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ADDING SPATIAL CONSIDERATIONS TO THE JABOWA MODEL OF FOREST GROWTH

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ABSTRACT

Classical ecological questions about the nature of communities and spatial pattern in vegetation may be answered through the integration of data from remote sensing with ecosystem simulation models. JABOWA and related forest growth models have successfully simulated small plots but are not adequate for large-area projections. Study of vegetation pattern requires selection of an appropriate spatial resolution or "grain size", which should be guided by the ecological phenomena studied and an understanding of the effects of adjacent units on one another. A forest sample plot size of 0.1 hectare is proposed as both ecologically appropriate and consistent with available resolution from remote sensing devices. The rationale and methodology for transforming JABOWA from a non-spatial "gap" model to a model with the capacity to simulate the growth of spatially-related forest plots are discussed.

I. INTRODUCTION

The resolution of many environmental and ecological problems requires knowledge about current vegetation and the ability to predict future characteristics of vegetation and environment over large areas. Forest vegetation constitutes a major portion of the world's biomass and production and is therefore of particular importance. Remote sensing can be used to determine current forest conditions and monitor changes. Projections of future states of a forest require computer simulations, for which initial conditions may be supplied by remote sensing. Current forest models are not adequate for large-area projections, which leads us to explore modifications to existing models that can lead to appropriate techniques.

Spatially and temporally consistent data sets obtained from remote sensing permit a new approach to some classical ecological questions about the nature of communities and spatial patterns in vegetation. Study of vegetation pattern requires: (1) choice of an appropriate spatial resolution or "grain size", which should be guided by the ecological phenomena studied and (2) an understanding of the effects of adjacent units on one another (for projection of future states of one forest stand, information about adjacent stands may be required). For mapping vegetation there is a third requirement, a method for classifying vegetation. All three requirements involve an understanding of the nature of vegetation patterns -- whether there are continua or mosaics of discrete units, the intensity and scale of variation over the landscape, and the repeatability of patterns or classes.

There exists no coherent body of theory dealing with appropriate resolution, characters, and procedures for classifying and mapping vegetation or ecosystem variables, or with the other issues of spatial patterns in vegetation. We believe that the integration of the spatially complete, uniform, and repeatable data sets from remote sensing with ecosystem simulation models offers a new and promising approach to these unresolved classical issues. This paper will address the rationale and methodology for transforming JABOWA from a non-spatial "gap" model to a model with the capacity to simulate the growth of spatially-related forest plots.

II. THE JABOWA MODEL OF FOREST GROWTH

Temporal patterns of forest growth have been successfully modeled for a wide

variety of forests using computer simulation. Most of these models are modifications of the JABOWA program, first developed for application to forests of the northeastern United States (Botkin et al., 1972). JABOWA and its descendants involve simplifying assumptions which ignore spatial relationships among forest plots and ignore the specific geographic location of trees within a plot. The crucial simplifying assumptions are that (1) all trees within a plot can affect all others in that plot and the effect does not depend on the exact locations within the plot; (2) trees on separate plots have no effect on one another; and (3) the seed source is assumed to be independent of any plot.

Although the original JABOWA model allowed the user to define any plot size, in its first application the program used a 10 x 10 meter forest sample, developed as part of the Hubbard Brook Ecosystem Study, for initial conditions. Even with the simplifying assumptions of no interaction with adjacent plots and non-spatial within-plot competition among trees, JABOWA has successfully reproduced competitive effects, dynamics of secondary succession, and changes in vegetation accompanying changes in elevation for mixed species, uneven-aged forest ecosystems of the northeastern United States and other areas. However, to study pattern and process in those ecosystems, it is desirable to extend the JABOWA model to include explicit spatial interactions both among trees and among plots. The impetus to extend the model to include plot interactions has become particularly strong with the advent of high-resolution, geographically-registered forest data obtained via remote sensing, which could be used both as initial conditions for a spatial model and to compare with simulation results.

III. WITHIN-PLOT SPATIAL INTERACTIONS

A. EFFECTS OF PLOT SIZE

The square 0.01 hectare plot used in the original version of JABOWA appears to adequately simulate the growth of northeastern U.S. forests. For southern U.S. forests, however, JABOWA was modified to simulate growth on a 0.08 hectare circular plot, an 8-fold increase in area, to accommodate an increase from 13 to 33 tree species (Shugart & West, 1977). Shugart and West's model, "FORET", was in turn modified by Hemstrom and Franklin to simulate forest succession in the Pacific northwest, in the "CONIFER" model (Trimble & Shriner, 1981, p. 43). Hemstrom

also collaborated with Adams on the "CLIMACS" model, in which the circular plot was enlarged to 0.2 hectare, or 20 times the Hubbard Brook plot size, to accommodate such large species as *Pseudotsuga menziesii* (Hemstrom & Adams, 1982; Dale & Hemstrom, 1984).

While plot size used in forest growth simulators has tended to increase, reflecting movement toward greater realism and the availability of faster data processing, the reverse trend has obtained in the resolution of remote sensing instrumentation. (Figure 1). We can now study remotely-sensed images composed of pixels corresponding to areas as small as 30 x 30 m with a fair measure of confidence as to pixel location. It thus appears that employing a plot size at or near the intersection of these two trends would be a practical and logical beginning for adding spatial interactions to JABOWA. Presently, that intermediate plot size is approximately 0.1 hectare, or ten times the original plot size of JABOWA.

The utility of a plot size of 0.1 hectare in modeling is supported by the studies of Shugart and West, who investigated the effects of plot size on the dynamics of a deciduous forest stand growth model (FORET). They found that individual trees could not grow to maximum size on a plot less than 0.04 hectare in area. Also, gap-phase replacement was poorly simulated on plots of 0.20 hectare and was absent on plots of 0.40 hectare, since the reduction in competition due to the death of a single tree is negligible when diffused over a plot of this size (Shugart & West, 1979).

Empirical analysis of plot size also points to the utility of 0.1 ha plots. Bormann (1953) found that plots of about 0.05 ha two 0.14 ha gives the best estimates of composition for tree vegetation. However, a single plot size is unlikely to give equally accurate information about all tree species.

Given a plot size of 0.1 hectare, how representative of the larger forest will samples be? One way of determining the efficacy of plot size is to plot a species-area curve. If there is a log-series distribution of species abundances and the area sampled is large, then the number of species per quadrat will be proportional to the logarithm of quadrat area (Pielou, 1977). This species/log area model has been modified by Kobayashi (1975) to yield a regression passing through the origin, i.e., no species at zero area.

From species-area curves, one can estimate the "minimal area", the smallest sample that contains all of the species of some minimum importance in a community. For temperate zone forests, empirical values of 200-500 m² have been given (Mueller-Dombois, 1974), so a plot of 0.1 ha satisfies the minimal area requirement (Figure 2).

Plots of 0.1 ha have been widely used by ecologists in studies of vegetation pattern; Rice and Westoby (1983) summarize measurements of plant species richness for this plot size for a number of sites throughout the world. Temperate closed-canopy forests usually have less than 50 species per 0.1 ha, most of these being shrubs or herbs. Often, 0.1 ha plots contain fewer than 10 tree species. Both the calculations of the forest model and the classification of the remote sensing imagery should be simplified because of this low number of species.

How useful will a plot size of 0.1 ha be for studying forest pattern? This will depend upon the degree of heterogeneity of the forest and its pattern or "grain". If the plot size is much larger than the "grain", pattern information will be lost; if the plot size is much smaller than the grain, the model may be needlessly complex. Available information and expert opinion suggest that a 0.1 ha plot is appropriate for study of vegetational patterns of interest in most forest vegetation. It is also near the practical limits of resolution of satellite remote sensing instruments.

B. EFFECTS OF PLOT SHAPE

In building a spatial model, plot shape might also be important. A square plot mandates only four nearest neighbors, so that interactions at the corners are problematic. Bormann (1953) determined that long rectangular plots give the best estimate of composition of the tree strata of some forests, but for best results, plots must be properly oriented with respect to patterns of variation in the environment and vegetation. Rectangular plots, especially elongate ones, lead to high likelihood of error due to edge effect. This can be reduced by using circular plots, since the perimeter is reduced relative to the area. Circular plots may also serve well in collecting field data. However, they present topological problems since they join neighboring plots only at single points.

The most useful shape for modeling plot interactions might be hexagonal,

with six nearest neighbors; or as an approximation, a hexagonal array of square or circular plots which functionally ignores the intervening space. For sampling North American boreal forests to obtain "ground-truth" for remote sensing studies, we have employed an array of 5 circular subplots that total 0.1 hectare, arranged in a circular plot of 60 m diameter (Figure 3). This array will be useful in testing spatial modifications to JABOWA.

C. OTHER SPATIAL CONSIDERATIONS

The success of existing versions and modifications of the JABOWA model suggest that the model is robust in relation to plot shape and other spatial considerations within a plot. Adding details such as the location of individual trees within a plot relative to one another greatly increases the resolution of the model (from a plot size resolution to an individual tree resolution). However, our experience shows that modeling forest growth at the individual tree level adds great complexity while providing little increase in realism concerning population, community, and ecosystem characteristics. Therefore, this should be the last focus of activities.

IV. PLOT INTERACTIONS

A. RECRUITMENT

A crucial simplifying assumption of the JABOWA model is that the availability of seeds of any species in a plot is independent of the trees on that plot. Since the model and its modifications have been generally successful in reproducing realistic temporal dynamics of forests, it is not at all certain that it will be necessary to change this assumption when geographic models are developed. Aside from direct competition for water, light and chemical elements among neighboring trees, the coupling between individual tree performance and population size and distribution in a forest stand is weak. Allen and Shugart (1983) suggest that the robustness of JABOWA-based models is due to implicit incorporation of such coupling as exists.

We suggest that spatial modeling of forests should be developed in stages, testing alternative hypotheses regarding spatial interactions, following the scientific method in always moving from the simplest assumptions to more complex assumptions, only as the more complex ones are necessary. A first step might be a version of JABOWA which is spatial only in that plots are located spatially as on a

LANDSAT scene, so that their relationship to one another and to spatial variations in topography, geology, hydrology, and soils are evident, but without interactions among plots. This would represent a first-level spatial model.

The second-level spatial model would add the influence of existing mature trees on recruitment. The first version of this model would make reproduction a function of the availability of seed-producing trees within a plot. This model would have a high probability of reaching extinction of all tree species since stochastic loss of a species would cause its permanent loss. The second version would make reproduction within a plot a function of the availability of seed-producing trees in some neighborhood of plots. The neighborhood size required to maintain long-term persistence of all species would be an important result of this version of the model; this result could be used to guide spatial coupling in future versions.

If the introduction of spatial variation in seed availability does not succeed in reproducing forest pattern, it may be necessary to further modify the recruitment model. Particularly in relatively stable forest communities, the seed source is probably almost constant and species diversity and population pattern are more strongly influenced by canopy-understory interactions. Thus, a third version of the recruitment model should include species-specific canopy tree influence on the fates of seedlings and saplings. Implementing such a model would necessitate species-specific knowledge of canopy-understory dynamics, for sapling abundance alone is seldom indicative of replacement success (Horn, 1981).

In the case of replacements of shade-tolerant, co-dominant species by one another, studies of sapling location alone may be sufficient to ascertain the probability that a tree of one species will be replaced by a sapling of the other species. (Woods & Whittaker, 1981) For more complex canopy gap dynamics, it may be necessary to alter the recruitment model to reflect either estimates of the transition probability from each gap-creating species to each available species, or estimates of total (multi-species) canopy influence on saplings of each species (e.g., Runkle, 1979; Woods, 1984).

B. ENVIRONMENTAL INTERACTIONS

A third-level spatial model would incorporate environmental interactions among plots. The most important environmental factor to consider would be water transport. In JABOWA, direct precipitation is the sole input of water to a plot and water storage and runoff are calculated based on soil type, soil depth, and temperature. A more realistic water balance could be achieved by keeping track of water movement between adjacent plots. In this approach, topographic and geologic influences on surface and subsurface water flow would become a part of the model. It would seem that the inclusion of such hydrologic--biologic spatial interactions would be necessary for realistic projections of the influence of forest vegetation on water runoff; however, our experience with the JABOWA model suggests that considerable simplification may be possible.

The next plot interaction to implement might be shading among adjacent plots. With 0.1 ha plots, tall trees on neighboring plots could easily block a significant amount of sunlight. For stands of smaller trees, this influence would diminish but might still be of importance in the suppression of shade-intolerant species. Moreover, slope and aspect will augment the shading effect of one plot upon another.

C. ADDITIONAL PLOT INTERACTIONS

Additional environmental factors which might produce interdependence among plots include: 1) snowmelt and drifting of snow; 2) the effects of climate and weather, such as windthrows upwind of a plot; 3) fire patterns, as influenced by topographic and geographic features; and 4) effects of pathogens and herbivores.

Some modeling has been done of fire spread and the spread of pathogens and insect pests in forests. In general, such models have used a lower level of resolution than the JABOWA model--cells in such models are a forest type, but individual stems are not identified, nor their size taken into account. An area of investigation in the future will be to examine the resolution of models required to consider these factors as they influence subsequent forest growth; it is not clear at this time whether the more highly-aggregated, lower-resolution models are sufficient, or whether a JABOWA-type model would be necessary. The best approach would be to pursue parallel lines of investigation.

The effects of acid rain and other air pollutants on forests have been modeled to some extent; JABOWA-based models have been used in a limited way to consider pollution effects. For example, JABOWA was used to estimate effects of CO₂ enrichment; the "FORTNITE" model added litter accumulation and soil nitrogen availability to the JABOWA program to investigate the effects of acid precipitation; and the "SILVA" model was developed to study the effects of SO₂ pollution (Botkin et al., 1973; Aber et al., 1982; Kercher & Axelrod, 1981). Again, spatial factors were not considered, and it is not clear at this time whether spatial distributions of the pollutants themselves need to be considered in making projections of the effects of pollutants on forest growth.

V. SUMMARY

In this paper we have discussed the need for models of forest growth that can be used for projecting forward from geographic-based information about forest stands, including information from remote sensing devices such as LANDSAT. Such models can be used to investigate classical ecological questions about the nature of communities and spatial patterns in vegetation. A forest sample plot size of 0.1 hectare is proposed as both ecologically appropriate and consistent with resolution available from remote sensing devices. We have suggested a series of steps proceeding from existing models, with spatial considerations added one by one, that would allow identification of those spatial details necessary for successful modeling of a forest which exhibits geographically-correlated pattern.

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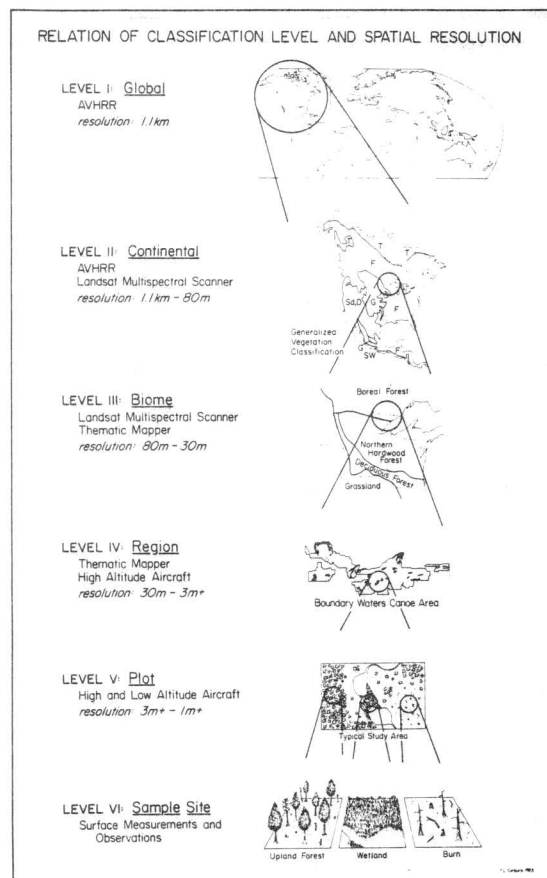


Figure 1: Hierarchical measurements needed for remote sensing techniques, from current work in Minnesota's Superior National Forest. Each site contains a circular plot 60 m in diameter for helicopter remote sensing. Following ground measurements and remote sensing from low-altitude aircraft, larger-scale measurements are next taken and tested from higher-altitude aircraft (Botkin et al., 1984).

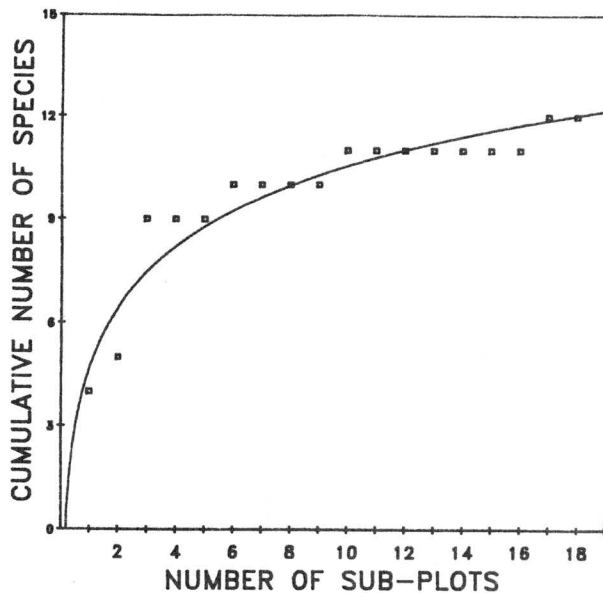


Figure 2: A species-area curve for stands of young (about 15 yr) aspen-dominated upland deciduous forest in the Superior National Forest of Minnesota indicates that the minimal area is less than 0.1 ha. The horizontal axis shows cumulative number of sub-plots (sub-plots are circular with radius of 6 m and total area of about 113 m²). The vertical axis is cumulative species richness. The 18 sub-plots are located in two 30 m radius plots in adjacent stands.

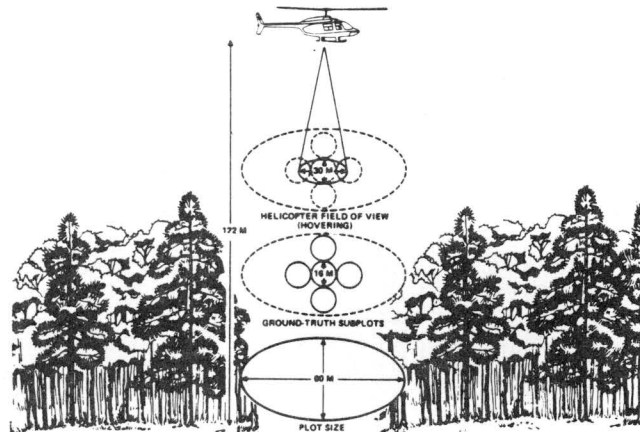


Figure 3: Within each 60 m diameter plot, five sub-plots were laid out, and tree stems were mapped, along with sub-canopy and understory vegetation. Spectral data for these stands were collected from a helicopter hovering approximately 120 m above the stand. The field of view of helicopter-mounted instruments is 30 m in diameter, corresponding to the pixel size of the Landsat Thematic Mapper.

AUTHOR BIOGRAPHICAL DATA

Daniel B. Botkin obtained his Ph.D. at Rutgers University, after which he joined the faculty of Yale University's School of Forestry and Environmental Studies. Dr. Botkin is now Chairman of the Environmental Studies Program and Professor of Biology and Environmental Studies at the University of California, Santa Barbara. He specializes in ecological research of wilderness areas. His current research emphasis is the study of the biosphere and has been supported by the National Science Foundation, the National Aeronautics and Space Administration, and the National Oceanographic and Atmospheric Administration. For more than a decade, Prof. Botkin has advised federal and state governments about the management of our natural resources, scientific research on wilderness, endangered species, and the use of satellite remote sensing for earth resources research. He is a member of the National Academy of Science's Space Science Board, which advises NASA about space research.

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