EVALUATION OF METHODOLOGY FOR DETECTING/PREDICTING MIGRATION OF FOREST SPECIES

Dale S. Solomon and William B. Leak[1]

Abstract: Available methods for analyzing migration of forest species are evaluated, including simulation models, remeasured plots, resurveys, pollen/vegetation analysis, and age/distance trends. Simulation models have provided some of the most drastic estimates of species changes due to predicted changes in global climate. However, these models require additional testing against field data to ensure their reliability. Remeasured plots would provide a basis for model testing, but the number of plots required to detect short term trends might be excessive. Remeasurement data from forested areas where there have been no land-use changes provide a clearer picture of migrational trends. A 60-year record from the Bartlett Forest provided estimates of species changes in relation to management versus no management, land type, and elevation. Migration rates based on historical pollen analyses are of limited value because these analyses are derived from small, scattered samples formed under physical/biological conditions much different from those of today. Age/distance trends from carefully chosen and specified study locations will provide estimates of recent migrational trends and rates of elevational change. Independent surveys of vegetation in areas where previous plots cannot be relocated are subject to the same limitations as remeasured plots.

INTRODUCTION

During the past decade, there has been renewed interest in plant migration due to the potential impacts of global climate change. Predictions have suggested major shifts in species ranges - even extinction - over the next 50 to 200 years in response to temperature shifts of up to 4.5 °C (e.g., Davis 1987; Peters 1990; Overpeck et al. 1991). Although some field studies have suggested actual changes in the elevational distribution of species due to climate change (Hamburg and Cogbill 1988; Grabherr et al. 1994), others show little or no detectable response (Solomon and Leak 1994; Leak and Smith[1]) that could be attributed to changes in climatic factors. We address this inconsistency by examining various approaches that are used to measure, detect, or predict species migration: simulation, remeasured plots, resurveys, interpretation of pollen records, and age/distance trends.

We use the term migration to mean the invasion of a species into a geographic region where it has not recently been able to grow due to climatic or edaphic conditions. Succession means the invasion or increased proportions of a species in an area where the species is readily able to grow but has been excluded due to stand dynamics or serial stage.

SIMULATION

Some of the most drastic predictions of climatically induced vegetation change have been derived from computerized simulation models or graphical approaches. For example, Overpeck et al. (1991) predicted shifts in plant ranges of 500 to 1000 km within periods as short as 200 years. Others (e.g., Davis et al. 1994) suggest the possibility of near extinction of species such as sugar maple and beech due to an inability to migrate rapidly enough to keep pace with the changing climate. Most modeling attempts follow a similar format (Pastor and Post 1988; Solomon and West 1987). First, future changes in temperature and precipitation variables are predicted through one of several general circulation models (GCM). Relationships between species occurrence and climatic variables are developed or inferred using modern or historical geologic data. Future ranges are then predicted that can be compared to estimated migration rates by species as evidenced in the pollen record. The strength of this approach is that there is a strong relationship between species and climate as well as a wealth of empirical regional data (Denton

---

[1]Research Foresters, USDA Forest Service, Northeastern Forest Experiment Station, Durham, NH 03824.

and Barnes 1987; Gajewski 1987; Prentice et al. 1991; Spear et al. 1994). Questions about this approach relate to the extreme variability in GCM output (Cooter et al. 1993) (Fig. 1), and the validity of these models (e.g., Charlson and Wigley 1994). In addition, little is known about the responses of vegetation to climatic change with respect to growth, reproduction, genetic potential, and migration. This remains an extremely complex subject that cannot be understood simply by developing empirical vegetation/climatic relationships.

Appendix

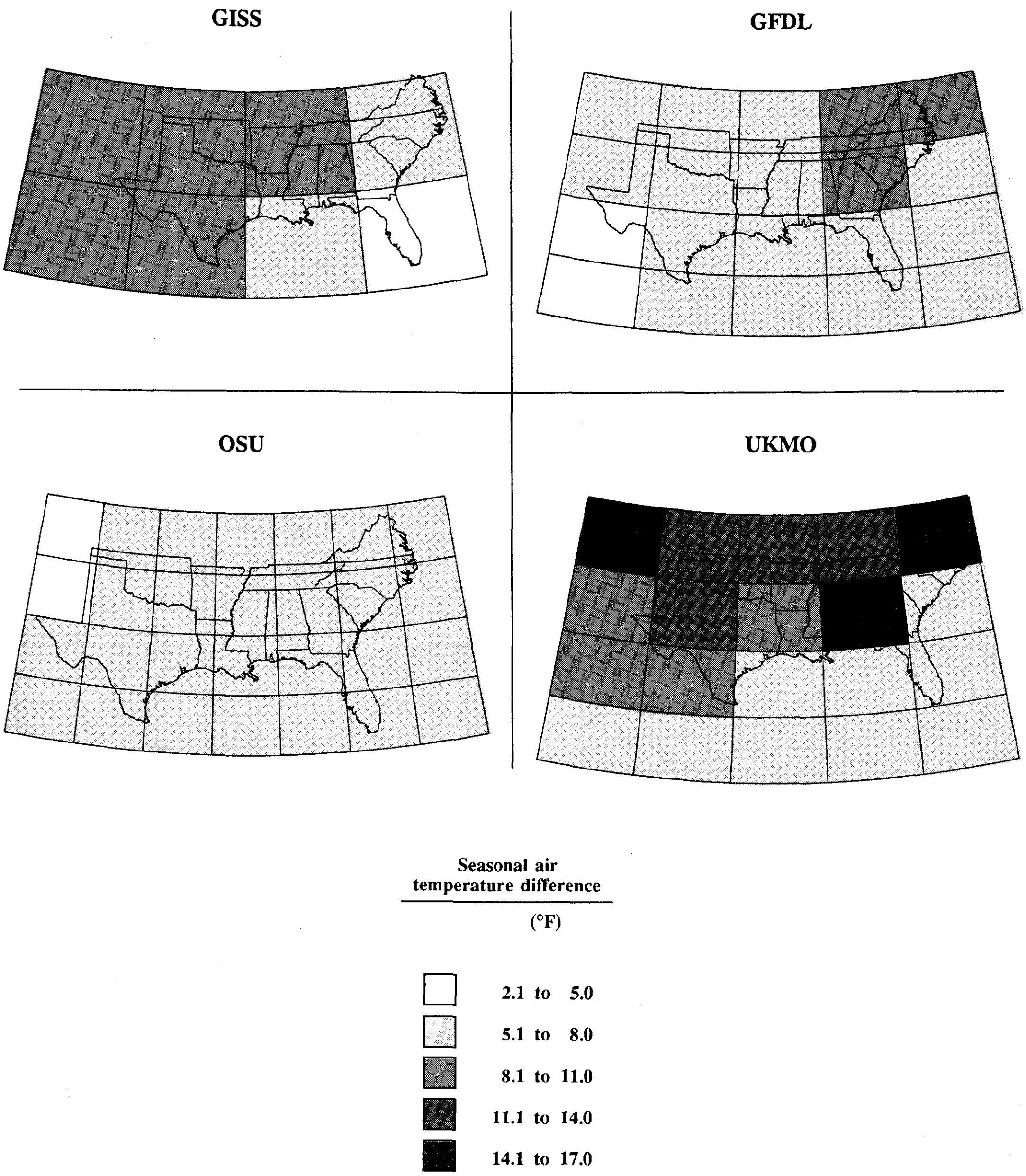

Figure 1. Winter season temperature increases after doubling the CO^2 concentration as predicted by four GCM models: GIS (Goddard Institute for Space Studies), GFDL (Geophysics Fluid Dynamics Laboratory), OSU (Oregon State University), and UKMO (United Kingdom Meteorological Office) (adapted from Cooter et al. 1993).

REMEASURED PLOTS

USDA Forest Service Forest Inventory and Analysis (FIA) plots are ideal for monitoring species migration. Also, they provide the data needed to test migrational models. One complication is that, on a regional scale, existing vegetation is responding to factors other than climate change. In New England, one dominant factor is natural successional change following prior disturbances from agricultural clearing and logging (Solomon and Leak 1994). This factor could easily mask any tendencies toward climatically driven changes in vegetation (Fig. 2, Table 1). A 24-year record on FIA plots in Maine indicated that white pine and balsam fir were declining in both average latitude and elevation. However, the area's land-use patterns suggested that these changes were not a reflection of climate change but the result of the invasion of abandoned agricultural land by these species.

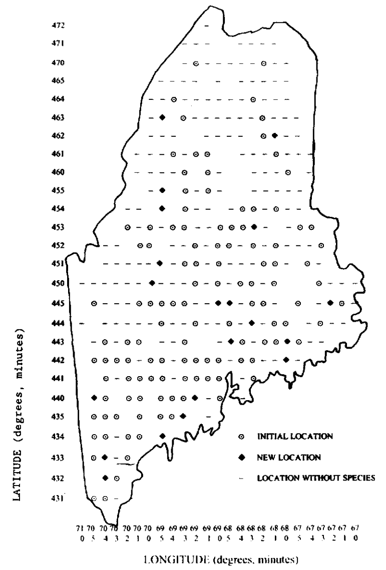

Figure 2. Initial locations in Maine with living white pine, new locations after an average 24-year period, and locations without white pine at either point in time (adapted from Solomon and Leak 1994).

Table 1. Average elevation (m) and latitude and longitude (degrees) of Maine plots occupied by major species at three measurement periods spanning 24-year average period from the 1950s and 60s to 1980s (adapted from Solomon and Leak 1994)

Measurement period	Red spruce	Hemlock	Balsam fir	White pine	Sugar maple	Beech	Red oak
				Elevation			
1	242(7)[a]	136(8)	238(7)	150(9)	265(10)	243(11)	121(16)
2	240(8)	135(8)	241(7)	142(9)	273(10)	250(11)	117(16)
3	237(7)	136(7)	231(7)**	134(8)**	272(10)	245(11)	119(14)
				Latitude			
1	45.66(.04)	44.98(.06)	45.69(.04)	44.82(.07)	5.64(.07)	45.41(.06)	44.15(.10)
2	45.68(.04)	44.96(.06)	45.71(.04)	44.73(.07)	45.62(.07)	45.42(.07)	44.12(.09)
3	45.64(.04)	44.95(.06)	45.65(.04)**	44.72(.06)*	45.58(.06)	45.40(.06)	44.10(.07)
				Longitude			
1	69.05(.04)	69.18(.08)	69.08(.04)	69.50(.08)	69.30(.07)	69.25(.07)	70.00(.14)
2	69.01(.04)	69.20(.08)	69.09(.04)	69.53(.08)	69.36(.07)	69.27(.07)	70.01(.14)
3	69.02(.04)	69.23(.07)	69.07(.04)	69.44(.07)	69.39(.06)**	69.26(.07)	70.05(.12)

Standard error in parenthesis; **Significant at 0.01 level; *Significant at 0.05 level.

Table 2. Percent of basal area by species, elevation class (E), year (Y), and deciduous or coniferous landtype (T) for unmanaged stands on Bartlett Experimental Forest, with significance tests (* = 0.05 level) among factors and interactions with year[1]

	Deciduous			Coniferous													
	200 to 350 m			200 to 350 m			500 to 650 m			650 to 820 m			T	E	Y	TY	EY
Species	1931	1940	1992	1931	1940	1992	1931	1940	1992	1931	1940	1992					
YB	14.5	11.5	6.9	12.9	12.1	6.6	12.9	14.	14.3	8.4	9.5	12.5	-	-	*	-	*
SM	6.2	5.9	6.6	2.9	2.8	2.6	11.7	11.	12.7	9.2	8.6	7.9	-	*	-	-	-
RM	19.3	22.4	25.7	21.9	24.6	29.2	9.3	8.3	8.2	8.2	7.4	6.4	-	*	-	-	*
PB	14.3	16.4	8.7	11.7	12.1	5.9	15.8	13.	5.5	21.6	21.8	6.6	-	-	*	-	-
WA	4.7	6.1	6.3	3.3	3.3	4.0	0.7	0.9	0.4	0.2	0.2	0.3	-	*	-	-	*
ASP	10.8	5.6	2.9	8.2	5.0	1.3	0.2	0.0	0.0	0.0	0.0	0.0	-	-	-	-	*
EH	6.9	7.9	14.9	13.3	13.5	24.8	3.0	3.4	7.8	1.1	1.2	3.0	-	*	*	-	*
RS	2.5	2.6	2.9	5.3	5.5	6.6	22.1	23.	25.9	34.5	34.9	43.4	*	*	-	-	-
BF	0.3	0.6	0.3	2.7	2.6	1.8	0.8	0.8	0.5	5.8	5.4	6.2	-	-	-	-	-

Note: YB=yellow birch, SM=sugar maple, RM=red maple, PB=paper birch, WA=white ash, ASP=aspen, EH=eastern hemlock, RS=red spruce, BF=balsam fir.

[1]Leak, W.B; Smith, M.L. Sixty years of management and natural disturbance in New England forested landscape. (In preparation).

Local sets of long-term plot data in unmanaged or lightly managed conditions allow some assessment of both successional and migrational tendencies[1] (Table 2). A 60-year record on the Bartlett Forest in New Hampshire provided information on species changes related to management, disturbance, land type, and elevation. On coniferous, unmanaged land types, eastern hemlock increased from 13 to 25 percent of the basal area in the 200- to 350-m elevational class, from three to eight percent in the 500- to 650-m class, and from one to three percent in the 650- to 820-m class. The results indicate that hemlock shows only a slight tendency to increase its elevational range, a result developed from an independent study of age/distance/elevational trends at Bartlett (Solomon and Leak 1994).

Effects of global climate change on expansion or contraction of elevational range appear minimal or nonexistent at present. However, red spruce increased from 34 to 43 percent of the basal area in the 650-820 class (Table 2), and from 22 to 26 percent in the 500-650 class. Apparently, red spruce populations are maintaining themselves well at these elevations despite warnings about growth decline or winter injury due to acid deposition. In summary, the use of permanent plots is a long-term solution that requires careful selection and analysis to confirm migrational tendencies or serve as a data base for model testing.

RESURVEYS

Under this topic we refer to remeasurements where the initial plots cannot be relocated. This type of information might include resurveys of general areas where earlier survey data are available (e.g., Grabherr et al. 1994) or surveys representing a sequence over time in comparable (but spatially different) locations (e.g., Hamburg and Cogbill 1988). Resurveys pose at least two special problems. First, species/area considerations make it necessary to use the same sampling protocol at each inventory so that the appearance or loss of species does not simply reflect a change in methodology. Second, in areas such as New England where there is high variability in environmental conditions over small spatial scales, it is difficult to resurvey without encountering different habitat conditions and different species.

POLLEN/VEGETATION ANALYSIS

Pollen records developed from bog and lake sediments provide long-term estimates of changes in vegetation on a regional level over a time scale established by carbon dating or historical markers (e.g., Spear et al. 1994). This approach provides general estimates of species migrational rates and indicates how communities might change with drastic fluctuations in climatic, edaphic, and competitive conditions during the analysis period.

Pollen diagrams can be constructed from shallow-humus profiles that provide local point estimates of changes in vegetation over shorter periods (several hundred years) (Foster et al. 1992). A time scale seems difficult to establish, though certain historical markers provide some basis for calibration. Apparently, this approach has not been used sufficiently to establish its value in determining recent migrational trends. A careful series of samples along an elevational gradient in an unmanaged landscape might prove useful.

AGE/DISTANCE TRENDS

Migrating species exhibit a sequential relationship between age and distance or elevation, that is, young plants will be out in front of old plants (Solomon and Leak 1994). The migration rate can be represented as the change in distance/change in time (Solomon et al. 1990).

$$\text{Migration rate} = \frac{d_{j-1} - d_j}{a_j - a_{j-1}},$$

where d_j = distance from parent stand and a_j = maximum tree age at d_j.

The age/distance approach is based on the premise that tree species under forested conditions gradually move away from a concentration of seed-producing trees (as opposed to discontinuous jumps), a concept that aligns with what we know about seedfall distribution and sprouting/suckering behavior (Davis 1987; Leak and Graber 1974). This approach requires intensive sampling of actual or predicted tree ages over a distance/elevational transect. It works best in carefully selected areas where there is a steep climatic gradient (on a mountain slope), no significant barriers to plant movement, and unmanaged stands. An example would be the forest species hemlock on Haystack Mountain, Bartlett, NH. While indicating an advancing front, new seedlings have not been established at higher elevations on new or different sites (Fig. 3).

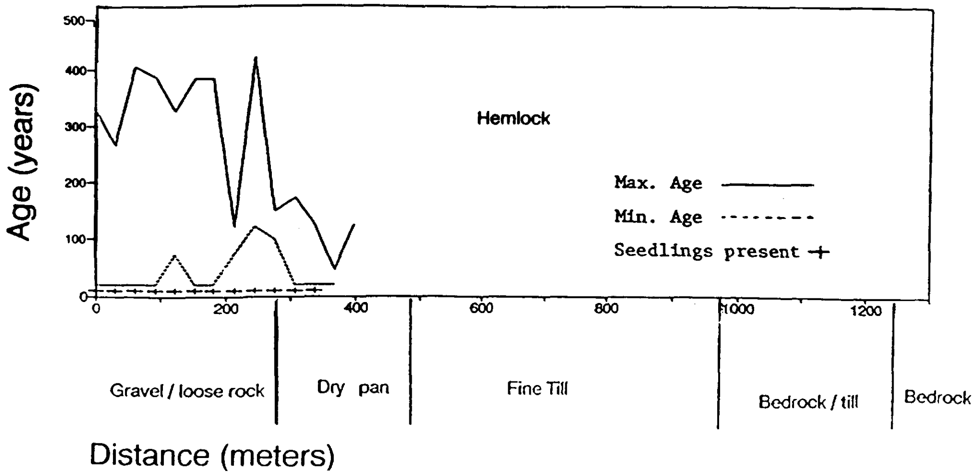

Figure 3. Example of an advancing front from the Bartlett Experimental Forest (adapted from Solomon and Leak 1994). Maximum and minimum ages over horizontal distance for hemlock on Haystack Mountain, Bartlett, NH.

DISCUSSION

Each of the methods discussed has certain advantages and disadvantages. The modeling approach is the only way to predict future scenarios. However, this approach currently is unreliable due to a lack of available data on climatic change and vegetation response. A series of permanent plots, such as FIA plots, should be made available to test modeling theories if or when actual climatic change begins. Such plots need to be selected carefully or screened to ensure that we do not confuse migrational change with successional rebound from prior disturbance. Resurveys of areas with previous vegetation histories is fraught with problems *except* that some of our long-term information on vegetation change can be obtained only in this fashion. Typical bog/lake pollen analyses seem unsuited for detecting current migrational trends, though they are useful in providing a historical and long-term perspective on vegetation response to drastic climatic scenarios. Short-term pollen-profile data from well-designed surveys (e.g., along elevational gradients) could provide interesting insights into recent elevational shifts, especially if accompanied by historical, local weather data. Likewise, studies of age/distance trends provide one-visit estimates of recent migrational change when carried out in carefully selected study sites. This method can provide fairly precise estimates of recent migrational rates as well as details on patterns of movement, obstacles (such as site conditions), and species interactions. A better understanding of successional response of both overstory and understory plant species to climatic changes would aid in the interpretation of apparent migrational trends.

LITERATURE CITED

Charlson, R. J.; Wigley, T. M. L. 1994. Sulfate aerosol and climate change. Scientific American. 270: 48-57.

Cooter, E. J.; Eder, B. K.; LeDuc, S. K.; Truppi L. 1993. General circulation model output for forest climate change research and applications. General Technical Report SE-85. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 38 p.

Davis, M. B. 1987. Invasions of forest communities during the holocene: beech and hemlock in the Great Lakes region. In: Gran, A. J.; Crawley M. J.; Edward, P. J., eds. Reprint from the 26th Symposium of the British Ecological Society on Colonization, succession and stability. Blackwell Scientific Publications, Oxford. 18: 373-393.

Davis, M.; Zabinski, C. 1992. Changes in geographical range from greenhouse warming effects on biodiversity in forests. In: Peters, R.L.; Lovejoy, T. E., eds. Proceedings, World Wildlife Fund conference on consequences of global warming for biological diversity. New Haven, CT: Yale University Press. 22: 297-308.

Denton, S. R.; Barnes, B. V. 1987. Tree species distributions related to climatic patterns in Michigan. Canadian Journal of Forest Research. 17: 613-629.

Foster, D. R.; Zebryk, T.; Schoonmaker, P.; Lezberg, A. 1992. Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England. Journal of Ecology. 80: 773-786.

Grabherr, G.; Gottfried, M.; Pauli, H. 1994. Climate effects on mountain plants. Nature. 369: 448.

Gajewski, K. 1987. Climatic impacts on the vegetation of eastern North America during the past 2000 years. Vegetatio. 68: 179-190

Hamburg, S. P.; Cogbill, C. V. 1988. Historical decline of red spruce populations and climatic warming. Nature. 331: 428-431.

Leak, W. B.; Graber, R. E. 1974. A method for detecting migration of forest vegetation. Ecology. 55: 1425-1427.

Overpeck, J. T.; Bartlein, P. J.; Webb, T., III. 1991. Potential magnitude of future vegetation change in eastern North America: comparisons with the past. Science. 254: 692-695.

Pastor, J.; Post, W. M. 1988. Response of northern forests to CO^2-induced climate change. Nature. 334: 55-58.

Peters, R. L. 1990. Effects of global warming on forests. Forest Ecology and Management. 35: 13-33.

Prentice, I. C.; Bartlein, P. J; Webb, T., III. 1991. Vegetation and climate change in eastern North America since the last glacial maximum. Ecology. 72: 2038-2056.

Solomon, A.; West, D. C. 1987. Simulating forest ecosystem responses to expected climate change in eastern North America: applications to decision making in the forest industry. In: Shands, W. E.; Hoffman, J. S., eds. The greenhouse effect, climate change, and U.S. forests. Washington, D.C.: Conservation Foundation. 304 p.

Solomon, D. S.; Leak, W. B. 1994. Migration of tree species in New England based on elevational and regional analysis. Research Paper NE-688. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 9 p.

Solomon, D. S.; Leak, W. B.; Hosmer, H. A. 1990. Detecting and Modeling the Migration of Tree Species in Response to Environmental Change. In: Burkhart, H.E.; Bonner, G.M.; Lowe, J.J., eds. Research in Forest Inventory Monitoring Growth and Yield Proceedings IUFRO S4.01 and S4.02. Virginia Polytechnical Institute and State University, Blacksburg, VA. Publication FWS-3-90.

Spear, R. W.; Davis, M. B.; Shane, L. C. K. 1994. Late quaternary history of low- and mid-elevation vegetation in the White Mountains of New Hampshire. Ecological Monographs. 64: 85-109.