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SPATIAL PATTERNS OF EARLY FOREST SUCCESSION FOLLOWING HARVEST IN LOOKOUT CREEK BASIN, OR

by

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INTRODUCTION

In the Pacific Northwest, rapid harvesting of forested lands has been offset by natural regeneration and planting of these areas. Early succession following wildfire in the Oregon Cascades region generally proceeds through stages of herbs and grasses and then broadleaf shrubs and seedlings before reaching young dense-crown Douglas fir (Franklin and Dyrness, 1988). Early succession following commercial harvest usually follows a similar track, but often at more extreme rates; examples of highly accelerated and severely stagnated stands are often found on managed lands (Perry et al., 1989).

Succession is the "orderly process of community development that is reasonably directional and, therefore, predictable." (Odum, 1969) The ecological role of succession after a disturbance is to establish progressively more stable and resilient plant communities on a site. Although the order of potential vegetation transitions on a site can be predicted, with larger growth forms replacing smaller ones, the rates and specific trajectories of succession vary considerably among communities. Neighboring communities often converge or diverge in their development. Harvest units planted with conifer seedlings still diverge considerably in development due to a variety of external factors.

The trajectory of forest succession after harvest is affected by factors at many different spatial scales (Frelich and Reich, 1995). Important factors at the scale of individual communities include seed source and severity of disturbance (Halpern and Franklin, 1990). Clearly, however, factors at larger scales have the potential to constrain the effects of these site factors. Topography and land management are two examples of watershed-to-regional scale factors that can directly or indirectly influence the setting for community development.

There is a growing demand for landscape-scale information on successional trends and the factors that contribute to divergence of post-harvest trajectories. Spatial models are increasingly being used for regional planning and research efforts, including future estimates of biodiversity and biogeochemical fluxes. Many such models require estimates of future forest status for individual elements of the landscape, requiring data on the projected rate and pathway of succession (Hall, 1990). For example, the overall carbon budget for a forested area is dependent on the age-class distribution of the forest; different rates of conifer establishment produce different measures of carbon flux over time, and therefore the rate of growth is an important input to models of future carbon flux (Harmon et al., 1990).

The general objective of this project was to test a method to document rates and pathways of early succession and investigate potential predictive factors on a landscape to regional scale. The method incorporates remote sensing, vector Geographic Information Systems (GIS), and raster GIS modeling. Similar projects have been conducted elsewhere with success. Hall et al. (1991) compared two dates of classified Landsat imagery and calculated probabilities of transition rates between successional states. Potential explanations for the spatial pattern of successional transitions were offered, but associations were not quantified. White and Mladenoff (1994) used a vector (polygon) GIS approach in their investigation of successional transitions in northern Wisconsin. The authors used historical and modern vegetation maps to document transitions in vegetation cover over a 120 year period, calculate transition probabilities, and formulate hypotheses for controlling processes, including landforms and history of ownership. With both of these methods, future forest composition can be easily estimated through transition probabilities. Since transition rates are estimated for the landscape as a whole, however, the future of individual stands cannot be predicted. Also, due to this lack of locational information, associations between rates and pathways of succession and explanatory factors can not easily be quantified.

The specific objectives of this project were (1) to verify the existence of divergent trajectories of early succession in post-harvest communities in the H.J. Andrews Experimental Forest and map their distribution, (2) to quantify associations between environmental and treatment factors and successional trajectories on a landscape scale, and (3) to evaluate the usefulness of generalized spatial databases for investigating these questions. The study focused on the first forty years of growth after harvest.

BACKGROUND

1. Definitions of scale

Many qualifiers of scale are used in this paper, including community, stand, site, unit, watershed, subbasin, basin, landscape, and region. These terms have no specific measure of area attached to them. Scale can be represented quantitatively, however, by two measures: grain (resolution) and extent. The scale of this study, for example, is a function of the smallest homogeneous unit (30 meter pixels) and the study extent (4,400 hectares). The spatial patterns in succession rates observed are intrinsically a function of these parameters.

Generalized scale qualifiers (such as stand, watershed, region) have developed because they have proved useful for various sciences. Patterns of phenomena have repeatedly been observed within the extents of these general landscape features; they often mark the boundaries between "closed" systems, due to confinement of ecological interactions (Swanson, et al. 1988).

When these terms are used in a particular study, however, they need to be explicitly defined. In this study, regional-scale refers to patterns in phenomena within major landform units, such as the Western Cascades of Oregon. Landscape-scale refers to patterns within a land area that includes several interacting ecosystems, generally hectares to square kilometers in extent (Turner, 1989). In this paper, the HJA is a landscape. Watershed-scale refers to patterns within 50-100 hectare watersheds within the study area. Stand, site, and community-scale refer to patterns below the grain of 30m pixels up to approx. 5 hectares.

2. Study area

The H.J. Andrews Experimental Forest (HJA) study site is in the western Cascade Range of Oregon, where it fully occupies the 15,800-acre drainage basin of Lookout Creek (Figures 1, 2). The basin is part of the Willamette National Forest. Elevation ranges from 410 to 1630 meters above mean sea level. Lower elevation forests are dominated by Douglas-fir *(Pseudotsuga menziesii)*, western hemlock *(Psuga heterophylla)*, and western redcedar *(Thuja plicata)*. Upper elevation forests contain noble fir *(Abies procera)*, Pacific silver fir *(Abies amabilis)*, Douglas-fir, and western hemlock. Common low-medium elevation seral/understory species are big leaf maple *(Acer macrophyllum)*, vine maple *(Acer circinatum)*, swordfern *(Polystichum munitum)*, rhododendron *(Rhododendron macrophyllum)*, Oregongrape *(Berberis nervosa)*, and salal *(Gaultheria shallon)*. Common high elevation seral/understory species are huckleberry *(Vaccinium membranaceum)*, beargrass *(Xerophyllum tenax)*, and vanillaleaf *(Achlys triphylla)* (Franklin and Dyrness, 1988).

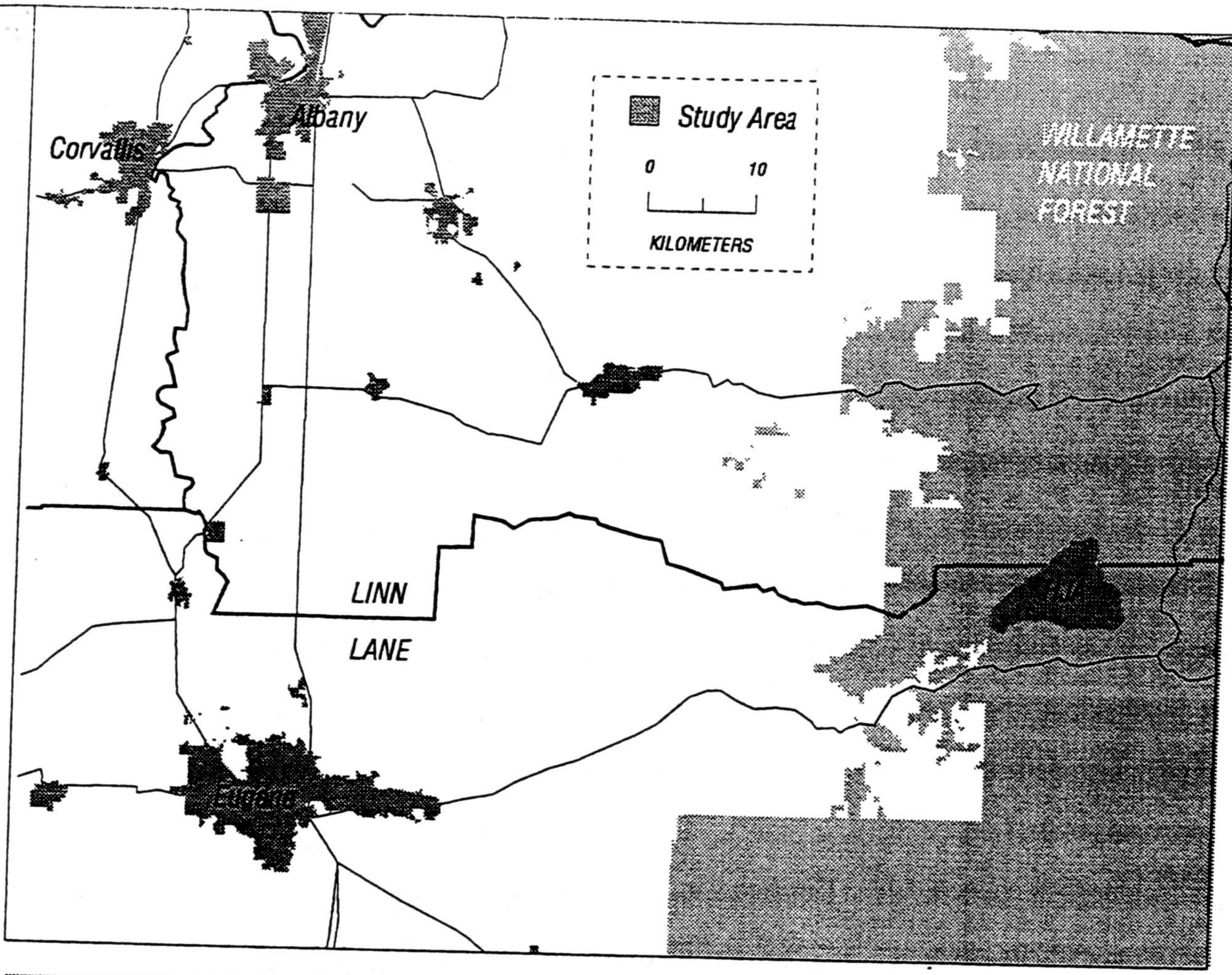


FIGURE 1

Study area location

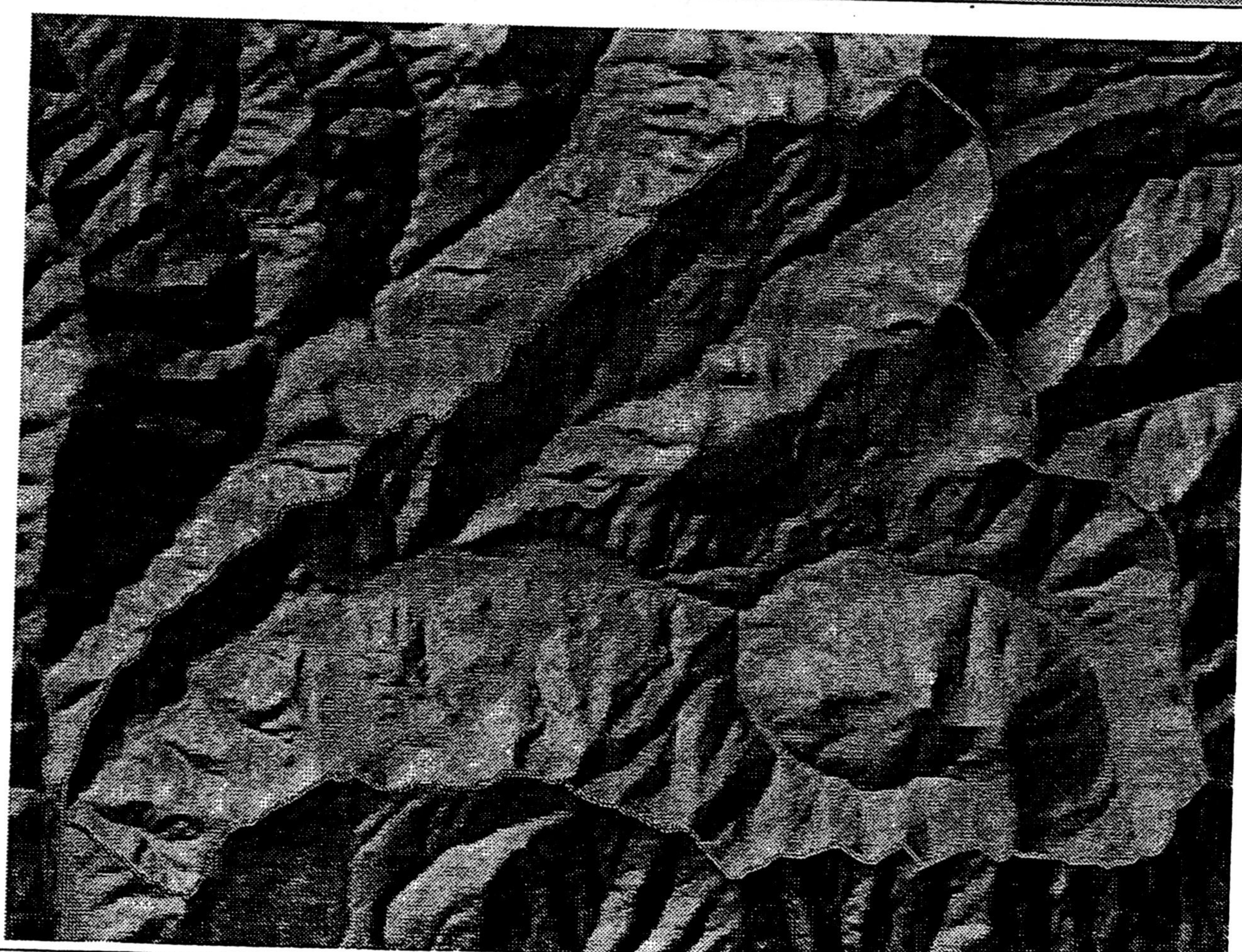


FIGURE 2

30m Digit Elevation Model (DE hillshaded 315 degre azimuth, 45 degree altitude

Just over 25% of the HJA has been harvested since 1950 in 150 units ranging from .5 to 92 hectares in size, averaging 10 hectares in size. Cutting progressed from primarily low elevation sites in the 1950's and 1960's to higher elevation sites in the 1970's and 1980's. Over 20% of the harvesting and 80% of the road construction occurred before 1970 (Jones and Grant, 1996). The most common management treatments used in HJA cutting units were to clear-cut the area, and then broadcast burn the site to prepare it for planting (McKee, 1996). Most units were planted with seedlings within a few years of burning, but about 7% of the area (7 units) was left to regenerate naturally. Pre-commercial thinning has taken place on many units.

Landscape-scale successional trends have not previously been investigated in the HJA. Long term study plots exist in scattered stands of different ages around the forest, but they are limited in size and distribution. Halpern and Franklin (1990) compared general post-harvest successional trends within two watersheds over a 20 year period, and determined that pre-disturbance community and burning intensity (soil disturbance) significantly affected the course of succession at their scale of analysis (192 2m x 2m plots scattered over a total of 120 hectares). The authors suggested that between-watershed differences might be explained in part by differences in larger scale environmental conditions. At a landscape scale, Fiorella and Ripple (1993) investigated spectral response of well regenerated and poorly regenerated stands throughout the HJA, and determined the usefulness of Landsat TM data, which has a 25m grain, for differentiating among early successional cover types in the region.

3. Factors influencing succession

There are many different conceptual and mechanistic models for the process of succession. The conceptual model utilized in a study of succession affects the selection and interpretation of potential explanatory factors. Halpern and Franklin (1990) determined that the communities they observed in the HJA were operating under the model of initial floristic composition, and the mechanisms of tolerance and inhibition. In this model, changes in community composition over time are attributed to differences in initial abundance, growth rate, and longevity of species. Other models of succession include those based on concepts of floristic relays and facilitation, where earlier stages of vegetation modify their environment and facilitate establishment of subsequent stages (Pickett et al., 1987).

Four explanatory factors are considered in this paper; three are environmental (elevation, slope aspect, and topographic convergence), and one is a treatment (planting). These variables do not influence succession directly. Direct environmental influences on succession include moisture, temperature, light, chemicals (soil nutrients), and physical influences such as frost, wind, and animals (Cleary et al., 1978). These factors influence the composition and survival of residual and invading species. They also influence planted seedling survival, and the potential for low or high ecological resiliency after the disturbances of harvesting and site preparation. Planting conifer seedlings can dramatically affect the path of succession in a community in that it prematurely introduces later successional species, and increases competition in the community for light, moisture and nutrients.

Topographic variables are indirect measures of environmental influences; they are rough covariates with direct factors. They are often used in spatial modeling, however, because they are easier to estimate on a regional scale. As elevation increases, air and soil temperatures drop, length of growing season decreases, damage to vegetation from wind and snow increases, and moisture from orographic precipitation increases. There is also evidence that at higher elevations, soil biology is more sensitive to disturbance; processes associated with harvesting and site treatments can shift the balance of soil microorganisms from primarily fungal to bacterial, which can lead to a downward spiral in soil conditions, and effectively a sort of reverse succession (Perry et al., 1989; McKee, 1996). Aspect is correlated with daily solar radiation, which indirectly affects temperature and soil moisture. In these latitudes, radiation loads and temperatures are higher on south aspects than on north aspects. At high elevations, minimum soil temperatures on south slopes can be higher than the maximum temperatures on north slopes (Cleary et al., 1978). The Topographic Convergence Index is a function of slope and topographic position that is theoretically representative of soil moisture. The TCI is calculated by the following formula:

$$\ln(\partial / \tan\beta)$$

where ∂ is the accumulated upslope area for a given unit, and β is the slope angle. A high value of TCI indicates wet soil. Soil is shallow on steep slopes and on ridgetops, and therefore often limited in moisture. As slope decreases and/or accumulated drainage area increases, as in a floodplain area, the level of soil moisture increases (Cleary et al., 1978).

The competition a young conifer seedling might receive from shrubs and hardwoods is predictable in part through knowledge of the pre-existing community structure. In their studies on watersheds 1 and 3, Halpern and Franklin (1990) determined that initially herb-rich communities maintained herb dominance until canopy closure began, initially shrub-dominated communities generally experienced a significant shrub phase, and initially tree-dominated sites progressed most rapidly towards canopy closure. Since plant communities are commonly arrayed along topographic gradients, topographic factors may be indirectly predictive of early successional pathways.

Method of harvest, timing of slash burning (spring vs. fall), and quality of conifer stock can all affect the nature of early regeneration on a landscape scale, but I did not test for these factors here. They may explain, however, patterns in early succession that the other factors do not explain. I hypothesize that many site-scale factors, such as seed source and soil disturbance intensity, are most likely affecting patterns of succession at scales smaller than the grain of the this study, or will not be captured with a generalized classification of successional rates.

METHODS

1. Data preparation

Three databases were used in the analysis: a 30m resolution U.S.G.S. Digital Elevation Model (DEM) (Figure 2), a classified 1988 Landsat TM satellite image (25m resolution) (Figure 3), and an ARC/INFO polygon coverage of harvest units in the HJA (Figure 4). All three coverages had been previously georeferenced and registered to each other at Oregon State University's Forest Science Laboratory, where this project was conducted. I did not attempt to quantify the quality of the registration. The coarsest resolution of the three coverages, 30m, was chosen for analysis, and the satellite image was resampled to this resolution using the nearest neighbor method (ESRI, 1992). The grain size (resolution) was chosen based on the smallest scale of variation observed in explanatory factors. All data were

Figure 3:

1988 VEGETATION

- Open
- Semi-Open
- Closed Mixed Hardwood/Conifer
- Young Conifer
- Mature Conifer
- Old Conifer

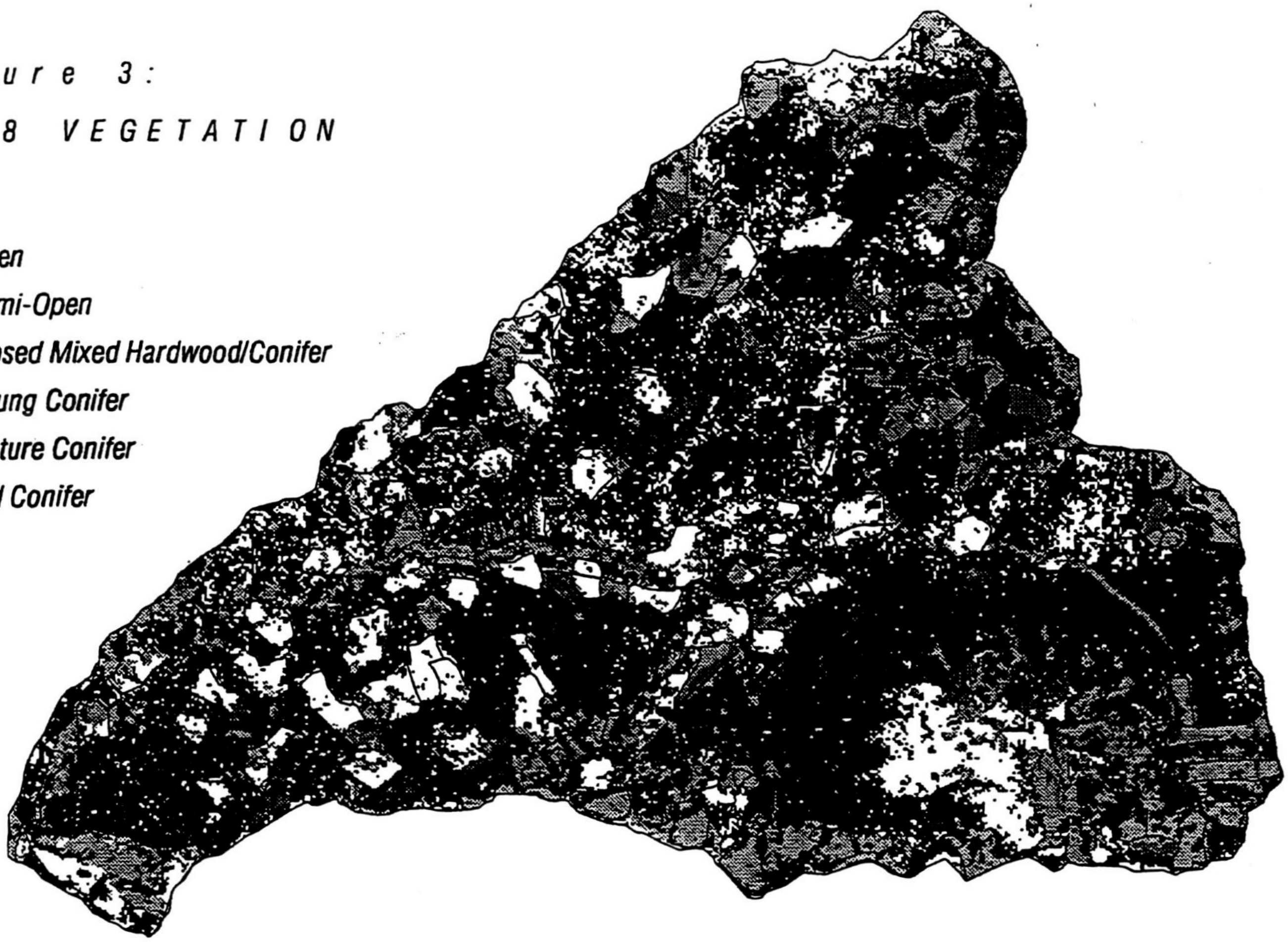
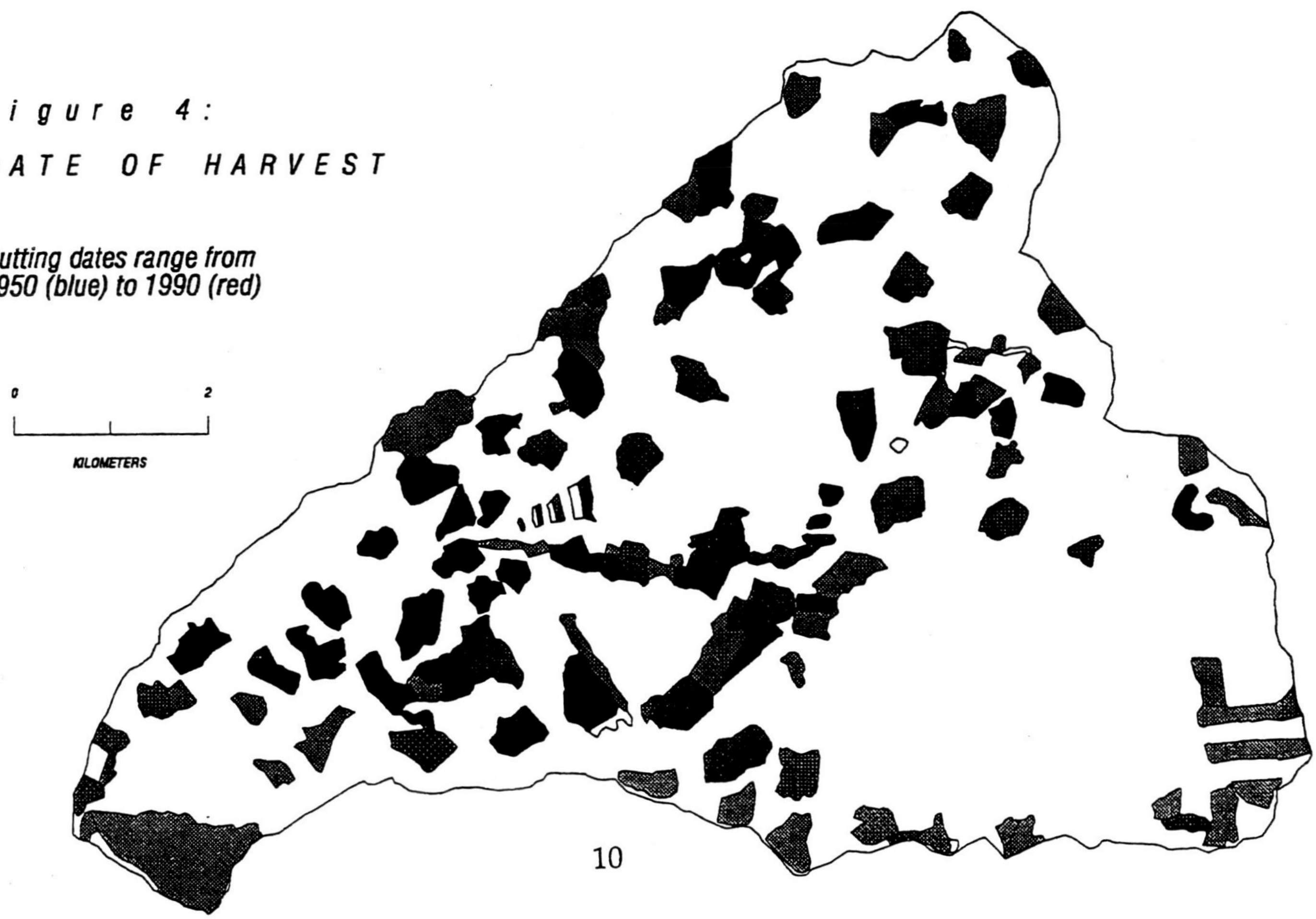


Figure 4:

DATE OF HARVEST

Cutting dates range from 1950 (blue) to 1990 (red)



converted into ARC/INFO GRID (raster) format for analysis. ARC/INFO Version 7.1 was used for all GIS operations and cartographic production.

The harvest unit coverage provided a template for the areas of the HJA. which are in the process of regeneration. The polygons were buffered inside one pixel width (30m) in order to avoid edge effects on the satellite image from surrounding trees and roads. Roads that entered into units that were visible on the satellite imagery, or were visibly affecting spectral response, were also removed from the template; these roads were isolated, buffered (30m), rasterized, and removed from the template grid. Along with being used for the template, the harvest unit coverage provided information on harvest date. Attributes on planting and thinning treatments were added to the coverage, and individual GRID layers were produced from the coverage representing each of these themes. The vegetation grid was checked visually for the influence of thinning on cover classification; only young conifer stands are extensively thinned, and if there were an influence on the reflectance values, these stands would be classed in a younger state, and should have been removed from the data set. No evidence of influence was observed, so thinned units were included in the analysis.

The satellite image, which covers a 1.2 million ha. area on the west side of the Cascade range, had been previously classified into twelve vegetation condition classes (Cohen et al., 1995). Only three of these classes were eventually used in this analysis: semi-open mixed hardwood/conifer (30-85% cover), closed mixed hardwood/conifer (>85% cover), and closed young conifer (<80 years). Low elevation (agriculture) and high elevation (lava parkland) classes were not present within the study area. Pixels classified as "mature" or "old-growth" conifer that fell within the clear-cuts were considered to be either trees left standing after harvest, or a result of positional or classification error, and were eliminated from the data set. The oldest cuts in the HJA. were only 38 years old in 1988, and therefore could not realistically be reaching these stages of growth. Landscape units classified as "open" were not considered because nothing could yet be said about their successional pathway; the few open areas that were not very recently cut (<6 years before the image was taken) were rock outcrops or other permanently open elements of the landscape.

The DEM was used for investigation of environmental influences on rate of succession. Three variables were derived from the DEM through functions in GRID (ESRI, 1992): elevation zones, aspect zones, and TCI. All DEM-derived variables were generalized into broad classes. Elevation was generalized to three classes (<900m, 900-1200m, and >1200m) corresponding to vegetation zones: western hemlock, Pacific silver fir, and mountain hemlock (Hemstrom, 1987). Aspect was generalized to four classes (N: 315-45°, E: 45-135°, S: 135-225°, W: 225-315°), and TCI to three (low, medium, high). The number of classes for each variable was chosen based on anticipated levels of variance in succession rates between classes. Total area for each class, within the HJA as well as within the cutting units, is displayed in Table 1.

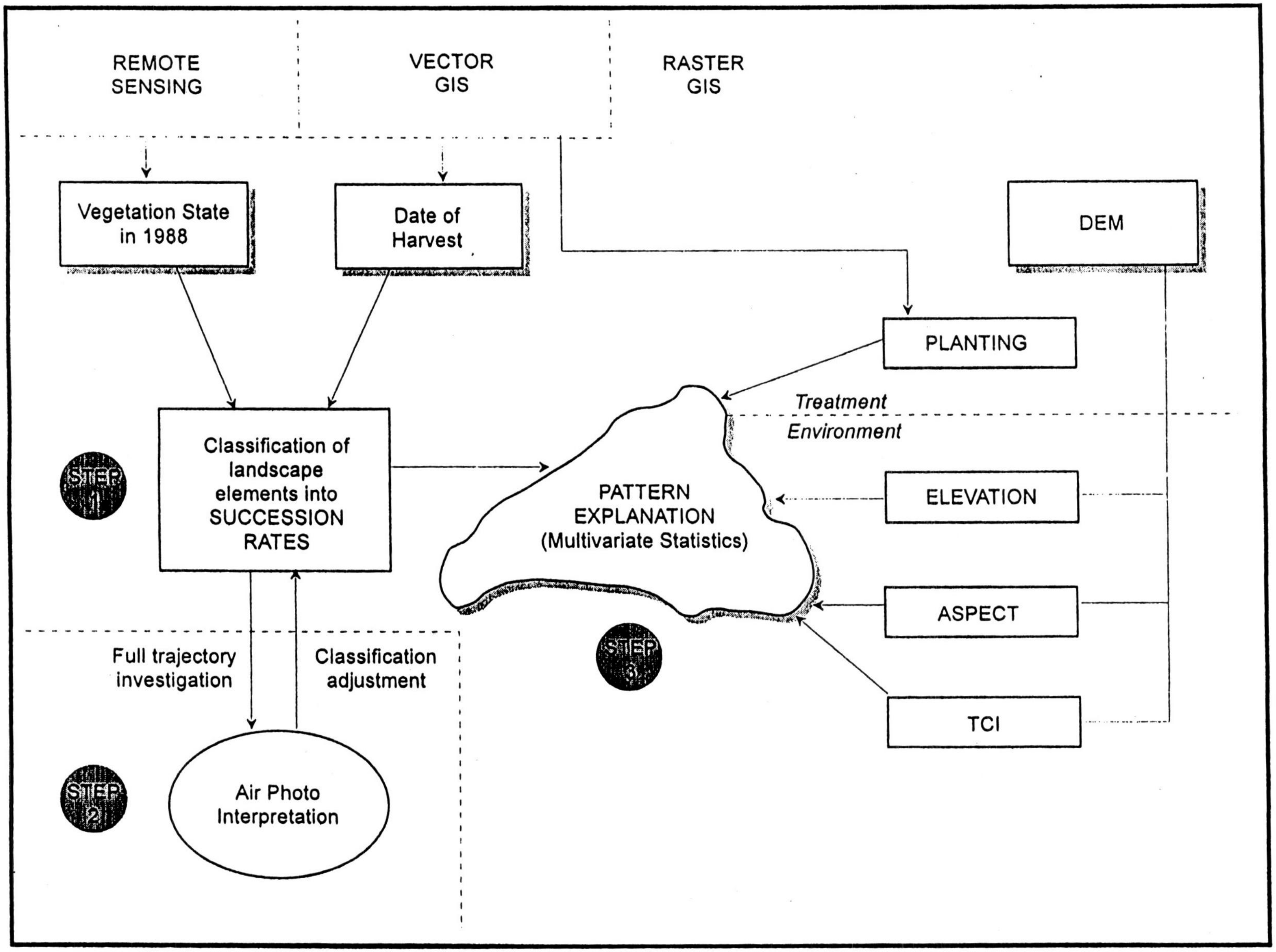
2. Classification into rates of succession

The three major elements of the project are shown in Figure 5. The first step in the project was to classify landscape elements (30m square pixel areas) in HJA. harvest units into rates of succession. Two data bases were used to determine rates: vegetation state (in 1988) and harvest date. These grids were combined, and succession rate classes assigned to each landscape element (pixel) based on their state of vegetation development in 1988 in relation to other elements of a similar age.

Table 1: Distribution of variable classes within region, study area, and samples. Values are percent area.

ELEVATION	LOW	MODERATE	HIGH	
HJA	42.72	33.04	24.24	
CUTTING UNITS	60.06	25.35	14.59	
SLOW SAMPLE	61.68	24.28	14.04	
FAST SAMPLE	61.95	24.16	13.88	
ASPECT	NORTH	EAST	SOUTH	WEST
HJA	28.69	11.59	29.58	30.14
CUTTING UNITS	28.71	10.96	32.63	27.71
SLOW SAMPLE	30.54	12.86	31.56	25.04
FAST SAMPLE	28.88	11.57	32.39	27.16
TCI	LOW	MODERATE	HIGH	
HJA	43.71	39.92	16.38	
CUTTING UNITS	42.06	39.16	18.78	
SLOW SAMPLE	41.71	37.39	20.89	
FAST SAMPLE	42.25	38.99	18.77	

Figure 5: Project flow chart



3. Investigation of full trajectories

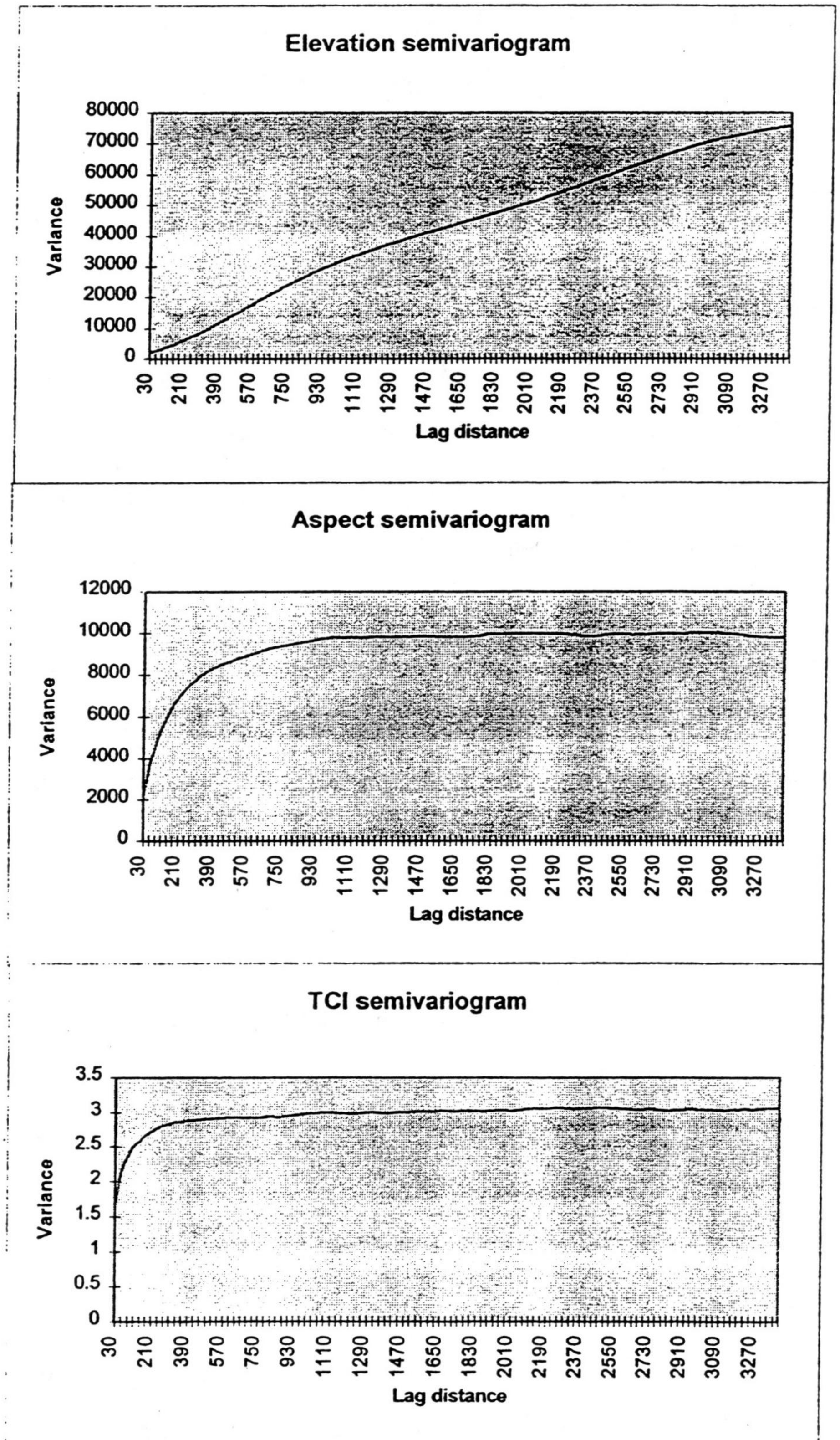
The rate classification was the result of a single-date observation of the units. To investigate the nature of the full successional trajectories of units, and be able to associate trajectory types with rates, I interpreted several air photo series' for sample sub-units (groups of four homogenous pixels) in different rate classes. I selected at least two samples each for every existing combination of rate class and vegetation state, and interpreted the successional state for each sub-unit at six different dates: 1959, 1967, 1973, 1979, 1988 and 1990. Sample locations were hand picked, rather than randomly selected, because of the need to sample homogeneous rate class clumps. Photos from 1959 and 1967 were black and white; photos from 1973, 1979 and 1990 were color. Photos from 1967 and 1973 were at a scale of 1: 16000; photos from 1959, 1979 and 1990 were at a scale of 1: 12000. 1988 photos were color infrared at a scale of 1: 62000. Four successional states were estimated: semi-open, closed mixed hardwood/conifer shrub, closed mixed hardwood/conifer trees, and young conifer. I decided to break down the "closed mixed" category for the air photo interpretation in order to investigate the amount of divergence that occurred within this category, as it is quite broad and includes several growth forms (sub-shrub, shrub and tree). The trajectories of sub-units in each rate class were then normalized to time since harvest, and averaged to smooth out the artificial dates of change created by static photo dates.

4. Explanation of spatial pattern

The third major step in the analysis was to quantify the associations, if any, between mapped successional rates and selected explanatory variables. Explanatory variables were tested separately for two general classes of succession rate - fast and slow - to see if different variables were important in producing different types of divergence. A binary grid was produced for each rate class; the class of interest was coded 1, and the remainder of the classes were coded zero. As a mask for extraction of data, random samples of approx. 1200 pixels (out of 6283) were taken from each rate class map. These grids were used as masks in GRID's SAMPLE function, along with grids for each of the explanatory factors - elevation, aspect, TCI, and planting. This GRID function produces an ASCII file with a value for every variable at every location in the mask grid (ESRI, 1992). I imported these sample files directly into SAS version 6.09 for statistical analysis.

The use of a random sample was necessitated by the occurrence of spatial dependence in mapped variables. Conventional linear (aspatial) tests of association assume independence of samples, which is violated by continuous spatial data such as a DEM. Spatial autocorrelation in elevation, aspect, and TCI within the study area is displayed in semi-variograms (Figure 6). In these plots, the point of interest is the range, or the value of lag distance where the plot levels out. This value indicates average size of a pattern; if samples are taken at a distance apart smaller than this value, they can be considered potentially spatially dependent. With these variables, at the scale considered, the range of aspect is approx. 500m and the range of TCI is approx. 300m; elevation displays a relatively constant gradient within this study area. Ideally, average sampling distance should be larger than the largest variable range. Due to the small size of my study area, however, this was not feasible. To minimize the problem of autocorrelation as much as possible, I sub-sampled from each rate class at a density just high enough to provide dispersion of samples across the landscape. Multiple random samples were taken for each model, and checked for a distribution across variable classes

Figure 6: Semivariograms calculated for environmental variables to determine optimum sampling distance. Lag distances, displayed here in 30m intervals, indicate distance apart of samples. The y-axis indicates the variance in sample values at that distance. The point at which the plot levels out (the range) is the scale of the spatial pattern in the variable.



that was similar to the distribution for the entire study area (Table 1). Only one subsample was then selected for each model.

I tested the null hypothesis that environment and treatments had no effect on rate of succession by calculating expected and observed percentages of area in each treatment class within a particular rate class, and assessing the significance of the difference between expected and observed using Chi-square tests of association. Chi-square statistics were estimated following Ramsey and Shafer (1993) as follows:

$$x = \sum (\text{Observed} - \text{Expected}) / \text{Expected}$$

Significance of the statistic is assessed from the proportion of values (p-value) from a chi-squared distribution on 1 degree of freedom that is greater than x . Significance was assessed between each individual variable and rate class.

Chi-square is a useful test for individual variables, but it does not test for covariance or interaction of variables, and I suspected that my data was displaying both of these phenomena. To investigate this, I modeled various combinations of explanatory factors using multiple logistic regression, following Hosmer and Lemeshow (1989). The dependent variable for these models was always binary - the presence or absence of slow or fast stands. The models were constructed using the GENMOD procedure in SAS with a logit link function and a binomial dispersion parameter (SAS, 1993). Linear regression was not an option due to the categorical nature of my data. Logistic regression uses the same general principles as linear regression, but fits a model based on maximum likelihood of an outcome, rather than on least squares (Hosmer and Lemeshow, 1989).

To determine the optimum combination of variables in each of my models, I calculated all combinations in every possible order, and evaluated the drop in deviance resulting from the addition of each successive factor.

The logistic regression models I constructed did not include planting as a factor because of missing interaction categories (i.e. no natural regeneration stands at high elevations); natural regeneration areas were removed from the data prior to model building, and only planted areas were considered.

RESULTS

1. Classification into rates of succession

The data distribution of vegetation state and harvest date for all pixels is shown in Figure 7. Stands which were young conifer in 1988 had a median harvest date of 1955, with harvest dates ranging from 1950 to 1982. Stands which had closed-canopy hardwoods or mixed conifer cover by 1988 had a median harvest date of 1962, with harvest dates ranging from 1950 to 1984. Stands with semi-open cover had a median harvest date of 1966, with harvest dates ranging from 1951 to 1987. Overlap in dates of harvest for different vegetation types suggested divergent rates of succession. Median dates of harvest for each vegetation state were used as class cut-off points for succession rate classes (Figure 8), providing a classification based on data distribution. For example, units that were cut before 1955 that were still in a semi-open state in 1988 were considered to be very slow (class 1). Six classes were initially determined with this method: (1)very slow, (2)slow, (3)expected/slow, (4)expected/fast, (5)fast, and (6)very fast (Figure 9). The histogram for this succession rate variable is shown in Figure 10.

Semi-open stands were never classified as fast or very fast, and young conifer stands were never classified as slow or very slow because these assumptions could not logically be made. Very few stands in this area spend more than a few years in a completely open state before establishing enough

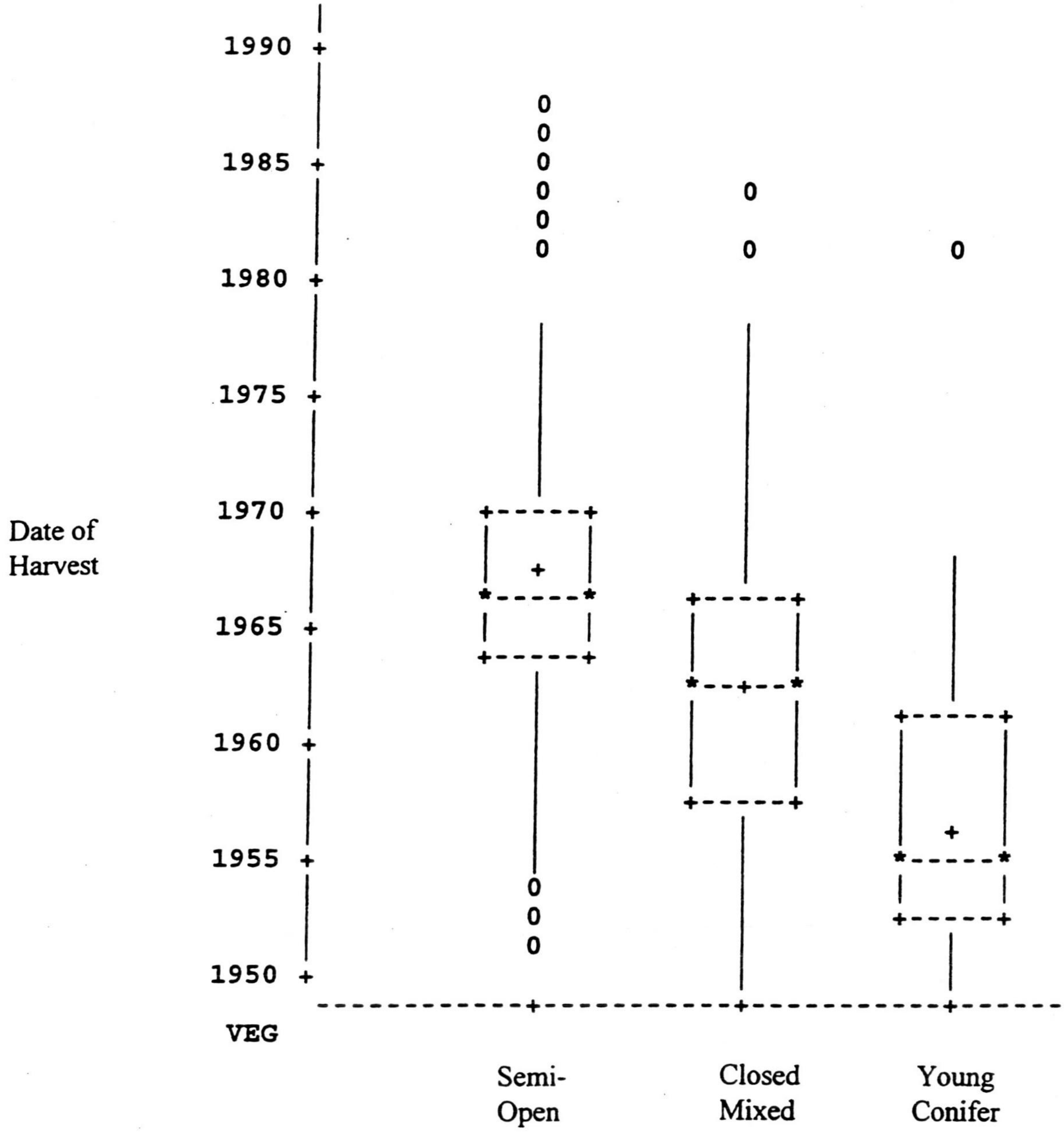


Figure 7: Distribution of harvest date by vegetation state in 1988 in the HJA. The median date of harvest for semi-open stands is 1966; for closed mixed stands, 1962; and for young conifer stands, 1955. Dates of harvest overlap considerably in the first interquartile range, suggesting divergent rates of succession.

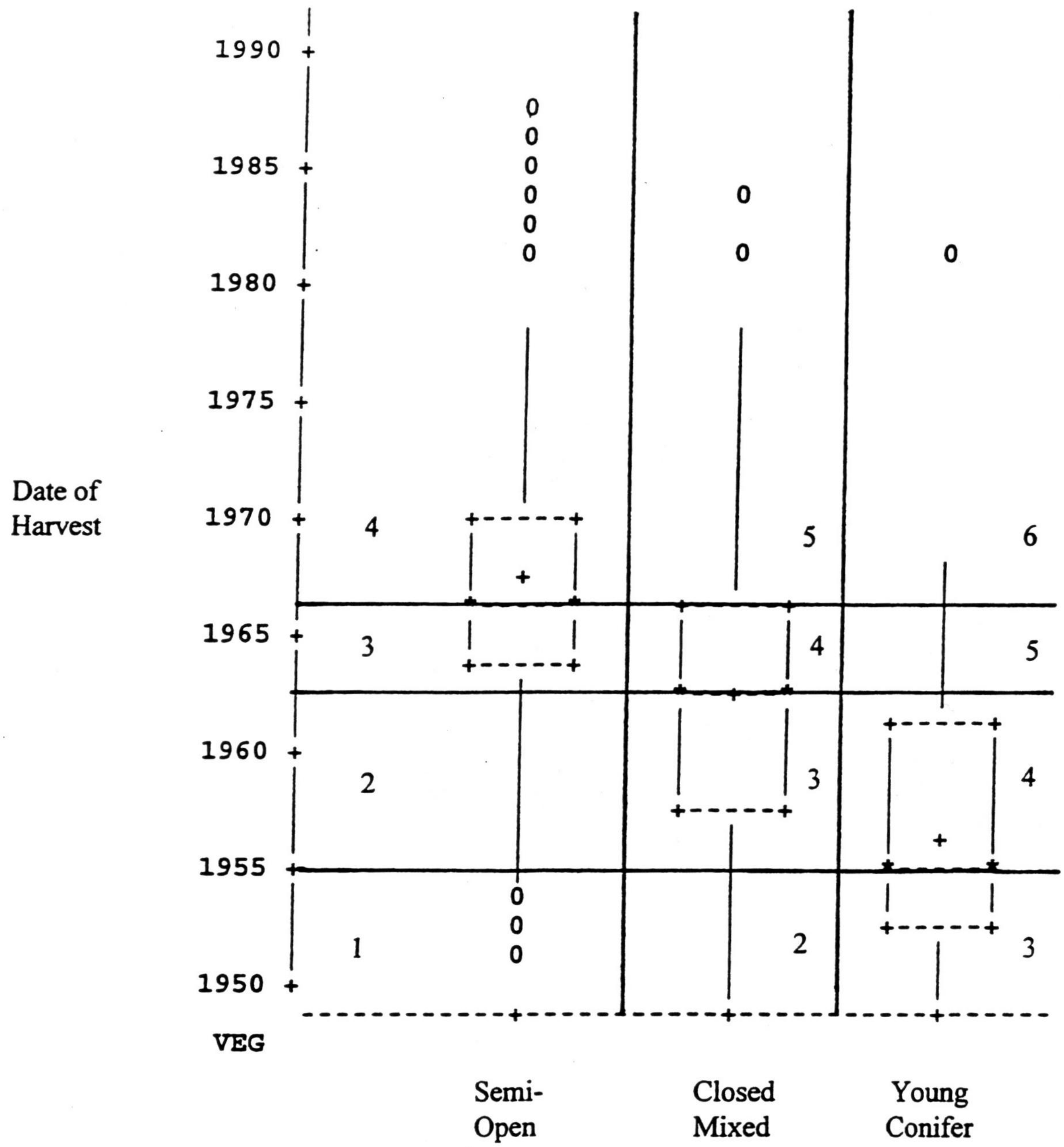


Figure 8: Rate classification assignment. Every 25m landscape element was assigned one of the following rate classes: (1) very slow, (2) slow, (3) expected/slow, (4) expected/fast, (5) fast, (6) very fast.

Figure 9:

SUCCESSION RATES

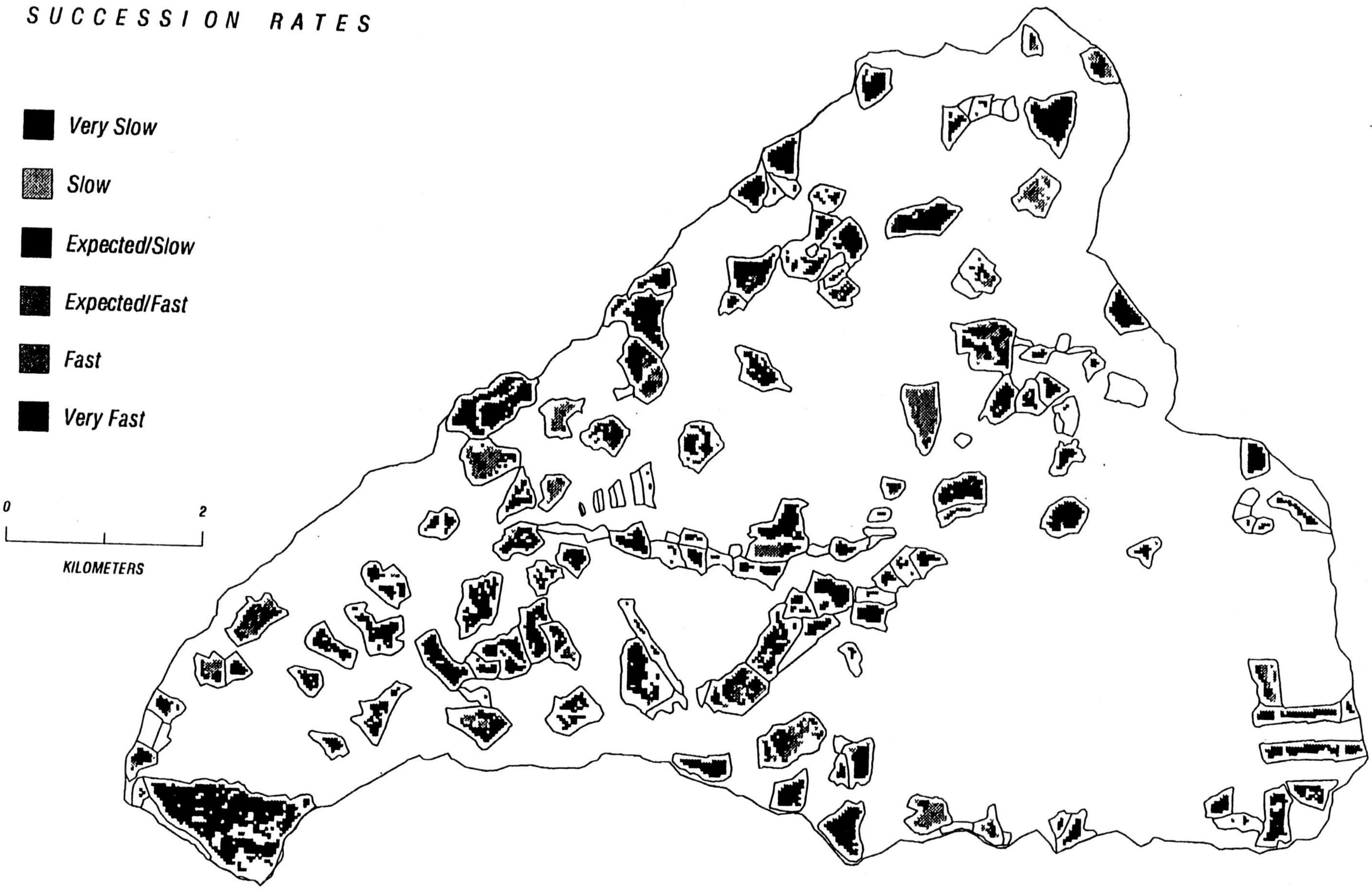
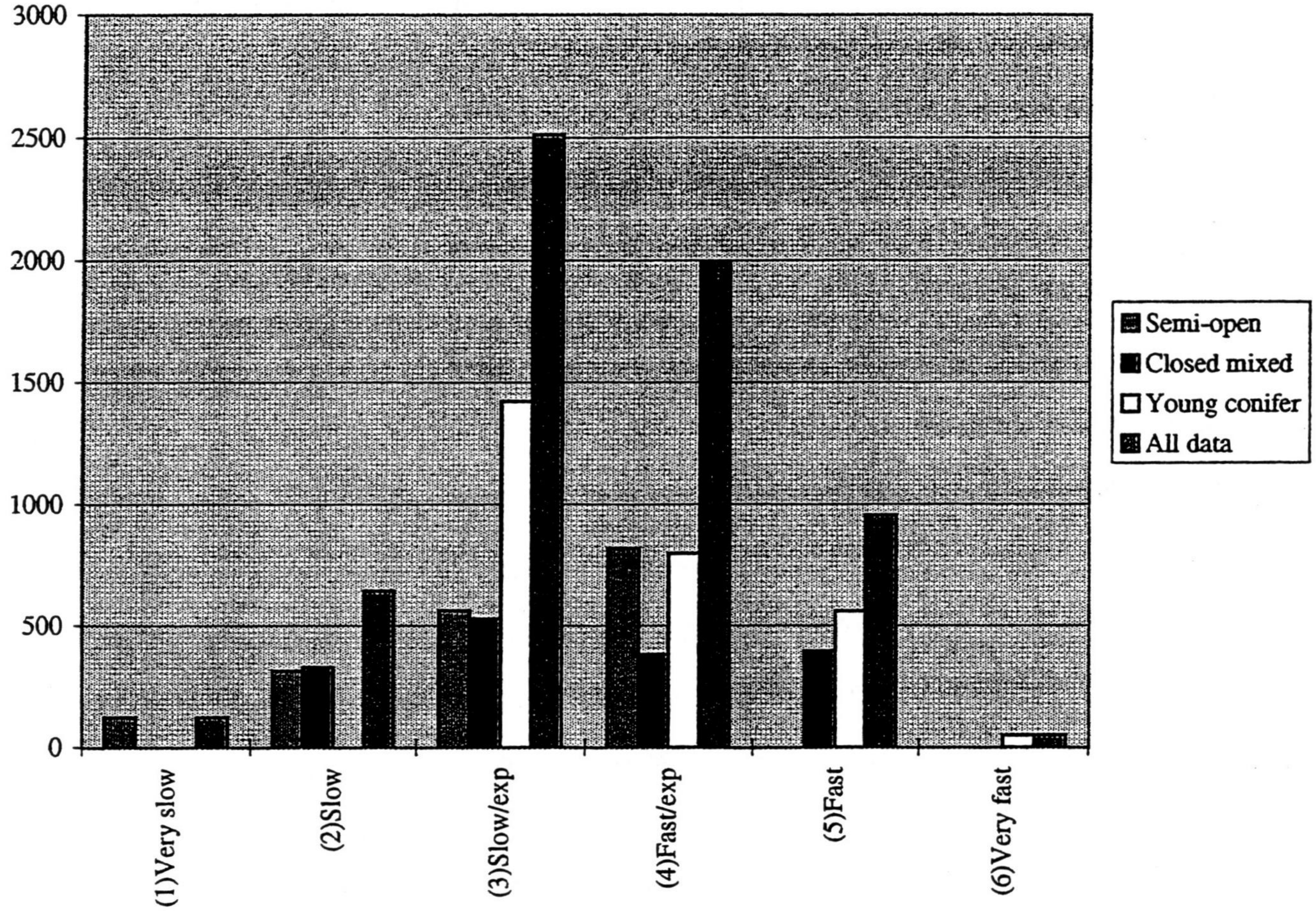


Figure 10: Histogram of succession rates in the HJA. The cover type categories represent vegetation state in 1988.



ground cover to be classified as "semi-open", and the observation time was not long enough to document transitions out of a young conifer state.

2. Investigation of full trajectories

A total of 27 stands were photo interpreted, at least two stands for each combination of rate class and vegetation state in 1988 (Figure 11). For example, areas classed as slow/expected could have been semi-open, closed mixed, or young conifer in 1988, so samples were taken for all these combinations (a total of six samples), whereas very slow areas were all semi-open in 1988, so only two samples were taken for this class. Three of the areas were classified in the 1988 image as semi-open, and were put in the slow rate class, but were actually closed hardwood shrubs and trees that were senescing or otherwise reflecting in soil-like spectral ranges and might have been placed in a different rate class if classified as closed mixed. The trajectories of these samples were eliminated from the full set prior to averaging of trajectories in specific rate classes, and two different samples were taken for this category.

The generalized trajectories appeared to be relatively distinct (Figure 12). However they did not appear to be distinguishable until about fifteen years after harvest, when most communities began to reach a closed canopy of hardwood shrubs while some stayed in a semi-open stage and others proceeded directly to young conifer. In general, the trajectories were of these three types. Due to a lack of samples in the most extreme categories (very slow and very fast), and the visual separation of trajectories into these types, the six original classes were collapsed into three (Figure 13). These trajectory classes –slow, average, and fast– were used for all subsequent analyses. The slow trajectory did not reach a young conifer stage, or even a closed canopy hardwood stage, within the observation time (35 years) but remained in a

Figure 11:

PHOTO INTERPRETATION SITES

Very Slow

Slow

Expected/Slow

Expected/Fast

Fast

Very Fast

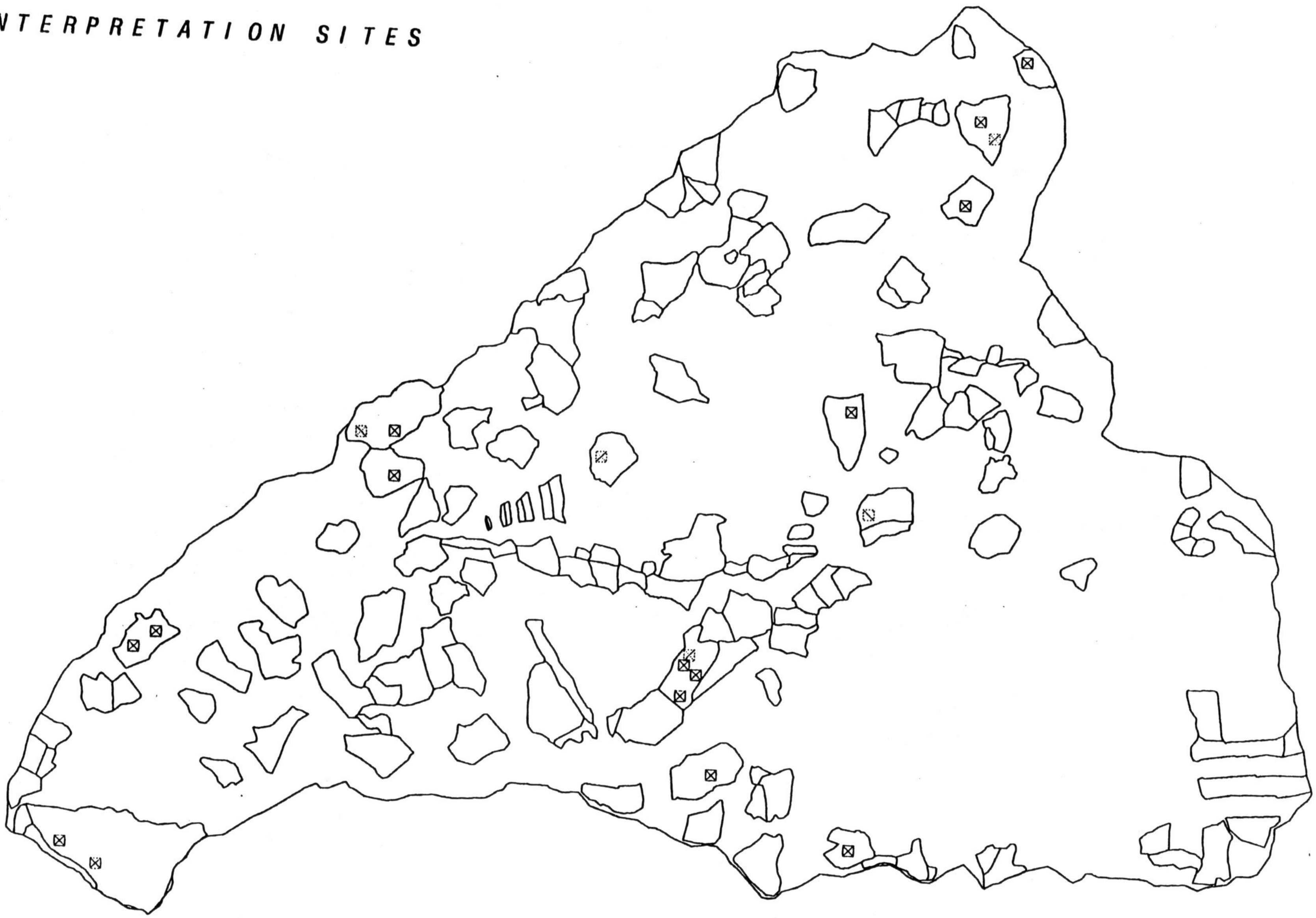


Figure 12: Individual trajectories from photo interpreted stands in specific rate classes were averaged to form these generalized trajectories. The successional states estimated were: (1) semi-open, (2) closed mixed shrub, (3) closed mixed trees, and (4) young conifer.

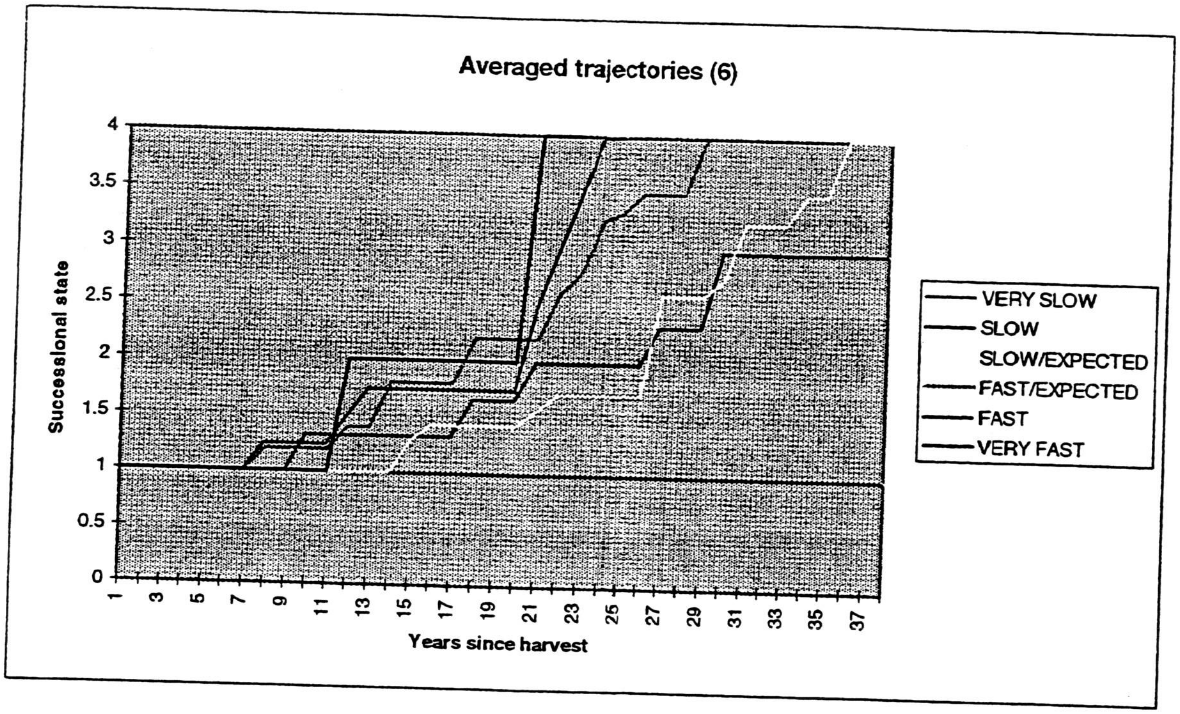
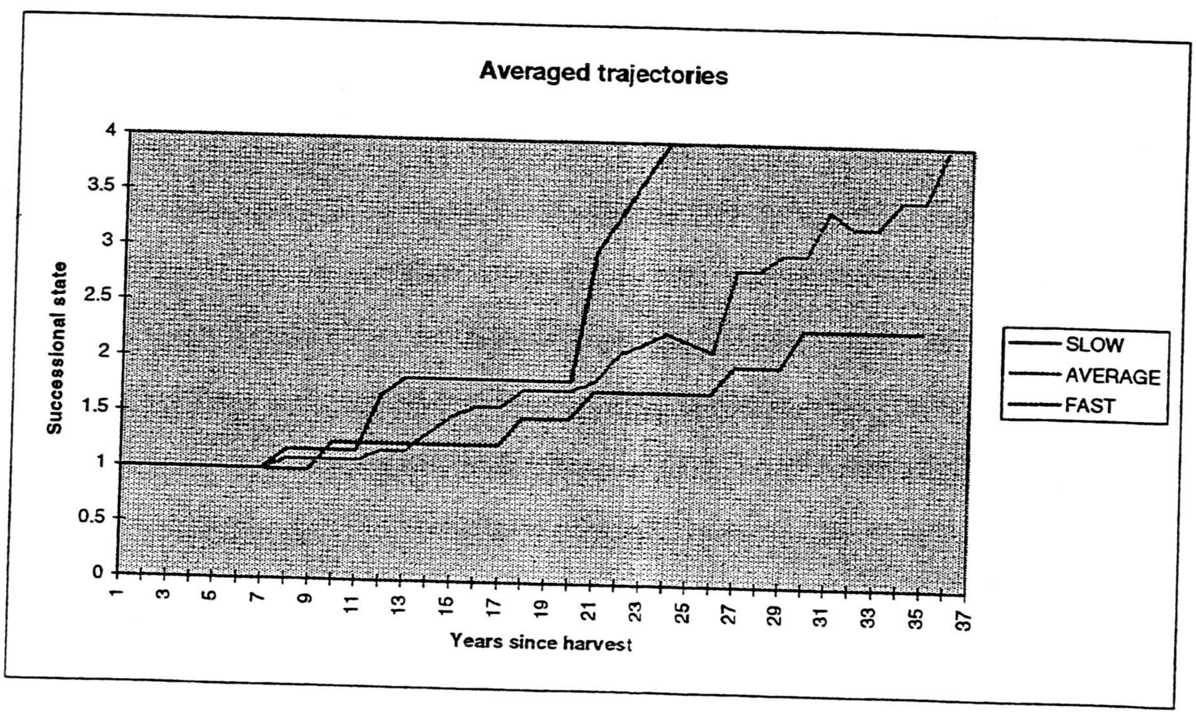


Figure 13: The six original rate classes were collapsed into three (very slow+slow, slow/exp+fast/exp, and fast+very fast), and individual trajectories were again averaged.



shrub state. The average trajectory proceeded relatively linearly, reaching young conifer at around 35 years, and the fast trajectory skipped from a semi-open/young shrub stage directly to young conifer between years 20 and 24.

3. Explanation of spatial pattern

Patterns in rate classes across the study area suggested that the disparate development of regenerating communities was not random at the chosen scale of analysis. Variation both between and within harvest units suggested explanatory factors at several nested scales. The associations of explanatory variables with successional rates are displayed visually in Figures 14-17.

In the initial Chi-square tests of association, planting was the only variable that displayed a significant association with rates of succession. Stands left to regenerate naturally were much more likely to be on slow trajectories, and much less likely to be on fast trajectories. Elevation and aspect were associated with slow stands when naturally regenerating stands were included in the study area, but when these areas were dropped for the logistic regression analysis, and I re-calculated the Chi-square statistics, the environmental variables were no longer significant on their own (Table 2). An explanation for the difference is that naturally regenerating stands were clumped in certain elevation and aspect classes, creating false trends in elevation and aspect and a confounding relationship with planting.

Environmental variables were also not significant individually in the multiple logistic regression analysis, but interactions between these variables were highly significant. In other words, elevation, aspect and TCI are significant predictors, but only when considered together. In the model for slow stands, interactions of elevation*aspect and aspect*TCI were highly significant; in the model for fast stands, elevation*aspect and elevation*TCI

Figure 14:

PLANTING AND SUCCESSION RATES

Figure 15:

ELEVATION AND SUCCESSION RATES

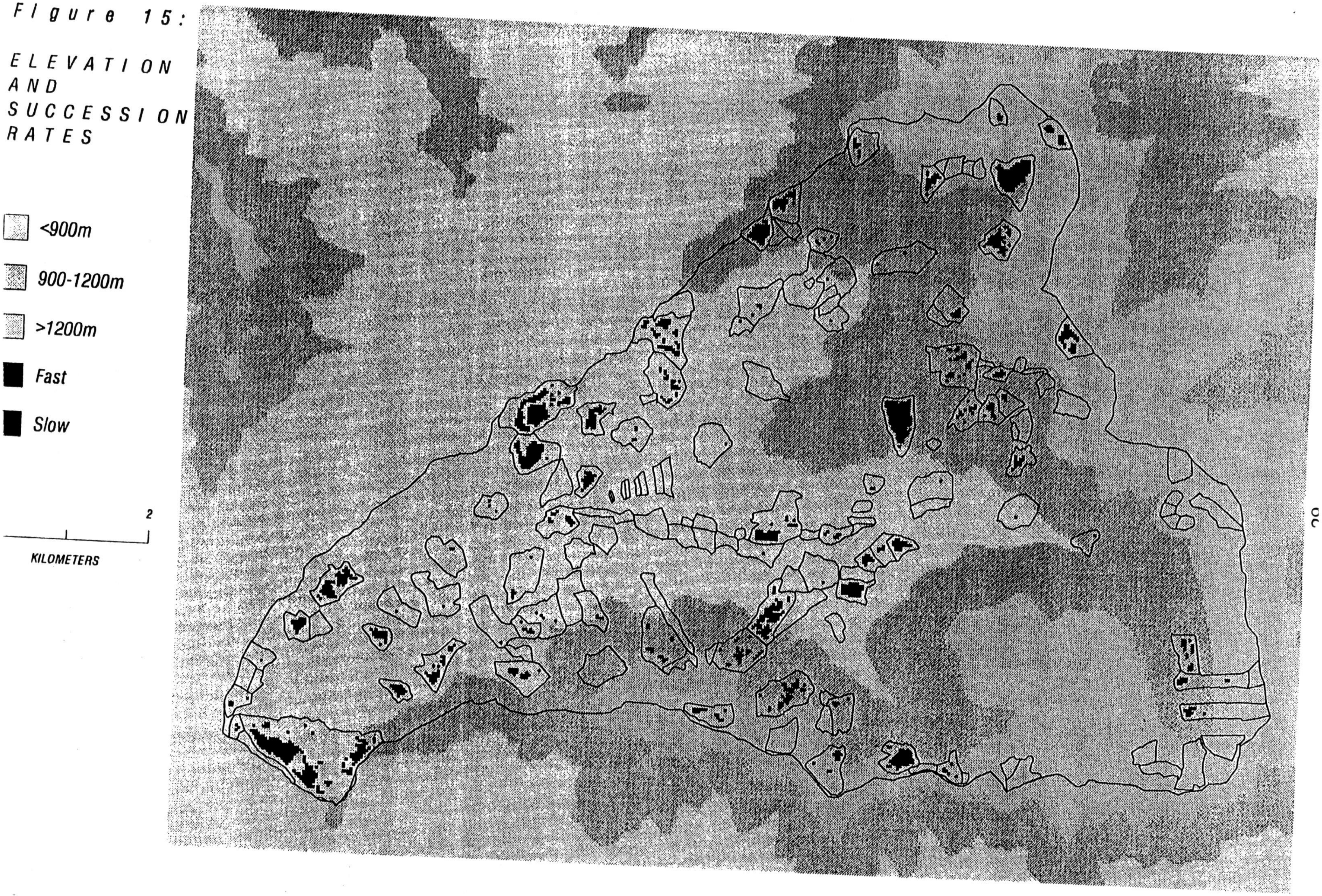


Figure 16:

ASPECT AND SUCCESSION RATES

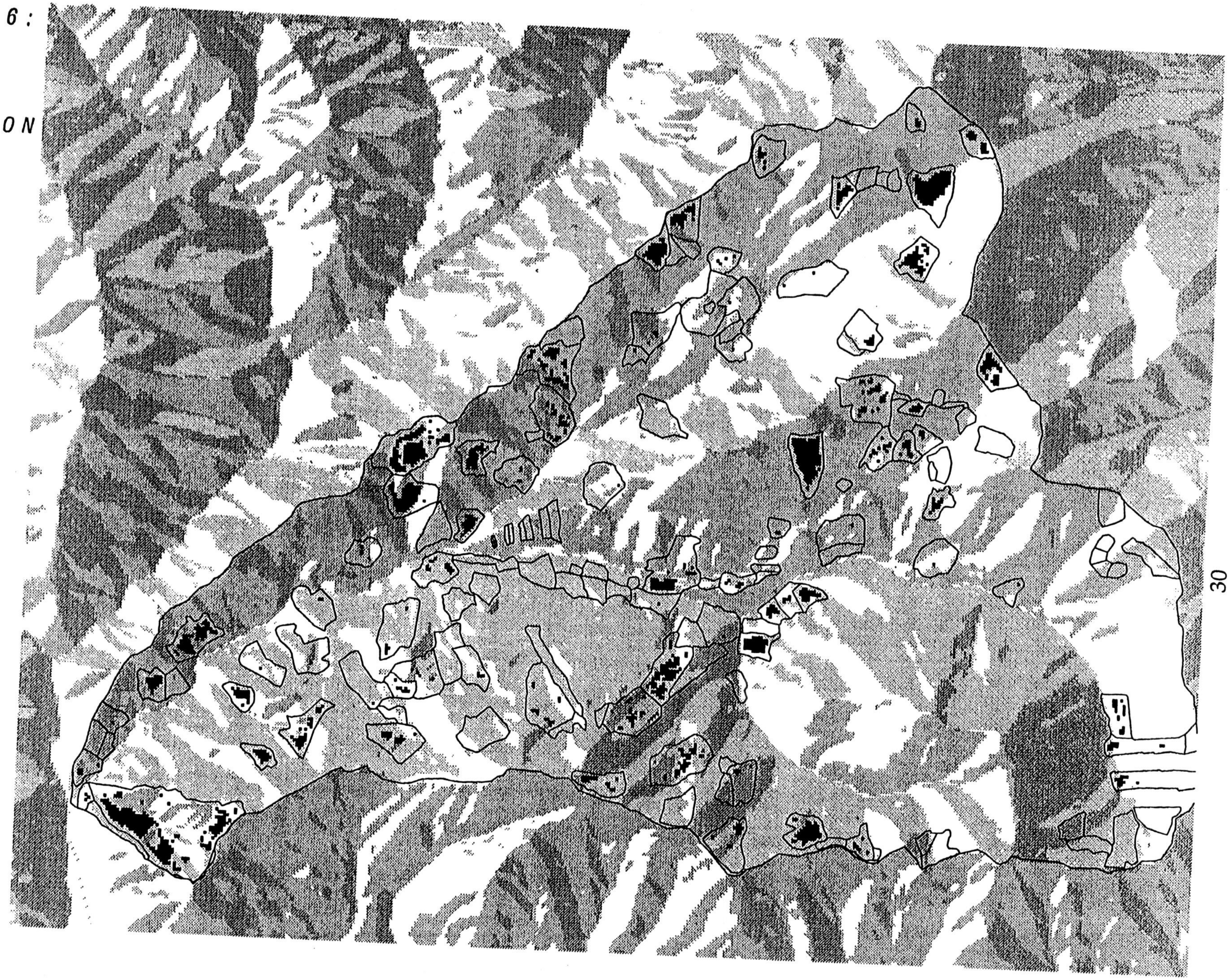
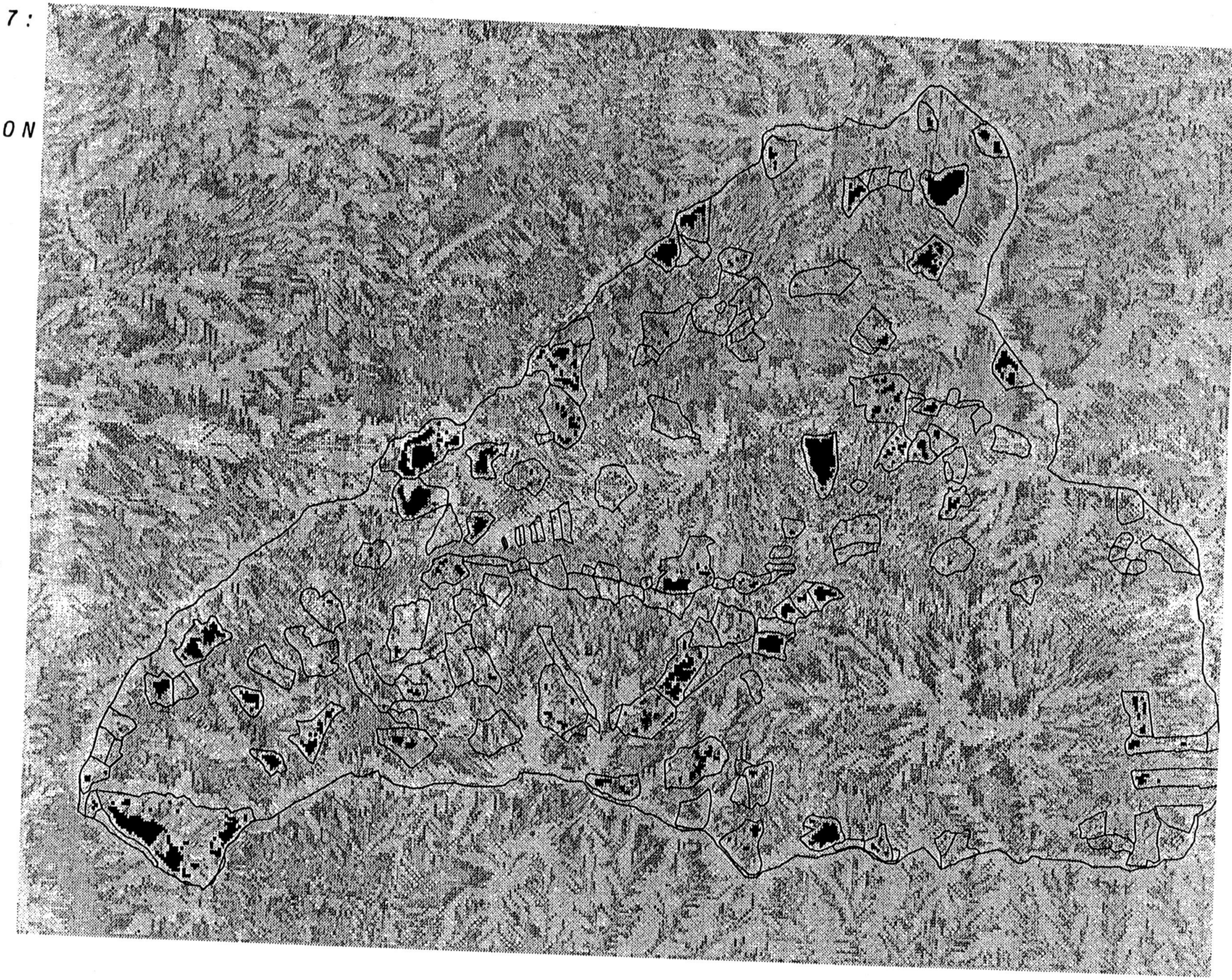


Figure 17:

TCI AND SUCCESSION RATES



Dry

Average

Wet

Fast

Slow

2

KILOMETERS

Table 2: Significance of Chi-square statistics for individual explanatory variables (P-values).

	Planted and natural regeneration areas	
	FAST	*SLOW*
PLANTING	0.001	0.001
ELEVATION	0.86	0.005
ASPECT	0.56	0.001
TCI	0.54	0.29

	Planted areas only	
	FAST	*SLOW*
ELEVATION	0.5	0.11
ASPECT	0.08	0.37
TCI	0.38	0.82

were highly significant (Table 3). The overall fit of the slow model was slightly better than that of the fast model, but both models were adequate, as assessed by the ratio of deviance to degrees of freedom (Table 3), which in both cases was less than one (SAS, 1993).

To investigate which specific combinations of variable classes were contributing to significance, and to be able to attach some ecological meaning to the results, I calculated odds ratios for all interaction terms. The odds ratio is basically a statement describing the outcome probabilities related to different explanatory variable classes. Odds ratios were calculated for fast and slow models based on the data from the entire study area (Table 4). The results display concurring trends between fast and slow models. At low elevations, south- and east-facing slopes are more likely (15x and 7x, respectively) than north to be on slow trajectories, and half as likely as north to be on fast trajectories. At moderate elevations, south and west slopes are more likely than north to be on fast trajectories, and south and east slopes are less likely than north to be on slow trajectories. At high elevations, south, east, and west slopes are all more likely (20x, 8x, and 4x) than north slopes to be fast growing.

Odds ratios were calculated for TCI, but some of the results were difficult to interpret. In general, the interactions were not as strong as those for elevation and aspect. On eastern aspects, dry ridgetops were 3x more likely than wet valley bottoms to be slow, and on north aspects, moderate soil moisture areas were 3x more likely than wet areas to be slow. At high elevations, low and moderate soil moisture areas were less likely to be fast than wet areas.

Table 3: Multiple logistic regression results (drop-in-deviance tests). The F-statistic tests the significance of the drop in deviance with the inclusion of the term. All interaction terms were significant regardless of their position entered into the model. No variables were significant individually, but must be retained in the models if interaction terms follow.

SLOW

Source	Deviance	DDF	F	Pr>F
INTERCEPT	835	1162	-	-
ELEVATION	831	1162	3.17	0.04
ASPECT	828	1162	1.57	0.19
TCI	827	1162	0.47	0.62
ELEV*ASP	792	1162	8.6	0.0001
ASP*TCI	776	1162	3.9	0.0006

FAST

Source	Deviance	DDF	F	Pr>F
INTERCEPT	1027	1149	-	-
ELEVATION	1025	1149	0.8234	0.44
ASPECT	1019	1149	2.6202	0.05
TCI	1018	1149	0.5299	0.59
ELEV*ASP	958	1149	12.1296	0.0001
ELEV*TCI	949	1149	2.779	0.026

Table 4: Odds ratios for interaction terms.

SLOW			**Aspect**		
Elevation		*WEST*	*SOUTH*	*EAST*	*NORTH*
	<900m	3	14.8	6.5	1
	900-1200m	0.94	0.54	0.17	1
	>1200m	3.7	0.72	0.42	1
FAST					
Elevation		*WEST*	*SOUTH*	*EAST*	*NORTH*
	<900m	1.1	0.62	0.54	1
	900-1200m	2.3	5.9	0.97	1
	>1200m	3.8	20.6	7.97	1

SLOW			**TCI**	
Aspect		*DRY*	*MODERATE*	*WET*
	WEST	1	0.55	1
	SOUTH	0.78	0.5	1
	EAST	3.6	0.75	1
	NORTH	1.77	3.5	1
FAST				
Elevation		*DRY*	*MODERATE*	*WET*
	<900m	0.9	1.1	1
	900-1200m	0.75	0.69	1
	>1200m	0.45	0.21	1

DISCUSSION

The statistical analyses indicate a dramatic change in the effects of aspect on growing conditions between low and moderate elevations. The combination of low elevation with high solar radiation loads creates excessively hot and dry growing conditions, while the combination of high elevation with low solar radiation creates excessively cold and wet growing conditions, poor soil aeration, and limited soil nutrients due to slow decomposition of organic matter (Cleary et al., 1978). At low elevations, water seems to be the limiting factor, while at high elevations, temperature seems to be the limiting factor. These results from the elevation/aspect interaction are consistent with the literature on effects of topography on growing conditions summarized earlier in the paper. Interpretation of TCI results required examining the specific data distribution. The high likelihood of slow stands on dry, east facing ridgetops is consistent with the results of the aspect*elevation interaction; I had expected the south facing stands to also display this trend. The likelihood of fast stands on wet, high elevation slopes, indicated by TCI*elevation odds ratios, seemingly contradicts the elevation*aspect results. However, it is a trend that is most likely influenced by one particularly large high elevation stand that, although it is on wet soil, is south facing; excess moisture here is not limiting because it is not as cold as the northern slopes. It is evident that all topographic factors must be considered together.

General growing conditions affect conifer seedling success as well as community composition and biological resiliency. The relative contributions of these processes towards determining a successional pathway can not be determined from this study. In their analysis of two single watersheds, Halpern and Franklin (1990) concluded that when interpreting processes determining paths of succession, "very similar changes in seral understory structure may come about through significantly different mechanisms." However, potential hypotheses can be constructed. In low elevation/south facing units, shrubs may compete better than conifer seedlings for scant water resources. In particular, species of *Ceanothus* can outcompete conifer seedlings because it is better at getting moisture from dry soil, and if well established, can make a site dryer than usual, making conifer establishment especially difficult (Cleary et al., 1978). This is most likely the case with many south and east facing slopes in the lower part of the HJA (McKee, 1996).

In my study of pre-harvest photos, I observed that many north facing sites at moderate-high elevations had large patches of tall shrubs, most likely red alder, mixed in with the more thinly spaced conifers. This suggests that conditions are better suited to these species initially, and combined with high frost potential, these areas are also less likely to have conifer seedling success. At the highest elevations in the watershed, there is evidence of a change in soil biology after harvest. On both north and south ridgetops at the highest elevations, stands exist that are stagnated in semi-open stages. However, the sample at high elevations was not large enough to impact the significance of the elevation*TCI factor for slow stands. Perhaps with a larger study area this factor would appear to be more significant.

In general, the distribution of slow stands in poor growing conditions suggests that as long as conditions are suitable, planted conifer seedlings seem to be able to outcompete other residual and invading species. Distribution of fast stands could indicate areas where the pre-existing community was tree-dominated; the generalized trajectory for these areas indicates a lack of a distinct shrub or hardwood phase.

Issues to consider when drawing these hypothesis include the appropriateness of the vegetation classification for construction of meaningful successional trajectories, and the appropriate selection of classes for DEM-derived variables. Ideally, I would have used a vegetation classification that was more specifically designed to separate early successional stages. For instance, the closed mixed category in this classification was quite broad, and included several growth forms. This classification works, but it could be improved with more detail. The classes selected for DEM-derived variables seem to have worked well, with the possible exception of TCI. TCI classes were chosen arbitrarily by visual distribution, and could have been improved with investigation of the functional differences in levels. More detail doesn't seem to be necessary in aspect classes, and elevation could even possibly be collapsed into two classes rather than three.

There were many potential sources for error in the various technical components of this project. First is the potential for error in the original databases, all of which were pre-existing. This would include classification error in the satellite image and the harvest records. The overall estimated accuracy of the classified image, which covers a 1.2 million hectare area, is 82%; accuracy for the semi-open class is 84%, and for closed mixed and young conifer, 88% (Cohen et al., 1995). Potential error in harvest records is unknown. The second potential source for error is in the GIS operations. This kind of error is often difficult to estimate. Changing data formats, such as from vector to raster, can shift boundaries and alter shapes, especially for linear features. Taking only the center of each harvest unit minimized this problem for the harvest unit coverage, but the roads were more difficult to manage. Elements of reflected roads were probably still present in the final data set. Changing data resolution can also shift boundaries, but in this project the change was minimal (from 25m to 30m, in the satellite image).

Transforming the DEM into variables can weaken its accuracy because existing errors are amplified. In a study relating DEM variables to vegetation patterns, Davis and Goetz (1990) found that their digital elevation model matched actual elevations reasonably well, but that only fair agreement existed between actual and mapped slope angle and slope aspect. Errors were concentrated in areas of rapidly changing slope and exposure, such as ridges and ravines.

The final GIS operation, the selection of data samples from all five coverages (rates, planting, elevation, aspect, TCI), was straightforward. Rasterized coverages were checked for registration prior to extraction of data, so error produced in this operation should have been minimal.

The classification of successional rates, although functional, was, in the end, not ideal because of the strength of the planting association, and the elimination of natural regeneration areas prior to model construction. Ideally, I would have calculated the succession rates again without the natural regeneration areas before I conducted the regression analysis. Because it was a site-specific classification, the rates would have been affected by this change. The "observation time" of the study was not really long enough to reveal anything about divergent development in naturally regenerating stands, given that only one stand reached full conifer canopy closure.

Finally, error in the statistical analysis could have resulted from stochastic error in sampling. Some of the random samples were highly volatile; the distribution of variable classes within random samples had a large effect on the outcomes due to the small overall sample size of "slow" and "fast" stands (Table 3). With "slow" samples of 100 pixels, divided into four aspect classes, a few pixels difference meant a big difference in the odds ratios. This is why odds ratios were calculated from the entire data set, using the model constructed from the sample.

CONCLUSIONS

The methods demonstrated in this paper are a sound approach to investigating successional trajectories on a landscape scale. Meaningful, albeit generalized, trajectories can be determined, and empirical associations can be made with topographic positions. The method would be particularly successful if within a particular study area, a full range of cutting dates occurred on all general landscape positions. Cutting history is somewhat patterned in the HJA., with cutting progressing generally to higher elevations over time. This trend could have distorted the results of this study, but I did not attempt to estimate to what degree.

One disadvantage to the method is that the classification constructed is only valid for a particular study area. The classes have been defined relative to the sample, rather than through a priori regeneration goals. One solution to tailoring the classification is to only consider certain groups of harvest units. However, the break-off points could also simply be chosen a priori, without regard to the observed distribution.

The next step to take in developing this methodology is to apply the results of the coefficients logistic regression models to topographic variables and reproduce a succession rate map. This would be an excellent test of the strength of the association, and would provide clues as to where in the forest the relationships do not hold, and therefore how the model could be improved with alteration of factors or the addition of other factors. A different model could also be tested, with a multinomial response variable, so that all rate classes could be modeled together.

It is unfortunate that planting could not be included in the multivariate analysis element of this study. Much could be learned from a similar analysis that included a greater distribution of naturally regenerating stands, including some harvested earlier in the century, in order to see to what degree planting mitigates or amplifies other environmental influences. The study extent could also be extended to include different ownerships, to see if this factor is also indirectly predictive.

One aspect of regional landscape modeling is that data consistency can be elusive. Spatial data often must be obtained from a variety of institutions and individuals whose standards and methods of digital encoding vary considerably. Landsat satellite imagery and digital elevation models are two types of databases that are easily obtained and relatively consistent across large regions. Harvest unit coverages are less consistent, but can be rectified with imagery if necessary, as the units themselves are usually highly visible on images. If further developed, the methodology described in this paper has potential for predicting trajectories of early succession for recently cut units as well as areas not yet harvested. As currently developed, it can illuminate the types of trajectories that exist, and some of the interactions of landscape-scale factors, natural and human-induced, contributing to divergence of these trajectories.

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Appendix 1: Photo interpretation results for all sub-units. Values are successional states interpreted: (1) Semi-open, (2) Closed mixed shrub, (3) Closed mixed tree, (4) Young conifer. Shaded trajectories were eliminated because of classification error.

A: Full trajectories

UNIT #	B13	B13	402	208	341	306	305	210	402	208	207	306	B13	WS1	WS1	402	601	109	701	381	WS1	402	109	381	WS1	109	109B
HARVEST DATE	52	52	52	57	55	61	61	62	52	57	57	61	52	66	66	65	59	67	61	67	66	65	67	67	66	67	67
3 RATE CLASS	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3
6 RATE CLASS	1	1	2	2	2	2	2	2	3	3	3	3	3	3	3	4	4	4	4	4	4	5	5	5	5	6	6
AGE: 1														1	1					1	1		1	1		1	1
2										1	1			1	1	1				1	1		1	1		1	1
3										1	1			1	1	1				1	1	1	1	1	1	1	1
4					1					1	1			1	1	1				1	1	1	1	1	1	1	1
5					1					1	1		1	1	1	1				1	1	1	1	1	1	1	1
6					1	1				1	1	1	1	1	1	1				1	1	1	1	1	1	1	1
7	1	1	1		1	1			1	1	1	1	1	1	1	1			1	1	1	1	1	1	1	1	1
8	1	1	1		1	1			1	1	1	1	1	1	1	2	1		1	1	1	2	1	1	1	1	1
9	1	1	1		1	1			1	1	1	1	1	1	1	2	1		1	1	1	2	1	1	1	1	1
10	1	1	1		2	1			1	1	1	1	1	1	1	2	1		1	1	1	2	1	1	1	1	1
11	1	1	1		2	1			1	1	1	1	1	1	1	2	1		1	1	1	2	1	1	1	1	1
12	1	1	1		2	1			1	1	1	1	1	1	1	2	1		1	1	1	2	1	1	1	1	1
13	1	1	1		2	1			1	1	1	1	1	1	1	2	1		2	1	1	2	1	2	1	2	2
14	1	1	1		2	1			1	1	1	1	1	1	1	2	3		2	1	1	2	1	2	2	2	2
15	1	1	1		2	1			2	1	1	1	2	1	1	2	3		2	1	1	2	1	2	2	2	2
16	1	1	1		2	1			2	2	1	1	2	1	1	2	3		2	1	1	2	1	2	2	2	2
17	1	1	1		2	1			2	2	1	1	2	1	1	2	3		2	1	1	2	1	2	2	2	2
18	1	1	1		3	1			2	2	1	1	2	1	1	2	3		4	1	1	2	1	2	2	2	2
19	1	1	1		3	1			2	2	1	1	2	1	1	2	3		4	1	1	2	1	2	2	2	2
20	1	1	1		3	1			2	2	1	1	2	1	1	2	3		4	1	1	2	1	2	2	2	2
21	1	1	2		3	1			2	2	1	1	3	1	1	2	3		4	1	1	2	3	3	2	4	4
22	1	1	2		3	1			2	2	2	1	3	1	1	2	3		4	1	3	2	3	3	4	4	4
23	1	1	2		3	1			2	2	2	1	3	1	1	3	3		4	1	3	4	3	3	4	4	4
24	1	1	2		3	1			2	2	2	1	3	1	1	3	3		4		3	4			4		
25	1	1	2		3	1			2	2	2	1	3	1	1	3	3		4			4					
26	1	1	2		3	1			2	2	2	1	3	1	1		3		4								
27	1	1	3		3	1			3	2	2	2	4				3		4								
28	1	1	3		3	1			3	2	2	2	4				3		4								
29	1	1	3		3	1			3	2	2	2	4				4		4								
30	1	1	3		3				3	2	2		4				4										
31	1	1	3		3				3	3	3		4				4										
32	1	1	3		3				3	3	3		4														
33	1	1	3		3				3	3	3		4														
34	1	1	3		3				3				4														
35	1	1	3		3				3				4														
36	1	1	3						4				4														
37	1	1	3						4																		
38	1	1	3						4																		
39																											

B: Averaged (6)

AGE	all 1	all 2	all 3	all 4	all 5	all 6
1			1	1	1	1
2			1	1	1	1
3			1	1	1	1
4		1	1	1	1	1
5		1	1	1	1	1
6		1	1	1	1	1
7	1	1	1	1	1	1
8	1	1	1	1.2	1.25	1
9	1	1	1	1.2	1.25	1
10	1	1.333	1	1.2	1.25	1
11	1	1.333	1	1.2	1.25	1
12	1	1.333	1	1.4	1.5	2
13	1	1.333	1	1.4	1.75	2
14	1	1.333	1	1.8	1.75	2
15	1	1.333	1.286	1.8	1.75	2
16	1	1.333	1.429	1.8	1.75	2
17	1	1.333	1.429	1.8	1.75	2
18	1	1.667	1.429	2.2	1.75	2
19	1	1.667	1.429	2.2	1.75	2
20	1	1.667	1.429	2.2	1.75	2
21	1	2	1.571	2.2	2.5	4
22	1	2	1.714	2.6	3	4
23	1	2	1.714	2.8	3.5	4
24	1	2	1.714	3.25	4	
25	1	2	1.714	3.33	4	
26	1	2	1.714	3.5		
27	1	2.333	2.6	3.5		
28	1	2.333	2.6	3.5		
29	1	2.333	2.6	4		
30	1	3	2.75	4		
31	1	3	3.25	4		
32	1	3	3.25			
33	1	3	3.25			
34	1	3	3.5			
35	1	3	3.5			
36	1	3	4			
37	1	3	4			
38	1	3	4			
39						

C: Averaged (3

1 (1 2)	2 (3 4)	3 (5 6)
	1	1
	1	1
	1	1
1	1	1
1	1	1
1	1	1
1	1	1
1	1.1	1.2
1	1.1	1.2
1.3	1.1	1.2
1.3	1.1	1.2
1.3	1.2	1.7
1.3	1.2	1.8
1.3	1.3	1.8
1.3	1.5	1.8
1.3	1.6	1.8
1.3	1.6	1.8
1.5	1.8	1.8
1.5	1.8	1.8
1.5	1.8	1.8
1.8	1.8	3
1.8	2.1	3.3
1.8	2.2	3.7
1.8	2.3	4
1.8	2.2	4
1.8	2.1	
2	2.9	
2	2.9	
2	3	
2.3	3	
2.3	3.4	
2.3	3.3	
2.3	3.3	
2.3	3.5	
2.3	3.5	
	4	
	4	
	4	