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Climate Change and Ecosystem Responses

David A. Perry[1] and Jeffrey G. Borchers[1]

Introduction

Many scientists predict that known increases in atmospheric concentrations of heat-trapping gases will increase average global temperatures from 1.5 to 4.5° C before the middle of the twenty-first century (Houghton and Woodwell 1989). Although not all scientists agree with this assessment of the "greenhouse effect," most do. According to Houghton and Woodwell (1989), "Seldom has there been such a strong consensus among scientists on a major environmental issue."

In this paper we briefly review current knowledge concerning the possible consequences of a changing climate for terrestrial ecosystems. Forests and grasslands of western North America figure prominently in the discussion, but our intent is to consider general principles rather than specific communities. Nevertheless, these principles are applicable to the fate and management of old-growth forests. First, we review the current climate-change scenarios and their implications for plant growth and physiology. Next we consider the severity and frequency of disturbances such as fire, insect outbreaks, and windstorms. Then we turn to the possible net effect of climate change on ecosystems, an effect that emerges from numerous interactions and feedback processes, and that is greatly affected by the speed with which species migrate. Finally, we discuss some approaches for mitigating possible impacts and for easing transitions from one community type to another.

A Brief Review of the Greenhouse Effect

The average surface temperature of the globe is determined by a complex of factors that includes the amount of energy received from the sun, the absorptive properties of the atmosphere, and the absorptive properties of the surface (in turn a function of the relative area of oceans, deserts, snowfields, forests, etc.). A high proportion of the energy absorbed by the earth's surface and lower atmosphere

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[1] Department of Forest Science, Peavy Hall 154, Oregon State University, Corvallis, Oregon 97331-5705.

is emitted as heat. Like a window, the atmosphere passes some of this heat on to space, while the rest is absorbed and emitted once again as heat.

At the root of the predicted climate change is the accumulation of an array of gases in the atmosphere that traps heat radiated from the planet surface. Carbon dioxide has received the most attention, but other gases are involved as well, such as water vapor, ozone, nitrous oxide, chlorofluorocarbons (CFSs), and methane. (Trends in greenhouse gases have been discussed by various authors in Abrahamson 1989.) Like CO_2, the latter four have been increasing in the atmosphere because of human activities. The widely publicized loss of ozone is occurring in the upper atmosphere, where the gas shields against ultraviolet radiation; however, ozone is increasing in the lower atmosphere.

Athough there is uncertainty about how climate will respond, there is no doubt that greenhouse gases are accumulating. Atmospheric CO_2 began climbing in the latter part of the nineteenth century because of the clearing of forests and plowing of prairies, which released to the atmosphere, as CO_2, the carbon once stored in biomass and soils. Burning of fossil fuels and accelerated deforestation since the 1940s have greatly exacerbated the effect. Around 1880, the atmosphere at 50°N latitude contained an average 292 parts per million (ppm) CO_2; in 1988, the average was about 345 ppm, and well over one-half of this increase has occurred since 1958 (From and Keeling 1986; MacDonald 1989). Using highly uncertain proportions, roughly two-thirds of the increase in CO_2 since the mid-twentieth century has come from burning fossil fuels and one-third from deforestation (Woodwell 1989).

Most public attention has focused on deforestation in the tropics, but the problem exists in northern forests as well. Harmon, Ferrell, and Franklin (1990) have shown that clearcutting old-growth Douglas-fir results in a net flux of CO_2 to the atmosphere that takes several hundred years to recoup, even when the cut forest is replaced by fast-growing young trees. In many areas of the world, including parts of the United States and Canada, cut forests are not being successfully regenerated; this means that, in these instances, carbon loss is not mitigated by the carbon-fixing capacity of young forests (Perry et al. 1989).

Greenhouse effects on climate are simulated with General Circulation Models (GCMs) which, because of limitations in both knowledge and computing power, do not adequately capture the extreme complexity of the earth's climate system. It does not follow that the predictions of the models are wrong, only that they are uncertain. But right or wrong, the models are the best predictive tool currently available.

Three widely used GCMs have recently been compared by Neilson et al. (1989). Not surprisingly, the models differed from one another in underlying assumption about climate behavior and varied somewhat in their predictions. However, they also showed consistencies. A doubling of preindustrial, atmospheric CO_2 concentration will be reached sometime in the twenty-first century. At that time, winter temperatures in the coterminous United States are predicted to increase to what would be the equivalent of a 4-degree to 6-degree southward shift in latitude (range 1° to 9.8° lat.); summer temperatures are predicted to increase to the equivalent of 5° to 11° southward (range 4.1° to 16° lat.). (For perspective, compare the climate of central Oregon and southern California, which differ by about 10° lat.) Note that summer is predicted to warm more than winter, a fact that, as we shall discuss, has many implications for ecosystem response. The magnitude of warming is predicted to vary from east to west across the United States, the greatest warming being in the Great Plains where the Dakotas may eventually develop a climate more like that of Texas. The models predict a warming in mountains equivalent to a 650-m to 900-m decease in elevation, so that most, if not all, alpine and subalpine ecosystems would probably disappear. If current emission trends continue, increases in CO_2, plus increases in other greenhouse gases, are predicted to take us into the "doubled CO_2" temperature regime in less than 50 years (Hansen et al., 1988). Other greenhouse gases are less abundant in the atmosphere than CO_2, but they have a much greater warming effect per molecule. One molecule of methane, for example, has 3.7 times more warming potential than one molecule of CO_2, whereas a molecule of nitrous oxide has 180 times more warming potential and a molecule of chlorofluorocarbon-12 has 10,000 times more (Lashof and Ahuja 1990).

The models are less consistent in predicting the greenhouse effect on precipitation, which is a crucial factor in ecosystem response. There is general agreement that warming will be greater at high than at low latitudes, and the consequent narrowing of the global temperature gradient seems likely to alter precipitation patterns, although the changes that might be expected remain unclear. However, warming—even with no change in precipitation—should increase the droughtiness of ecosystems because of greater evaporative demand caused by higher temperatures.

Climate Effects on Plant Physiology and Growth

The growth and overall health of plants result from numerous interactions within an ecosystem, and between an ecosystem and the atmosphere. The physiological processes within individual plants could be altered by three greenhouse-related factors: (1) warmer temperatures, (2) higher atmospheric CO_2, and (3) shifts in water availability.

Warmer Temperatures

Warmer temperatures will affect plant physiology through increased respiration relative to photosynthesis, longer growing seasons, and effects on the yearly developmental cycle.

The physiological processes of photosynthesis are relatively insensitive to change of temperature over a rather broad range, whereas the loss of carbon through respiration increases sharply with increasing temperature. Considering only these two factors, warmer temperatures would increase carbon loss more than carbon fixation and therefore would decrease net photosynthesis. On the other side of the ledger, longer frost-free seasons would allow plants to grow for a greater proportion of the year, increasing net carbon fixation. The degree to which plants could utilize longer growing seasons would depend on various factors, particularly the availability of water.

One of the most disruptive effects of warmer temperatures on plants could be confusion of yearly developmental cycles, which for most plant species are triggered by temperature cues. A notable example is Douglas-fir, which requires a period of cold temperature during winter in order to grow and develop properly during spring and summer (Lavender 1984; Leverenz and Lev 1987). It is uncertain how that species might respond if temperatures warm to the extent that the "chilling requirement" is not met.

Higher Atmospheric CO_2

Higher atmospheric CO_2 benefits the growth of some plants but not others; in particular, it enhances the efficiency with which plants use water. The connection between CO_2 and water use occurs because the CO_2 required to manufacture carbohydrates is absorbed through microscopic pores (stomates) in leaves that, when open, not only enable CO_2 to enter, but allow water to escape the leaf. In order to absorb CO_2 without losing excessive water, plants use environmental and physiological cues to regulate stomatal openings. Except in very moist environments, water conservation takes precedence over photosynthesis and stomates close during periods when plants could photosynthesize if they had access to CO_2. As atmospheric CO_2 increases, plants absorb more at a given degree of stomatal opening, hence are able to photosynthesize more at a given

amount of water loss. (Higher atmospheric CO_2 has other effects on plants that we will not discuss here. See Kramer and Sionit 1987; Rose 1989).

In studies completed to date, only one species—ponderosa pine—has responded negatively to enhanced CO_2 (Woodman 1989). Most species photosynthesize more when atmospheric CO_2 is increased, but they vary widely in the degree to which the increase translates into greater growth. For example, when atmospheric CO_2 is doubled, sugar maple photosynthesizes more than beech, but only the beech grows faster; the sugar maple spins off the additional carbon in respiration (C. D. Reid and B. R. Strain, paper presented at the American Institute of Biological Sciences meeting, 1989, Toronto, Ontario). However, such experiments dealing with plant responses have been limited to seedlings growing under controlled conditions; therefore, the results may not apply to plants in the field, particularly long-lived perennials such as trees and shrubs (Kramer and Sionit 1987). Few experiments showing increased efficiency of water use in a higher CO_2 atmosphere have been performed on drought-stressed plants, hence it is not clear that CO_2-induced increases in water-use efficiency will overcome such stress. Moreover, as we shall discuss later, better growth because of enhanced CO_2 might be offset by higher losses to insects.

Water Availability

Water is one of the biggest wild cards in terms of plant response to climate change. Should precipitation increase sufficiently to balance or exceed the increased water loss due to higher temperatures, productivity would potentially increase. If systems become more droughty, productivity would decline and plants would become more susceptible to insects and some kinds of disease.

The Net Effect on Plant Physiology

The net effect of the interacting factors we have discussed is difficult to predict and almost certainly will vary among plant communities, depending on the environments they now grow in and on the interactions and feedback processes within the ecosystem, which as yet are poorly understood. Other factors being equal, plants growing at high latitudes and high elevations stand to benefit from warmer temperatures, whereas those in warmer environments might reduce growth because of increased respiration. Plants at high elevations or in droughty environments stand to gain from increased CO_2: high-elevation plants benefit because the air thins and CO_2

levels decrease as elevation increases; dryland crops and plants in semiarid forests, grasslands, and deserts benefit because of greater water-use efficiency conferred by higher atmospheric CO_2. However, these beneficial effects could be readily canceled with decreases in precipitation.

Another important factor is how individual plant species within the same community react to environmental changes. If one species benefits more or suffers less than others, it may, through competition, reinforce the negative effects on its neighbors and come to dominate the community. For example, B. R. Strain suggests that the exotic annual weed, cheatgrass, will benefit more than native plants from climate change in western grasslands (paper presented at the AIBS meeting, 1989, Toronto, Ontario). On the other hand, conceivably some plant species could be mutually supportive during periods of stress (Amaranthus and Perry 1989; Borchers and Perry 1990; Perry et al. 1990).

Because these numerous uncertainties and complexities make prediction difficult, if not impossible, our best information will come from field observations of plant growth (though even these do not permit straightforward interpretation). Studies of tree rings indicate an upward trend in growth of at least some high-elevation and high-latitude forests over the past 100 or so years, except in periods of extended drought such as occurred during the 1930s (Garfinkle and Brubaker 1980; LaMarche et al. 1984; Bork 1985; Graumlich, Brubaker, and Grier 1989). In high-elevation forests of the southwestern United States, this trend has been attributed to the combined effects of warmer temperatures and increased CO_2, with the latter predominating since 1970 (LaMarche et al. 1984). Warmth is postulated to be the primary factor in high-elevation forests of the northern Cascade Range (Graumlich, Brubaker, and Grier 1989).

The way that trees will respond to climate change will vary with the environment they occupy, although the exact nature of the variation is not clear. In one analysis, Kienast and Luxmoore (1988) found that tree growth had increased since 1950 at eight of 34 sites throughout the northern hemisphere. All sites in which growth increased had moderate drought or temperature stress. On the other hand, Bork (1985) showed that over the past 100 years or so, Oregon ponderosa pine stands occupying the opposite ends of a precipitation gradient (but with little difference in elevation) had an upward growth trend, except during severe drought years, especially the 1930s. In the middle of the gradient, however, the trend was downward (Fig. 1). Differences among the stands might reflect the effect of water availability on tree response to greenhouse-related factors; however—and this is a key point—the large growth variability over the past few hundred years makes it difficult to attribute any change during the twentieth century to greenhouse factors.

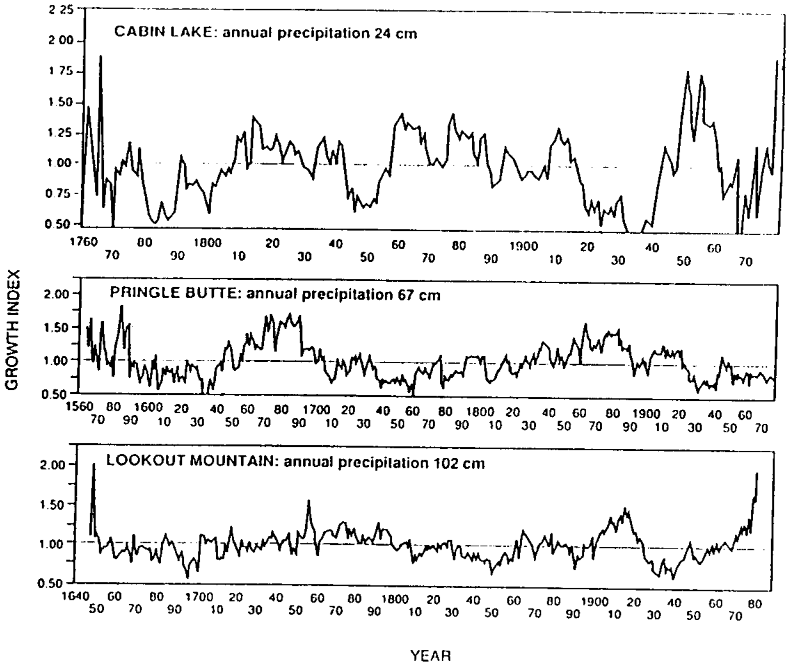

Fig. 1. Historic trends of ponderosa-pine growth across a precipitation gradient in central Oregon (from Bork 1985). The growth index is the average annual ring width in proportion to the average (1.00) for the period. Ring widths are adjusted to remove changes that are attributable to increasing circumference, rather than to the environment.

Climate Change and Ecosystem Disturbance

We usually perceive the pattern of vegetation on the earth's surface to be stable, particularly over short intervals such as a lifetime. Nevertheless, the landscape and its vegetation exist in a state of dynamic balance with the forces that have sculpted them. When these forces create events that are sufficiently rapid and large in scale, we perceive them as "disturbance." Both natural and human disturbances are agents of change in ecosystems. The type and frequency of disturbance may influence how rapidly vegetation responds to climate change (e.g., see Overpeck, Rind, and Goldberg 1990).

The projected shifts in average global temperature and precipitation are disturbances because the rates of change are from 10 to 60 times faster than historical values (Schneider 1989). We can hypothesize the effects of such climate change on some other, more typical disturbances. We emphasize that fire, insects, and disease have had a historical role in maintaining the current structure (e.g., vegetation patterns) and functions (e.g., nitrogen cycling) of ecosystems. But in a shifting climate, these same factors may become the means by which ecosystems are rapidly altered.

Biotic Disturbance.

In healthy ecosystems, invertebrate "pests" and other disease organisms generally remain in small numbers, with outbreaks often precipitated by plant stress (e.g., drought, nutrient deficiencies, pollution). It is reasonable to assume that many plant species will become stressed as temperature and precipitation change beyond their tolerance levels. This, and the possibility that insect populations may grow faster in warmer, drier climates, could lead to large outbreaks. For example, the Oregon Department of Energy (1990) predicts outbreaks of the balsam woolly adelgid (*Adelges piceae* [Ratzeburg]), a pest of subalpine fir. It is also possible, however, that climate changes will suppress some insects and pathogens.

Recent studies have shown that greater carbon : nitrogen ratios in plants grown under elevated CO_2 levels prompted defoliating insects to increase their consumption of leaves in order to acquire sufficient nitrogen (Fajer, Bowers, and Bazzaz 1989; Lincoln and Liu 1989). But it is not clear if the results of short-term controlled studies can be extrapolated to natural ecosystems; long-term physiological responses of plants to elevated CO_2 concentrations may be very different from short-term responses. For example, Kramer and Sionit (1987) suggest that greater plant growth might offset increased defoliation. In a CO_2-enriched atmosphere, trees may produce more biochemicals that defend against insect defoliators. These carbon-based compounds often are synthesized in response to defoliation, but are most abundant when plants have a "luxury" level of carbon from photosynthesis (Baldwin and Schultz 1983; Waring and Schlesinger 1985).

Abiotic Disturbance

Abiotic disturbances are factors such as ice, fire, wind, and short-term fluctuations in temperature and precipitation (White 1979). For instance, higher average ocean temperatures may increase hurricane severity (Emmanuel 1988); tree blowdowns, flooding, or other stresses may become more commonplace. Even without rapid climate changes, normal climatic variation—especially fluctuations in temperature and precipitation—can stress many ecosystems.

Fire is potentially the most rapid and extensive agent of change. Often the vegetation mosaic on a landscape is attributable to periodic fires of natural and human origin (Knight 1987). Given otherwise similar conditions, ecosystems in warmer, drier climates tend to have lower biomass and more frequent, less severe fires (Olson 1981; Agee 1990). This pattern is substantiated in the heterogeneous forests of the Pacific Northwest where the frequency of fire ranges from 10 to 15 years in dry, ponderosa pine forests (Bork 1985) to at least 400 years in some very moist forests of true fir (Hemstrom and Franklin 1982).

These present-day relationships between climate, fire regimes, and biomass suggest what may occur as conditions become warmer and drier. Fire frequency probably will increase, its severity exacerbated by biomass that accumulated when the climate was cooler and wetter (Clark 1988). The largely unpredictable interactions between fire and other factors of disturbance increase the likelihood of conflagration because one disturbance tends to trigger another. For example, extensive windthrow may exacerbate a bark beetle outbreak, and either of these may set the stage for fire more severe than that in undisturbed forest (Perry 1988; Dickman and Cook 1989).

Disturbance of Human Origin

Human intervention in natural processes has long affected landscapes, probably since the discovery of fire. Since that time, most of the planet has been altered in at least a small way by our activities (as it is being altered now by increased CO_2 in the atmosphere). In some cases the activity has had little visible impact, especially when it mimics a natural disturbance. For instance, partial harvest of forests followed by prescribed under-burning approximates the pattern of disturbance natural to some regions where wildfire is commonplace (e.g., the inland Northwest, the Southeast). In tropical rain forests, where wildfire is far less frequent, such a practice would be more disruptive to the ecosystem.

The exclusion of fire from many western forests during the twentieth century is a prime example of human interference with the natural disturbance regime. The resulting buildup of fuels and biomass can increase the severity of wildfire when it does occur (Kaufmann 1990). This is evident in many ponderosa pine forests where fire exclusion has altered species composition and the vertical structure of stands (Weaver 1974). In some ways, fire exclusion mimics a shift to cooler, wetter conditions; fire-intolerant species invade, biomass accumulates, and fires become less frequent but more severe. In the scenario for global climate change, conditions rapidly become warmer and drier, but biomass accumulations reflect a previous climate and a legacy of fire exclusion. The potential is great for catastrophic fires and, therefore, for large pulses of CO_2 into the atmosphere, which would reinforce the greenhouse effect.

Pollutants are a more insidious form of disturbances imposing stress on ecosystems. Acidic deposition has been implicated in the decline of large forested areas to central Europe (Schutt 1985), and of spruce in Canada and the northeastern United States (Johnson and Siccama 1983). The potential effects of such large-scale pollution can be easily confounded with climate change and other factors, as several authors have recently pointed out (McLaughlin et al. 1987; Pastor et al. 1987; Hamburg and Cogbill 1988). The confusion serves to remind us that pollution and rapidly changing climate may act synergistically; ecosystems already degraded by acidic deposition may collapse with rapid changes in temperature and precipitation.

Altered disturbance regimes resulting from climate change thus have the potential to affect greatly the structure and function of ecosystems. But it is the strength of naturally evolved, stabilizing mechanisms that will determine ecosystem response to climate change and associated disturbances.

Climate Change and Ecosystem Feedback Processes

Understanding ecosystem processes and interactions is the key to understanding vegetation dynamics as climate changes. Two fundamental interactions govern ecosystem behavior: *negative feedback* and *positive feedback* (see DeAngelis, Post, and Travis 1986). A hypothetical scenario using the global carbon cycle illustrates their circularity:

> 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.

Notice that the self-augmenting effect of Jack's positive-feedback loop amplifies the rate of temperature increase, while Jill's negative-feedback loop tends to stabilize temperatures. In this simplified scenario, the relative numbers of Jacks and Jills would determine how rapidly global temperature would increase. With ecosystems, however, feedback (especially positive feedback) can result in complex and, as yet, unpredictable behavior (DeAngelis, Post, and Travis 1986; Perry et al. 1989).

Global CO_2 Input

One of the most important unknowns regarding positive feedback in climate change is the effect that rising temperatures would have on input to the atmospheric CO_2 pool from decomposing detritus and soil organic matter. (Current models of climate change do not account for this feedback process.) Carbon stores in soil are large, about twice that in the atmosphere or vegetation (Post et al. 1982; Schlesinger 1984; Schneider 1989). Among ecosystems with similar productivity, soil carbon stores are generally lower in those having warmer climates (Meentemeyer 1978; Jenny 1980). Therefore, one would expect higher average temperatures to result in a transfer of carbon from soil reservoirs to the atmosphere. One estimate is that 15 percent of the carbon in soils and peats will be released over 50 years at the temperatures expected with a doubling of atmospheric CO_2 (Hobbie and Melillo 1984). In Pacific Northwest forests, carbon stored as coarse wood debris in old-growth forests exceeds soil stores by a large factor (Harmon, Ferrel, and Franklin 1990). This, too, may represent significant input into the atmospheric CO_2 pool should decomposition rates or the severity of fires increase.

These positive feedback loops among atmospheric CO_2, temperature, and soil carbon have the potential to turn with increasing rapidity, at least until other interactions within the soil or atmosphere constrain the cycle. However, details of the process remain poorly understood. We know relatively little about the stability of various reservoirs of carbon in soil, hence cannot predict how quickly soil carbon would be released to the atmosphere as temperature increases (Oades 1988).

Nutrient Cycling between Plants and Soil

Pastor and Post (1988) acknowledged the critical role of feedback between vegetation and soil when they modeled forest-productivity responses to CO_2-induced climate change. Their simulations of coniferous and deciduous forests of eastern North America suggest that soil-texture control over water availability could strongly influence the species that succeed in a warmer and drier climate. Eventually, coarse-textured soil would support only drought-tolerant, less-productive species; on fine-textured soil, however, productivity was predicted to increase because of an influx of deciduous species with faster intrinsic growth rates. In the latter case, the warm-temperature stimulus to productivity was amplified by a positive feedback between carbon and nitrogen cycles; faster decomposing litter from the newly established deciduous trees increased nitrogen availability, and thereby productivity. Consequently, carbon storage in biomass and soil increased. But on coarse-textured soil, lack of available water indirectly constrained positive feedback, and the influx of slower growing drought-tolerant species produced litter with a relatively slower decomposition rate. The simulations illustrate but one of many complications that arise in attempts to quantify carbon fluxes between ecosystems and the atmosphere.

Other elements besides carbon may affect feedback processes. Nitrogen, for example, is likely to be lost from ecosystems in large quantities because its fate is strongly linked to that of carbon (McGill and Cole 1981). To a lesser extent, this is true for phosphorus. Nitrous oxides released from the soil to the atmosphere (Firestone 1982) are also greenhouses gases that provide another positive feedback between warming and soil response to that warming. Increased decomposition in anaerobic soils (e.g., bogs) would release methane to the atmosphere (Mathews and Fung 1987). Releases of nitrous oxides in methane are particularly significant because, per molecule, methane has almost four times more warming potential than CO_2; nitrous oxide has 180 times more (Lashof and Ahuga 1990). Nutrients lost to groundwater or transported to streams by erosion might enhance the productivity of aquatic ecosystems (Gregory et al. 1987), perhaps to the point of eutrophication. The transfer of nitrogen, phosphorus, iron, and other nutrients from land to sea in sufficient quantities could trigger complicated feedback relationships among land, water, and atmosphere. If phytoplankton increased their growth because of nutrient input from land, the consequent absorption of CO_2 would constitute a negative feedback to the greenhouse effect. Because the major source of cloud-condensation nuclei over open ocean is a sulfur compound produced by some planktonic algae (Charlson et al. 1987), enhanced productivity of plankton theoretically could result in more cloud cover and reflectance. Clouds can either increase or reduce global warming rates, depending on their type. Those that form over oceans are likely to have a net cooling effect. (Monastersky 1989 discusses uncertainties about the role of cloud formation in climate change.)

Feedback Links between Plant and Soil Organisms

Plants exist in strong positive feedback loops with certain groups of soil organisms (Perry et al. 1989). Roughly 90% of plant species form *mycorrhizae*, a symbiosis between roots and the various fungi that colonize them. In return for nutrients, plants act as hosts and channel energy to the fungi (Harley and Smith 1983; Richards 1987). Generally, neither plant nor fungus can long survive without the other.

There are many examples of the importance of this relationship. Mine spoils have no mycorrhizal fungi if host plants have never been present; therefore plants cannot gain a foothold (Marx and Artman 1979; Harley and Smith 1983; Perry et al. 1989). Similarly, the cumulative effects of forest-harvesting activities can create poor conditions for tree regeneration. In southwest Oregon, deforestation can depress the soil activity of mycorrhizal fungi if all potential host plants are excluded from sites by harvesting, burning, and application of herbicides (Amaranthus and Perry 1987; Perry, Molina, and Amaranthus 1987). Over the years, seedling establishment and reforestation becomes increasingly difficult as fungal activity declines.

If the climate becomes warmer and drier, there is increased likelihood that disturbances and barriers to migration will disrupt critical positive feedback loops in the plant–soil system. Should this occur, patterns of vegetation on the landscape may change with surprising rapidity.

Plant Migration and Ecosystem Stability

Plant species will shift northward and upward in elevation in response to warming; however it is unlikely that they will move as fast as the warming rates. Models predict that the yearly temperature change will be the equivalent of a shift of several thousand meters southward in latitude. Trees migrated northward at the end of the last glaciation at a rate of only 100 m to 400 m per year (Davis 1981; Johnson and Adkisson 1986)—roughly 10% as fast as the predicted rate of temperature change. Moreover, such barriers to natural migration as freeways, farms, and housing development were not impediments 12,000 years ago. During previous migrations, birds such as jays and nutcrackers carried seeds of the nutbearing trees northward; however, these birds do not readily cross open land. How effectively will they be able to transport seeds across the modern landscape?

Migrations might be facilitated by humans if we summoned the will and money to do it. But even if armies were mustered to move plants and associated animals and microbes in the coming years, some species would encounter foreign and probably stressful environments. This would occur because shifts in the seasonal distribution of temperature or rainfall would not simply transfer climatic regimes from one area to another, but would produce wholly unique environments. For example, the northerly extension of North American hardwood forests is constrained by winter cold (Sucoff 1969); but if, as predicted, winter temperatures increase less than summer temperatures, the species composing this forest type would experience warmer, possibly drier, summers—even at their new northernmost extension (Neilson et al. 1989).

The large discrepancy between the rates of temperature change and species migration, coupled with the possibility of more frequent disturbances and entirely new climatic patterns, raises serious questions about the stability of ecosystems in coming decades. A crucial factor will be the degree of overlap between residents and emigrants, which would depend on both migration rates and the stability of existing communities. As we have seen, the response of communities to changing climates, hence their stability, is likely to be complex, including favorable and unfavorable effects on plant physiology, altered relationships among species, and increased stresses from fire, wind, pests, and pathogens.

The net effect is difficult or impossible to predict with certainty, but whatever trends are initiated are likely to be reinforced and accelerated by feedback within the system. The close feedback link between plants and soils is particularly critical (Perry et al. 1990). If resident species become stressed and weakened before migrants arrive and establish, soils could deteriorate. A site might become captured by weeds, greatly reducing its productivity; because degraded ecosystems store only a fraction of the carbon of healthy ones, the site having reduced productivity might create another strong positive feedback to the greenhouse effect. Such degradation involves complex and poorly understood changes in soil chemistry, physics, and biology and it is unlikely to be reversed by quick fixes such as fertilizing (Perry et al. 1989, 1990; Schlesinger et al. 1990). Because of this, it is essential that we prevent degradation rather than permit it and then try to reverse it.

Implications for Land Management

It is imperative that management of forests, rangelands, and agricultural lands include strategies of stabilizing ecosystems and facilitating the transition from one community type to another. This may decrease some short-term yields, but it will buy us—and more important, future generations—some degree of insurance in the face of a highly uncertain future.

Strategies of stabilization will vary from one area and community type to another; however, the following needs are common to all:

1. Soils must be protected by maintaining a cover of healthy perennial plants at all times. This can be accomplished by avoiding clearcutting in forestry; by rotating agricultural crops wherever feasible, and low till or no-till where it is not; and by preventing overgrazing of rangelands. Restoration efforts should be accelerated where soils are already partially or completely deteriorated, as has happened throughout much of interior western North America (and indeed throughout the world: deserts are spreading and cut forests are not being renewed).
2. The natural stabilizing mechanisms of ecosystems must be better understood and employed, rather than ignored or eliminated—as is often the case under intensive land management. Among the most important of these mechanisms are the redundancies provided by biodiversity *at every scale*: genetic diversity within the individual species, species and habitat diversity within local ecosystems, and diversity of landscapes within regions (Perry 1988; Perry et al. 1989, 1990). Preserving the legacy of ecosystems, such as old logs and snags in old-growth forests, is also an important component of this strategy because it may promote quicker restoration of the habitats and processes that are buffers to disturbance (Franklin et al. 1989).
3. Excessive utilization stresses ecosystems and must be avoided. In managed forests, this means conserving organic matter and nutrients, and eschewing overly short rotations. (See papers in Perry et al. 1989 for discussion of strategies for sustaining productivity in Pacific Northwest forest ecosystems.) In grasslands, it means preventing overgrazing. Schlesinger et al. (1990) argue that the widespread conversion of semiarid grasslands to arid shrublands in the southwestern United States in the past 100 years is a result of soil deterioration initiated by overgrazing. If so—and evidence for their thesis is good—overgrazing in drier climates would convert many grasslands to deserts, as evidenced elsewhere in the world.

Another possible strategy for stabilization is to increase ecosystem carbon storage by transferring it from above-ground plant parts where it is vulnerable to loss in fire, to below-ground reservoirs.

However, too little is known about soil carbon dynamics to determine how this might be done.

Historically, soils disturbed by intensive agriculture, forestry, and grazing have been significant sources of carbon to the atmosphere (Buringh 1984; Schlesinger 1984). Intact forests store significant amounts of carbon, and, as we mentioned earlier, conversion of old-growth Douglas-fir forests to young plantations decreases the carbon stored in the system, even when changes in the soil are not taken into account (Harmon, Ferrel, and Franklin 1990). Levels of timber harvest are influenced by many biological, social, and economic factors. It is time that the role of forests in maintaining the health of the global ecosystem also is factored into the equation.

We must develop and implement monitoring procedures that provide an early warning signal of deteriorating ecosystem health. Loss of essential nutrients to streams is one of these. Other possible signals that should be tested experimentally are: shifts in biomass, and particularly in types of soil organisms; increased emissions of trace gases from soils; changes in the maximum leaf area of sites; and changes in leaf chemistry. Except for nutrient loss to streams, these factors fluctuate somewhat in healthy systems—so we must begin monitoring soon in order to verify trends and to identify those variables that are most stable, hence the best indices of changing conditions.

Summary

Climate change will have complex effects on ecosystems. Warmer temperatures and greater atmospheric CO_2 concentration potentially benefit plant growth, but increased water stress could cancel or outweigh benefits. Disturbances such as insect infestations, wildfires, and windstorms are predicted to increase in frequency and severity and will exacerbate direct climatic stresses. Numerous interactions and feedback processes within ecosystems and among land, water, and the atmosphere are likely to come into play and could either stabilize ecosystems or push them rapidly toward instability. A particularly critical factor at the local ecosystem level is the strong, mutually reinforcing, positive feedback that occurs between plants and soils which, if broken, can lead to rapid degradation. Plant species will not migrate fast enough to keep up with the predicted rates of climate change. Management of forests, rangelands, and farms should incorporate practices that diminish possible negative impacts and ease the transition from one vegetation type to another. In particular, plant–soil links and the natural stabilizing mechanisms of ecosystems—many of which require biological diversity—should be protected.

Coda

History tells us that it is unwise to ignore potential disruptions of climate change, particularly when coupled with abusive land practices. A few thousand years ago, northern Africa and the mideast were fertile breadbaskets with extensive forests in the highlands. The interacting and mutually reinforcing effects of climate change, overgrazing, and deforestation resulted in the arid deserts that dominate that region today. That need not happen again; if it is to be avoided, however, we must develop a strategy and act now. Although there is much uncertainty as to how climate may really change, waiting for uncertain trends to become truths wastes valuable time. One does not wait until the house catches fire to buy insurance.

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