Effects of Global Climate Change on Vegetation Distribution

Statement of the Problem
Global CO₂ emissions may generate two classes of ecological impacts at the global scale. One involves the global carbon cycle and another involves the Earth’s biodiversity. Both are affected in large part by the potential redistribution of vegetation on the Earth. Currently, the many different kinds of unmanaged vegetation are adapted to today’s climate; as climate changes, each kind of vegetation must change as well, dying out in places where climate becomes too stressful, and prospering where climate becomes salubrious. As the Earth warms from increasing atmospheric greenhouse gases, the redistribution of vegetation can induce the terrestrial biosphere to become either a source of additional CO₂ (quickening the warming) or a sink for CO₂ (reducing the warming). Which course it will take is not known. For example, a warmer earth should support more forests that contain high carbon densities, but the warmest places on earth today support only sparsely-vegetated deserts. As vegetation changes, so do the ecosystems on which populations of plants and animals depend for their existence. Hence, biodiversity will also be impacted by vegetation redistribution. The NHEERL research effort of the 1990’s focused on the carbon cycle implications of vegetation redistribution.

Approach
Estimating future vegetation redistribution was based on developing predictive models. One group of models was designed to correlate the geography of climate with the geography of vegetation types. Then the future distribution of climate was used as a basis for redrawing the geography of the vegetation types (including agriculture). Once the new distributions of vegetation types were defined, the carbon they could store was calculated -- assuming that their current carbon densities would be supported in their future distributions.

A second group of models accounted mechanistically for processes which determine the growth, shifting density, and carbon uptake of vegetation during chronic climate change. These processes include the rapid dieback, reproduction, and slow regrowth of forests -- all processes which induce lags in vegetation response to rapid climate change. Although these processes could not be treated mechanistically in the correlative models described above, we did approximate the process effects in the correlative models, using values consistent with known biotic change rates.

Main Conclusions
The redistribution of global vegetation in response to climate and land use change during the next century is likely to generate a several-decade long pulse of carbon dioxide from the biosphere into the atmosphere. The result will enhance the buildup of greenhouse gases resulting from anthropogenic emissions.
Critical to the modeling effort was developing precise data bases for climate and vegetation (e.g., EPA/NOAA 1992, 1993). Early work used life form classifications (e.g., Sedjo and Solomon 1988; King and Neilson 1992). Later work used known climate thresholds to assemble different plant functional types (PFTs) in each ½ X ½ degree of latitude and longitude (Prentice et al. 1992). The presence of different combinations of PFTs defined biomes (temperate deciduous forest, cold grasslands, etc.). In addition to assessing vegetation redistribution impacts on the carbon cycle (e.g., Solomon, et al. 1993, 1996; Solomon 1996, 1997), we also assessed land use effects (Cramer and Solomon 1993, Leemans and Solomon 1993, Solomon and Leemans 1997), rapid tree dieback, differential availability of seeds, and slow regrowth of vegetation (Solomon and Kirilenko 1997, Kirilenko and Solomon 1998). Primary conclusions were:

1) The capacity of the terrestrial biosphere to remove and store atmospheric carbon should be greater under a warmer global climate.

2) The slow death and growth responses by vegetation would generate a pulse of carbon from vegetation 15-20% as great as that from anthropogenic emissions.

3) Increasing intensity of agriculture in higher latitudes would permanently reduce the capacity of the earth to store carbon below its’ current storage capacity.

A second modeling approach used climate correlations (rather than climate thresholds) to define the climate space occupied by U.S. vegetation types (Neilson et al. 1992), and then applied a physiology model which calculated the uptake of CO₂ by photosynthesis and emission of CO₂ by respiration in each vegetation type (Neilson 1993a, 1995). This approach used climate projections calculated by global climate models to define new vegetation distributions. Then, based on the new distributions of vegetation types, the projected balance of carbon uptake and emission from vegetation was determined. Expanded to a global scale (Neilson 1993b, 1998, Neilson and Marks 1994), this approach could simulate the direct effects of increasing CO₂ (a plant nutrient) on biomass storage. Applied to future climate conditions using several climate scenarios, this research suggested, but did not confirm, the potential presence of a multi-decade transient pulse of atmospheric carbon (Neilson 1993b, 1998).

The modeling effort could not estimate the effects on carbon storage of slow vegetation responses to rapid climate changes. Instead, carbon storage was projected assuming that climate and vegetation distributions are stable. However, “there is no indication that a stable climate will appear in the foreseeable future. Indeed, the global change problem to be assessed involves rapidly changing climate, not stable climate” (Solomon et al. 1996). Forest gap models were used to estimate the time-related responses of vegetation to rapid climate change. These models replicate the death, reproduction, growth, and maturity of trees, and the development of forest ecosystems (Solomon and Bartlelin 1992, Solomon and West 1993, Bugmann and Solomon 1995, 2000). Although assessment exercises with these models (Solomon and Bartlelin 1992, Bugmann et al. 2001) confirmed the potential for the long-term carbon pulse that was described by the static correlative
models, the gap models have not yet been applied on the globally-comprehensive basis needed to thoroughly evaluate the carbon pulse phenomenon.

**Measured Global Vegetation Biomes**

Map of measured global vegetation biomes, including land dominated by agriculture, from various literature sources compiled and mapped by J. S. Olson, *et al.*, 1983 (from Solomon and Leemans, 1997, p. 141). Notice the effects of low temperature limits to plant growth shown by the latitudinal bands of boreal vegetation in the polar regions, and the dominance of low moisture limits to plant growth (1) in temperate and regions, shown by the longitudinal bands of agricultural and natural vegetation, and (2) in tropical regions shown by the latitudinal presence of hot deserts along the subtropical convergence zone where sinking air blocks frontal passage and thus precipitation. The finer-scale complexity of the global biome distribution patterns is derived from the local and regional variations in soils, topography, and land use.
Modeled Global Vegetation Biomes

Map of modeled global vegetation biomes, including land suitable for agriculture. This map is defined entirely by known cardinal climate thresholds applied through the BIOME model, with no reference to the actual vegetation present. Modeled biomes are identified in the legend above (from Solomon and Leemans 1997, p. 141). Comparing this map with the previous one, notice that the model maintains the biome distribution patterns with regard to low temperature and low moisture dominance in polar, temperate and tropical regions, as well as many of the finer-scale biome distribution patterns derived from the local and regional variations in soils, topography, and land use. The ability to use climate data as proxy vegetation to reproduce the known patterns of biome distribution is critical to subsequent efforts aimed at projecting maps of future vegetation and carbon storage under climate warming scenarios.
**Future Global Vegetation Biomes**

Map of future global vegetation biomes, including land suitable for agriculture, under a future climate at the time atmospheric CO$_2$ concentrations double. The climate changes used to drive the BIOME model are among the mildest simulated by general circulation models of the atmosphere, that is, the global climate model (ECHAM-1 by the Max Plank Institute, Hamburg; see Greco et al. 1994) is only moderately sensitive to greenhouse gas concentrations.

Note the great increase in land suitable for agriculture toward polar areas, a feature which follows from expected climate changes: all general circulation models of the atmosphere (global climate models) project a greater increase in warming at the poles than at the equator, a greater warming in winter than in summer, and a greater warming at night than in daytime. As a result, the projected climate in high latitudes is expected to increase greatly in days with temperatures constantly above freezing, and in the annual growing season length. Indeed, polar growing seasons have already increased 12 to 18 days since 1980, as measured by satellites.

Note also that, compared with the previous map, this map shows areas of natural vegetation in temperate areas dominated by dryland biomes, especially thorn shrub vegetation, and boreal forests severely reduced as potential agriculture covers low latitude growing areas, with little space to grow toward the higher latitudes.
The **CO₂ Pulse**

Total carbon stored by the terrestrial biosphere in separate biomes and in total in Pg (petagrams, \(10^{15}\) g). Carbon storage is simulated for 500 years into the future, with a warming scenario from ECHAM-1, by the Max Plank Institute in Hamburg (Greco et al. 1994), from year 0 to that from a doubling of atmospheric CO₂ concentrations at year 100. Minus values represent release of carbon from the terrestrial biosphere to the atmosphere, positive values represent storage of carbon into the terrestrial biosphere from the atmosphere (from an unpublished version of the MOVE model (Kirilenko and Solomon 1998) which includes stochastic rather than constant rates of tree mortality and growth).

The total biomass of the terrestrial biosphere declines markedly for the first 100+ years of this simulation, defining the multi-decadal pulse of carbon to the atmosphere discussed in the text. Note that only grassland vegetation initially increases in biomass, as it replaces the woody vegetation types which dieback during early warming and which only gradually regrow to out compete the herbaceous vegetation.
References Cited


Annotated Bibliography of WED Research


Current scientific concerns regarding the impacts of global change include the responses of forest composition and biomass to rapid changes in climate, and forest gap models have often been used to address this issue. These models reflect the concept that forest composition and biomass in the absence of large-scale disturbance are explained by competition among species for light and other resources in canopy gaps formed when dominant trees die. Since their initiation 25 yr ago, a wide variety of gap models have been developed that are applicable to different forest ecosystems all over the world. Few gap models, however have proved to be equally valid over a wide range of environmental conditions, a problem on which our work is focused.

We previously developed a gap model that is capable of simulating forest composition and biomass in temperate forests of Europe and eastern North America based on a single model structure. In the present study, we extend the model to simulate individual tree species response to strong moisture seasonality and low temperature seasonality, and we modify the widespread parabolic temperature response function to mimic nonlinear increases in growth with increased temperature up to species-specific optimal values.

The resulting gap model, FORCLIM V2.9, generates realistic projections of tree species composition and biomass across a complex gradient of temperature and moisture in the Pacific Northwest of the United States. The model is evaluated against measured basal area and stand structure data at three elevations of the H. J. Andrews LTER site, yielding satisfactory results. The very same model also provides improved estimates of species composition and stand biomass in eastern North America and central Europe, where it originated. This suggests that the model modifications we introduced are indeed generic.

Temperate forests other than those we studied here are characterized by climates that are quite similar to the ones in the three study regions. Therefore we are confident that it is possible to explain forest composition and biomass of all major temperate forests by means of a single hypothesis as embodied in a forest gap model.


Future global carbon (C) cycle dynamics under climates altered by increased concentrations of greenhouse gases (GHGs) will be defined in part by processes which control terrestrial biospheric C stocks and fluxes. Current research and modeling activities which involve
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terrestrial C have focused on the response of unmanaged vegetation to changing climate and atmospheric chemistry. A common conclusion reached from applying geographically explicit terrestrial carbon models is that more C would be stored by equilibrium vegetation controlled by a stable GHG-warmed climate than by equilibrium vegetation under the current (stable) climate. We examined the potential impact on the terrestrial C cycle if global agriculture were to increase to the limits permitted by future GHG-induced climates. Climatic limits to global agricultural zones were determined, the new climatic limits to agricultural zones projected, and the amount of C the terrestrial biosphere would store under the new climate and agricultural conditions was calculated. We conclude that following a warming loss of C from agriculture could be as important as gain of C by climate effects. As much or less C would be stored by a terrestrial biosphere in which agriculture reached its new climatic limits as is stored by the current biosphere in which agriculture reaches its climatic limits. We project that agriculture alone could produce a C source of 0.3 to 1.7 Pg yr\(^{-1}\) if doubling of GHGs required 50 to 100 yr. The gains in agriculture would occur almost entirely in the developed countries of high latitudes, and the losses, in the less developed countries of the lower latitudes.


Two methods are investigated for interpolating daily minimum and maximum air temperatures (\(T_{\text{min}}\) and \(T_{\text{max}}\)) at a 1 km spatial resolution over a large mountainous region (830 000 km\(^2\)) in the U.S. Pacific Northwest. The methods were selected because of their ability to (1) account for the effect of elevation on temperature and (2) efficiently handle large volumes of data. The first method, the neutral stability algorithm (NSA), used the hydrostatic and potential temperature equations to convert measured temperatures and elevations to sea-level potential temperatures. The potential temperatures were spatially interpolated using an inverse-squared-distance algorithm and then mapped to the elevation surface of a digital elevation model (DEM). The second method, linear lapse rate adjustment (LLRA), involved the same basic procedure as the NSA, but used a constant linear lapse rate instead of the potential temperature equation. Cross-validation analyses were performed using the NSA and LLRA methods to interpolate \(T_{\text{min}}\) and \(T_{\text{max}}\) each day for the 1990 water year, and the methods were evaluated based on mean annual interpolation error (IE). The NSA method showed considerable bias for sites associated with vertical extrapolation. A correction based on climate station/grid cell elevation differences was developed and found to successfully remove the bias. The LLRA method was tested using 3 lapse rates, none of which produced a serious extrapolation bias. The bias-adjusted NSA and the 3 LLRA methods produced almost identical levels of accuracy (mean absolute errors between 1.2 and 1.3°C), and produced very similar temperature surfaces based on image difference statistics. In terms of accuracy, speed, and ease of implementation, LLRA was chosen as the best of the methods tested.

The proposed research will quantify white spruce growth and document its latitudinal stability at the tree limit in the central Brooks Range over the life span of the living trees. The goal is to link tree growth and tree position to summer temperature and precipitation. Historical records from 1929 to 1938 from work by Robert Marshall have been used to identify tree limit sites and provide information to interpret the present location of the tree limit.


Global climate change as currently simulated could result in the broad-scale redistribution of vegetation across the planet. Vegetation change could occur through drought-induced dieback and fire. The direct combustion of vegetation and the decay of dead biomass could result in a release of carbon from the biosphere to the atmosphere over a 50- to 150-year time frame. A simple model that tracks dieback and regrowth of extra-tropical forests is used to estimate the possible magnitude of this carbon pulse to the atmosphere. Depending on the climate scenario and model assumptions, the carbon pulse could range from 0 to 3 Gt of C yr⁻¹. The wide range of pulse estimates is a function of uncertainties in the rate of future vegetation change and in the values of key model parameters.


The continued accumulation of radiatively-active trace gases in the atmosphere may significantly alter the climate of the Pacific Northwest. Mean annual temperatures could increase 2° to 5°C. The seasonality of precipitation will likely remain the same, but with annual totals remaining unchanged or increasing 20%.

The potential effects of these climate changes on Northwest forests have been estimated using a variety of modeling approaches and climate scenarios. Overall, 26 to 90% of the area in the Northwest may change from one general vegetation type to another. Forest area in the Northwest could decrease 5 to 25%. Remaining forest land would differ in species composition, and likely be less productive than current forests. In Oregon, drier Douglas-fir dominated forests would increase in area, whereas the more productive western hemlock - Douglas-fir forests would decrease. Forest vegetation zones would rise in elevation from 500 to 1000m. Alpine and subalpine forests could disappear from all but the highest elevations in the region.

Detrital carbon stores in the Oregon Cascades could be reduced by as much as 30% with a 5°C climate warming. Assuming no change in forest productivity, there could be a net loss of 60 Mg of carbon per hectare from the same region. This compares to a decrease in
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carbon storage of 305-370 Mg per hectare resulting from conversion of old growth forests to young plantations.

Forest disturbances such as fire, wind and pest/pathogen outbreaks will likely increase in frequency, speeding vegetation change in response to climate change. Disturbances imposed on forests through timber management practices may also hasten the response of forests to climate change. Also, current management practices coupled with natural disturbances may inhibit establishment of new forests at the same time as older forests are changing.

There are two key limitations to the data presented here. First, the transient (time-dependent) dynamics of change have not been adequately investigated. How forests respond to a rapidly changing but variable climate is uncertain. Second, the direct effects of enhanced CO₂ concentrations on forest species growth have not been considered in any of the modeling simulations. Laboratory experiments suggest the potential for increased drought tolerance by individual plants under higher CO₂ concentrations. The landscape scale impacts of higher CO₂ concentrations on vegetation and water balance are uncertain.

In sum, natural and human caused disturbances of the landscape will play a major role in the response of regional forests to climate change. The interplay of forest management and natural forest processes needs to be considered in future assessments of climate change impacts on Northwest forests. They also must be considered in designing mitigation options for reducing the impact of climate change on regional forests.

Forest managers are thus presented with a difficult problem. How should current forests be managed given 1) our uncertainty of the magnitude and direction of future climate change and 2) the potential for large changes in forest composition and distribution if the climate does change as currently simulated by state-of-the-art climate models?


Modeling potential global redistribution of terrestrial vegetation frequently is based on bioclimatic classifications which relate static regional vegetation zones (biomes) to a set of static climate parameters. The equilibrium character of the relationships limits our confidence in their application to scenarios of rapidly changing climate. Such assessments could be improved if vegetation migration and succession would be incorporated as response variables in model simulations. We developed the model MOVE (Migration Of VEgetation), to simulate the geographical implications of different rates of plant extirpation and in-migration. We used the model to study the potential impact on terrestrial carbon stocks of climate shifts hypothesized from a doubling of atmospheric greenhouse gas concentration. The model indicates that the terrestrial vegetation and soil could release carbon; the amount of this carbon pulse depends on the rate of migration relative to the rate of climate change. New temperate and boreal biomes, not found on the landscape today, increase rapidly in area during the first 100 years of simulated response to climate change. Their presence for several centuries and their gradual disappearance after the climate ceases to change adds uncertainty in calculating future terrestrial carbon fluxes.

The large-scale distribution of crops is largely determined by climate. We present the results of a climate-crop prediction model based on the U.N. Food and Agriculture Organization crop-suitability approach, implemented in a GIS (geographic information system) environment using several global environmental databases. The model utilizes daily temperature and soil moisture conditions to determine the properties of the growing period. Crops are characterized by their variety-specific minimum growing period requirements and photosynthesis and respiration properties. Temperature and radiation during the growing period control the development of each crop. The model simulates crop-specific geographic distributions by demarcating the region where rain-fed productivity is possible. The model takes only non-irrigated crop productivity into account and the potential increase in productivity by technical means is not considered. The model therefore shows no potential yield in arid, irrigation-dependent regions. The simulated distributions of crops under current climatic conditions coincide largely with the current agricultural regions. Simulations with an atmospheric general circulation model (AGCM)-derived climate-change scenario illustrate changes in the agricultural potential. There are large regional differences in the response. Only high-latitude regions uniformly benefit from the climatic change with projected longer growing periods and an increased productivity. Most other regions, however, do not benefit significantly or even lose productivity after such change. In most of the latter regions differences in moisture availability control the change. The analysis shows that agricultural potential and impacts of climatic changes can be simulated comprehensively.


A Mapped Atmosphere-Plant-Soil System (MAPSS) has been constructed for simulating the potential biosphere impacts and biosphere-atmosphere feedbacks from climatic change. The system calculates the potential vegetation type and leaf area that could be supported at a site, within the constraints of the abiotic climate. Both woody vegetation and grass are supported and compete for light and water. The woody vegetation can be either trees or shrubs, evergreen or deciduous, and needleleaved or broadleaved. A complete site water balance is calculated and integrates the vegetation leaf area and stomatal conductance in canopy transpiration and soil hydrology. The MAPSS model accurately simulates the distributions of forests, grasslands, and deserts and reproduces observed monthly runoff. The model can be used for predictions of new vegetation distribution patterns, soil moisture, and runoff patterns in alternative climates.

A new biogeographic model, MAPSS, predicts changes in vegetation leaf area index (LAI), site water balance and runoff, as well as changes in Biome boundaries. Potential scenarios of equilibrium vegetation redistribution under 2 X CO₂ climate from five different General Circulation Models (GCMs) are presented. In general, large spatial shifts in temperate and boreal vegetation are predicted under the different scenarios; while, tropical vegetation boundaries are predicted (with one exception) to experience minor distribution contractions. Maps of predicted changes in forest LAI imply drought-induced losses of biomass over most forested regions, even in the tropics. Regional patterns of forest decline and dieback are surprisingly consistent among the five GCM scenarios, given the general lack- of consistency in predicted changes in regional precipitation patterns. Two factors contribute to the consistency among the GCMs of the regional ecological impacts of climatic change: 1) regional, temperature-induced increases in potential evapotranspiration (PET) tend to more than offset regional increases in precipitation; and, 2) the unchanging background interplay between the general circulation and the continental margins and mountain ranges produces a fairly stable pattern of regionally specific sensitivity to climatic change. Two areas exhibiting among the greatest sensitivity to drought-induced forest decline are eastern North America and eastern Europe to western Russia. Drought-induced vegetation decline (losses of LAI), predicted under all GCM scenarios, will release CO₂ to the atmosphere; while, expansion of forests at high latitudes will sequester CO₂. The imbalance in these two rate processes could produce a large, transient pulse of CO₂ to the atmosphere.


The prospect of global change, fostered by human impacts on the global climate and by extensive alteration of the natural landscape, has raised concerns over the fate of the earth's natural biological diversity. Unfortunately, a definitive theory on the causes of biological diversity has been elusive. The absence of such a theory makes it difficult to project the consequences of global change on biodiversity. The ideal theory of biodiversity must, at least, be able to explain the spatial patterns of biodiversity and their changes through time. Our intent, in this chapter, is to explore some of the spatial patterns of biodiversity and to propose a few mechanisms that appear to account for much of this pattern. We are particularly attentive to the potential climatic drivers of spatial patterns of biodiversity.

Diversity can be defined in many different ways. Two manifestations of diversity are addressed in this chapter: (1) diversity of form (i.e., physiognomy), and (2) diversity of species. Physiognomy is used here to refer to both the plant life forms that are used to characterize biomes (Beard 1978) and to vegetation structure within a biome (e.g., the different relative amounts of overstory and understory life forms). Species diversity has two components: richness and evenness (Whittaker 1972, Cody 1975). Species richness is the number of
species in a sample, while evenness refers to their relative abundances (Whittaker 1972, Cody 1975). We restrict our discussion to species richness.

Spatial patterns of both physiognomic and species diversity have resulted from processes on two vastly different time scales: evolutionary and ecological. Over evolutionary time, new species and life forms arise, but this process usually requires millennia for terrestrial plants. Over ecological time, from years to centuries, evolution can be assumed to be static, and spatial patterns of species diversity arise from different spatial arrangements of species due to climatic and substrate forcing or to ecological interactions. Evolutionary time frames and processes are not discussed in this chapter. Rather, we attempt to extract the different influences of climate over short time scales on spatial patterns of diversity across a range of spatial scales. In addition to the separation of potential causes of diversity patterns at different scales, we look for mechanistic relationships between climate at large spatial scales and patterns of diversity at large and small spatial scales.

Recent reports suggest that climatic change could cause biomes to shift several hundred kilometers across the earth and that the physiognomy of any given biome could rapidly change to something quite different (e.g., Solomon 1986, Neilson et al. 1989, Winjum and Neilson 1989, Neilson et al. 1990). Both types of change—spatial and physiognomic—could threaten the extinction of large numbers of species. The ecotones between major biomes are probably landscapes that are sensitive to climatic change (di Castri et al. 1988) and should possess patterns of biodiversity that are unique relative to more central biome areas. We first describe a theory of physiognomic diversity and spatial distribution as driven by large-scale climatic patterns. This theory should explain the general physiognomy within biomes, as well as the location of the ecotones between biomes. We then attempt to relate local patterns of species diversity to the distributions of biomes, with particular attention to the relationships between diversity patterns and ecotones at regional and local scales.


Current projections of the response of the biosphere to global climatic change indicate as much as 50% to 90% spatial displacement of extratropical biomes. The mechanism of spatial shift could be dominated by either 1) competitive displacement of northern biomes by southern biomes, or 2) drought-induced dieback of areas susceptible to change. The current suite of global biosphere models cannot distinguish between these two processes, thus determining the need for a mechanistically based biome model. The first steps have been taken towards the development of a rule-based, mechanistic model of regional biomes at a continental scale. The computer model is based on a suite of empirically generated conceptual models of biome distribution. With a few exceptions the conceptual models are based on the regional water balance and the potential supply of water to vegetation from two different soil layers, surface for grasses and deep for woody vegetation. The seasonality of precipitation largely determines the amount and timing of recharge of each of these soil layers and thus, the potential mixture of vegetative life-forms that could be supported under a specific climate. The current configuration of rules accounts for the potential natural vegetation at about 94% of 1211 climate stations over the conterminous U.S. Increased temperatures, due to global warming, would 1) reduce the supply of soil moisture over much of the U.S. by reducing the volume of snow and increasing winter runoff, and 2) increase the potential evapotranspiration (PET).
These processes combined would likely produce widespread drought-induced dieback in the nation's biomes. The model is in an early stage of development and will require several enhancements, including explicit simulation of PET, extension to boreal and tropical biomes, a shift from steady-state to transient dynamics, and validation on other continents.


Accurate prediction of the ecological impacts of climatic change is a pressing challenge to the science of ecology. The current state of the art for broad-scale estimates of change in biomes and ecotones between biomes is limited to equilibrium estimates of ecological change under some future equilibrium climate. Uncertainties in these estimates abound, ranging from uncertainties in future climate scenarios to uncertainties in our ecological models and finally to uncertainties in modelling the feedbacks between the climate and the biosphere. Ecologists and policymakers need to go beyond equilibrium estimates of biosphere change to transient responses of the biosphere as the climate changes. Ecotones between biomes have been suggested as sensitive areas of change that could be effectively modelled and monitored for future change. Ecotones are also important in influencing local and regional biodiversity patterns and ecological flows. The ecological processes that could affect change at ecotones and within biomes are discussed; they include internal ecosystem processes, such as competition, and external abiotic processes, most notably drought and related disturbances. Drought followed by infestations and fire appears to be the most likely process that could mediate ecological change under a rapidly changing climate. The impacts would be apparent all across biomes, not just at ecotones. However, specific predictions about the dynamics of ecotones can be made qualitatively, based on a theory of patch scaling and diversity in relation to abiotic stressors. Under current conditions, the size of homogeneous patches is expected to be small at ecotones, but to enlarge with distance from the ecotone. Directional climatic change should promote a coalescence of patches on one side of the ecotone and increased fragmentation on the other side. Ecotones should begin to blur as viewed from a satellite only to re-form at some later date in a new location. This view is in contrast to the notion that ecotones would retain sharp distinction and simply move across the landscape. These changes are presented as hypotheses based on theory and should be testable in a mechanistic modeling framework that is only now being developed.


During the 21st century, global climate change is expected to become a significant force redefining global biospheric boundaries and vegetation dynamics. In the northern hardwood - boreal forest transition forests, it should, at the least, control reproductive success and failure among unmanaged mixed forest stands. One means by which to predict future responses by the mixed forests is to examine the way in which they have responded to climate changes in the past. We used proxy climate data derived from Holocene (past 10,000 years) pollen records in the western Upper Peninsula of Michigan to drive forest gap models, in an effort to define regional prehistoric vegetation dynamics on differing soils. The gap models mimic forest
reproduction and growth as a successional process and, hence, are appropriate for defining long-term tree and stand dynamics. The modeled period included a mid-postglacial period that was warmer than today's climate. Model failures, made apparent from the exercise, were corrected and the simulations were repeated until the model behaved credibly. Then, the same gap model was used to simulate potential future vegetation dynamics, driven by projections of a future climate that was controlled by greenhouse gases. This provided us with the same "measure" of vegetation in the past, present, and future, generating a continuously comparable record of change and stability in forest composition and density. The resulting projections of vegetation response to climate change appear to be affected more by the rate than by the magnitude of climate change.
Migration of populations or species of trees ('tree migration') in response to climate change is of interest both to palaeoecologists who assess past vegetational as responses to climate change, and to global ecologists concerned with future climate change induced by increasing greenhouse gases (GHGs). A major difference between climate-driven tree migrations in prehistory and those expected in the future is the high speed of the latter climate change. The 4-6 km which temperate-zone July isotherms are predicted to move northward annually (Solomon et al. 1984) are about an order of magnitude more rapid than prehistoric rates deduced from palaeoecological evidence. Assuming prehistoric rates of warming matched the rate of tree migration (T Webb 1986; Prentice et al. 1991), fossil pollen data allow inference of 400 m yr\(^{-1}\) (Davis 1983) to 800 m yr\(^{-1}\) (Gear & Huntley 1991) of climate change and tree migration at most. The rate may be even slower if tree migration includes the establishment and maturity of the tree population (Bennett 1986) as well as the processes of seed transport, establishment, growth and seed production, normally defined as migration (e.g. Davis 1989; MacDonald et al. 1993).

The difference in definition is important for predicting the amount of carbon (CO\(_2\) is the most important of the GHGs) that will reside in the atmosphere in the future. The oceans provide the ultimate long-term control on atmospheric carbon concentrations (e.g. Sundquist 1985; Prentice et al. 1993). However, the terrestrial biosphere modulates the shorter-term changes in carbon content, measured over a few decades or centuries (Gammon et al. 1985; Keeling et al. 1995; Denning et al. 1995). Forests store about 2/3 of above-ground terrestrial organic carbon and over half of the carbon present in the world’s soils (Dixon et al. 1994). The presence of a few trees on the landscape (e.g. MacDonald et al. 1993), indicated by establishment and reproductive maturity of seed trees, contributes little carbon to terrestrial stocks. Instead, closed-canopy stands of mature mixed or pure species provide the dense carbon stocks of interest. These are associated with mature, stable populations.

Projections of global terrestrial carbon cycle dynamics under warmer climates of a doubled GHG concentration have used static vegetation models (Prentice & Solomon 1990). These projections hinge on the critical assumption that the migration of trees and the formation of mature, stable populations at new locations proceeds at the same rate as the climate change to which it is responding (Sedjo & Solomon 1989; Leemans 1989; Prentice & Fung 1990; Smith et al. 1992a, b; Smith & Shugart 1993a, b; Solomon et al. 1993). To date, these static model exercises have projected increased global terrestrial carbon storage under future warming, because large new land areas suitable for forest growth are created either by warming of high latitude treeless tundra, or by increased hydrologic cycle intensity in treeless steppe.

Yet, unchanged or decreased rather than increased carbon storage may result if forests cannot migrate and establish in the time required to attain the doubled GHG benchmark. The objective of the current paper is to estimate the time required for forests to develop in regions new to them, to estimate the time required for forests to die out where they become climatically obsolete, then to calculate the impacts of those times on future terrestrial carbon stocks.


Global temperature increases from greenhouse gases are expected during the 21st Century, possibly as early as the next decade. Warming is predicted to be greatest at highest latitudes. Initial attempts to document climate change will be hampered by the great inter-annual variability in weather at high latitudes and the scarcity of long-term weather records. Certain key properties of these environmental changes, however, can be defined, despite uncertainty concerning results from present climate models. A group of scientists meeting at Villach, Austria, in 1987 (Jaeger, 1988) agreed that 3 °C was a moderate estimate of average
global warming during the next century, while at high latitudes (60 to 90° N.), 0.6 to 0.7 °C per decade in winter and 0.1 to 0.2 °C per decade in summer are more probable climate change expectations. Results from the most recent climate model results are not very different and range from 0.4 to 0.8 °C per decade (Mitchell et al., 1990). In addition, results from both the Villach group and the more recent compilations agree that winter precipitation and soil moisture could increase at high latitudes as more precipitation falls, and as more precipitation falls as rain instead of snow. These climate changes are quite intense and rapid. For the next few decades, they may result in a much wider range of temperature and precipitation extremes than has ever been recorded in cold regions.