

BEYOND GLOBAL WARMING: ECOLOGY AND GLOBAL CHANGE

THE ROBERT H. MACARTHUR AWARD LECTURE

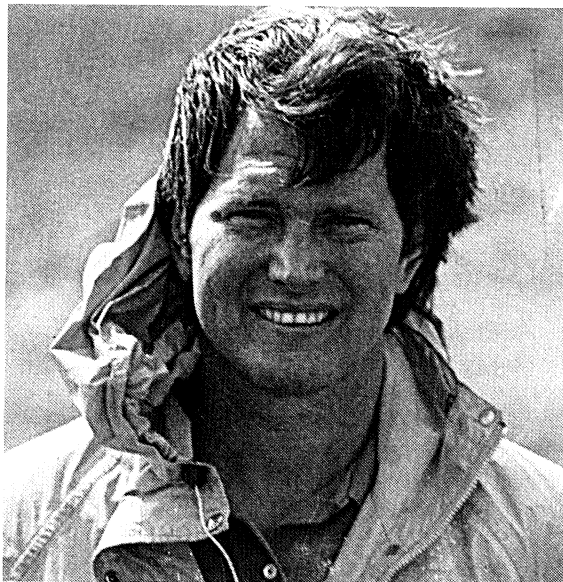
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Abstract. While ecologists involved in management or policy often are advised to learn to deal with uncertainty, there are a number of components of global environmental change of which we are certain—certain that they are going on, and certain that they are human-caused. Some of these are largely ecological changes, and all have important ecological consequences. Three of the well-documented global changes are: increasing concentrations of carbon dioxide in the atmosphere; alterations in the biogeochemistry of the global nitrogen cycle; and ongoing land use/land cover change. Human activity—now primarily fossil fuel combustion—has increased carbon dioxide concentrations from ~280 to 355 $\mu\text{L/L}$ since 1800; the increase is unique, at least in the past 160 000 yr, and several lines of evidence demonstrate unequivocally that it is human-caused. This increase is likely to have climatic consequences—and certainly it has direct effects on biota in all Earth's terrestrial ecosystems.

The global nitrogen cycle has been altered by human activity to such an extent that more nitrogen is fixed annually by humanity (primarily for nitrogen fertilizer, also by legume crops and as a byproduct of fossil fuel combustion) than by all natural pathways combined. This added nitrogen alters the chemistry of the atmosphere and of aquatic ecosystems, contributes to eutrophication of the biosphere, and has substantial regional

effects on biological diversity in the most affected areas. Finally, human land use/land cover change has transformed one-third to one-half of Earth's ice-free surface. This in and of itself probably represents the most important component of global change now and will for some decades to come; it has profound effects on biological diversity on land and on ecosystems downwind and downstream of affected areas. Overall, any clear dichotomy between pristine ecosystems and human-altered areas that may have existed in the past has vanished, and ecological research should account for this reality.

These three and other equally certain components of global environmental change are the primary causes of anticipated changes in climate, and of ongoing losses of biological diversity. They are caused in turn by the extraordinary growth in size and resource use of the human population. On a broad scale, there is little uncertainty about any of these components of change or their causes. However, much of the public believes the causes—even the existence—of global change to be uncertain and contentious topics. By speaking out effectively, we can help to shift the focus of public discussion towards what can and should be done about global environmental change.

Key words: biogeochemistry; carbon dioxide; education; global change; human population growth; land use change; nitrogen cycle; public policy; resource use.

INTRODUCTION

I will make two major points in this paper. First, human-caused global environmental change is with us now. Ultimately, it is driven by the rapidly growing human population and our high rates of resource consumption; proximately, global environmental change occurs as a number of interacting components that alter the structure and function of Earth as a system. There is strong public and governmental focus on one of these components, climate change or (simplistically) global warming, and many ecologists are involved in analyzing the likely implications of climate change for natural and managed organisms, populations, communities, and ecosystems (e.g., Peters and Lovejoy 1992, Kareiva et al. 1993). However, climate change is not the best known, not currently the most significant, and not the most permanent of the components of anthropogenic global change. Many of the other components of global change, and most of their consequences, lie partly or largely within ecological systems. Indeed, one of the fundamental causes of global change—human population growth—is an ecological phenomenon. As ecologists, we should recognize that addressing global change will require active collaborations with a wide range of scientists outside our field and with researchers outside the natural sciences, but we also should recognize that it is *our* responsibility to take the lead in dealing with major components of global environmental change.

Second, we will have to learn how to deal more effectively with certainty. Ecologists who address public policy or globally significant issues often are advised to learn to deal with *uncertainty*, because generally neither policy recommendations nor global extrapolations are amenable to statistical "certainty" at the 0.05 or 0.01 level. However, most of what I will discuss in this paper is both globally significant and not at all controversial, yet much of the educated public believes that our understanding of global environmental change is both uncertain and highly contentious. There are uncertainties, but there is also a substantial core of

knowledge, and it is our responsibility to see that it reaches policy makers and the public.

In this paper, I will summarize three components of global environmental change that have several features in common. All are well-documented, ongoing changes whose existence and global nature are beyond serious dispute; their proximate causes have been identified clearly; and all have direct causal connections to global climate change and/or the loss of biological diversity. The three that I have selected (drawn from a longer list of equally certain global changes) are: (1) the increasing concentration of carbon dioxide in the atmosphere; (2) alteration of the global nitrogen cycle; and (3) change in land cover and/or land use. For each component, I will describe how and why it is changing globally, and some of the known or likely ecological consequences of change. I will then describe how these and other equally certain components of global environmental change drive global changes in climate and biological diversity (Fig. 1) and briefly discuss the proximate and ultimate causes of change. Finally, I will suggest several steps that we can take to influence the course of global change.

COMPONENTS OF GLOBAL CHANGE

Increasing carbon dioxide

The change.—The fact that concentrations of carbon dioxide in the atmosphere are increasing is known to all ecologists; it is fair to describe this as the best documented global change. However, the uniqueness of the increase (at least in the past 200 000 yr), the thoroughness with which it has been documented, the level of certainty concerning its causes, and the multiple consequences of elevated carbon dioxide concentrations are not well understood by the educated public.

Atmospheric carbon dioxide concentrations have been measured continuously and extraordinarily carefully since 1957 (Keeling et al. 1989a). The results display two major signals: a seasonal cycle that reflects

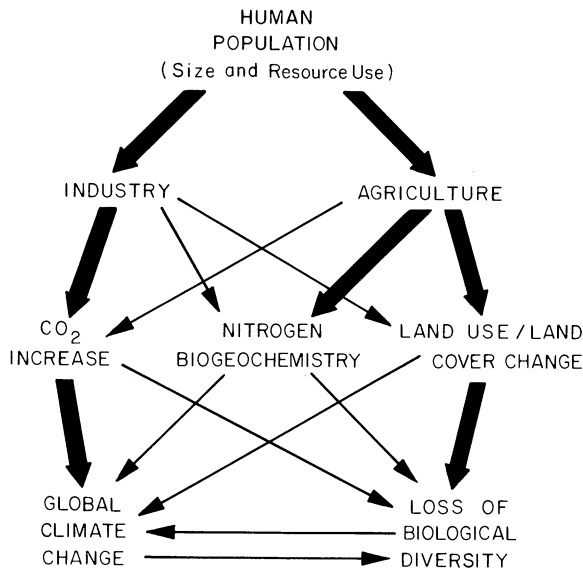


FIG. 1. The components of global environmental change emphasized in this paper, showing relationships among human population and activity, the well-characterized components of change discussed herein, and changes in climate and biological diversity. The wide arrows represent dominant effects.

the metabolism of terrestrial ecosystems in the northern hemisphere (Fung et al. 1987) and an accelerating increase in tropospheric concentrations throughout the period of record (Fig. 2). There can be no doubt that concentrations have increased, but if we had only the post-1957 observational record we could not rule out the possibility that the increase might be part of a natural fluctuation that we just happened to catch on the upswing. However, air bubbles trapped within the Greenland and Antarctic ice caps record the concentration of stable gases at the time the bubbles were isolated from the atmosphere (Raynaud et al. 1993), and measurements of carbon dioxide in this air demonstrate that concentrations were reasonably constant for several thousand years before the 19th century (Fig. 3). Carbon dioxide concentrations then began to increase at an accelerating rate, and results from analysis of the air bubbles fit seamlessly into the modern observations (Watson et al. 1990).

In the longer term, measurements of trapped air from a deep Antarctic ice core demonstrate that carbon dioxide concentrations have been variable on the time scale of glacial-interglacial cycles, with low concentrations during glacial periods, relatively high concentrations during interglacial times, and relatively rapid transitions in both temperature and carbon dioxide concentrations (Barnola et al. 1987, Raynaud et al. 1993). The modern increase is superimposed on this natural variation; it begins with carbon dioxide concentrations at their high interglacial level and goes up from there, outside of the range of the past (Fig. 4).

The recent increase is substantial, already nearly as large as the range between glacial minima and interglacial maxima, and it is 5–10 times more rapid than any of the sustained changes in the ice-core record (Fig. 4). Clearly, we are dealing with an unusual event in recent Earth history, one that coincides with the recent proliferation of the human population and our expansion of energy and resource use.

What causes this modern increase in carbon dioxide concentrations? Fossil fuel combustion is the most important source. First, there is more than enough of it; fossil fuel consumption releases ≈ 5.6 Pg (1 Pg = 10^{15} g) of CO_2 -C annually (Marland et al. 1988), while the annual increase in atmospheric CO_2 -C is ≈ 3.5 Pg (Keeling et al. 1989a). Indeed, there is real controversy over where the rest of the fossil fuel carbon (plus any net contribution from deforestation) goes (Fung 1993, Siegenthaler and Sarmiento 1993). Second, there is an unambiguous tracer of the carbon dioxide derived from fossil fuel. Radioactive ^{14}C , with a half-life of 5730 yr, is a minor constituent of atmospheric carbon dioxide and of the biota. The carbon in fossil fuels is millions of years old, so it is now wholly depleted in ^{14}C . To the extent that fossil fuel combustion causes the observed increase in atmospheric carbon dioxide, $^{14}\text{CO}_2$ in the atmosphere should be diluted by the addition of ^{14}C -depleted CO_2 from fossil fuels. That is precisely what has been observed (Suess 1955, Bacastow and Keeling 1974) (Fig. 5), up to the time when ^{14}C derived from nuclear explosions alters the record. Indeed, by using both ^{14}C and the stable carbon isotope ^{13}C , which differs in relative abundance between biosphere and atmosphere due to fractionation during photosynthesis (Farquhar et al. 1982, 1989), it is possible to calculate directly that most of the increase in CO_2 in the past several decades is due to fossil fuel combustion and not deforestation (Stuiver 1978, Keeling et al. 1989b).

Consequences of increasing carbon dioxide. The climatic consequences of increasing carbon dioxide con-

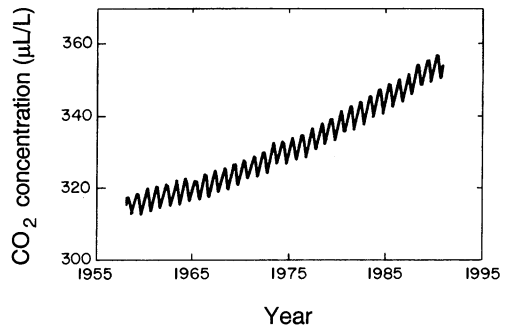


FIG. 2. Measured concentrations of CO_2 in the atmosphere at Mauna Loa, Hawaii. The annual cycle is driven by seasonal activity of terrestrial biota in the northern hemisphere, while the overall increase is driven primarily by fossil fuel combustion (Keeling et al. 1989a, b). From data in Keeling and Whorf (1991).

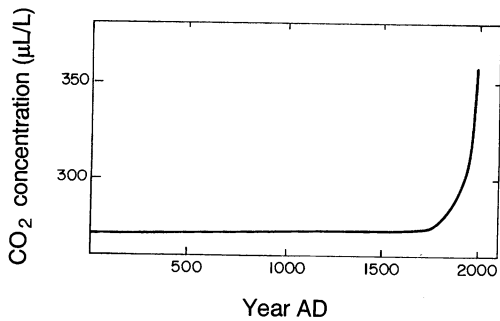


FIG. 3. Concentrations of CO₂ in the atmosphere over the past 2000 yr, determined by analysis of air bubbles trapped in the Greenland and Antarctic ice caps (Raynaud et al. 1993). Redrawn from Webb and Bartlein (1992).

concentrations have received a great deal of attention (e.g., Houghton et al. 1990), appropriately so because CO₂ will be responsible for more than half of the anticipated global warming over the next century (Lashof and Ahuja 1990, Rodhe 1990). Evaluations of the direct effects of elevated carbon dioxide on biological systems have been less prominent, even though photosynthetic rates of many plants can be enhanced by increased carbon dioxide concentrations over much of Earth (cf. Eamus and Jarvis 1989, Bazzaz 1990, Mooney et al. 1991). Much of the research on biological effects of elevated CO₂ that has been carried out was motivated (at least on the part of its sponsors) by a desire to determine the "β-factor" (Bacastow and Keeling 1974), the extent to which an increase in the concentration of carbon dioxide increases carbon storage in terrestrial ecosystems. Knowledge of β is important to analyzing the global carbon cycle and its regulation, but it is far from the whole story of the biological effects of elevated CO₂.

A few ecologists, notably F. A. Bazzaz and his colleagues, recognized early the enormous ecological implications of increasing carbon dioxide concentrations. Elevated carbon dioxide increases photosynthetic rates of most plants with the C₃ photosynthetic pathway, especially where other resources are not limiting. It increases both photosynthetic water use efficiency and integrated nutrient use efficiency (in that plants produce tissue with higher carbon/nutrient ratios) (Bazzaz 1990, Field et al. 1992). Many species of plants acclimatize to elevated CO₂ relatively quickly; many others do not, but maintain elevated growth rates indefinitely (Bazzaz et al. 1994) (Fig. 6). Accordingly, there is an enormous potential for effects on the community level, as some species gain a relative advantage from their large or sustained response to elevated CO₂ (Patterson et al. 1984, Bazzaz 1990).

Some generalizations about which species are favored by elevated CO₂ are emerging; for example, species with rapid growth rates may be more responsive than slower growing species (Hunt et al. 1991), and plants with the C₃ photosynthetic pathway should gain

relative to those with the C₄ pathway (Bazzaz 1990, Poorter 1993). The latter effect may cause shifts in the boundaries between C₄-dominated prairies and savannas and C₃-dominated forests. However, there are exceptions to these generalizations, and idiosyncratic effects that we cannot now predict may turn out to be the most important ones. For example, *Bromus tectorum*, the notorious Eurasian invader of the Intermountain West of the United States, is unusually responsive to elevated CO₂ in comparison with other C₃ grasses (Smith et al. 1987).

The effects of elevated carbon dioxide are not likely to be confined to plant growth and community composition. As noted above, plants that do respond to elevated carbon dioxide produce tissue with lower nutrient concentrations. As a consequence, individual herbivores must consume more tissue to acquire sufficient protein and other nutrients for growth and development (Fajer et al. 1991, Field et al. 1992); they generally grow more slowly, and suffer higher mortality in the process (Fig. 7) (Fajer et al. 1989). Similarly, decomposers may encounter lower quality tissue, with consequences for their own populations and for ecosystem-level nutrient cycling (Norby et al. 1986).

The potential effects of increasing carbon dioxide are not confined to terrestrial ecosystems. For example, Smith and Buddemeier (1992) point out that continued increases in the partial pressure of carbon dioxide in seawater will reduce the degree of oversaturation of aragonite, the form of calcium carbonate that represents the major building block of reef corals. The consequences of this change for the functioning of coral reef ecosystems are not yet known.

Overall, the increase in carbon dioxide represents a substantial alteration to the Earth system. The biological and ecological consequences of elevated CO₂ go well beyond the β factor, although an understanding

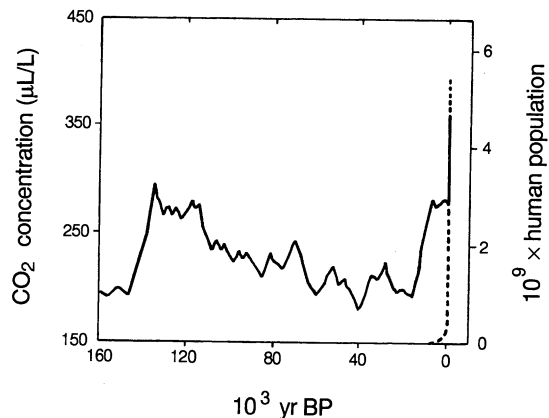


FIG. 4. Concentrations of CO₂ over the past 160 000 yr determined by analysis of trapped air bubbles from the Vostok ice core, Antarctica, and the estimated human population over the same time period. Carbon dioxide concentrations redrawn from Barnola et al. (1987).

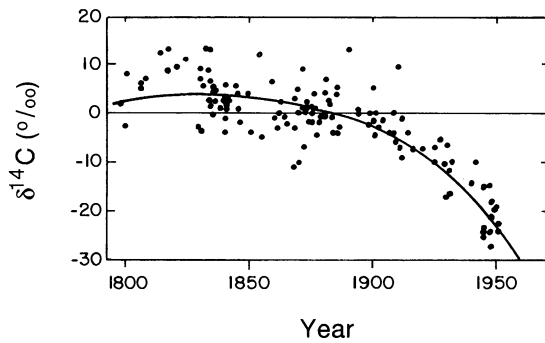


FIG. 5. The Suess effect: dilution of the δ¹⁴C in atmospheric carbon dioxide caused by combustion of ¹⁴C-depleted fossil fuels (Suess 1955). δ¹⁴C is calculated as:

$$\frac{(^{14}\text{C}/^{12}\text{C})_{\text{sample}} - (^{14}\text{C}/^{12}\text{C})_{\text{standard}}}{(^{14}\text{C}/^{12}\text{C})_{\text{standard}}} \times 1000.$$

●, the relative ¹⁴C enrichment in cellulose from known-age tree rings; —, the predicted ¹⁴C dilution from a model based on global patterns of fossil fuel combustion and atmosphere-ocean-biosphere carbon exchange. Redrawn from Bacastow and Keeling (1974).

of these effects would contribute substantially towards determining β. This ongoing change makes the periodic debates among ecologists concerning the virtues of working in pristine ecosystems vs. human-altered systems absurd; we all live and work in systems that are altered by human activity (Ludwig 1989).

Nitrogen biogeochemistry

The change.—The global nitrogen cycle is unique in that it consists of a large, well-mixed pool of N₂ in the atmosphere; a smaller quantity of C-, H-, or O-bonded N that cycles among plants, animals, soils, sediments, and solutions; and a set of relatively small, largely biologically mediated transfers between these pools (Schlesinger 1991). Moreover, the quantity of nitrogen available to organisms affects species composition, productivity, and the responsiveness of ecosystems to elevated CO₂ in many areas (Vitousek and Howarth 1991, Melillo et al. 1993).

The global nitrogen cycle also is extraordinary in the extent to which it has been modified by human activity. Under background conditions, biological nitrogen fixation in terrestrial ecosystems has been estimated at ≈100 Tg (1 Tg = 10¹² g) of N per year globally (Soderlund and Rosswall 1982); nitrogen fixation in marine ecosystems adds 5–20 Tg more (Carpenter and Capone 1983), while fixation by lightning accounts for 10 Tg or less (Soderlund and Rosswall 1982). In contrast to this natural background, industrial nitrogen fixation for nitrogen fertilizer now amounts to >80 Tg/yr. An additional 25 Tg of N are fixed by internal combustion engines and released as oxides of nitrogen, and ≈30 Tg are fixed by legume crops (over and above background N fixation on those lands) (Smil 1991, Vitousek

and Matson 1993). Accordingly, the global N cycle has now reached the point where more N is fixed annually by human-driven than by natural processes. This alteration is overwhelmingly a recent phenomenon (Fig. 8). Indeed, building on Turner et al. (1990), I estimate that 50% of all of the industrial N fertilizer used in human history through 1992 has been applied since 1982.

Moreover, these changes in nitrogen fixation understate the overall human effect on the global nitrogen cycle. In addition to fixing nitrogen, human activity mobilizes nitrogen from long-term storage pools through biomass burning, land clearing and conversion, and drainage of wetlands (Matson et al. 1987, Crutzen and Andreae 1990, Vitousek and Matson 1993). Both newly fixed and mobilized nitrogen can be transported in solution or in the atmosphere, and so alterations to the N cycle in a particular site can spread regionally or even globally.

Consequences of altered nitrogen biogeochemistry.—The enormous increase in the transfer to biologically available forms of a critical, often limiting nutrient can be expected to affect biological systems at all levels of organization, and at spatial scales from local to global. Globally, increased anthropogenic N fixation has occurred concurrently with an increase in atmospheric concentrations of the stable greenhouse gas nitrous oxide (Prinn et al. 1990) (Fig. 9). Detailed analyses of the global budget of nitrous oxide (cf. Keller et al. 1986, McElroy and Wofsy 1986, Matson and Vitousek 1990, Watson et al. 1990, Khalil and Rasmussen 1992) have sought to explain how global sources and sinks could be as much as 30% out of balance, as is necessary to account for the observed increase. The perspective pro-

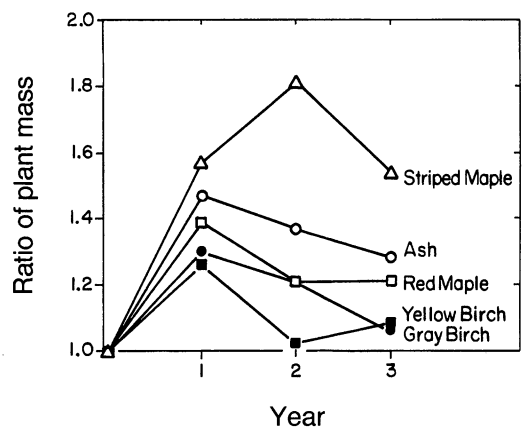


FIG. 6. The time course of growth enhancement caused by elevated CO₂ concentration for several New England tree species. The response ratio is calculated as growth of a given species at 680 μL/L CO₂ divided by its growth at 340 μL/L CO₂. All of the species initially respond positively, but they differ substantially in how long elevated growth rates are maintained. From Bazzaz et al. (1994); reproduced with permission.

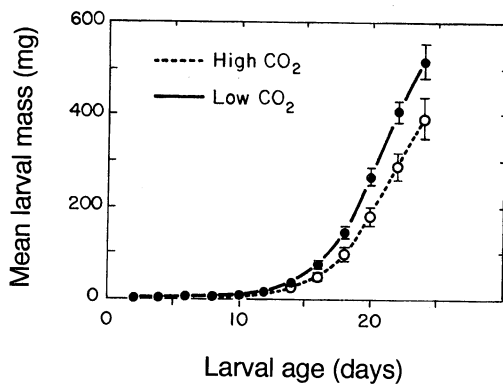


FIG. 7. Growth rate of the herbivorous caterpillar *Junonia coenia* on host plants grown at ambient (●—●) and elevated (○--○) CO₂ concentrations. From Fajer et al. (1989), reproduced with permission. Data are means \pm 1 SE.

vided by a nitrogen cycle that has been altered at least twofold by human activity raises different questions. Has this large anthropogenic increase in nitrogen fixation entrained a similar increase in nitrous oxide that has not yet occurred? Is that added nitrogen retained in terrestrial systems, causing carbon storage (Melillo et al. 1989, Aber et al. 1991)? Or is the anthropogenically fixed N lost from terrestrial ecosystems by other pathways? These alternative pathways could include volatilization of reactive nitrogen oxides, which can lead to the formation of tropospheric ozone (Logan 1985); volatilization of ammonia, which alters other aspects of atmospheric chemistry (Schlesinger and Hartley 1991); loss of nitrogen to aquatic systems, which can reduce water quality (Turner and Rabelais 1991); and denitrification to N₂, which would be benign.

On the ecosystem level, the possible effects of N deposition to terrestrial ecosystems (resulting from the fixation, mobilization, or application of N upwind) on carbon storage, nitrogen cycling, and trace gas emissions have been examined in a number of forest ecosystems (Melillo et al. 1989, Aber et al. 1991, Bowden et al. 1991, Kauppi et al. 1992). There is some evidence for increased nitrate leaching, emissions of N-containing trace gases, and enhanced carbon storage in such areas. There is also strong evidence that forest dieback in certain European forests can be caused, at least in part, by enhanced nitrogen deposition (Schulze 1989).

Alterations in the biogeochemistry of the nitrogen cycle also have significant effects on ecological processes at the population and community levels. Numerous experimental studies using fertilization with nitrogen demonstrate that in the many ecosystems where N supply limits primary production, added nitrogen leads to a concentration of dominance into one or a few nitrogen-responsive plant species (Tilman 1987, Berendse and Elberse 1990, Huenneke et al. 1990). Net primary production and biomass are increased by the addition of nitrogen, but overall species richness is decreased, often dramatically (Fig. 10).

Even without deliberate fertilization, the remarkable levels of nitrogen deposition observed over much of Europe (for example, a mean of 85 kg·ha⁻¹·yr⁻¹ in the interior of the Netherlands, resulting from intensive agriculture and internal combustion [Berendse et al. 1993]) have similar effects on ecosystems. Populations of nitrogen-demanding grasses such as *Brachypodium pinnatum* and *Molinia caerulea* have increased over time largely as a consequence of added N, while plants adapted to infertile soils have declined (Heil and Diemont 1983, Bobbink et al. 1988, Bobbink 1991). Overall, there has been a substantial decrease in within-community diversity (Bobbink and Willems 1987, Berendse and Elberse 1990). Diversity among communities may have decreased as well, because atmospheric N deposition increases nutrient availability in sites that formerly were infertile, and thereby favors the growth of nitrogen-demanding species everywhere. At present, western and central Europe are most strongly affected by excess N deposition. However, substantial areas in North America also receive anthropogenic N, and most of the recent growth in the use of N fertilizer is in the tropics (Vitousek and Matson 1993).

Additions of nitrogen can be expected to affect consumers, decomposers, and symbionts as well as plants. Increases in nitrogen concentrations in plant tissue favor the growth and survival of many consumers (the converse of the effects of elevated CO₂ discussed above) (Mattson 1980, Field et al. 1992) and can affect populations of predators and parasites as well (Loader and Damman 1991). The tissue produced by N-fertilized

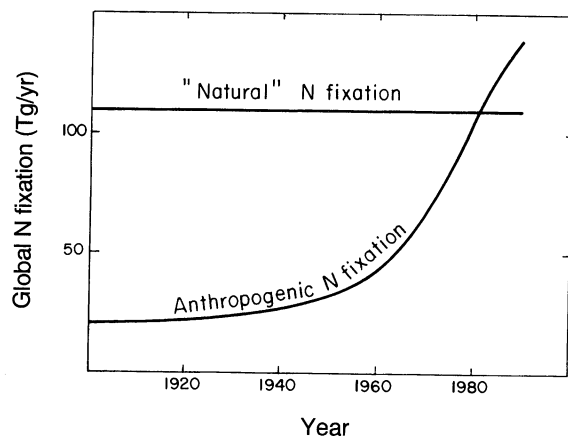


FIG. 8. Extent of human alteration of the global biogeochemical cycle of nitrogen. The "natural N fixation" line represents biological N fixation in natural terrestrial systems plus fixation by lightning; I assume that natural biological fixation has not changed recently, although it probably has declined due to land use change and increased N deposition. The "anthropogenic N fixation" line represents the sum of industrial N fixation for fertilizers, fixation during fossil fuel combustion, and fixation by leguminous crops (Smil 1991, Vitousek and Matson 1993). *Nitrogen biogeochemistry: The change* reports the modern fractions for each source.

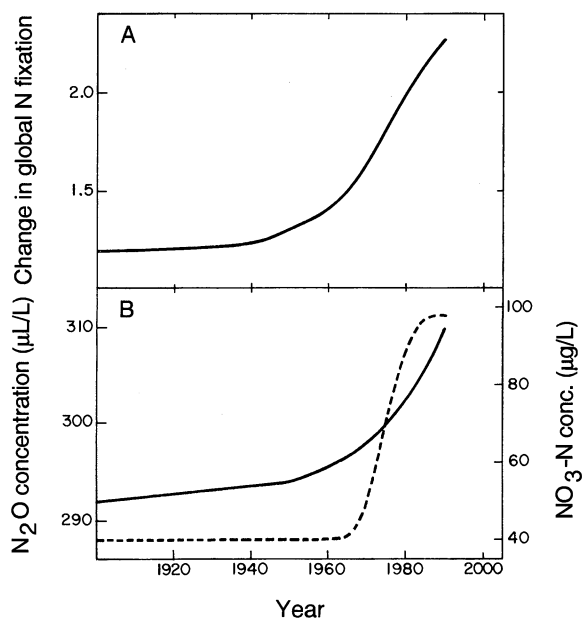


FIG. 9. Changes in global N fluxes during the 20th century. (A) Human alteration of global N fixation as the ratio of anthropogenic to total (anthropogenic plus natural) N fixation (from Fig. 8). (B) Concurrent patterns in atmospheric concentrations of the greenhouse gas nitrous oxide (—) (Watson et al. 1990) and in nitrate concentrations at the mouth of the Mississippi River (---) (Turner and Rabelais 1991).

plants often decomposes and releases nutrients more rapidly than that of conspecific unfertilized plants (Vitousek 1983, Berg et al. 1987). Moreover, where N deposition causes plant species replacement, the N-responsive species that are favored generally cycle more N externally through litter and produce more readily decomposable litter than do the species they replace, thereby driving a positive feedback towards increased availability of N (van Vuuren et al. 1992, Berendse 1993).

For symbionts, added nitrogen would be expected to decrease the activity of nitrogen-fixing organisms, as externally supplied N can replace energetically costly fixed N in plant metabolism. Moreover, to the extent that mycorrhizal fungi profit as a result of their importance in plant N nutrition, their populations could be altered by enhanced N deposition as well. In fact, there is strong evidence for a decline in many species of ectomycorrhizal fungi in the areas of Europe that are most affected by N deposition (Arnolds 1991).

As with the increase in CO_2 , human alteration of the nitrogen cycle represents an ongoing global change of which we are certain—certain that it exists, and certain that it is human-caused. This global change has consequences for climate through its effects on nitrous oxide emission and the carbon cycle, for biological diversity through its effects on local- and landscape-level diversity, and for ecological processes at all levels of organization from organisms to the Earth system.

Land use/land cover change

The change.—Land cover change is defined as alteration of the physical or biotic nature of a site, for example the conversion of forest to grassland, while land use change involves alteration of the way humans use land, as in the conversion of low-input agricultural land to high-input uses or vice versa (Meyer and Turner 1992). Land use change and land cover change can occur separately or simultaneously, but for convenience I will subsume both under “land use change” in this paper.

There is a reasonably strong consensus that land use change is now, and for some decades probably will remain, the single most important of the many interacting components of global change affecting ecological systems (Vitousek 1992, NRC 1993). Despite its importance, however, it is relatively difficult to quantify land use change as a global phenomenon; unlike the increase in CO_2 , it is not possible to install instruments on a tropical mountain, and let the evidence of global change come to you. Rather, land use change occurs in a heterogeneous way, hectare by hectare across Earth, and its global significance results primarily from the summation of many local changes in many local areas.

As yet, there is no direct global measure of land use change. More surprisingly, there is not even a direct measurement of deforestation, the most dramatic form of land cover change, even though the raw material for such an analysis has been available in civilian satellite imagery for more than two decades. Skole and Tucker

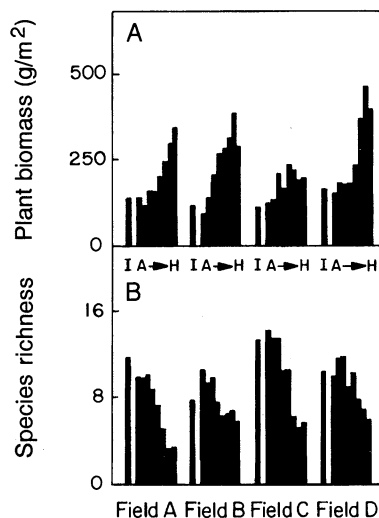


FIG. 10. Effects of eight levels of N fertilization on plant biomass (A) and plant species richness (B) in four Minnesota old fields. The results here are for the 4th yr of fertilization in each field. The plots represented with bars labelled “I” received no fertilizer, while those labelled A through H received equal quantities of phosphorus, potassium, and other nutrients plus 0, 1, 2, 3.4, 5.4, 9.5, 17.0, and $27.2 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ of N. Redrawn from Tilman (1987).

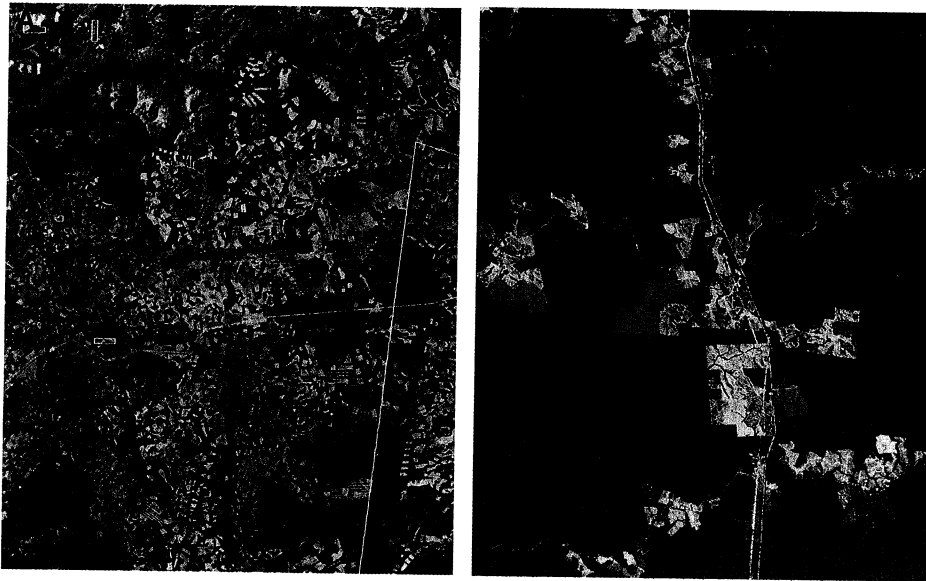


FIG. 11. LANDSAT-thematic mapper images of land use in Hood National Forest, Oregon in 1991 (A) and north of Manaus, Brazil in 1990 (B). Blue-black areas represent recently cleared and burned sites, pale orange areas represent established pasture or successional forest, and dark orange areas represent intact forest. Each image covers ≈ 1200 km². Photos from NASA-Goddard Space Flight Center, courtesy of C. J. Tucker.

(1993) recently used this imagery to make fine-scale measurements of rates of deforestation and habitat fragmentation across the Brazilian Amazon (Fig. 11), demonstrating in the process that there is no technical obstacle to a global analysis of deforestation.

In the absence of direct measurements, two summaries of the overall scale of human activities related to global land use change have been proposed. Kates et al. (1990) drew on the extensive analysis in *The earth as transformed by human action* (Turner et al. 1990) and concluded that about half of the ice-free terrestrial surface of Earth has been transformed (changed in state), managed, or utilized by human activity. Vitousek et al. (1986) used global data bases derived from studies of the global carbon cycle (cf. Ajtay et al. 1979, Olson et al. 1983) to estimate that nearly 40% of potential terrestrial net primary productivity (NPP) of Earth is used or dominated by humanity or foregone as a result of land use change. They calculated that 4% of current terrestrial NPP is consumed directly by humans and domestic animals, another 26.7% takes place in wholly human-dominated systems, and that 11.7% of potential terrestrial NPP is lost as a result of human activity (primarily the reduced NPP of many croplands in comparison with natural ecosystems) (Table 1). Neither of these analyses represents the overall effect of humanity on terrestrial ecosystems; after all, every system is affected by elevated CO₂. Rather, they represent the areas or quantities of energy that function in wholly different ways as a result of human use and human-caused land use change.

Consequences of land use change. The effects of land use change are felt on all levels of organization, from genetic to global. Land use change made the dominant

contribution to increasing concentrations of carbon dioxide in the atmosphere in the 19th century (Stuiver 1978), and it probably continues to make a small (relative to fossil fuels) net contribution now (Houghton et al. 1987, Detwiler and Hall 1988). Moreover, land use change is the most important cause of increases in atmospheric concentrations of the greenhouse gases methane and nitrous oxide (Matson and Vitousek 1990, Watson et al. 1990, Fung et al. 1991). Fires associated with land use change add nitric oxide and carbon monoxide to the atmosphere (Logan 1985, Keller et al. 1991), altering its reactive chemistry and bringing episodes of urban-like oxidant air pollution to extensive areas of the tropics (Crutzen and Zimmermann 1991, Fishman et al. 1991). Fires also produce aerosols that can affect energy balance and climate regionally and globally (Penner et al. 1992).

Land use change can also affect climate both locally and regionally by altering the ways that solar energy is partitioned. Conversion of forest to pasture increases albedo and decreases canopy roughness. On a local scale, the net effect is an increase in local temperature and a decrease in humidity; these in turn can affect the potential for forest regeneration, both directly and through their enhancement of the probability and intensity of fire (Uhl and Kauffman 1990). On a coarser spatial scale, recent simulation models suggest that converting all Amazonian forest to pasture would increase temperature, decrease precipitation, and alter patterns of atmospheric circulation over the region as a whole (Lean and Warrilow 1989, Shukla et al. 1990, Dickenson 1991). Desertification can have similar local and regional effects in semi-arid areas (Schlesinger et al. 1990).

TABLE 1. Terrestrial net primary production (NPP) used, dominated, or foregone as a result of human activity. From Vitousek et al. (1986).

Component	NPP (Pg/yr)
Total terrestrial NPP*	132
NPP used	
Consumed by humans	0.8
Consumed by domestic animals	2.2
Wood used by humans	2.4
Total	5.2 (4% of total)
NPP dominated	
Croplands†	15
Converted pastures†	10
Tree plantations†	2.6
Human-occupied lands†	0.4
Consumed from little-managed ecosystems‡	3
Land clearing	10
Total	41 (31% of total)
NPP lost to human activity	
Decreased NPP of cropland vs. natural systems§	10
Desertification	4.5
Human-occupied areas	2.6
Total	17 (together with the NPP dominated, 39% of total potential NPP)

* The global summary by Ajtay et al. (1979) was the basis for these calculations.

† This includes the total NPP of wholly human-dominated ecosystems.

‡ This category includes wood harvested and forage consumed by domestic animals on little-managed systems, and anthropogenic fires.

§ This accounts for a decrease (on average) in the NPP of crop systems compared to the natural systems they replace, due primarily to the substitution of annuals for perennials. If we follow Olson et al. (1983) and assume that cropland NPP is equal to or above that of natural systems, this component of loss disappears but is replaced by an equivalent amount of cropland NPP dominated by humanity.

Most importantly, one-third to one-half of the terrestrial surface, including some of the best land in terms of water supply and soil fertility, has been altered directly and substantially by human activity. This altered land is used by humans, by the plants and animals we have domesticated, and by other species that have attached themselves to our activities (e.g., rats and ragweed)—and the other 5–30 × 10⁶ species on Earth must persist on a reduced and decreasing fraction of land. Indeed, some major ecosystem types have been reduced to fragments or have virtually disappeared (e.g., tallgrass prairie, drought-deciduous tropical forest), and numerous species and genetically distinct populations have been lost in the process (Ehrlich and Wilson 1991, Wilson 1992, Ehrlich and Daily 1993, Myers 1993). The biotic effects of land use change are not confined to altered lands themselves; habitat fragmentation and edge effects influence substantial areas of otherwise undisturbed land (Redford 1992). For example, Skole and Tucker (1993) demonstrated that ≈230 000 km² of the Brazilian Amazon had been deforested by 1988, while >16 000 km² were in patches isolated as forest fragments, and another 341 000 km² were within 1 km of a deforested site. Moreover, land use patterns that decrease the size of each individual parcel of cleared land, such as size limits on clearcuts in U.S. national forests, increase the fraction of an area in which edge effects are important (Fig. 11). Studies of edge effects and of

habitat islands have a strong background in ecology, and ecological information can contribute a great deal towards understanding the genetic, population, and ecosystem consequences of this component of anthropogenic land use change (see Holsinger 1993 and other papers in Kareiva et al. 1993).

The effects of land use change are not confined to terrestrial ecosystems and/or the atmosphere. Carpenter et al. (1992) reviewed the likely effects of global climate change on freshwater ecosystems, but point out that:

To date, the most severe stresses on freshwater systems have come from watershed modifications and use and contamination of aquatic resources by humans.

Similarly, Smith and Buddemeier (1992) evaluated global change to coral reefs, concluding that:

Reef damage from anthropogenic environmental degradation [nutrient runoff, siltation, overexploitation] is widespread, represents a much greater threat than climate change in the near future, and can reinforce the negative effects of climate change.

Overall, land use change represents a major global change that is with us now, like increasing carbon dioxide and alteration of the global nitrogen cycle. Its current effects on biological diversity in particular are

greater than those of any other single component of global change, and they are likely to remain so for some decades. Indeed, I believe that a knowledge of rates of land use change is as important to predicting changes in biological diversity as a knowledge of increasing carbon dioxide is to predicting climate change. Land use change is not the only driver of change in diversity, but it is the most important one, and it interacts with most of the other components of global change.

OTHER WELL-DEFINED COMPONENTS OF GLOBAL CHANGE

Changes in CO₂, nitrogen biogeochemistry, and land use (Fig. 1) are far from the only components of global environmental change of which we are certain. Other well-documented global changes include:

The widespread distribution of synthetic organic compounds.—Highly persistent compounds such as DDT and PCBs have been used widely and have become globally distributed, with substantial effects on biota locally, regionally, and globally (Brown et al. 1990). More recently, increasing concentrations of the wholly human-made chlorofluorocarbons (CFCs) have depleted stratospheric ozone and increased UV-B (290–320 nm light) transmission in the Antarctic region (Rowland 1989, Solomon 1990), and there is increasing evidence of a reduction in marine productivity as a consequence of increased UV-B input (Smith et al. 1992). This component of global change is particularly interesting in that scientific research and political action have worked together successfully to reduce CFC emissions nationally and globally (Benedick 1991).

Altered biogeochemistry of global element cycles.—In addition to carbon and nitrogen (discussed above), the atmospheric portion of the sulfur cycle has been changed enormously by human activity. Emissions of sulfur dioxide from fossil fuel combustion exceed all natural gaseous emissions combined (Wigley 1989, Charlson et al. 1992). These emissions are concentrated in developed regions of the northern hemisphere, where sulfur dioxide emissions lead to sulfuric acid rain and enhanced sulfate aerosol concentrations. The region downwind of most industrial areas is affected by sulfuric acid rain (Schindler 1988, Johnson and Lindberg 1992), while sulfate aerosols serve as effective nuclei for cloud condensation. Model calculations suggest that anthropogenic sulfate aerosol loadings are sufficient to affect the energy budget of the northern hemisphere (Charlson et al. 1992).

In addition to elements that cycle through the atmosphere, human activity also has increased the mobilization of certain rock-derived elements far above natural background rates. This effect is particularly strong for phosphorus as a result of the mining of phosphate rock for fertilizer (Smil 1990) and for trace elements like lead and cadmium (Turner et al. 1990).

Harvesting by humanity.—Human use of natural populations has direct and indirect effects on the pop-

ulations of particular species, and those effects can then ramify to affect other populations, communities, and ecosystems. One striking example is the extinction of the Pleistocene megafauna of the Americas contemporaneous with the arrival of humans (Martin 1984)—a massive change, and one that is mirrored in the multiple extinctions that occurred when humans later reached isolated oceanic islands (Olson and James 1984, Steadman and Kirch 1990, Wilson 1992). More recent examples include the effects of hunting pressure on forest fragments in the tropics (Dirzo and Miranda 1991), and the harvesting pressures in freshwater and marine systems that drive substantial top-down alterations in ecosystem structure and function (Carpenter et al. 1991, Paine 1993). These biotic changes often are presented as local rather than global changes, but the majority of Earth's land and coastal marine area has been affected by them.

Biological invasions by non-native species.—Human activity moves many species across long-standing biogeographic barriers; the consequent biological invasions blur the regional distinctiveness of Earth's biota (Mooney and Drake 1986, D'Antonio and Vitousek 1992). I have a personal interest in this component of change; having been born and brought up in the Hawaiian Islands, where invasions are dramatic and devastating; having been stimulated to become an ecologist in part by reading *The ecology of invasions by animals and plants* (Elton 1958); and having spent years studying the ecosystem consequences of biological invasions. However, invasions are not just an island phenomenon; human mobility has brought about a massive interchange of Earth's biota that in itself represents a significant global change, one that can be shown to have affected biological diversity and ecosystem function in a number of cases (e.g., Singer et al. 1984, Vitousek and Walker 1989). Clear examples include the spread of fire-adapted African and Eurasian grasses to the Americas, Australia, and Oceania (Whisenant 1990, D'Antonio and Vitousek 1992) and the massive additions of non-native organisms to near-shore marine and freshwater communities (e.g., Carleton and Geller 1993). Even the deciduous forests of eastern North America have experienced the progressive decline of the American chestnut (*Castanea dentata*), American elm (*Ulmus americana*), and more recently American beech (*Fagus grandifolia*) and flowering dogwood (*Cornus florida*) in all or parts of their range as a consequence of introduced diseases (McCormick and Platt 1980, Huenneke 1983; C. Canham, *personal communication*).

Overall

It is certain that a substantial number of components of global environmental change are now ongoing, and it is equally certain that they are human-caused. I am not suggesting that all of these changes are wholly and inevitably devastating and must be reversed at all costs;

my point is simply that we should recognize that these are indisputably human-caused global changes, and we should make certain that others recognize it as well. In contrast, the ecological consequences of these changes, the interactions among components of change, and the local and global feedbacks resulting from alterations to ecological systems are not known as well; they offer a rich opportunity for ecological and interdisciplinary research (Lubchenco et al. 1991). Moreover, these components of change themselves represent the primary forces driving climate change and the loss of biological diversity (Fig. 1).

CLIMATE CHANGE AND LOSS OF BIOLOGICAL DIVERSITY

I will not discuss changes in climate and biological diversity in detail here; they have been described well elsewhere (cf. Houghton et al. 1990, Peters and Lovejoy 1992, Wilson 1992, Kareiva et al. 1993). However, it is worth noting that in the long term, these components of change may become dominant—climate change because climate sets constraints for management and for the distribution and abundance of all species, and the loss of biological diversity because it represents the one wholly irreversible component of global environmental change. Changes in both climate and biological diversity are known with less certainty than are changes in CO₂ concentrations, global biogeochemistry, or land use, although the lack of certainty derives from rather different sources in each case.

Climate change.—The most important uncertainties in global climate change (specifically, change caused by anthropogenic enhancement of the greenhouse effect) derive from the fact that temperature is more variable both spatially and temporally than is CO₂ concentration, and so human-caused change is much harder to detect against natural background variations. Global temperatures have been observed to increase in recent years, but the increase cannot be tied unequivocally to enhancement of the greenhouse effect (Wigley and Barnett 1990). Further, the level of complexity of the Earth system, and our lack of knowledge of many important interactions and feedbacks in it, make it unrealistic to expect that within a decade, global circulation models (GCMs) will be able to represent correctly the details of climate in a 2 × CO₂ Earth, maps displaying the mean July temperature and precipitation for 2060 globally by GCM grid cell to the contrary. The development of detailed management plans for particular species or communities in a current model's calculation of a 2 × CO₂ climate therefore is not the best use of ecologists' time. Ecological and interdisciplinary research on the processes governing how populations, communities, and ecosystems interact with climate change is more likely to be rewarding.

While the detection and the details of anthropogenic climate change remain uncertain, it can be said with confidence that the increasing concentrations of CO₂

and other greenhouse gases will cause increasing climate change; both simple physics and the results of all GCMs agree on that. Moreover, both paleoecology and climate models demonstrate unequivocally that climatic change is not a smooth or linear process (Schneider and Thompson 1979, Broecker 1987, COHMAP 1988, Webb and Bartlein 1992); thresholds and positive as well as negative feedbacks appear to be dominant features of the climate system's response to change. Greenhouse forcing probably is greater now than it has been in the Pleistocene (Webb and Bartlein 1992) and it is increasing rapidly. Accordingly, we are entering uncharted territory where it is difficult to know where the thresholds and feedbacks will be, but most likely they will be there.

Biological diversity.—For the loss of biological diversity, our uncertainties derive from lack of detailed information about a change that we know to be occurring. Our knowledge base for biological diversity arguably is better for species than it is for genetically distinct populations or for diversity at the ecosystem or landscape levels, and yet the majority of species on Earth have not yet been catalogued. Indeed, the total number of species on Earth cannot be estimated within a factor of 3 with any real confidence (Ehrlich and Wilson 1991, Wilson 1992).

On the other hand, we can use species/area curves from island biogeography to estimate the *fraction* of species whose loss is entrained by loss of habitat (land use change), even without knowing how many species exist (Wilson 1992). The standard estimate that the loss of 50% of a habitat eventually causes the loss of ≈10% of the species it supports is crude, but it is empirically based, and it can be improved. Perhaps more convincingly, we can analyze recent rates of extinction carefully in relatively well-known groups such as birds; for example, Wilson (1992) estimates that ≈2000 of the 11 500 species of birds that were extant several hundred years ago are now extinct as a consequence of human activity.

Most importantly, we can emphasize that the loss of biological diversity truly is irreversible. If anthropogenic CO₂ emissions stopped entirely, Earth's atmosphere would return close to background concentrations in some centuries; most land use change could be reversed on about the same time scale (not that either change is likely, or desirable globally). However, the loss of species and genetically distinct populations is permanent; overall species diversity of Earth might be re-established in one or a few million years following a human-caused mass extinction, but the combinations of genes, biochemistry, behaviors, and interactions represented by today's diversity would be lost forever.

CAUSES OF GLOBAL CHANGE

The causes of global environmental change lie proximately in the industrial and agricultural activities of human society, and ultimately in the spectacular pop-

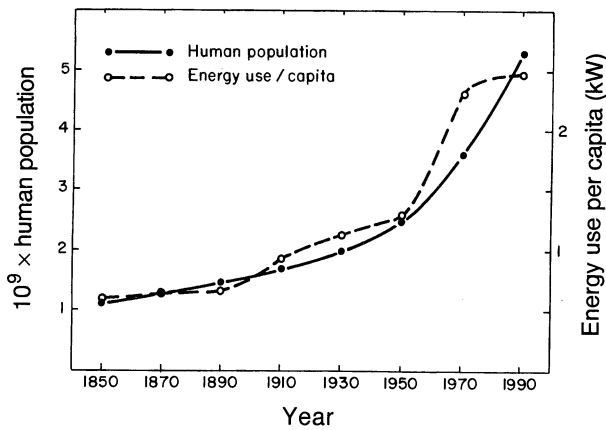


FIG. 12. The human population and per capita use of energy from 1850 to 1990. The product of these yields total energy use by the human population; population growth and growth in energy use per capita have contributed about equally to the 20-fold increase in humanity's use of energy since 1850. From information in Holdren (1991).

ulation growth of and increase in resource use by our species (Figs. 1, 12). It is clear that the current explosion of human activity is changing the way the world works, not just through an increasing exercise of dominion and control over nature, but also because the scale of our activity is so great that even our waste products loom large globally.

Moreover, the world will change a great deal more than it has already. Most likely the human population will double in the next century (Fig. 13). Energy use per capita in the most populous countries will increase, if living standards rise as they should (IPCC 1991, Johansson et al. 1993). The use of nitrogen fertilizer must increase more rapidly than does population in developing countries, or there will be widespread hunger, disease, and premature death (Smil 1991). Agriculture will continue to expand into marginal lands in regions with the most rapidly growing populations. However, the rates and extents of these changes are not fixed. It is possible that as a result of great effort, the human population will stop increasing before it doubles, then decline gradually (Fig. 13); at least equally likely, "business as usual" will prevail, and our population will triple before it stabilizes (or crashes). It is also possible that developing economies will follow an efficient and renewable-based path of energy development; more likely, the wasteful model of now-developed economies will be followed (Fig. 13).

WHAT CAN WE DO?

The pathways that human societies follow in population growth and resource use will make an enormous difference to the future state of humanity and of the Earth system, and anything that we can do individually or collectively to affect those paths is worth considering. I don't have the answers, but I do believe

that our developing understanding of the science of ecology; our recognition that while there may be "pure" ecology, there are no "pure" ecological systems; our ongoing development of multi- and interdisciplinary research and analysis through the International Geosphere-Biosphere Program and other efforts; and especially our teaching, are all crucial. In addition, I believe that ecologists should:

1. **Get active.**—As a science, we have spent some time thinking about what we *do* know; we should now spend some effort in communicating that to the public. As shown here, we know that several components of global change are real, ongoing, and human-caused; we can prove it. By speaking up, we can push public and academic discussion away from an enervating focus on uncertainty. It's reasonable to debate what should be done about particular components of global change; it's not reasonable to debate whether or not change is occurring.

2. **Get connected.**—Ecologists, indeed scientists generally, are good diagnosticians of human-environment

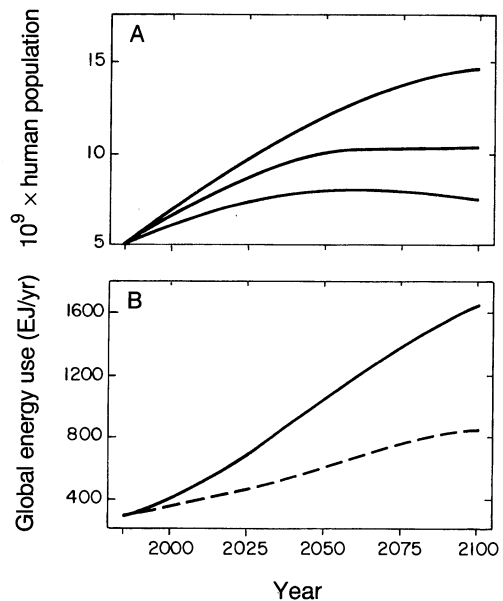


FIG. 13. Possible future pathways of human population growth (A, from United Nations Population Fund 1993) and overall energy use (B, from IPCC 1991) for the period 1985–2100. The middle projection for population is considered the most likely; it assumes that all nations will achieve a net reproductive rate of zero by early in the next century, although population sizes will continue to increase due to the effects of age structure. The lower curve assumes even more rapid achievement of zero net reproduction, while the upper assumes delays to the middle of the next century in achieving a zero net reproductive rate in some countries. For energy use (B), both projections assume high rates of economic growth; the upper one incorporates progressive but not revolutionary improvements in energy efficiency, while the lower assumes the accelerated introduction of energy-efficient technology. 1 EJ = 1 exajoule = 10^{18} J.

interactions; we aren't as good at managing or changing those interactions. Our colleagues outside the natural sciences, and outside academics, need our knowledge of how Earth is changing; we need theirs on what can be done about it. The effort we spend in finding non-scientists who will listen to what we have to say, the effort that goes into understanding their language and what they can teach us, is effort well spent. This is not an easy task; barriers of training, custom, reward systems, and institutional structure all are in the way. However, it must be done.

3. **Get real.**—The world has changed as a consequence of human action and will change more; we need to recognize, anticipate, and work with change at the same time as we work to minimize many of its consequences. One example: there is excellent ecological research being done on low-input, mixed cropping systems worldwide. That work has enormous potential for improving the lives of rural people on marginal lands, for maintaining the integrity of ecological systems in marginal areas, and for the development of our science. However, we also need to recognize that we live in an increasingly urban world and that much of the food for urban populations will be derived from intensive agriculture practiced on fertile lands. Ecologists could contribute a great deal to society (and to our science) by understanding and working to improve the efficiency and sustainability of such systems.

4. **Get involved in the Ecological Society.**—Through the Sustainable Biosphere Initiative (Lubchenco et al. 1991) and Office and through the Public Affairs Office, the Ecological Society of America has come a long way towards being a professional policy voice for ecology. The Society cannot take a stand on every environmental issue, but it can communicate what we know about ecological systems and global change: locally, regionally, nationally, and globally. It can also be a voice in the development of policies that affect the causes and consequences of global environmental change.

5. **Don't get down.**—We're the first generation with the tools to see how the Earth system is changed by human activity; at the same time, we're the last with the opportunity to affect the course of many of those changes. We cannot prevent global change. However, what we do *can* make a difference—individually by affecting particular human activities, collectively by helping to create policies and world-views that will affect which pathways of population growth and resource use human society follows. It is up to us.

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LITERATURE CITED

- Aber, J. D., J. M. Melillo, K. J. Nadelhoffer, J. Pastor, and R. D. Boone. 1991. Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. *Ecological Applications* 1:303–315.
- Ajayi, G. L., P. Ketner, and P. Duvigneaud. 1979. Terrestrial primary production and phytomass. Pages 129–182 in B. Bolin, E. T. Degens, and S. Kempe, editors. *The global carbon cycle*. John Wiley and Sons, Chichester, England.
- Arnolds, E. 1991. Decline of ectomycorrhizal fungi in Europe. *Agriculture, Ecosystems, and Environment* 35:209–244.
- Bacastow, R., and C. D. Keeling. 1974. Atmospheric carbon dioxide and radiocarbon in the natural carbon cycle: II. Changes from A.D. 1700 to 2070 as deduced from a geochemical model. Pages 86–135 in G. M. Woodwell and E. V. Pecan, editors. *Carbon and the biosphere*. National Technical Information Service, Springfield, Virginia, USA.
- Barnola, J. M., D. Raynaud, Y. S. Korotkevitch, and C. Lorius. 1987. Vostok ice core: a 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. *Annual Review of Ecology and Systematics* 21:167–196.
- Bazzaz, F. A., S. L. Miao, and P. M. Wayne. 1994. CO₂-induced enhancements of co-occurring tree species decline at different rates. *Oecologia* 96:478–482.
- Benedick, R. E. 1991. *Ozone diplomacy: new directions in safeguarding the planet*. Harvard University Press, Cambridge, Massachusetts, USA.
- Berendse, F. 1993. Ecosystem stability, competition, and nutrient cycling. Pages 409–431 in E. D. Schulze and H. A. Mooney, editors. *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, Germany.
- Berendse, F., R. Aerts, and R. Bobbink. 1993. Atmospheric nitrogen deposition and its impact on terrestrial ecosystems. Pages 104–121 in C. C. Vos and P. Opdam, editors. *Landscape ecology of a stressed environment*. Chapman and Hall, London, England.
- Berendse, F., and W. T. Elberse. 1990. Competition and nutrient availability in heathland and grassland ecosystems. Pages 93–116 in J. B. Grace and D. Tilman, editors. *Perspectives on plant competition*. Academic Press, San Diego, California, USA.
- Berg, B., H. Staaf, and B. Wessén. 1987. Decomposition and nutrient release in needle litter from nitrogen-fertilized Scots pine (*Pinus sylvestris*) stands. *Scandinavian Journal of Forest Research* 2:399–415.
- Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. *Journal of Applied Ecology* 28:28–41.
- Bobbink, R., L. Bik, and J. H. Willems. 1988. Effects of nitrogen fertilization on vegetation structure and dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grassland. *Acta Botanica Neerlandica* 37:231–242.
- Bobbink, R., and J. H. Willems. 1987. Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grassland: a threat to a species-rich ecosystem. *Biological Conservation* 40:301–314.
- Bowden, R. D., J. M. Melillo, and P. A. Steudler. 1991. Effects of nitrogen fertilizer on annual nitrous oxide fluxes from temperate forest soils in the northeastern United States. *Journal of Geophysical Research* 96:9321–9328.
- Broecker, W. S. 1987. Unpleasant surprises in the greenhouse. *Nature* 328:123–126.

- Brown, H. S., R. E. Kasperson, and S. Raymond. 1990. Trace pollutants. Pages 437–454 in B. L. Turner, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews, and W. B. Meyer, editors. *The earth as transformed by human action: global and regional changes in the biosphere over the past 300 years*. Cambridge University Press, Cambridge, England.
- Carleton, J. T., and J. B. Geller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. *Science* **261**:78–82.
- Carpenter, E. J., and D. G. Capone. 1983. Nitrogen fixation by marine *Oscillatoria* (*Trichodesmium*) in the world's oceans. Pages 65–103 in E. J. Carpenter and D. G. Capone, editors. *Nitrogen in the marine environment*. Academic Press, New York, New York, USA.
- Carpenter, S. R., S. G. Fisher, N. B. Grimm, and J. F. Kitchell. 1992. Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics* **23**:119–140.
- Carpenter, S. R., T. M. Frost, J. F. Kitchell, T. K. Kratz, D. W. Schindler, J. Shearer, W. G. Sprules, M. J. Vanni, and A. P. Zimmermann. 1991. Patterns of primary production and herbivory in 25 North American lake ecosystems. Pages 67–96 in J. Cole, G. Lovett, and S. Findlay, editors. *Comparative analysis of ecosystems*. Springer-Verlag, New York, New York, USA.
- Charlson, R. J., S. E. Schwartz, J. M. Hales, R. D. Cess, J. A. Coakley, Jr., J. E. Hansen, and D. J. Hofman. 1992. Climate forcing by atmospheric aerosols. *Science* **255**:423–430.
- COHMAP. 1988. Climate changes of the last 18,000 years: observations and model simulations. *Science* **241**:1043–1052.
- Crutzen, P. J., and M. O. Andreae. 1990. Biomass burning in the tropics: impact on atmospheric chemistry and biogeochemical cycles. *Science* **250**:1669–1678.
- Crutzen, P. J., and P. H. Zimmermann. 1991. The changing photochemistry of the atmosphere. *Tellus* **43**:136–151.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass-fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63–87.
- Detwiler, R. P., and C. A. S. Hall. 1988. Tropical forests and the global carbon cycle. *Science* **239**:43–47.
- Dickenson, R. E. 1991. Global change and terrestrial hydrology—a review. *Tellus* **43**:176–181.
- Dirzo, R., and A. Miranda. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. Pages 273–287 in P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, editors. *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. John Wiley and Sons, New York, New York, USA.
- 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.
- Ehrlich, P. R., and G. C. Daily. 1993. Population extinction and saving biodiversity. *Ambio* **22**:64–68.
- Ehrlich, P. R., and E. O. Wilson. 1991. Biodiversity studies: science and policy. *Science* **253**:758–762.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, England.
- Fajer, E. D., M. D. Bowers, and F. A. Bazzaz. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. *Science* **243**:1198–1200.
- Fajer, E. D., M. D. Bowers, and F. A. Bazzaz. 1991. The effects of enriched CO₂ atmospheres on the buckeye butterfly, *Junonia coenia*. *Ecology* **72**:751–754.
- Farquhar, G. D., J. R. Ehleringer, and B. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology* **40**:503–537.
- Farquhar, G. D., M. H. O'Leary, and J. A. Berry. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology* **9**:121–137.
- Field, C. B., F. S. Chapin, III, P. A. Matson, and H. A. Mooney. 1992. Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annual Review of Ecology and Systematics* **23**:201–236.
- Fishman, J., K. Fakhruzzaman, B. Cros, and D. Nganga. 1991. Identification of widespread pollution in the southern hemisphere deduced from satellite analyses. *Science* **252**:1693–1696.
- Fung, I. Y. 1993. Models of oceanic and terrestrial sinks of anthropogenic CO₂: a review of the contemporary carbon cycle. Pages 166–189 in R. S. Oremland, editor. *Biogeochemistry of global change: radiatively active trace gases*. Chapman and Hall, New York, New York, USA.
- Fung, I. Y., J. John, J. Lerner, E. Matthews, M. Prather, L. P. Steele, and P. J. Fraser. 1991. Three-dimensional model synthesis of the global methane cycle. *Journal of Geophysical Research* **96**:13 033–13 065.
- Fung, I. Y., C. J. Tucker, and K. C. Prentice. 1987. Application of advanced very high resolution radiometer vegetation index to study atmosphere-biosphere exchange of CO₂. *Journal of Geophysical Research* **92**:2999–3015.
- Heil, G. W., and W. H. Diemont. 1983. Raised nutrient levels change heathland into grassland. *Vegetatio* **53**:113–120.
- Holdren, J. P. 1991. Population and the energy problem. *Population and Environment* **12**:231–255.
- Holsinger, K. E. 1993. The evolutionary dynamics of fragmented plant populations. Pages 198–216 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Houghton, J. T., G. J. Jenkins, and J. J. Ephraums, editors. 1990. *Climate change: the IPCC scientific assessment*. Cambridge University Press, Cambridge, England.
- Houghton, R. A., R. D. Boone, J. R. Fruci, J. E. Hobbie, J. M. Melillo, C. A. Palm, B. J. Peterson, G. R. Shaver, G. M. Woodwell, B. Moore, and D. L. Skole. 1987. The flux of carbon from terrestrial ecosystems to the atmosphere in 1980 due to changes in land use: geographic distribution of the global flux. *Tellus* **39B**:122–139.
- Huenneke, L. F. 1983. Understory response to gaps caused by the death of *Ulmus americana* in central New York. *Bulletin of the Torrey Botanical Club* **110**:170–175.
- Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* **71**:478–491.
- Hunt, R., D. W. Hand, M. A. Hannah, and A. M. Neal. 1991. Response to CO₂ enrichment in 27 herbaceous species. *Functional Ecology* **5**:410–421.
- IPCC (Intergovernmental Panel on Climate Change). 1991. *Climate change: the IPCC response strategies*. Island Press, Washington, D.C., USA.
- Johansson, T. B., H. Kelly, A. K. N. Reddy, and R. H. Williams. 1993. *Renewable energy: sources for fuels and electricity*. Island Press, Washington, D.C., USA.
- Johnson, D. W., and S. E. Lindberg. 1992. *Atmospheric deposition and forest nutrient cycling*. Springer-Verlag, Berlin, Germany.
- Kareiva, P. M., J. G. Kingsolver, and R. B. Huey, editors. 1993. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Kates, R. W., B. L. Turner, and W. C. Clark. 1990. The great transformation. Pages 1–17 in B. L. Turner, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews, and W. B. Meyer, editors. *The earth as transformed by human action*. Cambridge University Press, Cambridge, England.

- Kauppi, P. E., K. Mielikäinen, and K. Kuusela. 1992. Biomass and carbon budget of European forests, 1971 to 1990. *Science* **256**:70-74.
- Keeling, C. D., and T. P. Whorf. 1991. Mauna Loa. Pages 12-15 in T. A. Boden, R. J. Sepanski, and F. W. Stoss, editors. A compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Keeling, C. D., R. B. Bacastrow, A. F. Carter, S. C. Piper, T. P. Whorf, M. Heimann, W. G. Mook, and H. Roeloffzen. 1989a. A three-dimensional model of atmospheric CO₂ transport based on observed winds: 1. Analysis of observational data. Pages 165-236 in D. H. Peterson, editor. Aspects of climate variability in the Pacific and the western Americas. Geophysical Monographs. American Geophysical Union, Washington, D.C., USA.
- Keeling, C. D., S. C. Piper, and M. Heimann. 1989b. A three-dimensional model of atmospheric CO₂ transport based on observed winds: 4. Mean annual gradients and interannual variations. Pages 305-363 in D. H. Peterson, editor. Aspects of climate variability in the Pacific and the western Americas. Geophysical Monographs. American Geophysical Union, Washington, D.C., USA.
- Keller, M., D. J. Jacob, S. C. Wofsy, and R. C. Hariss. 1991. Effects of tropical deforestation on global and regional atmospheric chemistry. *Climatic Change* **19**:145-158.
- Keller, M., W. A. Kaplan, and S. C. Wofsy. 1986. Emissions of N₂O, CH₄, and CO₂ from tropical soils. *Journal of Geophysical Research* **91**:11 791-11 802.
- Khalil, M. A. K., and R. A. Rasmussen. 1992. The global sources of nitrous oxide. *Journal of Geophysical Research* **97**:14 651-14 660.
- Lashof, D. A., and D. R. Ahuja. 1990. Relative contributions of greenhouse gas emissions to global warming. *Nature* **344**:529-531.
- Lean, J., and D. A. Warrilow. 1989. Simulation of the regional climatic impact of Amazon deforestation. *Nature* **342**:411-413.
- Loader, C., and H. Damman. 1991. Nitrogen content of food plants and vulnerability of *Pieris rapae* to natural enemies. *Ecology* **72**:1586-1590.
- Logan, J. A. 1985. Tropospheric ozone: seasonal behavior, trends, and anthropogenic influence. *Journal of Geophysical Research* **90**:10 463-10 482.
- Lubchenco, J., A. Olson, L. Brubaker, S. Carpenter, M. Holland, S. Hubbell, S. Levin, J. MacMahon, P. Matson, J. Melillo, H. Mooney, C. Peterson, H. Pulliam, L. Real, P. Regal, and P. Risser. 1991. The sustainable biosphere initiative: an ecological research agenda. *Ecology* **72**:371-412.
- Ludwig, D. F. 1989. Anthropogenic ecosystems. *Bulletin of the Ecological Society of America* **70**:12-14.
- Marland, G., T. A. Boden, R. C. Griffin, S. F. Hurang, P. Kancircuk, and T. R. Nelson. 1988. Estimates of CO₂ emissions from fossil fuel burning and cement manufacturing using the United Nations environmental resource statistics and United States Bureau of Mines cement manufacturing data. Carbon Dioxide Information and Analysis Center, Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Martin, P. S. 1984. Prehistoric overkill: the global model. Pages 354-403 in P. S. Martin and R. G. Klein, editors. Quaternary extinctions: a prehistoric revolution. University of Arizona Press, Tucson, Arizona, USA.
- Matson, P. A., and P. M. Vitousek. 1990. Ecosystem approach to a global nitrous oxide budget. *BioScience* **40**:667-672.
- Matson, P. A., P. M. Vitousek, J. Ewel, M. Mazzarino, and G. Robertson. 1987. Nitrogen transformations following tropical forest felling and burning on a volcanic soil. *Ecology* **68**:491-502.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* **11**: 119-161.
- McCormick, J. F., and R. B. Platt. 1980. Recovery of an Appalachian forest following the chestnut blight, or, Catherine Keever, you were right! *American Midland Naturalist* **104**:264-273.
- McElroy, M. B., and S. C. Wofsy. 1986. Tropical forests: interactions with the atmosphere. Pages 33-60 in G. T. Prance, editor. Tropical forests and the world atmosphere. Westview, Boulder, Colorado, USA.
- Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore, C. J. Vorosmarty, and A. L. Schloss. 1993. Global climate change and terrestrial net primary production. *Nature* **363**: 234-240.
- Melillo, J. M., P. A. Steudler, J. D. Aber, and R. D. Bowden. 1989. Atmospheric deposition and nutrient cycling. Pages 263-280 in M. O. Andreae and D. S. Schimel, editors. Exchange of trace gases between terrestrial ecosystems and the atmosphere. John Wiley and Sons, London, England.
- Meyer, W. B., and B. L. Turner. 1992. Human population growth and global land-use/cover change. *Annual Review of Ecology and Systematics* **23**:39-62.
- Mooney, H. A., B. G. Drake, R. J. Luxmoore, W. C. Oechel, and L. F. Pitelka. 1991. Predicting ecosystem responses to elevated CO₂ concentrations. *BioScience* **41**:96-104.
- Mooney, H. A., and J. A. Drake, editors. 1986. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.
- Myers, N. 1993. Questions of mass extinction. *Biodiversity and Conservation* **2**:2-17.
- Norby, R. J., J. Pastor, and J. M. Melillo. 1986. Carbon-nitrogen interactions in CO₂-enriched white oak: physiological and long-term perspectives. *Tree Physiology* **2**:233-241.
- NRC (National Research Council). 1993. The role of terrestrial ecosystems in global change. National Academy Press, Washington, D.C., USA.
- Olson, J. S., J. A. Watts, and A. J. Allison. 1983. Carbon in live vegetation of major world ecosystems. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Olson, S. L., and H. F. James. 1984. The role of Polynesians in the extinction of the avifauna of the Hawaiian Islands. Pages 768-780 in P. S. Martin and R. G. Klein, editors. Quaternary extinctions: a prehistoric revolution. University of Arizona Press, Tucson, Arizona, USA.
- Paine, R. T. 1993. A salty and salutatory perspective on global change. Pages 347-355 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, Massachusetts, USA.
- Patterson, D. T., E. P. Flint, and J. L. Beyers. 1984. Effects of CO₂ enrichment on competition between a C₄ weed and a C₃ crop. *Weed Science* **32**:101-105.
- Penner, J. E., R. E. Dickenson, and C. A. O'Neill. 1992. Effects of aerosol from biomass burning on the global radiation budget. *Science* **256**:1432-1434.
- Peters, R. L., and T. E. Lovejoy, editors. 1992. Global warming and biological diversity. Yale University Press, New Haven, Connecticut, USA.
- Poorter, H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO₂ concentration. *Vegetatio* **104/105**:77-97.
- Prinn, R., D. Cunnold, R. Rasmussen, F. Simmonds, F. Alyea, A. Crawford, P. Fraser, and R. Rosen. 1990. Atmospheric trends and emissions of nitrous oxide deduced from ten years of ALE-GAGE data. *Journal of Geophysical Research* **95**:18 369-18 385.
- Raynaud, D., J. Jouzel, J. M. Barnola, J. Chappellaz, R. J. Delmas, and C. Lorius. 1993. The ice core record of greenhouse gases. *Science* **259**:926-934.

- Redford, K. H. 1992. The empty forest. *BioScience* **42**:412-422.
- Rodhe, H. 1990. A comparison of the contributions of various gases to the greenhouse effect. *Science* **248**:1217-1219.
- Rowland, F. S. 1989. Chlorofluorocarbons and the depletion of atmospheric ozone. *American Scientist* **77**:36-45.
- Schindler, D. S. 1988. Effects of acid rain on freshwater ecosystems. *Science* **239**:149-157.
- Schlesinger, W. H. 1991. Biogeochemistry: an analysis of global change. Academic Press, San Diego, California, USA.
- Schlesinger, W. H., and A. E. Hartley. 1991. A global budget for atmospheric NH₃. *Biogeochemistry* **15**:191-211.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. *Science* **247**:1043-1048.
- Schneider, S. H. and S. L. Thompson. 1979. Ice ages and orbital variations: some simple theory and modeling. *Quaternary Research* **12**:188-203.
- Schulze, E.-D. 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest. *Science* **244**:776-783.
- Shukla, J., C. Nobre, and P. Sellers. 1990. Amazonian deforestation and climate change. *Science* **247**:1322-1324.
- Siegenthaler, U., and H. Oeschger. 1987. Biospheric CO₂ emissions during the past 200 years reconstructed by deconvolution of ice core data. *Tellus* **39B**:140-154.
- Siegenthaler, U., and J. L. Sarmiento. 1993. Atmospheric carbon dioxide and the ocean. *Nature* **365**:119-126.
- Singer, F. J., W. T. Swank, and E. E. C. Clebsch. 1984. Effects of wild pig rooting in a deciduous forest. *Journal of Wildlife Management* **48**:464-473.
- Skole, D., and C. J. Tucker. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* **260**:1905-1910.
- Smil, V. 1990. Nitrogen and phosphorus. Pages 423-436 in B. L. Turner II, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews, and W. B. Meyer, editors. *The earth as transformed by human action*. Cambridge University Press, Cambridge, England.
- Smil, V. 1991. Population growth and nitrogen: an exploration of a critical existential link. *Population and Development Review* **17**:569-601.
- Smith, R. C., B. B. Prézelin, K. S. Baker, R. R. Bidigare, N. P. Boucher, T. Coley, D. Karentz, S. MacIntyre, H. A. Matlick, D. Menzies, M. Ondrusek, Z. Wan, and K. J. Waters. 1992. Ozone depletion: ultraviolet radiation and phytoplankton biology in Antarctic waters. *Science* **255**:952-959.
- Smith, S. D., B. R. Strain, and T. D. Sharkey. 1987. Effects of CO₂ enrichment on four Great Basin grasses. *Functional Ecology* **1**:139-143.
- Smith, S. V., and R. W. Buddemeier. 1992. Global change and coral reef ecosystems. *Annual Review of Ecology and Systematics* **23**:89-118.
- Soderlund, R., and T. H. Rosswall. 1982. The nitrogen cycles. Pages 62-81 in O. Hutzinger, Editor. *Handbook of environmental chemistry*. Springer-Verlag, Berlin, Germany.
- Solomon, S. 1990. Progress towards a quantitative understanding of Antarctic ozone depletion. *Nature* **347**:347-354.
- Steadman, D. W., and P. V. Kirch. 1990. Prehistoric extinctions of birds on Mangara, Cook Islands, Polynesia. *Proceedings of the National Academy of Sciences* **87**:9605-9609.
- Stuiver, M. 1978. Atmospheric carbon dioxide and carbon reservoir changes. *Science* **199**:253-258.
- Suess, H. 1955. Radiocarbon concentration in modern wood. *Science* **122**:415-417.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* **57**:189-214.
- Turner, B. L. II, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews, and W. B. Meyer, editors. 1990. *The earth as transformed by human action*. Cambridge University Press, Cambridge, England.
- Turner, R. E., and N. N. Rabelais. 1991. Changes in Mississippi River water quality in this century. *BioScience* **41**:140-147.
- Uhl, C., and J. B. Kauffman. 1990. Deforestation, fire susceptibility and potential tree responses to fire in the eastern Amazon. *Ecology* **71**:437-449.
- United Nations Population Fund. 1993. *The state of world population 1993*. UNFPA/United Nations Population Fund, New York, New York, USA.
- van Vuuren, M. M. I., R. Aerts, F. Berendse, and W. D. Visser. 1992. Nitrogen mineralization in heathland ecosystems dominated by different plant species. *Biogeochemistry* **16**:151-166.
- Vitousek, P. M. 1983. Nitrogen turnover in a ragweed-dominated first-year old-field in southern Indiana. *American Midland Naturalist* **110**:46-53.
- . 1992. Global environmental change: an introduction. *Annual Review of Ecology and Systematics* **23**:1-14.
- Vitousek, P. M., P. R. Ehrlich, A. H. Ehrlich, and P. A. Matson. 1986. Human appropriation of the products of photosynthesis. *BioScience* **36**:368-373.
- Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* **13**:87-115.
- Vitousek, P. M., and P. A. Matson. 1993. Agriculture, the global nitrogen cycle, and trace gas flux. Pages 193-208 in R. S. Oremland, editor. *The biogeochemistry of global change: radiative trace gases*. Chapman and Hall, New York, New York, USA.
- Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i. Plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* **59**:247-265.
- Watson, R. T., H. Rodhe, H. Oeschger, and U. Siegenthaler. 1990. Greenhouse gases and aerosols. Pages 1-40 in J. T. Houghton, G. J. Jenkins, and J. J. Ephraums, editors. *Climate change: the IPCC scientific assessment*. Cambridge University Press, Cambridge, England.
- Webb, T. I., and P. J. Bartlein. 1992. Global changes during the last three million years: climatic controls and biotic responses. *Annual Review of Ecology and Systematics* **23**:141-174.
- Whisenant, S. 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. Pages 4-10 in *Proceedings from the symposium on cheatgrass invasion, shrub dieoff and other aspects of shrub biology and management*. U.S. Forest Service General Technical Report INT-276.
- Wigley, T. M. L. 1989. Possible climate change due to SO₂-derived cloud condensation nuclei. *Nature* **339**:365-367.
- Wigley, T. M. L., and T. P. Barnett. 1990. Detection of the greenhouse effect in the observations. Pages 243-255 in J. T. Houghton, G. J. Jenkins, and J. J. Ephraums, editors. *Climate change: the IPCC scientific assessment*. Cambridge University Press, Cambridge, England.
- Wilson, E. O. 1992. *The diversity of life*. Norton, New York, New York, USA.