

# Plant Migration and Climate Change

*A more realistic portrait of plant migration is essential to predicting biological responses to global warming in a world drastically altered by human activity*

Louis F. Pitelka and the Plant Migration Workshop Group

Terrestrial plants are notorious for their sedentary habits; indeed, that is one way our ambulatory species identifies them as members of the other kingdom. Of course, populations of plants do move, infiltrating new territory by creep of root and shower of seed. But how much does our self-absorbed species really know about these stately migrations? Do scientists know enough, for instance, to predict what would happen to plant communities if the earth's climate suddenly changed?

We seem to believe that we do. Forecasts of global warming are often illustrated with maps showing the poleward movement of plant species, as though the biosphere were made up of puzzle pieces that could be rearranged at will. In reality, it may take plant populations years or decades to move substantial distances. Moreover, today they must move through a landscape that human activity has rendered increasingly impassable. Under the circumstances, it is possible that many species might perish, caught in the double bind of climate change and habitat degradation. To reliably assess this risk, we need a better understanding of plant migration.

The interdisciplinary research required to predict how migration might constrain the response of the plant kingdom to climate shifts is just beginning. The evidence consists of diverse pieces. Some scientists have examined the fossil record of plant migrations following ancient climatic upheavals. Others have studied

contemporary invasions of exotic species. Still others have analyzed the mathematics of dispersal mechanisms and the interaction of those mechanisms with contemporary landscape patterning.

These three lines of research provide disparate—even contradictory—insights. Past migrations have been much faster than simple calculations based on seed dispersal by wind or by vertebrate animals would predict. Plants appear to be capable of long-distance jumps and of rapidly spreading from pre-established outlier positions. But it is also evident that human activity has greatly altered patterns of plant migration. People disperse seeds farther and faster than the seeds' own dispersal mechanisms can take them. But people also fragment the landscape, creating habitat patchworks that are usually less able to support either plant species or their animal conveyances than are undisturbed landscapes.

Some of these factors would seem to retard plant migration and others to accelerate it. Which factor or combination of factors will predominate for which species in the event of future climate change? And what will happen if the climate changes faster than it has in the past? Perhaps the only way to explore questions this complex is by means of computer models.

## The Fossil Record

The paleorecord provides compelling evidence that plant migration can be rapid enough to track climate change and that migrations can take place by means of sporadic long-distance leaps. For example, by mapping the accumulation of pollen in lake sediments at sites widely dispersed in time and space, paleoecologists have produced maps that indicate some tree species advanced rapidly during the early Holocene epoch (our own epoch, beginning about 10,000 years ago), fol-

lowing the retreat of the North American glaciers (see Figure 3). The high migration rates and the ability of species to jump large bodies of water reveal an underlying potential for relatively rapid response to climate change.

How many kilometers can a tree species traverse in a year? A plausible set of velocities can be calculated from analyses of past migrations. Indeed, these velocities might be especially pertinent because they describe movement across the northern temperate latitudes, exactly those regions where greenhouse-warming scenarios predict the most severe temperature change. In eastern North America, the migration velocities were as high as a kilometer a year. Moreover, these velocities seem to have been unaffected by dispersal barriers, even ones the size of the Great Lakes and the North and Baltic seas (Woods and Davis 1989, Kullman 1996).

Dispersal this rapid around seemingly significant barriers is a puzzle theoretical biologists have tried to solve for nearly half a century. How could trees move so fast and leap obstacles so broad? Simple calculations based on the ranges of birds or mammals that disperse seeds and on patterns of wind-borne seed movement do not predict such rapid migration. This outcome has led modelers to suspect that migration is accomplished mainly by rare long jumps that escape our observation (Clark *et al.*, in press). In addition, contemporary empirical studies (for example, measuring the amount of seed caught in traps placed near trees) do not pick up seed caught in vigorous up-lift that would then inject it into high-level circulatory patterns. Long jumps might create dispersed outlier populations, too sparse to be detected in the pollen record, that might serve as foci for rapid invasion when conditions became more favorable.

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Figure 1. Northern Europe was not always blanketed with Norway spruce, but over several thousand years *Picea albens* mounted an impressive migration that produced the dark-green forests that now fill images of Scandinavia such as this morning scene near Ingdal, Norway. The biological record of the large spruce migration provides evidence that plant populations can advance rapidly by establishing distant outlier populations. But predicting the plant migrations that might accompany a global warming is difficult, partly because of the complex effects of human alterations of the environment. For instance, *Picea* populations in plantations (such as one in Nordmoen, Norway, right, photographed during acid-rain research) sometimes exist south of the tree's natural range; they might be left stranded and less productive if global warming moves the range northward. (Photograph at right courtesy of Louis Pitelka.)

One rare documented example of the long-jump-and-outlier model of spread is the western migration of Norway spruce (*Picea abies*) across northern Europe during much of the Holocene and especially the spruce migration across western Sweden about 3,000 years ago (Bradshaw and Zackrisson 1990). Wood fragments found underneath living groups of *krummholz* (stunted, multi-stemmed) spruce in the Scandes Mountains demonstrate that spruce grew there as early as 8,000 years ago, more than 5,000 years before its presence could be inferred from pollen data (see Figure 4). Isolated trees hundreds of kilometers in advance of the migrating front apparently served as foci for the later invasion of *Picea*. Although the long-jump-and-outlier model of spread might seem far-fetched as a general explanation for rapid migration, studies of contempo-

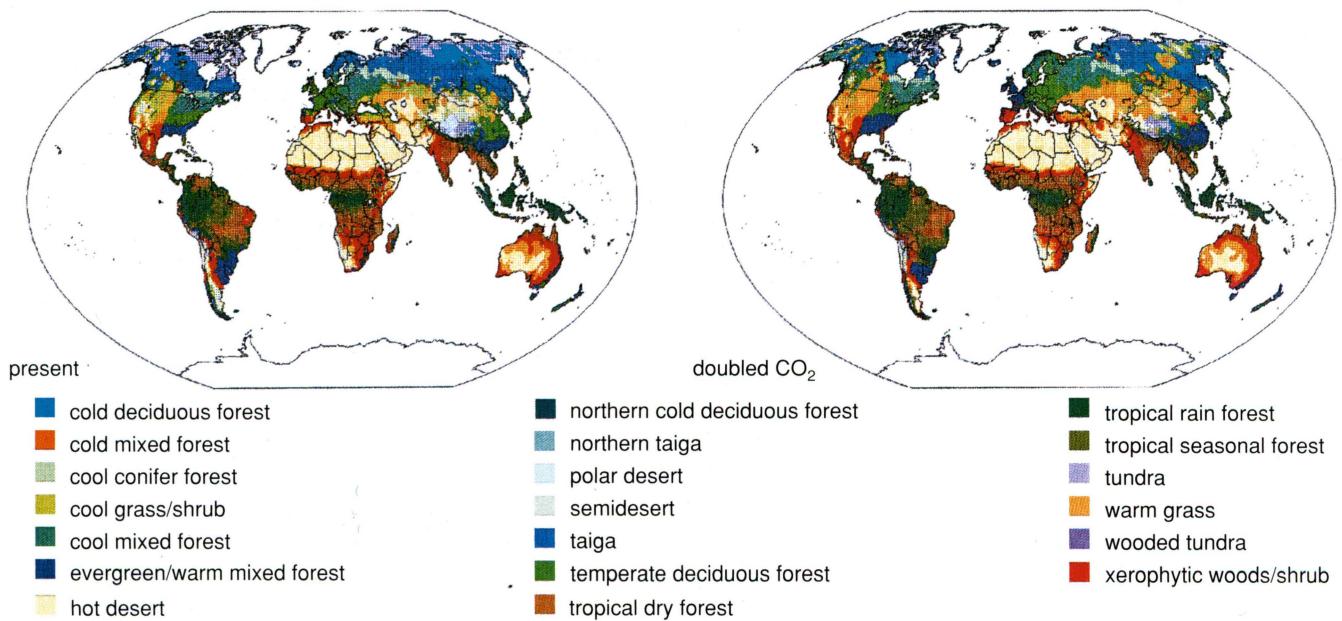
rary plant invasions suggest it is not limited to Holocene spruce.

Some scientists think that, with suitable technique, it may be possible to distinguish local from windblown pollen and thus to detect outliers even in the pollen record. One team used a "geographic method" to look for evidence of outlying colonies of eastern hemlock (*Tsuga canadensis*) and American beech (*Fagus grandifolia*) in the pollen record preserved in lake sediments from periods before human settlement in Michigan, Wisconsin and Minnesota. They were confident that pollen percentages consistently significantly higher than those at surrounding sites identified outlying colonies (Davis, Schwartz and Woods 1991).

The outlier model of spread is consistent with results from other lines of inquiry. Recent mathematical analyses



show that if a species' dispersal pattern (the spatial distribution of propagules around a source) is Gaussian, or bell-shaped, an invasion will exhibit constant-speed traveling waves. But if the pattern has "fat" tails (at least some seeds move especially long distances), invasion will accelerate (see, for example, Kot,



**Figure 2.** In many early simulations of climate change, vegetation ranges tended to shift around like puzzle pieces, ignoring the question of whether vegetation can migrate to match altered conditions. This map, produced by the BIOME1 model (Prentice *et al.* 1992), simulates the distribution of global natural vegetation for present climate conditions (*left*) and then under conditions brought on by a doubling of carbon dioxide levels in the atmosphere (*right*), based on a widely used general-circulation model of the atmosphere called GFDL (Manabe and Wetherall 1987). Ecologists have found, however, that plant migration is a far more complex phenomenon than such models suggest, and that feedback responses from vegetation subjected to climate change might alter the course of that change.

Lewis and van den Driessche 1996). Outlier populations, then, may increase the rate of invasion, exerting a continual outward pull that causes the wave to move forward faster and faster. Converging lines of evidence suggest, therefore, that once an outlier tree population was established across a barrier, the population rapidly filled in the intervening space (Davis, Schwarz and Woods 1991). In this context, it is interesting that the paleorecord indicates that migration rates slowed rather than accelerated in the later Holocene. This suggests they may have been limited by some factor other than intrinsic dispersal rates, such as the rate of climate change (Clark *et al.*, in press). In other words, plants may not have reached their maximum potential rates of spread.

On the whole, the picture that emerges from the fossil record is one of relatively rapid migration: Plants have moved fast enough to track climate change, and may be capable of faster migration than is seen in the paleorecord. These migrations have come in response to change that in some cases has been as fast as the rapid warming predicted for the next few decades. During the last glacial period, there were repeated episodes of warming in which the mean annual global temperature rose by 5 degrees Celsius or more within a few decades (Nicholls *et al.* 1996).

Holocene patterns of spread, however, do not guarantee rapid plant migra-

tion in response to future climate change. First, people have greatly altered landscapes since the early Holocene. Second, early Holocene range shifts indicate that patterns of spread may depend on many variables, including local topography, and not just the plants' intrinsic dispersal potential. Finally, the tree species whose pollen records are clearest are not necessarily representative of the entire plant community. Many different patterns of migration are found in the fossil record, and gaps in the record and problems in interpretation make it difficult to characterize these patterns precisely. A study of the paleorecord in southern Italy suggests that several tree genera—oak, beech and lime—kept pace with climate fluctuations in the last 15,000 years, advancing, retreating and advancing again, but perhaps they were able to do so because they had previously established outlier populations in nearby refuges, which served as a kind of hedge against change (Watts, Allen and Huntley 1996). In other regions there is no evidence for such rapid adjustments, although this might be because the pollen record lacks the temporal resolution needed to identify them.

### Contemporary Invasions

Clearly an exotic species invading a native plant community is not the same thing as a native species shifting its range in the wake of climate change. But in both cases plant populations

come to occupy new territory via dispersal and reproduction. And since invasions have occurred with increasing frequency in the past 200 years, we have detailed accounts that, judiciously weighed, provide an opportunity to learn about range adjustments.

Studies of contemporary plant invasions also provide evidence for the long-jump-and-outlier mechanism of spread. A particularly dramatic example is the recent expansion of cheatgrass, the Eurasian grass *Bromus tectorum*, in western North America (Mack 1986). This aggressive alien grass occupied most of its current range of about 200,000 square kilometers within the last decade of a 40-year invasion process (see Figure 5). The evidence suggests that *B. tectorum* arrived in the intermountain West, the region bounded by the Rocky Mountains to the east and the Cascade-Sierra Nevada ranges to the west, in the 1880s, as a contaminant in agricultural seed. Before 1900, the species had established itself in at least five locations in the region. Over the next 20 years at least 50 additional foci appeared, but the total area occupied by the grass was still small. Then, within only about 10 years (1920–1930), the grass filled in between these foci, becoming a dominant species throughout the region.

*B. tectorum* is just one of many examples of invasions that have two distinct phases: a quiescent phase, during which

ranges shift only slightly, followed by an active phase, during which something triggers explosive expansion (Forcella and Harvey 1981). The lag times of modern invasions range from decades to a century, numbers that provide an interesting commentary on the paleorecord of rapid migration. These periods are too brief to be picked up in fossil records, but they are long enough that plant populations might not persist if the climate changed as rapidly as some scenarios suggest it might.

It is difficult to see how the intrinsic migratory potential of an annual such as *B. tectorum* could limit its ability to adapt to future climate change, even if we assume it has a lag time of 40 years. But other species that have lower reproductive rates or take longer to reach reproductive maturity, such as trees and other perennials, could have longer lag times and might be stranded in unsuitable habitat by rapid climate change. This raises the unpleasant prospect that, in the event of rapid climate change, unwanted species—weeds—would be the species that would have little trouble shifting their ranges. Invaders by definition, most

weeds are capable of rapid propagation, spread and often adaptability; they are plants that over the course of evolution may have traded off other traits more valued by people. Thus it is likely that species that are more desired, and perhaps cultivated, might be vulnerable to extinction.

A second important lesson of modern invasions is that it can be very difficult to establish new populations. A study of attempts to introduce parasites and predators into pest insect populations in Canada found that the best predictor of successful colonization was simply how many times colonization was attempted (Bierné 1975). Similarly, newly founded outlier populations of plants may fail again and again, and even when they succeed, it may be a while before the founding populations can send out enough propagules to fill in the intervening ground. Repeated opportunity may thus be crucial to a species' ability to shift its range. As we discuss below, people have modified landscapes in ways that tend to reduce such opportunities.

The record of modern invasions also allows scientists to examine the relation be-

tween dispersal modes and migration rates. It is tempting to attribute the rapid spread of some species in the Holocene to their dispersal modes, but there is little evidence for such a link. To the contrary, differences in dispersal modes did not seem to matter; virtually all species migrated into new areas with apparently equal efficiency. (Again this observation must be interpreted cautiously. The fossil record may lack the temporal resolution needed to distinguish dispersal modes, or some factor other than dispersal modes may have limited rates of migration.)

Although plants have many different strategies for dispersing seeds, only three are long-haul mechanisms: dispersal by water, by wind, and by birds and large mammals. Although the northward-flowing rivers of northern Europe are thought to have played a role in the extremely rapid postglacial migrations of some woody taxa, such as hazel (*Corylus avellana*) (Huntley and Birks 1983), only wind and vertebrate transport are likely to be important for predicting large-scale migrations of broad classes of plants.

The distance a propagule falls from its source depends on wind velocity and

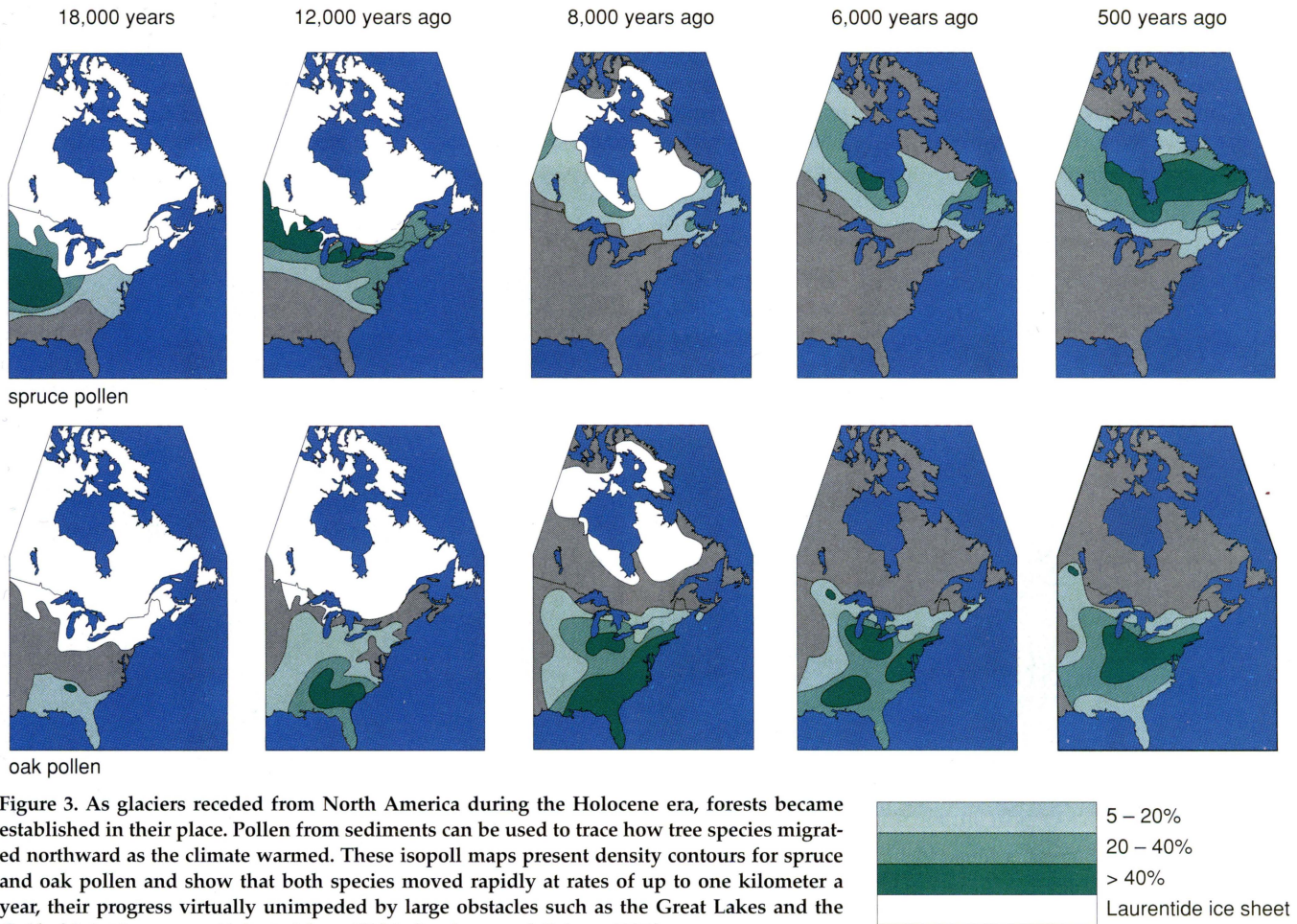


Figure 3. As glaciers receded from North America during the Holocene era, forests became established in their place. Pollen from sediments can be used to trace how tree species migrated northward as the climate warmed. These isopoll maps present density contours for spruce and oak pollen and show that both species moved rapidly at rates of up to one kilometer a year, their progress virtually unimpeded by large obstacles such as the Great Lakes and the Gulf of Saint Lawrence. (Adapted from Webb, Jacobson and Grimm 1987.)

“drag,” or resistance to fall (which is enhanced by seed wings or plumes). Windstorms may carry propagules long distances, especially if vigorous uplift lofts them higher than their normal release height. Although these events are difficult to observe, there is circumstantial evidence that they take place; for example, plants have rapidly colonized Krakatau and other newly formed volcanic islands.

Many plant propagules are adapted for dispersal by vertebrates (Webb 1986). Large terrestrial mammals and birds of all sizes are important agents of long-distance dispersal and can transport seeds tens of kilometers. Moreover, some species preferentially cache nuts along forest edges, which encourages spread (Johnson and Adkisson 1985). Blue jays, which exhibit this behavior, may have enabled Fagaceous trees such as beech to adjust easily to postglacial warming in eastern North America (Johnson and Webb 1989).

Interesting as these natural dispersal mechanisms are, they are not necessarily relevant to future range shifts; for some species, the natural dispersal mechanism is likely to be superseded by human agency. People routinely introduce and cultivate plants thousands of kilometers outside their native ranges, thus serving as a kind of super dispersal mechanism. The Chinese tallow (*Sapium sebiferum*), for example, was intentionally intro-

duced into South Carolina in the 1700s and has since spread throughout the southeastern United States. It is a serious threat to coastal prairie ecosystems, which are converted to woodland by this fast-growing tree. Remarkably, Chinese tallow is still sold in nurseries as an ornamental, even though it is known to be environmentally harmful (Stein and Flack 1996). Although human-assisted invasions have typically been considered ecological disasters, it is conceivable that people might cushion the effect of climate change for native species by moving seed longer distances than it could travel on its own.

Of course, dispersal is only the first step toward successful colonization. Plants must also successfully germinate, grow and reproduce in order to serve as the source of new propagules that can disperse in their turn. The likelihood of stray seed establishing itself depends on the existing vegetation and on the type and frequency of disturbances in the local environment. In the absence of disturbances, many plant communities are quite resistant to invasion. Shade from an established canopy or a thick leaf-litter layer can serve as a barrier to the establishment of both native and exotic plants. Plants also influence the chemistry of the litter and soil in ways that can render it inhospitable to invading plants. The unique soils in conifer forests, tun-

dra regions and wetlands are all self-protective in this way.

In general, the disturbance of an established plant community by fire, flood, windstorms, and burrowing or grazing animals renders it more vulnerable to invasion. This suggests that future climate changes that kill existing plants or lead to more frequent fires or windstorms would increase the probability that dispersed propagules would be able to establish themselves. But people have also profoundly altered disturbance regimes. Cheatgrass, for example, was able to establish itself so easily in part because settlers introduced livestock, and the grasses native to the intermountain West were intolerant of trampling. Large mammals introduced by people, such as water buffalo and wild boar, have also contributed to rapid spread of exotic invasive plants in Australia and Hawaii (Russell-Smith and Bowman 1992, Stone 1985).

The net effect of human agency is difficult to predict. Although people disturb large tracts of land by tillage and grazing, they also suppress some natural disturbances, such as wildfires. Fire suppression prevents the invasion of forests with dense understory vegetation by shade-intolerant saplings. On the other hand, it has allowed Midwestern oak woodlands to be invaded by fire-sensitive species such as buckthorn and Australian sclerophyll (drought-tolerant) forests to be in-

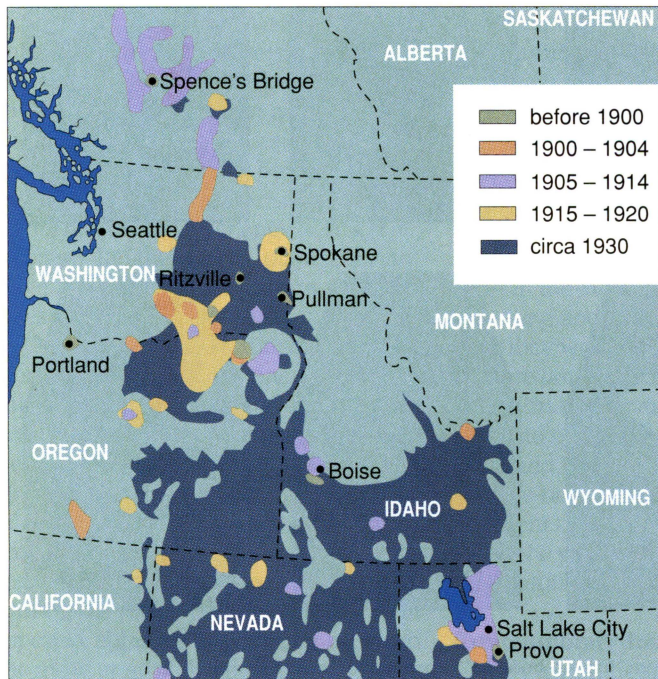


Figure 4. Cheatgrass, *Bromus tectorum* (right), invaded western North America during the past century, but the invasion (mapped at left) did not proceed at a steady pace. It appears to have had a quiescent phase, during which the plant's range shifted only slightly, followed by an active phase, in the years 1920–1930. Other examples of migrations by aggressive alien species also exhibit two stages. (Map adapted from Mack 1986; photograph courtesy of Richard Mack.)



Figure 5. Long-distance plant dispersal requires the help of water, wind and birds or large mammals. Plant propagules are adapted for various kinds of dispersal. Seeds of the milkweed (upper left) ride on the wind, just as cockleburrs ride on large, furry animals. Non-native plants often have human help. The Chinese tallow (*Sapium sebiferum*), introduced into South Carolina as a landscaping plant and still sold at nurseries, now threatens coastal prairie ecosystems. The photograph at right was taken at Old Santee Canal State Park near Charleston, where berry-laden tallow branches stand out against the darker leaves of another invasive species, the Chinese privet (*Ligustrum sinense*), imported for similar reasons and now also naturalized in the region. At lower left a cardinal enjoys tallow berries in winter, illustrating another common means of dispersal. (Photographs by: lower left, Lee Lowder, Old Santee Canal State Park; right, Lil Chappell.)

vaded by rain-forest species (Harrington *et al.* 1995).

Our species' flair for creating outlier populations of plants must also be considered. Because people have moved plants around the globe for horticultural and landscaping purposes, we may have set the stage for massive invasions by exotic species. Botanical gardens and similar large repositories of alien species have long been sources of plant invasions (Parker 1977), but such specialized facilities are not the only culprits. People routinely plant both native and alien species in their gardens and parks, far from the native ranges of these plants. Some of the most noxious plant invaders, such as the water hyacinth (*Eichhornia crassipes*), are probably escaped cultivars. Global climate change could trigger a new round of escapes, if conditions changed in such a way that species long occurring as agricultural weeds or maintained by cultivation outside their natural ranges were able to grow in the wild.

**What about Landscape Patterning?**

The record of modern invasions suggests that human agency acts to accelerate the migration of some species, particularly those that are adept hitchhikers or whose usefulness has captured our attention.

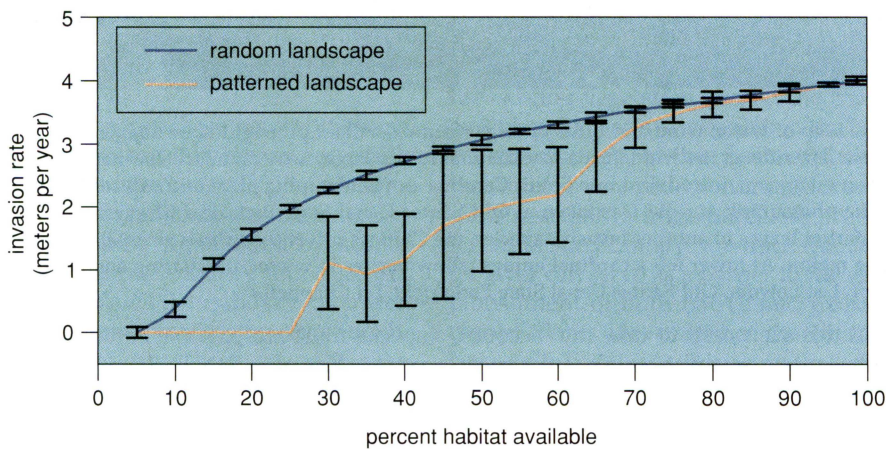
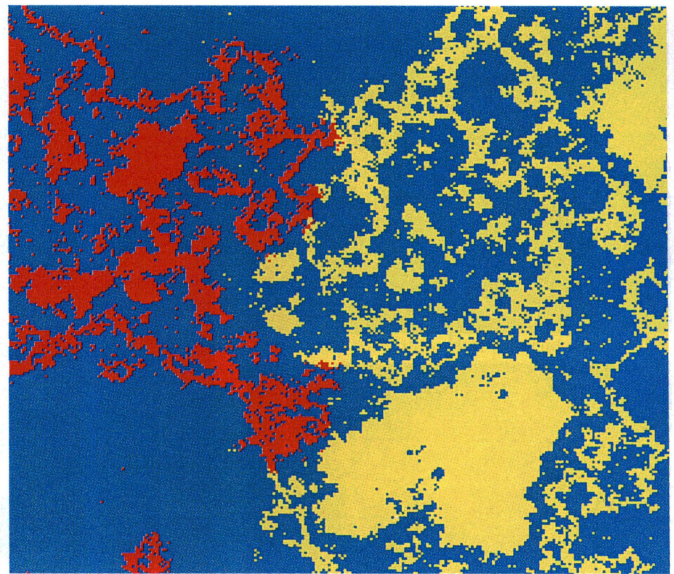
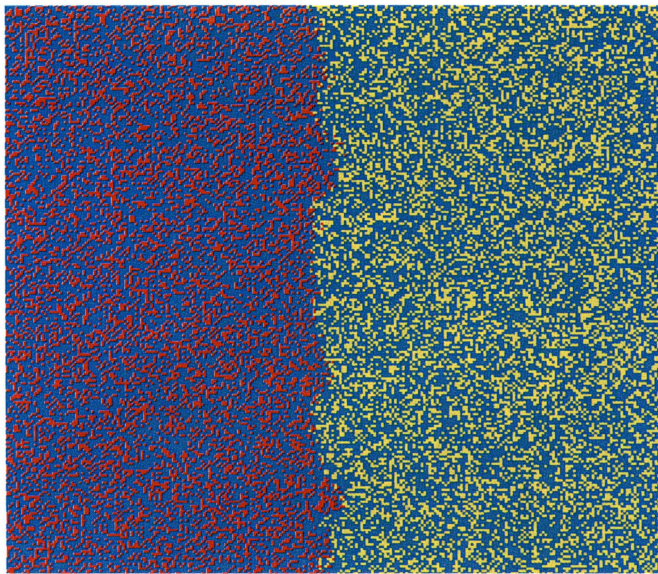
But this view fails to take into account what many scientists think is the most alarming effect of human activity: habitat fragmentation. Almost any aerial view of the earth reveals a patchwork landscape, in which undisturbed habitat exists as scattered islands in a sea of cultivated or developed land. Habitat destruction and fragmentation, by themselves, can drive species to extinction. Together with global climate change, they could lead to wholesale extinction, stranding plants in inhospitable landscapes without egresses. According to the Nature Conservancy, half of the endangered plant species in the U.S. are restricted to five or fewer populations (Schemske *et al.* 1994). If climate change renders these remnant sites inhospitable, there may not be enough plants left to launch migrations across largely hostile landscapes.

Landscape ecologists have developed several models that predict how habitat alteration might constrain plant migration. In general, the migratory rate is the product of the dispersal rate and the rate of population growth at the edge of the invasion. But if the plant population is spreading through a habitat mosaic, there is also a threshold effect: If the population is to expand at all, the fraction of the total habitat that is suitable for the

species must exceed some minimum value (see Figure 9). Finally, because many species persist as metapopulations, with local extinctions being balanced by colonizations, there is also a second subtler threshold: If the species is to persist, let alone spread, the number of populations also must not fall below some minimum value. Indeed metapopulation dynamics may explain why the geographic distribution of some plants is more restricted than physiological limits allow (Schemske *et al.* 1994).

These three theoretical rules have very down-to-earth implications. By carving up landscapes with roads, buildings and agricultural land, people reduce the availability of suitable habitat, reduce the number of populations in a metapopulation, and even depress dispersal rates and rates of population growth. In some cases, all of these factors will conspire to inhibit migration. There are known to be cases where the opposite is true—blue jays move between habitat islands, and such birds may move farther in a fragmented environment—but these cases are not the rule. Decreases in bird populations likely will reduce long-distance seed dispersal.

On the whole, habitat fragmentation is likely to have the greatest impact on



**Figure 6.** Landscape-ecology models predict how habitat alteration might constrain plant migration. If a plant population is spreading through a habitat mosaic, the models show there is a threshold effect: Some minimum fraction of the total habitat must be suitable if the population is to expand. These images show model predictions of the invasion of an invading annual plant species whose propagules are spread according to an exponential distribution with a mean distance of 1 meter and a maximum range of 6 meters. Each map has an area of 256 square meters, broken into one-meter sites. The invading species (red) is introduced onto the left side of the map and its asymptotic rate of invasion measured after 20 generations. In the random landscape (top left) the probability of any site being suitable is 0.4. A fractal algorithm was used to generate a patterned map (top right) in which habitat corridors for plant migration decrease in size and connectance as the fraction of suitable sites declines (but the overall probability remains 0.4). Above, the rate of invasion under each scenario is graphed (with bars representing 95 percent confidence intervals from 10 iterations) against the fraction of the map occupied by suitable habitat sites. Invasions slow significantly when the suitable habitat is less than 65 percent. (Images and data courtesy of Robert Gardner.)

species whose seeds are dispersed by large land animals. Landscapes are increasingly fragmented into parcels smaller than the home ranges of large vertebrates, and this refashioning is often accompanied by the hunting and local extirpation of species or the restriction of their movements. In parts of Africa, for example, even as introduced mammals contribute to the spread of some exotic plants, the substantial restriction of elephant populations may have far-reach-

ing consequences for native trees such as *Balanites wilsoniana* (one of the species called torchwood), for which they seem to be the exclusive or nearly exclusive dispersal agents (Chapman, Chapman and Wrangham 1992).

What is the upshot of these pressures on plant communities during climate change? We know that even during the Holocene, when only natural dispersal mechanisms were operating, entire plant communities did not migrate intact to

new ranges. Instead the compositions of biological communities were reshuffled by differences in the ability of species to re-establish themselves. Given that human activity accelerates the migration of some species and inhibits that of others, we can only expect that, in the future, this reshuffling would result in communities quite different from those we know today. Native species that rely on natural dispersal mechanisms would probably be slowed by habitat fragmentation. Those species that human beings actively disperse, such as timber or endangered species that we deliberately move to new sites, would be much less affected by fragmentation and might migrate faster than in the past. But so might species that take silent advantage of human mobility, such as weeds that are carried with harvested crops.

### Regional Problems

Although climate change is a global process, some of its most important consequences will take place on a regional scale. Looking at plant communities on this scale, one notices some plants such as forest trees that are cultivated near the limits of their natural ranges and others that are maintained in relatively small, isolated reserves. These classes of plants are vulnerable to climate change.

Norway spruce is currently the major commercial timber tree in southern Sweden, where it grows in naturally regenerated forests and in plantations outside its natural range. Depending on the pattern of climate change, future warming might alter considerably spruce's role in natural forests. And it might strand plantations even farther outside the

tree's natural range, threatening their productivity. Trees grown in heavily exploited agricultural landscapes have little opportunity for dynamic response to changing conditions. Replacing monoculture plantation systems with forestry systems that permit natural migration and regeneration, and that allow variation in species composition over time, will facilitate future species movements and might make the spruce a more viable species during warming.

Given the inexorable loss of habitat to human activity, conservationists often attempt to minimize species loss by arranging the remaining habitat in ways that increase its connectivity. Unfortunately many of these arrangements may be unlikely to function well through periods of climate change. For example, as a compromise between logging and conservation interests, a special system of habitat-conservation areas has been designed in the Pacific Northwest for the spotted owl. The expectation that this network of reserves on federal forest land will adequately protect the owl is based, however, on landscape-ecology models that assume old-growth forests in the targeted sites will regenerate at known rates (Lamberson *et al.* 1994). Because climate change is likely to alter the rates and patterns of regeneration of Douglas fir forests, it adds enormous uncertainty to these plans, yet it has not been factored into the calculations.

More generally we can think of our entire nature reserve and park system as a static network, with little flexibility in the face of climate change. Our reserves and parks are fixed in place; when the climate changes, what will become of the rare and unique species inhabiting these isolated sites? Even if other suitable sites exist, will these species be able to move to them?

One way to assess the risk to which climate change will expose endangered species is to calculate the average size of patches occupied by species and the mean distance between patches before and after different climate-change scenarios. Although we cannot say precisely what the effects of changes in these landscape features will be, we do know that marked reductions in either patch size or connectivity can threaten species. It is disheartening, for example, that the patch size and connectivity of old-growth forests in the Pacific Northwest have declined by more than an order of magnitude in the past 50 years (Groom and Schumaker 1993). This degree of landscape modification is certain to have

severe consequences for plant and animal migration.

### Global Consequences

At the global level we confront a difficult but potentially very important issue affecting not only plant migration but its significance: feedback between climate change and the biosphere. Changes in vegetation structure can affect the physical properties of the land surface, such as its *albedo* (the percentage of sunlight it reflects), surface roughness and canopy conductance to water vapor. Changes in vegetation structure and function can also influence the exchange of carbon dioxide and other radiatively active trace gases, such as methane and nitrous oxide, between the atmosphere and the biosphere. By these means plants can influence the percentage of incoming sunlight absorbed at the surface or the atmospheric concentration of greenhouse gases, and thus the rate and magnitude of climate change.

Positive feedback from the biosphere could exacerbate global warming. Models of earth's climate 6,000 years ago suggest that variations in the earth's orbit could not alone have produced the high annual average surface temperatures deduced from paleoclimate analyses. Instead orbital forcing must have been exaggerated by subsequent vegetation responses (Foley *et al.* 1994, TEMPO 1996). Because boreal forests absorb much more solar radiation than tundra does, poleward shifts in the location of the forest/tundra boundary during a period of warming can amplify climate changes by as much as 50 percent.

Moreover, under some circumstances, the carbon cycle might act as a second feedback loop. If during warming the rate of forest dieback on the southern edge of a forest range (in the Northern Hemisphere) were higher than the rate of forest expansion on its northern edge, there would be a net release of carbon to the atmosphere, exacerbating the greenhouse effect responsible for the climate change in the first place. What happens depends critically on the poleward migration rate. Calculations by one team suggest that transient carbon releases owing to this and related mechanisms might be substantial enough during predicted warming that the biosphere might no longer be the sink for carbon dioxide it is today (Smith and Shugart 1993).

How, then, do we make sense of the complex picture of plant migration described in this article? In order to accu-

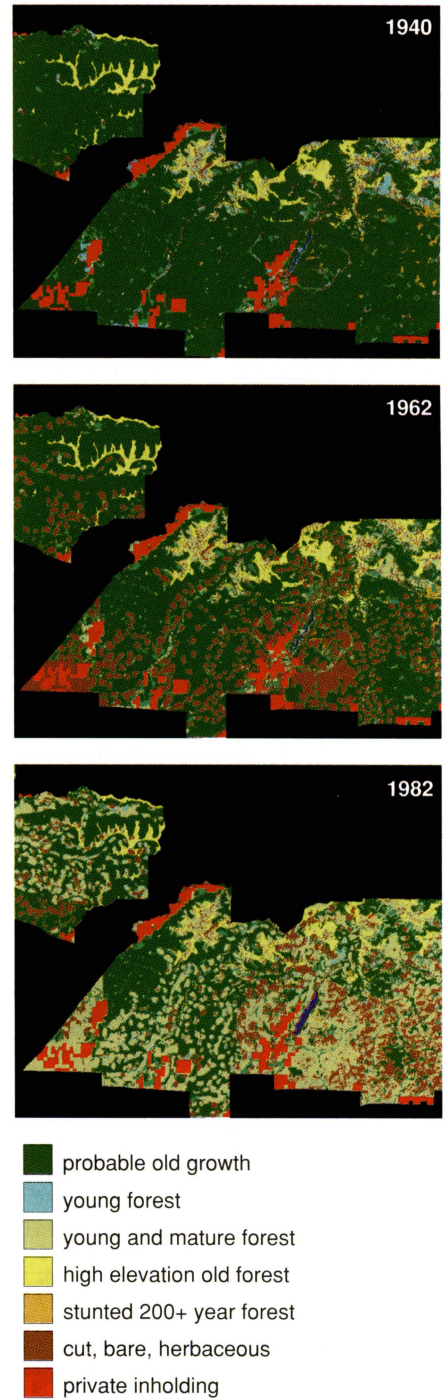


Figure 7. Ecological systems in old-growth forests in the Pacific Northwest may be particularly vulnerable to climate change because the size of old-growth patches and their connectivity have both declined dramatically as a result of cutting in recent years. These vegetation maps show a portion of the Olympic National Forest (approximately 38 × 46 kilometers) in 1940, 1962 and 1982. Each pixel represents a 57 × 57-meter patch of vegetation. Landscape modifications of this magnitude would be expected to have severe consequences for both plant and animal migration in a climate-change scenario. (Images courtesy of Nathan Schumaker, U.S. Environmental Protection Agency.)



rately predict future climate change, we must develop models that treat the biosphere as dynamic rather than static and that link changes in vegetation to global carbon and nitrogen cycles. The most comprehensive models of global vegetation, dynamic global vegetation models or DGVMs, can be used in combination with climate and carbon-cycle models to assess feedbacks between the biosphere and the general atmospheric circulation and the oceans (Foley *et al.* 1996).

DGVMs, like static models, include representations of photosynthesis, respiration, plant growth and decomposition, but they also include the processes of establishment, mortality and competition needed to simulate the waxing and waning of plant communities. Because they are global in scope, these models are necessarily coarse in some respects. For example, they typically describe the biosphere as a set of five to ten plant functional types, such as broad-leaf deciduous trees or needle-leaved evergreen trees, and they have a grid resolution no finer than half a degree, or about 50 kilometers.

Although several DGVMs have been used for preliminary assessment of the response of the biosphere to simulated

climate change, they do not fully capture biosphere dynamics. In particular, they lack any explicit representation of plant migration or of the interaction of dispersal processes and landscape patterning. Instead, they are typically executed in one of two “bracketing modes”: Either dispersal is assumed to be fully effective, so that ranges that have become newly hospitable are invariably colonized, or dispersal is assumed to be always limiting, so that plant types are unable to shift their ranges (Sykes and Prentice 1996).

Neither of these approximations is satisfactory. The first mode would be a realistic approximation only if the climate changed very slowly, which is not the eventuality of concern. The second mode is also unrealistic, because it is more likely that rapid climate change will promote a few species to dominance than that no species will be able to keep up. Theoretically, even one vigorous migrator could set in motion the feedback loops described earlier.

One challenge of upgrading the models will be to incorporate dispersal modes in the plant functional types. As we have mentioned, only two of the many plant dispersal modes are likely to be important in large-scale migrations of

functional types: wind and vertebrate dispersal. Wind dispersal is especially common among shade-intolerant species such as grasses and many forest trees, and these species often are highly clumped. Species dispersed by vertebrate animals—including perhaps 70 percent of tropical trees—may be either shade-tolerant or shade-intolerant but are often adapted to fill small gaps or patches of disturbed ground, growing as scattered individuals in highly diverse communities. These correlations might be exploited in the redefinition of functional types.

We still lack the knowledge to predict precisely how the interaction of dispersal modes and landscape patterning will affect the response to climate change. Given this predicament, the best approach might be to gradually narrow the range of possible outcomes by analyzing specific regions and vegetation types. For example, one could analyze the effect of climate change on Europe, which has many tree species with low dispersal rates and a highly fragmented landscape. This approach, together with that of evaluating various scenarios of climate change, offers our best hope of avoiding surprises in biosphere dynamics.

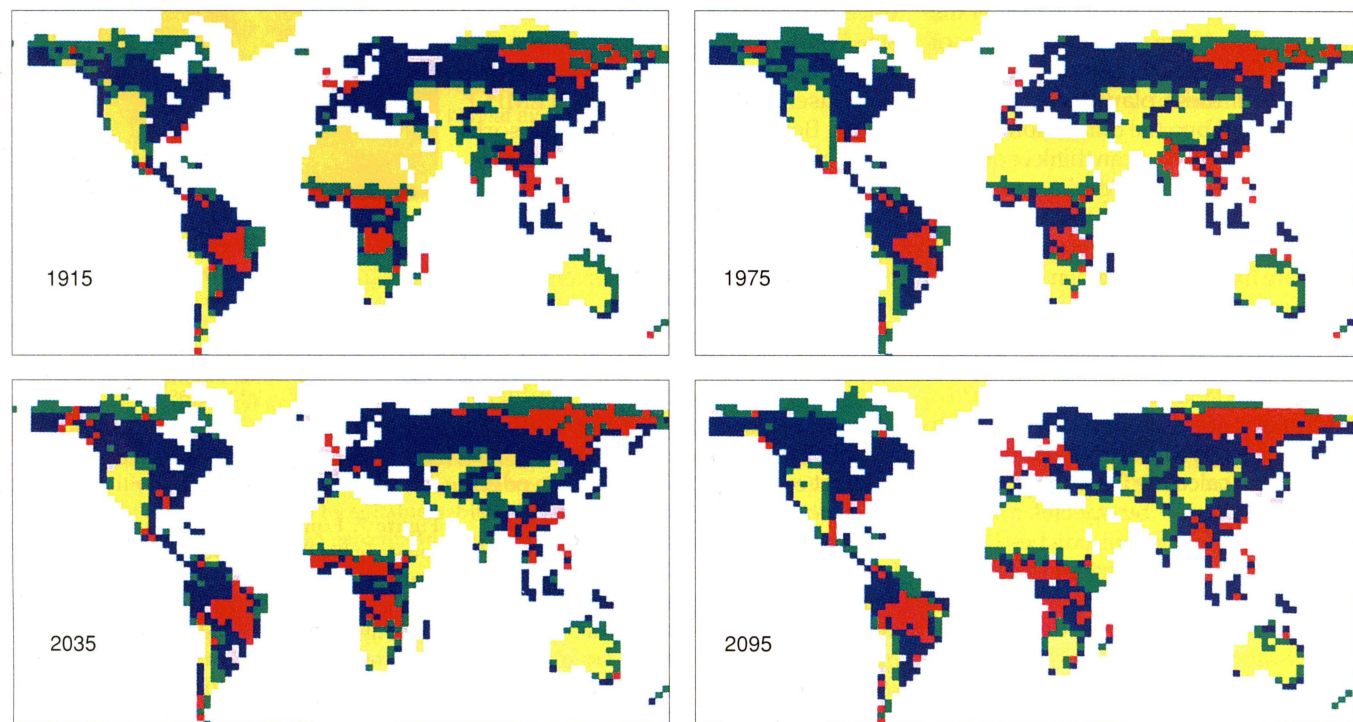


Figure 8. Linking climate models such as the one illustrated in Figure 2 with models of dynamic structural change in global vegetation could make it possible to predict biological responses to climate change and how these responses might affect the course of climate change. These preliminary simulations come from a DGVM, or dynamic global vegetation model, called IBIS (Foley 1996). In this simulation structural change in global vegetation is modeled based on population dynamics but no migration. The vegetation categories are desert (yellow), grassland (green), deciduous forest (red), mixed forest (pink) and evergreen forest (blue). The Hadley Centre general-circulation model of the atmosphere was used to predict climate change from known and predicted carbon dioxide concentrations from 1860 to 2099. (Preliminary unpublished model output courtesy of John Foley, University of Wisconsin; output maps by Alberta Fischer, Potsdam Institute for Climate Impact Research.)

It is not too soon to begin. In a recent issue of the journal *Nature* a team of scientists reported that measurements made from weather satellites between 1981 to 1991 had revealed a noticeable increase in the absorption of light by vegetation at northern latitudes. Not only has plant growth increased, the growing season has lengthened. Scientists cannot be sure what is causing the bloom, but it is certainly possible that the satellites have spotted one of the first signs of the effects of global warming on the biosphere.

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