

# The effects of global change on tropical ecosystems

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Revised 21 June 1996; accepted 9 April 1997

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## Abstract

Alteration of land use will continue to be the dominant driver of environmental change in the tropics for the next several decades. It can take the form of fundamental vegetation cover transformation, or of intensification of existing land use without substantial change in cover type. Atmospheric composition changes and resultant climate changes could become ecologically significant within the next century. Changes in atmospheric composition in the tropics are essentially the same as those in higher latitudes, despite differences in the source and sink strengths for trace gases. Such changes can affect the functioning of tropical ecosystems through several processes, principally those related to carbon and nutrient assimilation and their interactions. Atmospheric composition may also have an indirect affect on tropical ecosystems via its effects on the climate. Predicted temperature increases in the tropics are less extreme than at high latitudes, but could still be biologically significant, especially at the tropical margins. The structure and productivity of ecosystems of the subhumid and dry tropics are very sensitive to changes in water balance, which could be caused by a combination of changes in precipitation and temperature. It is presently not possible to predict rainfall changes at ecologically meaningful scales with any confidence. © 1997 Elsevier Science B.V.

*Keywords:* global change; tropical ecosystems; land cover; climate; atmosphere

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## 1. Introduction

This paper focuses on interpreting the ways in which the driving variables of ecosystem function are anticipated to change in tropical regions in the next century. ‘Driving variables’ are factors which impose change on the ecosystem

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from the outside. In other words, they control structure, species composition or process rates in the ecosystem, but are themselves largely independent of the ecosystem state, at least in the short term.

The phrase 'global change' has come to mean widespread trends (as opposed to fluctuations) in the global environment during the past two centuries, which are predicted to continue into the next century. Those trends which have become apparent since the 18th century are inferred to be of mainly anthropogenic origin, since this period coincides with the massive and ongoing expansion of the human population and the widespread adoption of technologies such as energy from fossil fuels and high-input agriculture. Global change consists primarily of three causally-linked aspects: land use change, atmospheric composition change and climate change.

The objectives of this paper are to describe and evaluate the principal mechanisms of global change as they relate to tropical ecosystems, identify the principal driving variables and highlight the ways in which the tropics differ from temperate regions with respect to ecosystem driving variables and the responses they elicit.

We define the tropics as those areas where low temperatures are not a primary constraint on ecosystem function. We believe the causes of large-scale environmental change in the tropics to differ more in degree than type from global change processes in high latitudes. The paper is, therefore, not intended as a general survey of the ecology of global change, but an attempt to identify those aspects which are especially important or unusual with respect to the tropics. The paper was prepared as background for a workshop on tropical soil carbon, so it emphasizes soil processes.

## **2. Global change in the tropics**

### *2.1. Land use and land cover change*

Land use and cover change in its most obvious form is the conversion of natural vegetation to agriculture. It preceded, and is partially responsible for, changes in atmospheric composition and climate. Although the combustion of fossil fuels is the dominant source of the observed increase in the atmospheric carbon dioxide (CO<sub>2</sub>) content at the present time (Watson et al., 1992), the release of CO<sub>2</sub> as a result of land use change is almost as important when integrated over the period from 1750 to the present (Houghton, 1994), and is probably still the dominant source of CO<sub>2</sub> in the many tropical regions.

Land use change is presently the most important aspect of environmental change in the tropics, and will probably continue to dominate for at least the next generation. Tropical countries are now undergoing the expansion and intensification of agriculture which has already occurred in the temperate

northern hemisphere, for instance in China a millennium ago, Europe in the 17th century and North America in the 19th century. The main factors driving land use change in the tropics are illustrated in Fig. 1. A principal cause is technological innovation, which on the one hand makes it possible to farm intensively in previously unproductive or uninhabited environments, and on the other hand has made it necessary to do so to support a growing human population. The understandable aspirations of people in developing countries for levels of consumption to match those enjoyed in developed countries is as much a cause of land use change as population growth itself.

The tropical forests are being cleared for timber yield and agriculture, at a rate of about 1% of the remaining tropical forest area per year, or  $15 \times 10^6$  ha  $\text{yr}^{-1}$  (Houghton, 1994). New croplands are also being created in areas which were once tropical savannas or wetlands, at a rate which is mostly undocumented but probably at least as rapid and extensive as forest clearing (see e.g. Madeley, 1993). There is a general intensification of land use throughout the tropics: more livestock per unit of pastoral land area; more inputs and outputs per unit of cropland; more frequent return to sites of slash and burn agriculture; more harvesting of fuelwood and timber.

Land use transitions are seldom unidirectional, but the rate of reversion from cropland to secondary forest or bush is even more poorly documented than the original clearing (Skole and Tucker, 1993; Skole et al., 1994). There is a continuous switching between agricultural production systems, driven by local social, economic and environmental factors, new technology, national policy decisions and the economics of global trade.

Radical land use change has a profound impact on almost all aspects of ecosystem structure and function. It is the main factor underlying the massive changes in biological diversity occurring in the tropics. Conversion of natural vegetation to cropland typically results in a loss of  $\text{CO}_2$  from the plant biomass

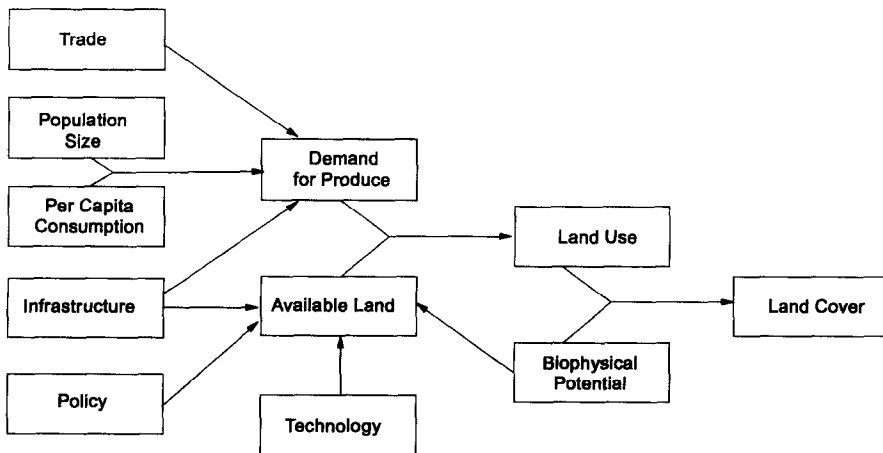


Fig. 1. The major factors driving land use and land cover change in the tropics.

and soil to the atmosphere. This loss is more rapid and more complete in the tropics than in temperate areas. Where fire is used for clearing, a large part of the cut plant biomass carbon is released within a few weeks and the remainder decays within a few years. Up to 50% of the soil carbon is released over a period of several decades (Scholes and Scholes, 1994). The rapid and large loss of soil carbon in the tropics is thought to be due to a combination of the climate (warmth and moisture promote decomposition) and the dominance of the soil carbon by easily-decomposed carbon fractions (as opposed to the more resistant humic substances).

The decline in soil carbon following cultivation is partly due to reduced carbon inputs to the soil, and partly due to increased decomposition of soil organic matter as a consequence of tillage. The decrease of inputs is usually not because the total productivity of the agroecosystem is less than the natural vegetation, but because a smaller fraction of primary production occurs below-ground, and a larger fraction of the aboveground production is removed as harvest, fuel or animal feed. The chemical composition of organic inputs also changes when the vegetation is altered from indigenous plants to crop species. Crop residues are typically more easily decomposed than the natural litters. Nutrient cycling becomes less tightly closed, resulting in losses through leaching, erosion and harvest. Soil fauna becomes less diverse and reduced in biomass (Lavelle et al., 1994). All of these changes can be ameliorated or reversed to some degree by specific management practices. For example, the carbon content of soil under well-managed tropical pastures may not differ greatly from that of the forests from which they were derived (Desjardins et al., 1994).

Land transformation is frequently the consequence of population immigration rather than growth of the local population. Human migration in the tropics is often attributable to political insecurity, environmental disasters and perceived differences in economic opportunities. Urbanization is a ubiquitous phenomenon in the developing world, creating new patterns of land use around urban centres. An example is the increased thinning of the woodlands around cities in tropical Africa for charcoal production. Urbanization does little to reduce the rate of land use change in rural areas, since it is mostly those with no access to land that move to towns, and urban dwellers continue to depend on food grown in rural areas. Infrastructural development has the effect of making new areas accessible to settlers, and creating markets for agricultural and forestry products. For instance, much of the deforestation in the Amazon is associated with road-building (Skole and Tucker, 1993). National and international policy decisions and macroeconomic factors can alter land use patterns relatively rapidly. An example is the preferential access to European Community markets for Botswanan beef, which is one cause of the increased exploitation of the Kalahari Basin.

Some of these changes are fundamentally unpredictable, and the complex interactions between even the reasonably certain processes will probably make

deterministic prediction of the location, rate and type of land use change an intractable problem for the foreseeable future. However, a series of more-or-less probable scenarios, for example based on inescapable relationships between population food needs, agricultural technology and land requirements, are attainable. For example, the population growth rate in Africa is high, and income growth per capita is low (or negative). If these conditions persist for the next two decades, large areas of Africa will be converted to cropland, since African farmers will not be able to afford the inputs needed to increase production per unit land area. The same scenario is probably not true for South-East Asia, where the incomes are rising and population growth is stabilizing. The situation in Latin America is somewhat in-between (Alcamo, 1994).

Building credible global change scenarios is likely to remain limited by our capacity to predict the human response to a changing environment. The Human Dimensions Programme, a joint venture by the International Geosphere–Biosphere Programme and the International Union of Social Sciences, targets this problem.

## 2.2. *Atmospheric composition*

Incontrovertible evidence for changes in atmospheric trace gas composition in recent decades has been provided by direct measurement, most famously by the observatory at Mauna Loa (Keeling et al., 1976), and confirmed at many other sites (Borden et al., 1991). Changes in the more distant past have been reconstructed from the analysis of gas trapped in ice cores (Neftel et al., 1982). The increase in concentration of ‘greenhouse gases’, those which block the re-radiation of energy from the earth’s surface, is predicted to lead to an increase in the global mean temperature, which in turn would trigger other climatic changes (Shine et al., 1990; Mitchell et al., 1995).

The global atmosphere mixes within weeks in an east–west direction, and over a period of a few years between the northern and southern hemispheres. The atmospheric composition in the tropics is, therefore, only markedly different from the global atmosphere with respect to short-lived components of local origin, such as CO resulting from biomass burning. For the more stable gases such as CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O and the man-made chlorofluorocarbons (CFCs), the tropical concentrations follow the global upward trends, with minor leads or lags associated with the global distribution of sources and sinks (Borden et al., 1991).

If emissions of CO<sub>2</sub> continue at 1990 rates, its atmospheric concentration will reach 450 ppm by 2050 (Houghton et al., 1990). If they continue to increase at their exponential historical rate of 0.5% per annum (the so-called ‘business as usual’ scenario) atmospheric CO<sub>2</sub> will reach 550 ppm (double the pre-industrial 270 ppm) in 2050. These predictions are based on the current relationship between the calculated quantities of emitted CO<sub>2</sub> and the observed atmospheric

CO<sub>2</sub> increase, which may not continue to hold in the future. The observed atmospheric increase is half of the emissions, due to the action of several poorly-understood carbon sinks.

There is still considerable uncertainty regarding the details of the global carbon cycle. Over 1 Gt (i.e. 10<sup>15</sup> g, or about one sixth of the annual anthropogenic emission) of carbon cannot be accounted for annually (Tans et al., 1990). If this 'missing sink' increases in strength as the atmospheric CO<sub>2</sub> increases, then the projections are overestimated. If, on the other hand, the sink becomes saturated, they are underestimates. The location of this 'missing sink' was initially thought to be oceanic, and later in the northern temperate terrestrial ecosystems. Recent inferences from the global distribution and isotopic composition of atmospheric CO<sub>2</sub> suggest that the sinks may be both tropical and temperate, and largely terrestrial (Siegenthaler and Sarmiento, 1993; Phillips and Gentry, 1994; Denning et al., 1995).

In the past few years the rate of increase of atmospheric methane has dropped from 0.9% per year to 0.4% per year, for unknown reasons. The overall upward trend is projected to continue, reaching 3250 ppb in 2050 under the 'business as usual' scenario, four times the pre-industrial level (Houghton et al., 1990). Methane has some important tropical sources and sinks. The sources include ruminants, paddy rice fields, wetlands and vegetation burning. Well-drained tropical soils under natural vegetation are probably a significant methane sink, but their methane consuming capacity needs more study before it can be generalized.

The processes leading to N<sub>2</sub>O emission are poorly understood, and the global inventory of known sources and sinks does not balance the observed unsteady atmospheric increase of 0.25% per year (Watson et al., 1992). The current concentration is 310 ppbv, up from about 288 ppbv in pre-industrial times, and increasing at about 0.8 ppbv per year (Khalil and Rasmussen, 1992). The main anthropogenic sources are believed to be related to industrial emissions and the use of nitrogenous fertilizers, and are thus presently predominantly northern-hemisphere and temperate. Tropical ecosystems are significant biotic sources (Bouwman et al., 1993). The N<sub>2</sub>O emissions from tropical forest soils temporarily increase when they are converted to pastures (Keller et al., 1993). As the land use intensifies in the tropics, and more manufacturing industry shifts to developing countries, tropical sources can be expected to increase in relative importance.

The trace gases associated with the formation of tropospheric ozone (itself a 'greenhouse gas') all have significant tropical sources. These gases are principally CO, NO<sub>x</sub> and hydrocarbons (including methane and a wide variety of other volatile organic compounds). Their concentrations, and the concentration of O<sub>3</sub>, are exceptionally high in the lower troposphere in the tropics during the dry months, when extensive vegetation burning takes place (Fishman et al., 1991; Lacuax et al., 1993). Savanna burning has been going on for millennia,

and there are no objective data to support or refute claims that the area burned has changed substantially at a global scale in recent decades. At a local scale, burning frequency has increased in some places and decreased in others. Biomass burning associated with tropical forest clearing and domestic fuel use are certain to have increased this century. Soils are a significant source of  $\text{NO}_x$ , especially in semi-arid climates (Parsons et al., 1996). Preliminary indications are that the savannas of the world are a major hydrocarbon source (Guenther et al., 1994). The atmospheric concentration record for these trace gases is too short, variable and incomplete to demonstrate an historical trend, and there are no convincing predictions for future changes.

### 2.3. *Climate*

Although the general mechanism for the ‘greenhouse effect’ is now widely accepted, it is not yet generally accepted within the scientific community that recent climatic trends, which are in the directions predicted by the hypothesis, are either statistically significant or indisputably attributable to an enhanced greenhouse effect. This uncertainty is largely due to the high inherent variability of the global climate system and the many possible sources of measurement error. Direct, unequivocal proof of global climate change will probably emerge this decade; some studies already claim to have proved aspects of it (Thompson, 1995). Evidence supporting climate change is at present mostly circumstantial, based on surrogate variables, such as retreating glaciers (Hastenrath, 1992) and rising sea levels, models of atmospheric physics and correlations between palaeoclimates and their atmospheres.

The mechanisms, magnitude and even direction of the second- and third-order changes which may occur in the global geosphere–biosphere system are still controversial. In particular, the potential stabilizing effects of some feedback mechanisms are not fully understood (Lindzen, 1992). For instance, will higher atmospheric  $\text{CO}_2$  stimulate photosynthesis sufficiently to slow down the future rise in the concentration of this gas, or will the increased temperatures cause more respiration, and accelerate the increase?

An increase in the global mean temperature is the most secure of the global climate change predictions. As the models have become more sophisticated, the predicted increase by the middle of the 21st century (the so-called ‘doubled  $\text{CO}_2$ ’ simulation) has converged towards the middle of the 1.9–5.2°C range. The models can predict the current global temperature and its distribution quite accurately. They predict that a future increase in global temperatures will be slightly more pronounced near the poles than near the equator, and that minimum temperatures will increase more than maximum temperatures (Mitchell et al., 1995).

Given that ecosystem processes in the tropics are generally not constrained by low temperatures, of what significance is a 2°C mean temperature increase?

Direct impacts on plant physiology will probably be small, since the temperature response of key enzymatic processes such as photosynthesis are relatively flat in the tropical temperature range. Some plants with a C3 metabolism may become uncompetitive in very hot areas. On the cooler margins of the tropics, the length of the growing season and plant production will increase, and frost risk decrease.

The indirect impact of a small temperature increase on plants could be substantial. One possible mechanism is through increased evaporative demand. A 1°C temperature rise in the semi-arid tropics (where water availability is the main constraint on ecosystem function) increases potential evapotranspiration by about a 15%. In reality this is likely to be balanced by a simultaneous increase in plant water use efficiency under elevated CO<sub>2</sub>, and possibly an increase in rainfall. Another mechanism of temperature impact on plants is through the differential temperature response curves of C3 and C4 plants (Culotta, 1995). In savannas, trees (C3) are in competition with grasses (C4). Higher temperatures favor C4 over C3, but will be partly counter-balanced by the advantages which elevated CO<sub>2</sub> gives to C3 plants.

The global circulation models (GCM) predict an increase in global precipitation of 5 to 15% with doubled CO<sub>2</sub> (Houghton, 1994). This follows directly from the increased evaporation at higher temperatures. However, precipitation will not necessarily increase regionally or locally, since water vapor can be transported great distances before it falls as rain. Rainfall associated with the inter-tropical convergence zone is tentatively predicted to increase, while a decrease seems likely in the dry tropics. From a tropical ecology point of view, a key uncertainty in the climate models is their poor performance in predicting rainfall at the local scale. The current spatial resolution of the climate models is too coarse to simulate the small-scale convective processes which deliver most tropical rainfall. For ecosystems driven by individual rainfall events, such as the semi-arid and arid tropics, this makes predictions of impacts very difficult.

For the next several years terrestrial scientists will probably have to make do with water balance predictions which are unsatisfactory from an ecological or agronomic point of view. Thereafter, improvements in computational capacity will allow finer-resolution climate models, including global models with smaller grids and high-resolution regional models nested within global models. Linkage of the climate models to better ocean models and dynamic vegetated surface models will provide more credible tools for exploring the reciprocal relationship between tropical ecosystems and the global climate.

### **3. Driving variables of tropical terrestrial ecosystems**

Ecosystems can be thought of as consisting of objects (such as organisms, the soil and the atmosphere) and their interactions. Biogeochemistry focuses on one



category of interactions, the fluxes of matter between objects. Community ecology mostly deals with what types of organisms are present and their non-material interactions. Both approaches are necessary to understand the totality of ecosystem function in the long term.

3.1. Process change: biogeochemistry

Fig. 2 is a simple representation of the biogeochemistry of terrestrial ecosystems. Two of the control points are particularly important: the assimilation of CO<sub>2</sub> and nutrients and their synthesis into living tissue; and the disassembly of dead organic molecules to release nutrients and CO<sub>2</sub>. The former process, known as primary production, occurs initially in the leaves of plants. The rate-controlling step has traditionally been regarded as the capture of CO<sub>2</sub> molecules (photosynthesis) and much research has been focused on the factors which control this process. Photosynthesis can be accurately predicted from radiation, temperature, atmospheric CO<sub>2</sub> concentration, and leaf properties such as stomatal conductance and the concentration of assimilatory enzymes (Hall et al., 1993). All of these factors will be altered to lesser or greater degree by

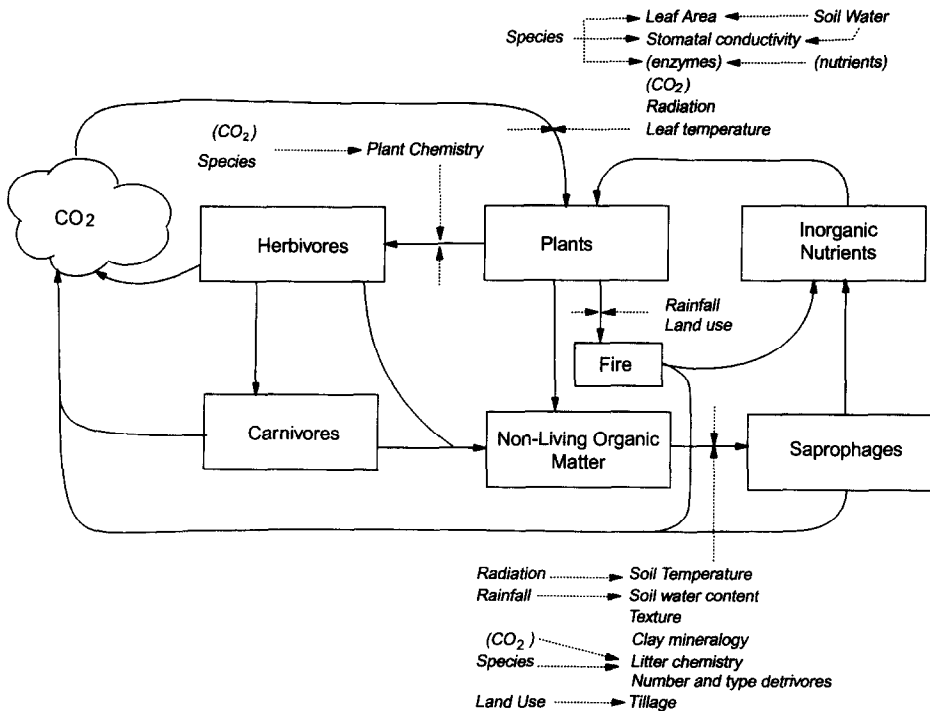


Fig. 2. A highly simplified model of a tropical terrestrial ecosystem. The key process control-points are shown as bow-ties, and their driving variables are in italics. The solid arrows are transfers of matter, while the dotted arrows are influences.

global change, so carbon assimilation will be affected. It is still unclear whether plants will acclimate to elevated  $\text{CO}_2$  in the longer term by down-regulation of the assimilatory process (Bazzaz, 1990, Culotta, 1995).

Predicting the net rate of carbon assimilation by an ecosystem requires a knowledge of species composition, vegetation structure (biomass and architecture) and the seasonal development of leaf area in addition to the abiotic drivers listed above. These variables are altered in the medium term by land use change, and in the long term by the link between climate and community composition discussed below.

It is clear from Fig. 2 that in ecosystems where nutrients are conserved and in limited supply, the rate of carbon cycling can in principle be controlled by the dissimilative processes as much as by the assimilative processes. Primary production can be constrained by the rate at which nutrients are freed from organic bondage and made available for assimilation. This process occurs principally in the soil and is mediated by the soil organisms. In the tropics, where radiant energy is abundant but soils are frequently nutrient-deficient, a strong argument can be made that most ecosystems are nutrient- rather than carbon-constrained. Therefore, the process limiting the rate of carbon cycling through the ecosystem is decomposition, except in high-input agroecosystems, where excess nutrients are supplied, and carbon assimilation may become rate-limiting.

Decomposition occurs in a number of overlapping steps, each of which releases a portion of the carbon and nutrients. Dead plant, animal and microbial tissues are consumed by bacteria and fungi, which convert part of the material into microbial biomass and respire the rest. The microbial biomass eventually dies and becomes substrate for decomposition itself. A small fraction of the microbially-processed material is converted to amorphous, structurally complex, high molecular weight organic compounds which are more resistant to further microbial decomposition. These, plus the partially decomposed particles of dead organisms, form the main reservoirs of soil carbon, nitrogen and sulfur. In weathered tropical soils they are also the main medium-term reservoir of plant-available phosphorus.

The rate of decomposition is controlled by temperature, soil moisture, the composition and size of the soil biota, and the accessibility and chemical composition of the substrate (Swift et al., 1979). Microbial access to organic substrates in the soil is controlled by the soil clay content and its mineralogy, directly and via its influence on soil structure. Substrate chemical composition is related to the vegetation type and its nutrient supply, particularly of nitrogen. Tropical vegetation is typically defended against herbivory (particularly by insects) by secondary chemicals such as tannins, which retard decomposition (Chapin, 1991). In the tropics, decomposition is particularly sensitive to the soil moisture regime and the land cover type.

A variety of models have been used to estimate changes in the soil carbon

and nutrient pools in response to environmental change. They range from simple (i.e. simple in structure and modest in data requirements; Post et al., 1982; Buringh, 1984; Janssen, 1984), to complex (many C-pools and linkages and demanding many parameters; Parton et al., 1987; Jenkinson, 1990; Rastetter et al., 1991). Computational and data constraints make it difficult to apply this last class of models at a global scale, but these limitations are rapidly being overcome. Most of the models were originally devised for a specific type of land use and environment, usually outside the tropics. They are increasingly applied in the tropics, often quite successfully (Sanford et al., 1991). In view of our limited insight into key aspects of C dynamics in soil–vegetation systems, further critical testing and improvements are needed before these models can be used with confidence to predict effect of global change in all ecosystems. In the long-term, climate affects non-organic soil properties such as the clay mineralogy, which in turn influence soil organic matter dynamics. Even the complex dynamic models do not include such long-term effects.

The production of fine roots is one of the major C inputs to the soil, but its rate in relation to soil fertility is still strongly debated (Hendricks et al., 1993). Less is known about other avenues of transfer of carbon from the root to the soil, such as the production of exudates and the sloughing of cells, except that they can be an important source of soil C, which will probably vary with the CO<sub>2</sub> content of the atmosphere (Lekkerkerk et al., 1990). The relationship between the chemical and physical nature of both plant material and the conceptual pools of soil organic matter used in the models needs clarification. The lignin-to-nitrogen ratio of plant material used in the Century model has proven to be a useful index of decomposability of plant material, but is probably too simplistic for many tropical litters. For instance, the breakdown of cellulose-rich litter may be stimulated by adding N but the reverse may be true in the long term for lignin-rich litter (Fog, 1988).

Oades (1989) points out that the physical or chemical protection of organic C is a quantitatively important, but very poorly understood. The commonly observed positive relationship between the clay contents of soil and its carbon content is captured in complex dynamic models by modifying the turnover rates of the pools as a function of soil texture. This approach gives satisfactory results in an area of similar mineralogy, such as the Great Plains region where it was developed. It is unlikely to be as successful in spanning the big difference between most tropical and temperate soils in soil mineralogy, which must strongly affect the accumulation of residual substrate. Trumbore (1997) observed a predominance of very young organic C in the ‘heavy’ (humified, clay-associated) fraction of a tropical surface soil. Temperate surface soils have a large amount of old organic C in that fraction. Practically all the current models consider a single soil surface horizon in the order of 0.2 to 0.3 m depth. In reality, rates of decomposition decrease strongly with soil depth (Hunt, 1977), and that decrease cannot be explained by differences in temperature and

moisture. In savannas, which make up the bulk of the tropical land area, the decomposition process can be accelerated by fire and herbivory. Both of these processes are highly influenced by land use decisions.

### 3.2. Changes in community composition

The theoretical basis for predicting the distribution of organisms in relation to climate is summarized in Fig. 3. All organisms have tolerance limits with respect to environmental variables such as temperature and moisture. In the presence of competing species, the physiological tolerance range is narrowed to that range where the organism is ecologically competitive. The competitiveness of most crop plants in the absence of human intervention is small, so the distribution is determined by the limits of the area that can be cultivated economically.

The defining limits may apply to only a particularly sensitive portion of the life history of the organism. This conceptual model only predicts the equilibrium distribution, and not the time required to reach it following environmental change; the latter requires consideration of the lifespan and dispersal rate of the organism. In the tropics the main factors determining plant species distribution are aridity (best indexed by the duration and seasonal pattern of plant-available

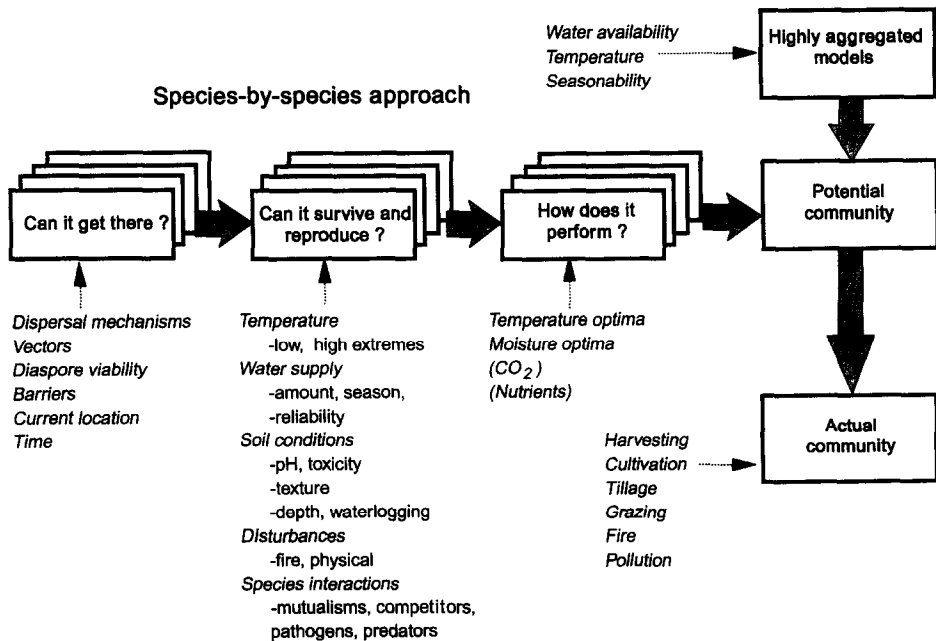


Fig. 3. Conceptual approaches to predicting the presence or absence of a given species, and its contribution to a community, under a changing environment.

soil water), the minimum annual temperature, specific soil requirements and the accidents of evolution and geomorphology.

Predicting community distribution from individual species tolerances is difficult in tropical ecosystems, which typically have hundreds of species and a rich array of community interactions such as competition and mutualism. One approach is to skip to a higher level of organization, and determine the environmental limits of broad vegetation types (biomes) as if they were species themselves (Ellery et al., 1991; Prentice et al., 1992). Water availability and its seasonal trend, and minimum temperatures emerge once again as the key factors in the tropics. Palaeobotanical information suggests that plants respond to climate change as individuals rather than as communities. Thus, a future climate could support biomes unknown in the present world. A more mechanistic approach uses basic ecophysiological arguments to define which ‘functional’ plant types can exist in a particular environment, and builds ‘functional’ vegetation types from these. These approaches all refer to potential vegetation cover. Increasingly in the tropics, the actual vegetation cover is determined more by human interventions than by the biophysical constraints.

The various approaches are beginning to converge. It is now possible, at the subcontinental scale, to run linked patch, biome and biogeochemical models, each at their own spatial and temporal scale (VEMAP, 1995). The biome models define the input parameters for the biogeochemical models, which in turn constrain a subsample of patch models. The patch models in turn provide the dynamics for the biome models. Such a system has yet to be attempted in the tropics.

#### **4. Conclusions**

For the next several decades, land use and land cover change will continue to be the most significant and obvious aspect of environmental change in the tropics. Demographic and economic factors will control the rate of these changes, and soil and climate and political factors will constrain their location. Thereafter the effects of atmospheric composition and climate change may become paramount.

The types and magnitudes of predicted potential changes in driving variables are sufficient to have far-reaching impacts on tropical ecosystems, according to known mechanisms. The processes of nutrient and carbon assimilation and dissimilation are the key points of interaction between the terrestrial biosphere, the atmosphere and the climate.

The future state of driving variables is not yet sufficiently predictable to make reliable forecasts of ecosystem responses. The development of models to translate abiotic drivers into biological impacts is already quite advanced, but must continue and accelerate in some areas. One such area is in the tropics.

## References

- Alcamo, J., 1994 (Ed.). *IMAGE 2.0: Integrated modelling of global climate change*. Kluwer, Dordrecht, 317 pp.
- Bazzaz, F.A., 1990. The response of natural ecosystems to the rising global CO<sub>2</sub> levels. *Ann. Rev. Ecol. Syst.* 21, 167–196.
- Borden, T.A., Sepanski, R.J., Stoss, F.W., 1991. *Trends 91: A Compendium of Data on Global Change*. Oak Ridge National Laboratory, 665 pp.
- Bouwman, A.F., Fung, I., Matthews, E., John, E., 1993. Global analysis of the potential for N<sub>2</sub>O production in natural soils. *Global Biogeochem. Cycles* 7, 557–597.
- Buringh, P., 1984. Organic carbon in soils of the world. In: Woodwell, G.M. (Ed.), *The Role of Terrestrial Vegetation in the Global Carbon Cycle: Measurement by Remote Sensing*. Wiley, Chichester, pp. 91–109.
- Chapin II, F.S., 1991. Effects of multiple environmental stresses on nutrient availability and use. In: *Response of Plants to Multiple Stresses*. Academic, New York, pp. 67–88.
- Culotta, E., 1995. Will plants profit from high CO<sub>2</sub>. *Science* 268, 654–656.
- Denning, A.S., Fung, I.Y., Randall, D., 1995. Latitudinal gradient of atmospheric CO<sub>2</sub> due to seasonal exchange with land biota. *Nature* 376, 240–243.
- Desjardins, T., Andreux, F., Volkoff, B., Cerri, C.C., 1994. Organic carbon and <sup>13</sup>C content in soils and soil size classes and their changes due to deforestation and pasture installations in eastern Amazonia. *Geoderma* 61, 103–118.
- Ellery, W.N., Scholes, R.J., Mentis, M.T., 1991. An initial approach to predicting the sensitivity of the South African grassland biome to climate change. *S. Afr. J. Sci.* 87, 499–503.
- Fishman, J., Fakhruzzaman, K., Cros, B., Nyanga, D., 1991. Identification of widespread pollution in the southern Hemisphere deduced from satellite analyses. *Science* 252, 1693–1696.
- Fog, K., 1988. The effect of added nitrogen on the rate of decomposition of organic matter. *Biol. Rev.* 63, 433–462.
- Guenther, A., Hewitt, C., Allwine, G., Berdowski, J., Dollard, G., Duyser, J., Ennis, C., Erickson, D., Fall, R., Geron, C., Gould, T., Graedel, T., Harley, P., Holland, E., Janson, R., Klinger, L., Lamb, B., Kerdu, M., McKay, B., Middleton, P., Monson, R., Pierce, T., Reed, B., Scholes, R., Simpson, D., Seuert, G., Steinbrecher, R., Tallamraju, R., Tarrason, L., Taylor, J., Trainer, M., Veldt, C., Yokouchi, Y., Westberg, H., Zimmerman, P., 1994. Global natural VOC emissions: an IGAC–GEIA inventory and assessment of uncertainties. *J. Geophys. Res.*, 100: 8873–8892.
- Hall, D.O., Scurlock, J.M.O., Bolhar-Nordenkamp, H.R., Leegood, R.C., Long, S.P., 1993. *Photosynthesis and Production in a Changing Environment*. Chapman and Hall, London, 464 pp.
- Hastenrath, S., 1992. Greenhouse indicators in Kenya. *Nature* 355, 503–504.
- Hendricks, J.J., Nadelhoffer, K.J., Aber, J.D., 1993. Assessing the role of fine roots in carbon and nutrient cycling. *Tree* 8, 174–177.
- Houghton, J.T., Jenkins, G.J., Ephraums, J.J., (Eds.), 1990. *Climate Change: The IPCC Scientific Assessment*. Cambridge University Press, Cambridge.
- Houghton, R.A., 1994. Balancing the global carbon cycle with terrestrial ecosystems. In: Zepp, R.G., Sontag, Ch. (Eds.), *The Role of Non-living Organic Matter in the Earths Carbon Cycle*. Wiley, Chichester, pp. 133–154.
- Hunt, H.W., 1977. A simulation model for decomposition in grasslands. *Ecology* 58, 469–484.
- Janssen, B.H., 1984. A simple model for calculating decomposition and accumulation of young organic matter. *Plant Soil* 76, 297–304.
- Jenkinson, D.S., 1990. The turnover of organic carbon and nitrogen in soils. *Philos. Trans. R. Soc. Lond. Biol. Sci.* 329, 361–369.

- Keeling, C.D., Bacastow, R.B., Bainbridge, A.E., Eckdahl, C.A., Geunther, P.R., Waterman, L.S., Chin, J.F.S., 1976. Atmospheric carbon dioxide variations at Mauna Loa Observatory, Hawaii. *Tellus* 28, 538–551.
- Keller, M., Veldkamp, E., Weitz, A.M., Reiners, W.A., 1993. Effect of pasture age on soil trace-gas emissions from a deforested area of Costa Rica. *Nature* 365, 244–246.
- Khalil, M.A.K., Rasmussen, R.A., 1992. The global sources of nitrous oxide. *J. Geophys. Res.* 97, 14651–14660.
- Lacuax, J.-P., Cachier, H., Delmas, R., 1993. Biomass burning in Africa: An overview of its impact on atmospheric chemistry. In: Crutzen, P.J., Goldammer, J.G. (Eds.), *Fire and the Environment: The Ecological, Atmospheric and Climatic Importance of Vegetation Fires*. Wiley, Chichester, pp. 159–191.
- Lavelle, P., Gilot, C., Pashanasi, B., 1994. Soil fauna and sustainable land use in the tropics. In: Greenland, D.J. (Ed.), *Soil Resilience and Sustainable Land Use*. CABI, Wallingford, pp. 291–308.
- Lekkerkerk, L.J.A., van de Geijn, S.C., van Veen, J.A., 1990. Influence of elevated atmospheric CO<sub>2</sub> levels on the carbon economy of a soil planted to wheat. In: Bouwman, A.F. (Ed.), *Soils and the Greenhouse Effect*. Wiley, Chichester, pp. 423–429.
- Lindzen, R., 1992. Absence of scientific basis. *Nat. Geogr. Res.* 9, 191–200.
- Madeley, J., 1993. Raising rice in the savannas. *New Sci.* 00-00, 36–38.
- Mitchell, J.F.B., Johns, T.C., Gregory, J.M., Tott, S.F.B., 1995. Climate responses to increasing levels of greenhouse gases and sulphate aerosols. *Nature* 376, 501–504.
- Neftel, A., Oeschger, H., Schwander, J., Stauffer, B., Zumbun, R., 1982. Ice core sample measurements give atmospheric CO<sub>2</sub> content during the past 40000 years. *Nature* 295, 220–223.
- Oades, J.M., 1989. An introduction to organic matter in mineral soils. In: Dixon, J.B., Weed, S.B. (Eds.), *Minerals in the Soil Environment*. Soil Sci. Soc. Am., Madison, WI.
- Parsons, D., Scholes, M.C., Scholes, R.J., Levine, J.S., 1996. Biogenic nitric oxide emissions from savanna soils as a function of fire regime, soil type, soil nitrogen and water status. *J. Geophys. Res.*, 23683–23688.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci. Soc. Am. J.* 51, 1173–1179.
- Phillips, O.L., Gentry, A.H., 1994. Increasing turnover through time in tropical forests. *Science* 263, 954–958.
- Post, W.M., Emmanuel, W.R., Zinke, P.J., Stangenberger, A.G., 1982. Soil carbon pools and world life zones. *Nature* 298, 156–159.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A., Solomon, A.M., 1992. A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.* 19, 117–134.
- Rastetter, E.B., Ryan, M.G., Shaver, G.R., Melillo, J.M., Nadelhoffer, K.J., Hobbie, J.E., Aber, J.D., 1991. A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO<sub>2</sub>, climate and N deposition. *Tree Physiol.* 9, 101–126.
- Sanford, R.L., Parton, W.J., Ojima, D.S., Lodge, D.J., 1991. Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: results of simulation modelling. *Biotropica* 23, 364–373.
- Scholes, R.J., Scholes, M.C., 1994. The effect of land use on non-living organic matter in the soil. In: Zepp, R.G., Sontag, Ch. (Eds.), *The Role of Non-living Organic Matter in the Earth's Carbon Cycle*. Wiley, Chichester, pp. 209–228.
- Shine, K.P., Derwent, R.G., Wuebbles, D.J., Morcrette, J.J., 1990. Radiative forcing of climate. In: Houghton, J.T., Jenkins, G.J., Ephraums, J.J. (Eds.), *Climate Change: The IPCC Scientific Assessment*. Cambridge University Press, Cambridge.

- Siegenthaler, U., Sarmiento, J.L., 1993. Atmospheric carbon dioxide and the ocean. *Nature* 365, 119–125.
- Skole, D., Tucker, C., 1993. Tropical deforestation and habitat fragmentation in the Amazon: Satellite data from 1978 to 1988. *Science* 260, 1905–1910.
- Skole, D.L., Moore III, B., Chomentowski, W.H., 1994. Spatial analysis of land cover change and carbon flux associated with biomass burning in Brazil, 1970–1980. In: Zepp, R.G. (Ed.), *Climate Biosphere Interaction: Biogenic Emissions and Environmental Effects of Climate Change*. Wiley, Chichester, pp. 161–200.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems*. Blackwell, Oxford.
- Tans, P.P., Fung, I.Y., Takahashi, T., 1990. Observational constraints on the global atmospheric CO<sub>2</sub> budget. *Science* 247, 1431–1438.
- Thompson, D., 1995. The seasons, global temperature and precession. *Science* 268, 59–68.
- Trumbore, S.E., 1997. Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. *Global Biogeochem. Cycles*.
- VEMAP, 1995. VEMAP Research Group: *A Comparison of Biogeography and Biogeochemistry Models in the Context of Global Change*. Natural Resource Ecology Laboratory, Colorado State University, Ft Collins, CO, USA.
- Watson, R.T., Meira Filho, L.G., Sanhueza, E., Janetos, A., 1992. Sources and sinks. In: Houghton, J.T., Callendar, B.A., Varney, S.K. (Eds.), *Climate Change 1992: The Supplementary Report to the IPCC Scientific Assessment*. Cambridge University Press, Cambridge, pp. 22–46.