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MODELING STRATEGIES FOR
PROJECTING VEGETATION TRENDS
IN AN AREA OF NORTHEASTERN
MINNESOTA

May, 1977

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MINNESOTA

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INTRODUCTION

In 1974 at the request of the Minnesota Environmental Quality Council, the State Legislature established the Regional Copper-Nickel Study to conduct a regional study of the possible impacts resulting from potential copper-nickel development in northeastern Minnesota. A major objective of this study is to characterize terrestrial life as it exists now and will exist in the future prior to development. The accomplishment of this objective is dependent upon the development of a process that will accurately predict trends in vegetation--i.e. a mathematical model that simulates succession. In this report I attempt to explore the possibilities of modifying proposed successional models found in the literature to suit this purpose.

Simplifying the task of characterizing terrestrial life in a 2000-square-mile study area, the Copper-Nickel Study team has focused its attention on a 560-square-mile area where mining development is most probable and for which data are immediately available (Fig. 1). Such data include the land-ownership, soil type, and vegetation cover type assigned to each one-hectare unit within this area. It is this MINESITE Area for which successional modeling will be examined (MINESITE, 1976).

MINESITE AND REGIONAL COPPER-NICKEL STUDY AREAS

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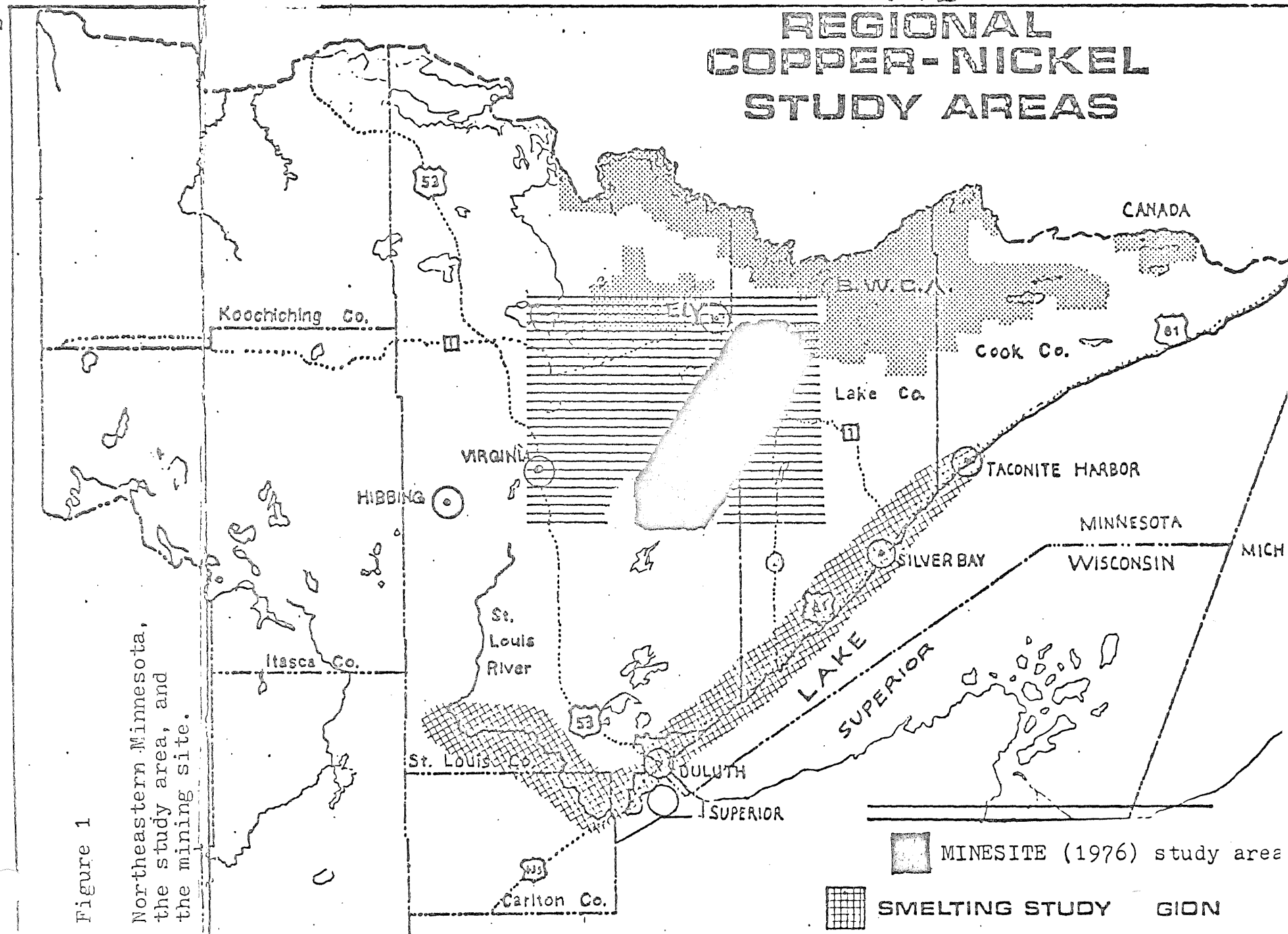




Figure 1

Northeastern Minnesota,
the study area, and
the mining site.

 MINESITE (1976) study area
 SMELTING STUDY AREA

Successional Models.

Modeling strategy is dictated by the reality to be described and an understanding of that reality. Given that:

generality measures the applicability of the model in different locations,
realism measures the degree to which the model corresponds to the biological concepts it represents, and
precision is the closeness of model predictions to observed data,

three possible modeling strategies exist according to Levins' (1966) widely-quoted classification. Each strategy sacrifices one of the above qualities so that the other two are maximized. Because the basic purpose of a successional model in our context is the accurate prediction of changes in vegetation over a relatively short period of time (25-100 years) in a particular region of northeastern Minnesota, a modeling strategy that sacrifices generality to realism and precision seems most appropriate. In this case, the most important parameters of these successional processes need to be identified and accurately measured. Yet succession is a poorly understood phenomenon, and consequently it is difficult to identify the parameters let alone isolate the more important ones. Hence, modelers of succession have resorted to using the second modeling strategy (sacrificing realism to generality and precision) in hopes that the unrealistic assumptions implied by the general mathematical equations they use will affect one another so that useful predictions from the model can be obtained.

Proposed successional models have taken on a variety of forms. As outlined by May (1973), general mathematical models are of four basic types. In both deterministic models, where the dependent variables are continuous, and stochastic models, where they are discrete, the independent variable may be either continuous (as in differential equations) or discrete (as in difference equations). In a successional model proposed by Shugart, Crow, and Hett (1973), a continuous dependent variable--the acreage of land dominated by a particular forest type--depends on the continuous variable of time. The flow of land between forest type compartments is described by a set of first-order linear differential equations. Similarly, Bledsoe and Van Dyne (1971) used such a compartment model to describe the abstract flow of energy or biomass from species to succeeding species during oldfield succession. In the stochastic models of Horn (1975) and Waggoner and Stephens (1970), the probabilities that a certain tree or plot dominated by a particular species is replaced by another is described by a finite Markov process. The dependent and independent variables are discrete. In the successional model by Leak (1970), probabilities that each tree in a forest will either produce one offspring that becomes established, produce no offspring, or die over the discrete interval of one year are given by species-specific birth and death rates. Finally,

a complex stochastic model that indirectly simulates forest succession by modeling tree growth was proposed by Botkin, Janak, and Wallis (1972). The model lumps deterministic equations for radial growth and growth in height, competition, and environmental effects. But tree birth and death are determined by species-specific probabilities so that both the dependent variable, the number of trees on a plot, and independent variable--time--are discrete.

Succession on the Mine Site.

Because the MINESITE Area is relatively large and thus heterogeneous, the most appropriate model would seem at the outset to be a form like that of Shugart et al. (1973) or a Markov model scaled up from describing the dynamics within a particular forest to describing the dynamics of many forest types within a region. In either case, the very large number of concrete vegetation types occupying particular unit areas are grouped into a finite number of abstract cover types. Succession is then modeled in some deterministic or stochastic fashion, while the total area of a region, constant over time, is partitioned among cover types. The basic structure of this model is described diagrammatically by what Shugart et al. (1973) term a "model topology." In such a diagram (Fig. 2), the boxes represent particular cover types, whereas the arrows represent



the flow of area from dominance by one cover type to that by another.

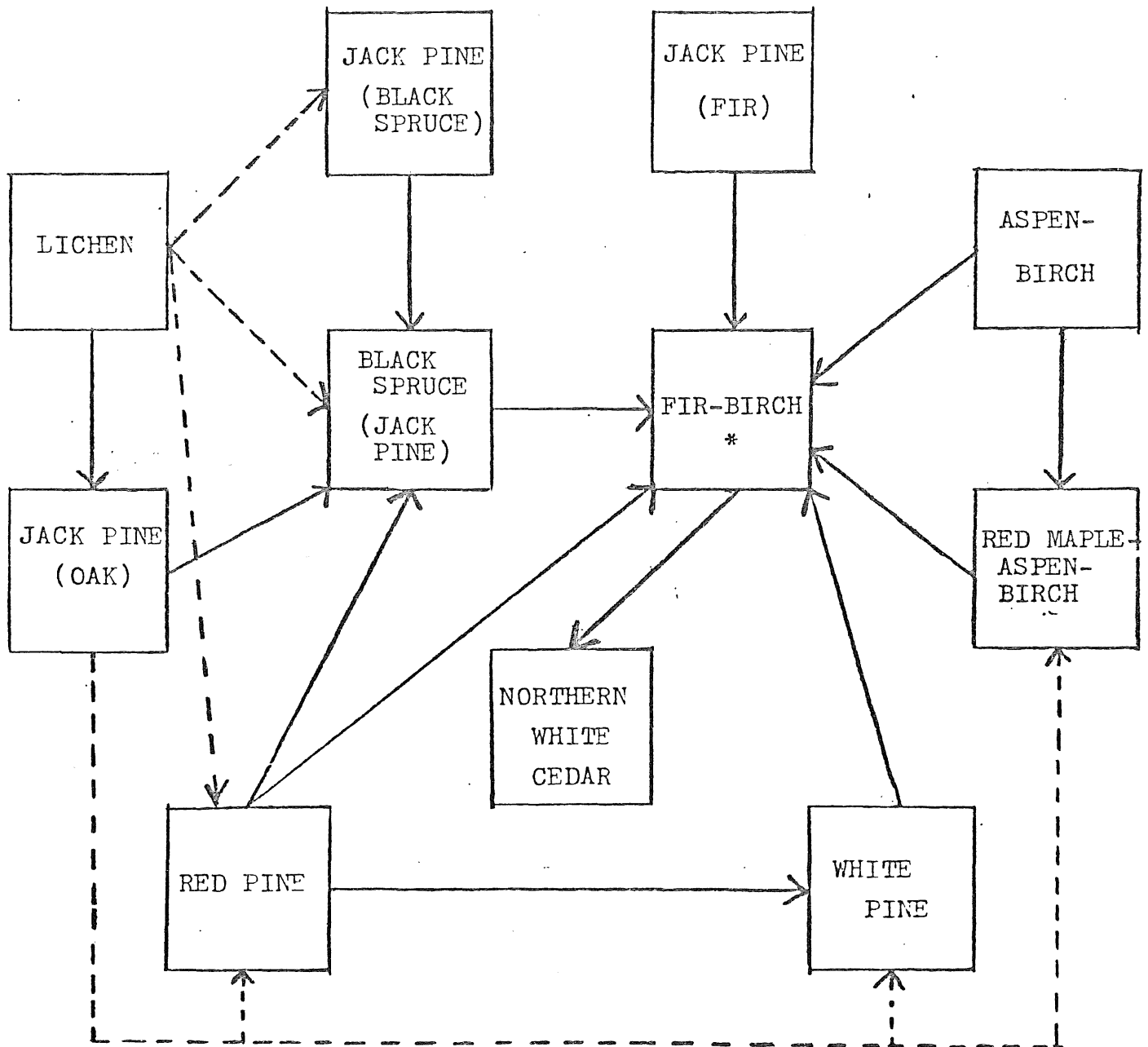
A logical approach on the MINESITE Area would involve modeling succession as it occurs naturally in the absence of natural or unnatural perturbations. Disturbances could then be incorporated later. Two basic problems are inherent in this technique. First, natural succession in northeastern Minnesota has not, as yet, been well documented. Two recent studies (Heinselman 1973, Ohmann and Ream 1971a, 1971b) examine natural succession in the Boundary Waters Canoe Area (BWCA) north of the MINESITE Area. A model topology on the probable dynamics of eleven statistically-defined cover types, is displayed in Figure 2. The magnitude of each arrow is not known. Stressing the importance of fire in natural ecosystems, Heinselman questions the existence of a true climax community for the area. Rather he views climax on a regional scale as a mosaic of cover types with no appreciable net change in the total area occupied by each over time in the absence of fire exclusion by man.

A second problem of modeling succession exists because the forests on the MINESITE Area are not 'virgin' (i.e. undisturbed by European man). Natural succession may not be predictable even by the best models for this intensively managed area where clearcutting is the most frequently used silvicultural system.

Figure 2

A model topology describing natural succession in the B.W.C.A. for those communities defined by Ohmann and Ream (1971b).

 probable trans.
 possible trans.



* Includes the budworm disturbed community

Indeed, the accuracy of predicting future trends in vegetation will rely heavily on an ability to predict future management policies.

Within the framework of the modeling objective and these associated problems, the remainder of this report will deal with the advantages, disadvantages, and possible alternatives to the deterministic model of Shugart et al. (1973).

THE MODEL OF SHUGART, CROW, AND HETT (1973)

Although deterministic models yield precise predictions, the accuracy of those predictions with respect to the real world can be approximated only after the model is verified with field data. The successional model of Shugart et al. (1973) is an example of one that was not tested.

Description and Problems.

The basic form of this model is a set of 'n' first order linear differential equations each of which represent the net flow rate of area into or out of cover-state x_i ($i=1,2,\dots,n$).

$$\begin{array}{l}
 dx_1/dt = a_{11}x_1 + a_{12}x_2 + \dots + a_{1n}x_n \\
 dx_2/dt = a_{21}x_1 + a_{22}x_2 + \dots + a_{2n}x_n \\
 \vdots \\
 \vdots \\
 \vdots \\
 dx_n/dt = a_{n1}x_1 + a_{n2}x_2 + \dots + a_{nn}x_n
 \end{array}
 \quad
 \begin{array}{l}
 dx_i/dt = \sum_{j=1}^n a_{ij}x_j \\
 \text{(where } i=j=1,\dots,n\text{)}
 \end{array}
 \quad (1)$$

The a_{ij} 's are coefficients that represent the transfer of area from the i^{th} to the j^{th} cover-state. These constants measure the rate of movement along the arrows between compartments in the model topology diagrams.

The model represented in compact matrix notation is

$$d/dt(\bar{X}) = A\bar{X} \quad (2)$$

where \bar{X} is an $n \times 1$ vector of the x_i 's and A is an $n \times n$ matrix of the transfer coefficients, a_{ij} being that value found in the i^{th} row and j^{th} column of the matrix. The diagonal elements of

this matrix (a_{ij}) have negative values and represent an output flow of area from the i^{th} state or these values are zero in the case of a climax state. This flow is partitioned as inputs of area among the remaining states so that the sum of all column elements is zero.

$$\sum_{j=1}^n a_{ij} = 0 \quad (\text{for all } i, j=1, \dots, n) \quad (3)$$

Applying equation 3 over all columns implies that area can neither enter nor leave the system or the region being modeled, which is reasonable. Such a system is said to be closed (Bledsoe and Van Dyne, 1971) and has the general solution:

$$x_i = \sum_{j=1}^n C_{ij} e^{\lambda_j t}, \quad (4)$$

where the λ_j 's are the eigenvalues of matrix A and the C_{ij} 's are constants that depend on the initial distribution of the region's area among the cover-states.

Each defined forest type of the region in question is further divided by Shugart et al. into three size classes--seedling, pole, and saw-timber. Growth in these vegetation types is then simulated over the region if each of the size categories represents a separate cover-state and thus one in the set of differential equations. As growth proceeds over time, area would flow from seedling, through pole, to the saw-timber size cover-state for any particular forest type.

The task of obtaining a matrix of transfer coefficients

is simplified by assuming that one forest type replaces another only after that earlier forest type has reached saw-timber size. The a_{ij} 's are then found by first measuring average growth in stands that make up a forest type and, second, by finding the probabilities that one forest type is succeeded by another (possibly measured by an average number of stems of the latter found in the understories below the former). The first step isolates the diagonal elements of the coefficient matrix, simplifying equation 1 to:

$$dx_i/dt = a_{ii}x_i \text{ with the solution } x_i = x_{i0}e^{-a_{ii}t} \quad (5)$$

where x_{i0} is the initial acreage in the i^{th} cover-state. The diagonal coefficient, a_{ii} , then is the reciprocal value of the time it takes for 63 percent of the initial area to leave the i^{th} cover-state because for $a_{ii} = 1/t$,

$$x_{it} = x_{i0}e^{-(a_{ii})(1/a_{ii})} = x_{i0}e^{-1} = .37(x_{i0}). \quad (6)$$

Coefficients other than the diagonals are determined by multiplying the probability (p_{ij}) that the j^{th} cover-state replaces the i^{th} forest saw-timber size cover-state by the diagonal element of the latter:

$$a_{ij} = p_{ij}a_{ii}. \quad (7)$$

Some time constants ($1/a_{ii}$) and transition probabilities (p_{ij}) used by Shugart et al. (1973) are shown in Tables 1 and 2.

According to the form of the model just described, the

Table 1

The time constants (in years) when 63 percent of the area occupied by one cover-state becomes occupied by the succeeding cover-state according to Shugart et al. (1973).

Forest type	Size class			
	seedling	pole	saw	total
Aspen	20	35	10	65
Jack pine	30	30	10	70
Fir-spruce	30	45	climax community	-----
Northern hardwoods	100	100	50	250
Red pine	100	100	100	300
White pine	100	150	200	450
Black spruce	80	80	80	240
Tamarack	100	100	90	290
White cedar	57	115	1000	1172

Table 2

The probabilities that the row cover-states are succeeded by the column cover-states according to Shugart et al. (1973).

	Succeeding state							Birch- ash- hemlock	White cedar
	Red pine	White pine	N.hard- woods	Hemlock	Sugar maple	Fir- spruce	Black spruce		
Aspen		.05	.55			.4			
Jack pine	1.0								
Red pine		1.0							
White pine			.7	.2	.1				
Northern hardwoods					1.0				
Tamarack							.8		.2
White cedar								1.0	

State
being
replaced

loss of area from a cover-state follows a negative exponential curve (Figures 3 and 4). Such an assumption is clearly unrealistic. This point is illustrated if one examines growth in any forest type simulated by the model. Consider, for example, the white pine forest type of Shugart et al. (1973) using their coefficients in Tables 1 and 2. By removing all inputs to this subsystem and initially setting 100 percent of the area dominated by white pine in the seedling size-class, the behavior of the system over time is easily identified (see the appendix) and is shown graphically in Figure 5. Two characteristics of these curves are worth mentioning. First, pole and saw-timber are immediately produced. Second and more important, only 50 percent of the initial seedling stands mature and give way to succeeding overstories in 400 years. However, only the most vigorous white pines reach such an age (Fowells, 1965). Growth is similarly underestimated for the other forest types listed in Table 1. This inconsistency might have caused the underestimation in abundance of the later successional forest types in Hahn and Leary's (1974) trial simulation using Shugart et al.'s (1973) model. If the transfer coefficients are increased to offset this amazing longevity exhibited by the forest stands, the loss of area becomes too great too quick so that the resulting curves are still unrealistic.

Figure 3

The loss of jack pine seedling area to the jack pine pole cover-state as implied by the Shugart et al. model (1973).

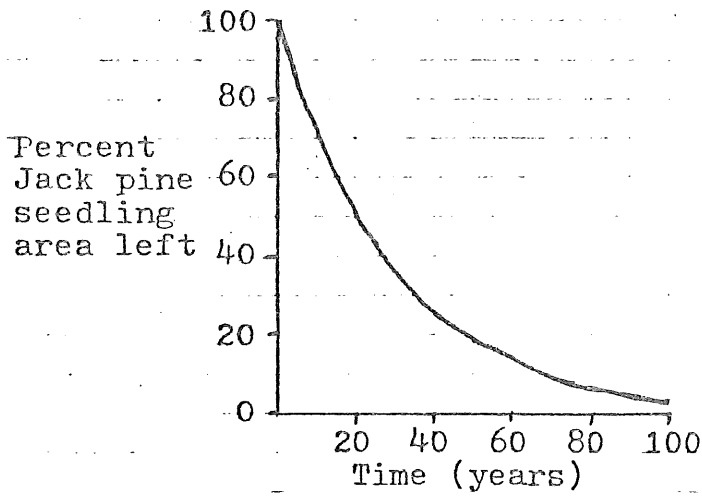


Figure 4

The loss of tamarack seedling area to the tamarack pole cover-state as implied by the Shugart et al. model (1973).

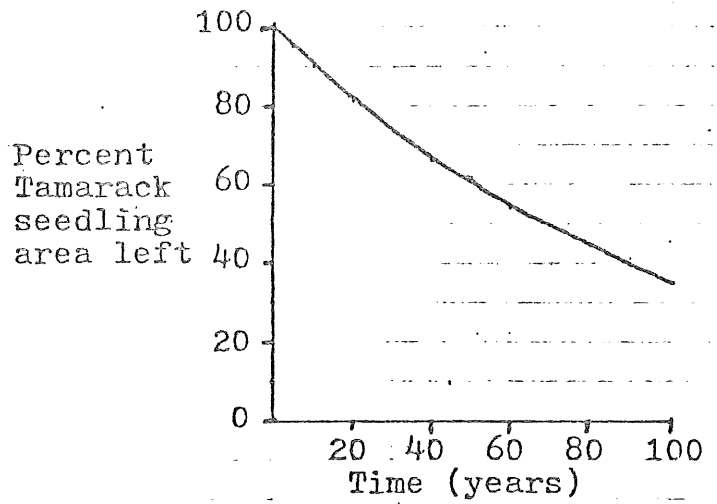
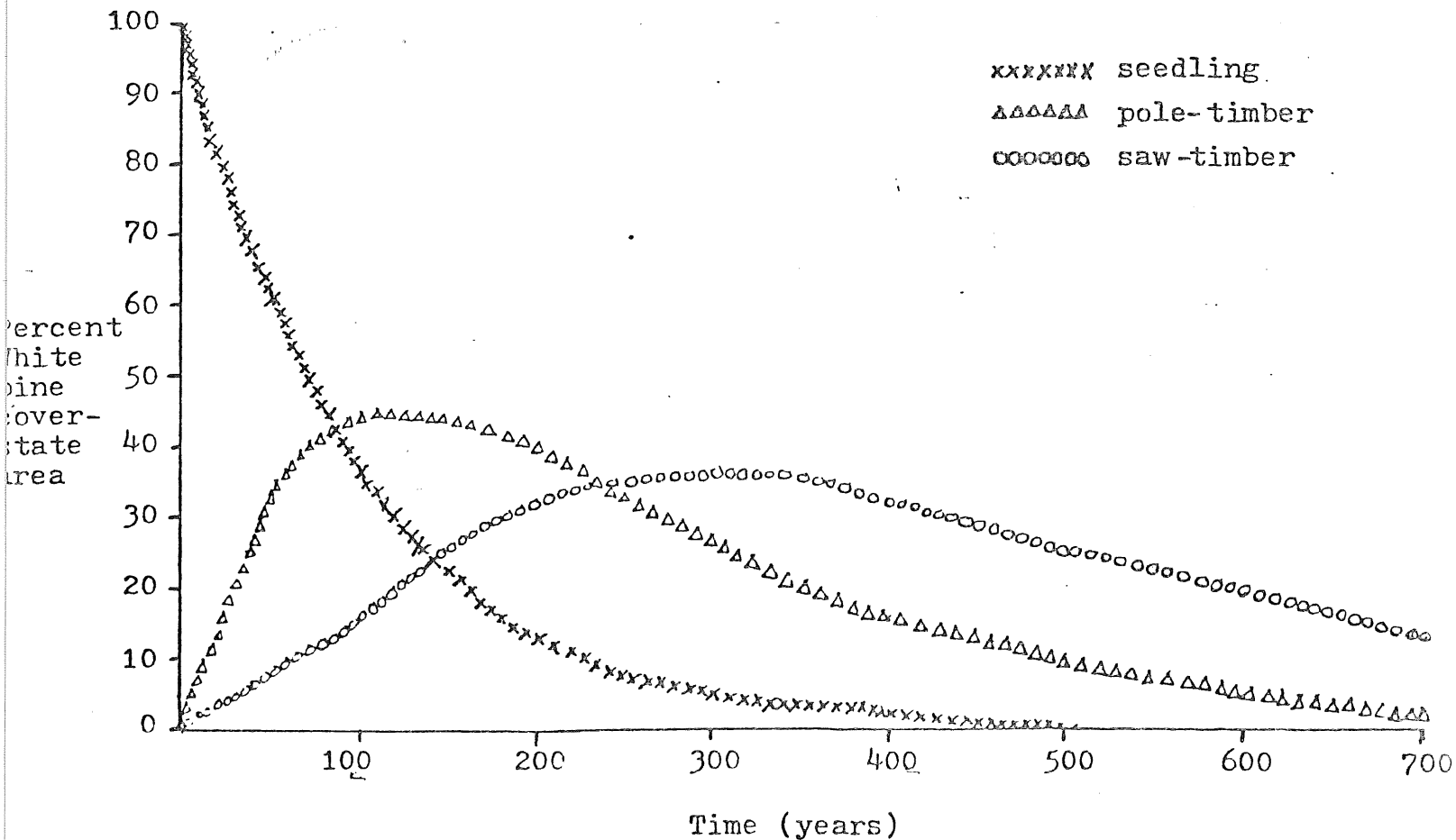


Figure 5

The decay of area from a white pine cover-state subsystem of the Shugart et al. model (1973).



THE COVER-STATE REPLACEMENT PROCESS

How does a curve behave which describes, over time, the decrease in the area of a cover-state that results from stand growth and mortality? As I have just shown, the assumption that the curve is negatively exponential (as in the model of Shugart et al. (1973)), is unrealistic. Nevertheless, such a simplification is probably acceptable over a very large and heterogeneous region. Over such a region, areas occupied by each forest type are composed of many different stands of varying ages and composition, occur on varying soil types and topography, and are subjected to varying climatic and other environmental conditions. These many stands are analogous to a population of phenotypically varying individuals. Mortality in such a population is often described by a continuous constant percent decrease in numbers over time, i.e. a negative exponential function (Lotka, 1925). The exponential curve then is a simplification of the complex cover-state behavior that attempts to account for heterogeneity over the region.

Instead of accounting for heterogeneity outright, an alternative approach to describing the cover-state replacement process involves building heterogeneity into a simpler mathematical system that describes replacement in a very homogeneous region. For reasons that will become evident as this discussion

proceeds, this approach is most compatible with the task at hand.

Consider a very homogeneous region on which grows one large, even-aged seedling stand where each surviving seedling reaches pole-size after 25 years. The loss in area occupied by this seedling cover-state would occur all at once (Fig. 6). If this same hypothetical region is occupied equally by five even-aged seedling stands of ages 0, 5, 10, 15, and 20 years, the loss from the cover-state would follow a curve shown in Figure 7. Finally, in such a region occupied by many even-aged seedling stands uniformly distributed in age and coverage, loss from the cover-state would ideally follow a straight line (Fig. 8), not an exponential curve. If the entire life span of an average stand can be divided into discrete time intervals representing ages, the growth of many stands over this homogeneous area can be simulated by allowing the area occupied by stands of a particular age to move to the next age-class as that interval of time passes. The time interval might be set as low as one year or as high as ten years. The form of this model for the interval $t=1$ unit is

$$\bar{X}_{t+1} = A\bar{X}_t \quad (\text{a Markov process}). \quad (8)$$

The diagonal elements of A are all set at -1 . Those elements just below the diagonals (a_{i+1}, a_i) are set at 1 in most cases.

A very bulky model will result when this method is used

Figure 6

Loss in area from a seedling cover-state if a homogeneous region is occupied by one even-aged seedling stand.*

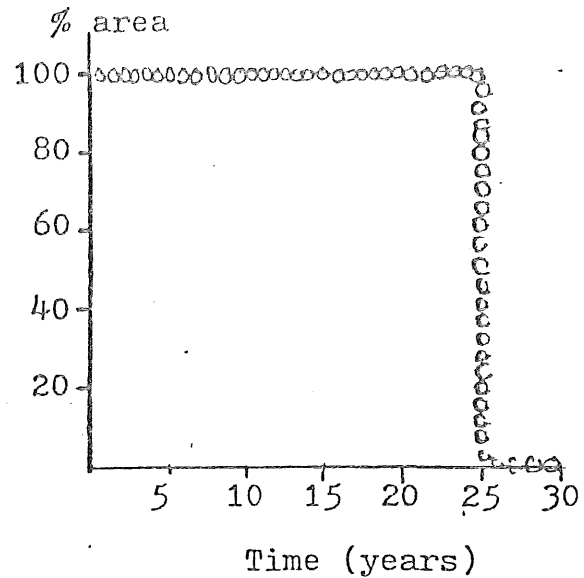


Figure 7

Loss in area from a seedling cover-state if a homogeneous region is equally occupied by 0, 5, 10, 15, and 20 year old even-aged seedling stands.*

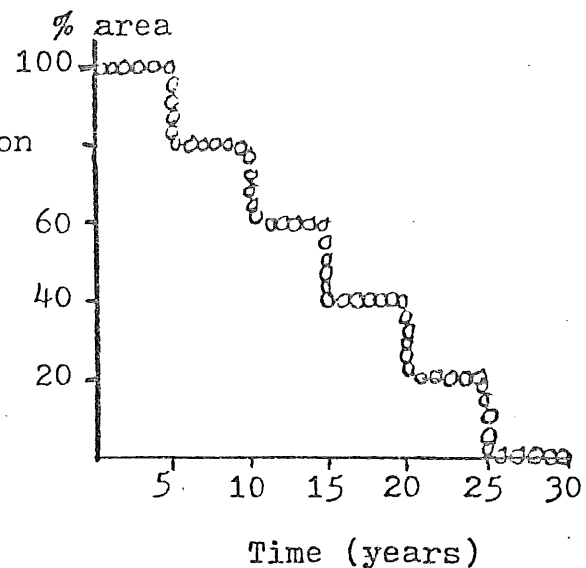
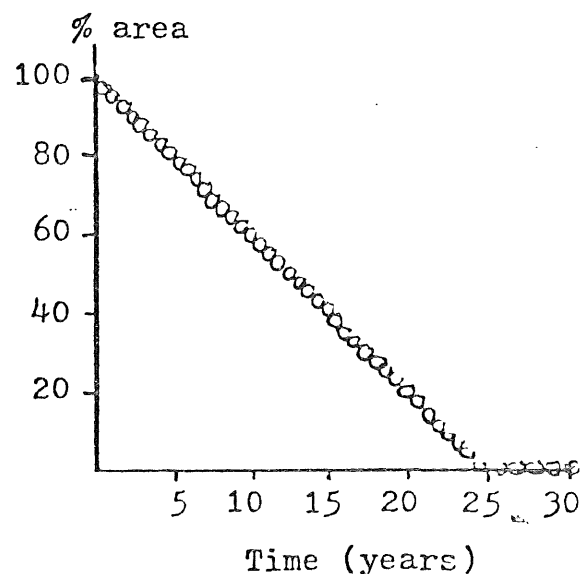


Figure 8

Loss in area from a seedling cover-state if a homogeneous region is equally occupied by seedling stands of all ages between 0 and 25 years.*



*In this homogeneous region, surviving seedlings become pole size in 25 years.

to simulate average stand growth for many forest types because a large number of variables or storage compartments (each representing an age-interval of a particular forest type) will be needed. However, such a simulation is not beyond the capacity of today's computers.

Two major unrealistic assumptions are inherent in this second model. First, all stands aren't necessarily even-aged. However, the abundance of uneven-aged stands in the MINESITE Area and possibly in a greater portion of northeastern Minnesota is probably negligible due to disturbance and the intolerant (of light) character of most indigenous species. Second, stands that make up a forest type grow at different rates depending on environmental factors, not at the same rate as assumed in the model. The level of complexity needed in the model to account for such heterogeneity will depend on the degree to which these growth rates vary about average values.

At the outset at least, the model is fundamentally and conceptually very simple. Further, only a moderate number of complications will probably be needed in the model since the region isn't as heterogeneous as one might initially think. For example, Grigal and Ohmann (1973) state that (1) "the narrow range of climatic conditions" and (2) "the broad range of plant tolerances" provide an explanation for the greater importance

of disturbance over other environmental factors in determining the composition of plant communities in the BWCA. Disturbance would tend to reduce regional heterogeneity. More importantly, timber management in the area dramatically simplifies the complex process of cover type replacement by maintaining most forest stands in an even-aged structure.

APPLYING THE ALTERNATE MODEL

Though stand age is often an important parameter of stand growth, growth is usually measured in terms of the average size of the trees composing the stand--specifically the average diameter at breast height (dbh). The Copper-Nickel Study group has recognized five size categories--seedling (0-1" dbh), sapling (1-5" dbh), pole (5-9" dbh), small saw (9-15" dbh), and a large saw-timber size class (15+" dbh). The problem with the alternate model then becomes one of relating stand age to the average dbh of trees in the stand.

The site index of a forest stand (the predicted average height of dominant trees at 50 years of age) gives a relative measure of an area's suitability for supporting the particular tree sources composing the stand. This value is obtained from published species-specific site index curves or from knowledge of the site itself--its soil type, topography, or its effect on other species growing in the area. If average stand dbh could be used in place of stand height in obtaining site index values, radial growth in many stands over a region could be modeled by further partitioning stands of a cover type into groups found on excellent, good, fair, and poor sites. Unfortunately, the average diameter of trees in a stand over time strongly depends on density. Although height growth may be great in stands on good sites, radial growth

will be very slow if the stand is too heavily stocked.

A definite relation between height and diameter may exist for the more intolerant species such as jack pine, aspen, and paper birch as natural thinning lessens the effects of crowding on tree diameter. Still, crowding in the stands of more tolerant trees will arrest radial growth. Properly managed stands, however, are periodically thinned to maximize growth. The stands are thinned to a prescribed density or basal area at a specific age. This unnatural thinning may also allow diameter to be roughly related to height.

Modeling Management in the MINESITE Area.

Obviously forest management doesn't always strictly follow prescribed guidelines. Such guidelines are also subject to change. It's not the purpose of this report to determine the extent that such guidelines are followed or change, however. Instead, an example of how the model might be applied to adequately stocked stands in managed forests using present guidelines is provided.

A model topology corresponding to the forest type management policies used in the Superior National Forest is shown in Figure 9. (Over 70 percent of the MINESITE Area is located in the Superior National Forest and is intensively managed by the U.S. Forest Service). This figure shows the flow of land between forest types when various stands reach rotation age. A few of these

Figure 9

A model topology describing how defined forest types (page 24) should be managed in the Superior National Forest (SNF, 1975). The circled numbers are the stand rotation ages in years. S.I.=site index (in feet)

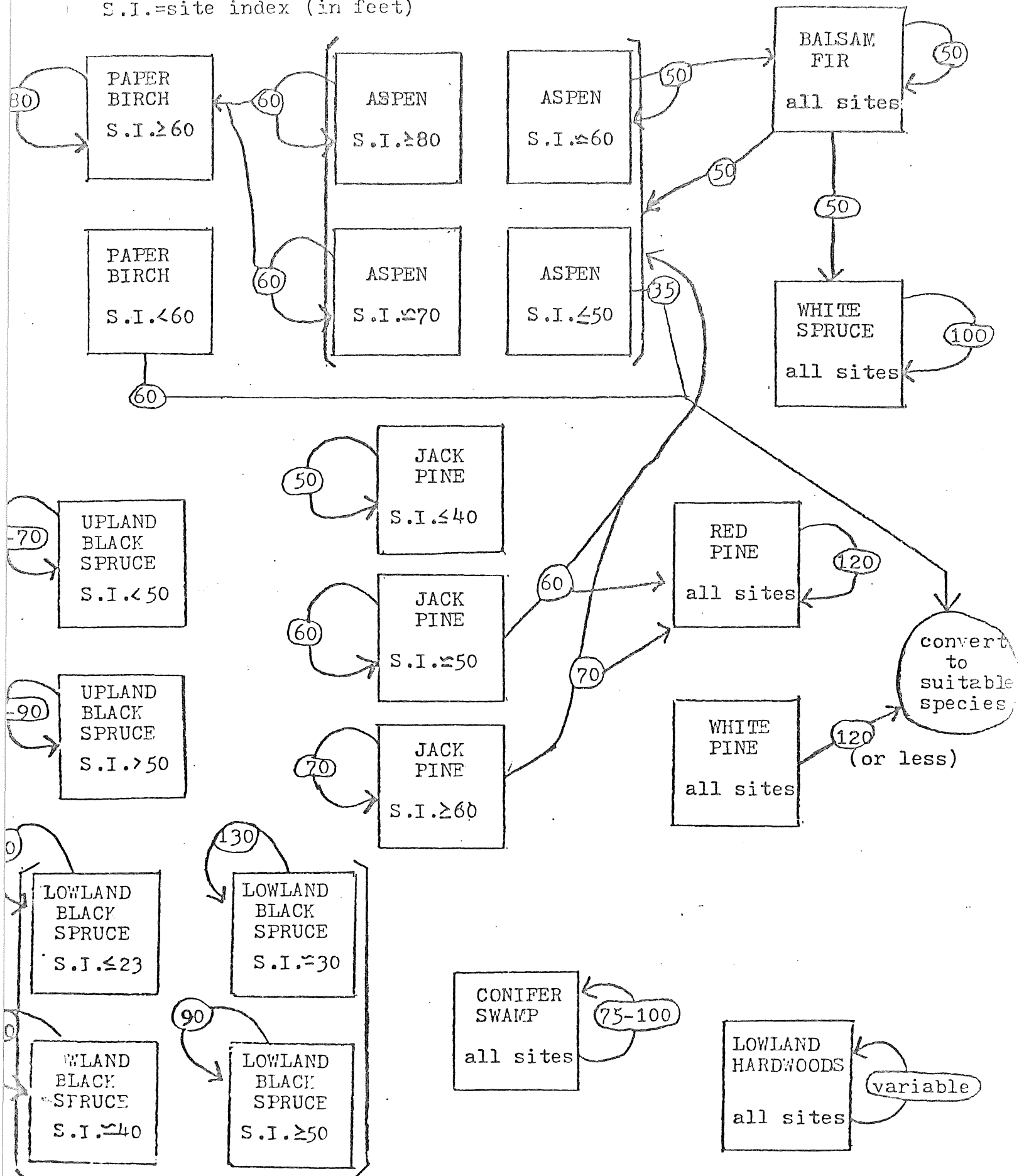


Figure 9 (continued)

Management's forest type definitions for adequately stocked stands. (Adequate stocking exists when the basal area (B.A.) of a stand is greater than 40 square feet per acre).

A. Upland forest types

1. A stand is managed for aspen when aspen:
 - a) makes up more than 80 percent of the crown density, or
 - b) is mixed with paper birch, white spruce, or both on sites that have a paper birch site index less than 60 and a white spruce B.A. less than 50 ft²/acre at the aspen rotation age.
2. A stand is managed for paper birch when paper birch:
 - a) makes up more than 80 percent of the crown density, or
 - b) is mixed with aspen, white spruce, or both on sites having a birch site index greater than 60 and a white spruce B.A. less than 50 ft²/acre at the birch rotation age.
3. A stand is managed for white spruce if white spruce:
 - a) makes up more than 50 percent of the crown density in a fir-spruce-aspen-birch mixture, or
 - b) has a B.A. greater than 50 ft²/acre at the rotation age of the dominant tree species.
4. A stand is managed for balsam fir if:
 - a) white spruce makes up less than 50 percent of the crown density in a fir-spruce-aspen-birch mixture, or
 - b) the total B.A., in fir stands, of paper birch, pine, and/or white spruce does not exceed 40 ft²/acre or the site is poor for those long-lived species, or
 - c) fir is needed for wildlife habitats.
5. A stand is managed for jack pine if jack pine:
 - a) makes up more than 80 percent of the crown density, or
 - b) is mixed with red pine, white spruce, or aspen on poor sites for those latter species or when not adequately stocked with those species.
6. A stand is managed for red pine if:
 - a) in mature stands, red pine is adequately stocked, or
 - b) in stands just older than 35 years, red pine has a B.A. greater than 25 and makes up at least 40 percent of the crown density, or
 - c) in stands younger than 35 years and adequately stocked, there are at least 100 well distributed red pine per acre.
7. A stand is managed for white pine according to the same principles that apply for red pine except when blister rust threatens the stand.

B. Lowland forest types

1. A stand is managed for black spruce if it makes up greater than 50 percent of the crown density.
2. A stand is managed for lowland hardwoods if red maple, ash, elm, and/or basswood make up more than 50 percent of crown density.
3. A stand is managed as a conifer swamp if neither black spruce nor lowland hardwoods make up 50 percent of the crown density.

forest types are handled as an example.

1. Aspen.

Assuming first, that all adequately stocked aspen stands in the MINESITE Area can be classified according to site index, and second, that average radial growth in these stands can be related to site index, Table 3a can be constructed using the yield tables of Kittredge and Gevorkiantz (1929). The model expressions corresponding to these roughly estimated parameters are shown in Figure 10a. The restrictions imposed on the subscripts require that, except for 50 percent of the aspen on poor sites, all stands are regenerated as aspen. That area not regenerated as aspen is arbitrarily converted to jack pine.

2. Paper Birch.

The same procedure used in the above treatment of aspen is used for paper birch using the yield tables of Cooley (1962). Birch stands on areas with a site index below 60 are 75 percent regenerated as birch and 25 percent as jack pine. The model expressions incorporating the parameters listed in Table 3b are shown in Figure 10b.

3. Jack Pine.

Table 3c is constructed using the yield data of Eyre and Lebaron (1956). All jack pine stands are regenerated as jack pine and, for simplicity, birch and aspen are converted only

Table 3a

The approximate ages that growing aspen stands on specified sites graduate from a size class or are harvested according to S.N.F. management guidelines and the yield tables of Kittredge and Gevorkiantz (1929).

		d.b.h. size class (inches)				
		0-1	1-5	5-9	9-15	15+
site index	80	5	25	55	60	--
	70	5	30	60	--	--
	60	5	35	50	--	--
	50	10	35	--	--	--

Table 3b

The approximate ages that growing paper birch stands on specified sites graduate from a size class or are harvested according to S.N.F. management guidelines and the yield tables of Cooley (1962)

		d.b.h. size class (inches)				
		0-1	1-5	5-9	9-15	15+
site index	70	5	30	60	80	--
	50	10	40	60	--	--

Table 3c

The approximate ages that growing jack pine stands on specified sites graduate from a size class or are harvested according to S.N.F. management guidelines and the yield tables of Eyre and Lebaron (1956).

		d.b.h. size class (inches)				
		0-1	1-5	5-9	9-15	15+
site index	60	5	25	50	70	--
	50	5	30	60	--	--
	40	5	35	50	--	--

Figure 10a

The model equations for aspen using a time interval of 5 years and the parameters listed in table 3a. ('t' is always some multiple of five years).

- acres of
the j^{th} aspen
- 1) age class on = $A80_j(t+5) = A80_i(t)$ $i=j-1$ for $j=2,3,\dots,12$
S.I. ≥ 80 $i=12$ for $j=1$
at time= $t+5$ $i, j=1,2,\dots,12$
 - 2) $A70_j(t+5) = A70_i(t)$ $i=j-1$ for $j=2,3,\dots,12$
 $i=12$ for $j=1$
 - 3) $A60_j(t+5) = A60_i(t)$ $i=j-1$ for $j=2,3,\dots,10$ $i, j=1,2,\dots,10$
 $i=10$ for $j=1$
 - 4) $A50_1(t+5) = (.5)(A50_7(t))$ $i, j=1,2,\dots,7$
 $A50_j(t+5) = A50_i(t)$ $i=j-1$ for $j=2,3,\dots,7$

For any 5 year interval t:

$$\begin{aligned} \text{aspen seedling acreage} &= A80_1(t) + A70_1(t) + A60_1(t) + \sum_{i=1}^2 A50_i(t) \\ \text{aspen sapling acreage} &= \sum_{i=2}^5 A80_i(t) + \sum_{i=2}^6 A70_i(t) + \sum_{i=2}^7 A60_i(t) + \sum_{i=2}^7 A50_i(t) \\ \text{aspen pole acreage} &= \sum_{i=6}^{11} A80_i(t) + \sum_{i=7}^{12} A70_i(t) \\ \text{aspen small saw acreage} &= A80_{12}(t) \end{aligned}$$

Figure 10b

The model equations for paper birch using a time interval of 5 years and the parameters listed in table 3b.

- 1) $PB70_j(t+5) = PB70_i(t)$ $i=j-1$ for $j=2,3,\dots,16$ $i, j=1,2,\dots,16$
 $i=16$ for $j=1$
- 2) $PB50_j(t+5) = PB50_i(t)$ $i=j-1$ for $j=2,3,\dots,12$
only $i, j=1,2,\dots,12$
 $PB50_1(t+5) = (.25)(PB50_{12}(t))$

For any 5 year interval t:

$$\begin{aligned} \text{paper birch seedling acreage} &= PB70_1(t) + \sum_{i=1}^2 PB50_i(t) \\ \text{paper birch sapling acreage} &= \sum_{i=2}^6 PB70_i(t) + \sum_{i=3}^8 PB50_i(t) \\ \text{paper birch pole acreage} &= \sum_{i=7}^{12} PB70_i(t) + \sum_{i=9}^{12} PB50_i(t) \\ \text{paper birch small saw acreage} &= \sum_{i=13}^{16} PB70_i(t) \end{aligned}$$

Figure 10c

The model equations for jack pine using a time interval of 5 years and the parameters listed in table 3c.

$$1) \text{JP60}_j(t+5) = \text{JP60}_i(t) \quad \begin{array}{l} i=j-1 \text{ for } j=2,3,\dots,14 \\ i=14 \text{ for } j=1 \end{array}$$

$$2) \text{JP50}_1(t+5) = \text{JP50}_{12}(t) + (.5)(\Lambda 50_7(t)) + (.25)(\text{PB50}_{12}(t))$$

$$\text{JP50}_j(t+5) = \text{JP50}_i(t) \quad i=j-1 \text{ for } j=2,3,\dots,12$$

$$3) \text{JP40}_j(t+5) = \text{JP40}_i(t) \quad \begin{array}{l} i=j-1 \text{ for } j=2,3,\dots,10 \\ i=10 \text{ for } j=1 \end{array}$$

For any 5 year interval t:

$$\text{jack pine seedling acreage} = \text{JP60}_1(t) + \text{JP50}_1(t) + \text{JP40}_1(t)$$

$$\text{jack pine sapling acreage} = \sum_2^5 \text{JP60}_i(t) + \sum_2^6 \text{JP50}_i(t) + \sum_2^7 \text{JP40}_i(t)$$

$$\text{jack pine pole acreage} = \sum_6^{10} \text{JP60}_i(t) + \sum_7^{12} \text{JP50}_i(t) + \sum_8^{10} \text{JP40}_i(t)$$

$$\text{jack pine small saw acreage} = \sum_{11}^{14} \text{JP60}_i(t)$$

to medium site jack pine. The corresponding model expressions are shown in Figure 10c.

This procedure could be repeated for some of the other forest types using, for example, the data of Meyer (1929) for white spruce and fir, Fox and Kruse (1939) for black spruce, and Eyre and Zehngraff (1948) for red pine. The point to be made is this: the model's flexibility enables the user to easily express when forests are harvested and the extent that a forest type is regenerated as the same or some other type.

Certainly not all stands are harvested at rotation age. Many stands are lost to succeeding understories because no markets exist for the overstory trees. Assuming that most stands are harvested at rotation age and properly regenerated, the model at least provides a framework on which to base less optimistic views of future management. Leuschner (1972) used a variety of management strategies in his model to obtain a rough estimate of future volumes of Lake States aspen. Likewise, in order that a good estimate of management's effects on MINESITE Area vegetation is obtained, model simulations should be run incorporating different management strategies.

Modeling Natural Succession in the MINESITE Area.

The portion of the region not subject to intensive management for one reason or another is subject to natural succession. In

the absence of management, the validity of the model decreases with the time of the simulation period as the model assumptions become increasingly violated--stands naturally become uneven-aged and mixed. Initially, stands are assumed to be even-aged and relatively pure. The two steps in applying the model to this portion of the region are analogous to those outlined by Shugart et al. (1973) described earlier.

1. Stand Growth is Modeled.

If it's deemed necessary and if the MINESITE Area vegetation inventory permits it, variability of stand growth about an average value can be accounted for by partitioning stands of forest types among different site index classes and density classes. Such subdivisions should obviously be kept to a minimum, however. The model is very large even before further complications are added.

Finding values for the average longevity of forest stands is a major problem. Longevity appears to depend on site quality and may depend on density as well. These values might be assumed to be a bit larger than the corresponding rotation ages but more study is needed in this area.

2. Transfer between Forest Types is Modeled.

The nondiagonal elements are calculated as before--using equation 7. The p_{ij} 's should be obtained from field data. For

example, Heinselman (1959) used the observed dominance of other species in understories to reflect the degree to which those species would replace aspen overstories in Minnesota. His results are listed in Table 4.

Fire, Drought, and Epidemics.

It is suggested that the frequency and effect on vegetation of fire, drought, and epidemics be ascertained from the past history of the area. These effects can then be expressed in the model by discontinuous means. As in the case of modeling different management strategies with different simulations, the effect and timing of these factors can also be added differently in a number of simulations to arrive at an overall average effect of each factor.

Table 4

The natural conversion of aspen to other cover types reflected by the dominance of the invading species in the understories of selected plots in Minnesota aspen-birch stands (Heinselman, 1954).

	Acres of Overstory Aspen-Birch Converted ($\times 10^3$)
Spruce-fir	570
Northern Hardwoods	290
Ash-elm	200
Mixed	150
Conifer Swamp	60
Oak	60
Inferior Hardwoods ¹	50
Pine	30
Total Complete Conversion ²	1410
Partial Conversion ³	1020
No Conversion ⁴	4370
Total	6800

¹ red maple, elm, ironwood, black and pin cherry.

² defined as $\geq 1050 \frac{\text{seedlings}}{\text{acre}}$, $\geq 650 \frac{(1 \text{ to } 3" \text{ dbh trees})}{\text{acre}}$, or $\geq 350 \frac{(3 \text{ to } 5" \text{ dbh trees})}{\text{acre}}$.

³ defined as 600 to 1049 " , 400 to 649 " , or 200 to 349 " .

⁴ defined as <600 " , <400 " , or <200 " .

CONCLUSION

The model of Shugart, Crow, and Hett (1973) is not recommended for use by the Copper-Nickel Study team for projecting vegetative trends in the MINESITE Area. It is neither immediately evident nor has it been demonstrated that this model accurately simulates natural succession over a large region. Also, by focusing on MINESITE's (1976) smaller and intensively managed region, the study group can collect a mass of data allowing them to at least qualitatively project, over a relatively short period of time, what will become of the many forest stands. The exponential increase or decrease in the cover-state area implied by the model of Shugart et al. (1973) would only prove to obscure these qualitative projections.

Instead, a Markov model is recommended. By reducing the system of linear differential equations to one of linear difference equations, the important factors affecting growth and replacement of forest stands can be more easily incorporated into a simulation.

The present and future state of the area's vegetation is greatly dependent on present and future forest management. It is believed that different management policies and their manifestations can be better simulated by the Markov model. In fact, the more important the role that management plays in

shaping the vegetation, the higher will be the degree to which the Markov model assumptions are met, and thus the more appropriate the model will be in obtaining projections.

One should remain critical of the ability of the Shugart et al. (1973) model to simulate natural succession. The same holds even more so for the Markov model even when its inherent assumptions are valid. As equations are added to account for the fact that not all stands are pure or grow at similar rates, the simulations may become more realistic. Still, the success of this model, like the many other successional models which embody the second Levins (1966) modeling strategy, depends largely on whether unrealistic effects inherent from the unrealistic assumptions cancel each other.

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APPENDIXSolving a System of Linear
Differential Equations

Shugart et al. didn't obtain an explicit solution for their model. Numerical approximation techniques were used instead. An explicit solution for a small subset of the set of differential equations can easily be found, however, by applying techniques found in any introductory textbook of linear algebra or differential equations. Such is done below so that growth and decay of white pine stands over a region can be visualized as predicted by the model in the absence of input acreages from other cover types.

The three equations that describe the growth of white pine stands are

$$\begin{array}{ll} \text{seedling} & dx_1/dt = (-1/100)x_1 \\ \text{pole} & dx_2/dt = (1/100)x_1 + (-1/150)x_2 \\ \text{saw} & dx_3/dt = (1/150)x_2 + (-1/200)x_3 \end{array}$$

$$\text{or} \\ d/dt(\bar{X}) = \begin{bmatrix} -1/100 & 0 & 0 \\ 1/100 & -1/150 & 0 \\ 0 & 1/150 & -1/200 \end{bmatrix} \bar{X} = A\bar{X} .$$

This system is complicated because the second and third equations contain variables other than that variable in the differential.

If the matrix A is similar to a diagonal matrix, D, made

up of its eigenvalues, the system can be reduced to eliminate

these other variables. All λ 's that are solutions of ' $\det(\lambda I_n - A) = 0$ '

(where I_n is the 3×3 identity matrix) are eigenvalues of A .

This follows from the definition of the eigenvector \bar{X} as ' $A\bar{X} = \lambda\bar{X}$ '

where \bar{X} is a nonzero solution of this equation only if the above determinant is zero. Since

$$\text{Det} \begin{bmatrix} \lambda + 1/100 & 0 & 0 \\ -1/100 & \lambda + 1/150 & 0 \\ 0 & -1/150 & \lambda + 1/200 \end{bmatrix} = 0$$

only when $(\lambda + 1/100)(\lambda + 1/150)(\lambda + 1/200) = 0$, $\lambda_1 = -1/100$, $\lambda_2 = -1/150$, and $\lambda_3 = -1/200$ are the eigenvalues and

$$D = \begin{bmatrix} -1/100 & 0 & 0 \\ 0 & -1/150 & 0 \\ 0 & 0 & -1/200 \end{bmatrix} .$$

The trick now is to find a matrix of columned eigenvectors, P , such that $\frac{d}{dt}(\bar{X}) = A\bar{X} = (PDP^{-1})\bar{X}$. Such eigenvectors are found by substituting each eigenvalue, λ_i , into $(\lambda_i I_n - A)\bar{X} = 0$ and solving for \bar{X} . When this is done for A above, one eigenvector is found to be associated with each eigenvalue.

$$\bar{X}_{\lambda_1} = \begin{bmatrix} 1/4 \\ -3/4 \\ 1 \end{bmatrix}, \quad \bar{X}_{\lambda_2} = \begin{bmatrix} 0 \\ -1/4 \\ 1 \end{bmatrix}, \quad \bar{X}_{\lambda_3} = \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix}, \quad \text{so} \quad P = \begin{bmatrix} 1/4 & 0 & 0 \\ -3/4 & -1/4 & 0 \\ 1 & 1 & 1 \end{bmatrix}$$

The inverse of P , denoted P^{-1} , as obtained using the so-called matrix inversion algorithm.

$$\left(\begin{array}{ccc|ccc} 1/4 & 0 & 0 & 1 & 0 & 0 \\ -3/4 & -1/4 & 0 & 0 & 1 & 0 \\ 1 & 1 & 1 & 0 & 0 & 1 \end{array} \right) \xrightarrow[\text{transformations}]{\text{linear row}} \left(\begin{array}{ccc|ccc} 1 & 0 & 0 & 4 & 0 & 0 \\ 0 & 1 & 0 & -16 & 12 & 0 \\ 0 & 0 & 1 & 4/3 & -4 & 1 \end{array} \right)$$

$$\text{so } P^{-1} = \begin{pmatrix} 4 & 0 & 0 \\ -16 & 12 & 0 \\ 4/3 & -4 & 1 \end{pmatrix}$$

Finally, setting $\bar{Y} = P^{-1}\bar{X}$, with $\frac{d\bar{Y}}{dt} = P^{-1}\bar{X} = D\bar{Y}$, the following expressions are obtained:

$$\frac{dy_1}{dt} = (-1/100)y_1 \quad \text{with solution } y_1 = C_1 e^{(-1/100)t}$$

$$\frac{dy_2}{dt} = (-1/150)y_2 \quad \text{with solution } y_2 = C_2 e^{(-1/150)t}$$

$$\frac{dy_3}{dt} = (-1/200)y_3 \quad \text{with solution } y_3 = C_3 e^{(-1/200)t}$$

Since $\bar{Y} = P^{-1}\bar{X}$ or $\bar{X} = P\bar{Y}$, an explicit solution for the subset model follows:

$$x_1 = (1/4)y_1 \quad \text{or } x_1 = (1/4)C_1 e^{(-1/100)t}$$

$$x_2 = (-3/4)y_1 - (1/4)y_2 \quad \text{or } x_2 = (-3/4)C_1 e^{(-1/100)t} - (1/4)C_2 e^{(-1/150)t}$$

$$x_3 = y_1 + y_2 + y_3 \quad \text{or } x_3 = C_1 e^{(-1/100)t} + C_2 e^{(-1/150)t} + C_3 e^{(-1/200)t}$$

By setting all areas at the outset of a simulation in the seedling size class with the initial conditions $x_{10} = 100$ \bar{A} , $x_{20} = 0$ \bar{A} , and $x_{30} = 0$ \bar{A} , the expressions become

$$x_1 = (100)e^{(-1/100)t}$$

$$x_2 = (-300)e^{(-1/100)t} - (100)e^{(-1/150)t}$$

$$x_3 = (100)e^{(-1/100)t} - (100)e^{(-1/150)t} + (100)e^{(-1/200)t}$$