LAGS IN VEGETATION RESPONSE TO GREENHOUSE WARMING

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Abstract. Fossil pollen in sediments documents vegetation responses to climatic changes in the past. Beech (*Fagus grandifolia*), with animal-dispersed seeds, moved across Lake Michigan or around its southern margin, becoming established in Wisconsin about 1000 years after populations were established in Michigan. Hemlock (*Tsuga canadensis*), with wind-dispersed seeds, colonized a 50,000 km^2 area in northern Michigan between 6000 and 5000 years ago. These tree species extended ranges northward at average rates of 20–25 km per century. To track climatic changes in the future, caused by the greenhouse effect, however, their range limit would need to move northward 100 km per °C warming, or about 300 km per century, an order of magnitude faster than range extension in the past. Yet range extension in the future would be less efficient than in the past, because advance disjunct colonies have been extirpated by human disturbance, and because the seed source is reduced due to reductions in tree populations following logging. Many species of trees may not be able to disperse rapidly enough to track climate, and woodland herbs, which have less efficient seed dispersal mechanisms, may be in danger of extinction.

Introduction

The speed with which the climate is expected to change in the next century presents a problem: can vegetation track climatic changes that occur so rapidly? Estimates of tracking stem from two kinds of evidence: experimental results from simulation models, and fossil or historical evidence of responses to known climatic events in the past.

Changes in Community Composition

Simulations of the response of a red spruce (*Picea rubens*) forest to a sudden 2 °C warming showed an immediate change in the understory, but delays of a century or more in the replacement of the canopy spruce by hardwoods (Davis and Botkin, 1985). The temperature change simulated in the model slowed the growth of canopy trees, but did not kill them outright. The temperature change was large enough, however, to lessen spruce seedling survival in the simulated plots, while permitting the establishment of seedlings of hardwood trees adapted to warmer climate. The canopy trees were thus replaced one by one at the end of their normal life span, as in the process of forest succession. Response was much more rapid when the simulations included disturbances. These had the effect of shortening the average life span of the dominant trees, thus speeding up replacement by under-

story saplings. This experiment suggests that forests subjected to frequent logging will adjust to climatic change more rapidly than forests in reserves.

Treering studies show that growth responses of individual trees occur within a year for most species (Brubaker and Cook, 1983). Responses at the population level are slower: even annual plants have taken more than seven years to colonize open sites in experimental desert plots (Brown *et al.*, 1986). Perennial prairie grasses show even longer lags following droughts (Tomanek and Hulett, 1970). Delays result from inadequate seed dispersal, or from competition from resident plants that continue to occupy a site, even after the environment has become unfavorable for seed production (Davis, 1986).

The fossil record of vegetation change in response to the sudden temperature drop during the Younger Dryas cold period 10,800 years ago is of particular interest, because the rate of change at that time was similar to the predicted CO_2-induced warming in coming decades. There is no evidence for a lag in vegetation response to the sudden cooling (Iversen, 1954), apparently because it was large enough to kill existing trees and shrubs. The parts of northwestern Europe that were affected by the cooling had supported tundra vegetation, or park-like woodland. Changes in the type of sediment deposited in lakes showed that at the time of the sudden cooling soil profiles were disrupted, and solifluction and mass-wasting occurred. These processes were initiated simultaneously over a wide region. This suggests that the temperature drop and accompanying frost action were sufficiently severe to kill the existing trees, while shrubs and mat-forming herbs were disrupted by frost action that broke apart incipient humus cover (Iversen, 1954; Tutin, 1969).

The abrupt warming at the end of the Younger Dryas 500 years later, in contrast, coincided with a halt in the input of silt and clay to sedimentary basins. Temperate herbaceous and shrubby species expanded immediately, while trees lagged several hundred years behind. Iversen attributed the lag in the development of forest to slow dispersal (Iversen, 1954), but Pennington (1986) has recently presented persuasive evidence that a lag in soil development slowed the expansion of forest. Several of the tundra plant and animal species that lived in Denmark during the Younger Dryas period were unable to migrate north rapidly enough to track the tundra to the arctic; these species and varieties became locally extinct as open habitats in southern Scandinavia were replaced by forest (Iversen, 1973; Degerböl, 1959).

In summary, climatic changes in coming decades may not be large enough to cause direct death of adult trees over large areas of the landscape, at least in temperate regions. If temperatures rise only 2 °C, vegetation may respond through changes in competitive relationships among plant species, resulting in changes in the relative abundances of dominant trees. Over large regions, these changes could lag decades behind the climatic changes, especially in undisturbed forests dominated by long-lived species.

Changes in Geographical Range

Changes in the geographical distributions of plants are also to be expected in coming decades. For each degree centigrade warming, ranges expand 100 km northward, while southern populations retreat. On the scale of tens of kilometers, and thousands of years, geographical limits of tree species have tracked past climatic changes quite closely (Webb, 1986; Prentice, 1986; Woods and Davis, 1989; Davis *et al.*, 1986a).

The question of interest is whether plant species *can* disperse and establish new populations rapidly enough within the next 100 years to occupy habitats that will become available, given warming of several degrees magnitude, and a rate of climatic warming that is at least one order of magnitude more rapid than any known previous climatic change.

The fossil record has provided useful information about the rate at which trees were able to advance across the landscape during the Holocene. The rates measured by the appearance of pollen in quantity at different latitudes represent actual (not potential) rates of range extension, averaging 10–45 km per century over long time periods (Firbas, 1949; Davis, 1981; Huntley and Birks, 1983). These observed rates have seemed very rapid to ecologists studying mechanisms of seed dispersal (van der Pijl, 1969), but we cannot say whether they represent maximum possible rates. Range extension in the past may have been closely constrained by changing climate (Webb, 1986; Prentice, 1986) or by rates of soil development (Pennington, 1986). It is difficult to devise rigorous tests that distinguish between biotic and climatic limitations (Davis *et al.*, 1986).

We have been studying range extension of American beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*) into the Great Lakes region of North America during the Holocene (Davis *et al.*, 1986a, b; Woods and Davis, 1989). The Great Lakes posed major geographical barriers 50–100 km in width, making obvious any difficulties forest trees may have had in dispersing seeds to new regions. The fossil pollen record shows that beech reached the western shore of Lake Michigan either by long-distance dispersal across the lake, or by dispersal from one habitat island to another through prairie landscape at the southern end of the lake. The latter route involved seed dispersal distances of several 10's of km between scattered pockets of woodland habitat (S. L. Webb, 1986, 1987), while the former route would have necessitated dispersal across 100 km of open water. There was a lag of 500–1000 years between the time of establishment of beech on the eastern shore and its establishment as a disjunct population on the western shore (S. L. Webb, 1987). The lag suggests that the probabilities of long-distance dispersal were low, resulting in slow average rates of colonization of regions separated by large geographical barriers (Davis *et al.*, 1986).

Hemlock provides an interesting contrast. Its small, winged seeds are shed throughout the fall and winter when they can be carried by wind along the surface of snow. Fowells (1965) reports dispersal distances of 1 km, but our data suggest

that occasional dispersal events carry seeds many tens of km beyond the parent plants, permitting the establishment of outlying colonies as much as 100 km beyond the main species front. The fossil pollen record suggests that hemlock spread rapidly over an area of 50 000 km^2 in eastern upper Michigan and northern lower Michigan between 6000 and 5000 years ago. It colonized this large area by spreading from multiple "infection" centers – small colonies that had been established within the previous millennium by long-distance dispersal of seeds from Ontario. There is no evidence of lags in the diffusion of this species that can be attributed to difficulty in crossing the Great Lakes.

The history of beech and hemlock suggest that seed dispersal is far more effective than short-term observations would suggest. However, in the present-day environment, conditions are quite different. Important natural dispersal agents may be less abundant or missing altogether. For example, S. L. Webb (1986) postulates that the passenger pigeon was an effective dispersal agent; this species, formerly very abundant, is now extinct. A second difference between modern and prehistoric conditions concerns the availability of sites for establishment. Weeds diffuse readily over the modern landscape partly because habitats suitable for them are abundant. Forest trees may be more specific: for example, in the Upper Great Lakes region hemlock seedlings characteristically become established on rotted logs.

Discussion

Lags in the adjustment of species abundances to climate will be small in the heavily disturbed communities that cover most of the landscape. Lags will last a decade or two at most; logging companies can decide to harvest forests that are no longer growing rapidly and replace them with species that are better adapted to the changed climate. It seems likely that through accident or purposeful management most of the common species of trees and herbs will be dispersed by humans to the new habitats that become climatically suitable for them. Included in this generalization are commercially valuable species of herbs or trees, and common weeds.

Lags will be a serious problem, however, for unmanaged forests, natural areas and for reserves. Although reserves are small in area, comprising a tiny fraction of the total landscape, they have great importance as reservoirs of species diversity. In fact most reserves in North America were established for the express purpose of protecting habitat for one or more rare and endangered species. Because climatic change during the next century *may* not be large enough to kill the canopy trees outright (assuming a best-possible-case-scenario with a change of 1–2 °C), they may persist and the habitat will appear superficially unchanged, even as a different group of tree seedlings becomes abundant in the understory, changing competitive conditions for rare woodland herbs. Changes in the soil may occur, such as decomposition rates for forest litter and thus nutrient availability (Pastor and Post, 1988).

Lags in changes of canopy trees in reserves may prove important, because when

even-aged canopy trees do die without replacement, a major change in community type occurs relatively suddenly. The forest as we know it disappears, together with the conditions of light, microclimate and soil that are critical for the valued understory species the reserve was designed to protect. Studies are needed for reserve species to predict the time course of response to climatic warming; modeling of specific reserve communities would be particularly helpful.

Dispersal to climatically suitable regions will be difficult for most rare species. The seed source is less abundant than under natural conditions, because populations are small. Natural vectors are reduced, and target areas (reserves in climatically favorable regions) are extremely small. It is also unclear whether the target areas will contain the precise conditions necessary for the establishment of woodland species. Intervention and purposeful transplanting of rare plants may be necessary. The success of these horticultural efforts is uncertain because the conditions that favor establishment of many woodland plant species are not well known.

The problem of preserving rare species can be illustrated by the case of hemlock (Davis, 1988). Although abundant elsewhere, hemlock is listed as a rare and endangered species in Minnesota; only fourteen localities for hemlock have been identified within the state – isolated stands 50–100 km west of the main species boundary in Wisconsin. Since Euro-American settlement in the late 19th century, half of these stands have disappeared. The trees were either cut down, burned in postlogging fires, or killed by exposure after surrounding forest was logged. Most of the stands consisted of single trees or small populations of 3–12 individuals; the one large stand of 1000 or more trees was completely destroyed by logging and fire. As a result less than 1% of the original hemlock population in the state still survives (Calcote, 1986).

In Minnesota hemlock appears limited by low precipitation and hot summers; it will doubtless become extinct within the state as the result of future climatic changes. However, it will expand its range elsewhere, as outlying colonies occur everywhere beyond the limits of the species (Fowells, 1965). To the north such outliers could serve as centers of infection, facilitating hemlock colonization of new habitats in the manner we have observed in the fossil record (Davis *et al.*, 1986b). This will not occur, however, if hemlock colonies everywhere have suffered the same fate as those in Minnesota.

In Wisconsin, where the tree grew abundantly, its numbers have been much reduced by disturbance. Hemlock reproduces poorly following logging; logging characteristically converts hemlock stands to maple-basswood (*Acer-Tilia*) forest. In most of Wisconsin and Michigan, rotted logs provide the principle sites for hemlock seedling establishment; these sites are rare in logged-over areas. At the present time, even in those forests where hemlock does become established, browsing by deer prevents the seedlings from surviving to the sapling stage (Anderson and Loucks, 1979; Frelich and Lorimer, 1985).

In conclusion, outlying colonies have been decimated, the main population is much reduced in density and therefore produces fewer seeds, and soil changes and

increased browsing prevent establishment. This means that diffusion rates today for hemlock will be much lower than observed in the fossil record, resulting in a delay in the colonization of new areas by this species. The fossil record shows that hemlock extended its range at an average rate of 20 km/century, although much higher rates occurred for a short time in eastern Michigan, when numerous pre-existing outlying colonies expanded, apparently in response to climatic change (Davis *et al.*, 1986b). Future range extension will have to occur at least 10 times the average Holocene rate, or 200 km per century, to track the expected temperature rise. In other words, expansion of pre-existing outlying colonies is the only possible means whereby it could expand northward rapidly enough to track climatic warming.

The problems of diffusion to new areas under future conditions will be similar, but more severe, for most herbaceous species, many of which are rare throughout their ranges. Preservation strategies must be developed on a case by case basis, as each species will present new problems. In particular danger are rare plants that grow only in forested habitats, and that depend on soil conditions produced by the litter of particular canopy trees. Where dispersal of trees is too slow to track the climate, old-growth forest trees will be replaced for a time by secondary species. The ecosystem-level effects of changes like this can be large because of the influence of litter on nutrient availability (Pastor and Post, 1988). Interventions will be difficult before the ecosystem-level processes involved are better understood.

Graham (1986) argues persuasively that plant/animal interactions were largely responsible for the Late-Quaternary extinctions of large mammals; the individualistic responses of plant species to climatic changes disrupted communities, changing habitat and fodder conditions for mammals. A similar argument is made here, that plants that are interdependent will be the most difficult to protect. In the face of rapid climatic change, each species will respond with a different time lag, disrupting plant communities for many decades (Davis, 1986).

Beginning now, and extending into the next century, reserves and natural areas will have to operate as zoos already do for large mammals. Preserve managers will have to learn to propagate plants, transplanting them to areas that are predicted to become favorable for them and attempting to preserve genetic diversity in the face of diminishing natural populations. The prospect of attempting such a massive effort for hundreds of species that are difficult to grow in cultivation seems overwhelming.

Even where species are not lost altogether, we face a loss of diversity on a regional basis, as species become extinct in marginal areas. The most useful intervention to prevent extinction would be the immediate dedication of large areas of landscape as reserves, with adequate provision for corridors for migration of species toward those latitudes where they may be able to survive the climatic changes of the next 100 years.

References

Anderson, Roger C., and Loucks, Orie L.: 1979, 'White-Tail Deer (*Odocoileus virginianus*) Influence on Structure and Composition of *Tsuga canadensis* Forests', *J. Appl. Ecol.* **16** 885–861.

Brown, J. H., Davidson, D. W., Munger, J. C., and Inouye, R. S.: 1986, 'Experimental Community Ecology: The Desert Granivore System', in Diamond, J. and Case, T. J. (eds.), *Community Ecology* Harper and Row, New York, pp. 41–62.

Brubaker, Linda B. and Cook, Edward R.: 1983, 'Tree-Ring Studies of Holocene Environments' in H. E. Wright, Jr. (ed.), *Late-Quaternary Environments of the United States: The Holocene* Vol. 2. Univ. of Minnesota Press, Minneapolis, pp. 222–224.

Calcote, R. R.: 1986, 'Hemlock in Minnesota: 1200 Years as a Rare Species', M. S. Thesis, Univ. of Minnesota, Minneapolis, MN.

Davis, M. B.: 1981, 'Quaternary History and the Stability of Forest Communities', in D. C. West, H. H. Shugart, and D. B. Botkin (eds.), *Forest Succession: Concepts and Application.* Springer-Verlag, New York, pp. 132–177.

Davis, M. B. and Botkin, D. B.: 1985, 'Sensitivity of Cool-Temperature Forests and their Fossil Pollen Record to Rapid Temperature Change', *Quaternary Research* **23**, 327–340.

Davis, M. B.: 1986, 'Climatic Instability, Time Lags, and Community Disequilibrium'. in Diamond, J. and Case. T. J. (eds.), *Community Ecology*, Harper and Row, New York, pp. 269–284.

Davis, M. B., Woods, K. D., Webb, S. L., and Futzma, R. P.: 1986a. Dispersal versus Climate: Expansion of *Fagus* and *Tsuga* into the Upper Great Lakes Region', *Vegetatio* **67**, 93–104.

Davis, M. B., Mack, J. H., and Calcote, R. R.: 1986b, 'Diffusion of Hemlock (*Tsuga canadensis*) into Michigan and Wisconsin during the Holocene', *Ecol. Soc. Amer. Program*, 1986, p. 128.

Davis, M. B.: 1988, 'Climatic Change and Extinctions of Forest Species', in G. Woodwell (ed.), *Biotic Impoverishment*, Cambridge University Press, Cambridge England (in press).

Degerböl, M. and Krog, H.: 1959, 'The Reindeer (*Rangifer tarandus L.*) in Denmark. Zoological and Geological Investigations of the Discoveries in Danish Pleistocene Deposits', Biol. Skr. Kgl. Dan. Videnskab. Selsk., 10.

Firbas, F.: 1949, *Spät und Zeitliche Waldegeschichte Mitteleuropas Nördlich der Alpen*, Vol. 1. Gustav Fischer, Jena.

Fowells, H. A.: 1965, *Silvics of Forest Trees of the United States*, USDA Forest Service Handbook No. 271. Govt. Printing Off., Washington, D.C.

Frelich, Lee E. and Lorimer, Craig G.: 1985, 'Current and Predicted Long-term Effects of Deer Browsing in Hemlock Forests in Michigan, U.S.A.', *Biological Conservation* **34**, 99–120.

Graham, R. W.: 1986, 'Response of Mammalian Communities to Environmental Changes during the Late Quaternary', in Diamond, J. and Case, T. J. (eds.), *Community Ecology.* Harper and Row, New York, pp. 300–313.

Huntley, B. and Birks, H. J. B.: 1983, *An Atlas of Past and Present Pollen Maps for Europe: 0–13000 Years Ago*, Cambridge Univ. Press, Cambridge, England.

Iversen, J.: 1954, 'The Late-Glacial Flora of Denmark and its Relation to Climate and Soil', *Dansk. Geol. Unders. II Series*, No. 80. pp. 87–119.

Iversen, J.: 1973, *The Development of Denmark's Nature Since the Last Glacial, Dansk Geol. Unders. V. Series*, No. 7-C, 126 pp.

Pastor, J. and Post, W. M.: 1988, 'Response of Northern Forests to CO_2 Induced Climatic Change', *Nature* **334**, 55–58.

Pennington, W.: 1986, 'Lags in Adjustment of Vegetation to Climate Caused by the Pace of Soil Development: Evidence from Britain, *Vegetatio* **67**, 105–118.

Pijl, L. van der: 1969, *Principles of Dispersal in Higher Plants*, Springer Verlag, New York.

Prentice, I. C.: 1986, 'Vegetation Responses to Past Climatic Variation', *Vegetatio* **67**, 131–141.

Tomanek, G. W. and Hulett, G. K.: 1970, 'Effects of Historical Droughts on Grassland Vegetation in the Central Great Plains', in Dort, Jr., W. and Jones, Jr., J. K. (eds.), *Pleistocene and Recent Environments of the Central Great Plains.* Univ. of Kansas Spec. Univ. Kansas Press, Manhattan, KS, pp. 203–210.

Tutin, Winifred (Pennington): 1969, 'The Usefulness of Pollen Analysis in Interpretation of Stratigraphic Horizons, both Late-Glacial and Post-Glacial', *Mitt. Internat. Verein. Limnol.* **17**, 154–164.

Webb, S. L.: 1986, 'Potential Role of Passenger Pigeons and Other Vertebrates in the Rapid Holocene Migrations of Nut Trees', *Quaternary Research* **26**, 367–375.

Webb, S. L.: 1987, 'The Holocene Extension of Range of American Beech into Wisconsin: Paleoecological Evidence for Long-Distance Seed Dispersal', *Ecology* **68**, 1993–2005.

Webb, T., III.: 1986, 'Is Vegetation in Equilibrium with Climate? How to Interpret Late-Quaternary Pollen Data', *Vegetatio* **67**, 75–92.

Woods, Kerry D. and Davis, Margaret B.: 1989, 'Paleoecology of Range Limits: Beech in the Upper Peninsula of Michigan', *Ecology* **70**, 681–696.