage of carbon in plant and microbial communities and attempt to integrate "up," across broader spatial and temporal scales. We summarize, in a top-down fashion, what is known about the stocks and flows of carbon in the global carbon cycle. After that, we turn to a more bottom-up approach to examine in greater detail what is known about the underlying biology and ecology.

CARBON CYCLING AND CARBON SINKS (TOP-DOWN APPROACHES) Although carbon-cycle feedbacks to climate on million-year time scales are dominated by

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exchanges with the carbon in carbonate rocks (by far the largest stock of carbon on the planet), the weathering and sedimentation rates governing this exchange are so slow that they can be neglected as far as anthropogenic climate change is concerned. On the more relevant time scales of months to centuries, carbon-related feedbacks to climate will be controlled by exchanges of carbon between the earth's atmosphere and the terrestrial and oceanic reservoirs. To a first approximation, these exchanges are assumed to have been in steady-state prior to anthropogenic perturbations. An important aspect of the global carbon cycle for the understanding of carbon-related feedbacks is the quarter-century-long debate—still only partially resolved—about the fate of excess carbon released into the atmosphere by human activities (14). This debate exists because the observed increase in atmospheric CO_2 (together with the calculated increase in oceanic uptake) since preindustrial times has been insufficient to account for all the carbon emitted due to human activities during this period (assuming that terrestrial ecosystems would have neither gained nor lost carbon if not for the losses from human land-use changes). All told, accounting for the period between 1750 and 1990, the atmosphere is "missing" an estimated 60–100 Pg[1] of carbon (8–13% of the current atmospheric inventory, and one third to one half of the emissions from all human fossil-fuel burning (14–16), an amount too large to be accounted for by uncertainties in the budget terms (14). This means that either our understanding of oceanic carbon uptake processes is seriously flawed or the assumption that terrestrial ecosystems remained in steady-state (apart from land-use changes) is in error.

Table 2, which shows the most recent consensus estimates of sources and sinks for excess CO_2 in the 1980s, includes a carbon sink term due to northern-hemisphere forest regrowth. This term reflects important progress made on the "missing carbon" problem in the last 10 years that indicates the initial assumption of steady-state for terrestrial biota is in error. The evidence comes from several sources, including (*a*) the spatial distribution of atmospheric CO_2, which, together with known patterns of atmospheric circulation, allows inference of the location on the surface of carbon sinks and sources [which indicates a substantial northern-hemisphere sink in the midlatitudes; (17, 18)]; (*b*) variations in the atmospheric O_2 concentration; and (*c*) variations in the $^{13}C/^{12}C$ ratio in atmospheric CO_2. The second of these methods allows discrimination between oceanic and vegetative uptake of CO_2 because oceanic CO_2 uptake does not involve O_2 exchange, whereas the carbon flows associated with decomposition, plant respiration, and photosynthesis do. Accurate measurement of the atmospheric CO_2-O_2 anticorrelation thus provides an independent constraint on the size of the ocean sink. The third method allows discrimination between

[1]Pg $= 10^{15}$ g.

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Table 1 Taxonomy of terrestrial ecosystem feedback mechanisms

Feedback mechanism	Brief description of feedback mechanism	Sign[a]	References[b]
Atmospheric CO_2/N_2O			
CO_2 plant fertilization	Increased CO_2 can stimulate photosynthesis, but respiration can be both stimulated and suppressed	(−)	44–50, 52–54, 57–62, 66
CO_2 enrichment of soil and litter	Increased CO_2 has negligible direct effect, but indirect effect can result in lower N availability, constraining any stimulatory effect on plant growth	(+)	67–70
Climatic effects on plants	Increased CO_2 and warming may affect photosynthesis and respiration in a way difficult to determine net effect. Warming may also cause increased water stress and temperature shifts away from optimum, reducing CO_2 uptake	(+/−)	45, 71–73, 75, 155
Climatic effects on soil	Warming causes increased soil respiration, but effects vary according to moisture availability; interactions with N can lead to either stimulated plant growth or release of N_2O	(+/−)	76–87
Fire frequency	Warming may increase fire frequency and thus reduce biomass C storage by changing age class structure and possibly geographic distribution of many species; soil respiration and nitrogen availability could also be affected	(+)	95–100
Atmospheric CH_4			
Peatland response	Warming will increase CH_4 production in high-latitude peatlands. Changing soil moisture will influence both CH_4 production and consumption, with net effect uncertain; changes in topography may also increase CH_4 release	(+/−)	102, 103, 105, 106, 109, 111, 113, 114

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Atmospheric albedo			
Dust and aerosol load	Climate change and socioeconomic factors cause deforestation, land degradation, and aggravate desertification, adding to the atmospheric dust and aerosol burden, which enhances cooling effect	(−)	115, 118, 121, 122, 124, 126, 128–130
Surface albedo			
Poleward biome shift	Warming induces poleward expansion of boreal forest into tundra, decreasing albedo and thus increasing radiation absorption; paleo studies suggest large feedback	(+)	133, 134, 137–141
Land use change	Climate change and socioeconomic factors cause deforestation, increasing albedo, altering hydrologic cycle, which affects regional climate; global climatic effects remain unresolved	(?)	144, 145, 147–154, 161, 162
Latent and sensible heat transfer to atmosphere			
Vegetative respiration	Increased CO_2 and warming can affect transpiration and hence surface cooling associated with latent energy flux in opposite directions; regional impacts may be very large	(+/−)	45, 73, 155–160

[a]The sign of the feedback mechanism refers to the effect on global climate change.

[b]Some references here address the nature of ecosystem-climate feedback more explicitly than others. Other references not listed here, but cited in the text, provide additional background and context for the understanding of ecosystem-climate feedbacks.

Table 2 Sources and sinks for excess carbon, 1980–1989

Reservoir	Average flux (Pg C/year)
Sources	
Fossil fuels	5.5 ± 0.5
Deforestation and land use	1.6 ± 1.0
Total	7.1 ± 1.1
Sinks	
Atmosphere	3.3 ± 0.2
Oceans (modeled)	2.0 ± 0.8
Northern hemisphere forest re-growth	0.5 ± 0.5
Total	5.8 ± 1.0
Imbalance (inferred terrestrial sink)	1.3 ± 1.5

Source: Schimel et al (21).

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oceanic and terrestrial sinks because terrestrial uptake of CO_2 strongly discriminates against ^{13}C relative to ^{12}C. Application of these latter two methods points, consistent with the first method, to a northern-hemisphere terrestrial sink for the missing carbon (15, 19, 20). However, some argue, based on model results, that most of the terrestrial sink should be in tropical forests (22). Additional support for a terrestrial (as opposed to oceanic) sink is given by a recent study of plant growth in high northern latitudes (20a) and by models of the effects of increased CO_2 concentrations and increased nitrogen deposition, which predict increases in terrestrial productivity and carbon sequestration (21). The recent IPCC assessment concluded, however, that aside from a few field measurements of whole-system carbon fluxes in mid-to-high–latitude forests [which do show net carbon sequestration; (23, 24)], "experimental confirmation from ecosystem-level studies is lacking. As a result, the role of the terrestrial biosphere in controlling past atmospheric concentrations is uncertain, and its future role difficult to predict" (11, p. 79).

Modeling studies that attempt to better understand the details of the mechanisms controlling this sink are ongoing (26, 27). In the meantime, most predictions of future CO_2 concentrations (including those of the IPCC) assume a biospheric sink due entirely to CO_2 fertilization tuned to reproduce concentrations observed in the 1980s, given estimates for other CO_2 sources and sinks. This fertilization effect is then assumed to continue to operate in the same way into the future, implying a sink that increases monotonically with CO_2 concentrations (28). This approach is risky, as there is a high degree of uncertainty regarding the processes responsible for the inferred terrestrial sink. If terrestrial sequestration levels off, and/or other feedbacks come into play, future atmospheric CO_2 concentrations could be much different than current predictions suggest.

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The missing carbon problem is intimately connected to the question of carbon-cycle feedbacks. If increased terrestrial CO_2 uptake is a negative feedback monotonic in atmospheric CO_2 (e.g. if it is due to a simple CO_2 fertilization efffect that increases with CO_2 concentration, independent of anything else), then the extrapolation approach used by the IPCC is a reasonable one. If, however, the sink is due in part to processes other than CO_2 fertilization (for example, increased nitrogen deposition, as discussed e.g. in 26)—or is not a feedback at all (such as forest regrowth that accidentally coincided with the atmospheric rise in CO_2 and will stop when the forests finish regrowing)—this assumption may be problematic. Moreover, if there are feedbacks in the carbon cycle that are not in current models and that only begin to take effect after substantial warming is realized, then the extrapolation of a biospheric sink could be substantially in error.

TEMPORAL PATTERNS OF CO_2 AND CLIMATE Looking at patterns of atmospheric CO_2 and temperature across time provides clues about a possible linkage between the two. There is evidence on at least three time scales that CO_2 and global temperature are correlated: the ice-core data of the last 220,000 years, the ice-core data of the last several hundred years, and the direct measurement of temperature and CO_2 over the last several decades. The ice-core record—the longest so far is from the Vostok station in Antarctica (29–31)—indicates that over the last 220,000 years (which extends from before the last interglacial period to the present), atmospheric CO_2 and temperature were highly correlated, with changes in CO_2 concentration apparently lagging temperature changes (at least during cooling) by about 1000 years. At the end of the last glacial period (18,000 years ago), the temperature was about 5°C cooler, and atmospheric CO_2 concentrations were about 80 ppm (170 Pg carbon) below modern preindustrial levels (14).

The source of the increase in atmospheric carbon since the last glacial period may well have been the oceans, because the terrestrial biosphere most likely gained carbon as the earth warmed and the biota spread (32). The role of terrestrial biota is subject to some controversy, however. Prentice & Fung (33), using a model based on correlations between present-day vegetation and present-day climate to predict vegetation distribution (and hence, carbon storage) under different climate regimes, have suggested that net terrestrial carbon storage during the last glacial period was about the same as today. At the other extreme, Adams et al (32) infer from the pedological and sedimentological pollen record that during the last glacial maximum there was 1300 Pg less carbon in the terrestrial biosphere, implying that glacial terrestrial carbon storage was less than half of what it is now. Carbon isotope data on glacial oceanic ^{13}C (from the marine benthic record) and glacial atmospheric ^{13}C (from ice cores)

indicate that the carbon storage difference is in the range of 270 to 720 Pg, values in between the two extremes (34–36). In any case, increases in atmospheric CO_2 between the last glacial period and the recent preindustrial period clearly involved substantial carbon transfers from the ocean.

There also appears to be a correlation between CO_2 and global temperature over the last several hundred years. Atmospheric CO_2 data from the 1400–1900 time period appear to show a fall, followed by a rise, in CO_2 concentrations at the same time as the slight cooling of the so-called "little ice age" of the seventeenth century (37). Finally, the CO_2 anomaly (the residual variation after the seasonality and upward trend are removed) over the past several decades shows a high correlation (with a several-week lag) with the temperature anomaly over the same time period (38). This correlation includes the recent (mid-1991–1994) large slowdown in atmospheric CO_2 growth (the 1.5 ppm deviation from expectation is equivalent to a loss of 1.6 Pg of carbon from the northern hemisphere atmosphere). This "Pinatubo carbon anomaly" (so named because it began a few weeks after the volcanic eruption) is apparently (based on trends in atmospheric ^{13}C and O_2) due to an increased terrestrial sink (19, 20, 39). Several recent modeling studies illustrate plausible mechanisms by which interannual climatic variations such as the Pinatubo effect could be causing variations in terrestrial carbon storage (40–42). These short-term variations in climate and carbon hold particular promise for developing and testing our understanding of climate-carbon feedbacks on time scales relevant to addressing anthropogenic global warming.

In sum, the overall pattern of top-down approaches over a range of time scales, and at temperatures and CO_2 concentrations at or below current ones, is consistent with a net positive feedback, but the apparent mechanisms are different (long-term variations between glacial periods are ocean driven, while the recent interannual variations appear to be driven by terrestrial biota), and the details poorly resolved.

ECOLOGICAL FEEDBACK MECHANISMS (BOTTOM-UP APPROACHES) Carbon feedbacks from the terrestrial biosphere will come about principally as a consequence of impacts on either or both of the two basic living pools of ecosystems: the autotrophs (principally chlorophyll-containing plants), which fix carbon from the atmosphere during the course of photosynthesis; and the heterotrophs (principally microorganisms), which typically obtain their energy needs from the oxidization of reduced carbon compounds.

There are two principal types of carbon feedback mechanisms that should be distinguished. In CO_2 feedbacks, changing levels of atmospheric CO_2 directly cause perturbations to the carbon cycle without involving climatic shifts as an intermediate step. In climate feedbacks, the effects of rising atmospheric GHG

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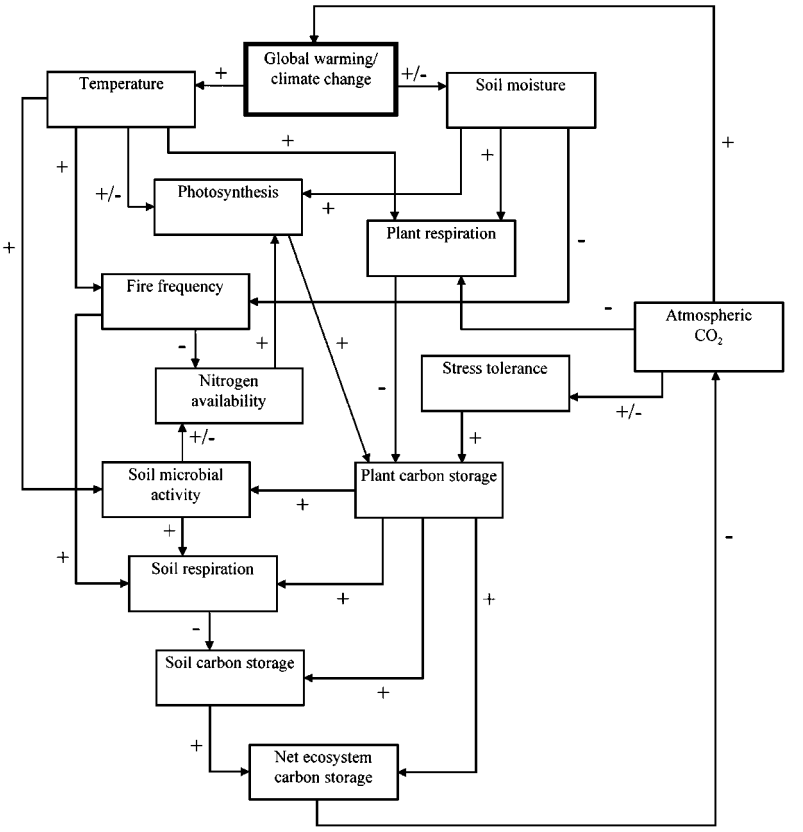


Figure 3 Possible climatic feedback paths in a hypothetical ecosystem [see also Figure 1 of Harvey (43)].

concentrations are felt indirectly as a result of induced climate change (Figure 3). The combined net effect of both types is difficult to predict, however, because each is likely to simultaneously involve both positive and negative feedback mechanisms. For example, where global warming causes both soil warming (which stimulates microbial activity and, hence, soil respiration) and drying (which suppresses it), the sign of the net feedback will depend, all else being equal, on which effect is stronger. Despite the clear need for experimentally tested predictions of simultaneous CO_2 and climate feedbacks, most experiments conducted so far have focused on the direct CO_2 effect alone, some have focused on climatic effects, and fewer still have attempted to combine the two. No field experiment so far has realistically (i.e. without chambers) manipulated

both climate and CO_2 levels at the ecosystem level (12). Below we briefly review first the CO_2 effects on plants and soil individually and then the climatic effects.

CO_2 fertilization and plants Numerous experiments demonstrate that increasing the supply of CO_2 generally increases photosynthetic uptake by plants from many different ecosystems under many different conditions (44), a negative feedback (assuming that the increased photosynthesis will lead to long-term increases in carbon storage in plant biomass or soils). Indeed, such experiments provide much of the empirical basis for the general assumption discussed in the previous section that the missing carbon is in the biosphere.

The detailed response of plants to elevated CO_2 depends, first of all, on the biochemical pathway of photosynthesis used by the plant. For C_3 plants (95% of known plant species), the biochemistry predicts that increases in intercellular CO_2 typically should raise the photosynthetic CO_2 uptake rate, all other things being equal (45). With the C_4 photosynthetic pathway, on the other hand, the enhancement of photosynthetic uptake due to elevated CO_2 should be relatively lower (46). Many experiments generally confirm this prediction (47, 48), but some show no difference between C_3 and C_4 plants (6), or even instances of effects in the opposite direction (50). Since photorespiration increases with the atmospheric O_2/CO_2 ratio, increasing intercellular CO_2 concentrations greatly decreases leaf photorespiration in C_3 plants (51). The effect of elevated CO_2 on the metabolic dark respiration of plants is much less clear (52), and experiments show opposite effects with different species [e.g. Oechel & Strain (53) vs Gifford et al (54)]. On balance, if increases in photosynthesis are not canceled by increases in respiration, carbon stocks in plant biomass will grow, and some fraction of anthropogenic CO_2 will be sequestered.

The overall long-term global plant response to elevated CO_2, however, may not be straightforwardly predictable from the experimental data base, which consists largely of short-term studies that are conducted in potted plants or greenhouses under conditions of high resource availability, or on individual plants or monocultures. Studies with conditions that closely approximate real-world field conditions (in which multiple plant individuals and species interact with each other within communities in resource-limited environments with long acclimation times) are few in number. Of some 1500 publications on the subject, only 2% deal with natural vegetation in situ (55, 56), and these more realistic experiments sometimes confound the predictions that might have been made from simpler experiments.

For example, in the first CO_2-enrichment experiment conducted over multiple growing seasons on the ecosystem scale in a natural arctic tundra (57, 58), an initial period of enhanced carbon uptake was followed by reestablishment of CO_2 flux homeostasis after three years (a result caused by a downward

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readjustment in plant photosynthetic capacity). In treatments that combined CO_2 elevation with heating, the CO_2 fertilization effect persisted after three years (but appeared to be declining). Another prominent study showed no significant CO_2 fertilization effect in an experimentally constructed tropical ecosystem (59, 60), even though models often predict that CO_2 fertilization should be greatest where the temperature is highest (e.g. 22). The interactive effect of CO_2 and temperature has also been shown in smaller-scale studies (61, 62). The effect of mineral nutrient availability (such as nitrogen) on the magnitude of the CO_2 effect is another key variable, one which is subject to some controversy. For example, it is often stated that plants that are nutrient-limited should in general be much less responsive in absolute terms to elevated CO_2 (e.g. 51), and some studies appear to support this (59, 63), but the generality of this claim is strongly disputed by others (22, 44).

Increased CO_2 availability means that plants can partially close their stomata (tiny openings on the epidermal layers of plants where gaseous exchanges take place), thereby reducing water loss without suffering a decrease in carbon uptake. This leads to increased water-use efficiency (denoted WUE and defined as the ratio of the weight of dry matter produced to the amount of water transpired), an effect that indicates that CO_2 fertilization should be especially effective in water-limited ecosystems and may aid vegetation found in arid and semi-arid regions (64, 65). Stomatal closure could also ameliorate air pollution–related stress, since the stomata serve as the key entry point for gaseous pollutants like tropospheric O_3 and SO_2 [(66); but see Allen & Amthor (45) who find that CO_2-induced inhibition of respiration could increase vegetation's susceptibility to certain pollution-related stresses, since the products of respiration often aid in the detoxification process].

CO_2 enrichment effects on soils and litter The potential for elevated CO_2 to increase the biotic carbon sink depends not so much on CO_2-induced changes in plant photosynthesis or net primary productivity (carbon flow) but on whether these lead to increases in plant biomass or soil organic matter (carbon stock). Thus, the behavior of the litter and soil carbon pools in response to elevated CO_2 is key. Elevated CO_2 is not expected to have a significant direct impact on rates of litter and soil decomposition (67). The reason is that partial pressures of CO_2 in the soil atmosphere are already tens of times higher than atmospheric levels, so incremental increases of 300–600 ppm in the atmosphere will have only small percentage impacts on CO_2 in the soil atmosphere. The principal effects are thought to be indirect ones mediated by plant responses, which can result in changes in litter quality and the soil environment, thus affecting the microbial communities that mediate litter decomposition (Figure 3). One possibility [the "Bazzaz hypothesis" (68)] is that a rise in CO_2 will result in an increase in plant

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and litter C:N (decline in litter quality), which in turn will cause a decrease in soil nitrogen availability (from reduced nitrogen mineralization associated with decomposition and increased microbial immobilization). The decreased nitrogen availability could limit plant growth, thus imposing a negative feedback constraint on the initially positive responses of plants to elevated CO_2. But other outcomes are possible. Elevated CO_2 can stimulate plant root activity and exudation, thereby stimulating microbial activity and increasing nitrogen availability (69). It has recently been suggested that a similar effect might also be caused by increases in soil moisture brought about by decreased plant transpiration (70).

Climatic effects on plants The short-term effects of temperature and moisture on plant physiology have been well studied (71, 72). Plant photosynthesis and respiration tend to respond differently to temperature. Above 0°C, gross photosynthesis responds rapidly at first to rising temperature before leveling off and eventually declining to zero again at very high temperatures (typically >40°C), owing to protein denaturation. Plant respiration, in contrast, tends to rise slowly at first and then rapidly at higher temperatures, potentially by 10–35% or more per 1°C if water availability is sufficient (73). Net photosynthesis, therefore, achieves its maximum at the intermediate optimum temperature where the marginal rates of increase of gross photosynthesis and respiration with temperature are equal. Whole-plant growth rates also tend to follow this pattern and to allocate resources to their photosynthetic apparatus so that their optimum growth temperature tends to be near mean growing-season temperatures of their environment (72). A plant photosynthesizing at its optimum rate can therefore be expected to suffer a short-term decline in CO_2 uptake if temperature shifts in either direction; in the longer term, however, acclimation to temperature is common (74), although shifts in the competitive balance among species in a community are likely.

Water stress is well known to decrease photosynthetic uptake and growth in a wide range of plants (72, 75). Such effects occur when plants increase their water-use efficiency by reducing stomatal conductivity, which in turn inhibits the inflow of CO_2 and thus carbon uptake. In certain regions then, such as continental interiors where soil drying is often projected to accompany warming (reviewed in 43), a decrease in carbon uptake via photosynthesis might be expected. Because this effect could be ameliorated by the elevated CO_2 effects that will accompany climate change, however, the combined net effect on carbon storage is difficult to predict.

Climatic effects on soils and soil respiration The cycling of carbon in the soils of natural ecosystems on the time scale of anthropogenic climate change will be controlled primarily by the heterotrophic soil microorganisms, which play a central role in the decomposition of organic carbon compounds. Microbial

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activity and respiration are strongly influenced by soil temperature and moisture levels (76). As with plants, warming generally accelerates (up to the point of protein denaturation) the chemical reaction rates of respiration. The effect of moisture changes depends on which of three moisture regimes apply: At low moistures, respiration increases with increasing water availability; over a broad intermediate range, increasing moisture has little effect; and at high levels, saturating and flooding conditions limit oxygen availability to the point where anaerobic decomposition takes over and rates of organic matter decomposition slow substantially (76).

The correlation between climate and soil respiration rates across a range of ecosystems has been well established. These patterns clearly show that as temperature and moisture increase, so do in situ soil respiration rates. This same pattern is well demonstrated in laboratory incubations of soil and litter as well (e.g. 77, 78). Based on these patterns, and on models built upon them, a number of studies have predicted that global warming will induce significant loss of carbon from soils (79–84). As with CO_2 enrichment effects, however, it is important not to consider these effects alone, because the fate of the nitrogen mineralized along with the carbon may play an important role in what actually happens to carbon in the whole ecosystem (85). The mineralized nitrogen could be (*a*) assimilated by plants, resulting in a net negative feedback due to enhanced plant growth (86); (*b*) immobilized by microbes, resulting in a positive feedback, as anticipated by the above results; or (*c*) lost from the ecosystem via leaching or via gaseous loss (as N_2 and N_2O) after nitrification and denitrification (87), conceivably adding an N_2O-based feedback (positive in this case) to the carbon effect.

Ecosystem-level experiments There have been relatively few manipulation studies of climatic effects at the ecosystem level. The ones that do exist reveal that ecosystem-level interactions tend to make the overall response much more difficult to predict than the simple trends expected from understandings of short-term individual plant physiological responses. For example, in a nine-year study of warming and nutrient additions on arctic tundra, there were large effects on individual species, but because of differential and opposing responses of different species, the whole ecosystem response was much less significant. In addition, even focusing on individual species' responses over the short-term (3 years) gave poor predictions of their long-term (9 years) responses. Also, as with the ecosystem-scale investigations of CO_2 enrichment, many of the important effects of elevated temperature were those mediated by the indirect responses brought about by changes in nutrient cycling (88).

Several field manipulation studies on the effect of warming in natural ecosystems have been done that show the potential for significant impacts on trace gas

fluxes, at least in the short term. Peterjohn et al (89, 90) measured increases in carbon loss via soil respiration in response to a soil-warming manipulation in a mid-latitude forest. In a field-warming manipulation study in a Rocky Mountain meadow, Saleska et al (SR Saleska, J Harte & MS Torn, submitted) measured a reduction in net ecosystem carbon storage (photosynthesis and respiration combined) in heated plots that was on the order of 100 g carbon per square meter during one growing season (92). Another study (in the Alaskan tundra) of ecosystem-level carbon exchange, although not a manipulation, hypothesized that measured net carbon losses in arctic tundra in recent years were due to concurrent trends in warming and drying in the Arctic (93). If these results from the Alaskan tundra are extrapolated to the circumpolar Arctic, Oechel et al (93) calculate that 0.2 Pg carbon per year may have been lost to the atmosphere from these regions during the 1980s. Thus, at the global scale, it can be said that the future effect of anthropogenic greenhouse gas emissions on carbon storage over time will depend on complex interactions of the carbon and nitrogen cycles, as they are influenced by rising CO_2 concentrations, climate change, and nitrogen deposition, among other factors.

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FIRE AND THE CARBON CYCLE Studies of ecosystem response to climate change have largely emphasized the direct, rather than indirect, effects of changes in temperature and precipitation on biogeochemical processes and on the geographic ranges of organisms and ecosystem types. Climate change, however, can also affect ecosystems through a wide variety of indirect mechanisms (94), one of which is warming-induced change in the frequency or intensity of fire.

The importance of fire in determining dominant vegetation types and biospheric carbon storage has been emphasized for boreal (95) and temperate (96) ecosystems. Suffling (95) developed a model that accounts for 65% of the geographic distribution of dominant species assemblages in a boreal transect of Ontario as a function only of the mean fire-free interval, which is used to calculate the probability of survival to reproduction for each competing species. Species with the highest probabilities of reproducing are predicted to be the dominant vegetation types in each region. Kurz et al (96) show that substantial reductions in biomass carbon storage can result from changes in the age-class structure of forests induced by increases in fire frequency and regeneration delay, even in the face of a CO_2 fertilization effect that could increase the average biomass for each individual age class. They also emphasize the asymmetry in rates and risks between the potential for forests to continue to gradually accumulate carbon and the potential for increased disturbance to rapidly reverse this process.

The effect of increases in fire frequency on soil carbon storage was emphasized in a study of boreal forests by Kasischke et al (97). They point out that

there are large carbon stocks in the ground layer of boreal forests, much of which can be oxidized directly by fire. In addition, for several decades following a fire, summer soil temperatures will be substantially elevated and the soil active layer overlying permafrost will increase in depth, leading to higher rates of soil respiration. Overall, Kasischke et al find that increased fire frequency in boreal forests could lead to an average net release of 0.3–0.8 Pg carbon per year for a 50–100-year period, despite a small increase in live biomass due to warming (but not accounting for any direct effects of higher CO_2 concentrations).

Another important interaction that needs to be further investigated is the effect of changes in fire regimes on nutrient availability and hence carbon cycling. In particular, Kuhlbusch et al (98) have estimated that biomass burning results in denitrification of 10–50 TgN per year or 5–50% of global nitrogen fixation. While most of this total comes from tropical ecosystems, particularly natural and human-induced grassland fires, increased fire frequency could also have a substantial impact on nitrogen availability in forested ecosystems.

Likely changes in fire frequency induced by global warming have been studied for Canada (99) and Northern California (100). Results for Canada and northern parts of the United States based on the Canadian General Circulation Model show significant increases in the Canadian Fire Weather Index (FWI) over the continental interior, with decreases over much of eastern Canada. The areas where FWI is predicted to increase, however, are concentrated where most fire activity currently occurs, while fire is already only a minor problem in the areas where FWI is predicted to decrease. Torn & Fried (100) used a much more detailed fire-simulation model to examine the implications of a doubled-CO_2 climate on fire dynamics in Northern California. This model incorporates the effects of fire-control activity and predicts the area burned in contained fires as well as the number of fires expected to escape containment. Results indicated likely increases in both the area burned and the number of escapes, with grassland fires being most severely affected. There were, however, considerable differences in the magnitude of the changes predicted, depending on which general circulation model results were used as inputs to the fire model, indicating that further improvements in prediction of regional changes in climate are needed before the detailed results of this type of exercise can be considered reliable.

Methane Feedback

Methane (CH_4) is the second most important (after CO_2) greenhouse gas perturbed by human activity, responsible for 19% of the direct warming effect (radiative forcing) of GHGs since preindustrial times (21). Current concentrations of over 1700 ppb are well over twice preindustrial background levels. Methane

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emissions are dominated by biological sources; anaerobic decomposition of organic matter in natural wetlands, rice paddies, and landfills is responsible for about 40% of the identified net sources (101). Changes in the rate of methane oxidation by atmospheric hydroxyl radicals (OH) and of biological methane oxidation also play an important role in the global methane budget. The strong dependence of these processes on environmental conditions suggests a potential for substantial climate change feedbacks, although quantitative estimates of the magnitude of these feedbacks remain highly uncertain. Potential feedback processes involving methane have been recently reviewed (102, 103).

Strong coupling between climate and atmospheric methane is clearly indicated in the Vostok ice-core record (30, 31). Glacial periods are characterized by methane concentrations of 300–400 ppb with interglacial values of 600–750 ppb (101, 104). This coupling is also found on shorter time scales, such as the Younger Dryas period, during which methane concentrations declined by several hundred ppb (101). Significant variations in methane concentrations that are not linked to changes in global temperature have also been documented recently. In a high-resolution study of methane concentrations from 8000 to 1000 years before the present (yr BP), Blunier et al (104) found variations of up to 15%, with minimum values of about 600 ppb occurring near 5200 yr BP. No similar feature is found in the oxygen isotope record, but evidence from lake levels and other precipitation proxy records is interpreted as suggesting that the observed methane variations are primarily due to changes in the extent of wetlands.

In contrast to CO_2, the glacial-interglacial changes in methane concentrations are almost certainly terrestrial in origin and most likely result from the increases in wetland areas and emission rates that accompanied the retreat of ice sheets and warming (51). It has also been suggested that large releases of methane from hydrates could have been a major factor in the glacial-interglacial transition (105). The potential for a significant positive feedback to anthropogenic global warming due to the release of methane from hydrates has recently been evaluated by Harvey & Huang (9) but will not be discussed further here, as it is not directly linked to terrestrial ecosystems.

High-latitude peatlands store large quantities of carbon and are thought to have the largest potential for a positive feedback from global warming. The ecology and biogeochemistry of these ecosystems have been recently reviewed by Gorham (106), who estimates total carbon (C) stocks of 450 PgC and annual methane emissions of 14 TgC. This methane flux estimate is less than half of several previous estimates (e.g. 101, 103, 107–109), and uncertainty remains high owing to large spatial and temporal variability. For example, a recent detailed study of diverse microsites in Manitoba found substantially higher average emissions than those used by Gorham but had standard deviations that

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were often more than 100% of the mean flux (110). Nonetheless, statistically significant correlations were found as a function of temperature at the water table surface and of water table height, water chemistry, and vegetation characteristics. The importance of soil characteristics and the need to distinguish between labile and refractory carbon pools have been emphasized in a review of peatland feedback processes by Bridgham et al (111).

To evaluate the potential for changes in methane flux to produce climate feedbacks, it is essential to distinguish between gross and net emissions. Net methane emissions or consumption, as measured in chamber studies, is the difference between two substantially larger terms, namely gross methane production and methane consumption within the soil column. Gross methane consumption by soils is estimated to be of the same order of magnitude as atmospheric oxidation by reaction with OH, or ~600 Tg per year (112). This level of consumption implies that gross methane production in wetland and other soils must be several times net methane emissions. As pointed out by Torn & Harte (113), this creates the potential for much larger feedbacks to climate change than would be expected by considering only the net flux, because a relatively small percentage change in either methane production or consumption independently can yield a relatively large change in net emissions.

Methane production and consumption respond differently to the key environmental controls of soil temperature and soil moisture. Biological production (methanogenesis) appears to respond more strongly to temperature than biological oxidation (methanotrophy) and is strongly suppressed at temperatures below about 10°C (110). Soil moisture influences both methanogenesis and methanotrophy by limiting the diffusion of oxygen or methane into soil pore spaces; anaerobic conditions are necessary for methanogenesis, and sufficient methane and oxygen are required for methanotrophy. Torn & Harte (113) found that methanotrophy can also be reduced by soil moisture levels below about 25% gravimetric moisture. Thus methanogenesis increases linearly with soil moisture, whereas methanotrophy exhibits an inverted U-shape relationship. Changes in soil moisture, then, have the potential to produce both positive and negative feedbacks through changes in methane consumption, while warming will produce a net positive feedback, as methane production increases faster than methane consumption (Figure 4). Accurately predicting the net effect requires a detailed model of surface hydrology because increases in production due to warming may not result in increased emissions if the water table simultaneously drops, allowing this methane to be oxidized before it reaches the atmosphere.

Failure to treat these processes separately is likely to result in a significant underestimate of potential changes in methane emissions with a changing climate. For example, Christensen & Cox (114) assumed the same temperature

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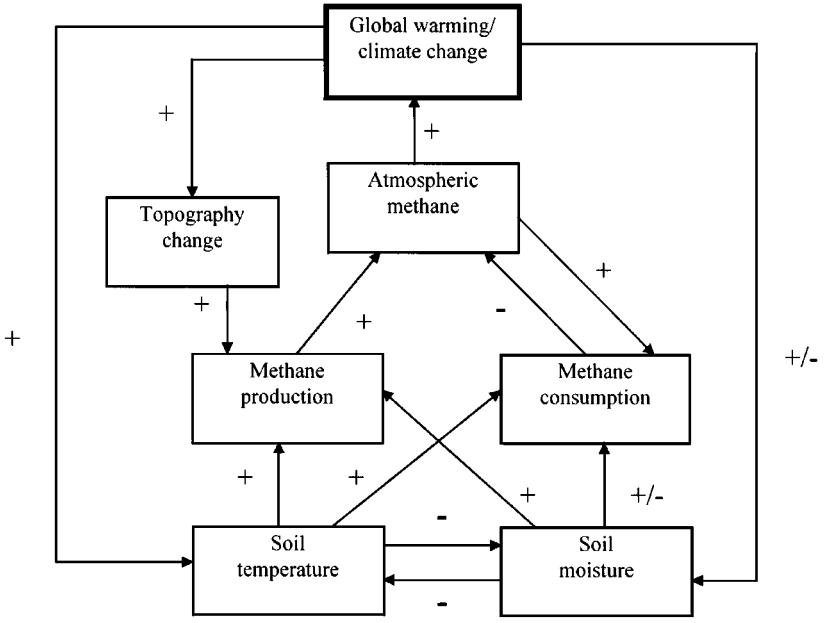


Figure 4 Methane feedback diagram.

relationship for both methanogenesis and methanotrophy and considered a scenario in which 50% of tundra area experiences a 4°C temperature increase and a 10% precipitation increase while the remaining tundra area experiences a 4°C temperature increase and a 10% precipitation decrease. These assumptions lead to only a very modest increase in net methane emissions from 35 Tg per year to 38 Tg per year. Even their model, however, showed the potential for much greater increases in emissions when run with the climate predictions of the UK Meteorological Office single-column model. Comparing five-year runs for $1 \times CO_2$ and $2 \times CO_2$ conditions for a specific location resulted in a 56% increase in methane emissions. This much larger effect was due in part to the 17% increase in soil moisture obtained at this location, but it also reflected the effect of increases in the thaw season and thaw depth that were incorporated in this simulation but not in the sensitivity test described above.

Physical and ecological changes in peatlands resulting from global warming may also significantly affect methane emissions. Bubier et al (110) find that methane emissions are strongly related to vegetation cover and microtopographic features, with particularly high emissions found in transition zones between permafrost and wetland environments. This may relate to the role that plants can play in transporting methane from anaerobic soil layers to the

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atmosphere and to root exudates as a source of labile organic matter, as well as to differences in hydrology (111). This suggests that degradation of permafrost leading to the collapse of peat plateaus could cause additional increases in methane emissions not captured by temperature and moisture relationships that assume fixed topography. Considering these additional factors, Hogan (103) concludes that global warming could lead to more than a doubling of methane emissions from high-latitude wetlands, depending on changes in soil moisture conditions, and estimate that the increase could be in the range of 5–65 Tg CH_4 per year. Other factors that can influence wetland extent should also be examined, such as changes in beaver activity and shifts in agricultural activity that may be induced by climate change. For example, Bridgham et al (111) found that increased beaver activity in Voyageurs National Park, Minnesota, has led to an almost fourfold increase in methane emissions since 1940. Overall, given the huge stock of carbon stored in peatlands and the potential for very large changes in methane emission rates, significant feedbacks from this source are possible with global warming, despite the relatively modest magnitude of current emissions.

Dust and Aerosol Particle Feedback

Unlike GHGs, dust and aerosol particles appear to be having a net cooling effect on the Earth's surface. Of the various terrestrial types of these particles, windblown mineral dust and smoke aerosols from forest fires may be the most affected by climate change and thus represent potential sources for feedbacks. Quantifying the magnitude of such feedbacks will not be easy, since, for reasons discussed below, understanding the global climatic effect of dust and aerosols is more difficult than assessing the warming associated with GHGs.

First, these particles have a brief lifetime (typically hours to weeks) in the lower atmosphere, which results in a globally inhomogeneous distribution, in contrast to the relatively uniform distribution of long-lived GHGs. Second, dust and aerosol particles can trap outgoing infrared radiation (much like a GHG), but it seems their most prevalent—and best understood—effect on climate is to screen out incoming solar radiation. And third, comparison of data sets of dust and aerosol is often confounded by differences in the particle size measured, an important characteristic that determines a particle's atmospheric behavior (115).

Aerosols affect solar radiation directly and indirectly. The direct effect involves the scattering and absorption of incoming solar radiation, whereas the indirect effect—which is more difficult to quantify—involves the transformation of these particles into cloud condensation nuclei that in turn enhance cloud albedo and may even extend a cloud's lifetime. The net effect of this ultimately depends on the underlying surface (116). Over high-albedo areas such as the polar ice caps or snow-covered surfaces, absorption of sunlight by large amounts

of mineral dust and aerosol particles may result in less solar reflectance (117). In fact, Overpeck et al (118) provide evidence suggesting that some of the warming responsible for abrupt glacial terminations during the Pleistocene was dust induced. Over low-albedo areas like the oceans and forests, the presence of dust and aerosols results in greater solar reflection, producing surface cooling.

Scientific understanding of the climatic significance of dust and aerosol—in particular its offsetting effect to GHG-induced warming—has improved considerably in recent years. For example, the IPCC's most recent "best estimate" for average global warming by the year 2100 fell by roughly one third to 2°C compared to previous estimates, owing mostly to the inclusion of aerosol cooling in GCM predictions (119). It has also been demonstrated that incorporating the effects of aerosol greatly improves the agreement between observed and simulated temperature trends over the last century at the global and regional scales (120).

Mineral or soil dust is perhaps the largest of all natural and anthropogenic aerosol sources in terms of its total mass load, accounting for the release of approximately 1500 Tg per year into the atmosphere (115). Significant sources of soil dust typically include arid and semi-arid regions, where large expanses of unconsolidated material are subject to wind erosion and weathering. Tegen & Fung (121) provided evidence that a large portion—perhaps up to 50%—of the total atmospheric dust load can be attributed to "freshly exposed surfaces from disturbed sources," which include eroded soils, deforested areas, and transient desert boundaries such as the Saharan/Sahelian border in Africa. Such disturbed sources could be the result of climatic change and variability, anthropogenic interference, or a combination of both, thus confounding the business of assigning feedbacks to clearly identifiable factors induced by climate change. The implication of Tegen & Fung's findings is that mineral dust can no longer be considered part of the constant natural background against which GHG forcing is estimated.

Other natural, terrestrial sources that may be influenced by climate change include biological debris (ca 50 Tg per year), sulfates from biogenic gases (ca 90 Tg per year) and organic matter from biogenic non-methane hydrocarbons (ca 55 Tg per year) (115). The total annual mass of natural dust and aerosols (ca 3000 Tg per year including volcanic aerosols and sea salt) accounts for approximately 80–90% of all (i.e. natural and anthropogenic) global emissions of these particles, but natural dust and aerosols only account for about half of the negative forcing attributable to the total global dust and aerosol "burden" (115, 122). This phenomenon can be explained by two general distinguishing characteristics of anthropogenic particles. (*a*) Anthropogenic sulfate particles due to fossil-fuel combustion and metal smelting tend to be smaller than, say, windblown dust and thus remain suspended in the troposphere for a longer

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period (i.e. several days vs a day or less) and have a greater light-scattering efficiency. (*b*) Key anthropogenic sulfate compounds tend to be more hygroscopic (i.e. bind more readily with atmospheric water vapor), enabling them to scatter more incoming radiation than dry, natural particles (123).

Climate change could potentially alter the current natural, and in some cases anthropogenic, rates of dust and aerosol emissions in the following ways. The duration and intensity of drought periods in continental interiors could increase; similarly, the expected increase in the rate of evapotranspiration could lead to drier soils if there is insufficient compensation from the projected increase in precipitation; an expansion of arid into semi-arid lands and of semi-arid into grass- and shrublands may take place; human dislocations as a result of either sea-level rise, depleted water resources, or altered agricultural productivity could cause greater rates of "freshly exposed surfaces" as people search for new agricultural lands and new sources of fuelwood; and the average interval between "natural" fires, due to drier conditions in some regions, could decrease, releasing emissions of smoke aerosols.

Decreased rainfall has indeed been projected for many of the world's deserts, including large parts of the Saharan, northern Arabian, the Sonoran, and central and western Asian deserts (124). However, deserts are already subject to large fluctuations in annual precipitation, so the initial stages of climate change may not bring about conditions considerably outside current, natural variability (124). This may partially explain why Monserud et al (125) projected that deserts were the most stable areas in a simulation of biome redistribution under climate change induced by CO_2 doubling (see below). Nevertheless, if more frequent drought-like conditions exacerbate the desertification process in arid and semi-arid lands, the result could be larger plumes of windblown dust as the severity of wind erosion becomes more intense (126). Schlesinger et al (127) hypothesize that, along grassland/shrubland margins, once-uniform soil resources under grasslands become increasingly heterogeneous upon the intrusion of shrublands. This retards the accumulation of needed minerals in the soils and in turn promotes the further spread of shrubland, thus increasing the area of bare soil vulnerable to wind erosion. Whether driven by climate change or land-use practices, greater land degradation may, for instance, enhance even further the African dust load currently observed in the North Atlantic trade winds (128); and globally, this could increase the mean negative forcing associated with dust from "disturbed sources," currently estimated at about -1 W/m^2 with a regional maximum over the Arabian Sea of -25 W/m^2 (129).

The potential for more frequent natural forest fires under global warming is addressed in the section on carbon feedbacks. In addition to CO_2 emissions, the burning of biomass releases fine particulate aerosols to the atmosphere, but it is difficult to predict how the heating and cooling effects of these emissions

will interact at the regional and global scales. Unnatural fires (i.e. biomass burning related to deforestation) have been occurring on a large scale primarily in the tropical latitudes over recent decades. These fires are perhaps the second largest source of anthropogenic aerosols after sulfate (115); Penner et al (130) estimated, with a fair degree of uncertainty, that the global net (i.e. direct plus indirect) cooling effect of these aerosols is roughly -2 W/m^2, but more recently, their effect was assessed to be much lower (115). For reasons briefly mentioned above and in the section on surface albedo feedback, these emissions, currently characterized as anthropogenic, may increasingly become linked with factors associated with global climate change.

Overall, it seems such feedbacks would likely be negative (Figure 5) for the following reasons. An increase in the mineral dust load due to greater

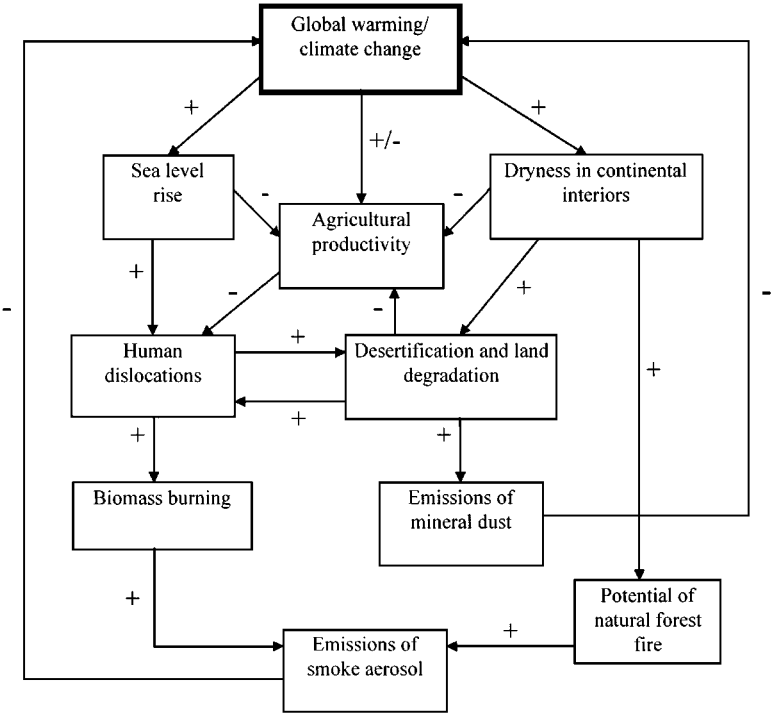


Figure 5 Through a combination of climatic and anthropogenic effects, the most significant feedbacks involving mineral dust and aerosol would be negative, since a greater release of such emissions would generally enhance atmospheric albedo, the result of which would be a cooling effect. Over certain areas with a high surface albedo, such as the high latitudes or some high elevation ranges, increased levels of mineral dust could cause warming.

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desertification and land degradation would likely remain confined to low-albedo areas in the low- to mid-latitudes and thus contribute to regional cooling. The increase in biomass burning, due to either the increased frequency of natural fire cycles or tropical deforestation, would release smoke aerosols and directly affect incoming solar radiation, which would also result in cooling. This latter effect would, however, be offset, either completely or partially, by the concurrent release of CO_2. The importance, magnitude, and geographical significance of these potential feedbacks remain highly uncertain.

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ENERGY FLOWS

Surface Albedo Feedbacks

This section focuses on changes in surface albedo that may ensue as a result of both biome redistribution and deforestation and how such changes could act as feedbacks. Differences in albedo among vegetation types are primarily the result of differences in color, vegetation density, canopy height, and leaf area index. Tropical forests, for instance, have a much lower albedo than, say, arid regions and therefore absorb much more incoming solar radiation; likewise, boreal forest—the circumpolar, subarctic forest dominated by conifers—has a lower albedo than tundra, a treeless plain of the Arctic and Antarctic characterized by short grasses.

Global changes in temperature and other parameters such as precipitation patterns, evaporation rates, and sea level can induce changes in vegetation cover both directly and indirectly. Direct effects include shifts in the geographical distribution of large-scale classes of vegetation types or biomes. Indirect effects may be land-use transformations such as tropical deforestation. The main driving force of the latter is and will continue to be non-climatic factors like economic and population growth; however, the consequences of anthropogenic climate change on agricultural productivity, water supply, and human migration could increase demand for agricultural and pastoral lands, fuelwood, and timber, aggravating rates of deforestation.

BIOME SHIFTS As is evident from pollen and plant fossil data, the last glacial maximum approximately 18,000 years ago resulted in vegetative shifts equatorward, whereby tundra and boreal forests were pushed into the present-day areas of the lower Great Lakes, Western and Central Europe, and vast mid-sections of Russia. Tropical forests, although altered less dramatically, were partly occupied by savannas. [See a simulation of these past changes in (131)]. In like but opposite manner, anthropogenic warming over the next century may induce a poleward migration of biomes, with the most dramatic shifts occurring in high northern latitudes, where the greatest amounts of warming are projected (28).

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The ability of species to adapt and migrate will depend strongly on the rate of temperature increase, which, as projected by the IPCC (119), is likely to fall between 0.1°C and 0.35°C per decade. Even the low end of this range is a faster rate of warming than any that has occurred during the past 10,000 years. Based on paleo studies, it appears unlikely that most species will be able to match the migration rate required (based on the IPCC's projections) to maintain their current climatic conditions (132). Thus, in addition to possible biome shifts, there may also be large rates of forest dieback during the transient phase (i.e. before a new climatic equilibrium is reached). Species migration rates will also depend on soil characteristics such as moisture and nitrogen availability. As suggested by Pastor & Post (133), interactions between vegetation and water and nitrogen availabilities may produce a bifurcation in the forest response to climate change. This would be characterized by increased vegetative productivity where soil moisture is not limiting and nitrogen availability is enhanced, and decreased productivity where both soil moisture and nitrogen become more limiting.

Models that simulate the effects of climate change on biome distribution (biogeography or biome models) are in qualitative agreement that shifts will be greatest in high northern latitudes. More detailed comparisons among the models, however, are difficult because many use different vegetation classification schemes, different numbers of classifications, and entail different sensitivities to climatic perturbations, particularly with regard to their hydrologic responses to changes in temperature and atmospheric CO_2 (134). Furthermore, although the models are well suited to identify which biomes will undergo stress due to climate change, they are less adept at describing what the new vegetation patterns will be (125). Current models have an insufficient ability to simulate seed dispersal, shifts in vegetative competitive balances, adaptive responses at micro scales, and the likelihood of damage due to fire, insects, and disease. In addition, radiative feedbacks due to surface albedo changes following biome shifts, or any other type of biome modification, are rarely built into simulations. Some more recent models, however, are able to couple large-scale vegetation distribution with biogeochemistry (135) and vegetation dynamics, including a simplified representation of competition among certain vegetation types (136).

The Integrated Model to Assess the Greenhouse Effect (IMAGE 2; 137), which can simulate vegetative transformations under climate change, projected the following biome shifts between 1990 and 2050: encroachment of boreal forests into roughly 40% of the tundra region; migration of conifer forests northward into 22% of the boreal forest zone; and the replacement of 78% of the conifer forests by a mixed forest type. These changes in the high northern latitudes were largely attributed to high rates of warming. Biome shifts in the lower latitudes (e.g. desert to warm grassland) were less dramatic and were attributed, primarily, to increased water-use efficiency through CO_2 fertilization

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(137). The modified Budyko model, which projects vegetation patterns under various doubled CO_2 scenarios using a dryness index and potential evaporation, demonstrated similar results (125). One comparison (confined to the coterminous United States) of three biogeography models' responses to three separate GCM warming scenarios, with and without doubled CO_2 effects, demonstrated major northward shifts of eastern forests (134).

Paleo studies, in combination with GCM simulations, provide some insight into how such large-scale changes can produce feedbacks. Foley et al (138) examined the effects that boreal forests may have had on the earth's climate during the mid-Holocene period 6000 years ago, a time of high-latitude warming due to variations in the Earth's orbit. Paleo evidence suggests that during this time boreal forests extended beyond the current northern treeline [see, for example, (139) for an explanation of the magnitude of this biome shift through a positive surface albedo feedback]. The inclusion of this expanded boreal coverage in a GCM for mid-Holocene conditions lowered the regional land surface albedo from 0.36 to 0.26, resulting in 8 W/m^2 of additional solar radiation absorbed at the surface. Thus, the initial 1.8°C warming caused by orbital variations was, averaged annually, further increased by 1.6°C in high latitudes. According to the authors, this large positive feedback brought about by northward migration of the boreal forest—the same type of biome shift expected as a result of anthropogenic warming—may explain the magnitude of warming during the mid-Holocene, which apparently cannot be attributed to orbital changes alone.

A similar modeling study (140) of a past cold period—an interglacial-to-glacial shift 115,000 years ago—led to the same conclusion: Orbital variations, along with lower atmospheric CO_2 concentrations relative to present amounts, were not sufficient in isolation to produce the extensive glaciation that observational evidence supports. Only when the model allows high-latitude land surface albedo to increase by roughly 0.3–0.4 (representing expanded tundra) is enough incoming solar radiation reduced to decrease temperatures even further, which in turn causes greater tundra expansion. De Noblet et al (141) examined the same past cold period, but coupled a biome model iteratively with a climate model. As in other studies, initial orbital changes did not cause the onset of a glaciation but did cool summer temperatures enough so that subsequent iterations with the biome model resulted in progressively greater amounts of tundra. These studies suggest that biome shifts in the high northern latitudes can act as a strong positive feedback (Figure 6), exacerbating any initial forcing, whether it be the cooling and warming caused by changing orbital cycles or the warming expected from rising concentrations of GHGs.

LAND-USE CHANGES Assuming anthropogenic warming may be, at least in part, responsible for future land-use conversions, how will these conversions

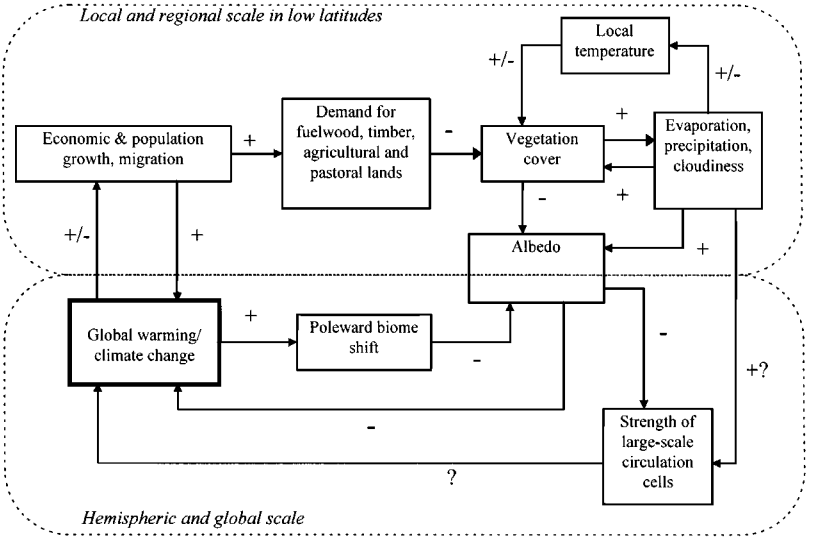


Figure 6 At the local and regional scale, economic and population growth, along with migration, have been and will continue to be the dominant driver towards rates of tropical deforestation. Climate change will play a secondary but important role. Tropical deforestation raises surface albedo, which decreases evaporative cooling and thus increases local and regional temperatures. This in turn can raise albedo further, resulting in a positive feedback process. Climatic effects beyond the deforested region, such as the weakening of large-scale circulation cells, have been identified, but the larger effects on climate change remain unclear. At the global and hemispheric scale, both paleo studies and GCM simulations suggest that anthropogenic warming will result in a poleward migration of boreal forest into the tundra zone, which decreases surface albedo, raises temperatures further, and thus causes a self-enforcing, positive feedback loop.

either intensify or dampen climatic change? Information on this comes largely from the low latitudes where deforestation rates have been estimated at 15.4 million hectares per year (142).

Two of the most important feedbacks to consider regarding deforestation involve the change in surface albedo and the release of carbon to the atmosphere. [The estimate for current emissions from tropical land-use change is 1.6 $\pm$ 1.0 PgC per year (143)]. In this section we focus primarily on albedo-climate feedbacks, although other factors like moisture availability and surface roughness must eventually be included as well. Currently, there is a lack of information on surface characteristics of tropical vegetation, but most estimates of tropical forest albedo fall between 0.11 and 0.13 (144, 145), significantly lower than most other terrestrial landscapes across the globe. This low albedo is the result of relatively dark color, dense vegetation, and deep canopy, the combined effect of which is to trap incoming solar radiation quite effectively. Thus, conversion

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from tropical forests to grazing lands results in the largest albedo increase, possibly as high as 0.25; conversion to agricultural crops can produce an albedo between 0.18 and 0.25; and replacement with plantation forests increases the albedo only slightly (144, 146).

An increase in surface albedo, by itself, will lead to a decrease in surface temperature. According to one study (147), total deforestation, along with other land-use changes such as desertification, irrigation, dam-building, and urbanization, resulted in a global surface land albedo increase of between 0.00033 and 0.00064 over the period 1954–1984, corresponding to a global temperature decrease of between 0.06°C and 0.09°C (well within the magnitude of natural climate variability). Bonan et al (148) simulated the climatic impacts of replacing all forests north of 45° North (N) with bare soil—admittedly an extreme scenario, but one which isolates the influence of northern forests on our current climate and may provide an upper bound of this effect due to large-scale logging. The result, largely caused by a high increase in surface albedo, was a drastic cooling, which was most severe in April when temperatures were as much as 12°C cooler. These effects extended beyond the deforested region: At 30°N air temperatures were 1.67–3.2°C cooler; and even at 10°N, temperature decreases of 1°C were identified. This study is consistent with the simulations of biome shifts to the extent that it demonstrates the large influence of surface albedo on climate in the high latitudes.

With tropical deforestation, it is more difficult to establish a straightforward relationship between surface albedo changes and surface temperature changes. Indeed, an increase in surface albedo following deforestation will, in isolation, result in a lower surface temperature due to less absorbed solar radiation. However, because of other concurrent, offsetting factors discussed below, many simulations have shown surface temperature increases following deforestation (147, 149–152). These regional temperature changes were largely confined to their respective deforested region, but their magnitude is considerable (see bottom three references of Table 3), often in the higher range of the IPCC's 1.0–3.5°C projected increase for average global surface temperature by 2100 (119). These simulations likely represent an upper bound for regional warming due to deforestation because virtually all of the tropical forest for, say, Amazonia was replaced with pasture or similar landscape. More recent simulations (153, 154) projected much smaller temperature increases for the Amazon Basin and even temperature decreases for other tropical areas in Africa and Southeast Asia (see top two references of Table 3).

Latent Heat Feedbacks

CLIMATIC EFFECTS Plant transpiration results in the loss of water vapor through stomatal openings to the atmosphere. The water vapor emitted through transpiration plays an important role in several ways. Most importantly, it contributes

Table 3 Model results of regional surface temperature changes due to deforestation

Deforested area	Temperature change	References
Amazon Basin replaced with scrub grassland	+0.3°C	154
SE Asia replaced with scrub grassland	−0.2°C	
Tropical Africa replaced with scrub grassland	−0.02°C	
Amazon Basin replaced with scrub grassland	+0.3°C	153
SE Asia replaced with scrub grassland	−0.7°C	
Amazon Basin and SE Asian tropical forests replaced with tall grass-covered scrubland with a few large trees	+2.8°C in Jan. +1.5°C in July	152
Amazon Basin replaced with pasture	+2.5°C	151
Amazon Basin replaced with pasture	+1–3°C	150

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to the amount of atmospheric moisture, a function especially crucial in areas like the Amazon where roughly 50% of rainfall is recycled from local evapotranspiration (149); and due to the energy required to transform water into water vapor, it acts to cool leaf surfaces and transfer latent heat to the atmosphere. This latent heat flow, together with other non-vegetative sources of evaporation, constitutes one of the three major mechanisms of energy transfer from the earth's surface to the atmosphere (the other two being radiation and convection of sensible heat). Altered rates of plant transpiration can therefore act as feedbacks by changing surface temperature through changes in the latent energy flux (Figure 7), but effects are expected to be regional in nature, particularly in areas of vast vegetation such as the tropics and boreal zone.

As discussed in the section on carbon feedbacks and CO_2 fertilization, most, but not all, plant species exhibit increased stomatal resistance in an enriched CO_2 environment (155, 156), which can lead to a decrease in transpiration.

Henderson-Sellers et al (155) simulated the effects of doubling stomatal resistance—a simplified representation of how vegetation may respond to the expected doubling of atmospheric CO_2—in our current climate and found a global surface temperature increase of 0.13°C. The largest regional temperature increase (2°C) was in the boreal zone, where the latent energy flux decreased by -15 W/m^2 and the subsequent increase in the sensible heat flux was 15 W/m^2. Pollard & Thompson (156) increased stomatal resistance by a factor of two, which also produced a 2°C temperature rise in the boreal zone, where transpiration was reduced by one fourth; in the Amazon, where transpiration was reduced by one half and the latent heat flux by -120 W/m^2, temperatures increased by as much as 4°C.

Many other model simulations have allowed doubled atmospheric CO_2 concentrations to influence stomatal and hence the transpiration/latent-heat

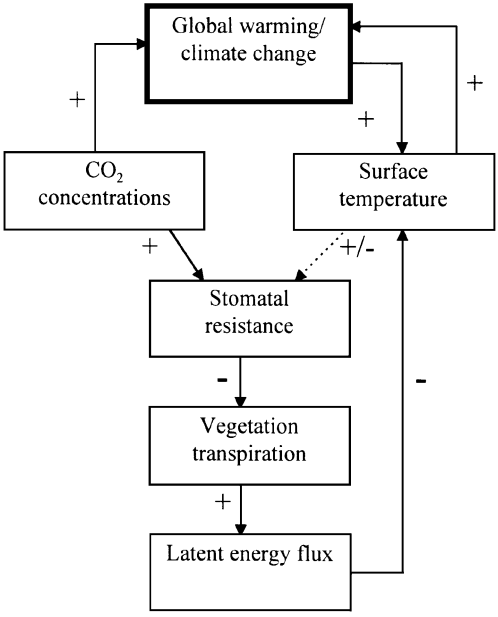


Figure 7 Transpiration-related feedbacks involving both material exchanges and energy flows. (Based in part on Figure 1 of Reference 155.)

response. Sellers et al (157), using a coupled biosphere-atmosphere model, found that, without allowing for physiological effects, the doubled CO_2–induced temperature increase in the tropics was 1.7°C, but it rose to 2.6°C when stomatal conductance (and photosynthesis) was allowed to respond. Friend & Cox (158) also employed an interactive atmosphere-vegetative model and found that doubled CO_2 reduced overall transpiration by 25% (and that the resultant decline in surface humidity increased stomatal resistance even further). Friend & Cox also demonstrated that the increase in leaf area index, due to the enrichment effects of higher ambient CO_2, could be insufficient to offset the reduction in transpiration per unit leaf area.

Clearly there is a need to understand the combined effects that increases in both CO_2 concentrations and global average temperature will have on transpiration and latent heat fluxes. Modeling studies by Henderson-Sellers et al (155) and Sellers et al (157) suggest that the synergistic effects of CO_2-induced stomatal resistance and CO_2-induced warming may be significantly different than either perturbation in isolation. For example, the effects of increased stomatal resistance could be strong enough to offset a warming-induced global

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intensification of the hydrologic cycle, resulting in a net reduction of evapotranspiration in some regions.

Important questions for this discussion have been addressed by Jarvis & McNaughton (159): Is it stomatal resistance or the supply of energy that controls transpiration? Can changes in transpiration witnessed at small scales (e.g. leaf, plant, canopy) be extrapolated to the global scale? The authors noted that regional evapotranspiration is primarily determined by net radiation and temperature, and that, with increasing scale, transpiration's sensitivity to changes in stomatal resistance is progressively weakened. These conclusions, confirmed later by the same authors (160), are primarily due to a growing number of stabilizing, offsetting factors that arise with increasing scale. Such factors include an increase in leaf temperature (as demonstrated in the above studies), which has the tendency to increase transpiration, and the resultant increase in the leaf-to-air vapor pressure difference.

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COMBINED LATENT HEAT AND SURFACE ALBEDO FEEDBACKS FROM DEFORESTATION One consistent outcome among deforestation-climate simulations is an overall reduction in the strength of the hydrological cycle, resulting in decreased rates of precipitation, evapotranspiration, and amount of cloudiness. Most simulations indicate a greater reduction in precipitation (by 10–30%) than in evaporation (147, 149–161), thereby extending the length of the dry season, which has serious implications for any hopes of reestablishing tropical forests following extensive deforestation because their current distribution is characterized by areas with either a short dry season or no dry season (151). Drying could also increase surface albedo even further, if for example significant amounts of land become bare. However, the decrease in cloudiness would cause atmospheric albedo to decrease, so it is difficult to project the net albedo feedback.

Decreased evapotranspiration, and thus evaporative cooling, is the key factor that offsets a reduction in surface energy due to increased surface albedo. This factor largely accounts for the temperature increases in Table 3. Lower evapotranspiration rates following deforestation are essentially the result of decreased leaf and stem area, which reduces water-holding capacity; decreased surface roughness—the primary factor that determines the nature of the aerodynamic exchange between the surface and the lower atmosphere—due to a change to shorter and smoother vegetation; and decreased available soil moisture, primarily due to a reduction in average root depth [e.g. from 127 to 61 cm (149)]. Loss of evapotranspiration reduces the local source of moisture and thus contributes to lower precipitation and decreased cloudiness. Decreased precipitation may in turn further reduce soil moisture availability and thus rates of evapotranspiration. The increase in surface albedo can affect moisture sources external to the

deforested region by reducing the available energy at the surface, which in turn weakens ascent and boundary-layer convergence. Decreased cloudiness affects the amount of available surface energy in two ways: Incident solar radiation increases but is offset to some degree by the higher surface albedo following deforestation, and infrared radiation reflected from clouds back down to the surface decreases. The net effect of this may be radiative cooling, which in the more recent studies has had a stronger effect, thus explaining the much smaller temperature changes in the deforested areas (Table 3).

Combining the information about latent heat and surface albedo feedbacks leaves an ambiguous picture as to how the effects of changes in vegetation cover in the tropics, or elsewhere, may act as feedbacks on global climate change. Clearly, at the regional and local scale, deforestation causes, among other things, an increase in surface albedo, a weakened hydrological cycle and, most importantly, reduced evaporative cooling. In most cases, these effects raise temperatures and could lead to further increases in surface albedo, resulting in a possible positive feedback loop. However, the extent to which changes brought on by deforestation may act as a feedback on global climate change remains unclear. Certainly the climatic impacts of deforestation will not remain confined to Amazonia, tropical Africa or Southeast Asia. Potential effects on large-scale features of the climate system like the Hadley Cell have in fact been demonstrated (162), but the question of how such changes may interact with those ushered in by anthropogenic warming has until now received little attention. Deforestation caused by socioeconomic factors may continue to have a much more dramatic impact on tropical ecosystems than global climate change over the coming decades. Over this period, deforestation may also cause perturbations to the regional climate that are similar in magnitude to those brought about by global climate change.

CONCLUSION

We have reviewed a rapidly growing literature on feedbacks between climate change and terrestrial ecosystems. Paleoclimate studies suggest that biogeochemical feedbacks may have played an important role in the large climate swings that the earth has undergone during the last 220,000 years by amplifying relatively weak orbital forcings. While the mechanisms that operated in the past may or may not play a role in human-induced global climate change over the coming decades to centuries, work ranging from manipulation experiments at individual sites to global-scale ecosystem models is demonstrating the potential for important interactions that are not yet incorporated in most global climate change simulations. We note, for example, that the current IPCC global warming scenarios incorporate a negative feedback from CO_2 fertilization of

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photosynthesis, but they do not include a range of ecological interactions and responses to climate change that are likely to limit or reverse the carbon sequestration projected on the basis of the fertilization effect alone. Similarly, general circulation models incorporate an ice-albedo positive feedback, but they do not currently include the vegetation-albedo feedback that is likely to substantially amplify this process. Feedbacks involving methane are also likely to be positive. Other feedback processes, such as changes in latent heat flux, are likely to substantially affect climate change at the regional level, although their global implications are less clear. While the processes involved are complex and there are both positive and negative feedback loops, it appears likely that the combined effect of the feedback mechanisms reviewed here will be to amplify climate change relative to current projections, perhaps substantially if the underlying climate sensitivity due to strictly physical feedback mechanisms is toward the upper end of the uncertainty range adopted by the IPCC. The risk that biogeochemical feedbacks could substantially amplify global warming has not been adequately considered by the scientific or the policymaking communities.

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