14. Forest Responses to Changing Climate: Lessons from the Past and Uncertainty for the Future

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The earth's climate has undergone dramatic and long-term changes through natural processes many millennia before humans influenced global climate. Considerable evidence indicates that increasing concentrations of carbon dioxide and other greenhouse gases in the earth's atmosphere will lead to near-term warming, perhaps as much as 2 to 4°C in northeastern North America. Given that the distribution of vegetation on earth has varied with past climate change, it is reasonable to expect that future climate change will affect forest composition and distribution. For reasons both ecological and economic, it is desirable to understand and be able to predict the extent and nature of the changes that might be expected in northern forests in response to climate warming.

This chapter offers insights as to how one might analyze potential future changes in forest composition and also elucidates the numerous complicating biological and anthropogenic factors that create uncertainty about forest responses to changing environments in the future. In particular, we explore vegetation–climate interactions of the past using paleoecological and paleoclimatic information to reveal patterns that have implications for the future. Furthermore, we examine predictive models of vegetation change in response to climate warming that are based largely on our

understanding of current forest–climate relationships and of physiological characteristics of vegetation. We also explore specific biological factors, such as survival, reproductive capacity, and rate of dispersal, that influence how individual species respond to changing climate conditions, and we assess the potential ramifications of interspecific and intraspecific variation in forest responses to changing environments. Finally, we conceptualize anthropogenic stressors as a "new" set of driving variables that can either shape or constrain evolutionary responses to new environmental situations. To that end, we explore the potential "costs" of pollution as a selective agent, the implications of forest fragmentation, and even intensive forest management on both forest ecosystem stability and our ability to anticipate future forest responses.

Paleoecological Evidence of Past Climates and Vegetation Patterns

Holocene Climates of the Northeast

The climate of the Quaternary Period, which is roughly the last two and a half million years, has fluctuated widely. It is characterized by regular cycles consisting of ice ages followed by brief warm intervals known as interglacials, of which the Holocene is the most recent. The regularity of the ice-age cycles has been linked convincingly to three orbital parameters that affect the amount of energy reaching the earth's surface. These "Milankovitch cycles" include changes in (1) the precession of the equinoxes with a periodicity of approximately 19,000 to 22,000 years, (2) the tilt of the axis of the earth with a periodicity of approximately 42,000 years, and (3) the eccentricity of the earth's orbit around the sun with a periodicity of approximately 100,000 years (Imbrie and Imbrie, 1979). Hays et al. (1976) demonstrated that these three cycles were strongly evident in the geochemistry of ocean sediments deposited during the Quaternary and argued that the changing energy flux set the timing of long-term glacial–interglacial sequences.

Of the three cycles, the precessional cycle has most affected Holocene climates because it has changed the date of the year that the earth comes closest to the sun (perigee). At present, perigee occurs on January 5, in the heart of the northern winter. Approximately 9,000 to 11,000 years ago in the early Holocene, perigee occurred in the summer. As a result, seasonality in the early Holocene was increased, that is, summers were relatively warmer and winters relatively cooler than in the Northern Hemisphere today.

A record of climate change in the Holocene consistent with such changes in insolation and reduction in seasonality can be found in sedimentary deposits that have remained in place over many centuries. For thousands of years, lakes and peat bogs have passively monitored vegetation shifts caused by climate change, human activities, and other related

phenomena in the study area. Cores of lake sediments or peat deposits resemble strip-charts that have recorded past vegetation change and have provided a chronology through radiocarbon dating (Jacobson, 1988). Such stratigraphic evidence has been used to infer that temperatures during much of the previous 10,000 years were as much as 2°C warmer and that net moisture was considerably lower than today (COHMAP, 1988; Webb et al., 1994). The climate 6,000 years ago in the upper Midwest was characterized by mean July temperatures approximately 2°C warmer than at present (Bartlein and Webb, 1985). The fact that mean July temperatures in central Europe were also 2°C warmer at that time (Huntley and Prentice, 1988; Prentice et al., 1996) reinforces the notion that hemispheric or global phenomena were involved.

Changes in moisture balance per se (precipitation minus evaporation) in the Holocene have been the focus of studies of past lake levels in Minnesota (Digerfeldt et al., 1992), Wisconsin (Winkler et al., 1986; Winkler, 1988), and Cape Cod (Winkler, 1985). Additional data relating to past water-level changes have been compiled from throughout the northeastern United States (Webb et al., 1993) and eastern North America (Harrison, 1989; Webb et al., 1994). Paleohydrologic research of this kind has consistently shown that lake levels were relatively low during the early to middle Holocene and that they have risen to present levels only in the past few millennia (Fig. 14.1). This is consistent with warmer and drier conditions early in the Holocene changing to cooler and moister conditions in its latter stages.

Forest Responses to Holocene Climate Change in the Northeast

Paleoecoiogists have used pollen analysis of lake and peat deposits to reconstruct the distribution and abundance of plant taxa during the Holocene. Data from hundreds of such studies completed during the last several decades have been used to create isopoll maps that show temporal changes in distribution and abundance of selected plant taxa, including forests of the northeast (Jacobson et al., 1987; Webb et al., 1994). The North America Pollen Database, an outgrowth of Webb's COHMAP database, is now available to the public at the National Oceanic and Atmospheric Administration (NOAA) National Geophysical Data Center in Boulder, Colorado.

Northeastern forests have been strongly influenced by changing temperature and moisture regimes during the present interglacial. Synoptic maps of pollen data spanning the past 20,000 years reveal that most modern vegetation assemblages, even at the biome scale, have been in their present configuration for no more than 6,000 to 8,000 years (Webb, 1987; Jacobson et al., 1987; Overpeck et al., 1991). Also, these results have shown that continent-wide changes in distribution and abundance of plant taxa are species-specific, consistent with Gleason's (1926) individualistic

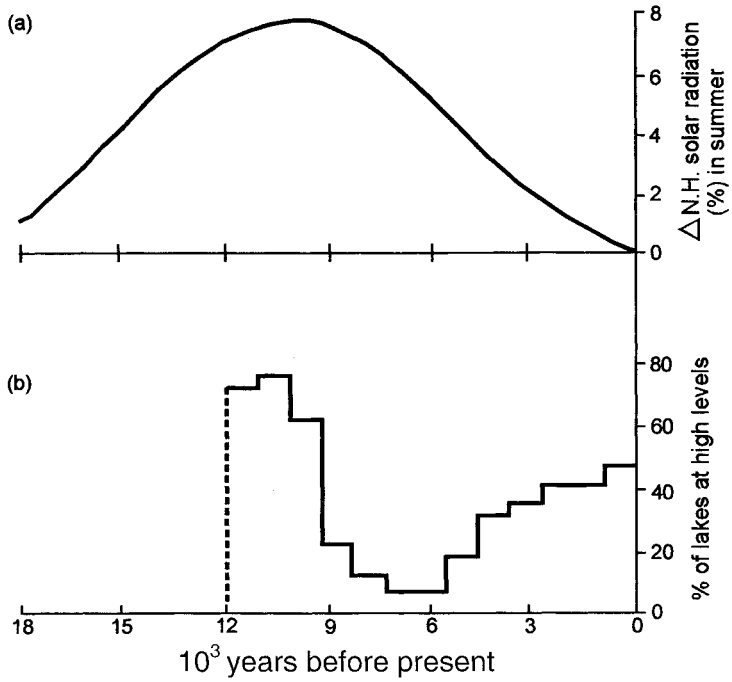

Figure 14.1. (a) Holocene variation in solar radiation during summers at mid-latitudes in the Northern Hemisphere. The pattern results from precession of the equinoxes. (b) Summary data for Holocene lake levels in eastern North America, showing the proportion of sites with relatively high levels through time (by implication, times of moist water-balance) (after Webb et al., 1994).

concept of plant–species responses (Davis, 1983; Jacobson et al., 1987). Contrary to popular belief, modern communities are not highly organized, finely tuned units representing long periods of co-evolution among species. Rather, present communities are merely transitory combinations of taxa that have been responding individualistically to continual and sometimes major climate changes (Hunter et al., 1988).

Eastern White Pine Case Study

Eastern white pine (*Pinus strobus* L.) is just one of many species whose Holocene distribution has been studied using pollen analysis (Jacobson, 1979; Jacobson and Dieffenbacher-Krall, 1995). The data show that changes in eastern white pine populations accompanied major changes in Holocene climate (Fig. 14.2). Eastern white pine was widely distributed in the early to middle Holocene (10,000 to 6,000 years ago), a time of warmer and drier climate than occurs today. As was noted earlier, this was a period of lowered lake levels that, along with other sedimentary data,

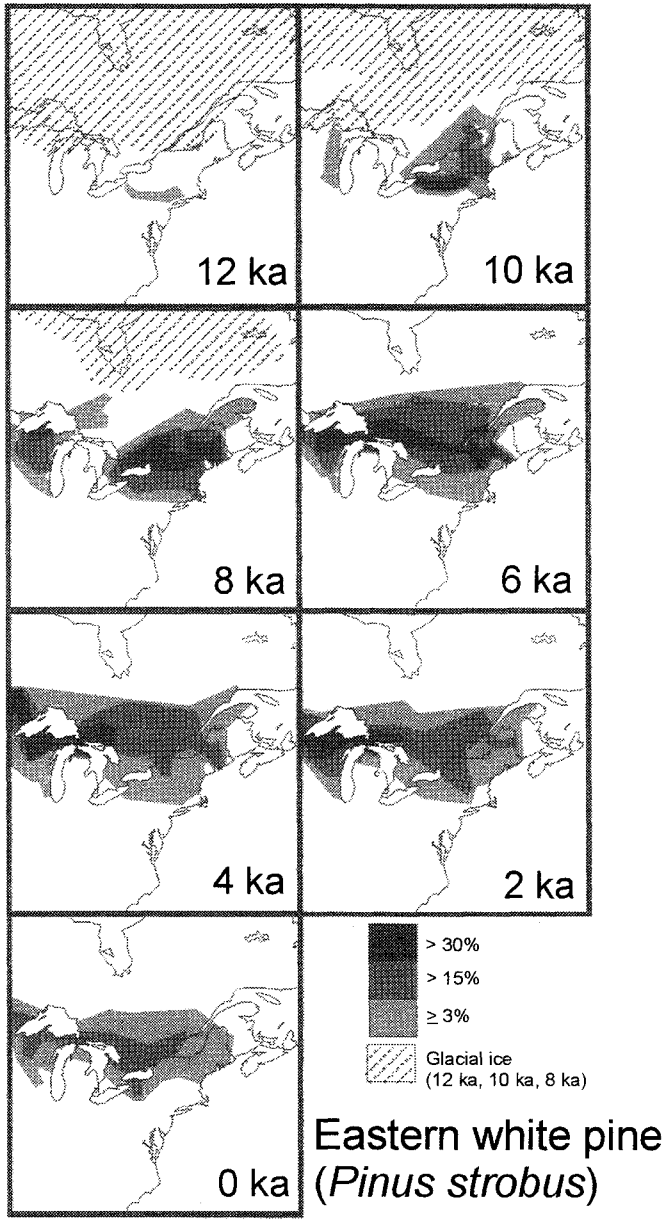

Figure 14.2. Isopoll maps showing areas of abundant white pine (*Pinus strobus*) during the past 12,000 ^{14}C years (estimated from ^{14}C pollen). Fossil pollen data from approximately 140 sites are summarized by lines of equal proportional representation across northeastern North America. Time designated in kiloanni (ka).

indicate that relatively dry conditions prevailed throughout the early Holocene in the Great Lakes–New England region (Webb et al., 1993).

Paleoecological evidence shows that eastern white pine made its first post-glacial appearance in Virginia (Craig, 1969), perhaps moving in from a full glacial location on the exposed continental shelf. It reached northern New England by 10,000 years ago (Davis and Jacobson, 1985), the central Great Lakes region by 9,000 years ago (Brubaker, 1975), and Minnesota and western Ontario by 7,000 years ago (Jacobson, 1979; Björck, 1985).

In the early Holocene, large concentrations of eastern white pine occurred in both the eastern Great Lakes–New England region and an area west of Lake Michigan. In general, regions of high abundance of eastern white pine were also areas in which forest fires were frequent and precipitation was probably not much greater than evapotranspiration. The relatively high fire frequency of the early to middle Holocene would have helped to create conditions favorable for seedling establishment (Jacobson and Dieffenbacher-Krall, 1995). Early Holocene sediments in many New England lakes have high proportions of pollen from eastern white pine and oak (*Quercus* spp.) (Fig. 14.3), along with many charred particles from past fires (Anderson et al., 1986; Patterson and Barkman, 1988; Anderson et al., 1992). Similar evidence was found in Nova Scotia (Green, 1982). The close relationship between climate and fire frequency has been well-established in detailed studies by Clark (1988, 1989).

Eastern white pine reached its northernmost extent about 4,000 years ago, with areas of high abundance shrinking substantially and shifting southward thereafter. This coincides with climate cooling that has allowed boreal taxa to move southward. Another factor in the late-Holocene decline in eastern white pine is the decrease in frequency of fire. Further details of these late-Holocene changes may be found in Jacobson and Dieffenbacher-Krall (1995).

The western range limit of eastern white pine occurs today where precipitation equals evapotranspiration (Transeau, 1905). Unless its habitat is manipulated by human activity, white pine does not thrive when conditions become too cool or moist, for example, at the southern margins of the boreal forest in northern New England and adjacent Canada where disturbance by fire may be too infrequent for widespread establishment of seedlings. The current abundance of eastern white pine in the Northeast results largely from abandonment of farmland during the last 150 years.

Isopoll maps of other taxa (Jacobson et al., 1987; Webb et al., 1994) provide a useful context for evaluating regional changes in eastern white pine. Other data show that in the early to middle Holocene, both eastern white pine and eastern hemlock (*Tsuga canadensis* [L.] Carr) were present at elevations as much as 300 to 400 m higher than their present upper limit in the White Mountains of New Hampshire (Davis et al., 1980). Jackson and Whitehead (1991) documented similar elevational patterns for tree

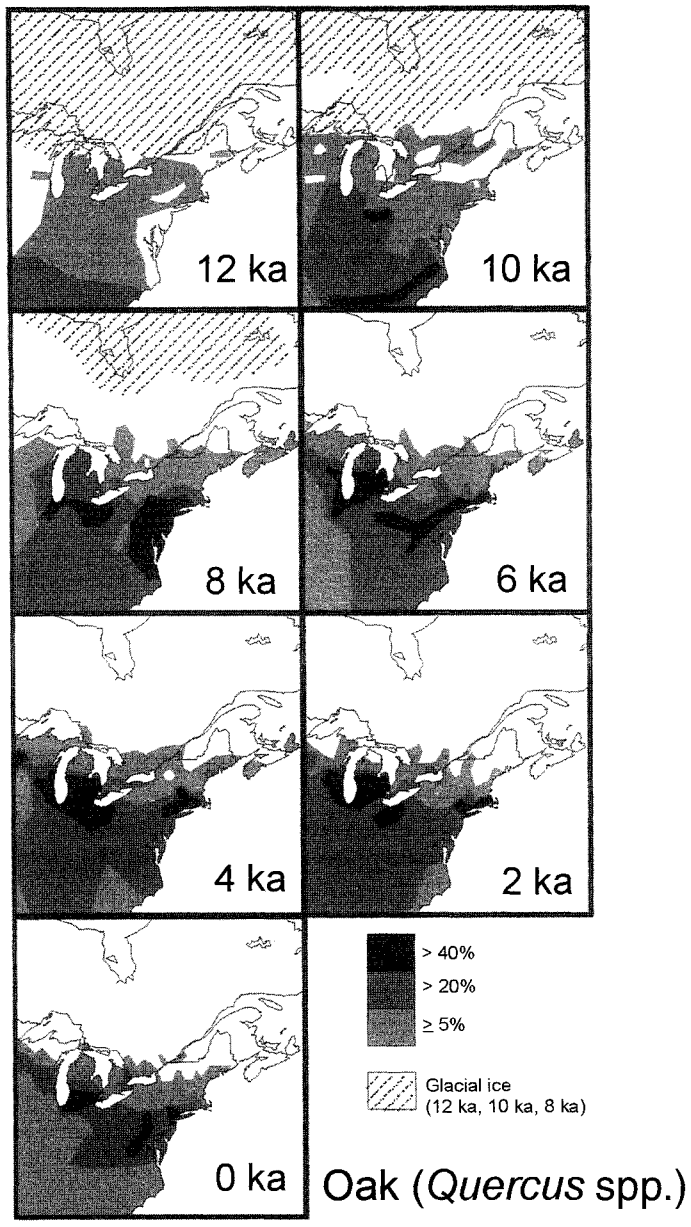

Figure 14.3. Isopoll maps showing areas of abundant oak (*Quercus* spp.) during the past 12,000 ^{14}C years (estimated from ^{14}C pollen). Fossil-pollen data from approximately 600 sites are summarized by lines of equal proportional representation across northeastern North America. Time designated in kiloanni (ka).

taxa growing in the Adirondack Mountains of New York. Paleoecological studies of the later Holocene show that the boreal forest of eastern Canada developed only in the past 6,000 years (Webb, 1987) and that hemlock has been abundant in the forests of the eastern Great Lakes–New England region for that same period of time (Fig. 14.4). Other data show that southern populations of spruce (*Picea* spp.) shifted from Canada into the northern tier of states from Maine to Minnesota in the past 1,000 to 1,500 years, accompanied by a general decrease in abundance of eastern white pine that has continued to the present (see Fig. 14.2). Small populations of balsam fir (*Abies balsamea* [L.] Mill.) were scattered throughout the northeast during most of the Holocene, but they, too, expanded recently to form the spruce–fir forests of today. The spatial array of changes has been influenced by variations in importance of fire (Foster, 1983) and other disturbances.

Spruce Case Study

Acadian forests of Maine and the adjacent Canadian provinces are characterized by abundant spruce and fir. These constitute a major resource for both the forest products industry and the millions of recreational users who enjoy the north woods. The health of these forests is so important that any threat to their productivity or aesthetics is of immediate public concern. During the last few decades, factors such as spruce budworm outbreaks, cutting practices, and various other land use issues have been the subject of major public discussions in the Northeast. However, spruce–fir forests may be as vulnerable to future changes in climate as to any of these often-debated factors.

Isopoll maps demonstrate that dramatic changes occurred in the abundance of spruce in Maine and adjacent areas, especially during the last few centuries. Spruce and, to some extent, fir had relatively little presence in the northeastern forest during most of the last 9,000 years (Fig. 14.5). Only in the last few centuries have spruce and fir covered the Acadian region as densely as they do today (Schauffler, 1998). Another way to think about this is that the older spruce trees living today in northern Maine, some 250 years or more old, have been living for roughly half the time in which recent spruce forests have densely covered the Acadian region.

Populations of spruce and fir are closely linked to climate and have responded to cooling in the late Holocene. Several lines of evidence indicate that the climate of New England became cooler starting several thousand years ago—and that it turned dramatically cooler just a few hundred years ago. A similar trend is well-documented for many areas of Europe and even New Zealand, where the recent cooling is often referred to as the "Little Ice Age." The best current estimates of the cooling in Maine and along the southern margin of the boreal forest in Canada indicate a reduction of perhaps 1°C in mean July temperature during the

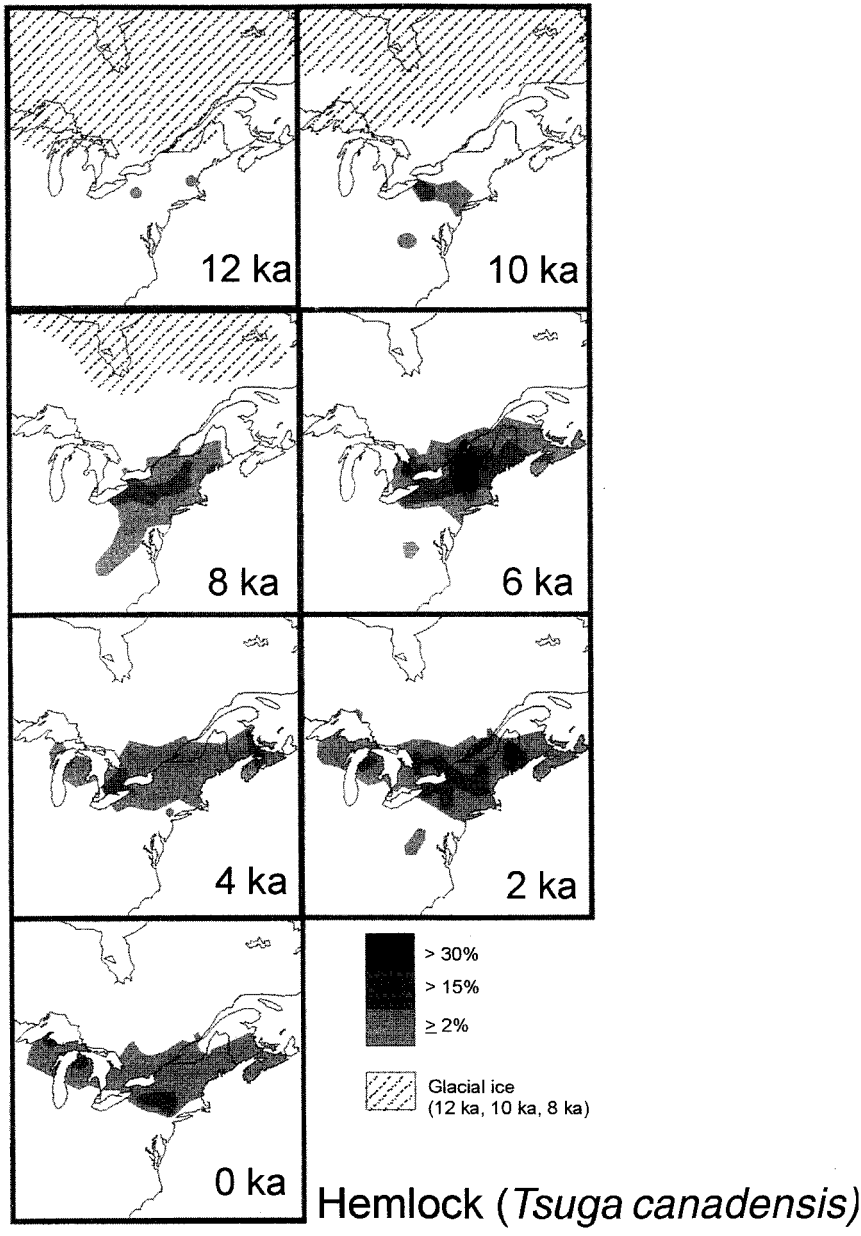

Figure 14.4. Isopoll maps showing areas of abundant hemlock (*Tsuga canadensis*) during the past 12,000 ^{14}C years (estimated from ^{14}C pollen). Fossil-pollen data from approximately 450 sites are summarized by lines of equal proportional representation across northeastern North America. Time designated in kiloanni (ka).

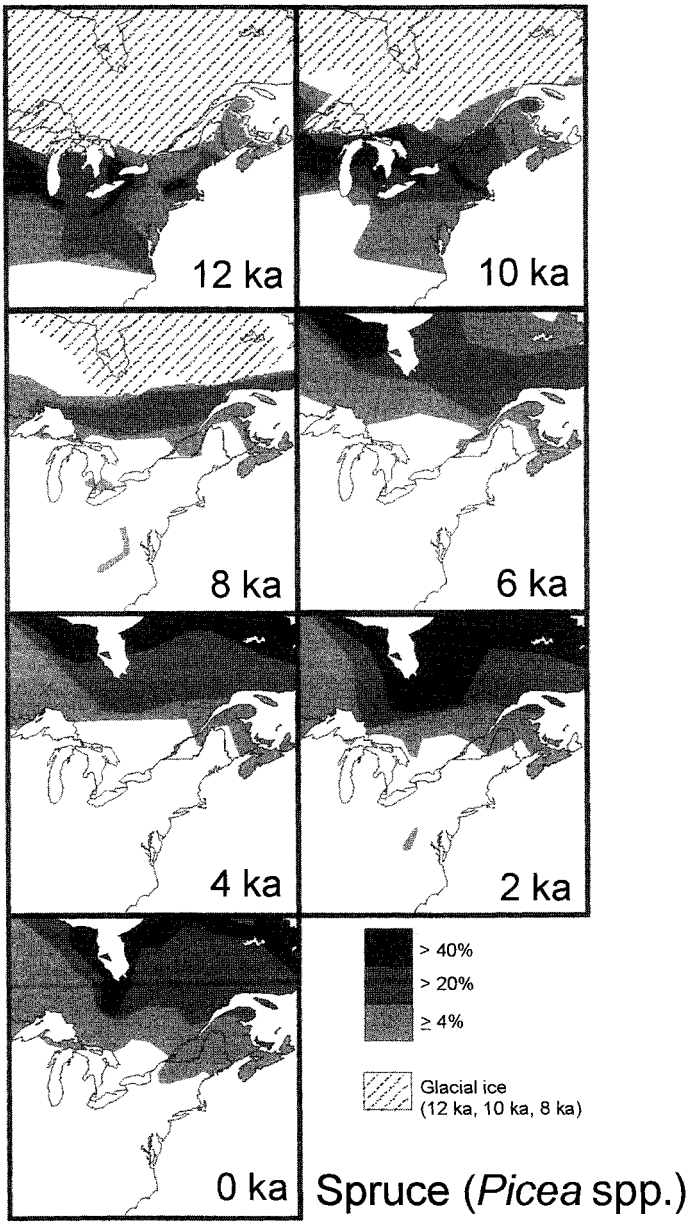

Figure 14.5. Isopoll maps showing areas of abundant spruce (*Picea* spp.) during the past 12,000 ^{14}C years (estimated from ^{14}C pollen). Fossil-pollen data from approximately 600 sites are summarized by lines of equal proportional representation across northeastern North America. Time designated in kiloanni (ka).

"Little Ice Age" (Gajewski, 1988). This change is ecologically significant because spruce survival along the southern margin of its range is thought to be limited by summer heat and drought. The examples of spruce and eastern white pine migrations of the past demonstrate the independent nature of species responses to changing climate and provide insights into the dynamic nature of species/environment relationships.

Modeling Species Responses to Changing Climate

Evaluation of paleoecological evidence is one approach for predicting future forest composition in response to climate change. The second general approach involves using mathematical models to predict how changes in climate will affect the distribution of vegetation. Increasing evidence exists of a general warming trend on the planet (MacCracken, 1995; Wigley, 1995), and various global circulation models predict a further 1 to 4.5°C temperature increase over the next century (Kattenberg et al., 1996). Major changes may occur in the earth's living systems, including temperate forests. Using models to predict vegetation response may greatly help in understanding potential impacts of global climate change.

Several approaches have been used to model possible species responses, each of which has merit. These models use modern calibrations of various types and at various spatial scales. For example, Nielsen (1995) and Kittel et al. (1995) have developed climate–vegetation models based essentially on continent-scale calibration of biomes. Other efforts have included stand-scale modeling approaches to estimate forest responses to climate changes (Pastor and Post, 1986; Post and Pastor, 1990, among others). Still another type of model, Prentice's BIOME model, was derived from a physiology-based analysis of how plant life-forms relate to climate regions of the world (Prentice et al., 1996; Haxeltine and Prentice, 1996). Indeed, because these models cannot be truly validated (Rastetter, 1996), multiple avenues of research are encouraged, with the hope that results may eventually converge (Hobbs, 1994; VEMAP members, 1995; Lauenroth, 1996). This section provides a brief overview of some of the models that have been used. It then explains in more detail one empirical approach to modeling specific species responses and finally uses that approach to present two possible scenarios of tree biodiversity effects using multiple species overlays.

Overview of Approaches

Two major approaches have been used to model potential responses of vegetation to climate change: the empirical approach using correlative/statistical models and the mechanistic approach using biogeography and biogeochemistry models. The first uses empirical relationships of

current vegetation–climate patterns to predict potential vegetation distribution following climate change, while the latter incorporates physiological characteristics of the vegetation. Because modeling is an active area of research, all approaches are becoming more sophisticated and intertwined.

Empirical Approach Using Correlative/Statistical Models

Many researchers have successfully recreated current vegetation patterns via climate–vegetation analysis and using specific regression relationships (Booth, 1990; Bonan and Sirois, 1992; Box et al., 1993; Huntley et al., 1995). Iverson and Prasad (1998) used regression tree analysis (described in detail in a following section) that uses climate as well as soil, topographic, and land cover information to derive vegetation–environment relationships. Once relationships to current vegetation are established, the climate is changed according to various global change scenarios to derive potential future vegetation distribution maps. These models must assume that species are bounded by modeled characters, so that factors such as changes in species competition and CO_2-derived water use efficiency cannot be incorporated (Loehle and LeBlanc, 1996). Still, they provide valuable insights into potential species shifts under various global climate change scenarios.

Mechanistic Approach Using Biogeography and Biogeochemistry Models

At least five biogeography models and 20 biogeochemistry models now exist (Neilson et al., 1998); they use physiological characteristics of vegetation to predict future vegetative distribution from climate change. Two primary biogeography models are the Mapped Atmosphere-Plant-Soil System (MAPPS), developed by Neilson and associates (Neilson, 1995; Neilson and Marks, 1994), and the BIOME3 model (Haxeltine et al., 1996). Both models calculate the potential vegetation type (up to 45 vegetation types globally for MAPPS and 18 for BIOME3) and leaf area that a site can support (at local, regional, or global scales), as constrained by local vegetation and hydrologic process and the physiological properties of plants (Neilson et al., 1998). These two models have been used extensively by the Intergovernmental Panel on Climate Change to better assess potential regional vegetation changes according to various climate change scenarios (Watson et al., 1998). Efforts are now underway to incorporate continuous feedback from vegetation effects into dynamic models of global vegetation change (Foley et al., 1996; Neilson and Running, 1996).

Biogeochemistry models simulate carbon and nutrient cycles of ecosystems, but tend to lack the ability to predict vegetation types at a given location. In an exercise to compare among three of the primary

biogeochemical models as well as three biogeography models, the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) was devised to assess model capabilities and the potential impacts of global warming on U.S. ecosystems (VEMAP members, 1995). They used TEM (Raich et al., 1991), CENTURY (Parton et al., 1988), and BIOME-BGC (Running and Hunt, 1993). The VEMAP process determined that all models can adequately simulate vegetation under the current environment, but that alternative climate scenarios produce divergences, even to the level of producing vegetation responses of opposite sign. The biogeochemical model PnET, used thus far primarily in the eastern part of the U.S., has done an excellent job of producing physiologically based estimates of primary productivity, annual drainage, and photosynthesis (Aber and Federer, 1992; McNulty et al., 1994).

All of the above modelling efforts have shown that environmental drivers, as modified by disturbance processes, generally control the distribution of tree species. These relationships are increasingly being scrutinized and verified. Within a region, species vary primarily due to regional climatic factors, whereas variations in terrain, soil, and land use history factor principally in more local studies. Geographical information systems (GIS) allow predictive mapping of vegetation based on the species-environment relationships.

Response of Species Using Regression Tree Analysis Models

We describe here an empirical modeling approach called regression tree analysis (RTA) to evaluate potential future habitat that is suitable for species to occupy given any potential future climate scenario. If we assume the species will be able to migrate to the new habitat, it will represent potential future distributions for the species. RTA is a relatively new technique in the ecological sciences that uses repeated resampling of the data to develop empirical relationships between response and predictor variables, rather than the more restrictive distributional assumptions in classical regression functions. This alternative modeling approach creates models that are fitted by binary recursive partitioning whereby a data set is successively split into increasingly homogeneous subsets to elucidate relationships between predictor and response variables (Clark and Pregibon, 1992).

The RTA approach seems appropriate for predicting landscape-level distributions of species from environmental data. Its use has grown with that of geographical information systems that allow model outputs to be readily mapped across landscapes. There are few, but increasing, ecological examples of the use of RTA (e.g., Davis and Goetz, 1990; Michaelsen et al., 1994; Reichard and Hamilton, 1997; Flemming, 1997). For this chapter, RTA was used to evaluate the relationship of 33 environmental variables to 80 eastern tree species importance values,

and then used the derived relationships to predict their present and potential future importance values. The methods and assumptions involved in this effort are described in detail in Iverson and Prasad (1998), and were used to produce an associated atlas of all 80 species (Iverson et al., 1999).

The intention was to create RTA models that best match current distribution of species importance values, then project potential future distributions after climate change. For this, we substituted current climate variables with the projected outputs from two scenarios of equilibrium climate under $2\times CO_2$: the GFDL (Geophysical Fluid Dynamics Laboratory) (Wetherald and Manabe, 1988), and GISS (Goddard Institute of Space Studies) (Hansen et al., 1988). Though $2\times CO_2$ will likely occur by the year 2100, the longevity of trees, genetic variation, and the presence of remnant refugia would dictate that the possible outcomes shown in these models would take centuries to take full effect.

Regression trees were generated for 80 tree species in the U.S. Department of Agriculture (USDA) Forest Service's Forest Inventory and Analysis (FIA) database. Species importance value (based on basal area and number of stems) was the response variable, along with the 33 predictor variables mentioned above. The regression trees were generated and used to predict the importance value for each species by county.

The tree diagram produced for each species provided information on the primary driving variables for the species. Predicted current distributions matched current FIA data quite well for most species. For example, the primary variable controlling the importance value of eastern hemlock was July temperatures followed by soil characteristics, such that the modeled current distribution and abundance of eastern hemlock matches actual data reasonably well (see color insert Fig. 14.6). Eastern hemlock grows well on moist, cooler sites with good drainage, but will grow under a variety of soil conditions (Godman and Lancaster, 1990). The county-level of resolution is therefore adequate to capture the major environmental variables driving its distribution, and conditions represented by county averages are adequate to model the species.

In general, the more specialized the species is with respect to edaphic conditions, the less accuracy in the RTA model predictions because county-resolution data would not be expected to consistently capture the appropriate information for the RTA process. Projected species distributions, following equilibrium of predicted climate changes, show major shifts for many species. The GISS and GFDL scenarios would reduce area of eastern hemlock by 14% in the U.S., with over 40% loss in area-weighted importance value (see Fig. 14.6). The difference maps show the loss of importance to be primarily in New York and southern New England, while increases could occur in the upper Midwest (see Fig. 14.6). Because of differential shifts among species in area and importance, forest communities would also be expected to differentially change in compo-

sition. Regression tree analysis can be considered a valuable tool to understand species–environment relations. By operating at a species level, RTA gives an indication of potential changes in community dynamics and biodiversity.

Multiple Species Assessments

Using regression tree analysis, we can begin to make overall assessments regarding possible changes in forest composition under global climate change scenarios. Of course, overlaying multiple species projections means that, in addition to the assumptions listed by Iverson and Prasad (1998), we must assume that competition among species will not significantly alter the result of linearly combining the 80 single species models created by RTA.

Species Richness

By combining the maps for all 80 species, we can count the number of species projected to occur in each county and map the result (see color insert Fig. 14.7). Doing so, we see that the overall species richness is not projected to change wildly. However, a general homogenization occurs whereby those locations in the western part of the study area with currently the lowest species diversity are projected to gain some species, and some of the areas of rich diversity in the southern part of the country (e.g., Mississippi) are projected to lose some species. Florida also shows a possible gain in species, although diversity is currently artificially low there because its many endemic species did not meet the criteria for entering into the RTA modeling. As shown in Fig. 14.7, Minnesota and Wisconsin would lose some species, while areas that are now highly diverse, such as along the Ohio River and Mississippi River, would remain diverse.

Dominant Genera

In an effort to begin assessing possible changes in forest type, we combined the information for all 80 species and assigned a genera code to the species that had the highest importance value for each county. This process was done for current climate as well as the GISS and GFDL climate scenarios. Maps were then generated showing genera with the highest importance value from current and projected future conditions (see color insert Fig. 14.8). To aid in visual comparisons, only those 14 genera were mapped that had at least 15 counties in which they were dominant under current climate conditions, and the same legend was used for the two future scenarios. A comparison of the three maps shows the loss of all fir (mostly balsam fir) from Maine and most of the *Populus* spp. (mostly quaking aspen) from the northern states. Eastern cottonwood (*Populus*

deltoides Bartr.) remains important in the western part of the study region. Maple (*Acer* spp.) also is greatly reduced in the future scenarios; red maple (*Acer rubrum* L.) is mostly eliminated from dominant position, while sugar maple (*Acer saccharum* Marsh.) appears infrequently in the Midwest and boxelder (*Acer negundo* L.) occupies a prominent position in the western counties.

The primary increase is with pine (*Pinus* spp.), primarily loblolly pine (*Pinus taeda* L.). This species is shown to move quite dramatically northward, yet, along with longleaf pine (*Pinus palustris* Mill.), retain the current area but diminish in importance in the Southeast (see Fig. 14.8). In New England, again pine is prominent, but here it is white pine, which is projected to replace the fir forests in Maine. Ashes (*Fraxinus* spp.) and elms (*Ulmus* spp.) would gain prominence in the midwest under the future climate change scenarios. The oaks (*Quercus* spp.) would also expand under future (warmer and drier) conditions, especially in the GFDL scenario in which primarily post oak (*Quercus stellata* Wang.) would take over loblolly pine in overall importance in many instances.

Both paleoecological studies and modeling efforts have clearly shown that communities are *ad hoc* mixtures of species and cannot be expected to move together as intact communities if future conditions change. Modeling exercises such as these are laden with assumptions, but they do begin to give a picture as to how species and forests could respond if the climate changes. The model outputs for spruce–fir and eastern white pine match historical patterns described in the case study presented earlier in the chapter. Efforts such as these are needed to begin to learn what the nature of our nation's future forests might look like under a globally changed climate.

Factors Contributing to Uncertainty in Predicting Future Forest Composition

Paleoecological studies and modeling efforts provide strong evidence that global warming will eventually change the geographical distribution of vegetation. However, forecasting the details of species migration presents a significantly more difficult challenge because a number of important factors are not well known. Accurately predicting future forest composition requires both an understanding of how the environment will change and how individual species will respond to that change. Considerable effort has been expended to predict future climate change, but many questions still remain, particularly about future precipitation patterns and the frequency of disturbance events. Also not yet clear is the extent and nature of predicted change in such factors as ambient air temperature increases, atmospheric ozone enrichment, and the concentration of acid inputs.

The response of tree species to complex environmental changes will be of fundamental importance to the continued adaptation, health, and sustainability of northern forest ecosystems, yet species responses to environmental change have been treated only in simple terms. For the most part, the determinants of the boundaries of any particular species are poorly understood. Many models attempting to forecast species distribution in response to global warming begin with the assumption that species can exist only within their present temperature and/or moisture regimes (Botkin and Nisbet, 1992; Davis and Zabinski, 1992). While perhaps initially appealing, there is substantial evidence that many other factors are also influential in delimiting species boundaries and distributions (Woodward, 1987). Without accurately addressing the variety of factors that influence species distribution and responses to changing environments, predictions of species migration in response to changing climate will be erroneous, perhaps greatly so. Consideration must certainly be given to life history and competition factors that influence species establishment and survival, including the potential responses and influence of exotic plant species and pathogens to climate change. Anthropogenic factors and the differential response of species and populations within species to such factors represent a new complicating element in predicting future forest composition. Anthropogenic stresses may transform some species through selective action and modify the extent, nature, and ability of populations or species to adapt or respond to climate changes.

Impact of Life History and Competition Factors

Despite many uncertainties, we do know the general categories of factors that influence species distribution. For a species to maintain a presence at a particular location, there must be (1) a physical environment (including climatic, edaphic, and fire-history factors) that permits successful completion of the plant's life stages, (2) a supply of seeds (or an effective vegetative propagation method), (3) an absence of decimating herbivores and pathogens, and (4) an ability to successfully compete with other species. If a species is absent from a particular location, it may be because the species' physiological tolerances have been exceeded at one or more stages in its life cycle. Alternatively, it may also be because past events have excluded the species from the area, or the species is not competitive with others that are present, or fires or pests preclude survival. If a species exists at a particular location, it is because that species has traits that enable it to outcompete other species on that site. As such, for a species to successfully occupy a site, it must be able to access that area, successfully colonize the site and remain competitive, and replace itself. Present ecological configurations certainly reflect competitive successes, but do not necessarily reflect the only situations in which a species could be successful.

We can generalize about the relative importance of environmental factors on species distribution. In the boreal and temperate regions, low temperatures are frequently thought to limit poleward expansion of species ranges. Where forests abut steppe, drought and/or fire are probably limiting agents. In most other situations, interspecific competition is likely to be the dominant factor limiting species distribution. Examples of effective interspecific competition strategies may include more aggressive reproduction, phenological synchrony with physical and/or biological components of the environment, or more effective methods to withstand insect or pathogen attack. By Woodward's (1987) analysis, the equator-ward margins of species ranges tend to be established by competitive forces. Unfortunately, though, the precise factors that determine species ranges are myriad and idiosyncratic. The number of factors and paucity of information about them led Franklin and others (1992) to conclude that, aside from the general tendency for species to migrate poleward and uphill as climates warm, "... surprises (exceptions to our logical predictions) will probably be the rule."

Robustness of Natural Populations

Where trees exist at their physiological limits, climate changes could induce rapid death. While some express concern about this possibility (Botkin and Nesbit, 1992), others have noted the ability of mature trees to withstand altered climates for considerable lengths of time (Brubaker, 1986). Support for the latter view comes from historical data indicating that during the past 10,000 years North American spruce trees existed in climates that were significantly warmer than in any part of their current ranges (Davis, 1978). There is general recognition from paleoecological data that the distribution of vegetation was nonanalogous with climate prior to about 6,000 to 7,000 years ago (Woodward, 1987; Overpeck et al., 1991). This suggests that factors other than physiological tolerance were determining the southern portions of the range of spruce. It also suggests that the phenotypic plasticity of spruce is greater than that evident from the range of environments inhabited by spruce today.

The degree to which climate change can be tolerated before mortality is accelerated is not well known for any tree species, but provenance tests indicate that it is probably substantial. In provenance tests, trees of a single species representing a wide range of habitats are planted together at one or more locations for comparison. In most cases, such tests reveal considerable genetic differentiation among populations from disparate parts of the species' range. As a general rule, trees from northern populations are slower-growing than their southern relatives (except when low temperatures injure trees from southern provenances) when grown in common garden, and they suffer almost no mortality when grown

hundreds of miles south of their origin. Clearly, northern populations of most temperate and boreal zone species have no difficulty tolerating climates more than 5°C warmer on an annual basis. The only exception may be with trees having substantial winter chilling requirements. For example, red maples from Massachusetts exhibit sporadic and delayed spring budbreak and have poor survival when grown in Florida (Perry and Wang, 1960). This possibility should be examined carefully because some climate models project that much of the future warming will be experienced in the winter (Woodward, 1992). Observations of horticultural plantings also suggest that species can be grown in climates far warmer than any place in their natural range.

While increasing warmth, per se, will probably not be injurious to most established trees, results could be different if accompanied by drought. The anticipated warming, of course, will be accompanied by increased atmospheric carbon dioxide (CO_2) concentration. A number of studies have shown that increased CO_2 concentration should increase the growth of trees under well-watered conditions (Teskey et al., 1998). More importantly, perhaps, other studies have shown that increased CO_2 will reduce transpiration by allowing more CO_2 to enter through partially closed stomata (Jarvis and McNaughton, 1986). The reduction in transpiration that is expected to accompany increased CO_2 concentration may well offset the effects of increased drought that could occur. Indeed, Woodward (1992) projects that the world's forested area will increase despite increased dryness if atmospheric CO_2 concentration doubles. These projections are based on extrapolations from small plot studies and, thus, are subject to considerable error when applied on a global scale. Nevertheless, it is expected that higher CO_2 concentrations will partially offset the effects of decreased moisture availability, but the degree of compensation is not firmly established.

Provenance tests also indicate that trees from moist areas generally suffer greater mortality than trees from drier sites, especially when planted on sites in the drier portions of the species' range. For example, loblolly pine from North Carolina (with wetter growing seasons) grew much faster than native populations in Arkansas (with drier growing seasons). However, after 25 years, the North Carolina trees show pronounced mortality (Wells and Lambeth, 1983). The exact cause of death was not known, but it was correlated with drought. Plasticity in drought tolerance has not been quantified for any species, but appears to be smaller than for tolerance of high temperatures.

Empirical information from provenance tests and horticultural plantings, albeit based on trees in largely noncompetitive growing environments, demonstrates the great resiliency of forest tree species, especially relative to high temperatures. Coupled with the relatively rapid rate of predicted climate warming, these data and experiences highlight the

possibility that many species distributions may not simply shift northward or upward, but may actually remain competitive in their current locations and actually expand their distributions.

Regeneration Success in Changed Climates

The inherent robustness of natural populations will likely enable existing trees to withstand warmer temperatures currently predicted to accompany higher atmospheric CO_2 levels. Concerns have been raised, however, about the ability of these trees to regenerate in a warmer and perhaps drier climate (Franklin et al., 1992).

The ability to regenerate depends on the ability of existing trees to produce seeds and for those seeds to germinate and survive. Various climatic parameters can influence seed production. Cold temperatures have been shown to restrict seed production in some species, such as little-leaf linden (*Tilia cordata* Mill.), at the northern extremities of their range (Pigott, 1981). On the other hand, viable seed production in American beech (*Fagus grandifolia* Ehrh.) is an inexplicably uncommon event in the southern portion of its range, exclusive of Mexico. Physiological stress has been shown to increase seed production in many species, at least in the short term. Conversely, stress that depletes carbon reserves can result in poor seed production, and severe drought stress can lead to flower and fruit abortion. Numerous other climatic factors could potentially affect seed production as well. However, no generalizations can be made at this time. Some species will undoubtedly show increased seed production, and others less. In most cases, though, there is no reason to expect seed production will be inhibited following warming.

A greater concern is that a warmer and drier environment may reduce germination and seedling survival. The most sensitive stage of a tree's life is the beginning. Losses in this period are very high, owing mostly to conditions that are inhospitable at this vulnerable stage. On sites that are prone to drought or lethal temperatures, such as south-facing slopes, higher temperatures would exacerbate losses. The area affected by these lethal agents would increase to some degree. Furthermore, germination could be reduced or unfavorably delayed in species with unmet cold stratification requirements. These unknown factors related to seed germination and success of the seedling stage in forest trees all contribute to uncertainty in predicting future forest composition.

Uncertain Rates of Migration

Paleoecological studies have indicated that the ranges of many species have migrated throughout history in response to changing environmental conditions. As climate warmed, species ranges typically shifted to higher latitudes and higher altitudes; as climate cooled, the reverse occurred.

Other, more subtle, changes in species ranges could also occur to adjust for climate changes, such as a species inhabiting cool, moist microsites if the climate becomes warmer and drier. The ability to adjust their distribution to changing environmental conditions ensured continued representation of many forest tree species after such upheavals as the Quaternary's glacial periods.

Of course, individual trees did not change location; rather, a shift occurred in the distribution of the range of the overall species at historical rates of approximately 10 to 50 km per century (Schwartz, 1993). Consider the example of climate cooling. More seedlings on the southern portion of the species range would likely become established than on the northern edge of the species range. In time, more seedlings would germinate southward than northward, and the species range as a whole would shift southward. If a topographical obstacle, such as a high mountain range or water body happens to get in the way of this southward migration, the species may be unable to migrate far enough southward to withstand a significant climatic cooling. In fact, this scenario may have occurred for a number of northeastern forest tree species during glacial periods; many species found a "glacial refugium" in the southern Appalachian region. If the Appalachian Mountains were aligned east–west instead of north–south, perhaps many of these species would have been unable to migrate far enough southward to endure the climatic cooling experienced during glaciation.

Uncertainty exists about the nature and extent of future climatic change and its effect on migration of forest tree species. Although it is tempting to speculate that climate change may be too rapid for forest tree species to successfully migrate or that large gaps may be created that can restrict species dispersal, historical evidence indicates that climate changes in the past have been more rapid than changes projected for the next few centuries without any great restriction to species movement. It is possible, however, that species rates of migration could be so different that some species may be "overrun" and obliterated by more competitive species. Furthermore, it is unclear to what extent species migration might be influenced by human activities, such as being restricted by forest fragmentation or aided by the planting of trees. Migration is an important component that needs to be addressed in predicting future forest composition.

Competition from Exotic Species

The competitive influence of exotic species, including both nonnative plant competitors and exotic pathogens (insects and diseases), also contributes uncertainty to predictions of how northern forests will respond to environmental change. Whether part of the planned extension of a species range or the result of an uncoordinated release, the addition of nonnative tree species to northern forests would likely interact with the competitive

dynamics already influenced by environmental change and further alter forest community structure. In fact, because exotic species often aggressively fill new or undeveloped niches within ecosystems, there is reason to believe that some exotics could thrive in an environment in which traditional niches are redefined in response to environmental change. Empirical observations of the survival, growth rate, and successful establishment of exotic species in northern forests, such as Norway spruce (*Picea abies* [L.] Karst.), common buckthorn (*Rhamnus cathartica* L.), common lilac (*Syringa vulgaris* L.), and black locust (*Robinia pseudoacacia* L.), demonstrate that aggressive exotic species can modify the composition of forested landscapes, especially in disturbed areas. The widespread existence of mature forest plantations, including both non–North American and off-site native species, and abundant ornamental plantings provide a ready source of exotic germ plasm for dissemination. Likely variation in the net physiological responses and resulting competitive fitness of native species, combined with uncertainties about the possible interplay of introduced species, raises substantive questions about our ability to accurately predict the outcomes of complex and potentially dynamic environmental change.

Perhaps of greater concern are the potential impacts of exotic insects and diseases. Exotic pathogens, such as chestnut blight, Dutch elm disease, and gypsy moth, have already modified the dynamics and composition of north temperate hardwood forests. If warm temperatures permit the spread of insects and diseases that are currently held at bay by cold, or if drought increases the acreage affected by fire or the susceptibility of some trees to secondary stresses, the impact on forest health and future composition would be substantial. Although the effects of fire may be mitigated by human fire-control activity, it is likely that unpredictable insect and disease epidemics will materialize. Abundant present day empirical information supports this contention. Recent epidemics of Scleroderris canker, pear thrips, the Asian longhorn beetle, and the apparent aggressive northern migration of the hemlock wooly adelgid and hemlock looper illustrate the potential influence of exotic pathogens on native forests. The globalization of forest industry and frequency of long-distance travel and transport has enhanced pathways for exotic introductions. Indeed, this element of uncertainty can have truly frightening implications.

Indeed, the potential for significant climate-driven changes in the distributions of north temperate forest tree species will likely blur the distinction between some species thought to be "native" vs. "exotic" to a specific region or habitat. In the same way that some very adaptable Eurasian exotic plant or pathogen species may have become widespread and competitive in the northeast, the potential exists for some currently native northeastern species to become dominant as an "exotic" of sorts in some new environment. For example, recent data documents a dramatic

ecological expansion in the distribution of red maple throughout eastern forests, which is expected to shift wildlife populations and alter biodiversity of these forests (Abrams, 1999). The expansion is attributed to a combination of the species being an ecological generalist and changes in habitat disturbance patterns, including the suppression of forest fires (Abrams, 1999). Under new disturbance regimes associated with changing climate, other species may emerge as dominant generalists to alter the distribution and composition of future forests.

Impact of Anthropogenic Factors

Anthropogenic factors also need to be incorporated into future environment scenarios because human influences on the earth's ecosystems are substantial and growing (Vitousek et al., 1997). Through a variety of enterprises (e.g., industry, agriculture, recreation, and international commerce), humans are transforming fundamental natural processes such as climate, biogeochemical cycling, and even the biological diversity upon which evolutionary change depends (Vitousek et al., 1997). Although a dominant component of this global transformation is climate change, there are many other environmental factors that could affect the health and sustainability of forests. Prominent among these is a diverse pool of pollutant inputs. The list of airborne chemicals that northern forests receive is long, and probably restricted only by current monitoring limitations. Principal contaminants include acid deposition (which is dominated by four ionic constituents: hydrogen [H^+], nitrate [NO_3^-], sulfate [SO_4^{2-}], and ammonium [NH_4^+]) and gaseous pollutants (primarily ozone [O_3], sulfur dioxide [SO_2], and oxides of nitrogen [NO_x] in addition to elevated CO_2) (Mohnen, 1992). Trace additions of heavy metals (e.g., lead, mercury, and arsenic) and numerous man-made toxins (e.g., polychlorinated biphenyl [PCB] congeners, polycyclic aromatic hydrocarbons [PAHs], dichlorodiphenyltrichloroethane [DDT]), and derivatives also occur (Baisden et al., 1995; Hoff et al., 1996; Golomb et al., 1997a,b).

Although climate change and pollution are often emphasized, northern forests also contend with a host of other anthropogenic influences, including changes in land use and associated forest fragmentation and the possible impacts of intensified forest management. Alone and in combination, these and other anthropogenic forces are changing forest environments and the selection pressures that shape forest communities and will affect the future distribution of species.

Direct Threats to Tree Health and Survival

It is increasingly evident that some anthropogenic factors directly alter tree physiology and influence the health and survival of forests. The impact of gaseous air pollutants on eastern white pine and acid deposition on red spruce (*Picea rubens* Sarg.) provide vivid examples.

Eastern white pine, although a robust species from both ecological and paleoecological perspectives (Jacobson and Dieffenbacher-Krall, 1995), may very well be injured by air pollution more than any other tree species in eastern North America and is particularly sensitive to O_3 and SO_2 pollution (Gerhold, 1977). Morphological and physiological symptoms of air pollution injury in eastern white pine include direct foliar injury, growth reductions, depressed photosynthetic rates, and mortality (Karnosky and Houston, 1979). It has been demonstrated that greater than 10% of the sensitive trees and 5% of trees intermediate in sensitivity in a population died as a result of air pollution–induced viability selection (i.e., reduced growth rate and competitive ability for light, water, etc.) over several years (Karnosky, 1980). Most estimates suggest that the proportion of trees sensitive to air pollution in a population may vary between about 5 and 25%, and many of the sensitive individuals have been lost from natural populations. In northern Ohio, it is estimated that 40% or more of a native eastern white pine population may have been lost as a result of air pollution–induced selection (Kriebel and Leben, 1981). Although the population is adapting to changing pollution levels, such selection for pollution resistance results in an immediate loss of forest productivity. Also, pollution-induced mortality would be expected to reduce genetic diversity that may be needed for future adaptation to anthropogenic stress, such as climate warming.

The response of red spruce to acid deposition is more indirect and physiologically complex, but further illustrates an anthropogenic threat to forest health, survival, and potential evolutionary development. It has recently been documented that acid inputs directly leach calcium from the membranes of leaf cells, decrease cell stability, reduce cold tolerance, and enhance the potential for secondary freezing injury (DeHayes et al., 1999; see Chapter 6). In fact, acid-induced reductions in cold tolerance are of sufficient magnitude (3 to 10°C) to explain the now common and widespread freezing injury to red spruce observed in northern montane forests over the past 40 years (Johnson et al., 1988; DeHayes, 1992; Johnson et al., 1996) and growth and vigor losses typical of red spruce decline (Wilkinson, 1990; Tobi et al., 1995). Most northern evergreen species develop a tolerance to low temperature that protects leaves from freezing injury even at temperatures well below the lowest ambient temperatures experienced. In contrast, the current-year foliage of red spruce achieves a maximum cold tolerance that is barely sufficient to prevent freezing injury during most winters (DeHayes, 1992; Schaberg et al., 2000). As a consequence of this low baseline hardiness, acid-induced reductions in cold tolerance make red spruce uniquely vulnerable to freezing injury (DeHayes et al., 1999; see Chapter 6). The study of acid deposition's influence on red spruce cold tolerance has provided a detailed mechanistic model of how a pollutant can alter tree physiology and forest

health. This case study also exemplifies how variation in stress response can have profound ecological consequences.

Substantive differences in survival following exposure of eastern white pine to gaseous air pollution and red spruce to acid deposition compared with other apparently less sensitive species highlight the possibility that variation in species responses to anthropogenic change could be an important force in shaping the composition, form, and function of tomorrow's forests.

Heterogeneity of Species Responses to Environmental Change

To further complicate predictions of future forest composition, the response of trees to any given environmental change will not be uniform. If existing research is any indication, a major source of variability will likely be at the species level.

Numerous studies have evaluated potential differences in the physiology of tree species following perturbations in temperature, water availability, atmospheric gases, or pollutant loading that may accompany climate change. And, almost uniformly, these studies detect significant differences in species responses to environmental perturbation. Table 14.1 provides examples of studies that examined the impact of these perturbations on a broad range of physiological traits for eastern North American tree species. Collectively, these examples include evaluations of eight different climate change factors, three crossed factors, 24 tree species, and a range of physiological parameters including seed germination, growth, foliar injury, cold tolerance, carbohydrate storage, water transport capacity, cation nutrition and mortality (see Table 14.1). Yet, despite the diversity exemplified here, one commonality is clear: in each study, meaningful differences in response were detected among the species evaluated (see Table 14.1).

If trees in forests showed the same heterogeneity in response depicted in Table 14.1, one consequence would be great uncertainty in predicting the overall impacts of environmental change. This uncertainty is fueled, in part, by the many levels of response that require integration in order to determine "net responses." For example, even for a single climate change factor (e.g., acid rain) and a single tree species (e.g., sugar maple), the physiological impact could be seemingly positive for one trait (e.g., increased extension growth and leaf weight under low soil nutrient conditions, Raynal et al., 1982b), neutral for a different trait (e.g., seed germination, Table 14.1, Raynal et al., 1982a), and potentially negative for yet another (e.g., increased foliar cation leaching, Table 14.1, Lovett and Hubbell, 1991). So, to understand the net impact of even a solitary climate change factor on a single species, one has to integrate impacts on all physiology throughout the life and reproductive cycle of that species. Once this was accomplished for each species, this information would have

Table 14.1. Examples of Differential Responses of Eastern North American Tree Species to Individual or Combined Environmental Change Factors

Factor	Species Compared	Response	Reference
CO_2	*Acer rubrum* L. *Acer saccharum* Marsh. *Betula papyrifera* Marsh. *Fagus grandifolia* Ehrh. *Pinus strobus* L. *Prunus serotina* Ehrh. *Tsuga canadensis* (L.) Carr	Relative to plants receiving 400 μl l^{-1} CO_2, shade tolerant *A. saccharum*, *F. grandifolia*, and *T. canadensis* seedlings had the greatest stimulation of biomass accumulation in response to elevated CO_2 (700 μl l^{-1}), *P. serotina* and *B. papyrifera* showed intermediate increases, whereas *A. rubrum* and *P. strobus* experienced insignificant increases in biomass growth.	Bazzaz et al., 1990
Temperature	*Abies balsamea* (L.) Mill. *Picea rubens* Sarg.	Mature montane *P. rubens* trees dehardened 3 to 14°C during a natural midwinter thaw, whereas sympatric *A. balsamea* trees showed no evidence of dehardening.	Strimbeck et al., 1995
O_3	*A. rubrum* *Betula alleghaniensis* Britton *Fraxinus americana* L. *Liquidambar styraciflua* L. *Liriodendron tulipifera* L. *P. serotina* *Quercus alba* L. *Quercus rubra* L.	Following 12 weeks of experimental exposure to 0, 0.075 or 0.15 ml l^{-1} O_3 seedlings showed a range of leaf stippling and defoliation responses. *P. serotina* was the most sensitive to O_3, followed by *L. styraciflua*, *L. tulipifera*, *F. americana*, *A. rubrum* and *B. alleghaniensis*. *Q.* spp. exhibited no foliar injury.	Davis and Skelly, 1992
UV-B	*Picea glauca* (Moench) Voss *Picea mariana* (Mill.) B.S.P. *Pinus banksiana* Lamb.	All seedlings experienced reductions in dry weight following 16 weeks of high supplemental UV-B (150 W cm^{-2}) relative to low additions (1.1 W cm^{-2}). Shade tolerant *P. glauca* and *P. mariana* showed greater reductions (45 and 40%, respectively) than *P. banksiana* (29%).	Yakimchuk and Hoddinott, 1994
Acid precipitation	*A. rubrum* *A. saccharum* *B. alleghaniensis* *P. strobus* *T. canadensis*	The impact of pH 3.0, 4.0 or 5.6 treatment solutions on seed germination was tested. Compared with pH 5.6, germination was inhibited at pH 4.0 and 3.0 for *A. rubrum* and at pH 3.0 for *B. alleghaniensis*. No inhibition was observed for *A. saccharum* or *T. canadensis*. Germination was stimulated by decreasing pH for *P. strobus*.	Raynal et al., 1982

Nitrogen deposition	*A. balsamea* *A. rubrum* *Acer spicatum* Lam. *Betula* spp. *P. rubens*	Following 7 years of low level nitrogen additions (0 to 31.4 kg N $ha^{-1}yr^{-1}$) to montane forest plots, *P. rubens* had the highest rates of annual mortality (% trees that die per species), followed by *A. balsamea* and *Betula* spp. No *Acer* spp. mortality was noted.	McNulty et al., 1996
Water stress	*Populus deltoides* Bartr. *Thuja occidentalis* L. *A. saccharum* *Juniperus virginia* L.	Xylem tensions causing a 50% loss in hydraulic conductivity were lower (a more positive Ψ) for *P. deltoides*, intermediate for *T. occidentalis* and *A. saccharum*, and greater for *J. virginiana.*	Tyree et al., 1994
Ca depletion	*P. strobus* *A. saccharum*	For both pH 3.8 and 5.0 mist treatments, *A. saccharum* canopies lost approximately 6 times more Ca ($\mu g\ m^{-2}$ leaf area) than *P. strobus* canopies.	Lovett and Hubbell, 1991
$CO_2 \times N$	*Populus tremuloides* Michx. *Q. rubra* *A. saccharum*	Seedlings were exposed to 2 levels of atmospheric CO_2 (355 or 650 $\mu l\ l^{-1}$) and 2 soil NO_3 treatments (1.25 or 7.5 mM). Significant $CO_2 \times NO_3 \times$ species interactions were found for shoot length ($P \leq 0.05$). *P. tremuloides* shoot growth increases were almost solely associated with NO_3 treatment, whereas *Q. rubra* and *A. saccharum* had growth increases responsive to both CO_2 and NO_3.	Kinney and Lindroth, 1997
$CO_2 \times$ UV-B	*P. banksiana* *P. mariana* *P. glauca*	Seedlings were exposed to CO_2 (350 or 370 $\mu l\ l^{-1}$) and UV-B radiation (1.1 $\mu W\ cm^{-2}$ or 150 $\mu W\ cm^{-2}$). A $CO_2 \times$ UV-B interaction ($P \leq 0.05$) for height growth was found for only *P. banksiana*. For this species, UV-B treatment fully offset increases in growth associated with CO_2.	Yakimchuk and Hoddinott, 1994
$CO_2 \times$ water stress	*P. tremuloides* *A. saccharum*	Seedlings were grown under ambient or elevated CO_2 (350 or 700 $\mu l\ l^{-1}$) and under well-watered or drought conditions. A $CO_2 \times H_2O \times$ species interaction for foliar hexose levels ($P \leq 0.06$) was found. For *P. tremuloides*, drought-induced reductions in hexose concentration were partially offset by elevated CO_2. In contrast, *A. saccharum* experienced increases in foliar hexoses with drought, but these increases were reduced by elevated CO_2.	Roth et al., 1997

to be compiled and tested to determine how these physiological changes could impact competition and survival among species. In addition, the complexity in response would only increase as the mix of environmental change factors is augmented to more closely resemble field conditions. Even limited study of differences in response to combinations of environmental factors has identified significant interactions with tree species (see Table 14.1). Considering the probability that multi-factor interactions with tree species occur, the interplay of species responses to complex mixes of environmental change factors in the field are likely to be different from results of simplified experimental simulations. These differences could have great importance if they influence the dynamics of species competition that have helped establish and sustain existing forest communities.

The models that have been used so far to predict future forest composition (examples described earlier in this chapter) have been valuable first steps in the ever-evolving prediction process. Refinements can made after results of these models are evaluated. Heterogenetity of species response and other factors affecting species distribution will need to be addressed in future prediction models.

Genetic Variation in Response to Changing Environments

Forest tree species clearly have the potential to respond in dramatically different ways to changing environmental conditions, including climate warming and elevated levels of CO_2 and other greenhouse gases. That is, species × environment interactions, a measure of the differential response of species to varying environmental conditions, are expected to be substantial. Similarly, although perhaps less intuitive, different populations and individuals within a single species also exhibit considerable genetic variation in response to changing environmental conditions. Such genotype × environment interaction may reflect an adaptive response of populations to anthropogenic stressors, adding uncertainty about how complex forest systems may respond to global environmental changes. Because forest tree species are dynamic and exist as an aggregate of potentially genetically variable and divergent populations, it is not reasonable to expect individuals of a given species to uniformly respond to changing environmental conditions.

Genetic variability has been documented in the response of eastern forest tree species to an array of anthropogenic stressors, including tropospheric O_3, acid deposition, elevated CO_2, elevated nitrogen, and temperature stress (Table 14.2 on pages 526–527). The findings highlight both the resiliency and adaptability of forest tree species and also the potential for complex responses to interactive stresses in environments where competition for limited resources is prevalent. For example, Berrang et al. (1986, 1989) demonstrated genetic variation in ozone sensitivity

among populations of quaking aspen (*Populus tremuloides* Michx.). Interestingly, their data show that high ambient levels of ozone in certain locations have differentially selected against sensitive aspen genotypes resulting in populations with greater average resistance to both artificial ozone fumigations (Berrang et al., 1986) and exposure under ambient field conditions. Trees originating from locations with low ambient O_3 levels were generally most sensitive to O_3 exposure. Thus, it appears that natural selection for O_3 tolerance has occurred relatively quickly in this species because anthropogenically elevated levels of O_3 had existed for only about 60 to 70 years prior to the study. Important, however, is the fact that more than a 3-fold difference in O_3 injury was observed among clones within some populations, including the highly selected populations that had evolved greater O_3 tolerance. As such, it seems that a relatively short period (perhaps a single generation) of ozone selection was enough to enhance tolerance with little evidence of a reduction in genetic variation.

Recent evidence has suggested that plant species may also exhibit genetic variation in response to global change factors, such as CO_2-enriched environments. As such, it might appear that rising CO_2 levels would result in selection favoring genotypes and populations that exhibit increased productivity in CO_2-enriched atmospheres leading to enhanced carbon sequestration in terrestrial ecosystems and a concomitant reduction in future atmospheric CO_2 levels. However, empirical data suggests a more complex form of selection pressure and population response. Bazzaz et al. (1995) have shown that experimental populations of yellow birch (*Betula alleghaniensis* Britt.) exhibited responses to enriched CO_2 that were both genotype-specific and density-dependent (see Table 14.2). That is, under conditions of minimal competition, all half-sib families of yellow birch that were tested exhibited a growth enhancement in response to elevated CO_2. However, the magnitude of the family response varied genetically. For instance, the fastest-growing family at ambient CO_2 levels was the slowest growing in the CO_2-enriched atmosphere. Under high density, maximum competition conditions, variation among genotypes in CO_2 responsiveness was greater, but the overall magnitude of the response was considerably less than in minimal competition environments. An enriched CO_2 atmosphere appeared to result in pronounced shifts in genetic composition, even though overall productivity enhancements were small. The authors concluded that CO_2 enrichment intensified interplant competition and that selection favored genotypes with a greater ability to compete for resources other than CO_2. While this may result in the evolution of populations with a greater competitive ability on the one hand, there is little evidence to suggest the evolution of increased CO_2 responsiveness or carbon sequestering on the other. Furthermore, the increased selection intensity evident in CO_2-enriched environments would be expected to contribute to a loss of genetic diversity in these populations and perhaps

to influence population responses to other localized or global-scale environmental changes.

These examples illustrate the dynamic nature, potential evolutionary responsiveness, and overall resiliency of forest tree populations in the face of anthropogenically induced environmental change. However, they also highlight the challenge in predicting species-level responses to changing climatic conditions because forest tree populations have been, and will continued to be, faced with a potentially new set of environmental changes that are not well understood. Such changes may lead to the evolution of resistance or population elimination, greater or lesser competitive abilities, reductions in overall levels of genetic diversity and responsiveness, and/or individuals and populations that exhibit greater levels of fitness in new environments. There clearly is uncertainty. In fact, the only certainty is that environments and selection pressures and forest tree populations themselves will be different from those of the past. As such, extensive variability among and within species will make accurate prediction of overall responses to anthropogenic change difficult at best. However, because genetic and phenotypic variability is fundamentally important to biological survival, the presence and persistence of such variability as the raw material for future evolutionary adaptation will impart the greatest likelihood of continued health and stability within northern forests.

Potential Threats to Evolutionary Adaptation

Forest trees possess and depend upon extensive levels of genetic diversity for their adaptive potential and for overall forest ecosystem stability (Gregorius, 1996). Anthropogenic disturbances, such as air pollution selection, forest fragmentation, and intensive timber harvesting or management regimes, and perhaps even mutagenic effects of pollution (Grant, 1998), could alter the size and structure of tree populations, levels of genetic diversity, and gene flow, which are the foundations of species adaptation and evolution. The genetic foundation of forest ecosystem stability lies at the population level, which is the unit of adaptation and evolution (Gregorius, 1996). As such, loss of genetic variability within populations poses a potential threat to evolutionary adaptation.

Fitness vs. Flexibility: Potential "Cost" of Resistance to Anthropogenic Factors

Forest tree species generally possess very high levels of genetic diversity, and much of the genetic polymorphism is concentrated among individuals within populations. The ubiquitous presence of genetic variation in forest trees implies that selection for resistance to stressors (e.g., pollution) may be occurring in natural populations. The previously cited example with trembling aspen (Berrang et al., 1986, 1989) illustrates this relationship.

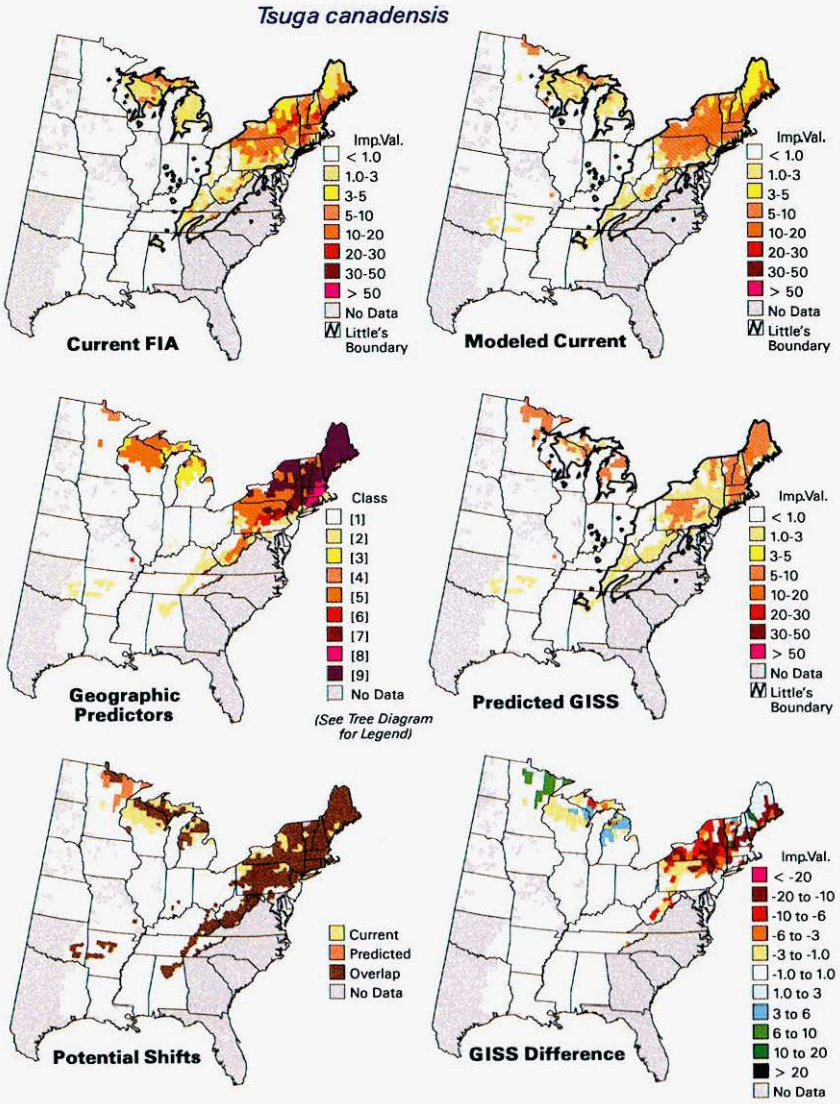

Figure 14.6. Example model outputs for eastern hemlock (*Tsuga canadensis*), including (UL) actual county importance value (IV) as calculated from FIA data; (UR) modeled current IV from the RTA model; (ML) predicted future IV after climate change according to the GFDL GCM; (MR) predicted future IV after climate change according to the GISS GCM; (LL) difference between modeled current and predicted future IV according to the GFDL model; and (LR) difference between modeled current and predicted future IV according to the GISS model.

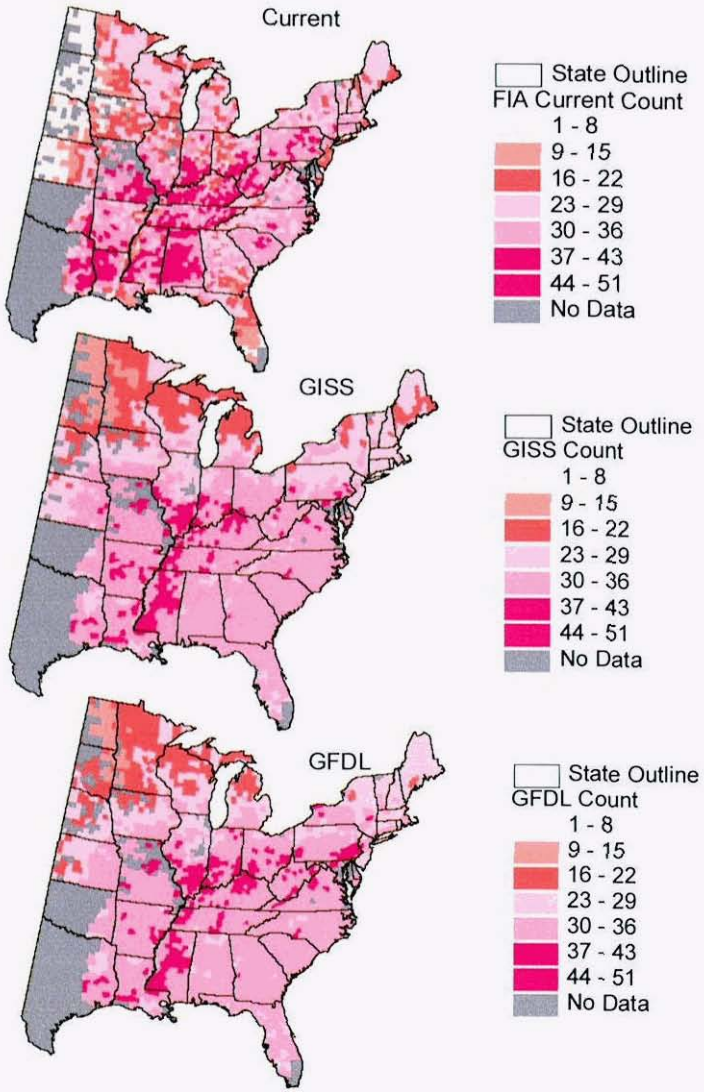

Figure 14.7. Estimated species richness, of the possible 80 common tree species in the eastern U.S., for (top) current times according to FIA data; (middle) future climate according to the GISS scenario; and (bottom) future climate according to the GFDL scenario.

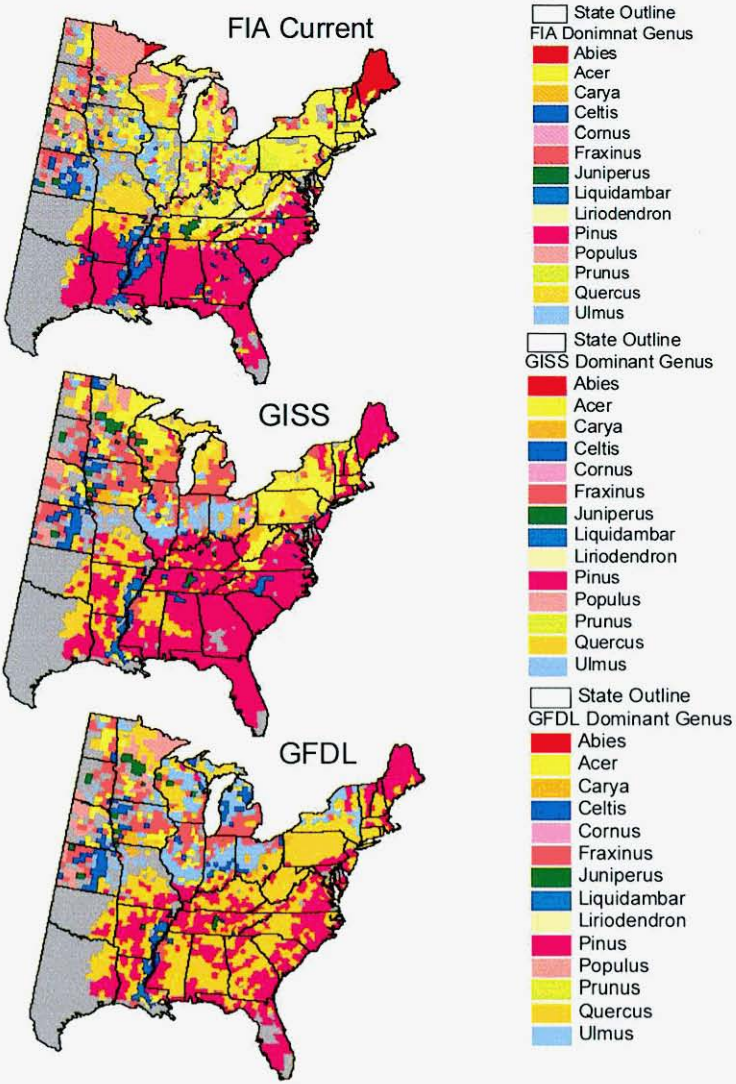

Figure 14.8. Estimated dominant genera, by county, based on the 80 common tree species in the eastern U.S., for (top) current times according to FIA data; (middle) future climate according to the GISS scenario; and (bottom) future climate according to the GFDL scenario.

The review by Pitelka (1988) provides additional examples. The extent of a physiological or evolutionary "cost" of resistance is not clear. Resistant individuals clearly have the benefit of increased fitness in the presence of changing environmental conditions. However, such fitness may come with a price: loss of genetic variation that could lead to decreased flexibility of the population to respond to future environmental change.

Competition experiments indicate that resistant plants are less able to compete and survive in environments lacking the pollution stress and that there can be rapid selection against tolerant individuals once pollution stress declines (Pitelka, 1988; Winner et al., 1992). Although "costs" of resistance may indeed be real, they are expected to vary with the physiological mechanism(s) involved and, therefore, might be expected to vary among co-occurring resistant species exposed to the same pollutant (Parsons and Pitelka, 1992). As such, competitive balances and species composition may be altered.

From an evolutionary standpoint, the "cost" of pollution selection in terms of loss of genetic diversity will be influenced by numerous factors, such as the selection intensity, the magnitude of resistance and pattern of its inheritance, and the life cycle of the population/species under selection. Given the episodic nature of most air pollution (acid deposition, ozone, sulfur dioxide) exposures, high levels of genetic diversity in trees, and the relatively long life cycles of tree species, one might expect a relatively slow rate of loss of genetic diversity in response to air pollution selection in most tree species. The persistence of genetic diversity in ozone resistance among trembling aspen clones from relatively resistant populations is consistent with this expectation. If, however, pollution-induced mortality is high, as Kriebel and Leben (1981) have indicated for eastern white pine populations from Ohio, then one would expect the residual population to effectively experience a bottleneck, genetic drift, and a reduction in genetic diversity. That is, genetic diversity and the potential for evolutionary change may be reduced as a result of the random loss of alleles (including alleles unrelated to the actual cause of mortality) associated with reduced population size as well as the byproduct of intensive pollution selection. Pollution-induced changes in both the genetic structure and levels of genetic diversity of forest tree populations will influence the evolutionary opportunities and pathways possible in the future in response to new selection pressures and intensities.

Forest Fragmentation

Fragmentation of forest ecosystems has occurred as a result of agriculture, urban and suburban development, and road construction. Fragmentation serves as a potential migration barrier that can inhibit species or population dispersal in response to environmental change, especially latitudinal migration expected in response to climate warming. Certainly,

Table 14.2. Examples of Genetic Variation in Responses of Eastern North American Tree Species to Individual or Combined Environmental Change Factors

Factor	Species Compared	Response	Reference
Temperature	*Picea rubens* Sarg.	Freezing injury of trees from 12 provenances growing in a NH plantation was assessed for 4 winters. Trees from Quebec, NY, and New Brunswick were consistently among the least injured, whereas trees from MA and NH were consistently among the most injured.	DeHayes et al., 1990
O_3	*Populus tremuloides* Michx.	Ozone sensitivity of offspring derived from populations in 5 national parks with differing ambient O_3 levels was evaluated. Populations varied significantly in ozone-induced foliar injury resulting from both fumigation and ambient exposure. This provides evidence of natural selection for ozone tolerance.	Berrang et al., 1986, 1989
Acid precipitation	*Acer rubum* L.	Trees from 3 seed sources grown in plantation were sprayed with simulated rain solutions of pH 5.2, 4.2 or 3.2 on 5 dates over the growing season. Evaluations of throughfall chemistry revealed small but significant differences among provenances ($P \leq 0.05$) in the concentrations of Ca, Fe, and Zn leached from canopies.	Schier, 1987
N	*Betula papyrifera* Marsh.	Seedlings from 4 populations were grown with either low or high soil N treatments (20 or 80 N supplied at NH_4NO_3) for 3 months. Populations differed in average root biomass and root/shoot ratios following treatment ($P \leq 0.01$).	Wang et al., 1998

Water stress	*A. rubrum*	Seedlings from 4 seed sources (2 wet sites and 2 dry sites) were subjected to 3 levels of water stress. Wet site seed sources wilted sooner in response to water stress than dry site sources. However, at all levels of water stress, growth was greatest for wet site seedlings.	Townsend and Roberts, 1973
CO_2	*B. alleghaniensis*	Experimental populations were exposed to CO_2-enriched atmosphere. CO_2 enhanced biomass in noncompetitive situations. In high density stands, enriched CO_2 resulted in significant shifts in genetic composition and only small productivity enhancements.	Bazzaz et al., 1995
CO_2 and temperature	*Pinus banksiana* Lamb.	Seedlings from 15 maternal families were grown in growth chambers with either 390 $\mu l\ l^{-1}$ CO_2 and simulated ambient temperatures or 700 $\mu l\ l^{-1}$ CO_2 and ambient + 4°C temperatures. Families differed ($P \leq 0.05$) in their instantaneous water use efficiency (WUE) following treatment.	Cantin et al., 1997
CO_2 and temperature $\times$ N	*P. banksiana*	Seedlings in the above study were also divided into subplots that received either 5 or 100 $\mu g\ g^{-1}$ N fertilization. A CO_2 and temperature $\times$ N $\times$ family interaction ($P \leq 0.05$) was found for WUE.	Cantin et al., 1997
$CO_2 \times O_3$	*P. tremuloides*	Rooted cuttings from one O_3-tolerant and one O_3-sensitive clone were exposed to either O_3-reduced air, 0.10 $\mu l\ l^{-1}$ O_3, 150 $\mu mol\ mol^{-1} CO_2$, or elevated O_3 and CO_2. Simultaneous $O_3 + CO_2$ exposure decreased photosynthetic carboxylation efficiency more than the O_3 treatment alone for the O_3 tolerant clone only.	Kull et al., 1996

paleoecological lessons have shown that forest tree species have survived changing environmental conditions by dispersing to more suitable environments. Such dispersal is expected to be constrained in today's increasingly fragmented forests throughout the north temperate zone. Historical rates of migration (10 to 50 km per century) are not likely to occur within a fragmented habitat (Schwartz, 1993). Realizing this, current investigators are assessing more realistic migration scenarios based on species regeneration characteristics and actual landscapes (Schwartz et al., 1996; Iverson et al., 1999).

Equally as important, however, fragmentation subdivides populations into small subunits that could become prone to inbreeding or, more importantly, subject to localized extinction as a result of random demographic uncertainties, such as catastrophic events or periodic reproductive failure (Lande, 1988). As noted by Ledig (1992), such partial extinctions (i.e., loss of populations) represent a loss of genetic diversity and threat to evolutionary development because they may result in the breakup of a complex structure of locally adapted populations.

Small, fragmented populations are expected to experience inbreeding, genetic drift, and an erosion of genetic variability and evolutionary potential within subpopulations, especially if isolation and small population size persists for multiple generations. Under such conditions, genetic divergence among populations is expected to increase, while genetic diversity within populations becomes eroded. While individual populations perhaps become vulnerable to environmental stresses because of genetic uniformity, the genetic distance and isolation of surviving populations could conceivably lead to further evolutionary division and separation. Empirical data from modern-day marginal populations reinforces such theoretical predictions. Table 14.3 shows that relatively small, isolated marginal populations of pitch pine and red spruce exhibit reduced heterozygosity and genetic polymorphism compared with large

Table 14.3. Estimates of Genetic Variability for Central and Marginal Populations of Pitch Pine and Red Spruce

Species	No. of Populations	Polymorphic Loci (%)	Heterozygosity (%)	Reference
Pitch pine				
Central	3	71 a[a]	24.6 a	Misenti,
Marginal	3	56 b	20.9 b	1990
Red spruce				
Central	6	40 a	8.9 a	Hawley and
Marginal	5	36 a	6.2 b	DeHayes, 1994

[a] Means within species followed by the same letter are not significantly different by analysis of variance.

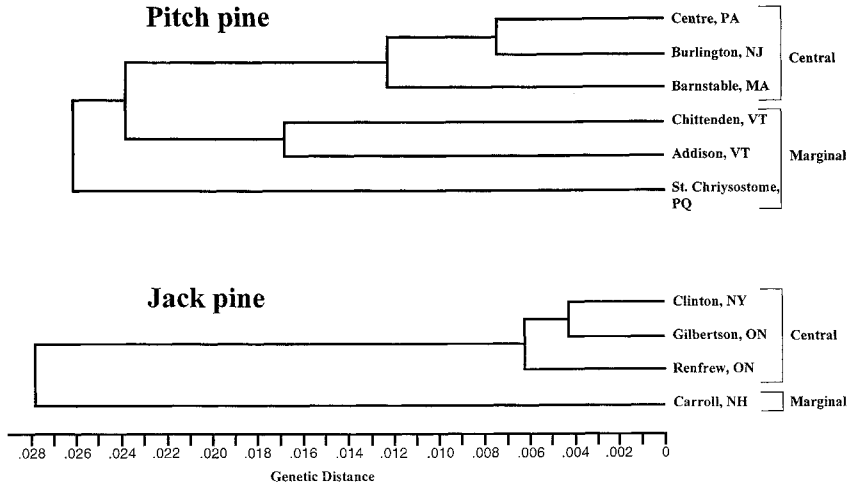

Figure 14.9. Phenogram of genetic distance estimates depicting the degree of genetic differentiation among marginal and central populations of pitch and jack pines.

central populations, and genetic distance estimates among marginal populations of pitch and jack pines are at the extremes for most conifer species (Fig. 14.9). The latter presumably have resulted from genetic drift. Indeed, fragmentation does alter the genetic structure of forest tree populations. Although population subdivision in response to changing environmental conditions is not an entirely new phenomenon, the prevalence and expected increasing rate of fragmentation in today's north temperate forests is unprecedented and a potential threat to evolutionary adaptation.

Intensive Forest Management

Forest management and harvesting practices that include selective logging can conceivably alter the genetic structure of forest tree populations and the evolutionary potential of forest tree species, especially when the intensity of selection is high. Selective cutting could also increase inbreeding, which would be expected to reduce reproductive output and viability (Ledig, 1992). However, very little empirical information has been generated about the influence of intensive forest management practices on the genetic structure, diversity, and mating systems within forest ecosystems. Neale (1985) and Neale and Adams (1985) found that shelterwood harvesting had little impact on the genetic structure of Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests and attributed population resiliency to exceedingly high levels of genetic diversity in that species and

the almost pure, high density Douglas-fir stands. In contrast, Cheliak et al. (1988) reported that phenotypically selected white spruce (*Picea glauca* [Moench] Voss) trees possessed on average only 75% of the genes found among randomly selected trees from the same population. Thus, a loss of some genes and changes in gene frequencies would be expected in response to selective cutting.

Indeed, recent studies have demonstrated that selective logging can alter the genetic structure of residual populations and presumably the potential for populations to adapt to future environmental changes. Buchert et al. (1997) contrasted genetic diversity parameters between preharvest and postharvest gene pools in virgin, old-growth stands of eastern white pine in central Ontario. Following harvesting-driven reductions in tree density of about 75%, the following changes in population genetic structure were observed: 25% reduction in number of alleles, 33% reduction in polymorphic loci, and an 80 and 40% loss of rare and low frequency alleles, respectively. The latent genetic potential of these stands was reduced by about 50%, and the ability of these gene pools to adapt to changing environmental conditions was likely compromised. Given the selective logging history of eastern white pine over the past century or so, one might conclude that harvesting has caused genetic erosion in this species with some loss of evolutionary potential.

The influence of selective logging on the genetic structure of eastern hemlock is more complex, but also demonstrates a dysgenic influence of selective logging on the population. Hawley et al. (1998) compared genetic diversity parameters between an unmanaged control stand and stands that had undergone fixed diameter limit cuts or selection cuts three times over the past 40 years (years 0, 20, and 40) as part of a long-term replicated silvicultural experiment at the Penobscot Experimental Forest in eastern Maine. Residual stands that had undergone intensive and repeated diameter limit cuts, leaving only the very worst trees in terms of size and form, had significantly higher levels of heterozygosity, polymorphic loci, and effective number of alleles per locus. These seemingly counterintuitive results reflect an apparent association between rare alleles and defective phenotypes in eastern hemlock. Several alleles that occurred at very low frequencies ($P < 0.03$) in the natural unmanaged stand occurred at a higher frequency in the diameter limit cut because the defective residual trees preferentially possessed these rare alleles. That is, rare alleles conferred a negative fitness impact (i.e., slow growth and poor form) on eastern hemlock trees. In fact, 68 and 24% of the residual trees from the diameter limit cut possessed at least one or two rare alleles, respectively, compared with 26 and 6% and 32 and 2% for the unmanaged and selection cut stands, respectively. Although these results contrast dramatically with the harvest-induced loss of such alleles and potential positive evolutionary implications of rare alleles suggested for eastern white pine, they nonetheless illustrate that intensive human-induced manipulations of

forest tree populations have altered the genetic structure, long-term adaptability, and productivity of north temperate forest ecosystems.

Summary: The Net Effect

One fact is certain: responses of tree species to changing global environments are exceedingly complex. As such, meaningful predictions of future forest composition are challenging and inherently uncertain. Our best understanding of future forest composition from contemporary models based on species relationships to climate and site characteristics indicates substantial geographical shifts for many species in response to climate warming. In addition, forest communities are expected to change in composition. Both the paleoecological record and predictive models indicate that individual species rather than intact communities will disperse and that forest communities will transition to a new mixture of species able to co-exist on the same site for a period of time.

Issues of substantial uncertainty include the rate of change in forest species composition, migration pathways, and the implications of interspecific competition. One scenario is that most tree populations will be maintained in place for an extended period, despite a warming climate. The ability of existing trees to survive, produce seeds, and adapt should allow such maintenance. If the physiological tolerances of existing species are not exceeded, they should remain in place until other, more competitive, invaders become established. At that point, they will be eliminated. And by the time more successful invaders enter the site, species fading from one location will have migrated to more favorable locations. However, a more likely scenario is that of global climate change causing the demise of some species because better adapted species will outcompete them. Disease, insects, and drought are the primary agents that are expected to create these situations, and disturbance frequency will strongly influence the rate of change in forest composition. That is, rapid change will likely follow disturbance. In the absence, of disturbance living trees will likely persist and only be replaced as gaps occur.

Anthropogenic factors, including pollution exposure, exotic plants and pathogens, and a diverse array of other direct and indirect human influences on forests, represent a new "wild card" that can profoundly influence species responses to global climate change. Neither the paleoecological record nor modern day models reflect this sort of biotic and abiotic disturbance. Extrapolations of existing research regarding the impact of single or simple combinations of anthropogenic stressors suggest that the health and survival of individual trees, specific tree populations, and perhaps even some species, will likely be degraded in the years ahead if predicted levels of climate change and pollutant exposures are realized. However, because actual stress exposure combinations will

probably be more complex than mixes already tested, predictions based on existing data can only produce generalized potential outcomes. Our modern-day experiences with the impacts of aggressive exotic species, especially exotic insects and diseases, indicate potential for a dramatic influence on the migration, establishment, and reproductive success of forest tree species growing in altered environments.

Whatever the response to individual or multiple stressors, evidence of extensive variation in stress response both within and among species suggests that North American trees currently have a broad capacity for differential response and potential adaptation to environmental change. However, climate change and pollutant additions are not occurring in isolation from other anthropogenic changes. Other factors, including increased forest fragmentation and intensive silvicultural management, could alter the genetic structure of and diversity within northern forests. Collectively, these activities have probably altered the level and distribution of genetic diversity that confers the adaptability nècessary for trees to persist across environments that vary spatially and over time. This may have important consequences for the response of forests to global climate warming.

Because of existing and ever-increasing forest fragmentation, migration in response to climate warming may be impeded and evolutionary change may be the only viable means for some species to respond to and cope with changing climates over the long term. Forest tree species depend on high levels of genetic diversity for their adaptive potential and for overall forest ecosystem stability. If the reproductive and/or genetic structure within species or populations is altered due to population reduction and isolation, as is evident in marginal populations of many species today, or the influence of anthropogenic selective forces, then the adaptability and stability of many forest ecosystems in response to changing climates may also be compromised. In this context, perhaps the greatest anthropogenic threat to northern forests lies in the combined dangers of unprecedented climate change, pollution exposure, and competition from exotic plants and pathogens concomitant with a degradation of the genetic diversity needed for adaptation and survival. Indeed, our understanding of and ability to predict forest responses to changing climates may now be influenced as much by uncertainty as by the well-documented lessons from the past.

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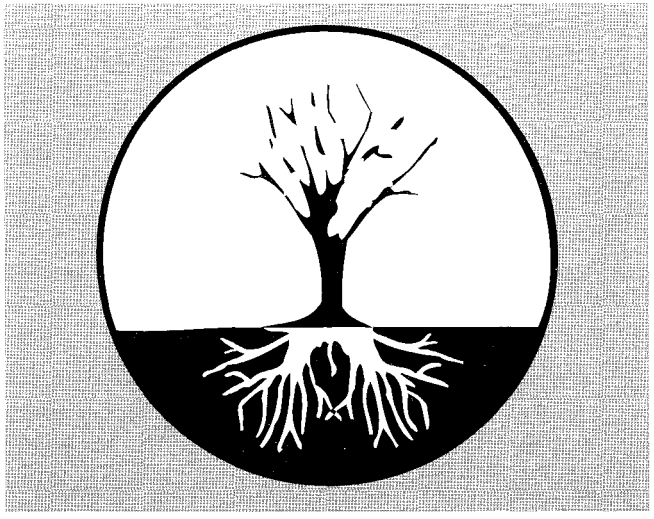

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