

Biological Feedbacks to Climate Change: Terrestrial Ecosystems as Sinks and Sources of Carbon and Nitrogen

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Introduction

Life profoundly influences Earth's climate through its influences on the cycling and storage of chemical elements and the absorption and reflection of solar energy (Lovelock 1979; Lovelock and Whitfield 1982, 1988; Holland, Lazar, and McCaffrey 1986). The manner in which the biosphere responds to the greenhouse effect—the accumulation of atmospheric gases trapping heat radiating from Earth's surface—will either dampen climate change or magnify it. However, the net effect of the direct and indirect interactions of atmosphere, land, and water is a complex, poorly understood issue with critical implications for both the magnitude and rate of climate change.

The concept of *feedback* indicates a special class of interaction in which the factors that produce a result are themselves modified by that result. This concept is crucial to understanding the potential impacts of climate change, and much has been written on one or more aspects of feedbacks to climate change (see the reviews by Haughton and Woodwell [1989]; Lashof [1989]; Bazzaz [1990]; Graham, Turner, and Dale [1990]; King et al. [1990]; Perry and Borchers [1990]; Ausubel [1991] and Neilson and King [in press]). Herein, we bring together and build on past work; we begin by defining and

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contrasting *positive* and *negative* feedbacks, briefly discuss possible atmospheric feedbacks to climate change, then move to the major thrust—how terrestrial ecosystems create biological feedbacks to climate change by acting either as sources or “sinks” (reservoirs) of the key, and strongly linked, elements carbon and nitrogen. Although oceans contain by far the largest amounts of carbon stored on Earth, yearly carbon fluxes between land and air are similar in magnitude to those between oceans and air (Moore and Bolin 1986/87); therefore, changes in amounts of carbon stored on land could substantially affect global warming. Nitrogen is of interest for two reasons. The “greenhouse gas” nitrous oxide (N_2O) has 180 times more warming potential per molecule than carbon dioxide (CO_2). Moreover, nitrogen is commonly believed to be the most limiting element in many land and water ecosystems; hence changes in the amount of available nitrogen are likely to strongly influence the ability of ecosystems to take up and store carbon.

Feedbacks Defined

The concept of feedback, first applied to biological systems with the development of cybernetics in the late 1940s (von Bertalanffy 1968), is simply illustrated by Perry and Borchers' (1990) hypothetical example:

Jack drives his car up the hill to fetch some water. As it is a warm summer day, he switches on the air conditioner to feel cooler. This increases fuel consumption and CO_2 emissions, which in turn add to global warming. Jack turns up the air conditioner still more, thereby increasing the CO_2 output, and the cycle begins anew. Jill, on the other hand, has no air conditioner. As Jack's habits make Jill's drive up the hill uncomfortable on summer days, she decides to drive less and walk in the shade. The hotter it gets the less she drives. Her behavior, in opposition to Jack's, has a moderating effect on global temperature.

In natural systems, feedbacks are more complex than our example here and hence more difficult to analyze (Lashof 1989). *Negative* feedbacks like Jill's which dampen the magnitude of “the original signal” (in this case, Jack's using his air conditioner), abound and tend to stabilize systems. *Positive* feedbacks like Jack's, which amplify the magnitude of “the original signal,” are also common, but have a Jekyll-Hyde character. An example is *mutualisms*, a common relationship in Nature in which two or more species interact for the benefit of both or all. They entail a positive feedback that contributes

significantly to the productivity and vigor of biological communities, strengthening the system. But mutualisms also are an “Achilles heel”: stress in one partner can reflect in the other, rapidly weakening the system. Moreover, systems dominated by positive feedbacks can change very rapidly, a phenomenon that probably underlies the current, rapid degradation of many global ecosystems (Perry et al. 1989) and may have triggered the periods of rapid climate change that are known to have occurred (Broecker 1987). So, positive feedbacks are of greater concern than negative because of the possible “runaway” behavior they induce in a system.

In climate dynamics, the “signal” impinging on the biosphere is a change in global temperature. As a simple example, suppose the amount of the greenhouse gas CO_2 were to double. The associated warming of high-latitude wetlands could increase emissions of the greenhouse gas methane (CH_4). Because CH_4 has 3.7 times the warming potential of CO_2 (Lashof and Ahuja 1990), its additional release would act as a positive feedback to the doubling of CO_2 and further amplify the greenhouse effect.

However, global-scale feedbacks comprise many processes whose interactions are not always well understood. In a more complex example, again suppose that average global temperature were to increase from higher concentrations of atmospheric CO_2 . The associated warming would decrease the extent of the Arctic permafrost zone, increase the length of the Arctic growing season, and create conditions more favorable for organic matter to decompose in tundra soil. The greater decomposition would act as a positive feedback, prompting faster release of CO_2 and CH_4 , which would amplify the rate of global warming and increase Arctic temperatures. To complicate matters, this positive feedback would be offset by the negative feedback resulting from increasing CO_2 uptake and carbon storage by tundra vegetation in response to the improved growing conditions. Because information is lacking about the magnitude of the two feedbacks, the net outcome is difficult to predict. Moreover, further complications might arise when the feedbacks involve processes that are slow to respond to “signals” or that respond to “signals” nonlinearly (Lashof 1989).

Although the concept of feedback is vitally important to understanding and modeling system behavior, it has definite limits. As systems become more complex, they become less amenable to analysis as a simple sum of positive and negative feedbacks. Complex, interconnected systems, of which Earth is the prime example, behave as wholes, not as sums of parts (Ashby 1966)—a critical point we return to at the close of the paper.

The Atmosphere: Feedbacks to Climate Change

Greenhouse Gases

Significant greenhouse gases include water vapor, carbon dioxide, methane, nitrous oxide, ozone (O_3), and chlorofluorocarbons (CFCs). Global budgets of carbon dioxide, carbon monoxide (CO), methane, and nitrous oxide reveal that biological processes account for most of the movement of these elements among land, air, and water. Because the biosphere is expected to respond significantly to human-induced climate change, the concentrations of natural greenhouse gases might also be influenced, producing the potential for positive or negative feedbacks to climate change.

After water vapor, carbon dioxide is the dominant greenhouse gas. Its concentration is determined by many factors collectively characterized as the global carbon cycle. That cycle includes large fluxes between air and land, and air and ocean. The atmospheric CO_2 concentration in the northern hemisphere oscillates seasonally by about 7 parts per million (ppm) (Keeling et al. 1989) due to net uptake by plants (through photosynthesis) in summer and release (via respiration) in winter. The amplitude of the seasonal cycle has been increasing since the early 1970s, suggesting increased biological activity in the mid- to high latitudes (D'Arrigo, Jacoby, and Fung 1987).

Atmospheric CO_2 concentration has varied widely over geological time but ranged between 200 and 300 ppm over roughly the last 100,000 years (Barnola et al. 1987). Long-term changes in CO_2 concentration appear to be responses to, rather than initiators of, climate change and generally act as positive feedbacks; that is, climate change may be initiated by periodic changes in the amount of sunlight reaching Earth's surface, but biospheric or other factors that change concentrations of atmospheric CO_2 and other greenhouse gases amplify the original change. The current global concentration of CO_2 is approximately 350 parts per million (ppm), having risen from 280 ppm in the 1800s (Neftel et al. 1985); further increases in concentration over the next few decades will depend on population growth and energy policy as well as the response of the biosphere to climate change.

Two gases with relatively long atmospheric lifetimes are methane (10 years) and nitrous oxide (120 years). Atmospheric concentrations of both gases are also currently increasing, most likely because of human activity, and are predicted to account for approximately 25% of the increase of global temperature due to the increasing greenhouse effect over the next several decades (Ramanathan et al. 1985). Methane also influences the depletion of stratospheric ozone which

protects Earth from excessive ultraviolet radiation. During and between previous ice ages, atmospheric concentrations of methane and nitrous oxide increased during periods of warming, suggesting they were part of a positive feedback to warming (Khalil and Rasmussen 1989). However, future feedbacks associated with these two gases are highly uncertain (Lashof 1989). Natural sources may increase because of warming at high latitudes where amounts of potentially decomposable belowground organic matter are large. Moreover, large amounts of pre-existing methane may be released from marine sediments or from frozen high-latitude soils. The sink for methane may be decreasing, thus increasing its atmospheric lifetime and concentration.

Chemical Reactions in the Atmosphere

The atmospheric concentration of CO_2 is determined by the balance between the amounts of CO_2 released from land and oceans, and the amount taken up. However, the concentration of other important greenhouse gases depends on chemical reactions that take place within the atmosphere, and these chemical reactions depend, in turn, on biologically produced compounds that are not greenhouse gases, but that react with greenhouse gases to alter their chemical state. Consider the greenhouse gas CH_4 (methane). In the jargon of chemistry, CH_4 is "reduced," meaning it has an abundance of electrons. When CH_4 reacts with compounds that are deficient in electrons it is "oxidized," i.e., it gives up electrons, in the process changing its chemical state to one that is rather quickly removed from the atmosphere in rain and dust. It follows that the atmospheric concentration of CH_4 depends in part at least on the concentration of oxidizing compounds, or the "oxidation state" of the atmosphere. The most important oxidizing compounds in the atmosphere are the hydroxyl radical (OH) and ozone, particularly the former. The biosphere affects the atmosphere's oxidation state, thus the concentration of many important greenhouse gases, through the production of reduced compounds that react with and consume atmospheric OH and ozone. CH_4 is one such compound; others, that are not greenhouse gases, include CO, a variety of hydrocarbons other than CH_4 (collectively termed NMHCs, or nonmethane hydrocarbons), and H_2 . Changes in the distribution and condition of vegetation in response to climate change will create feedbacks via emissions of these trace gases.

The oxidation of carbon monoxide appears to be the dominant consumer of hydroxyl radicals (~70%, Crutzen and Andreae 1990). Thus, an increased source of CO would tend to increase the atmo-

spheric lifetime and hence concentration of methane. There is considerable uncertainty about global CO sources, but CO concentration appears to be rising at 1 to 2% per year (Levine, Rinsland, and Tennille 1985; Zander et al. 1989), most likely due to emissions related to fossil-fuel and biomass burning, as well as increases in methane emissions from rice cultivation and livestock (Khalil and Rasmussen 1990). Photochemical models suggest a possible decrease in hydroxyl radical concentration because of these increases in CO and methane (Levine, Rinsland, and Tennille 1985; Thompson, Huntley, and Stewart 1990). Biospheric factors that affect the concentration of OH, and thus may affect biospheric feedbacks to climate change, include direct ecosystem emission of CO, which remains poorly quantified (Harriss et al. 1990); methane releases from wetlands; and CO originating from plant emissions of NMHCs. The potential increase in catastrophic fire also should produce a significant source of CO, CH₄, and NMHC.

Because emission of methane from wetlands is apparently sensitive to temperature (Harriss et al. 1990), it could be expected to rise as high-latitude wetlands warm. The extent of wetlands under future climate scenarios has not been projected, however, and recent studies indicate a great sensitivity of annual emissions of methane to site water balance (Bolle, Seller, and Bollin 1986). Atmospheric methane concentrations seem to have increased during previous periods of warming (Khalil and Rasmussen 1989), suggesting that natural methane emissions probably will increase with any future warming.

NMHCs are among the most reactive natural greenhouse gases, with atmospheric lifetimes of hours to days. They are emitted by most types of vegetation, but amounts vary widely depending on vegetation type and environmental factors such as temperature and light (Zimmerman et al. 1978). Oxidation of NMHCs and related CO provides a significant sink for OH radicals in the planetary boundary layer (Jacob and Wofsy 1988) but also to a great extent via oxidation of CO (an intermediate in the NMHC oxidation pathway) in the troposphere. The exponential increase in amounts of NMHCs emitted by plants with increasing temperature (Tingey, Evans, and Gumpertz 1981) suggest that the warming associated with climate change is likely to increase amounts emitted locally. Changes in the area occupied by forests also will alter the magnitude of global NMHC emissions (Turner et al. 1991).

The increased emission of chemically reduced gases from both manufactured and natural sources in response to climate change suggests that the atmospheric overall oxidation state could be expected to decrease in the coming decades—that is, the atmospheric

lifetime of many greenhouse gases will increase. Potentially counterbalancing factors include increasing tropospheric ozone, NO, NO₂, and water vapor, all of which promote the formation of hydroxyl radicals (Thompson, Huntley, and Stewart 1990). Crutzen and Andreae (1990) have suggested that amounts of ozone might increase at the industrialized latitudes because of fossil-fuel related to NO, NO₂, CO, and hydrocarbons, and in the tropics due to biomass burning. The relatively long atmospheric lifetime of CO and CH₄ means that they are well mixed in the atmosphere, and will tend to deplete OH globally. More sophisticated models than are currently available are needed to evaluate future possibilities. However, all analyses point to a strong role of the biosphere in regulating global atmospheric chemistry.

Cloud Condensation Nuclei

The biosphere also may influence climate via production of cloud condensation nuclei (the particles around which clouds form). Natural sources of cloud condensation nuclei include dimethylsulfide (DMS) over oceans and plant-derived particulates, and NMHCs over land. The brightness of clouds has a large effect on the global albedo (reflecting power), hence the global energy balance; therefore, even a small increase in amount of cloud cover could counteract the radiative forcing of a doubling of atmospheric CO₂ (Dickinson 1986).

Charlson et al. (1987) have hypothesized that DMS production associated with phytoplankton responds to environmental variables affected by climate change. Under warming conditions, DMS flux is projected to increase, thus providing a higher global albedo and a negative feedback to warming. Recent modeling has suggested the long-term strength of that feedback may be relatively small (Foley, Taylor, and Ghan 1991), but there remains great uncertainty about the short term. It seems likely that human influences on nutrient availability may also substantially affect DMS production over the next few decades.

The role of vegetation NMHCs in cloud albedo is even more uncertain (Chatfield, in press). However, the aerosol counts in the Amazon Basin, for example, include a large organic component, originating in part from NMHCs. As with the case of DMS, a warmer climate might promote greater biospheric release of NMHCs, thus more cloud condensation nuclei causing a negative feedback to warming. At this point, however, the complexity of the relationships of cloud condensation nuclei, cloud albedo, and amount of cloud cover makes it difficult to realistically predict whether the biospheric feedbacks related to cloud condensation nuclei will be positive or

negative. But these hypotheses are providing a strong impetus to further research.

The Land: Feedbacks to Climate Change

The accumulation of greenhouse gases and subsequent global warming have the potential to affect the structure and functioning of ecosystems on land and—by extension—the interaction of these ecosystems with air and water, in two general ways: first, through direct effects of temperature, atmospheric CO₂, and altered precipitation on the physiology of individual organisms and the interactions among individuals; and second, through large-scale reorganizations of ecosystems triggered by species migrations and altered disturbance regimes. Although the first has received more attention by scientists, large-scale reorganizations of ecosystems have the greater potential for producing strong feedbacks to global warming.

Along with their control over water cycling, terrestrial ecosystems will influence global warming most directly by acting either as a sink for excess CO₂ (dampening the greenhouse effect) or—by giving up some of the CO₂ currently stored on land—as a source for it (magnifying the greenhouse effect). The land could act as a sink for carbon if plant growth on a worldwide basis (global net primary productivity [NPP]) increased, and particularly if forests, which store more carbon than other vegetation types, expanded. Even if NPP increased, however, the land could act as a net source of carbon, rather than a sink, if decay of organic matter stored in soils offset increased plant production. Increases in NPP would be transitory if ecosystems became overly stressed by drought, disturbances such as wildfires and insect infestations, or inability of plants to migrate fast enough to keep pace with climate change. We shall return to these in more detail later.

Carbon is removed from the atmosphere by photosynthesis and returned to the atmosphere by respiration and fire, both of which oxidize organic matter (hence the close coupling between the carbon and oxygen cycles). Photosynthesis by land plants removes roughly 110 gigatons (Gt) of carbon from the atmosphere each year (one Gt = 10⁹ metric tons, or 10¹⁵ g); this is about one-seventh of the atmosphere's carbon, and 20 times more carbon than is released each year through fossil-fuel burning (Houghton 1987; King et al. 1990; Post et al. 1990). Of the amount removed by photosynthesis, about one-half is respired and returned to the atmosphere; most of the rest is stored in aboveground and belowground biomass and soil humus. A small amount (about 0.4 Gt per year) is exported to streams and oceans (Schlesinger and Melack 1981). Soils are the largest

carbon reservoir on land, holding 3 to 4 times more than living vegetation (Post et al. 1982; Dixon and Turner 1991). Forests contain most of the carbon stored in living vegetation on land and strongly influence the seasonal fluxes of CO₂ between land and air. For example, the annual rhythms of growth and decay of the boreal forests (conifer-dominated forests of the far north) account for 30% of the yearly change in atmospheric CO₂ measured at Mauna Loa, Hawaii (D'Arrigo, Jacoby, and Fung 1987). It follows that the fate of forests will play an important role in determining future climate.

Most researchers assume that carbon stores in undisturbed terrestrial ecosystems are in steady state—that is, amounts shunted to storage reservoirs during any given year are balanced by equivalent losses to decay of older organic matter. However, this clearly is not the case in disturbed ecosystems. For example, one of the earlier pulses of CO₂ into the atmosphere during modern times came not from burning fossil fuels, but from the accelerated decomposition of soil organic matter that accompanied the rapid expansion of agriculture during the latter part of the nineteenth century (Wilson 1978). Destruction of forests is thought to have contributed up to one-third of the CO₂ that has accumulated in the atmosphere in this century (Woodwell 1989); however, there is considerable uncertainty about just how much carbon is stored in forests, which in turn raises questions about how much CO₂ has been pulsed to the atmosphere through deforestation (Post et al. 1990). Data gathered during the 1980s indicate that both tropical and boreal forests contain significantly less carbon in living vegetation than previously believed (Brown and Lugo 1984; Botkin and Simpson 1990; Brown, Gillespie, and Lugo 1989). Botkin and Simpson (1990) suggest that, worldwide, terrestrial vegetation may contain only one-third to one-fourth of the amount cited during the 1970s and early '80s.

In general, the global carbon cycle is poorly understood. Of the 5 Gt known to be released by fossil-fuel burning, and the 2 Gt thought to be released in deforestation, less than one-half has accumulated in the atmosphere (Houghton and Woodwell 1989). So where does the rest go? Until recently, scientists assumed the "missing" carbon was absorbed by the oceans; this means the strongest sink should be in the southern hemisphere, which has a much higher proportion of ocean to land than the north does. However, computer modeling (Tans, Fung, and Takahashi 1990) indicates that global patterns of atmospheric CO₂ can best be explained by a strong carbon sink in the northern hemisphere; either the northern oceans are exceptionally strong sinks, or the sink lies on land—most logically the boreal forests of North America and Eurasia. As we discussed earlier, the amplitude of the seasonal cycle in atmospheric

CO₂ has been increasing over the past few decades, which suggests that forests in the northern hemisphere might be growing more (Jarvis 1989); however, the magnitude of change is relatively small and cannot account for the "missing" CO₂. Schlesinger (1990) argues that soils are unlikely to be soaking up the extra carbon. The ability of scientists to do more than speculate about carbon sinks on land is severely limited by lack of data (Dyson 1990).

With this background, we now turn to the question of whether global warming will trigger terrestrial ecosystems to be sinks or sources of excess atmospheric CO₂, respectively dampening or magnifying the greenhouse effect. This complicated issue involves numerous poorly understood factors (Bazzaz 1990). We concentrate here on the likely effects on (a) plant physiology and growth; (b) soil carbon stores; (c) soil nutrient fluxes, as influenced by loss of soil organic matter; and (d) redistribution and reorganization of major vegetation types, especially as influenced by disturbance regimes. Of these factors, change in vegetation types and disturbance seems likely to play the major role, particularly when considered in interaction with increasing human pressure on land—in its own right a powerful degrading force likely to be exacerbated by climate change (e.g., Eamus and Jarvis 1989; Perry et al. 1990; Schlesinger 1990b; Neilson and King, *in press*).

Plant Physiology and Growth

How climate change might affect plant physiology has been much discussed in the literature, particularly with regard to higher atmospheric CO₂ (e.g., Jarvis 1989; Adams et al. 1990; Bazzaz 1990; Eamus and Jarvis 1989; Graham, Turner, and Dale 1990; Perry and Borchers 1990). To briefly summarize, higher atmospheric CO₂ frequently produces increased plant growth under controlled conditions, but this effect is often transitory and is not always confirmed in field studies. From a strictly physiological standpoint (*i.e.*, not accounting for disturbance and migration), the ability of plants to sequester CO₂ is limited by the availability of other resources. Controlled studies indicate that at least some trees produce relatively more roots and form more mycorrhizal fungi in environments with high, rather than low, levels of CO₂ (Norby et al. 1987; O'Neill et al. 1987a, b), which should allow them to gather more nutrients and water. Moreover, higher atmospheric CO₂ allows many plant species (the so-called C3 plants) to use water more efficiently (Bazzaz 1990). Nevertheless, in unfertilized and unirrigated ecosystems nutrients and water will probably constrain the ability of plants to significantly enhance their growth solely because of higher atmospheric

CO₂ (e.g., Billings et al. 1984). Studies of single plant species growing in pots in a growing chamber—which dominate the literature on this issue—are unlikely to accurately reflect what happens in Nature (Jarvis 1989; Bazzaz 1990).

Warmer temperatures might have several conflicting effects on plant productivity. Respiration, hence CO₂ loss, will increase, as will evaporative demand, which will tend to deplete soil moisture more rapidly. On the other hand, longer growing seasons could increase plant productivity, but once again this depends on other limiting factors, especially soil water, which is likely to be exhausted and limit growth even if the frost-free season extended well into autumn. However, if a longer frost-free season were accompanied by fall rains, plant productivity could significantly increase. In some ecosystems, plants could benefit from having less soil water.

Greenhouse effects on both the total amount and seasonal distribution of precipitation are the major wild cards in predicting response of terrestrial ecosystems (Neilson et al. 1989; Perry and Borchers 1990). The total amount of water vapor will increase with warmer temperatures because of greater evapotranspiration—the loss of water from soil both by evaporation and by transpiration of plants growing there. However, it does not follow that precipitation also will increase, at least not uniformly across the globe. In fact, models predict that the interiors of the North American and Eurasian continents and certain areas of the tropics will become drier (Mitchell and Warrilow 1987; Neilson et al. 1989). The most significant effect of climate change may be changes in the spatial and temporal variability of climate rather than changes in global averages.

Soil Carbon Stores

The amounts of carbon stored in soils reflect the balance between inputs by plants and losses through erosion and microbial decomposition. Whereas photosynthesis is relatively insensitive to temperature, microbial activity—hence the rate at which organic matter is decomposed by soil microbes—increases sharply with temperature. It follows that, other factors remaining equal, warmer temperatures will increase decomposition rates: without a concomitant increase in the amount of carbon added to soils, carbon will be moved from soils to the atmosphere, reinforcing the greenhouse effect. Using a model developed at Rothamsted Agricultural Research Station in England, Jenkinson, Adams, and Wild (1991) estimated that the "most likely" scenario for temperature increase (0.03° C per year) would release 61 Gt of soil carbon to the atmo-

sphere by the year 2050, assuming no change in soil moisture or plant growth and excluding wetlands. That is about 19% of the carbon that will be released by fossil-fuel burning over the same period, if fuels continue to be burned at current rates.

The Jenkinson et al. (1991) estimate represents a drop of about 5% in global carbon stores in the soil, although local declines may be considerably larger. Woodwell (1986) estimates that soils in the boreal zones could lose 10% to 50% of their carbon over the next few decades because of increased decomposition, but Lashof (1989) thinks that is an overestimate. Comparison was made of soil carbon in two old-growth forests on the H. J. Andrews Experimental Forest (Oregon Cascade Range). One of the forests was at 800 m elevation and the other was at 1,600 m elevation; the lower-elevation forest contains about one-half less soil carbon than the latter (D. A. Perry and T. Bell, unpublished data). The average temperature difference between these two stands is roughly equivalent to that expected for the doubled- CO_2 climate—which suggests that, if the difference in soil carbon between the two stands is a result of temperature and not mineralogy or some other factor, the higher elevation forest will lose one-half of its soil carbon as it comes into equilibrium with the new climate. How representative these two stands may be of the rest of the Cascades is unknown. Unfortunately, scientists suffer from a lack of knowledge about how much carbon is stored in soils and how stable it is.

Feedbacks to climate change created by carbon loss from wetlands are of particular concern. Although covering less than 3% of the land surface, wetlands are estimated to contain nearly 15% of global soil carbon. Microbes that decompose organic matter in wetland soils can operate in that oxygen-poor environment through a metabolic pathway that produces CH_4 rather than CO_2 ; CH_4 has nearly 4 times more warming potential than CO_2 (Lashof and Ahuja 1990). Another class of microbes particularly active in oxygen-poor environments converts nitrate into N_2O , which has 180 times more warming potential per molecule than CO_2 . Increased activity of these wetland microbes with warmer temperatures could produce a strong positive feedback to the greenhouse effect.

In areas that become drier as well as warmer, as is predicted for the interiors of North America and Eurasia and for parts of the tropics, soil organic matter content is likely to drop sharply. Where warmth is not accompanied by drought, and ecosystems are not unduly stressed, carbon added to the soil because of greater plant productivity could somewhat compensate for increased decomposition of soil organic matter. However, though the magnitude is uncertain, it is likely that there will be a net movement of carbon

from soils to the atmosphere, reinforcing the greenhouse effect. How fast this may happen is uncertain, but it will probably be on the order of decades rather than centuries. The few available studies indicate that an appreciable fraction of soil organic matter is readily decomposed. For instance, prairie soils in Missouri lost 80% of their carbon within 30 years of being plowed (Balesdent et al. 1988).

Soil Nutrient Fluxes

Organic matter profoundly influences the biology, chemistry, and physics of soils. Litter and soil humus are the primary reservoirs of nitrogen in ecosystems, and are also important reservoirs of phosphorus and sulphur. Much of the physical structure of soils, hence their porosity to water and air, arises from the ability of organic compounds to aggregate minerals. A significant proportion of the soil's electrical surface charge comes from carbon compounds, and that charge helps keep soluble nutrients such as calcium, potassium, and magnesium from leaching to streams. Some nutrients, such as iron, are highly insoluble (hence unavailable to plants) unless they are combined with an organic molecule. Finally, carbon compounds are the energy source for the microbes and soil invertebrates that cycle nutrients. It follows, then, that soil carbon losses will affect numerous aspects of soil structure and processes, and could significantly alter nutrient fluxes to water and air.

The following discussion focuses on nitrogen for two reasons. First, 98% or more of soil nitrogen occurs in organic molecules; hence it is the nutrient that stands to be most directly affected by soil carbon loss. Second, nitrogen is considered to be the most limiting element in temperate and boreal ecosystems (but not in the tropics), and perhaps in the oceans as well (marine biologists disagree about whether nitrogen, phosphorus, or iron limits productivity in the oceans); therefore, altered nitrogen storage and cycling could initiate significant feedbacks to climate change through effects on primary productivity. Accelerated decomposition of soil organic matter due to warmer temperatures will free nitrogen from organic bonds, converting it to more mobile, inorganic forms. Relatively large amounts of nitrogen might be released. Jenkinson et al.'s (1991) estimate of a 61 Gt decline in global soil-carbon stores in a doubled- CO_2 climate would free roughly 3 Gt of nitrogen over the next 60 years. To put some perspective on that number, in the unlikely event that all the freed nitrogen went to rivers and ultimately oceans, the amounts added annually to oceans would increase 2 to 6 times.

Since most temperate ecosystems are limited by nitrogen, some nitrogen released from decomposing organic matter will act as a

fertilizer and enhance plant growth (Billings et al. 1984; Oberbauer et al. 1986). Because woody plants contain much more carbon per unit of nitrogen (known as the *C/N ratio* to ecologists) than humus, conversion of humus nitrogen to plant nitrogen would result in significantly more carbon being taken up in new growth than was released in decomposition. For instance, depending on the *C/N ratio* of soil organic matter, a net drop of 12 to 30 g of soil carbon would free roughly 1 g of nitrogen; a nitrogen-limited tree that used that 1 g to support new growth could perhaps sequester 150 g of carbon as net photosynthates. One Gt of nitrogen transferred from humus to trees would result in a net transfer of roughly 125 Gt of carbon from the atmosphere to land—about 25 years' worth of fossil-fuel burning at the 1980 rate.

Although this inadvertent nitrogen fertilization would appear to provide a strong negative feedback to global warming, two lines of argument suggest that this will not be the case. First, comparison of Pacific Northwest sites with high and low levels of nitrogen shows that when root and mycorrhiza growth is considered along with aboveground growth, forests differ little in their total productivity: those on nitrogen-poor sites invest more growth belowground and less aboveground (Edmonds et al. 1989). Therefore, a burst of nitrogen from decomposing organic matter may trigger a shift from belowground to aboveground growth, where the carbon and nitrogen are more vulnerable to loss in wildfire. Second, even if total productivity were increased by greater nitrogen availability, other factors—nutrients other than nitrogen, water, herbivory (predation by plant eaters), disturbances, degradation due to land use—are likely to become limiting before a significant proportion of the additional nitrogen can be soaked up. Most tropical forests are thought to be limited by phosphorus rather than nitrogen (although that may change, because their nitrogen stores are being lost at an alarming rate through burning by humans [Crutzen and Andrea 1990; Kauffman, Till, and Shea, in press, 1992]; hence they are unlikely to retain much, if any, of the freed nitrogen. German forests that are being inadvertently fertilized with nitrogen by acid precipitation have become limited—and even severely stressed—by shortages of magnesium and potassium (Oren et al. 1988). The ability of western conifers to respond to nitrogen fertilizer is often restricted by other nutrients (Edmonds et al. 1989; Velasquez-Martinez 1990; Mika and Moore 1991). Thus, whereas some of the nitrogen freed as a result of soil carbon losses will fuel plant growth, an unknown but probably significant proportion will either be converted to gas and escape to the atmosphere or be leached to streams.

Conversion by soil microbes of mineral nitrogen to gas could

significantly reinforce global warming, depending on how much N_2O production increases with climate change. Soils are believed to be the primary source of N_2O to the atmosphere, but detailed knowledge is sketchy (Banin 1986; Bowden 1986). As previously noted, marshes, bogs, and other wetlands will almost certainly be major sources of N_2O ; lowland moist tropical forests may be significant sources as well. Only crude estimates of N_2O fluxes to the atmosphere are possible. The rate of denitrification is known to increase from 40% to 60% with each $10^\circ C$ rise in temperature (in scientific jargon, the Q_{10} of the process is 1.4 to 1.6; Bowden 1986). Estimates of current rates of N_2O emission from soils range from less than 5×10^{12} g per year to over 120×10^{12} g per year. Applying the Q_{10} value, an average temperature rise of $3^\circ C$ over the next 50 years would increase N_2O emissions by between 0.03×10^{12} and 0.75×10^{12} g per year. Although N_2O is a much stronger greenhouse gas than CO_2 (Lashof and Ahuja 1990), that amount of yearly increase in N_2O emissions from soils has only 0.03% to 10% of the warming potential of the CO_2 released each year from fossil-fuel burning.

Amounts could be higher than that simple calculation indicates, however. Some nitrogen freed from organic matter in well-drained upland soils may be converted to gas, but most of that not taken up by plants is likely to leach to surface waters, where it might either have little effect or stimulate productivity, depending on amounts. Too much nitrogen entering streams and estuaries could cause eutrophication and, in fresh waters, diminish water quality.

The amount of nitrogen released to streams during warming is likely to vary widely from one area to another, depending on total soil organic matter and its stability, and on the degree to which plants can sequester the nitrogen converted from organic to mineral forms. Experience with fertilization in the Pacific Northwest suggests that forests may sequester at most 100 to 200 kg/ha of additional nitrogen before becoming limited by other factors.² As we discussed earlier, Pacific Northwest forests (and probably other forests as well, at least conifers) may respond to extra nitrogen by shifting growth from belowground to aboveground tissues with little change in total growth, in which case the additional nitrogen sink afforded by higher decomposition will be relatively small. If so, the amount of nitrogen entering surface waters globally could increase several fold, depending on amount and rate of carbon losses. Locally, amounts could be much higher. High-elevation forests on the west slopes of the Cascades could release as much as one-third to one-half of their total soil nitrogen to streams—2,000 to 4,000 kg/ha—as they come into equilibrium with a warmer climate. Over what period that might occur is unknown.

Not all of the nitrogen and other nutrients leached from upslope ecosystems goes directly to streams. Streamside plant communities are very effective nutrient absorbers; studies have shown that 65% to 75% of the dissolved nitrogen in soil solution is removed before entering surface waters (Lowrance et al. 1984; Peterjohn and Correll 1984). However, the ability of streamside vegetation to pull nutrients out of solution would be reduced if plants there become stressed by drought or other factors related to climate change. Moreover, not all of the nitrogen that reaches streams will flow eventually to estuaries; far from being simple pipes connecting land to the sea, streams effectively retain nutrients. As with upslope ecosystems, primary productivity of streams is frequently limited by nitrogen and would almost certainly be stimulated to some degree by added nitrogen, particularly in the Pacific Northwest. In a small (first-order) stream draining an old-growth watershed on the H. J. Andrews Experimental Forest in the Oregon Cascades, more than 50% of dissolved nitrogen entering the stream in either organic or inorganic forms was removed from water before it left the watershed. Twenty-five to 100% of the nitrogen experimentally added to a larger (fifth-order) stream on the H. J. Andrews was removed from stream-water within 300 m (Lamberti and Gregory 1989). Increased nitrogen concentration in water actually increases the rate at which aquatic plants and microbes take up nitrogen. Nitrogen uptake would be enhanced further by warmer water temperatures, which would stimulate biological activity, and by lower summer flows (due to lower precipitation and earlier snow melt), which would slow the movement of nutrients through stream reaches and thereby increase the probability of a given nutrient molecule being taken up. The situation is complex, but the evidence suggests that, in the Pacific Northwest at least, less than half of the nitrogen released from upslope ecosystems as a result of soil carbon loss would be exported to the ocean.

Redistribution and Reorganization of Major Vegetation Types

The degree to which forest area expands or contracts will be an important determinant of whether terrestrial ecosystems dampen the greenhouse effect by sequestering atmospheric carbon or reinforce it by releasing some carbon to the atmosphere. Three issues are involved: (a) the distribution of vegetation types when they have come into equilibrium with future climate; (b) the so-called transient response (Solomon 1986), the period of redistribution and reorganization that precedes a new equilibrium; and (c) disturbances

(human caused and natural) that, through impacts on soils and biodiversity, degrade systems and prevent them from responding to what may be more favorable climatic conditions. Transient responses and disturbance are likely to dominate the landscape, and consequently the nature of feedbacks to global warming over the next few centuries (Solomon 1986; Neilson et al. 1989; Perry et al. 1990; Perry and Borchers 1990; Sirios and Payette 1991). However, most computer models predicting the effect of climate change on terrestrial carbon stores have assumed that vegetation is in equilibrium with the new climate. Such "equilibrium" approaches are probably unrealistically optimistic; nevertheless they are useful because their results represent "best case"—that is, the scenario that produces the strongest negative feedback to global warming.

So what do equilibrium models say about the distribution of vegetation on a warmer Earth? A logical place to expect forest area to expand is in the far north, where warming is predicted to significantly exceed the global average. Indeed, some models predict that the current boundary of boreal forest will extend into what is now tundra, perhaps by hundreds of kilometers (Neilson et al. 1989; Smith and Tirpak 1989), something that would significantly mitigate global warming. In contrast, another model (Emanuel, Shugart, and Stevenson 1985), which assumes no change in precipitation (hence reduced soil-water storage), predicts that tundra will be replaced by cold desert or shrublands. Should available soil water decline, models predict that current northern forests will shift to less productive, drought-resistant types, and in some areas perhaps even to grasslands (Emanuel, Shugart, and Stevenson 1985; Pastor and Post 1988; Bonan, Shugart, and Urban 1990).

Equilibrium models also disagree about whether the area in tropical forest will expand or contract; again, the wild card is water. One model (Prentice and Fung 1990), for instance, predicts that vegetation in equilibrium with a doubled- CO_2 climate would store 38% more carbon in living biomass and 1% more in soils than currently. That prediction results primarily from a 75% increase in the area covered by tropical forest as a result of higher precipitation. In that scenario, the additional carbon stored by expanded forests would lower atmospheric CO_2 by 128 ppm, significantly dampening the greenhouse effect (the increase in atmospheric CO_2 between 1850 and 1989 was about 60 ppm; Houghton and Woodwell 1989). The more conservative model of Emanuel, Shugart, and Stevenson (1985), predicts less forest and more grasslands and deserts in a doubled- CO_2 climate. Using this model, Schlesinger (1990a) estimates that soils alone would store 45.5 Gt less carbon than currently.

Equilibrium models have a number of significant limitations. For

instance, climate change is unlikely to simply produce shifts in current climatic zones, but rather to create entirely new combinations of temperature and moisture. Where vegetation types occur is sensitive not only to the amounts of precipitation, but to its seasonality, a factor seldom accounted for in equilibrium models (Neilson et al. 1989). Another unknown factor is the temporal and spatial variability in future climate, which may be more important in determining vegetation patterns than changes in average temperature and moisture. However, the major problem with equilibrium models does not lie in their assumptions about future precipitation patterns, but in the fact that many forests and grasslands are currently severely stressed, and a growing number of ecosystems have been and are being degraded by land-use practices, chronic insect infestations, and/or pollution (Perry et al. 1989; Schlesinger 1990b; Kauffman 1991). Even if changing climate produced more favorable growing conditions, the ability of degraded systems to respond favorably is doubtful.

Even for plant communities healthy enough to expand, equilibrium models beg the question of just how expansion will occur and ignore possible impacts from intensified natural disturbances. These are not trivial issues. Although there have been significant changes in the distribution of vegetation as Earth moved into and out of ice ages, so far as is known none of these occurred at anywhere near the rate that climate is expected to change in response to the greenhouse effect. Pollen preserved in bogs shows that, at the end of the last ice age, tree species in the U.S. upper Midwest migrated northward at an average rate of 20 to 25 km per century—about one-tenth of the rate that would be required to keep up with predicted temperature change during the coming decades (Davis 1989). Moreover, many barriers to migration exist today that did not at the end of the last ice age (farms, cities). This raises significant questions about the stability of biological communities whose members are increasingly maladapted to the climate (Neilson et al. 1990; Perry et al. 1990). What will happen during the period when species are migrating and biological communities are reorganizing? Will communities existing on a given site phase out slowly while newcomers phase in, making an orderly transition? Or will existing communities become stressed to the point of collapse before the arrival of newcomers that can stabilize the processes and cycles vital to ecosystem health? A gradual, orderly transition might be little noticed on the scale of decades. A disorderly one, however, could greatly disrupt the ability of terrestrial ecosystems to sequester carbon and protect soils, and exacerbate the effects of climate change.

Healthy ecosystems are resilient toward the disturbances and cli-

matic fluctuations to which the individuals of a community are adapted. This suggests that a slow, orderly transition of community types is possible, despite the rapidity of climate change. The issue is clouded, however, by the fact that many communities are not healthy, and by the probability that wildfire, insect infestations, and windstorms will become more severe as climate changes (Neilson et al. 1989; Overpeck, Rind, and Goldberg 1990). Wildfires, in particular, have the potential to pulse large amounts of carbon into the atmosphere and disrupt the orderly transition from one mature community type to another. Immature, early successional communities are likely to do well in such a regime, a point we shall return to. That climate change will trigger intensified wildfires is supported by a strong historic link between the incidence of wildfires in North America and periods of warmer-than-average temperature (Clark 1988). Fire is a natural part of many forest types but, when too frequent and/or severe, it can exceed the system's natural resilience mechanisms and lower site productivity. Sirois and Payette (1991) show that past periods of frequent wildfire in northern Canada have converted boreal forest to tundra, concluding that models that do not account for fire and early postfire recovery conditions provide an unrealistic indication of the effect of changing climate on these ecosystems.

Moist tropical forests—already burning at unprecedented rates because of land-use practices (Kaufman et al. 1990; Kauffman and Uhl 1990)—are particularly vulnerable to wildfire because the trees are not adapted to survive or quickly recover from fire (Kauffman et al. 1992). Intact forests in the moist tropics rarely dry out enough for fires to burn; however, forests that have been logged or fragmented into small blocks burn readily (Uhl, Kauffman, and Cummings 1988). Parts of landscapes that are highly flammable—such as dry pastures—serve as centers for ignition and spread of fires, increasing the risk to those parts that are not highly flammable. This is a problem not only in the tropics, but in the Pacific Northwest, where highly flammable young plantations can propagate fire into relatively resistant old-growth stands (Perry 1988; Franklin et al. 1989).

More fires would of course pulse large amounts of CO₂ to the atmosphere, and smaller amounts of the strong greenhouse gases CH₄ and N₂O. Vegetation regrowing after fire would reabsorb at least some of the CO₂, though even with rapid regrowth it could take from several decades to several hundred years to reaccumulate the amount of carbon stored in old-growth forests (Harmon, Ferrell, and Franklin 1990). How fast communities recover from wildfire or other disturbances during a period of changing climate is an open

question. Plants native to the temperate and boreal zones generally tolerate wide climatic fluctuations and are well adapted to fire, but a plant community that is maladapted to its climate seems unlikely to stage a robust recovery following catastrophic disturbance. On the one hand, disturbance could create openings that make it easier to newcomers to establish—if those newcomers have arrived. Otherwise, weedy annual plants, which disperse very effectively, are likely to become more abundant, and the ability of terrestrial vegetation to reabsorb the carbon released in fires and to stabilize soils will be greatly diminished. In some cases at least, an extended weedy period produces changes in soil biology and structure that make it more difficult for trees to establish (Perry et al. 1989, 1990). Even if weeds do not dominate a site, increased fire frequency and severity could result in nutrients being lost from sites faster than they are replenished through natural processes, which would in turn significantly diminish the ability of mature plant communities to recover and sequester carbon (Kauffman, Till, and Shea 1992).

Should terrestrial ecosystems become chronically stressed through intensified disturbances or inability to adapt to new climates, the strong nutrient sinks and physical stabilization of soils provided by plants and associated microorganisms would become weakened, and more nutrients would be transported to surface waters through leaching and erosion. Deforestation in the Himalaya Mountains provides an extreme, but unfortunately common, example of how severe disturbance of terrestrial ecosystems can have serious repercussions on rivers and ocean margins. Between 30 and 75 metric tons of soil are estimated to erode yearly from each hectare of deforested land in Nepal (Myers 1986). Erosion of former forest land in Nepal and India is so severe that a number of river beds in the Ganges system are rising at a rate of 15 to 30 cm per year; in the Bay of Bengal, accumulating sediment is producing a gigantic shallow covering some 50,000 km² (Myers 1986). Not all mountain soils are as unstable as those of the Himalayas, but there is little doubt that erosion and nutrient leaching will increase if climate change triggers a more severe disturbance regime in upland forests.

The conclusion that emerges from all this is that predictions of significant dampening of the greenhouse effect by expanding forests are most probably wrong. More likely, the current trend of global forest degradation will accelerate and, as a by-product, significant amounts of carbon will be released to the atmosphere and both on-site and downstream impacts of erosion increased. It is difficult to quantify with any accuracy how disturbance and migration may influence carbon storage on land; the best that can be done is to bound the possibilities. Neilson and King (in press) modeled several

scenarios investigating the interplay between CO₂ released from wildfire in northern forests and CO₂ absorbed by expanding tropical forests. In their most optimistic scenario, CO₂ released in northern fires was absorbed by the expanding tropical forests, resulting in no net pulse of CO₂ to the atmosphere. In their most pessimistic scenario, northern forests burned extensively over the next 50 years, and tropical forests failed to expand, resulting in a net pulse of 166 Gt of carbon from aboveground biomass to the atmosphere—equivalent to about 30 years' worth of fossil-fuel burning and a strong positive feedback to global warming. Moreover, even that pessimistic scenario did not consider carbon losses from soil and litter.

No one knows how extensively northern forests might burn in the future, although the historic evidence indicates that wildfires will increase. The future of tropical forests is clearer: in the absence of radical changes in land use, these forests are going to continue contracting rather than start expanding, which means they are going to be a source of CO₂ to the atmosphere rather than a sink. But how much of a source? Consider the year 1987 in Amazonia: 35,000 fires burned more than 20 million ha (Kaufman et al. 1990), roughly 40% of which was in primary forest cleared for pasture, and the remainder in cleared secondary forest and previously established pasture (Setzer et al. 1988). Cattle pastures in Amazonia—most of which degrade quickly—store only about 3% as much carbon in 1 ha of aboveground living biomass as mature forest (Kauffman, Till, and Shea 1992). If Amazonian forests continue to be converted to pasture at the 1987 rate, by the year 2050 they will store roughly 150 Gt less carbon in aboveground biomass than in 1990; if soil carbon losses were accounted for, that figure would increase, though it is unclear how much. Reduced carbon storage in Amazonia alone would match about 30 years worth of fossil-fuel burning. And that is only Amazonia: other areas throughout the tropics are being similarly degraded. If we add to that the CO₂ from fires in northern forests, disruptions on land could pulse even more carbon into the atmosphere over the next several decades than fossil-fuel burning.

But even that bleak scenario does not represent a "worst" case. A significant proportion of precipitation, at least in the tropics, results from cycling of water by forests. For instance, about 50% of the rainfall that sustains the forests of Amazonia results from water cycled by the forests themselves (Salati 1987). Declines in precipitation following tropical deforestation have been noted since Columbus recorded this in his journals in the early 1500s. In the 1900s, precipitation declines have been recorded in deforested areas of Panama, Malaysia, India, the Philippines, and the Ivory Coast (Windsor, A. S. Rand, and W. M. Rand 1986; Myers 1988). As tropical

forests are converted to pastures or degraded through logging and shifting cultivation, it is entirely possible that, at some critical level of deforestation, entire regions such as Amazonia will dry out solely because the internal water cycle is disrupted. The combination of declining precipitation and increased fire susceptibility because of land-use practices could result in catastrophic collapse of remaining forests. Lest this begin to sound like science fiction, consider the fact that, in 1983, a massive forest fire on the island of Borneo burned an area of moist tropical forest nearly the size of Taiwan (3.5 million ha)—an event that is unprecedented in recorded history.³

Coda

Earlier we stressed the need to understand complex systems as wholes rather than as parts. Ashby (1966, p. 54) states the situation thusly in his introductory text on cybernetics:

When there are only two parts joined so that each affects the other, the properties of the feedback give important and useful information about the properties of the whole. But when the parts rise to as few as even four, if every one affects the other three, then twenty circuits can be traced through them; and knowing the properties of all twenty circuits does *not* give complete information about the system. Such complex systems cannot be treated as an interlaced set of more or less independent feedback circuits, but only as a whole.

Behavior of the global ecosystem—which has far more than four interconnections—is unlikely to be captured by even very complicated models. This fact has important implications for decision making. Whereas much of science and technology is predicated on the ability to predict and control, a complex, highly integrated system such as Earth is inherently unpredictable and subject to threshold changes that are unlikely to yield to quick technological fixes. The bottom line is that no one knows which way climate change will take us, and no one will until it is too late to do something about it. The rational response is not to “wait and see,” but to act now. Necessary steps include both reducing carbon emissions and enhancing carbon uptake and storage (Flavin 1990). Carbon emissions can be lowered by reducing the amounts of fossil fuels that are burned (the responsibility of the industrialized countries), slowing deforestation (the responsibility of the Global community), and adopting minimum tillage agricultural systems. Various approaches have been suggested for enhancing carbon uptake, all of which center on increasing the productivity of plants on land and in the

oceans; the most feasible (albeit very expensive) of these is reforesting the large areas of degraded forest lands.

Planting trees and providing tropical countries the incentives to halt deforestation are important steps, but climate change is unlikely to be significantly slowed while industrialized countries continue burning fossil fuels at current rates. Rosenfeld and Botkin (unpublished ms. 1989; for information contact Dan Botkin, Biology and Environmental Science, U.C. Santa Barbara) calculate that world forest area would have to be doubled to balance carbon emissions from fossil fuels—something that is unlikely at best and probably impossible. Moreover, newly planted trees will take decades to soak up appreciable amounts of carbon; meanwhile, forests may become increasingly stressed by changes in climate that are already set in motion, reducing their ability to sequester carbon. Arguments against reducing fossil fuel consumption center on the economy, however considerable energy savings are possible with little or no impact on lifestyles. Rosenfeld and Botkin conclude that “With the proper political leadership, we could reduce energy intensity in industrial countries by 50%, using existing technology, and still maintain the quality of life. . . .” Ultimately, climate change, as well as other stresses such as pollution, loss of biodiversity, and degradation of soils and water, will only be adequately dealt with by striking at the root problems—overpopulation in the third world, overconsumption in the industrialized world, and the growing gap between rich and poor.

Summary

The major effect of vegetation on carbon fluxes to and from the atmosphere will be reorganization and redistribution of forests due to disturbance and migration. Because they store the bulk of terrestrial carbon, forests will play a key role. Boreal forests could extend onto current tundra, but only if precipitation increases enough to balance increased evapotranspiration. No plants except weeds are likely to migrate fast enough to keep pace with climate change. Should frequency and severity of fire increase, as is predicted, northern forests are likely to become a source of CO₂ to the atmosphere rather than a sink. Some models predict that tropical forests will expand, in which case they would be a strong sink for CO₂; other models predict they will contract. However, when land-use practices are taken into account, tropical forests doubtless will contract regardless of what happens with climate. Hence the tropics are much more likely to be a CO₂ source rather than a sink. In terms of carbon fluxes, changes in terrestrial vegetation are more likely to signifi-

cantly reinforce the greenhouse effect than to dampen it. The nitrogen released from accelerated decomposition of soil organic matter might stimulate forest productivity somewhat, but several lines of argument suggest that will not provide a significant negative feedback to warming. Amounts of nitrogen leached to streams could increase several-fold, increasing stream productivity. Should mountain forests become severely stressed, the resulting erosion would greatly increase sedimentation of streams, rivers, and estuaries. Because the global ecosystem is complex, unpredictable, and subject to threshold changes that could be difficult or impossible to reverse, a "wait and see" attitude is not an appropriate response to impending climate change.

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Notes

1. N release from organic matter is estimated using a global average soil C/N ratio of 17.3, calculated from data given in Post et al. (1982) and Post et al. (1985). Current flux of N from rivers to oceans is from Rosswall (1983).

2. That estimate assumes that only one-half of the fertilizer applied gets to trees (Edmonds et al. 1989). Fertilization may not accurately indicate how trees will respond to increased decomposition rate (Ingestad 1982).

3. Wolf (1985) asks how a fire of that magnitude could occur in an area that gets 5 times more rain than New York or London. The answer appears to be an anomalous drought, apparently related to an El Niño, exacerbated by extensive modification of the mature rain forest by shifting cultivators.

References

- Adams, R. M., C. Rosenzweig, R. M. Peart, J. T. Ritchie, B. A. McCarl, J. D. Glycer, R. B. Curry, J. W. Jones, K. J. Boote, and L. H. Allen, Jr. 1990. Global climate change and U.S. agriculture. *Nature* 345:219-224.
- Ashby, W. R. 1966. An introduction to Cybernetics. Science Editions. New York: John Wiley & Sons. 295 pp.
- Ausubel, J. H. 1991. A second look at the impacts of climate change. *Am. Sci.* 79: 210-221.
- Balesdent, J., G. H. Wagner, and A. Mariotti. 1988. Soil organic matter turnover in long-term field experiments as revealed by carbon-13 natural abundance. *Soil Sci. Soc. Am. J.* 52(1):118-124.

- Banin, A. 1986. Global budget of N₂O: The role of soils and their change. *The Science of the Total Environment* 55:27-38.
- Barnola, J. M., D. Raynaud, Y. S. Korotkevich, and C. Lorius. 1987. Vostok ice core provides 160,000-year record of atmospheric CO₂. *Nature* 329:408-414.
- Bazzaz, F. A. 1990. The response of natural ecosystems to the rising global CO₂ levels. *Ann. Rev. Ecol. Syst.* 21:167-196.
- Billings, W. D., K. M. Peterson, J. O. Luken, and D. A. Mortensen. 1984. Interaction of increasing atmospheric carbon dioxide and soil nitrogen on the carbon balance of tundra microcosms. *Oecologia* (Berlin) 65:26-29.
- Bolle, H. J., W. Seiler, and B. Bolin. 1986. Other greenhouse gases and aerosols. Assessing their role for atmospheric radiative transfer. Pp. 157-203 in B. Bolin, B. R. Doos, J. Jäger, and R. A. Warrick, eds. *The greenhouse effect, climatic change and ecosystems*. SCOPE 29. New York: John Wiley & Sons. 541 pp.
- Bonan, G. B., H. H. Shugart, and D. L. Urban. 1990. The sensitivity of some high-latitude boreal forests to climatic parameters. *Climate Change* 16:9-30.
- Botkin, D. B., and L. G. Simpson. 1990. Biomass of North American boreal forest. *Biogeochemistry* 9:161-174.
- Bowden, W. B. 1986. Gaseous nitrogen emissions from undisturbed terrestrial ecosystems: An assessment of their impacts on local and global nitrogen budgets. *Biogeochemistry* 2:249-279.
- Broecker, W. S. 1987. Unpleasant surprises in the greenhouse? *Nature* 328:123-126.
- Brown, S., A. J. R. Gillespie, and A. E. Lugo. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Sci.* 35(4):881-902.
- Brown, S. and A. E. Lugo. 1984. Biomass of tropical forests: A new estimate based on forest volumes. *Science* 223:1290-1293.
- Charlson, R. J., J. E. Lovelock, M. O. Andreae, and S. G. Warren. 1987. Oceanic plankton, atmospheric sulphur, cloud albedo, and climate. *Nature* 326:655-661.
- Chatfield, R. B. Ephemeral biogenic emissions and the Earth's radiative and oxidative environment. In S. H. Schneider, ed. *Proceedings of the Chapman Conference on the Gaia Hypothesis*. (in press).
- Clark, J. S. 1988. Effect of climate change on fire regimes in northwestern Minnesota. *Nature* 334:233-235.
- Crutzen, P. J., and M. O. Andreae. 1990. Biomass burning in the tropics: Impact on atmospheric chemistry and biogeochemical cycles. *Science* 250:1669-1678.
- D'Arrigo, R., G. C. Jacoby, and I. Y. Fung. 1987. Boreal forests and atmosphere-biosphere exchange of carbon dioxide. *Nature* 329:321-323.
- Davis, M. B. 1989. Lags in vegetation response to greenhouse warming. *Climatic Change* 15:75-82.
- Dickinson, R. E. 1986. How will climate change: The climate system and modelling of future climate. Pp. 221-231 in B. Bolin, B. R. Doos, J. Jäger, and R. A. Warrick, eds. *The greenhouse effect, climatic change and ecosystems*. SCOPE 29. New York: John Wiley & Sons. 541 pp.
- Dixon, R. K., and D. P. Turner. 1991. The global carbon cycle and climate change: Responses and feedbacks from belowground systems. *Environmental Pollution* 73: 245-262.
- Dyson, F. J. 1990. Carbon dioxide in the atmosphere and the biosphere. (Radcliffe lecture given at Green College, Oxford, on October 11, 1990.) Institute for Advanced Study, Princeton, New Jersey, U.S.A.

- Eamus, D., and P.G. Jarvis. 1989. The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forests. *Advances in Ecological Research* 19:1-55.
- Emanuel, W. R., H. H. Shugart, and M. P. Stevenson. 1985. Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. *Climatic Change* 7: 29-43.
- Edmonds, R. L., D. Hinkley, M. C. Feller, P. Sollins, A. Abee, and D. D. Myrold. 1989. Nutrient cycling: Effects on productivity of Northwest forests. Pp. 17-35 in D. A. Perry, R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C. R. Perry, and R. F. Powers, eds. *Maintaining the long-term productivity of Pacific Northwest ecosystems*. Portland, Oregon: Timber Press.
- Flavin, C. 1990. Slowing global warming. Pp. 16-38 in *State of the world 1990*. New York: W. W. Norton.
- Foley, J. A., K. E. Taylor, and S. J. Ghan. 1991. Planktonic dimethylsulfide and cloud albedo: An estimate of the feedback response. *Climatic Change* 18:1-15.
- Franklin, J. F., D. A. Perry, T. D. Schowalter, M. E. Harmon, A. McKee, and T. A. Spies. 1989. Importance of ecological diversity in maintaining long-term site productivity. Pp. 82-97 in D. A. Perry, R. Meurisse, G. Thomas, R. Miller, J. Boyle, J. Means, C. R. Peiry, and R. F. Powers, eds. *Maintaining the long-term productivity of Pacific Northwest ecosystems*. Portland, OR: Timber Press.
- Graham, R. L., M. G. Turner, and V. H. Dale. 1990. How increasing CO₂ and climate change affect forests. *BioScience* 40(8):575-587.
- Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247:699-702.
- Harriss, R. C. 1989. Historical trends in atmospheric methane concentration and the sensitivity of methane outgassing from boreal and polar regions. Pp. 79-84 in *Ozone depletion, greenhouse gases, and climate change*. Washington, D.C.: National Academy Press.
- Harriss, R. C., G. W. Sachse, G. F. Hill, L. O. Wade, and G. L. Gregory. 1990. Carbon monoxide over the Amazon basin during the wet season. *J. Geophys. Res.* 95:16927-16932.
- Holland, H. D., B. Lazar, and M. McCaffrey. 1986. Evolution of the atmosphere and oceans. *Nature* 320:27-33.
- Houghton, R. A. 1987. Terrestrial metabolism and atmospheric CO₂ concentrations. *BioScience* 37(9):672-678.
- Houghton, R. A., and G. M. Woodwell. 1989. Global climatic change. *Scientific American* 260(4):36-44.
- Jacob, D. J., and S. C. Wofsy. 1988. Photochemistry of biogenic emissions over the Amazon forest. *J. Geophys. Res.* 93:1477-1486.
- Jarvis, P. G. 1989. Atmospheric carbon dioxide and forests. *Phil. Trans. R. Soc. Lond.* B 324:369-392.
- Jenkinson, D. S., D. E. Adams, and A. Wild. 1991. Model estimates of CO₂ emissions from soil in response to global warming. *Nature* 351:304-306.
- Kauffman, J. B. 1991. Fire effects on standing tropical forest trees in the Brazilian Amazon. *Biotropica* 23:219-234.
- Kauffman, J. B., K. M. Till, and R. W. Shea. 1992. Biogeochemistry of deforestation and biomass burning. In D. B. Dunette and R. O'Brien, eds. *The science of global change: Environmental impacts of human activity*. Washington, D.C.: American Chemical Society. (in press).

- Kauffman, J. B., and C. Uhl. 1990. Interactions of anthropogenic activities, fire and rainforests in the Amazon Basin. Pp. 117-134 in J. G. Goldammer, ed. *Fire in the tropical biota*. NY: Springer-Verlag.
- Kaufman, Y. J., A. Setzer, C. Justice, C. J. Tucker, M. G. Bereira, and I. Fung. 1990. Remote sensing of biomass burning in the tropics. Pp. 371-399 in J. G. Goldammer, ed. *Fire in the tropical biota*. NY: Springer-Verlag.
- Keeling, C. D., R. B. Bacastow, A. F. Carter, S. C. Piper, T. P. Whorf, M. Heimann, W. G. Mook, and H. Roeloffzen. 1989. A three-dimensional model of atmospheric CO₂ transport based on observed winds: Analysis of observational data. Pp. 165-236 in *Aspects of climate variability in the Pacific and the Western Americas*. Geophysical Monograph 55. Washington, D.C.: American Geophysical Union.
- Khalil, M. A. K., and R. A. Rasmussen. 1989. Climate-induced feedbacks for the global cycles of methane and nitrous oxide. *Tellus* 41B:554-559.
- Khalil, M. A. K., and R. A. Rasmussen. 1990. The global cycle of carbon monoxide: Trends and mass balance. *Chemosphere* 20(1-2):227-242.
- King, G. A., J. K. Winjum, R. K. Dixon, and Lynn Y. Arnaut, eds. 1990. Response in feedbacks of forest systems to global climate change. Corvallis, Oregon: Environmental Research Laboratory, U.S.E.P.A. (EPA/600/3-90-080).
- Lamberti, G. A., and S. V. Gregory. 1989. Influence of channel geomorphology and riparian zones on nutrient retention in stream ecosystems. Pp. 33-39 in D. L. Abell, ed. *California riparian systems—Protection, management and restoration for the 1990s*. University of California, Davis: University of California Press.
- Lashof, D. A. 1989. The dynamic greenhouse: Feedback processes that may influence future concentrations of atmospheric trace gases and climatic change. *Climatic Change* 14:213-242.
- Lashof, D. A., and D. R. Ahuja. 1990. Relative contribution of greenhouse gas emissions to global warming. *Nature* 344:529-531.
- Levine, J. S., C. P. Rinsland, and G. M. Tennille. 1985. The photochemistry of methane and carbon monoxide in the troposphere in the 1950 and 1985. *Nature* 318:254-257.
- Lovelock, J. E. 1979. *Gaia: A new look at life on Earth*. Oxford: Oxford University Press.
- . 1988. *The ages of Gaia*. New York: Norton. 252 pp.
- Lovelock, J. E., and M. Whitfield. 1982. Life span of the biosphere. *Nature* 296:561-563.
- Lowrance, T., R. Todd, J. Fail, Jr., O. Hendrickson, Jr., R. Leonard, and L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. *BioScience* 34: 374-377.
- Mika, P. G., and J. A. Moore. 1991. Foliar potassium status explains nitrogen fertilization response in the Intermountain Northwest, USA. *J. Water, Air, Soil Poll.* (in press).
- Mitchell, J. F. B., and D. A. Warrilow. 1987. Summer dryness in northern mid-latitudes due to increased CO₂. *Nature* 330:238-240.
- Moore, B. III, and B. Bolin. 1986/1987. The oceans, carbon dioxide, and global climate change. *Oceanus* 29(4):9-15.
- Myers, N. 1986. Environmental repercussions of deforestation in the Himalayas. *J. World For. Res. Manage.* 2:63-72.
- . 1988. Tropical deforestation and climate change. *Environmental Conservation* 15:293-298.

- Neftel, A., E. Moor, H. Oeschger, and B. Stauffer. 1985. Evidence from polar ice cores for the increase in atmospheric CO₂ in the past two centuries. *Nature* 315: 45-47.
- Neilson, R. P., and G. P. King. Continental scale biome responses to climatic change. In D. H. McKenzie, E. Hyatt, and J. McDonald, eds. *Ecological indicators*. Elsevier Science Publications. (in press).
- Neilson, R. P., G. A. King, R. L. DeVelice, J. Lenihan, D. Marks, J. Dolph, W. Campbell, and G. Glick. 1989. Sensitivity of ecological landscapes to global climatic change. U.S. Environmental Protection Agency Publication, EPA-600-3-89-073, Corvallis, OR; NTIS-PB-90-120-072-AS, Washington, D.C.
- Norby, R. J., E. G. O'Neill, W. G. Hood, and R. J. Luxmoore. 1987. Carbon allocation, root exudation and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO₂ enrichment. *Tree Physiology* 3:203-210.
- Oberbauer, S. F., N. Sionit, S. J. Hastings, and W. C. Oechel. 1986. Effects of CO₂ enrichment and nutrition on growth, photosynthesis, and nutrient concentration of Alaskan tundra plant species. *Can. J. Bot.* 64:2993-2998.
- O'Neill, E. G., R. J. Luxmoore, and R. J. Norby. 1987a. Elevated atmospheric CO₂ effects on seedling growth, nutrient uptake, and rhizosphere bacterial populations on *Liriodendron tulipifera* L. *Plant and Soil* 104:3-11.
- O'Neill, E. G., R. J. Luxmoore, and R. J. Norby. 1987b. Increases in mycorrhizal colonization and seedling growth in *Pinus echinata* and *Quercus alba* in an enriched CO₂ atmosphere. *Can. J. For. Res.* 17(8):878-883.
- Oren, R., E.-D. Schulze, K. S. Werk, and J. Meyer. 1988. Performance of two *Picea abies* (L.) Karst. stands at different stages of decline. VII. Nutrient relations and growth. *Oecologia* (Berl.) 77:163-173.
- Overpeck, J. T., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* 343:51-53.
- Pastor, J., and W. M. Post. 1988. Response of northern forests to CO₂-induced climate change. *Nature* 334(6177):55-58.
- Perry, D. A. 1988. Landscape patterns and forest pests. *The Northwest Environmental Journal* 4(2):213-228.
- Perry, D. A., M. P. Amaranthus, J. G. Borchers, S. L. Borchers, and R. E. Brainerd. 1989. Bootstrapping in ecosystems. *BioScience* 39(4):230-237.
- Perry, D. A., and J. C. Borchers. 1990. Climate change and ecosystem responses. *The Northwest Environmental Journal* 6(2):293-313.
- Perry, D. A., J. C. Borchers, S. L. Borchers, and M. P. Amaranthus. 1990. Species migrations and ecosystem stability during climate change: The belowground connection. *Conservation Biology* 4:266-274.
- Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: Observation of a riparian forest. *Ecology* 65:1466-1475.
- Post, W. M., W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger. 1982. Soil carbon pools and world life zones. *Nature* 298:156-159.
- Post, W. M., J. Pastor, P. J. Zinke, and A. G. Stangenberger. 1985. Global patterns of soil nitrogen storage. *Nature* 317(6038):613-616.
- Post, W. M., T.-H. Peng, W. R. Emanuel, A. W. King, V. H. Dale, and D. L. DeAngelis. 1990. The global carbon cycle. *Am. Sci.* 78:310-326.
- Prentice, K. C., and I. Y. Fung. 1990. The sensitivity of terrestrial carbon storage to climate change. *Nature* 346:48-50.

- Ramanathan, V., R. J. Cicerone, H. B. Singh, and J. T. Kiehl. 1985. Trace gas trends and their potential role in climate change. *J. Geophys. Res.* 90:5547-5566.
- Salati, E. 1987. The forest and the hydrological cycle. Pp. 273-296 in R. E. Dickinson, ed. *The geophysiology of Amazonia*. New York: John Wiley & Sons.
- Schlesinger, W. H. 1990a. Evidence from chronosequence studies for a low carbon-storage potential for soils. *Nature* 348:232-234.
- . 1990b. Vegetation an unlikely answer. *Nature* 348:679.
- Schlesinger, W. H., and J. M. Melack. 1981. Transport of organic carbon in the world's rivers. 1981. *Tellus* 33:172-187.
- Setzer, A. W., M. C. Pereira, A. C. Pereira, Jr., and S. A. O. Almeida. 1988. Relatório de Atividades do Projeto IBDF-INPE "SEQUE"; Inst. Pesquisas Espaciais (INPE), Pub. No. INPE-4534-RPE/565; INPE. Sao Paulo: Sao Jose dos Campos. 54 pp.
- Sirois, L., and S. Payette. 1991. Reduced post-fire regeneration along a boreal forest-forest-tundra transect in northern Quebec. *Ecology* 72:619-627.
- Smith, J. B., and D. Tirpak, eds. 1989. The potential effects of global climate change on the United States. Report to Congress. EPA-230-05-89-050. Washington, D.C.: U.S. Environmental Protection Agency. 413 pp.
- Solomon, A. M. 1986. Transient response of forests to CO₂-induced climate change: simulation modeling experiments in eastern North America. *Oecologia* (Berlin) 68: 567-579.
- Tans, P. P., I. Y. Fung, and T. Takahashi. 1990. Observational constraints on the global atmospheric CO₂ budget. *Science* 247:1431-1438.
- Thompson, A. M., M. A. Huntley, and R. W. Stewart. 1990. Perturbations to tropospheric oxidants, 1985-2035. 1. Calculations of ozone and OH in chemically coherent regions. *J. Geophys. Res.* 95:9829-9844.
- Tingey, D. T., R. Evans, and M. Gumpertz. 1981. Effects of environmental conditions on isoprene emission from live oak. *Planta* 152:565-570.
- Turner, D. P., J. V. Baglio, A. G. Wones, D. Pross, R. Vong, and D. L. Phillips. Global climate change and isoprene emissions from vegetation. *Chemosphere*. (in press).
- Uhl, C., J. B. Kauffman, and D. L. Cummings. 1988. Fire in the Venezuelan Amazon 2: Environmental conditions necessary for forest fires in the evergreen rainforest of Venezuela. *Oikos* 53:176-184.
- Velazquez-Martinez, A. 1990. Interacting effects of stand density, site factors, and nutrients on productivity and production efficiency of Douglas-fir plantations in the Oregon Cascades. Ph.D. thesis, Department of Forest Science, Oregon State University.
- von Bertalanffy, L. 1968. *General systems theory*. New York: George Braziller. 295 pp.
- Wilson, A. T. 1978. Pioneer agriculture explosion and CO₂ levels in the atmosphere. *Nature* 273:40-41.
- Windsor, G. M., A. S. Rand, and W. M. Rand. 1986. Variation in rainfall on Barrow, Colorado Island. Balboa, Panama: Smithsonian Tropical Research Institute (report).
- Wolf, E. C. 1985. Challenges and priorities in conserving biological diversity. *Interciencia* 10(5):236-242.
- Woodwell, G. M. 1986. Global warming and what we can do about it. *Amicus Journal* 8:8-12.
- . 1989. Biotic causes and effects of the disruption of the global carbon cycle. Pp. 71-81 in D. E. Abrahamson, ed. *The challenge of global warming*. Washington, D.C.: Island Press.

- Zander, R., P. Demoulin, D.-H. Ehhalt, and U. Schmidt. 1989. Secular increase of the total vertical column abundance of carbon monoxide above central Europe since 1950. *J. Geophys. Res.* 91:11021-11026.
- Zimmerman, P. R., R. B. Chatfield, J. Fishman, P. J. Crutzen, and P. L. Hanst. 1978. Estimates on the production of CO and H₂ from the oxidation of hydrocarbon emissions from vegetation. *Geophys. Res. Lett.* 5:679-682.

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Effects of Global Climatic Change on Forests in Northwestern North America

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This is how it happens, the Dinosaur said. Drought, fire, hurricanes and floods. Throw in a little radon, and the next thing you know, you're extinct.—Steve Palay in *The Oregonian*, Sept. 25, 1988

Introduction

Dense coniferous forests characterize the Pacific Coast of northwestern North America. Such species as Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Pacific silver fir (*Abies amabilis*) are dominant trees.

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