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THE RELATIONSHIP BETWEEN LAND-USE CHANGE AND CLIMATE CHANGE

Virginia H. Dale

Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831-6038 USA

Abstract. Land-use change is related to climate change as both a causal factor and a major way in which the effects of climate change are expressed. As a causal factor, land use influences the flux of mass and energy, and as land-cover patterns change, these fluxes are altered. Projected climate alterations will produce changes in land-cover patterns at a variety of temporal and spatial scales, although human uses of the land are expected to override many effects. A review of the literature dealing with the relationship between land-use change and climate change clearly shows that (1) in recent centuries land-use change has had much greater effects on ecological variables than has climate change; (2) the vast majority of land-use changes have little to do with climate change or even climate; and (3) humans will change land use, and especially land management, to adjust to climate change and these adaptations will have some ecological effects. Therefore, an understanding of the nonclimatic causes of land-use change (e.g., socioeconomics and politics) are necessary to manage ecological functions effectively on regional and global scales.

Key words: climate change, relation to land-use changes; forests, affected by climate change; global circulation models; global models of vegetation change; greenhouse gases, sources of; human-induced climate change; land-cover changes; land-use changes, non-climatic causes; land-use change and climate change; modeling carbon flux.

Introduction

During the next few decades, global ecological changes are expected to have major impacts on ecological, social, economic, and political aspects of human society. The ecological impacts include changes to biodiversity, productivity, migration, and sustainability. Climate and land-use changes are two major global ecological changes predicted for the future. Heretofore, causes and consequences of human-induced climate change and land-use activities have largely been examined independently (but see Turner et al. 1993). However, climate change and land use affect each other.

Land-use activity contributes to climate change, and changes in land-cover patterns are one way in which the effects of climate change are expressed (Fig. 1). *Land use* refers to the management regime humans impose on a site (e.g., plantations or agroforestry), whereas *land cover* is a descriptor of the status of the vegetation at a site (e.g., forest or crop). *Land-use effects on climate change* include both implications of land-use change on atmospheric flux of CO_2 and its subsequent impact on climate and the alteration of climate-change impacts through land management. *Effects of climate change on land use* refers to both how land use might be altered by climate change and what land management strategies would mitigate the negative effects of climate change.

Many resources are being expended to study causes and effects of climate change (Houghton et al. 1990). However, there is concern that the results of these studies may not be relevant to decision makers because the research does not deal with major factors influencing climate change impacts (OTA 1993: p. 111). The Sustainable Biosphere Initiative of the Ecological Society of America therefore commissioned this paper in order to evaluate the importance of land use in considering climate change impacts.

The purpose of this paper is to review current practice in assessing and modeling land-use change as it relates to climate change and to identify areas in which research is needed to supply critical information for such assessments and models. The emphasis is on global and regional landscapes, for these are the spatial scales at which land-use and climate-change interactions occur. The most productive research areas for enhancing our understanding of global ecological changes are identified.

Land-Use Contributions to Climate Change

Human activities influence climate change by altering the distribution of ecosystems and their associated fluxes of energy (e.g., latent and sensible heat and ra-

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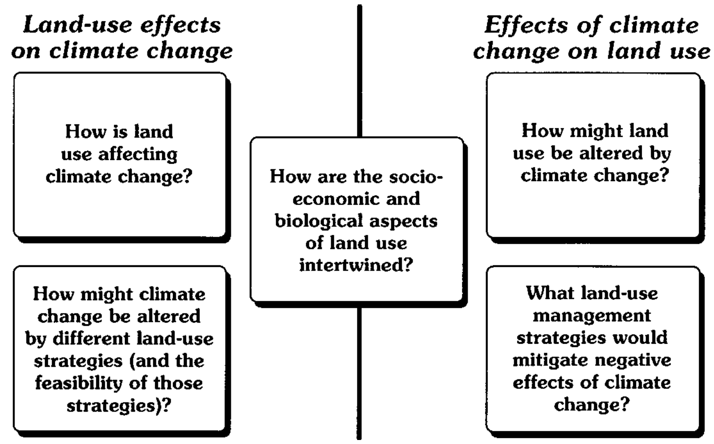

FIG. 1. Relationship between land-use change and climate change.

diative exchanges and mass (e.g., water vapor, trace gases, and particulates). Here, we focus on how land-use change can affect those fluxes.

At the landscape scale, changes in land-cover patterns can directly impact energy and mass fluxes. For example, when large areas of forests are cleared, reduced transpiration results in less cloud formation, less rainfall, and increased drying. Simulations of the deforestation of Amazonia indicate that evapotranspiration and forests would be replaced by either desert or pasture (Dickinson 1991). Although the model results are variable, they do indicate the sensitivity of regional climate to the type and density of vegetation.

Both field studies (Segal et al. 1988) and model simulations (Pielke et al. 1997) suggest that spatially alternating bands of transpiring vegetation with dry soil on a scale of tens of kilometers can influence atmospheric circulation and cloud formation. Because land-surface characteristics influence surface temperatures and latent heat flux, the contrasting characteristics of adjacent land-cover types can induce convection that enhances clouds and precipitation.

Increased albedo and its subsequent effects on climate also result from changes in land-surface characteristics (Dickinson 1991, Sagan et al. 1979). Changes in land cover can alter the reflectance of the earth's surface and induce local warming or cooling; generally, as albedo increases, surface temperatures decline. Desertification can occur when overgrazing of savanna vegetation alters surface albedo and surface water budget and thus changes the regional circulation and precipitation patterns. Overgrazing can also increase the amount of suspended dust that, in turn, causes radiative cooling and a decline in precipitation.

Increased atmospheric concentration of greenhouse gases that result in global climate change (Ramanathan 1988) is discussed at length below because (1) a wealth of data is available and (2) it illustrates how changes in particular land-cover categories can dominate the impact. Table 1 summarizes the industrial and biotic sources of the primary greenhouse gases: carbon dioxide, methane, nitrous oxide, and chlorofluorocarbons. At the global scale, human activities influence the greenhouse effect by releasing greenhouse gases into the atmosphere and by changing the patterns of carbon storage through land-use activities. The discussion below focuses on effects of greenhouse-gas emissions due to land use rather than those due to industrial activities.

Carbon dioxide

The anthropogenic release of CO_2 has increased greatly since the industrial age began and fossil fuels began being intensively used as an energy source. Currently, ≈61% of the anthropogenic greenhouse forcing can be attributed to CO_2 increases (Shine et al. 1990). During the past century (1850 to 1980), fossil fuels accounted for the release of 150–190 Pg of carbon (PgC) (Rotty 1987), and land-use change accounted for the release of 90–120 PgC (Houghton and Skole 1990) with land-use changes making the greater contribution prior to about 1910 (Fig. 2).

Houghton et al. (1983) estimated that the world's total forested area in 1700 was 6042×10^6 ha. Dixon et al. (1994) estimated that the area in 1987–1990 was 4165×10^6 ha. Comparing these two figures leads one to believe that >30% of the world's forests have been cleared since 1700 (not including areas that were cleared and grew back to forests). This large-scale deforestation has resulted largely from agriculture expansion. World Resources Institute (1992) estimates that 1478×10^6 ha were in cropland and 3323×10^6 ha were in permanent pasture by 1989. These areas constitute 11% and 25% of the world's land area, respectively, and represent increases of 2.2% and 0.1% since 1979. During that time the area in forest decreased by 1.8%, to 4095×10^6 ha. Deforestation and the associated agricultural expansion are particularly important because clearing induces carbon losses from the soil and vegetation, and forests contain ≈90% of

TABLE 1. Annual global emissions of the primary greenhouse gases, from industrial and biotic sources.

Gas	Contribution to greenhouse effect (%)†: Since start of industrial age	Contribution to greenhouse effect (%)†: During last decade (1980–1990)	Atmospheric life-time (yr)‡	Global warming potential relative to CO_2 over 500 yr†	Source	Annual emissions§	Share (%) of total greenhouse-gas emissions‖
CO_2	61	56	50–200	1	Industrial	5800 Tg C¶	78
					Biotic		
					Tropical deforestation	600–2600 Tg C#	22
CH_4	15	11	10	9	Industrial	80 (45–100) Tg C	16
					Biotic		
					Natural wetlands	120 (100–200) Tg C††	24
					Ruminant fermentation	80 (65–100) Tg C	16
					Rice paddies	50 (25–70) Tg C††	10
					Landfills	40 (20–70) Tg C	8
					Biomass burning	30 (20–80) Tg C††	6
					Oceans and freshwater	30 (6–45) Tg C††	6
					Animal wastes	30 Tg C††	6
					Sewage	30 Tg C††	6
					Termites	10 (10–100) Tg C††	2
N_2O	4	6	150	190	Industrial	0.1–0.3 Tg N	3
					Fertilizer	0.1–2.2 Tg N	15
					Biotic		
					Tropical soils	2.2–3.7 Tg N	39
					Temperate soils	0.7–1.5 Tg N	15
					Biomass burning‡‡	0.02–0.2 Tg N	2
					Oceans	1.4–2.6 Tg N	27
					Unknown	??	
CFCs	12	24	65–130	510–4500	Industrial	1.090 Tg	100
					Biotic	0 Tg	0

Note: The greenhouse gases considered here are only those directly released as a result of human activities. Tropospheric ozone, which is formed as a result of other emissions, contributes another 5% to the total. The major greenhouse gas, water vapor, is not directly under human control but will increase in response to global warming.

† Shine et al. (1990).

‡ Houghton et al. (1990).

§ Watson et al. (1990) unless indicated otherwise. Note: 1 Tg = 10^{12} g.

‖ Percentages are calculated using the mean or median value. Rounding may cause the sum to not be 100%.

¶ Marland (1990).

Houghton et al. (1987), Detwiler and Hall (1988), and Hall and Uhlig (1990).

†† Neue (1993).

‡‡ Kuhlbusch et al. (1991) demonstrate that significant quantities of molecular nitrogen (5–20 Tg N/yr) are also released by biomass burning.

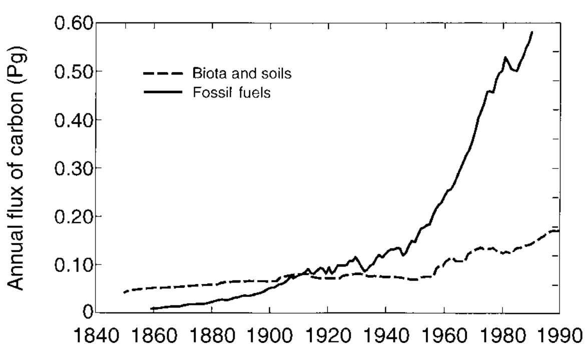

FIG. 2. Historical contributions to atmospheric CO_2 concentrations from greenhouse gases (Marland et al. 1989) and land-use change (Houghton 1994). (Note: 1 Pg = 10^{15} g = 10^9 metric tons.)

the carbon stored in global vegetation (calculated from the estimated biomass in forests compared to that in all vegetation using data in Whittaker and Likens [1973]).

Carbon releases from terrestrial ecosystems that result from land-use change are difficult to quantify accurately because of uncertainties in (1) the rates of land clearing and abandonment, (2) the estimates of the carbon stored in the vegetation and soils of managed and unmanaged ecosystems, and (3) the fate of carbon subsequent to land-use changes. It is clear that the location of major land clearing and abandonment has changed with time and that the form and magnitude of the carbon released from terrestrial ecosystems have also varied.

Before 1930, the primary biotic contributions of CO_2

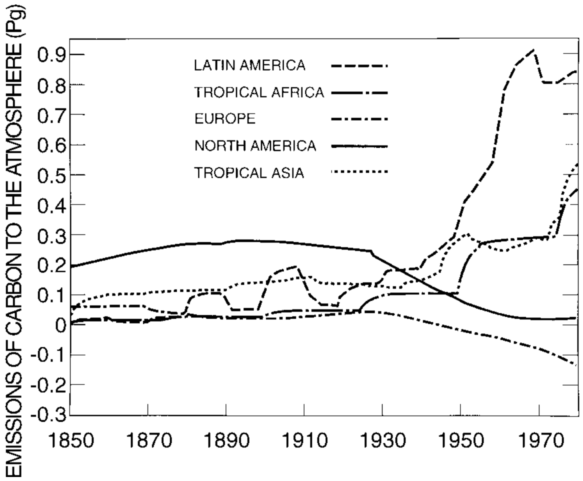

FIG. 3. Terrestrial release of CO_2, by continent, due to land-use change. Reprinted from Dale (1994: Fig. 2) with permission of Springer-Verlag, New York, New York, USA.

were from the clearing of the temperate forests in the northern hemisphere and from the losses of soil carbon because of agriculture (Fig. 3). Some of these temperate areas are now reforested, and today's 112×10^6 ha of forest plantations worldwide constitute a carbon sink as the growing trees rapidly accumulate carbon (Dixon et al. 1994). Currently, the most important changes in CO_2 storage are caused by tropical deforestation; $\approx 15.4 \times 10^6$ ha are being cleared each year (Table 2). Although large regions of the tropics are set aside for protection from forest harvesting, the degree to which forests are protected depends on political pressures within a government, population pressures within a country, the availability of other resources to sustain the lives and livelihoods of that population, economic pressures from within and without the country, the political stability of governments, the number and ability of law enforcement agents to uphold the laws, and the respect the citizens have for the laws. These factors are unpredictable in most developing countries.

Natural wetlands can also process and transfer significant amounts of CO_2 (Armentano 1980) and other greenhouse gases. The reduction of natural wetlands, largely caused by drainage for agriculture, has resulted in a reduction of a biotic source of CO_2. A computer model indicated that by 1990 28–38% of the temperate-zone carbon source had been eliminated by agricultural drainage (Armentano and Menges 1986).

Retrospectively estimating land clearing and wetland conversion has been complicated by the historic use of a large number of land-cover classification systems. Richards and Flint (1994) found changes in the classification system to be the major difficulty in compiling their 100-yr history of land-use changes in south and southeast Asia. A proposed vegetation classification logic for remote-sensing data (Running et al. 1994) and recent computer advances with geographic information systems (GISs) make estimation of potential vegetation repeatable and quantifiable (Iverson et al. 1994). Remote-sensing imagery makes it possible to measure land-cover patterns since 1972 (when LANDSAT was first established), and current remote sensing can detect and distinguish a diversity of land-cover types (Townshend et al. 1991).

But knowing the current and historic land cover is not enough. The amount of carbon stored in the terrestrial system also affects carbon releases, and the amount and form of carbon stored in vegetation and soils varies by vegetation type, prevailing temperature and precipitation conditions, prior disturbances, the state of recovery, and current management. The Terrestrial Carbon Model (Houghton et al. 1983) provides a basis for ascertaining the kind and status of data needed to estimate the amount of and changes in vegetal and soil carbon. That model assumes that carbon in vegetation and soils declines with disturbances, and recovers a portion of its initial value if the disturbance ceases and does not recur. The data required for the model have been derived for major vegetation types for each of the continents, and a complete description

TABLE 2. Rates of annual deforestation in the tropics. Values are from FAO (1993) unless indicated otherwise.

	No. of coun-tries	Land area (10^6 ha)	Forested land (10^6 ha)			Annual defor-estation, 1981–1991		Protected areas (10^6 ha)		Plantation areas in 1990 (10^6 ha)‡	
			1700	1980	1990	10^6 ha†	%/yr	Forested conser-vation areas	Closed forests	Indus-trial	Nonin-dustrial
Tropical Africa	40	2236.1	1358§	568.6	527.6	4.1	0.7	39.3	9.3‖	1.4	1.6
Tropical Asia and Pacific	17	892.1	855§	349.6	310.6	3.9	1.2	42.3	17.5‖	9.2	23.1
Tropical Latin America and Caribbean	33	1650.1	1445†	992.2	918.1	7.4	0.8	125.9	14.0‖	5.1	3.5
Total	90	4778.3	3658	1910.4	1756.3	15.4	2.7	207.5	40.8	15.7	28.2

† Entries are the average per year of the total for 1981–1991.
‡ Industrial refers to commercial forests; nonindustrial refers to privately owned forests.
§ Houghton et al. (1983).
‖ World Resources Institute (1992).

TABLE 3. Parameters used in the Terrestrial Carbon Model (Houghton et al. 1983) to define the changes in the carbon in vegetation and soils during the transformation of a natural ecosystem to agriculture, during cultivation, and following abandonment.

Category	Parameter
Carbon in vegetation	Undisturbed vegetation ''Recovered'' systems Agricultural crops Pasture Tree crops Degraded lands
Carbon in soils	Undisturbed systems ''Recovered'' systems Croplands Pasture Cleared systems (after the initial rapid decline) Degraded lands
Time required for an abandoned system to ''recover''	Carbon in vegetation Soil carbon
Fraction of carbon assigned to decay pools after clearing	Released immediately Released within 1 yr Released over 10 yr Released over 100 or more years
Decay of wood	k values for exponential equation†
Carbon in agricultural soils	Minimum value
Soil carbon decay	Time required for initial, rapid change in soil carbon following clearing
Time required for carbon in soil to reach minimum value	Croplands Pasture

† Where wood decay is given by the following equation: $B_t = B_0 e^{kt}$ where t = time, B_t is the biomass of wood at time t, and $k < 0$.

of these parameters is provided by Houghton et al. (1983) (Table 3). Both the remote-sensing-imagery and the Terrestrial Carbon Model approaches suffer from the same Achilles heel. They both rely on the determination of a single value to represent a vegetation type within a region. However, the basic parameters may vary from vegetation type to vegetation type more than is currently documented.

It is possible is gain an understanding of the sort of data needed to estimate carbon flux by reviewing the parameters used in the Terrestrial Carbon Model (Table 3). Carbon in the vegetation has been estimated in two ways, both of which assume that carbon constitutes about half of vegetation biomass (Reichle et al. 1973). Brown and Lugo (1992) point out that ecologists typically measure biomass in pristine forests, whereas foresters typically obtain biomass estimates from large statistical samples of forests that include a variety of stand histories. Thus, the ecologists' measures of biomass are generally higher than the foresters', and the foresters' estimates characterize average conditions of existing forests more accurately.

In computer models of regional land-use change (e.g., Houghton et al. 1983), carbon flux is modeled in a simplified manner. Carbon in ''recovered'' ecosystems is generally modeled as a portion of the biomass in the original system. In some cases, it is simply represented as 90% of the original value. However, recovered ecosystems may actually contain <90% of the original carbon, depending on how ''recovery'' is defined. In such models, carbon in crops and pastures is almost uniformly given a value of 5×10^6 g/ha. In reality, however, carbon content varies depending on the species planted, soils, use of fertilizers or irrigation, and prevailing climate. Even so, given economic constraints, agricultural lands are probably more similar (have less variance in biomass) than forests. In addition, the models usually assume that the time required for an abandoned system to recover is a constant regardless of vegetation type. However, based on a study of plant succession in the eastern Amazon, Uhl et al. (1988) suggest that the time for vegetation to recover to initial biomass levels may vary from 100 to 500 yr, depending on the intensity of the land use (particularly soil compaction by cattle).

In incorporating the effects of soil into assessments of vegetative cover, the spatial heterogeneity of soil properties complicates obtaining representative measures of soil conditions and maps of soil taxonomy. Yet as Schlesinger (1991) has pointed out, soil carbon and its changes, difficult as they may be to measure, may be key factors in accurately determining carbon flux. To estimate carbon flux, a major research need is information on soil characteristics (e.g., water-holding capacity, soil depth, texture, pH, redox potential, and hydrologic regime) and the roles played by the vegetation, detritus, and other biota.

Once the carbon content of abandoned systems is determined, the rate of change in carbon storage must be established. It depends on the carbon initially in the vegetation and soils, the time to ''recovery,'' and the carbon content of soils and vegetation of a system considered to be recovered (Table 3). These factors are a function of the nature of the surface of the soil, soil depth, the carbon and nutritive content of the soil, prevailing weather conditions, slope of the soil surface, suitability for revegetation, the presence of sources of seed for regeneration of the forest, and many more conditions.

Methane

Methane is a chemically active trace gas produced by anaerobic processes. Since the industrial age began, methane has grown to comprise ≈17% of the anthropogenic greenhouse forcing (Shine et al. 1990; Table 1). Methane is a very powerful greenhouse gas with a radiative effectiveness that is about 9 times that of CO_2. Wetlands are the largest natural source and contribute ≈22% of the total release of CH_4 to the atmosphere (see review by Harris et al. [1993]). Any activity that disturbs the soils of these wetlands (e.g., drainage for agriculture or forestry use) can affect anaerobic processes. Rice paddies are another major source of methane, with the amount being released depending on agricultural practices (fertilization, mulching, water management, plant density, and rotations), soil characteristics, and season (Neue 1993). The 41% increase in wetland rice production since 1951 has increased methane releases from this source (Neue 1993). Emissions from natural wetlands and rice paddies are particularly sensitive to temperature and soil-moisture changes and may be affected by future climate changes. For example, modeling studies suggest that northern high-latitude wetlands are a potential source of methane under warmer and wetter conditions than presently occur (Harris et al. 1993).

Biomass burning also releases methane, and thus the increase in rates of forest cutting (much of which is subsequently burned) correlates with the increase in methane release (Crutzen and Andreae 1990). Emissions of methane from ruminants depend on the density of animals as well as the type of food consumed. Increases in populations of cows and sheep have occurred as elephant and bison herds have decreased, which make it difficult to calculate the changes in methane emissions. It is unclear how much termites contribute to the methane flux because of uncertainties in the global termite population and the consumption of biomass by termites. If the termite population declines, methane from that source will correspondingly decrease. The anaerobic activity of landfills is another major source of methane to the atmosphere that increases with the growth in human population.

Nitrous oxide

Nitrous oxide is produced from a diversity of biological sources in soils and water. Nitrous oxides comprise ≈4% of the anthropogenic greenhouse forcing over the past five centuries, but their contribution has increased with the spread of human activity (Shine et al. 1990). Nitrous oxide is ≈190 times more effective radiatively than CO_2. The major background source of nitrous oxide (prior to human activities) was tropical forest soils (Matson and Vitousek 1987, 1990). Oceanic release of N_2O occurs through both nitrification in near-surface waters and denitrification in oxygen-deficient deep waters (e.g., Joye and Paerl 1993).

Within the biotic sphere, human activities and particularly agriculture have had a major influence on the flux of nitrous oxides. The release of nitrous oxides to the atmosphere has increased with human activities as a result of tropical land clearing and replacement by agriculture (Luizao et al. 1989), biomass burning (Crutzen and Andreae 1990, Cofer et al. 1991), and degassing of irrigation water (Ronan 1988). Emission of nitrous oxide has been increased by the use of fertilizers (EPA 1990) and by the expansion of the area in nitrogen-fixing leguminous plants in agriculture (Eichner 1990). However, our understanding of the global budget for nonindustrial and nontransport-related nitrous oxide is not complete because of uncertainties in the fluxes and a paucity of information on some of the processes (Vitousek and Matson 1993).

Ecological Effects of Climate Change

Climate change affects terrestrial ecological systems at a variety of temporal and spatial scales (Graham et al. 1990; see Table 4). To predict particular effects of climate change, the expected precipitation and temperature patterns for particular regions and times need to be known. However, there is a high degree of variability in projections of temperature and precipitation from general circulation models (GCMs) for any particular area (Mitchell 1989, J. T. Houghton et al. 1990). Therefore, it is not currently possible to provide a prediction of expected changes for particular biomes or landscapes. However, the ecological processes that would likely be susceptible to climate change are readily identified. At this time there is no direct evidence of any effects of human-induced climate change on ecosystems. Therefore, analysis of anticipated effects relies on models or historical and paleoecological evidence.

Global responses to climate change involve alterations in energy, carbon, or water fluxes of vegetation, which, in turn, depend on the spatial distribution of the different vegetation types. The Holdridge life-zone classification (Holdridge 1967) has been used to ex-

TABLE 4. Four biotic levels of organization that participate in the terrestrial response to climate and CO_2 change (modified from Graham et al. 1990: Table 1.)

Level of organization	Spatial scale	Temporal scale	Major processes	Relevant human activities
Biosphere	Global	Years to millennia	Energy, carbon, and water fluxes	Deforestation; fossil-fuel burning
Biome	Subcontinental	Years to millennia	Evolution/extinction; migration; disturbance	Plant breeding; land management; conservation
Landscape	$10–10^4$ ha	Years to centuries	Disturbance; nutrient cycling; production; water use; succession; competition	Pollution; exotic pests; fire suppression; flood control; forest management; soil management
Tree	$10^{-2}–10^3$ m^2	Minutes to decades	Phenology; reproduction; physiological processes	Fertilizing; watering; weeding; breeding

amine potential global shifts in major ecosystems with climate change (Emanuel et al. 1985, Lashof 1987, Prentice and Fung 1990, Smith et al. 1992). The Holdridge classification scheme relates the distribution of major ecosystem complexes to mean annual biotemperature, mean annual precipitation, and the ratio of potential evapotranspiration to precipitation. Smith et al. (1992) compare potential impacts on vegetation distribution of the climate changes projected by four GCMs. All four climate-change scenarios suggest a decrease in the area of tundra and desert and an increase in grassland area. The model projections also show forest areas increasing toward the poles, an increase in the extent of tropical forests into areas now occupied by subtropical or warm temperate forests, and a shift of the boreal forest zone into areas now occupied by tundra. All scenarios suggest an increase in terrestrial carbon storage ranging from 8.5×10^{12} kg to 180.5×10^{12} kg. Using the Holdridge classification approach to estimate effects of climate change on vegetation assumes that vegetation complexes move as a fixed unit in time and space, that vegetation distribution is solely correlated to climate (e.g., soils are not considered), and that equilibrium solutions exist (Smith et al. 1992).

This view is a great simplification of the real situation: at the biome level, species respond to climate change through migration, extinction, or adaptation to new disturbance regimes (Table 4). The potential for plants to evolve in response to climate change depends on genetic variation. The response to climate change has generally been via migration rather than evolution, and the potential for extinction is enhanced by (1) barriers to migration and (2) low genetic diversity.

Disturbance intensity, frequency, and duration are likely to change with climate (Overpeck et al. 1990). A number of examples of such environmental disturbances caused by climate change can be given. With a doubling of CO_2, the frequency of Caribbean hurricanes may double (Wendland 1977), and the destructive potential of hurricanes may increase by 40–60% (Emanuel 1987). Natural fire frequency, duration, and intensity are closely tied to storm occurrences and therefore to precipitation regimes. Insect outbreaks are a function of the prevailing moisture and temperature conditions, insects' physiological responses to extremes, and plant stress. In addition to direct mortality, these disturbances are important, for it is through disturbances that species replacement occurs more rapidly (Franklin et al. 1992). Climate change may have little direct effect on existing mature forests whose trees live hundreds of years; however, the ability of long-lived trees to reproduce and grow under new climate regimes may be best observed in areas that have been disturbed.

Landscape responses to climate changes may take years to centuries to express themselves and may occur in terms of nutrient cycling, water use, production, succession, competition, and response to changes in disturbance regimes (Table 4). Climate change affects nutrient cycling by changing litter decomposition rates, plant nutrient uptake, and/or internal cycling. Species shifts associated with climate change may also change patterns of nutrient cycling (Pastor and Post 1988). Vegetation's water use is a complex interaction of water-use efficiency, soil characteristics, and climate. Therefore, it is difficult to predict a general response of how water use will be affected by climate change. Productivity will likely decrease in some places and increase in others, depending on the spatial distribution of temperature and precipitation changes. Succession patterns and competitive interactions are likely to be altered with climate change, but it is difficult to make specific predictions because of the complex nature of these interactions. Pastor and Post (1988) show that the landscape response to climatic warming depends on the spatial pattern of soils and the nutrient-cycling properties of the vegetation. As at the biome level, disturbance frequency and intensity will modify the responses of vegetation to climate change. Wetlands are particularly susceptible to changes in disturbance regimes (OTA 1993, Michener et al. 1997). Sea-level rise would alter the distribution and condition of wetlands by altering the area they currently cover and changing the species they support. In the short term (5–20 yr), extreme weather events (such as storms, floods, droughts, and fires) may disrupt vegetation growth. These effects may be particularly severe in wetlands previously disturbed by human activities.

Climate changes can directly affect land use in a

TABLE 5. Human causes and consequences of land-cover change.

Causes†	Consequences: Typical land-cover changes	Typical activities that modify land cover	Ecological characteristics affected
Population growth	Forest harvesting	Irrigation	Biodiversity
Affluence	Agricultural expansion	Fertilization	Habitat
Technology	Urbanization	Forest degradation (thinning, coppicing, gathering wood)	Soil quality
			Productivity
Political economy	Second home development	Introduction of exotics	Extractable resources
Political structure	Flooding	Landscape fragmentation	Water quality
Attitudes and values			Regional and global climate

† From Turner et al. (1993).

number of ways. Climate-change effects on agriculture are probably the best known. Direct climate effects include changes in crop yield and spatial shifts of agricultural potential (Parry 1990, Easterling et al. 1993). Decreasing rainfall can lead to the need for irrigation. Changing temperature or rainfall patterns can change which crops are most suitable for an area; however, land managers can frequently identify replacement varieties or crops that perform equally well under new climate conditions. Indirect effects include altered farm profitability, regional productivity costs, regional and national food production, and the number of people at risk of hunger (Parry 1990, Rosenzweig and Parry 1994). For example, climate-change-induced alterations in agricultural productivity in one region can affect productivity in another region (e.g., loss of productivity in the Northern Hemisphere may lead to greater demand from the Southern Hemisphere). Also, climate-induced changes in disturbance regimes can indirectly affect land-use practices (e.g., the frequency of fire, wind, or insect outbreaks may affect the potential for forest harvesting).

The predicted rise in sea level from global warming will have major impacts on coastal zones and estuaries. As some areas are lost and replaced by higher-elevation sites, humans will build new commercial and industrial facilities. Currently, the human population is concentrated in coastal zones. For example, 53% of the United States population lives in counties within 80 km of the coast (NOAA 1990). Therefore, modifications of coastal zones will have significant impacts on social and economic systems.

CAUSES OF LAND-USE CHANGE

The major drivers of land-use changes are human population, affluence, technology, political economics, political structure, attitudes, and values (Turner et al. 1993; see Table 5). The importance of these factors varies with the situation and the spatial scale of analysis. Human population growth can be considered an ultimate cause for most land-use changes; however, local demographics as well as consumption per capita and its variability can modify the effects of population. Economic incentives set by government policies are a key cause of deforestation. Quantifying the effects of land-use change from a long-term economic perspective that includes environmental feedbacks is useful, for it emphasizes the opportunity for government policy on sustainability to modify negative effects of deforestation.

The question of how climate changes affect the major drivers of land-use change can be answered by postulating many scenarios of the effects of local or regional temperature and precipitation changes on land-use practices. Existing policies, economics, and attitudes may no longer be applicable in a changing world; new technologies may be developed to deal with the problems; and people's attitudes and values may change. It is not useful here to go through some of those scenarios, for only a small set could be thoroughly discussed. Rather, it is important to note that climate change can affect these land-use drivers and that the directions of the impacts must be considered to understand the effects of climate change.

Typical land-cover changes include forest harvesting, agricultural expansion, slash-and-burn agriculture, urbanization, and flooding (e.g., for rice cultivation). A number of common themes relate the drivers to particular land-cover patterns. For example, local population increase leads to urbanization and a decline in the natural land-cover types of the region. Elucidating these themes (and exceptions to them) would help us understand better the causes of specific land-use patterns. Turner et al. (1993) emphasize that theories relating human causes of land-use change to changes in land cover are not fully developed. Correlations among these phenomena at the global level do not always hold for local or regional scales. For example, global or regional population growth may not always be the prime cause of agriculture expansion. Therefore, case studies of the relation between human drivers and land-cover changes for specific regions are useful.

However, determining the primary causes of land-use changes is difficult. For example, Rondônia, Brazil, is a region that has undergone rapid deforestation since 1968 because of colonization projects along a road system that was paved in 1984, largely accomplished through funding from the World Bank. Between 1970

TABLE 6. Ecological effects of land-cover changes.

Land-cover changes	Examples of effects
Intensity of use	Loss of soil fertility; eutrophication; toxification
Total area deforested	Carbon release; desertification
Size of clearing	Soil erosion; forest recovery time; loss of mycorhizal associations
Size of forest patches	Decline in species diversity
Extent of forest edge	Wildfire damage
Spatial array of clearings	Restrictions on animal movements; spread of disturbances

and 1988, 37 500 km^2 (18% of the area in Rondônia) were cleared (Stone et al. 1991) as a direct result of the road and colonization projects. It is difficult to discern the ultimate causes of the colonization in Rondônia. Forestra (1991) proposes three reasons: social, political, and economic. The social reason for the colonization program was to relieve the pressures of population growth along the coastal zones of Brazil. However, 73% of the colonists' families moved from farm regions of south and southwest Brazil (Pedlowski and Dale 1992). The political reason for settling Rondônia was to encourage Brazilians to settle in the frontier community that was once a part of Peru. The economic reason was that the president of Brazil offered colonization of Rondônia as a solution to the famine resulting from a recent drought. Individual farmers have specific reasons for migrating to Rondônia, but many of them moved because of the opportunity to work on their own land (Pedlowski and Dale 1992, Jones et al. 1995). Thus, Rondônia was colonized and deforested for a variety of reasons.

Modification of land-cover types should also be considered in development of land-use theories. Typical land-cover modifications include irrigation, fertilization, introduction of exotic species, forest degradation, and landscape fragmentation. Forest degradation occurs when the forest type is retained yet structural features of the forest are changed. For example, removal of limbs and small trees for firewood reduces the forest biomass. Species introduction (e.g., the introduction of the European boar into the southern Appalachians) may reduce the diversity of the natural land-cover type. And fragmentation occurs when a land-cover type is segmented by roads, transmission lines, or a managed land cover (e.g., agriculture).

ECOLOGICAL EFFECTS OF LAND-USE CHANGE

Ecological effects of land-use conversion include changes in biodiversity, habitat availability, soil erosion and degradation, productivity, extractable resources, and water quality (Table 5). These changes largely occur as a direct result of changes in the land-cover pattern (Table 6). Over a period of decades, these well-documented effects of land-use change exceed the effects anticipated from human-induced climate change (Burke et al. 1991). Biodiversity reductions occur when a natural land cover is replaced by a new cover type that does not support some of the former species. On a local scale, diversity is lost when a forest is replaced by agriculture. The reduction in diversity can also be indirect through habitat modification. Currently, tropical deforestation is one of the major threats to biodiversity because of habitat alteration and loss (Wilson 1988).

Habitats are changed by almost all land-use modifications. Fragmentation can reduce species diversity (Fahrig and Paloheimo 1988) through changes in natural processes (e.g., disruption of seed dispersal) or the addition of new processes (e.g., competition with exotic species). Landscape fragmentation can cause declines in habitat and reduce or eliminate some animal or plant species. For example, as the preferred habitat for a species becomes less connected, the species may not have sufficient breeding habitat to survive (Dale et al. 1994*a*). Such effects largely depend upon the habitat size requirements for the species and the ability of the species to move across areas outside its preferred habitat. In addition, increases in the amount of edge habitat may compromise some species. For example, populations of neotropical migrant birds are being reduced by increases in cowbirds that parasitize nests of other bird species more frequently along forest edges, which are close to abundant food resources of agricultural areas and grasslands (Brittingham and Temple 1983). Predation can also increase along habitat edges (Yahner and Scott 1988).

Land-use activities can also increase the area of some habitats, such as in Northern Wisconsin where logging has increased the area and connectedness of early successional forests (Mladenoff et al. 1993). The larger area of successional forest has resulted in the abundance of species associated with those forests (such as white-tailed deer and grouse) and a decline in species sensitive to patchiness or roads (Thiel 1985).

Soil-quantity and soil-quality changes occur when land-management practices cause erosion or export soil nutrients as agricultural or forest products. Currently, topsoil is being lost from the agricultural lands in the world at the rate of $\approx 25 \times 10^{12}$ kg [25×10^9 metric tons]/yr (National Research Council 1992). The concept of sustainability is important to introduce in conjunction with soil quality, for frequently land-management practices are considered to be sustainable without considering the long-term implications on soil-quality degradation.

Both the natural and the managed productivity of a system can be altered by land-management practices. Use of fertilizers and irrigation are known to increase productivity. On the other hand, export of products from the land can reduce natural productivity.

Loss of extractable resources (e.g., fruit, rubber) is another consequence of land-use changes. For example, indigenous people generally manage the use of natural extractable resources in a responsible manner when their populations are stable (Anderson 1990). However, developed countries promote landscape uses that typically do not take advantage of extractable resources. Thus, many species having potential for food, fiber, or pharmaceutical drugs are being eliminated (Wilson 1988).

Water resources are compromised by increased demand, reduced capacity of the land to filter water, and increased pollution. These pressures are particularly apparent in arid regions, such as the southwestern United States. In their review of global change effects on freshwater ecosystems, Carpenter et al. (1992) find that freshwaters are tightly linked to climate and land use. In particular, watershed modifications and use and modifications of aquatic resources by humans stress freshwater ecosystems and must be considered in concert with climate-change effects.

Certain land-use activities can modify the effects of climate change on ecological systems at the biome and landscape levels (Table 4) through their effects on energy fluxes. These land-use activities include land management and conservation at the biome scale and fire suppression, flood control, forest management, and soil management at the landscape scale.

At the biome scale, impacts of a particular climate change may be exacerbated by human activities. For example, forest cutting, road development, and urban expansion create land-cover patterns that may impede the natural processes of seed dispersal and plant establishment that might otherwise compensate for changes occurring in the forest. On the other hand, some human activities may mitigate effects of climate change on forests. For example, some tree species may not be able to migrate to the regions where climate change produces appropriate habitats, but seedlings of those species could be intentionally planted.

At the landscape scale, agricultural management using fertilizers, crop rotation, irrigation, selection, or genetic engineering may reduce changes in crop yields or productivity that might otherwise occur with climate change. Predicting how agriculture systems respond to climate change requires information on how and when climate will change, information that is not now available nor is likely to be available soon. However, some possible adaptations are known (Rosenberg 1992): (1) Changes in length of the growing season can be countered with the use of cultivars that require either longer or shorter growing seasons. (2) Photoperiod limitations can be overcome by traditional plant-breeding procedures. (3) Greater warming or desiccation can be dealt with by using drought- and heat-resistant strains of crop species. (4) Moisture-conserving tillage methods can be adopted. (5) Dryland agriculture may no longer be economic in some areas, and demand for irrigation water may decrease; however, demand for irrigation may increase elsewhere (although greater demand for water may limit the potential for irrigation). (6) Improvements in irrigation efficiency can compensate somewhat for increased water demands. In agriculture, capital investments are relatively small (compared to those for forestry) and can be modified in a short time period with changing environmental conditions.

Methods for Studying Interactions Between Land-Use and Climate Changes

Historical and paleoecology studies

Historical and paleoecological evidence shows that the effects on forests of climate change have been significant. Because species' responses to climate change have been complex (Davis 1989), it is difficult to predict patterns of responses. For example, with climate warming, intact forest ecosystems have not moved northward as a unit; instead, species have responded individually. Different combinations of tree species occur today than in the past. Also, the order of species entry into an ecosystem has been unique or has occurred with time lags (Campbell and McAndrews 1993). Thus, understanding the functional response of species and ecosystems to climate change is required.

Although historical and paleoecological studies of effects of climate change on forests provide much information about responses in the past, their results cannot be directly applied to future conditions for two reasons. First, the current size, age, and species composition of temperate forests are unique and have been strongly affected by human activities. Second, global temperatures are predicted to increase at an unprecedented rate.

Field and greenhouse studies

Field and greenhouse studies of the interactions of climate change and land-use change are hampered by the logistical difficulties of implementing changes at the scale of entire ecosystems. Elucidating effects of one of these changes is difficult to do with sufficient size and replication of plots. Therefore, many field and greenhouse studies focus on one or a few aspects of predicted climate change or land-use change. For example, the effects of soil degradation or reduced precipitation can be experimentally documented. The challenge of field and greenhouse studies of changes at the scale and complexity of a forest is to design studies that deal with specific interactions or that provide information that can be extrapolated to larger scales.

An example of the type and scale of experiment required to investigate impacts of climate change is the throughfall displacement experiment (TDE) being performed in an upland forest of the Walker Branch Watershed in East Tennessee (Turner et al. 1992). The TDE is a stand-level manipulation experiment that provides the appropriate environment for mechanistic studies of ecosystem response to changing climatic conditions. Approximately 25% of the throughfall on the ''dry'' plot is being collected in polyethylene troughs and transported by gravity though pipes to the ''wet'' plot. The experimental system is able to produce statistically significant differences in soil water content for years having both extremely dry and extremely wet conditions. Biological and chemical characteristics of two treatment plots and a control plot (each covering 0.6 ha) are being monitored for 5 yr. These characteristics include: forest growth and the physiological responses of major tree and understory species, leaf-area index, herbivore activity, litterfall, understory competition, litter composition, soil organic matter and microbial populations, nutrient availability, soil and soil solution chemistry, and biogeochemical cycling processes.

Models

Understanding how current land cover will respond to transient patterns of global temperature, precipitation, solar radiation, etc. requires reliance on computer models that can deal with some of the complexities of the vegetation and climate systems. Because human activities are an important determinant of many land-cover types, the influence of humans must be included in some of the modeling studies. Human use of the land is largely influenced by available resources and social and economic conditions, so socioeconomic models must be paired with ecological models to understand the complex responses of modern ecosystems.

This discussion of models that relate land-use change and climate change builds upon recent reviews of land-use models (Dale et al. 1993*a*) and models used to understand ecological impacts of climate (Smith et al. 1992, Pacala and Hurtt 1993, Dale and Rauscher 1994). The challenge here is to consider how modeling approaches can be used to examine land-use and climate-change interactions. Of the 14 categories of climate-change models that Dale and Rauscher (1994) reviewed, they found that only three types considered land-use change.

Global models.—Global models of vegetation change have been used to project vegetation patterns under changing climate. Climate-change scenarios have been provided for these models in three ways. One approach uses mesoscale climate models to predict regional climate processes, such as the location of the arctic frontal zone, which is a good predictor of the boundaries of the boreal forest biome (Michaels and Hayden 1987). A second approach is to scale up a community demographic model by using functional plant groups instead of species, because the number of species that would need to be simulated on a global scale is overwhelming (Prentice et al. 1989). Functional plant types are groups of species that germinate and grow under similar sets of environmental conditions (e.g., dry-deciduous sclerophyll). The third approach correlates projected empirical models of climate and vegetation in a spatial context by using the Holdridge life-zone classification system (Emanuel et al. 1985).

Global models can be used to examine the relative influence of land-use change, biomass estimates, and the fate of carbon after land management on terrestrial carbon flux (including CO_2 fertilization and carbon sequestration). In such models, the problem of modeling interactions between climate change and land use is one of scale. Because of the large area involved, global models must rely on pixel sizes of about 1 km or larger; however, land management frequently occurs on a much smaller spatial scale. At such scales, it is difficult to model interactions among land-use drivers, topography, transportation networks, and climate change.

Regional models.—The region or landscape is the scale at which land-use changes frequently occur and at which estimates of climate change can be made. Currently, regional climate-change models' predictions do not agree on projected temperatures or precipitation for any area. However, regional models can be used to examine scenarios of land management and climate change to determine sensitive variables and features of the region. Regional vegetation and land-use models focus explicitly on how changes in the regional pattern of vegetation affect the carbon budget or other properties, a process in which the cause of land-use change plays a key role. As a result, these models may have complex socioeconomic components. All of these models are spatially explicit in the sense that they refer to actual land patterns, although some patterns may be hypothetical. Regional-vegetation and land-use models are exemplified by the studies of Rotmans and Swart (1991), Kurz et al. (1992), Southworth et al. (1991), Dale et al. (1993*b*), Bogdonoff et al. (1985), and Grainger (1990).

An example of a regional model illustrates the approach. Southworth et al. (1991) and Dale et al. (1993*b*, 1994*b*) have developed spatially explicit simulations of land-use changes in central Rondônia, Brazil. The Dynamic Ecological–Land Tenure Analysis (DELTA) model operates at the individual-farm level (using digitized maps of farms that average 101 ha in size). The model simulates changes in the impacts and spatial arrangement of farm practices and carbon release over 40 yr. The typical land-use scenario simulates farmers clearing an increasing amount of forest up to year 3 and stopping most of the clearing by year 7, at which time about half of the lot is cleared. This model's projections under this scenario compare to activities of farmers in central Rondônia (Dale et al. 1994*b*).

Global climate-change effects on the central Amazon may result from economic pressures rather than temperature or precipitation alterations. The DELTA model is used to explore the implications of increased demand for agricultural productivity that may result from reduced productivity in the temperate zones with climate warming. This simulation can be done in a variety of ways in the model: decreasing the likelihood that farmers leave the farms, increasing the value of production, and increasing the importance of the link to the market via primary and secondary roads. In all cases, the model outputs were similar to the typical case discussed in the previous paragraph and by year is resulted in >80% deforestation (Fig. 4). The reason for this similarity is probably that without technology changes, the farmers cannot clear land at a faster rate and cannot increase their productivity.

Thus, the model suggests that the increase in demand of agricultural products from the tropics would have to be accompanied by technological advances for there to be an impact on the carbon released and rate of fragmentation of areas that are already subjected to farming. New areas may still come under pressure to clear forests for agriculture expansion. The exercise shows that the model needs to consider technology development as a driver to fully explore this case. Such modeling experiments illustrate the limitation of existing models and the direction for new developments.

Landscape-transition models.—Landscape-transition

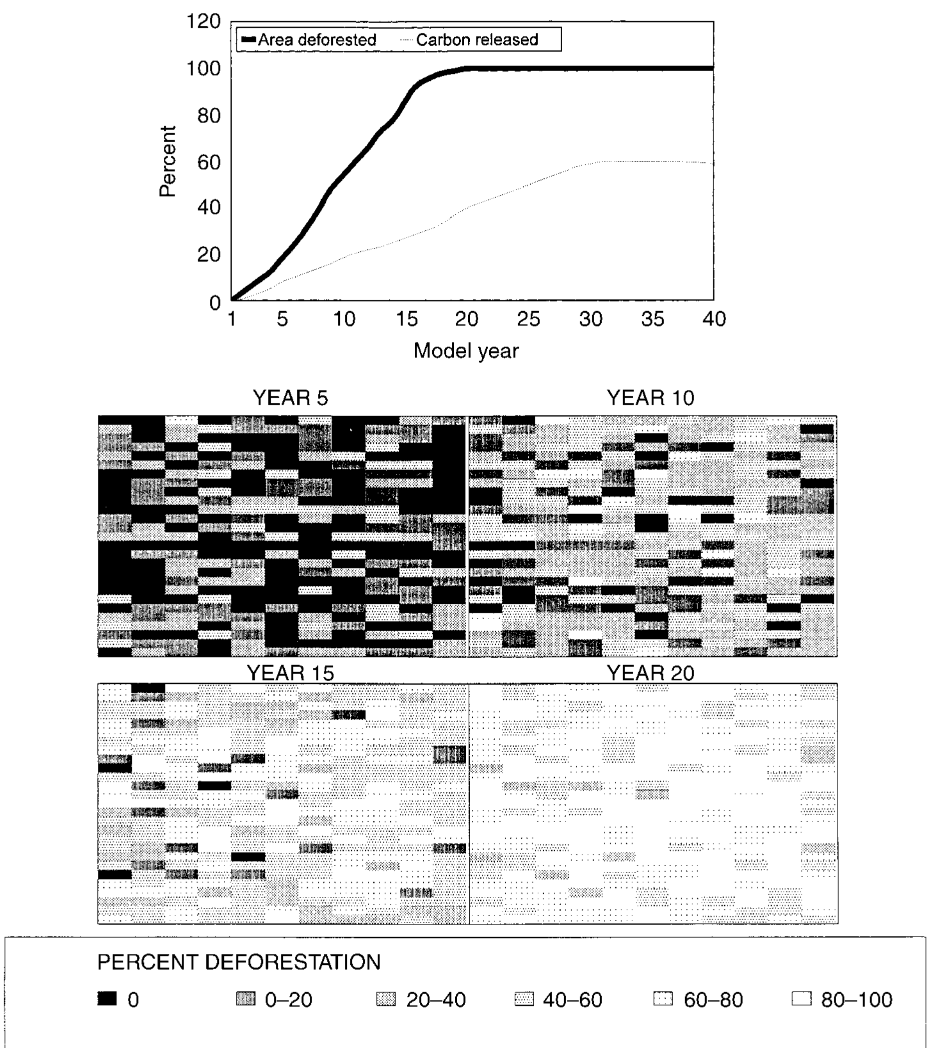

FIG. 4. Example of spatially explicit simulation of land-use changes in central Rondônia, Brazil, using DELTA, a regional-scale vegetation and land-use model that operates at the individual-farm level. *Top:* Simulated mean forested area cleared and carbon released over 40 yr for 296 plots. The model is described by Southworth et al. (1991) and Dale et al. (1993*a*, *b*). *Bottom:* Spatial patterns of the forested areas in the first 20 yr.

models use a cellular-automata approach to explore effects of changes in the location, size, shape, and composition of vegetation boundaries. The cellular-automata approach tracks interactions within and between each location in the spatial model. Landscape-transition models that can incorporate land-use and climate changes are exemplified by Turner et al. 1991, Schwartz 1992, and Gardner et al. 1994.

Gardner et al. (1994) developed a cellular-automata model that explores the spatial distribution of two competing species (a generalist and a specialist) with a severe perturbation in the abundance of the species, such as might be caused by a severe drought. The simulation was run for 100 generations, with and without a land-use modification (e.g., forest harvesting) that causes habitat destruction in either a blocked or fragmented fashion (Fig. 5). Simulated land-use changes altered the habitat types by preventing the specialists from being able to germinate. Survival of the specialists was greatest with no harvesting and no drought (Fig. 5). With larger areas of the forest being harvested, survival and abundance of the specialist species declined.

Summary.—In summary, global, regional, and landscape models can address issues relevant to the interaction between land use and climate change. However, the models have typically been used only to consider one type of change. The interaction between climate and land-use changes is clearly amenable to modeling studies.

Future Steps in Elucidating the Interactions Between Land-Use Change and Climate Change

Ecological research

Approaches for study and modeling.—

1) Interdisciplinary studies of land-use and climate-change effects are necessary. For example, economic, political, and social changes must consider ecological responses, and vice versa. Also, biologists need to work with climatologists to develop climate models at spatial scales that are useful in assessing the state of the biotic system. Scientists need to be aware that many problems are not solvable based on a single-discipline approach.

2) Spatially explicit models at local and regional scales are necessary to relate land-use changes to climate change. Many management questions are at the landscape or regional scale, and land management tends to occur at these scales. If these models have biologically relevant and socioeconomically meaningful interfaces and outputs, then these models can meet many of the management needs.

Topics and questions to be addressed.—

1) Relation between causes of land-use and actual land-cover changes—How can the causes and effects of these relations be clarified?

2) Paleoecology—How have species and ecosystems responded to climate changes in the past? Note that predicted changes are different from past climate alterations.

3) Agriculture—What are best land-use practices on tropical and temperate soils? Can use of native species

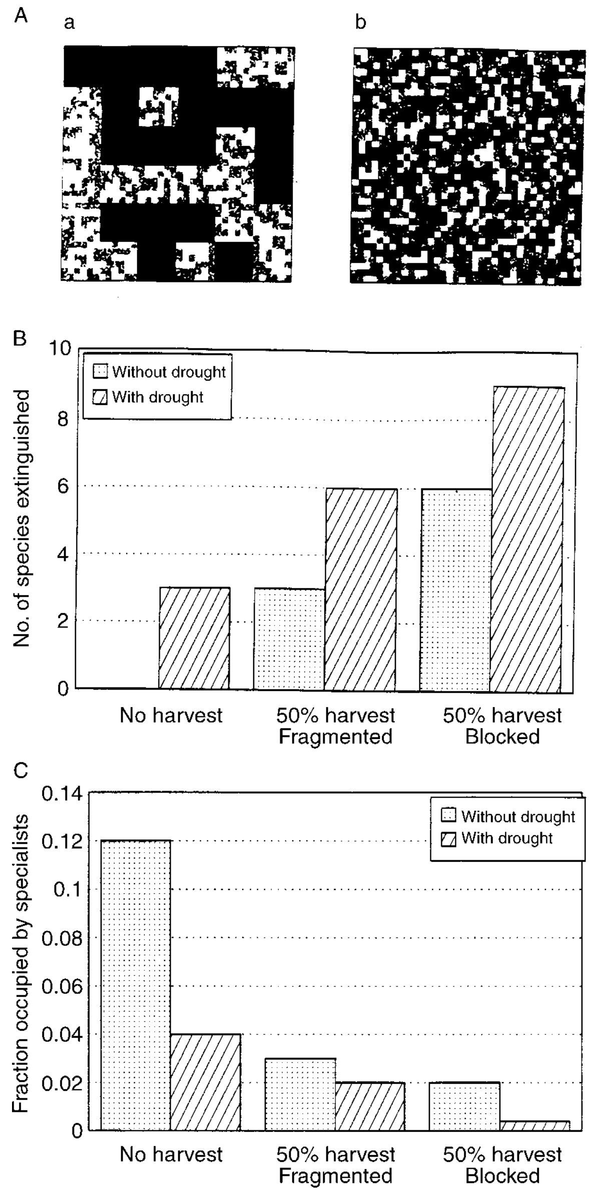

FIG. 5. Example of output from cellular-automata model (Gardner et al. 1994) used to explore the spatial distribution of two competing species (a generalist and a specialist) facing severe perturbation in abundance (e.g., caused by severe drought). The simulations were run for 100 generations and replicated 10 times. (A) Land-use modification (e.g., forest harvesting) causing habitat destruction was done in a blocked (a) or fragmented (b) manner. The black areas were subject to the land-use change. These harvesting schemes were used in the landscape-transition model to arrive at (B) the number of extinctions and (C) the fraction of the landscape occupied by specialists at the end of the simulation.

offset climate-change effects on agriculture? Can use of species from warmer environments offset effects of temperature increases?

Monitoring.—Information needs to be collected on how climate change (as compared to other confounding factors, e.g., land-cover change) will affect

1) the spatial distribution of natural vegetation (particularly rare species or those at the edges of their ranges), human population, land-use practices, and land-cover types;

2) the distribution of natural and human-induced species movements (including movements of humans);

3) the distribution and frequency of disturbances (e.g., hurricanes, tornadoes, fires, and insects) and the responses of organisms to disturbance; and

4) changes in patterns of economic growth and the resulting need for land-use change (e.g., for agricultural expansion).

Education

Scientists need to assist policy makers, stakeholders, and the general public by:

1) providing information linking climate change and land use;

2) defining what climate change would mean (in an ecological, social, health, political, and economic sense); and

3) relating people's lifestyles and energy choices to environmental consequences (e.g., demonstrating the effects of automobile and other energy use on climate change, pointing out the repercussions of local and regional land-use activities on the global environment, and identifying the per capita impact of human population and consumption).

Conclusions

There are two aspects to considering impacts of land use: effects of land use on climate change and the effects of human-induced climate change on land use (Fig. 1). The direct ecological effects of the land-use and climate change are dominated by the land-use change effects, at least over the period of a few decades. Because climate-change effects are largely determined by land-cover patterns, land-use practices set the stage on which climate alterations can act.

Determining the effects of climate change on land use involves resolving direct biophysical effects as well as management responses to climate impacts. Climate change might constrain or mandate particular land-management strategies (e.g., irrigation); however, these options will be different for each case.

In summary, land-use changes are having major ecological repercussions at a variety of biological scales. Being able to project effects of particular land-management strategies requires an understanding of the socioeconomic and biological aspects of land-use decisions. Such research will involve interdisciplinary efforts and will provide a better understanding of potential impacts of global change.

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