

# ASSESSING THE ABILITY OF PLANTS TO RESPOND TO CLIMATIC CHANGE THROUGH DISTRIBUTION SHIFTS

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**Abstract:** Predictions of future global warming suggest northward shifts of up to 800 km in the equilibrium distributions of plant species. Historical data estimating the maximum rate of tree distribution shifts (migration) suggest that most species will not keep pace with future rates of human-induced climatic change. Previous plant migrations have occurred at rates typically ranging from 15-50 km per century. A simulation model, which incorporates the effects of forest fragmentation and habitat loss, predicts maximum potential migration responses of trees may be only 1-10 km per century, or two orders of magnitude below that required to keep pace with predicted climatic warming. These predicted migration rates suggest that plants will fail to respond adequately to even modest climatic changes. Gauging the actual response of forest species to climatic change, and then appropriately managing forest resources poses several problems. First, we do not know the distribution limits of most forest species with the degree of precision to detect migration events on a 1-10 km scale. Second, many species may become vulnerable to extinction by their inability to migrate, leaving them geographically isolated from regions within their climatic tolerance. Third, while the distributions of species can be artificially expanded if climate does warm, this is not currently part of acceptable conservation management practice. Deciding whether or not to artificially enhance species ranges forces a choice between species preservation and historical community composition models for conservation. A pressing concern for forest management is to discover how climate change, anthropogenic habitat change, and doubled CO<sub>2</sub> interact to alter forest species performance and regeneration within habitats they currently occupy. Range edges are the first place to look for key changes in these ecological responses.

## INTRODUCTION

General circulation models, estimating climatic change during the next century in response to a doubling of the atmospheric CO<sub>2</sub> and other trace gases, suggest warming sufficient to trigger major changes in the earth's living systems. These environmental changes will affect virtually all plants and animals. Predicted terrestrial responses include altered: 1) plant-insect interactions (e.g., Lincoln et al. 1986); 2) plant-soil relationships (e.g., Luxmoore et al. 1986); 3) biome boundaries (e.g., Solomon 1986); 4) distributions of crop production areas (e.g., Rosenzweig 1993); and 5) distributions of individual species (e.g., Davis and Zabinski 1992), to name but a few. In order to manage natural resources, for extractable resources (e.g., timber trees) as well as for broadscale biological diversity, it is imperative that we understand the full suite of possible responses of species to the spectrum of climatic change scenarios. Toward this end, I review here what is known regarding the abilities of forest plants to respond under the combined forces of climatic change and anthropogenically altered habitats. Finally, I make research recommendations based on perceived gaps in this knowledge.

### The Climate Scenarios

Various Global Circulation Models (GCM's) predict 2 to 6 °C temperature increases during the next century, as atmospheric CO<sub>2</sub> doubles (Mitchell et al. 1990). Predicted global increases in temperature vary strongly with season and latitude with higher latitudes experiencing greater temperature increases, particularly during the winter months. Thus, for North America, winter temperatures in the boreal forest under a doubled CO<sub>2</sub> environment may be increased by as much as 12 °C over current conditions. Further, growing season precipitation is, in general, predicted to decrease over much of North America, resulting in lower soil moisture. Model predictions, however, are recognized as a first approximation at a very complex problem in atmospheric chemistry and physics.

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The variables predicted by the GCM's (mean seasonal temperature and precipitation), however, are not likely to be the variables that are most important to plant growth (e.g., Woodward 1995). Solomon (1984), for example, modeled vegetation change based on climate projections using growing degree days, a variable one could estimate from, but not modeled by, GCM's. Frequently, it is the extremes of climate (e.g., drought frequency and severity, frost free days, lowest minimum temperatures) that may be the most important variables used to estimate responses of plants to their environment (Graumlich and Brubaker 1995). Unfortunately, climatologists cannot easily model these parameters. Rind et al. (1989) suggest that, whatever the exact magnitude of climate change, variability in weather is likely to increase. The biotic consequences of increased climatic variability are likely to be complex and unpredictable.

### The Plant-Climate Relationship

Correlations between climate and plant distributions are widespread and well known (e.g., Good 1931, Cain 1944, Pigott 1970, Woodward 1987, Denton and Barnes 1987, and Grime 1990). Further, vegetation has been responsive to large-scale changes in climate with most tree species altering their distribution limits hundreds to thousands of kilometers during the past 10,000 years (Davis 1981, COHMAP 1988). Likewise, recent climatic shifts have resulted in measurable changes in the distribution and performance of plant species. For example, about a dozen coniferous species in North America alone have shifted their growth forms or distribution limits northwards during the past 100 years (see references in Graumlich and Brubaker 1995). The manifestations of these changes vary from changes in growth forms and increased seedling recruitment at tree line to expansion of tree line and increased elevation of successful growth (e.g., Kullman 1983). The observed increases, however, are not uniformly observed even where climate has warmed. In addition, some range shifts are a result of changes in precipitation, different disturbance regimes, or simply a brief series of relatively warm temperatures (Graumlich and Brubaker 1995). In yet other cases, tree line has recessed owing to changes in disturbance rates (Payette and Gagnon 1979). Evidence of recent tree line shifts are abundant in both directions (Graumlich and Brubaker 1995). These observed changes in treeline are often dependent on proximate ecological factors as well as climatic factors. Nonetheless, the physical evidence of the response of trees to their environment suggests that climatic warming will result in differential recruitment, growth, and survivorship of plants in and around their distribution limits. Our primary limitation in predicting species level responses to future climatic change is that we lack a mechanistic understanding of the climatic limitations of virtually all plants (except see Pigott and Huntley 1978, Cannell and Smith 1986, Richardson and Bond 1991). Even for important timber species much work remains on the physiological relationship between plants and climate to develop mechanistic models of climatic control on plant germination, growth, survivorship, and seed production.

Despite not fully understanding the mechanistic relationship between plants and climate, we can make assertions about the magnitude of vegetation change that ought to result of predicted future warming. Plant distributions correlate with mean annual temperature isobars (e.g., Denton and Barnes 1987). At present mean annual temperature isobars are distributed at approximately 100-125 km latitudinal intervals in eastern North America (Melillo et al. 1990). If plant-climate relationships remain intact, an increase in 5 °C may result in distribution shifts of 500 km for the equilibria ranges of most plants. Predictions of equilibrium plant distribution shifts become even more dramatic if one also considers both seasonal temperatures and precipitation. Davis and Zabinski (1991) predict that northward shifts of the equilibria distribution for plants could exceed 800 km. A pressing question then becomes: can plants keep pace with the predicted magnitude of climatic forcing?

### FUTURE PLANT MIGRATION RESPONSE

Historical data suggest that plants will not keep pace with climatic warming. Most trees migrated to their current distributions at rates of 10-50 km per century (Davis 1981). Presuming our climate models are correct, historical migration rates are an order of magnitude too slow to keep pace with future warming. One must question, however, whether these past migrations were limited by rates of climatic change, or by the dispersal abilities of the plants. Detailed palynological studies have detected considerable lags in response to climatic change (e.g., Davis et al. 1986, Pennington 1986), suggesting that historical migration rates were at, or near, the limit set by the dispersal

abilities of trees. Further, the relative constancy of maximum migration rates through time, among regions, and among species, suggests that these migrations were limited by rates of seed dispersal and not climatic change, which varied through time and among regions, and to which species responses vary (Huntley 1989). Thus, Holocene migration rates may be good predictors of maximum migration rates for most species.

A few species, however, migrated much faster than 50 km per century. *Picea glauca* expanded from southern Alberta, through Northwest Canada to Alaska (nearly 2000 km) from 10,000 to 9,500 ybp (Anderson and Brubaker 1993, Ritchie et al 1983, Graumlich, and Brubaker 1995). This may be interpreted as a rapid expansion of the population with little to no dispersal limitation. Alternatively, treeline expansions may often be a result of krummholz vegetation beginning to grow upright as a result of amelioration and thus indicative of rapid population expansion without range expansion (Graumlich and Brubaker 1995). Thus, it is not clear what the actual migration rate of *P. glauca* was 10,000 ybp. Another issue complicating specific response predictions is that the climate of the past represents a unique combination of events that are unlike any potential climatic change of the near future. For example, summer insolation was higher, and winter insolation lower, 10,000 ybp owing to the perihelion (the point in orbit at which the earth is closest to the sun) occurring in summer rather than winter, as at present. Thus, there were probably higher seasonal extremes, creating different temperature and moisture regimes (Graumlich and Brubaker 1995). Indeed, there is evidence of past vegetations that have no modern analog (e.g., Jacobson and Grimm 1986). Nonetheless, there is a broad consensus that the predicted magnitude of climate change would require migration rates to far exceed any historical rates of vegetation change (Overpeck et al. 1991) and that rates are likely to be limited more by the biology of species than the rates of change in the environment (Huntley 1991).

Regardless of how well past climate reflects future climate scenarios, an additional factor that must be considered is that past migration rates are based on a different landscape. Past migration rates are estimated from regions where trees moved from largely forested regions into largely forested regions. Future migrations for many forest species will be within the context of a largely fragmented forest landscape (Peters 1991). The effect of habitat loss on potential migration has been stochastically modeled using a simulated landscape in which dispersal and colonization is a function of the distance between occupied and unoccupied patches (Schwartz 1993). This model varied dispersal and colonization probabilities to fit either one of two functions (inverse power function or negative exponential function) based on empirically derived seed density data (e.g., Harper 1977, Portnoy and Wilson 1993). These models were calibrated to result in a migration rate of 50 km per century when 80 percent of the habitat cells were available for occupation. In sequential runs: 1) dispersal function (inverse power or negative exponential), 2) habitat availability (10-90 percent), and 3) within stand frequency (10-90 percent) were varied to characterize the effect of habitat loss on migration potential. Assuming 50 km per century to be an average maximum migration rate under a saturated environment (80 percent habitat availability), Schwartz (1993) predicted migration rates under low (10-30 percent) habitat availability to be from 1-10 km per century, yet another order of magnitude below that predicted to keep pace with climatic change (Figure 1).

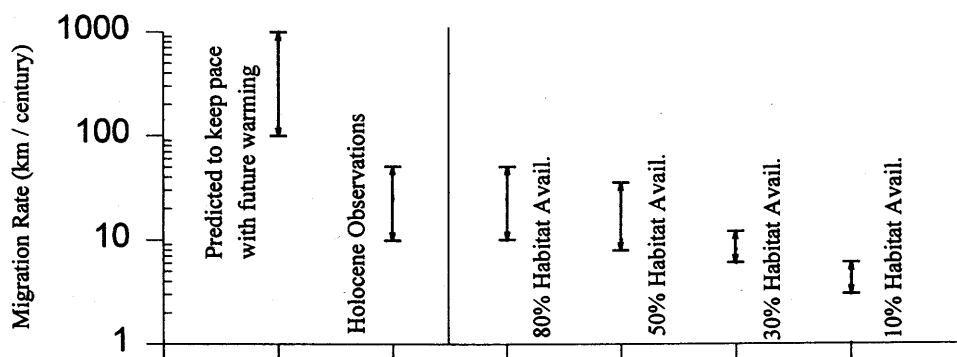


Figure 1. A schematic diagram of variation in tree migration rates comparing: 1) rates that would be required to keep pace with climate change; 2) observations of Holocene migration rates (based on palynological data); and 3) varying levels of habitat availability in a simulated landscape (redrawn from Schwartz 1993).

## The Potential for Species Loss

If plants can not migrate to keep pace with future climatic warming, then species may be vulnerable to extirpation as a result of climatic change because the current distribution of a species may become disjunct from a region of suitable climate (Peters 1991). Schwartz (1991) estimated the magnitude of this extinction potential using a compendium of 316 rare forest taxa of the Southeastern United States (Kral 1983). Using the north-south distribution breadth of species as a measure of sensitivity to extinction, Schwartz (1991) found that a substantial portion of the rare southeastern U.S. forest taxa are potentially vulnerable to extirpation under even modest warming, and that most rare taxa (> 85 percent) have north-south distributions of less than 500 km, the predicted baseline northward shift to keep pace with future warming (Figure 2). Naturally, not all, or even most, of these potentially vulnerable species are truly at risk. Many species are restricted by edaphic conditions, biogeographical boundaries or ecological factors, and not climate. Other species are in mountainous regions where relatively short geographical shifts upslope may be within the realm of migration potential. The point is that the risk of species loss is potentially large, and owing to our lack of a mechanistic understanding of the plant-climate relationship for most species, we have little ability to predict which species are truly at risk. We do not know which species are, or are not, limited by climate, and this lack of knowledge poses a conservation problem.

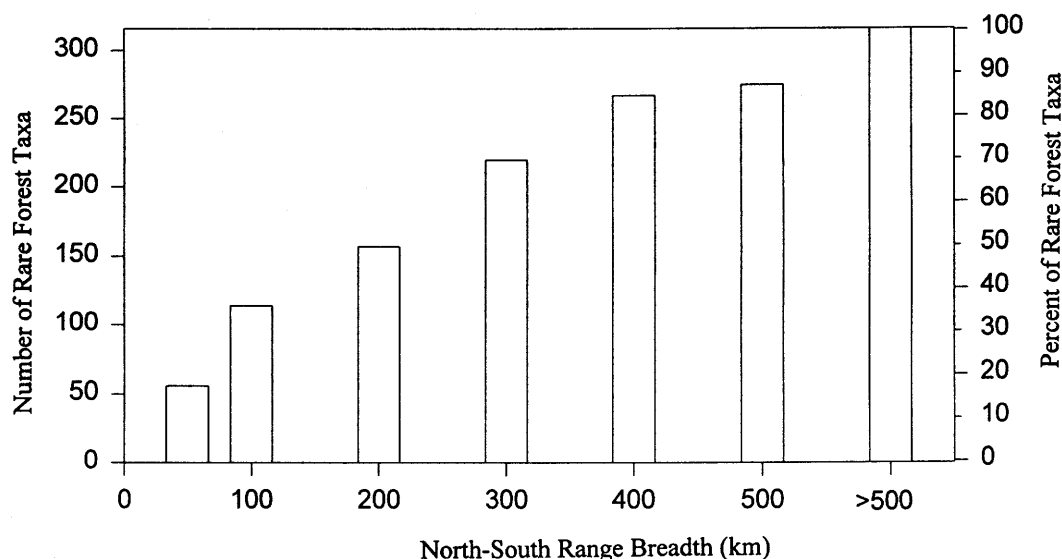


Figure 2. A histogram of the number of 316 rare forest species characterized by north-south distribution breadths of differing widths. The number of species in each range breadth category represent an upper estimate of the number, or percent, of species that are potentially vulnerable to extinction under different degrees of climatic change, assuming climatic control of distributions and an inability to migrate sufficiently to keep pace with future warming.

The lack of ability to migrate in response to climatic change for many species does not pose an insurmountable conservation problem. Certainly distributions can be altered through human intervention. This management activity, however, creates a conservation dilemma: we do not sanction range expansion as an acceptable conservation practice. Conserving historically accurate representatives of natural communities is, perhaps, the most common management directive and a common conservation goal. Intentional introduction of species perceived to be vulnerable to extinction into new habitats compromises traditional conservation efforts. Thus, if migration lag is severe, and causes species loss problems, then we must balance our efforts between two opposing conservation objectives: species conservation and maintaining community integrity (Schwartz 1994).

## CONCLUSIONS

How do we address the critical issues of climatic change and forest management given our sparse ecological knowledge? I suggest three areas of research that may focus our attention on the critical knowledge gaps in this area. First, we need spatially explicit models of predicted species range expansions in order to test whether species are, in fact, responding to climatic change. Work in this area has begun with an expansion of the simulation model of Schwartz (1993) to relax restrictions on the spatial scale and life histories of species modeled and to apply the model to real species in real landscapes (Schwartz and Iverson, personal communication). These spatially explicit models provide a testable hypothesis regarding the role of climate change in shifting species range boundaries. Knowledge of specific distribution limits, however, limits the extent to which we can test these hypotheses. Precisely indentifying the distribution limits of a few critical species would allow the model to be empirically tested.

The second area of emphasis is to increase our mechanistic understanding of the plant-climate relationship. By targeting species of particular interest we can begin to assess which species are likely to become vulnerable to climatic change. A good place to start would be to contrast species that have historically shifted their range boundaries, versus those that merely expanded their distributions during the Holocene. *Fagus grandifolia* and *Picea glauca* provide a good contrast in this regard. During the last full glacial both species were found in region that is now the Southeastern U.S. During the Holocene, *F. grandifolia* expanded its distribution northward, such that it is now distributed from Florida to Ontario, while *P. glauca* shifted its distribution northward, such that it is found from the Great Lakes and New England to northern Canada (Figure 3). Species that shift their distributions in response to future climatic changes are at greater risk than those that expand their distributions.

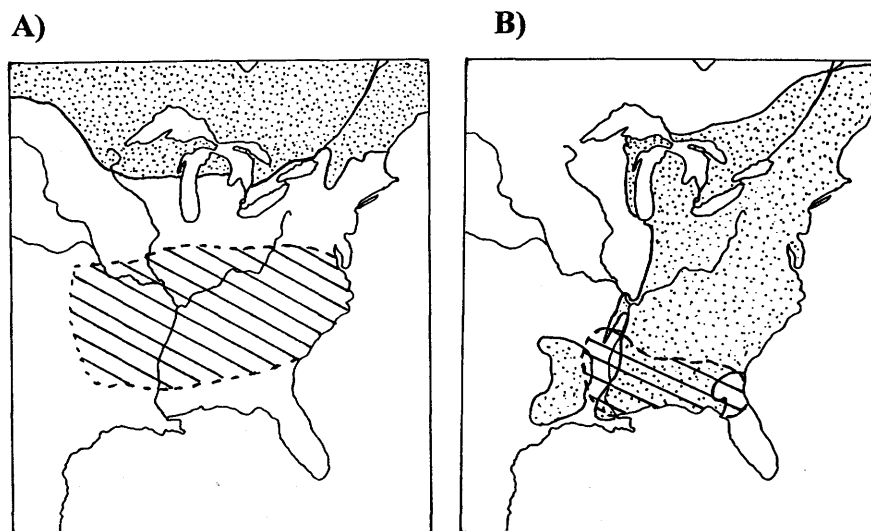


Figure 3. An estimate of the distribution of A) *Picea glauca* and B) *Fagus grandifolia* at 14,000 ybp (hashed) compared to the current (stippled) distributions showing a Holocene expansion of *F. grandifolia* compared to a wholesale shift in the distribution of *P. glauca*.

The third area of emphasis is relating species interactions and other dynamic ecological processes to estimates of species' responses to warming. Within stand changes in abundance may be the most immediate and strong effect of a changing climate. Thus, studying the interaction of climate to other ecological factors may best help us to understand changing abundances within forested communities. For example, rates of disturbance have observed to be a strong correlative factor that can drive treeline response in conjunction with climate change (e.g., Payette and Gagnon 1979). On a global scale most grasslands are disturbance maintained. Changes in the disturbance regime may swamp climate change in the rates of movements of both species and community boundaries. Alternatively, differences in modern species abundances, such as high deer densities resulting high herbivory rates on *Tsuga*

*canadensis* seedlings (e.g., Alvorson et al. 1988), seem likely to overwhelm the species' ability to respond to climate change through migration. The lack of passenger pigeons, an important presettlement seed disperser (Webb 1986), may also strongly affect the ability of trees to respond to climatic change.

Finally, we expect northward range limit expansions to be slow and fear that southern range limit contractions may be swift. Thus, we must focus our attention on ecological processes at both southern and northern distribution limits of species. Curtis (1959) defined a "tension zone" for the vegetation of Wisconsin as a region that is unusually rich in species distribution limits. Focusing research on "tension zones" allows us the ability to best capture the dynamic processes associated with climate change in a human-altered landscape. Further, sites that are characterized by anomalous microclimates, such as warm south-facing slopes, within these tension zones may be the most sensitive to early signs of climatic change. Lags are often observed in short term responses to climatic change owing to the fact that adult trees are less sensitive to the vagaries of climate than are juveniles; field studies targeting regeneration success and failure will most likely to detect critical changes in the response of species to their environment.

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