

# Potential Changes in Tree Species Richness and Forest Community Types following Climate Change

Louis R. Iverson\* and Anantha M. Prasad

*Northeastern Research Station, USDA Forest Service, Delaware, Ohio 43015, USA*

## ABSTRACT

Potential changes in tree species richness and forest community types were evaluated for the eastern United States according to five scenarios of future climate change resulting from a doubling of atmospheric carbon dioxide (CO<sub>2</sub>). DISTRIB, an empirical model that uses a regression tree analysis approach, was used to generate suitable habitat, or potential future distributions, of 80 common tree species for each scenario. The model assumes that the vegetation and climate are in equilibrium with no barriers to species migration. Combinations of the individual species model outcomes allowed estimates of species richness (from among the 80 species) and forest type (from simple rules) for each of 2100 counties in the eastern United States. Average species richness across all counties may increase slightly with climatic change. This increase tends to be larger as the average temperature of the

climate change scenario increases. Dramatic changes in the distribution of potential forest types were modeled. All five scenarios project the extirpation of the spruce–fir forest types from New England. Outputs from only the two least severe scenarios retain aspen–birch, and they are largely reduced. Maple–beech–birch also shows a large reduction in area under all scenarios. By contrast, oak–hickory and oak–pine types were modeled to increase by 34% and 290%, respectively, averaged over the five scenarios. Although many assumptions are made, these modeled outcomes substantially agree with a limited number of predictions from researchers using paleoecological data or other models.

**Key words:** climate change; species richness; forest types; GIS; statistical model; eastern United States.

## INTRODUCTION

The Earth's climate is always changing, but evidence is mounting that a warming trend is occurring (MacCracken 1995; Wigley 1995) and that human activities have a disrupting influence that is accelerating this dynamic process (Kattenberg and others 1996). The increasing concentrations of carbon dioxide (CO<sub>2</sub>) and other greenhouse gases in the Earth's atmosphere likely will lead to warming, perhaps by as much as 3° to 4°C globally over the next century and even more in the higher latitudes (Watson 1999). This warming

trend would cause major changes in all living systems, including forests. It has been estimated that the composition of one-third of the planet's forests could be altered markedly due to climate changes (Melillo 1999; Shriener and Street 1998).

In this paper, we review several approaches that are used to study the effects of climate change on forests, including earlier paleoecological, mechanistic, and statistical modeling. All three methods have been used to predict potential vegetation outcomes following climate change. We also present the results from an empirical modeling effort that estimates species richness and forest composition now and in the future for a series of climate change scenarios.

Received 12 May 2000; accepted 20 October 2000.

\*Corresponding author; e-mail: liverson@fs.fed.us

## Paleontological Studies

It is well known that climate is an overall regulator of vegetation, that species distributions in the past have varied as climate changed, and that we can expect plant species to continue to shift in range and abundance as the climate continues to change (see, for example; Woodward 1987). In North America, paleontological studies of plants during the Holocene warming provide the best evidence that plant ranges do indeed shift with climate. These studies have shown that: (a) species generally shifted northward (Delcourt and Delcourt 1988); (b) species did not shift in unison—that is, the rates and direction of migration differed among taxa, and species assemblages did not remain the same (Davis 1981; Webb 1992); and (c) variations in competition and dispersal mechanisms seemed to have little influence on vegetation migration patterns or rates—that is, historical data show little distinction in past migration patterns between trees with wind-dispersed propagules and trees with animal-dispersed propagules (Malanson 1993). During the Holocene, species tended to remain in equilibrium with the climate even though it was changing, as migrations were occurring over thousands of years and over a relatively uninterrupted landscape. However, under current global circulation models (GCM), the climate will change at a faster rate; moreover, natural migrations will be inhibited in today's fragmented and human-dominated landscapes (Iverson and others 1999b). Thus, it is difficult to assess what the future may hold for forest species and communities.

## Mechanistic Models

The second general approach to predicting potential forest response to climate change uses mechanistic, or simulation, models (Pitelka and Plant Migration Working Group 1997). These models mechanistically incorporate the physiological characteristics of the ecosystem as biogeography (that is, model species composition), biogeochemistry (that is, model nutrient and carbon cycles), or combination models. Currently, at least five biogeography models and 20 biogeochemistry models are being used in the context of climate change modeling (Neilson and others 1998). Two primary biogeography models are the Mapped Atmosphere–Plant–Soil System (MAPSS), developed by Neilson and others (Neilson 1995; Neilson and Marks 1994) and the BIOME3 model (Haxeltine and others 1996). Both models calculate the potential vegetation type and leaf area that a site can support, as constrained by local vegetation and hydrologic process and the

physiological properties of plants (Neilson and others 1998).

Biogeochemistry models simulate carbon C and nutrient cycles of ecosystems, but most lack the ability to predict vegetation types at a given location. Four primary biogeochemical models being used for global change modeling include TEM (Raich and others 1991), CENTURY (Parton and others 1993), BIOME-BGC (Running and Hunt 1993), and PnET (Aber and Federer 1992; McNulty and others 1994). Efforts are under way to make comparisons among the models (for example, VEMAP 1995) and to incorporate continuous feedbacks from vegetation effects into dynamic models of global vegetation change (Foley and others 1996; Neilson and Running 1996).

## Statistical Models

In a third approach to predict the potential effects of climate change, statistical models generally use empirical data to define relationships between current species distributions and environmental (especially climate) drivers. The climate is then “changed” by various GCM, and the statistical relationships are extrapolated forward to define possible new species distributions. When incorporated into a geographic information system (GIS), potential future distributions can be mapped in this manner. Statistical models used to define the relationships include regression, general linear models, general additive models, regression tree models (used here), and most recently, multivariate adaptive regression splines (Prasad and Iverson 2000). Statistical models usually are used to assess current and project possible future distributions for individual species rather than community types or biomes. Sometimes called “envelope analysis,” such models can define broad relationships for a large number of species and can be the basis for additional studies and fine-tuning. There are many examples of statistical models used for predictive mapping (Franklin 1995). With respect to climate change, Sykes and others (1996) evaluated 19 north European tree species, Box and others (1999) evaluated 125 woody species in Florida, Morse and others (1993) evaluated more than 15,000 vascular plant species in the United States, Thompson and others (1998) evaluated 16 tree species in the West, and Iverson and Prasad (1998b) evaluated 80 eastern tree species.

## Model Assumptions

All models carry assumptions that must be acknowledged when interpreting results. First, mod-

els are dependent on the inputs (that is, garbage in, garbage out); thus, errors in the input layers of potential species drivers or tree species sampling can create uncertainty. Using the county as a sampling unit minimizes a portion of this uncertainty because as the input layers are homogenized so that fine-scale error from mapping and map overlay will be mostly avoided. On the other hand, the large sampling unit prevents adequate model building on species that require rare or highly specific habitats. Therefore, the work reported here uses only 80 common species of the eastern United States.

Second, potential climate scenarios created by the various GCM often can make a large difference in the model outputs. Here, we use five GCM scenarios to assess this range of uncertainty.

Third, most models also assume that tree species occur in all environments where it is possible for them to survive, that they cannot survive outside this range, and that they are in equilibrium with climate. In fact, the opposite is probably true for many species (Loehle and LeBlanc 1996). Therefore, we report here the potential changes in suitable habitat for various forest types, not the predicted actual range changes. Within the potential suitable habitat, colonization success will depend on a suite of additional variables, such as edaphic barriers, landscape connectivity, and dispersal distances and rates. We are addressing this topic in related research (Iverson and others 1999b).

Fourth, statistical models cannot account for changes in physiological and species-interaction effects in the model outputs. As a result, there is no way to assess changes in competition among the "new" species mix, nor is there any way to account for changes in water-use efficiency or temperature acclimation in the species (Neilson 1995; Wayne and others 1998).

Still, in a world where there are lots of unknowns, statistical models have many advantages. They enable relatively rapid analysis for numerous individual species, allow interpretations that are understandable, provide for the integration of multiple factors operating on a species, identify possible key relationships and species for future experimentation and modeling, and are able to estimate a potential suitable habitat into which simulation models can predict future migration (Iverson and others 1999b). In one comparison between an empirical forest growth model and a forest gap simulation model where both models attempted to emulate 30 years of actual forest growth for two sites in Kentucky, the empirical model performed better (Yaussy 1999).

## Species Richness

Statistical models have also been used to evaluate species richness. Several researchers have used regression approaches to estimate species richness of vegetation (see, for instance, Conroy and Noon 1996; Heikkinen and Neuvonen 1997; Quian 1998; O'Brien 1998; Iverson and Prasad 1998a). For example, one group used regression approaches to relate plant and animal species richness in North America to energy balance (Currie 1991; Currie and Paquin 1987). Another approach in modeling species richness is to model individual species ranges and then sum them across a spatial grid to obtain estimates of richness (Skov and Borchsenius 1997). This was the approach taken here to estimate current and potential future species richness.

## METHODS

### DISTRIB Model

We used an empirical modeling approach called regression tree analysis (RTA), sometimes called classification and regression trees (CART), to predict suitable habitat for an individual tree species given a potential future climate scenario. RTA is well suited for predicting landscape-level distributions of species from environmental data. It is based on recursive sampling of the data to split a data set, based on a single predictor variable at each split, into increasingly homogeneous subsets until another split is infeasible. It thus readily forms prediction rules and automatically incorporates the possibility of interactions among the predictors (Breiman and others 1984). The variables that operate at large scales usually split the data early in the model, whereas variables that influence the response variable at more local scales operate later. The use of RTA and other predictive modeling procedures has grown with that of GIS, which allows the mapping of model outputs across landscapes. There is an increasing number of ecological examples of the use of RTA (for instance, Michaelsen and others 1994; Lynn and others 1995; Hernandez and others 1997; Reichard and Hamilton 1997; Franklin 1998; Dobbertin and Biging 1998; Iverson and Prasad 1998b).

DISTRIB is the RTA model framework that we used to model potentially new species distributions or suitable habitat across more than 2100 counties in the eastern United States. We used DISTRIB to evaluate the relationship of 33 environmental variables to 80 tree species importance values (based on basal area and number of stems by species on more than 100,000 plots from USDA Forest Service For-

est Inventory and Analysis data) (Hansen and others 1992). We then used the derived relationships to predict tree species present and potential future importance values. The environmental variables, calculated at the county level by area-weighted averaging, included attributes of soil, land use/land cover, elevation, landscape pattern, and climate. Selected soil variables included total water-holding capacity, pH, percent organic matter, percent clay, percent slope, and percent weight of rock fragments 8–25 cm, all from the STATSGO database (Soil Conservation Service 1991). The current and projected future monthly temperature, precipitation, and potential evapotranspiration outputs were acquired in  $10 \times 10$  km format (US Environmental Protection Agency 1993) or  $0.5 \times 0.5^\circ$  format from USDA Forest Service personnel at Corvallis, Oregon (R. Neilson, R. Drapek personal communication). From these, mean annual temperature, January temperature, July temperature, mean potential evapotranspiration (PET), mean temperature May–September (MAYSEPT), and the ratio of July–August precipitation to potential evapotranspiration (JARPPET) were derived.

We wanted to create models that best match current distribution of species importance values and then project potential future distributions following climate change. To accomplish this, we swapped current climate variables, within DISTRIB, with the projected outputs from the following five scenarios of equilibrium climate under doubled  $\text{CO}_2$  levels ( $2 \times \text{CO}_2$ ): (a) Geophysical Fluid Dynamics Laboratory (GFDL) model (Wetherald and Manabe 1988), (b) Goddard Institute of Space Studies (GISS) model (Hansen and others 1988), (c) United Kingdom Meteorological Office (UKMO) model (Wilson and Mitchell 1987), (d) Hadley Centre for Climate Prediction and Research (Hadley) model (Mitchell and others 1995), and (e) Canadian Climate Centre (CCC) model (Laprise and others 1998). Hadley and CCC are transient scenarios; that is, 30-year climatic averages were estimated for the period 2071–2100 (R Neilson personal communication).

These five scenarios give a range of possible outcomes in equilibrium climate at  $2 \times \text{CO}_2$ . Hadley has the least radical change in temperatures, especially January temperature (+0.9°C, averaged across the eastern United States), whereas UKMO predicts a large change in January temperature (+8.2°C). Annual precipitation shows a range of –44 to +242 mm among scenarios, with UKMO (+116 mm) and Hadley (+242 mm) having the highest increases in predicted precipitation.

The DISTRIB model uses equilibrium  $2 \times \text{CO}_2$

GCM conditions to predict potential future distributions. It essentially predicts suitable habitat for each species, with the assumption that species colonization will occur at all suitable sites. There is no time component to the model, however, though predictions from the Intergovernmental Panel on Climate Change show that if  $\text{CO}_2$  emissions were maintained at 1994 levels, the  $2 \times \text{CO}_2$  level could be reached by the end of the 21st century (Houghton and others 1996). In a parallel effort, our team is combining outputs from DISTRIB to that of SHIFT, a spatially explicit simulation model, to more realistically model tree distributions over the next 100 years (Iverson and others 1999b). Obviously, the typical longevity of trees and the presence of refugia will create large lag times, especially for southern limits to shift (Loehle 1996). Also, biological competition is not considered in the single-species outcome for DISTRIB. Instead, the model produces a species list and the potential ranges from which the possible makeup of future communities can be estimated. By operating at a species level, DISTRIB indicates potential changes in community dynamics and biodiversity. The outputs of these 80 individual species models have been published in atlas form under two (hardcopy: Iverson and others 1999a) and five (online: Prasad and Iverson 1999) climate change scenarios. In this paper, we use the single-species model outputs to evaluate the potential changes in forest types and richness that may result from climate change.

### Multiple Species Assessments

With RTA, overall assessments can be made regarding possible changes in forest composition under global climate change scenarios. Of course, overlaying multiple-species projections assumes that species interactions will not significantly alter the result of a simple linear combination of the 80 single-species models created by DISTRIB. Because there are errors in the models for individual species, additional caution is urged in interpreting multiple-species maps because of the additive effects of superimposing single-species maps. This limitation must be considered when interpreting the resultant maps.

*Species richness.* By combining the maps for all 80 species, the number of species projected to occur in each county were counted and mapped. This procedure was used for each of the five global climate change scenarios as well as the current situation.

*USDA Forest Service forest types.* Forest type maps were developed for current climate and each scenario based on rules that sum (for each county)

the importance values of most of the key species defining the forest type. The Forest Service has predefined the types, and species were assigned based on associations according to Hansen and others (1992). Most, but not all, species listed in Hansen and others (1992) were available for summing into associations, since predictive outputs were available for only the 80 most common species in the eastern United States (that is, those reported in Iverson and others 1999a). The county was then classed according to the highest-ranking score for each of the 10 classes for the eastern United States (Table 1). We recognize that when we aggregate and classify data to the county level, we introduce scale-dependent biases because some counties are much larger than others. Therefore, some smaller forest types may be underrepresented in areas (for example, white pine in northern Minnesota) where the counties are proportionately larger. This bias could be excessively great if we had also included the western United States, with its enormous counties, in this analysis.

An additional rule set was needed for the oak pine forest type because it was a sum of many major oaks and pines; yet the class was intended to identify forests with mixtures of at least 50% oak and 25%–50% pine species (Merz 1978). For this situation, if the rule (from Table 1) determined the class to be oak/pine, the following statements were applied:

1. If loblolly/shortleaf (class 4) was greater than oak/hickory (class 6), the county would be reclassified from oak/pine to loblolly/shortleaf, because the pine component exceeds 50%.
2. If oak/hickory (class 6) was more than twice that of loblolly/shortleaf (class 4), the county would be reclassified from oak/pine to oak/hickory because there was likely to be less than a 25% pine component.
3. If neither 1 or 2 apply, the county remains classed as oak/pine (class 5).

*Average forest type map.* An “average” forest type map was created by averaging the importance values for each species over all five GCM scenarios and then applying the rules of Table 1 to produce the map. For some, this average map can give an indication of what may happen based on a set of future climate scenarios. Others will prefer to examine the range of outcomes established by the five scenarios.

*Forest type agreement map.* The forest type agreement map was created by determining, for each county, how many different forest types are pre-

dicted among the five climate change scenarios. If all five scenarios output the same potential forest type, the agreement map would show a “1”; if each scenario output a different forest type, the agreement map would show a “5.” Thus, the map gives some indication of spatial uncertainty, since there will be areas of major confluence as well as disparity among the models.

## RESULTS

### Species Richness

The total number of species from the pool of 80 common eastern species is shown for current and potential future scenarios in Figure 1. Overall species richness is not projected to change substantially among the five scenarios or when compared to the modeled current situation. The mean (and range) species counts per county, in increasing order, are 26.3 (1–51) for the current situation according to the forest inventory data, 28.6 (10–42) for the modeled current situation, 29.7 (9–42) for Hadley, 30.3 (10–44) for GISS, 31.2 (12–44) for GFDL, 31.5 (10–44) for CCC, and 32.6 (10–45) for UKMO. Thus, average species richness of these 80 common species may increase slightly under the equilibrium climate scenarios depicted. The rank order of richness roughly corresponds to increasing severity of the scenarios: there is a slight overall increase in potential species richness with increasing severity (especially temperature) of the GCM. The models themselves (including the model representing current conditions) tend to homogenize richness, so that the range between low and highly diverse counties is reduced.

Locations in the western part of the study area that currently have the lowest species diversity are modeled to have additional species in the future, and some of the areas of rich diversity in the southern part of the country (for example, Mississippi) are modeled to have reduced species richness (Figure 1). Florida also shows a possible gain in species, although diversity is artificially low there because its many endemic species did not meet the criteria for entering into the RTA modeling. Box and others (1999) have more species ( $n = 124$ ) and spatial detail in their analysis of Florida. Minnesota and Wisconsin are modeled to lose some species, although areas that are now highly diverse such as along the Ohio and Mississippi Rivers are modeled to remain diverse (Figure 1). Overall, the well-known pattern of decreasing diversity as one moves toward higher latitudes is maintained both cur-

**Table 1.** Breakdown of Forest Types by Class (Based on Summing of Importance Values for Indicated Species in Each Class)

Class	Forest Type	Abbreviation	Species
1	White/Red/JackPine	WRJP	<i>Pinus strobus</i> <i>Tsuga canadensis</i>
2	Spruce/Fir	SF	<i>Abies balsamea</i> <i>Thuja occidentalis</i>
3	Longleaf/Slash Pine	LnSLP	<i>Pinus palustris</i> <i>P. elliotii</i>
4	Loblolly/Shortleaf Pine	LbShP	<i>Pinus taeda</i> <i>P. echinata</i> <i>P. virginiana</i>
5	Oak/Pine	OP	<i>Pinus strobus</i> <i>P. echinata</i> <i>P. virginiana</i> <i>P. taeda</i> <i>Quercus rubra</i> <i>Q. falcata</i> <i>Q. phellos</i> <i>Q. nigra</i> <i>Q. coccinea</i> <i>Q. stellata</i>
6	Oak/Hickory	OH	<i>Quercus alba</i> <i>Q. rubra</i> <i>Q. coccinea</i> <i>Q. prinus</i> <i>Q. velutina</i> <i>Q. stellata</i> <i>Carya sp.</i> <i>C. cordiformis</i> <i>C. glabra</i> <i>C. ovata</i> <i>C. tomentosa</i> <i>Liquidambar styraciflua</i> <i>Liriodendron tulipifera</i>
7	Oak/Gum/Cypress	OGC	<i>Q. phellos</i> <i>Q. falcata</i> var. <i>pagodaefolia</i> <i>Liquidambar styraciflua</i> <i>Ulmus americana</i> <i>Acer rubrum</i> <i>Taxodium distichum</i> <i>T. distichum</i> var. <i>nutans</i> <i>Nyssa aquatica</i> <i>N. sylvatica</i> var. <i>biflora</i>
8	Elm/Ash/Cottonwood	EAC	<i>Acer rubrum</i> <i>Ulmus americana</i> <i>Fraxinus nigra</i> <i>F. americana</i> <i>Plantanus occidentalis</i> <i>Populus deltoids</i> <i>Salix sp.</i> <i>Salix nigra</i>
9	Maple/Beech/Birch	MBB	<i>Acer rubrum</i> <i>A. saccharum</i> <i>Fagus grandifolia</i> <i>Betula alleghaniensis</i> <i>Prunus serotina</i> <i>Juglans nigra</i>
10	Aspen/Birch	AB	<i>Populus tremuloides</i> <i>P. grandidentata</i> <i>Betula papyrifera</i>

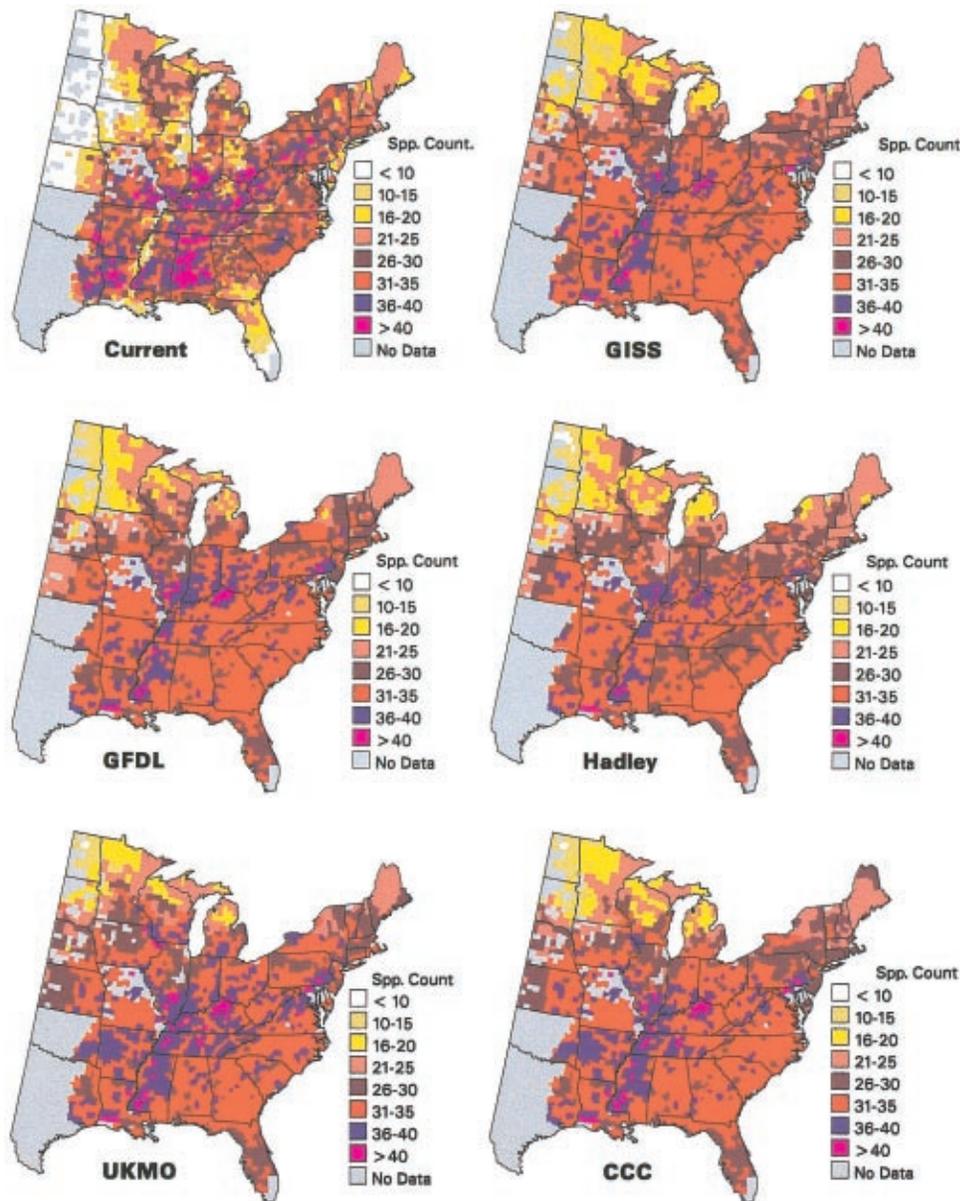


Figure 1. Current tree species richness as determined from forest inventory data and potential future richness with five scenarios of climate change.

rently and among all scenarios (Pianka 1966; Currie and Paquin 1987).

### USDA Forest Service Forest Types

In the algorithm for determining forest type, no distinction was made on how forested the county is, only that there are forest inventory data from at least one plot from that county. Therefore, there is a classification of forest type even for many of the counties in the prairie region, counties that rarely exhibit forested polygons on general forest maps (Figure 2). Currently, there is a sizable extent of each of the 10 forest types except for class 1 (white-red-jack pine), which is shown only for several

counties in New England (0.2% of land area). This estimate is low for white-red-jack pine because it exists in combination with more widespread types that swamp out the minor types within for example, the large counties of northern Minnesota. The oak-hickory occupies 28%, elm-ash-cottonwood and maple-beech-birch each occupy 17%, and loblolly-shortleaf pine occupies 11% of the eastern United States (Figures 2 and 3).

When climate change scenarios are applied to the 80 species and then aggregated into the forest types, changes in the distribution of potential forest types are dramatic (Figures 2-4). All five scenarios depict the extirpation of the spruce-fir forest types from

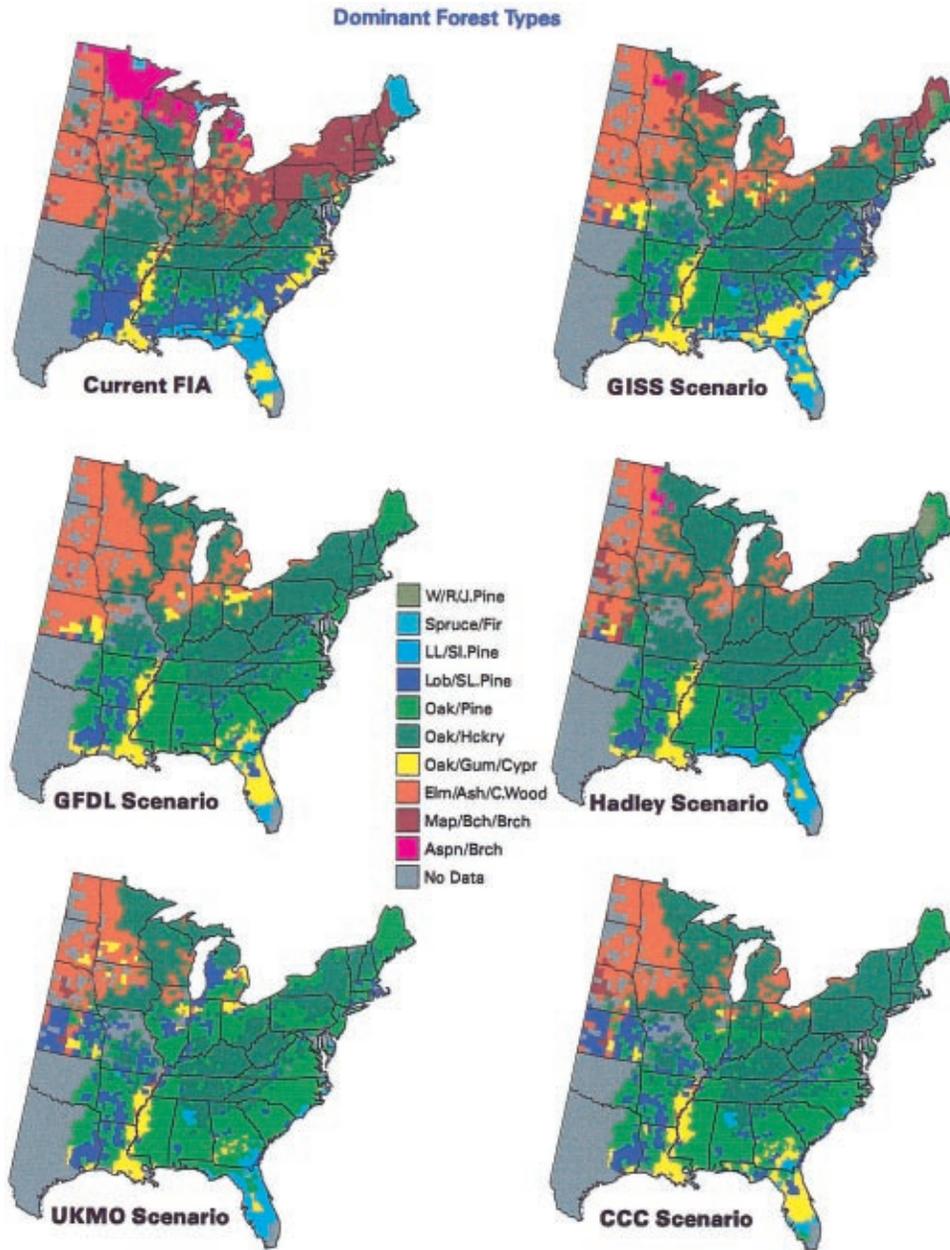


Figure 2. Current forest types as determined from forest inventory data and potential future forest types with five scenarios of climate change.

New England, and outputs only from Hadley and GISS (the least radical scenarios for temperature and precipitation changes) retain aspen–birch. Maple–beech–birch also shows a large reduction in area. Hadley and GISS show the most maple–beech–birch retained (1.6% and 4%, respectively), but the other three scenarios yield estimates of 0.5% or less for maple–beech–birch.

The loblolly–shortleaf pine type also shows a decrease for each scenario. The percentage cover of this type is projected to range from 4.2% for Hadley to 11% for GISS, which is about the same as the current situation. However, the individual species

models do not show losses of loblolly or shortleaf pine individually, but rather significant gains (Iverson and others 1999a; Iverson and Prasad forthcoming). In this case, the relatively greater gains in several oak species, especially post oak (*Quercus stellata*), allowed the summed importance value for oak to exceed 50%, whereas summed pine fell to 25%–50% of the total. This resulted in a classification of oak–pine or even oak–hickory (but still with sizable amounts of loblolly and shortleaf pine). When only *Q. stellata* was removed from this calculation, the loblolly–shortleaf pine amounts increased under all scenarios compared to the current

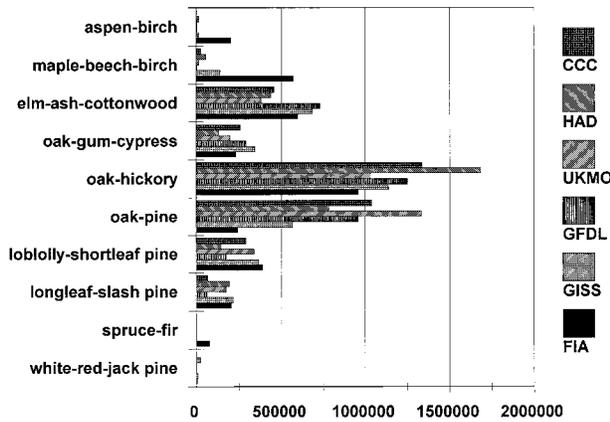


Figure 3. Total area occupied by forest types currently and potentially in the future.

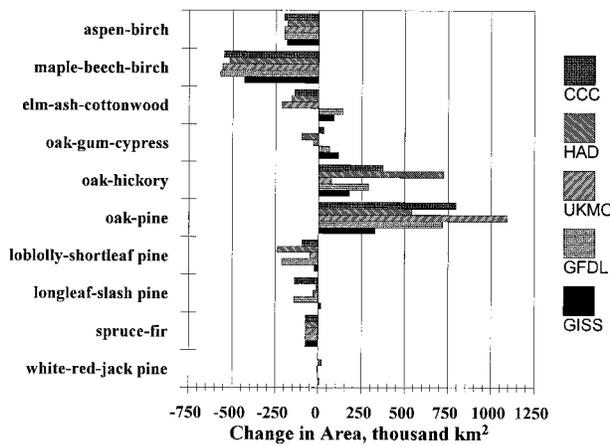


Figure 4. Potential change in area occupied by forest types with five scenarios of climate change.

situation. The high impact of *Q. stellata* in the forest type algorithm can be attributed to the following factors: (a) The predicted importance value of the species is driven primarily by the ratio of precipitation to PET in July and August (Prasad and Iverson 1999) and temperature variables that differ considerably in several of the scenarios; (b) the generic DISTRIB model for this species is less satisfactory because of the nature of RTA, where slight changes in certain variables sometimes allow large changes in the potential importance value. The use of multivariate adaptive regression splines (MARS) has been shown to improve on this drawback of RTA (Prasad and Iverson 2000).

The longleaf-slash pine (LnSIP) type also showed diminished area in every scenario but GISS (Figures 2–4). Like loblolly-shortleaf pine, the longleaf and slash pines were modeled individually to increase in area and importance for most scenarios (Iverson

and Prasad forthcoming), but the greater increases in oak pushed some of the area into the oak-pine or oak-hickory classes. Without *Q. stellata*, the longleaf-slash pine type also would have shown an overall increase.

The oak-hickory (OH) and oak-pine (OP) types are projected to increase for all five scenarios (Figures 2–4). Oak-hickory ranges from 29% for UKMO to 48% for Hadley (compared to 28% currently). Oak-pine ranges from 16% (GISS) to 38% (UKMO), compared to only 7% currently. However, these percentages also are significantly influenced by *Q. stellata*. If this species is excluded, the percentages would be lower, but these two forest types would still increase under every scenario.

The remaining forest types, oak-gum-cypress (OGC), elm-ash-cottonwood (EAC), and white-red-jack pine (WRJP), showed mixed results. The UKMO scenario shows WRJP as eliminated from the eastern United States, whereas Hadley shows an increase to 0.8% from the current 0.2% total coverage. With EAC, GISS and GFDL show an increase, although the other three scenarios show a decrease. UKMO and Hadley both predict decreases in OGC, whereas the other scenarios show an increase for this type (Figure 4).

If we assume that each suite of climate change scenarios have some validity and that they encompass the range of future possibilities, we can create an “average” map of potential future forest type distributions (Figure 5a) along with an “uncertainty” map showing the agreement among the five scenarios (Figure 5b). Compared to current coverages, the average map shows that over the eastern United States, oak-hickory expands by an average of 34%, primarily to the north and east (Figure 5a). The oak-pine type expands by roughly 290% and is represented throughout the Southeast. The spruce-fir is eliminated and the aspen-birch and maple-beech-birch types are reduced dramatically (–97% and –92%, respectively) and largely replaced by oak-hickory and oak-pine. The loblolly-shortleaf pine type is reduced by 32% and shifts north and west. The oak-pine type replaces this loblolly-shortleaf pine type in its current zone. The longleaf-slash pine type is reduced by an average of 31%.

The uncertainty map shows that for a large section (45%) of the study area, all five scenarios agree on a single potential future forest type (Figure 5b). This area is located primarily along the Appalachians, Great Plains, and Gulf states. Much of the area of relatively higher confidence is the oak-hickory type, which is modeled to stay as the oak-hickory type with each of the five scenarios.

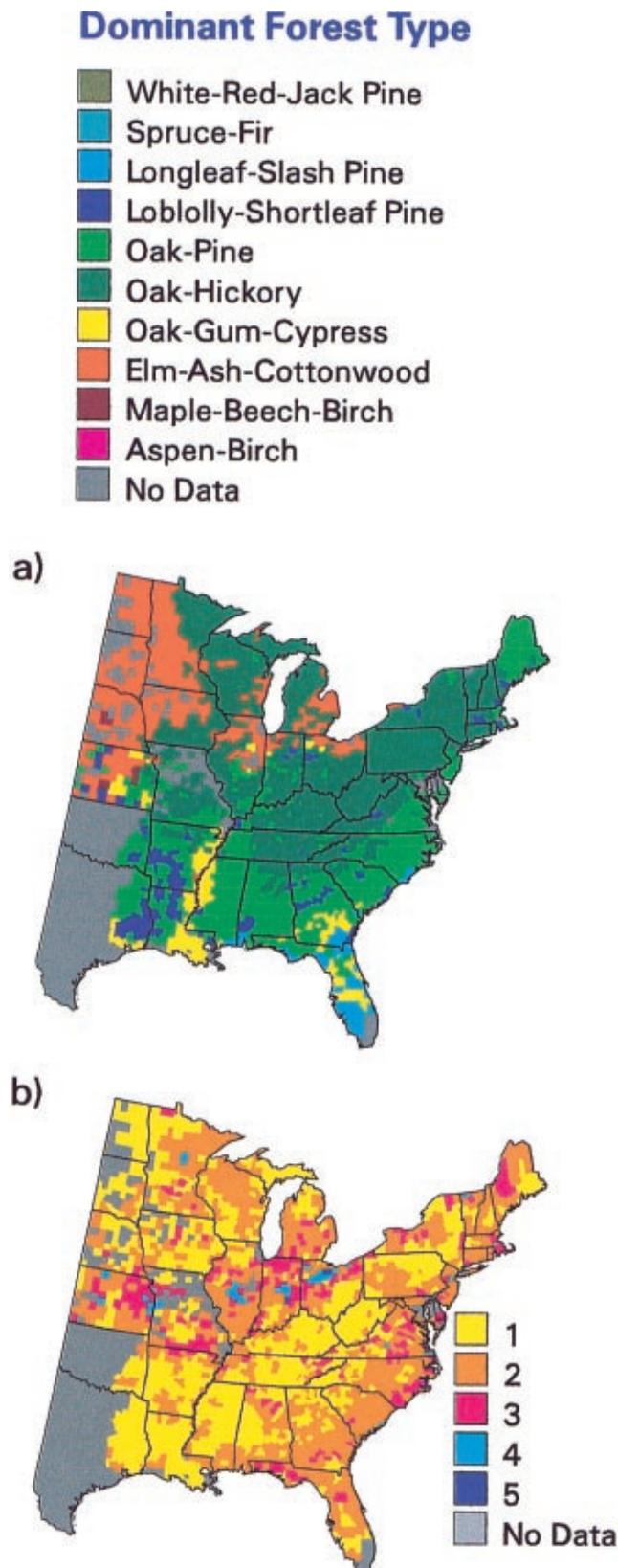


Figure 5. (a) "Average" forest type map based on five scenarios of climate change. (b) Variability of forest types, as modeled from five scenarios of climate change.

Another type projected for retention is elm-ash-cottonwood in the upper Great Plains (Figures 2 and 5). An additional 43% of the area, located primarily along the Atlantic coast and in the Great Lakes region, shows two potential forest type outcomes. The remaining area, primarily the Ohio River valley and west, has higher uncertainty (three to five potential outcomes).

These changes in community types reflect the responses of individual tree species. Averaged across all five scenarios, seven of the 80 species modeled were projected to be reduced in regional importance by at least 90%: bigtooth aspen (*Populus grandidentata*), quaking aspen (*P. tremuloides*), sugar maple (*Acer saccharum*), northern white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), red pine (*Pinus resinosa*), and paper birch (*Betula papyrifera*). Another 24 species would decline by at least 10%. Regional importance increased for 35 species; 12 species, including four species of oak and one hickory, increased by 100% or more. Most species were projected to move to the north, several species by 100–530 km (Iverson and Prasad forthcoming). On the basis of the results of these model experiments, the severity (from most to least severe) of the GCM scenarios with regard to forest type shifts appears to be:

UKMO > CCC > GFDL > GISS ≫ Hadley

This observation is based primarily on the evaluation of individual species and the distance that their "center of gravity" of suitable habitat would move under the various scenarios (Iverson and Prasad forthcoming). For example, the total number of species potentially moving more than 200 km north or beyond the US border is 27 for UKMO, 22 for CCC, 18 for GFDL and GISS, and eight for Hadley. The optimum latitude of seven species mentioned earlier is north of the US border for at least three scenarios. The number of species with their optimum latitude moving only slightly (less than 20 km either north or south) is highest for Hadley (35); for the other scenarios, the number of species ranges from 25 to 28.

## DISCUSSION

There is a potential for significant changes in forest community types in the eastern United States according to various scenarios of climate change. The impact may be greater regionally—for example, in the northern tier of states. These potential changes, in turn, could have large impacts on regional biodiversity and the socioeconomics of the affected re-

gions. The two forest types most likely to expand are oak–hickory and oak–pine. These expansions would have secondary implications. Oak–hickory supports a variety of species that rely on heavy mast production. More than 180 different kinds of birds and mammals use oak acorns as food, including squirrels, blue jays, red-headed woodpeckers, deer, turkey, quail, mice, chipmunks, ducks, and raccoons (Rogers 1990). The oak–pine type also supports a diverse associated flora and fauna.

Several forest types are projected to contract. All five GCM scenarios project that spruce–fir will move beyond the US border. Closely linked to climate, this type moved south into New England only in the past few centuries during the Little Ice Age (DeHayes and others 2000). The southern boundary of spruce–fir is probably limited by summer heat and drought. In our regression tree model, growing-season (May–September) temperature is the primary variable regulating balsam fir (*Abies balsamea*) (Iverson and others 1999a). Therefore, it is reasonable to expect that the type will be easily extirpated from the eastern United States as the temperature increases again. Spruce–fir supports moose and deer, especially in the winter, and a variety of other associated flora and fauna.

The aspen–birch type also is modeled to be greatly reduced in the East. Aspen is limited first to areas of water surplus (that is, areas where precipitation exceeds evapotranspiration) and then to minimum or maximum growing-season temperatures (Perala 1990). Our models show that anticipated average increases in temperature are responsible for driving both trembling aspen (*Populus tremuloides*) and paper birch northward (Iverson and others 1999a). These species are important in many regions, where they are often the only abundant hardwoods among conifer forests. Aspen–birch also provides food and shelter for wildlife (Safford and others 1990; Perala 1990).

The maple–beech–birch type makes up much of the current northern hardwoods. It is prominent in New England, New York, and Pennsylvania, and includes species such as red (*Acer rubrum*) and sugar (*A. saccharum*) maple, black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). Our models for this region show losses in the maples, beech, and yellow birch with concomitant increases in oak species, such that the area becomes classified as oak–hickory (Figure 2). This shift, in turn, would cause shifts in associated flora and fauna. Species specialized for the maple–beech–birch type could be squeezed considerably. Interestingly, this potential trend is opposite that observed today, for red maple is

slowly taking over many oak–hickory areas in the absence of fire (Abrams 1998).

Although the loblolly–shortleaf and longleaf–slash pine types show potential decreases under most scenarios (Figure 4), the pine species themselves were not modeled as individually reduced by climate change (Iverson and others 1999a). The proportionately greater potential increase in oak, especially post oak, resulted in the conversion of some pine type to oak–pine type. Pinelands provide valuable habitat for a variety of mammals and birds, including white-tailed deer, gray and fox squirrels, rabbits, bobwhite quail, wild turkeys, mourning doves, pine warblers, brown-headed nuthatches, and Bachman’s warblers. Old-growth longleaf pine stands also are important to the red-cockaded woodpecker (Baker and Langdon 1990).

The results of these model experiments compare favorably for those few species and forest types that have been studied previously. Using paleoecological data, Jacobson and Dieffenbacker-Krall (1995) predicted that white pine (*Pinus strobus*) would be favored and spruce–fir would be decreased under climate change. Flannigan and Woodward (1994) predicted a large northward shift of red pine (*Pinus resinosa*). Overpeck and others (1991) predicted the same trend for these two northern pines, but they also predicted large increases in oak abundance across the northern Great Lakes region and New England. In addition, they predicted a large northward shift in paper birch (*Betula papyrifera*) and a large northward expansion for southern pines. Joyce and others (1990) predicted a northward expansion for loblolly pine (*Pinus taeda*). In all cases, the model outputs reported here concur. Predictions of potentially large northward expansions have been made for several similar species in Europe, including *Picea abies*, *Abies alba*, *Tilia cordata*, *Quercus ilex* (Huntley and others 1995), *Fagus sylvatica*, *Betula pendula*, *Quercus robur*, and *Quercus petraea* (Sykes and Prentice 1996). More generally, the biogeography simulation models MAPSS and BIOME3 corroborate those shown here with a northward shift in forest types (Neilson and others 1998).

Both simulation and statistical models have value in determining potential impacts of climate change. The first incorporates physiological characteristics of the vegetation; the latter uses empirical relationships of current vegetation–climate patterns to predict potential vegetation distribution following climate change. All approaches are becoming more sophisticated and intertwined, and all require a series of assumptions that prevent the outcomes from being truly validated (Rastetter 1996; Rykiel 1996).

Therefore, researchers look for convergence of models to gain credibility (VEMAP Members 1995; Lauenroth 1996). In this way, various modeling approaches, including statistical models, can be used to search for convergence regarding possible future outcomes. Convergence of model outcomes with the paleoecological evidence adds credibility to predictions of future vegetative states.

Both paleoecological studies (for example, Webb 1992) and modeling efforts such as this one have shown that communities are ad hoc mixtures of species and cannot be expected to move together as intact communities if future conditions change. Macro modeling exercises such as this study are laden with assumptions, but they do provide a picture of how species and forests might respond if the climate continues to change. Macro studies identify emerging trends for the region, presenting a more accurate picture of how species and forests would shift regionally. Based on these efforts, we can begin to see what our nation's future forests might look like under a globally changed climate.

#### ACKNOWLEDGMENTS

This project was supported by the USDA Forest Service's Northern Global Change Program (R. Birdsey, Program Manager). Andy Hansen, Virginia Dale, Daniel Yaussy, John Aber, Lee Frelich, and an anonymous reviewer provided technical reviews, and Martin Jones provided an editorial review. The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the US Department of Agriculture or the Forest Service of any product or service to the exclusion of others that may be suitable.

#### REFERENCES

- Aber JD, Federer CA. 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92:463–74.
- Abrams MD. 1998. The red maple paradox. *BioScience* 48:355–64.
- Baker JB Langdon OG. 1990. *Pinus taeda* L. Loblolly pine. In: *in* Burns RM, Honkala BH, editors. *Silvics of North America*. Volume 1, Softwoods. Agriculture handbook 654. Washington, DC: USDA Forest Service. p 497–512.
- Box EO, Crumpacker DW, Hardin ED. 1999. Predicted effects of climatic change on distribution of ecologically important native tree and shrub species in Florida. *Clim Change* 41:213–48.
- Breiman L, Friedman J, Olshen R, Stone C. 1984. Classification and regression trees. Belmont CA: Wadsworth. 358 p.
- Conroy JJ, Noon BR. 1996. Mapping of species richness for conservation of biological diversity: conceptual and methodological issues. *Ecol Appl* 6(3):763–73.
- Currie DJ. 1991. Energy and large-scale patterns of animal- and plant-species richness. *Am Nat* 137:27–49.
- Currie DJ, Paquin V. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* 329:326–27.
- Davis MB. 1981. Quaternary history and the stability of forest communities. In: West DC, Shugart HH, editors. *Forest succession: concepts and application* New York: Springer-Verlag. p 132–53.
- DeHayes DH, Jacobson GL, Schaber PG, Bongarten B, Iverson LR, Kieffenbacker-Krall A. 2000. Forest responses to changing climate: lessons from the past and uncertainty for the future. In: Mickler RA, Birdsey RA, Hom JL, editors. *Responses of northern forests to environmental change*. New York: Springer-Verlag. p 495–540.
- Delcourt HR, Delcourt PA. 1988. Quaternary landscape ecology: relevant scales in space and time. *Landscape Ecol* 2:23–44.
- Dobbertin M, Biging GS. 1998. Using the non-parametric classifier CART to model forest tree mortality. *For Sci* 44(4):507–16.
- Flannigan MD, Woodward FI. 1994. Red pine abundance: current climatic control and responses to future warming. *Can J For Res* 24:1166–75.
- Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, Sitch S, Haxeltine A. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance and vegetation dynamics. *Global Biogeochem Cycles* 10:603–28.
- Franklin J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Prog Phy Geog* 19:474–99.
- Franklin J. 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *J Veget Sci* 9:733–48.
- Hansen J, Fung I, Lacis A, Rind D, Lebedeff S, Ruedy R. 1988. Global climate changes as forecast by Goddard Institute for Space Studies three-dimensional model. *J Geophys Res* 93: 9341–64.
- Hansen MH, Frieswyk T, Glover JF, Kelly JF. 1992. The Eastwide forest inventory data base: users manual. General technical report NC-151. St. Paul MN: US. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 48 p.
- Haxeltine A, Prentice IC, Creswell ID. 1996. A coupled carbon and water flux model to predict vegetation structure. *J Veget Sci* 7:651–66.
- Heikkinen RK, Neuvonen S. 1997. Species richness of vascular plants in the subarctic landscape of northern Finland: modelling relationships to the environment. *Biodiversity Conserv* 6(9): 1181–202.
- Hernandez JE, Epstein LD, Rodriguez MH, Rodriguez AD, Rejmankova E, Roberts DR. 1997. Use of generalized regression tree models to characterize vegetation favoring *Anopheles albimanus* breeding. *J Ame Mosquito Control Assoc* 13(1):28–34.
- Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K. 1996. *Climate change 1995: the science of climate change*. Cambridge (UK): Cambridge University Press 572 p.
- Huntley B, Berry P, Cramer W, McDonald AP. 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. *J Biogeog* 22:967–1001.
- Iverson LR, Prasad AM. 1998a. Estimating regional plant biodiversity with GIS modeling. *Diversity Distributions* 4(2):49–61.
- Iverson LR, Prasad AM. 2001. Potential tree species shifts with

- five climate change scenarios in the eastern United States. For *Ecol Manage*. Forthcoming.
- Iverson LR, Prasad AM. 1998b. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecol Monogra* 68:465–85.
- Iverson LR, Prasad AM, Hale BJ, Sutherland EK. 1999a. An atlas of current and potential future distributions of common trees of the eastern United States. General technical report NE-265. Radnor, PA: USDA Forest Service Northeastern Research Station, 245 p.
- Iverson LR, Prasad AM, Schwartz MW. 1999b. Modeling potential future individual tree-species distributions in the eastern United States under a climate change scenario: a case study with *Pinus virginiana*. *Ecol Model* 115:77–93.
- Jacobson GL Jr, Dieffenbacher-Krall A. 1995. White pine and climate change: insights from the past. *J Fore* 93:39–42.
- Joyce LA, Fosberg MA, Comanor JM. 1990. Climate change and America's forests. General technical report RM-187. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 12 p.
- Kattenberg A, Giorgi F, Grassl H, Meehl GA, Mitchell JFB, Stouffer RJ, Tokioka T, Weaver AJ, Wigley TML. 1996. Climate models—projections of future climate. In: Houghton JT, Meira-Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K, editors. *Climate change 1995: the science of climate change*. Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press; p 285–357.
- Laprise R, Caya D, Giguère M, Bergeron G, Côté H, Blanchet JP, Boer GJ, McFarlane N. 1998. Climate and climate change in western Canada as simulated by the Canadian Regional Climate Model. *Atmosphere–Ocean* 36:119–67.
- Lauenroth WK. 1996. Application of patch models to examine regional sensitivity to climate change. *Clim Change* 34:155–60.
- Loehle C. 1996. Forest response to climate change. *J Fore* 94(9): 13–5.
- Loehle C, LeBlanc D. 1996. Model-based assessments of climate change effects on forests: a critical review. *Ecol Model* 90: 1–31.
- Lynn H, Mohler CL, DeGloria SD, McCulloch CE. 1995. Error assessment in decision-tree models applied to vegetation analysis. *Landscape Ecol* 10:323–35.
- MacCracken MC. 1995. The evidence mounts up. *Nature* 376: 645–46.
- McNulty SG, Vose JM, Swank WT, Aber JD, Federer CA. 1994. Regional-scale forest ecosystem modeling: database development, model predictions and validation using a Geographic Information System. *Clim Res* 4:223–31.
- Malanson GP. 1993. Comment on modeling ecological response to climatic change. *Clim Change* 23:95–105.
- Melillo JM. 1999. Warm, warm on the range. *Science* 283: 183–4.
- Merz RW, editor. 1978. *Forest atlas of the Midwest*. St. Paul MN: USDA Forest Service, North Central Forest Experiment Station, 48 p.
- Michaelsen J, Schimel DS, Friedl MA, Davis FW, Dubayah RC. 1994. Regression tree analysis of satellite and terrain data to guide vegetation sampling and surveys. *J Veget Sci* 5:673–86.
- Mitchell JFB, Johns TC, Gregory JM, Tett S. 1995. Climate response to increasing levels of greenhouse gases and sulphate aerosols. *Nature* 376:501–4.
- Morse L, Kutner LS, Maddox GD, Honey LL, Thurman CM, Kartesz JT, Chaplin SJ. 1993. The potential effects of climate change on the native vascular flora of North America: a preliminary envelopes analysis. Palo Alto, CA: Electric Power Research Institute, TR-103330.
- Neilson RP. 1995. A model for predicting continental-scale vegetation distribution and water balance. *Ecol Appl* 5(2):362–85.
- Neilson RP, Drapek RJ. 1998. Potentially complex biosphere responses to transient global warming. *Global Change Biol* 4:505–21.
- Neilson RP, Marks D. 1994. A global perspective of regional vegetation and hydrologic sensitivities from climatic change. *J Veget Sci* 5:715–30.
- Neilson RP, Prentice IC, Smith B. 1998. Simulated changes in vegetation distribution under global warming. In: Watson RT, Zinyowera MC, Moss RH, editors. *The regional impacts of climate change: an assessment of vulnerability*. New York: Cambridge University Press. p 439–56.
- Neilson RP, Running SW. 1996. Global dynamic vegetation modelling: coupling biogeochemistry and biogeography models. In: Walker B, Steffen G, editors. *Global change terrestrial ecosystems*. New York: Cambridge University Press. p 461–5.
- O'Brien EM. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *J Biogeog* 25:379–98.
- Overpeck JT, Bartlein PJ, Webb TI. 1991. Potential magnitude of future vegetation change in eastern North America: comparisons with the past. *Science* 254:692–5.
- Parton WJ, Scurlock JMO, Ojima DS, Gilmanov TG, Scholes RJ, Schimel DS, Kirchner T, Menaut H-C, Seastedt T, Garcia Moya E, Kamnalrut A, Kinyamario JL. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochem Cycles* 7:785–809.
- Perala DA. 1990. *Populus tremuloides* Michx. Quaking aspen. In: Burns RM, Honkala BH, editors. *Silvics of North America*. Volume 2, Hardwoods. *Agriculture handbook* 654, Washington, DC: USDA Forest Service, p 555–69.
- Pianka, ER. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100:65–75.
- Pitelka LF, Plant Migration Workshop Group. 1997. Plant migration and climate change. *Am Sci* 85:464–73.
- Prasad AM, Iverson LR. 1999. A climate change atlas for 80 forest tree species of the eastern United States [database]. [www.fs.fed.us/ne/delaware/atlas](http://www.fs.fed.us/ne/delaware/atlas).
- Prasad AM, Iverson LR. 2000. Predictive vegetation mapping using a custom built model-chooser: comparison of regression tree analysis and multivariate adaptive regression splines. Proceedings, of the 4th International Conference on Integrating GIS and Environmental Modeling: problems, prospects and research needs. <http://www.colorado.edu/research/cires/banff/upload/159/index.html>, banff, Alberta, Canada.
- Quian H. 1998. Large-scale biogeographic patterns of vascular plant richness in North America: an analysis at the generic level. *J Biogeog* 25:829–36.
- Raich JW, Rastetter EB, Melillo JM. 1991. Potential net primary productivity in South America: applications of a global model. *Ecol Appl* 1:399–429.
- Rastetter EB. 1996. Validating models of ecosystem response to global change. *BioScience* 46:190–7.
- Reichard SH, Hamilton CW. 1997. Predicting invasion of woody plants introduced into North America. *Conserv Biol* 11:193–203.

- Rogers R. 1990. *Quercus alba* L. White oak. In: Burns RM, Honkala BH, editors. *Silvics of North America*. Volume 2, Hardwoods. Agriculture handbook 654. Washington, DC: USDA Forest Service. p 605–13.
- Running SW, Hunt ER Jr. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. In: Ehleringer JR Field CB, editors. *Scaling processes between leaf and landscape levels*. San Diego, CA: Academic Press. p 141–58.
- Rykiel EJ. 1996. Testing ecological models: the meaning of validation. *Ecol Model* 90:229–44.
- Safford LO, Bjorkbom JC, Zasada JC. 1990. *Betula papyrifera* Marsh. Paper birch. In: Burns RM, Honkala BH, editors. *Silvics of North America*. Volume 2, Hardwoods. Agriculture handbook 654, Washington DC: USDA Forest Service. p 158–71.
- Shriner DS, Street RB. 1998. North America. In: Watson RT, Zinyowera MC, Moss RH, editors. *The regional impacts of climate change*. New York: Cambridge University Press. p 253–330.
- Skov F, Borchenius F. 1997. Predicting plant species distribution patterns using simple climatic parameters: a case study of Ecuadorian palms. *Ecography* 20:347–55.
- Soil Conservation Service. 1991. State soil geographic data base (STATSGO) data users guide. Miscellaneous publication 1492. Washington DC. US Department of Agriculture, Soil Conservation Service. 88 p.
- Sykes MT, Prentice IC. 1996. Climate change, tree species distributions and forest dynamics: a case study in the mixed conifer northern hardwoods zone of northern Europe. *Clim Change* 34:161–78.
- Sykes MT, Prentice IC, Cramer W. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. *J Biogeog* 23:203–34.
- Thompson RS, Hostetler SW, Bartlein PJ, Anderson KH. 1998. A strategy for assessing future changes in climate, hydrology, and vegetation in the western United States. USGS circular 1153. [http://greenwood.cr.usgs.gov/pub/circulars/c1153/c1153\\_4.htm](http://greenwood.cr.usgs.gov/pub/circulars/c1153/c1153_4.htm).
- US Environmental Protection Agency. 1993. EPA-Corvallis model-derived climate database and 2×CO<sub>2</sub> predictions for long-term mean monthly temperature, vapor pressure, wind velocity and potential evapotranspiration from the Regional Water Balance Model and precipitation from the PRISM model, for the conterminous United States. Digital raster data on a 10 × 10 km, 470 × 295 Albers Equal Area grid, in “Image Processing Workbench” format. Corvallis OR: US Environmental Protection Agency, Environmental Research Laboratory.
- [VEMAP] Vegetation/Ecosystem Modeling and Analysis Project. Members. 1995. *Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO<sub>2</sub> doubling*. *Global Biogeochem Cycles* 9:407–37.
- Watson R. 1999. Common themes for ecologists in global issues. *J Appl Ecol* 36:1–10.
- Wayne PM, Reekie EG, Bazzaz FA. 1998. Elevated CO<sub>2</sub> ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts. *Oecologia* 114:335–42.
- Webb T III. 1992. Past changes in vegetation and climate: lessons for the future. In: Peters RL, Lovejoy TE, editors. *Global warming and biological diversity*. New Haven CT: Yale University Press. p 59–75.
- Wetherald RT, Manabe S. 1988. Cloud feedback processes in a general circulation model. *J Atmos Science* 45:1397–415.
- Wigley TML. 1995. A successful prediction? *Nature* 376:463–4.
- Wilson CA, Mitchell JFB. 1987. A doubled CO<sub>2</sub> climate sensitivity experiment with a global climate model including a simple ocean. *J Geophys Res* 92(D11):13315–43.
- Woodward FI. 1987. *Climate and plant distribution*. Cambridge UK: Cambridge University Press. 174 p.
- Yaussy DA. 1999. Comparison of an empirical forest growth and yield simulator and a forest gap simulator using actual 30-year growth from two even-aged forests in Kentucky. *For Ecol Manage* 126:385–98.