MODELING FOREST SUCCESSION

by

Samuel J. Harbo, Jr.

Institute of Statistics
Mimeographed Series No. 844
September 1972

ABSTRACT

HARBO, SAMUEL JAMES, JR. Modeling Forest Succession. (Under the direction of ARTHUR WELLS COOPER and DON WILLIAM HAYNE).

A simulation model is developed to aid in explaining the processes involved in forest succession. The model requires information of species changes at randomly located points and the probability of such changes. Covering of a point by a plant's aerial parts is the characteristic used in determining state. A full, or unsimplified, model is specified first, but due to the complexity of succession and hence of the full model, various simplifications are specified. In the simplified reduced model, plant states at a point are specified on an age-group basis, with each age group having an associated transition matrix whose entries are the probabilities of state changes for plants of that age group to the next older age group. Feedback relationships portraying interactions between species, as well as between age groups, are specified in the model. A seed vector containing the probabilities of a point being covered by a species' seed also is specified. The model is programmed for a digital computer.

Five simulated successions illustrate some uses of the model.

The rationale followed in determining which simplifications should be used in reducing the complexity of a model and the model-field study interactions are discussed.

MODELING FOREST SUCCESSION

by

SAMUEL JAMES HARBO, JR.

A thesis submitted to the Graduate Faculty of
North Carolina State University at Raleigh
in partial fulfillment of the
requirements for the Degree of
Doctor of Philosophy

DEPARTMENT OF EXPERIMENTAL STATISTICS
DEPARTMENT OF BOTANY

RALEIGH

1 9 7 2

APPROVED BY:

Co-Chairman of Advisory Committee

Co-Chairman of Advisory Committee

BIOGRAPHY

I was born on March 3, 1929, at Hanska, Minnesota. I was reared at that locality and received my first 12 years of formal education there. I attended the University of Nebraska, receiving a Batchelor of Science Degree in Soil Conservation in July, 1951.

After serving three years in the United States Navy, I enrolled at the University of California, Berkeley, spending three semesters there. I then enrolled at the University of Alaska, receiving a Master of Science Degree in Wildlife Management from that institution in 1958.

I was employed as a wildlife biologist by the Alaska Department of Fish and Game from 1958 to August, 1961. At that time I entered graduate study at North Carolina State University. During the periods August, 1961 to July, 1964 and June, 1966 to July, 1967 I was in residence at North Carolina State University completing the course requirements for my doctoral program.

In September, 1964 I accepted a teaching position at the University of Alaska; I am currently employed there.

I married Gayle Whitten on May 1, 1958. We have four children; Lisa Ann, 12 years; Lora Kay, 10 years; Keith William, 7 years; and Sam Jens, 4 years.

ACKNOWLEDGMENTS

I wish to express my appreciation to the co-chairmen of my advisory committee, Professors A. W. Cooper and D. W. Hayne, for their advice and guidance. I also wish to thank the other members of the committee, Professors H. L. Lucas, C. Proctor and H. R. van der Vaart, for their constructive criticisms.

I am grateful for the financial support I received during my doctoral study. I held a Research Assistantship with the Cooperative Wildlife Statistics Project for one year and a National Institute of Health Fellowship through the Biomathematics Program for three years.

I also wish to express special gratitude to my wife, Gayle, and my children for their patience, sacrifice and encouragement during the course of my study.

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Vegetation is a dynamic phenomenon, yet many investigators have tended to treat it as though it were static. Numerous treatises have dealt with spatially-related change and variability in vegetation, and the methodologies to measure, reduce or remove that change or variability. Numerous workers, concerned with vegetation modification with time, have recorded time-related vegetation changes, but they also have collected the data as though vegetation were static. Methodologies, both collecting and analytic, have not been developed to handle the dynamic aspect. Partly as a consequence, the roles of the processes involved in the principal dynamic aspect of vegetation, succession, are not well understood, even though succession has been an important topic in ecology for over half a century. Some of the deficiencies in our understanding undoubtedly also reflect the complexity of plant succession, and I believe some also reflect the orientation of many succession studies. F. C. Clements' overwhelming influence on ecological perspective in the early 1900's, and to some extent even today, stimulated many studies devoted to chronicling the products of succession, and presumably the invariance of the climax vegetation, but not the processes themselves.

The complexity of natural phenomena usually is of sufficient magnitude so that field studies conducted without supporting experimental and theoretical investigations are incapable of explaining, in a causal relationship context, the phenomena. That assertion particularly applies to vegetation, and to vegetation study. An additional complication usually associated with vegetation study is

the length of time required for completion of vegetation processes, and the subsequent manifestation of change. A hundred years or more may be required before a relatively unchanging forest stand re-occupies an abandoned field, for example. Since man's impatience and urgency demand answers now, not 100 years from now, telescoping of the time span is essential.

The present study, considering vegetation is a dynamic phenomenon, attempts to evaluate the roles played in vegetation development by the various processes involved in succession. I attempt to develop a model that is complementary to an associated field study and which will provide a means for collecting the information needed to resolve such questions as the role of chance, competition and other factors in determining plant groupings. The model is designed with special reference to forest succession and is structured to aid in telescoping of the time span.

LITERATURE REVIEW

Introduction

The stimulus for community ecology and succession study largely is due to three men, Frederic Clements, Henry Cowles and Eugene Warming. Their works stressed the concepts of community and plant succession.

Warming (1909), and many earlier workers, recognized that species are not randomly distributed but form associations of varied physiognomy. Warming believed that the study of associations involved determining which species associate together, why they associate, why the associations have a characteristic physiognomy, why each species has its own special "habit and habitat," and the means plants employ in order to live in a given environment. These points of inquiry still are current.

Cowles (1899) studied the succession of sand dune vegetation near Lake Michigan. He believed that vegetation was the joint product of past and present environments, and to understand the development of vegetation, succession must be studied. Such studies should attempt to discover the "laws" governing vegetation changes.

Clements (1916) accepted the community not only conceptually but factually. He believed in the importance and near organismic equivalence of communities, which prompted the questions of how communities arose, why some were replaced by others and why some seemed to persist indefinitely. To Clements, communities, and not individual species, are the important elements in succession, because the motive force in succession lies in the responses or functions of groups of

individuals. These responses or functions, producing different moisture regimes or soil structure, or other habitat reactions, depend on the life form of the group. A life form able to produce reactions causing stabilization received Clements' term dominance; plants of that life form were termed dominants. The concept of dominance and dominants is a focal point in Clements' view of succession.

Clements (1928) also considered competition an important factor in succession. He indicated that competition occurs only when plants are more or less equal; a dominant tree-understory herb relationship is not one of competition but is one of dominance and subordination. A tree seedling and herb could compete, however. Also, the dominants influence the competitive balance of the understory by modifying the environment. Although competition contributes to a community's reaction upon its habitat, Clements believed that dominance was of much greater importance.

Past Approaches to Vegetation Study

Clements strongly influenced the direction of vegetation study in North America during the first half of the 20th century. He stressed the regularity and directional aspect of succession and the ultimate invariance and importance of the terminal stage, labeled the climax community. Clements' emphasis of the units of vegetation and of successional invariance caused many of the North American plant ecologists to focus their attention on community classification and on detailing community sequences in succession.

Concurrent with the development of the climax concept, various other ecological schools or traditions developed. Most were classificatory in nature (Whittaker, 1962), and most accepted explicitly or implicitly a "natural" unit of vegetation (McIntosh, 1967). This belief in "natural" and floristically homogeneous units of vegetation influenced the sampling and analytic methodology used in vegetation study. In one widely-accepted approach to vegetation study, the Braun-Blanquet approach (Braun-Blanquet and Furrer, 1913; Braun-Blanquet, 1932), such methodology is an important and integral aspect of the approach. The approaches based on the objective reality of vegetation units gradually became known as the community-type approach to vegetation study (McIntosh, 1967).

Not all workers believed in the invariance of succession or the objective reality of plant communities, however one, H. A. Gleason, conceding that units of vegetation exist (Gleason, 1917) although they may be only coincidences (Gleason, 1926), stressed that the development and maintenance of vegetation results from the development and maintenance of the component individuals. Gleason reasoned that plant composition is determined by environmental sorting of immigrants from surrounding areas, and inasmuch as adjacent areas possess similar environments and receive immigrants from the same or very similar plant populations, areas of similar, but not precisely the same, vegetation should result. Gleason recognized that dense vegetation can modify and control the environment and consequently species composition and abundance, but he reasserts that the establishment or non-establishment of a plant on an area is determined by the arrival

or non-arrival of a propagule and by the environment encountered, and not by the vegetation *per se*. The result, according to Gleason, is that these two primary causes determine the plant life on every "minimum area," and as a consequence large areas of very similar vegetation do not occur. This concept of plant association Gleason termed the *individualistic* concept.

Concurrent with development of the individualistic concept, a Russian, L. G. Ramensky (1926), independently developed a similar philosophy regarding plant groupings. Ramensky shared Gleason's belief in the ecological individuality of each species, and that each plant reacts individually to the environment it encounters. Ramensky emphasized that plant cover changes continuously in space and that sharp boundaries between locally homogeneous plant groupings are exceptional, requiring special explanation such as human interference, discontinuous alteration of other factors, etc.

Gleason's and Ramensky's concepts of vegetation received little support until Stanley Cain's paper appeared in 1947 (Cain, 1947). Cain argued that each species in a vegetation stand has its individual area of occurrence and a more or less unique ecological amplitude and modality. Consequently, a floristic natural area occurs if the limits of areas of occurrence of a large number of species fall in the same place. In essence, a floristic natural area is characterized by the exclusiveness of a number of plants. As a consequence, associations are local phenomena and are individualistic because they cannot be more extensive than the superposition of areas of the species involved.

Curtis and McIntosh (1951), working in the prairie-forest floristic province of Wisconsin, also attacked the question of the objective reality of a plant community. They stipulated that only within floristic provinces, which have uniform flora and are similar to Cain's natural areas, can plant associations possibly achieve objective reality. The two investigators studied relatively natural, undisturbed stands of deciduous forests growing on upland forms in southern Wisconsin, deleting from study heterogeneous stands but accepting homogeneous ones regardless of their species composition. The two workers attempted to classify the stands into groups, using an index termed importance value. Several orderings, based on different assemblages of species, were tried. No discrete grouping of species was apparent; rather, the entire collection of species formed a continuum. Curtis and McIntosh conclude that their findings substantiate Gleason's individualistic association hypothesis, but with the restriction that the available flora's physiological potentialities and the existing environment limit the species combinations that can occur.

Whittaker (1956), working in the Great Smoky Mountains concurrent with, but independent of, the work in Wisconsin, sampled the vegetation without regard to apparent plant associations. The findings were related to known environmental gradients, using an analytic technique that Whittaker termed direct gradient analysis. Whittaker reasoned that the existence of valid vegetation types, and their relationship fo environmental gradients, would be revealed by abrupt changes in species composition and distinct groupings of species' maximum points,

when various plant characteristics were plotted on environmental gradients. Abrupt changes and distinct groupings did not occur; Whittaker concluded that species are not organized into distinct units but that stands and vegetative types are mainly continuous with one another. Although using different sampling and analytic techniques, Whittaker's conclusions support those of Curtis and McIntosh.

The studies by Cain, Curtis and McIntosh, and Whittaker changes the perspective of ecological thought in North America, causing re-evaluation of Clements' climax-oriented approach and provoking re-appraisal of Gleason's individualistic concept. The organismic equivalence and invariance of a community were placed in doubt, and the regularity of the successional process was questioned.

Numerous studies concerning succession have appeared since Gleason's advancement of the individualistic hypothesis. Some studies, such as Wells' (1928) study of the successional relationships of plant communities on the North Carolina coastal plain, considered communities as concrete entities; but other studies were less community-oriented and more autecological in nature (dePeralta, 1935; Pessin, 1939; Baldwin, 1940). A broader approach to successional studies appeared, however. Billings (1938), for example, explained old-field succession of woody species in terms of interspecific competition, individual species competition and species-induced environmental changes.

Keever (1950) studied the herbaceous vegetation that precedes the woody in old-field succession and found that competition, plant-induced environmental changes and timing of the life cycles

significantly influenced succession. She also observed that a species can modify the environment in a way detrimental to its own survival and that insufficient seeding rates can delay a species' attainment of dominance. Many other workers also have recognized the importance of seeding rates, and numerous studies have dealt with the variability in seed production and the factors influencing seeding rates and seed germination (Bormann, 1953; McVean, 1953; Black, 1958; Allen and Trousdell, 1961; Shoulders, 1961; Harper and McNaughton, 1962; Phares and Rogers, 1962; Stephenson, 1963).

The conflicting views regarding vegetation have resulted in two distinct trends in the approach to vegetation interpretation. The first trend, probably arising with the advent of scientific interest in vegetation, treats vegetation as composed of "well-defined, discrete, integrated units" (McIntosh, 1967). This trend is called the community-type concept. The second trend, termed continuum concept, holds that vegetation changes continuously and is not differentiated, except arbitrarily, into sociological entities (McIntosh, 1967). Although considered a linear descendent of the individualistic hypothesis, the continuum concept originated in the works of Curtis and McIntosh (1951) and Whittaker (1956). These two trends have created a community-contiuuum controversy that has influenced vegetation study. A discussion of some points of controversy and their influence on vegetation study follows.

Some investigators apparently interpret their findings in a manner consistent with their view of vegetation. Poore (1956), for example, specifies that a plant community should be described

according to its present characteristics rather than according "to what it has been or what it is thought about to become." Daubenmire (1966), on the other hand, stresses the need to consider stability when studying vegetation. He recommends that only areas of "maximum homogeneity" be sampled, and preferably only climaxes, or potential climaxes on areas judged to have preclimax vegetation, be considered. Monk (1968) succinctly illustrates the vegetation concept-interpretation interaction by stating (p. 303),

> That earth is continuously covered by vegetation is probably the only fact all vegetation analysts would accept. . . . It would be safe to say that if two researchers of the vegetation continuity-discontinuity schools were permitted to examine the same 1000 "community stands" the resultant would be a continuum on the one hand and a community-type classification on the other. One side would argue that the subjective sample selection is an end in itself whereas the other would propose methodology, state of succession, etc.

Leith (1968) claims that the goals of the two concepts are different: the goal of the community-type approach is a vegetation map while the goal of the continuum approach is the "key-lock explanation of each single species demand on the environment." Leith finds nothing wrong with either approach, except when pertinent information is ignored: for example, when continuum advocates deny the existence of characteristic species and the community-type advocates ignore overlaps. Monk (1968) claims that the community-type adherents minimize and the continuum advocates maximize the importance of the transition zones. Both Monk and Leith agree that in unraveling the causal relationships between vegetation and environment, the continuum approach seems most promising.

An investigator's concept of vegetation influences the methodology he selects (Yarranton, 1967a). A basic aspect, selection of study areas, is influenced. Community-type adherents traditionally have used subjective selection (McIntosh, 1967); they claim it is a major advantage of their approach (Becking, 1957; Poore, 1956 and 1962). Daubenmire (1966) believes that the areas must be subjectively sampled to insure "maximum homogeneity" or the samples will be virtually worthless. Continuum advocates reject that contention, arguing that areas must be objectively chosen, at least for some broadly defined vegetation type, so that preconceived ideas regarding the vegetation do not influence the selection process (Cottam and Curtis, 1949; Curtis and McIntosh, 1951; Whittaker, 1952 and 1962; Goodall, 1963). Cottam and McIntosh (1966) cite the need to sample the majority of an area's vegetation, and not only those parts that are amenable to grouping into discrete associations. Some investigators question whether sampling, and in particular random sampling, of vegetation is possible or useful. Egler (1968) infers that sampling is questionable if stands of vegetation are "coincidental phenomena, with each stand having the chance possibility of being 'significantly' different from the others." Major (1958) argues that sampling can be carried out only within a defined population. Therefore, defining qualitatively homogeneous populations is a prelude to sampling. Major believes that vegetation is not a random chaotic assemblage of plants but is ordered. He concludes that random sampling of <u>all</u> of an area's vegetation would be useless.

Current Approaches and Problems

The continuing community-continuum controversy has accentuated the need to critically evaluate the kinds of vegetation information collected and the methodologies required for their collection. Harper (1967) notes that measures of population turnover are completely obscured by methodologies used in most vegetational studies. Only if individual plants are marked and repeatedly observed can population turnover be assessed. Harper conjectures that plant species plasticity and the ability to reproduce vegetatively are the two main reasons why plant ecologists have not stressed numbers.

Yarranton (1966), concerned with vegetation variation and the sampling methods required for its elucidation, postulates that variation is determined by the distributional patterns of species comprising the vegetation. These patterns can be analyzed in physical terms in real space, or by "abstract statements" of plant interrelationships that may be explicable in terms of real space. Plot sampling methods are suitable for the former, Yarranton claims, but plotless methods are required for the latter.

An analysis of each species' distribution with respect to environmental variables and other species is required for evaluating the individualistic hypothesis (Yarranton, 1967b). Time is an important factor requiring incorporation in the analytic scheme (Yarranton, 1967b; Becking, 1968). Becking, stressing the need to consider the dynamic aspect of vegetation, cautions that the time scale used in a study can influence an investigator's perspective. Becking believes that community descriptions are only relevant as momentary time-lapse pictures of the ever-changing community.

The degree of integration or organization in a plant community is an important consideration in vegetation study. Two of the early workers, Clements and Gleason, differed greatly in their views of integration; Clements believed communities possessed a high degree of integration, but Gleason felt it was inconsequential. The difference in emphasis still persists among current investigators. Poore (1964), analyzing the evidence supporting integration, indicates that two factors, opportunity and competition, determine the composition of a community. Opportunity determines the species composition of the propagules reaching the area, and competition sifts out those species that will persist in the environment encountered. This sifting and selection, according to Poore, establishes a dynamic balance in the community that is reflected in community structure and pattern. This structuring, and possibly other manifestations of competition, lends inertia to the community and tends to inhibit community change. Poore believes that to understand natural vegetation we must understand integration's role. Detailed studies of the autecology of species under competitive conditions of natural communities are needed. Poore suggests that integration should be an essential part of the definition of community.

Understanding the selective processes operative during development of a community is essential in order to understand the nature of vegetation structure (Anderson, 1965). Knowing the quantitative and qualitative importance of both the intensity and duration of selection is required. Anderson postulates that the ultimate structure of vegetation depends upon the parts played by chance and

selection; if selection is weak and intermittent, chance plays a substantial role. But, if selection is intense and persistent, chance contributes only slightly. Based on a study in northwest Iceland, Anderson et al. (1966) concluded that intense selection exerted by the "harsh" environment limited the number of successful species; a weakly developed, climatically controlled continuum resulted. Poore (1967) suggests that opportunity and selection operate differentially on different segments of a vegetation's flora. He contends that the occurrence of the less common tree species in a tropical forest is correlated with physical environmental factors, which implies that selection has influenced the distribution of those species. The more common species, however, appear to be influenced less by environmental factors than by chance of dispersal and establishment. Not all workers agree with Poore's interpretation, however (Austin and Greig-Smith, 1968).

The complexity of vegetation undoubtedly is causing ecologists to seek special tools and techniques. Austin and Greig-Smith (1968) indicate as much when they criticize Whittaker's (1967) assertion that the simpler ordination techniques are more likely to provide advances in ecological understanding than are the more elaborate techniques. Slobodkin (1965) stresses the point that field studies cannot stand alone, stating (p. 349),

> . . . it is almost certain at the moment that field observation by itself, in the absence of laboratory and theoretical study, is almost useless in providing explanations (of field phenomena). . . theoretical and laboratory analyses can provide limits for the possible functions of various processes in the field . . . making possible, decisions between various alternative hypotheses with respect to field data.

Quantitative analytic techniques are increasing in importance in vegetative study. Goodall (1963), for example, used geometric models based on vegetation space having an axis for each species comprising the vegetation and plotting each sample area as a point in that space. He stressed that the distribution of points in vegetation space reflects two completely distinct factors: 1) the frequency distribution of the different sites, and 2) the "adaptations" of species locally available to the ecotope and to each other. Goodall observes that if clumping of points depends only on unequal availability of sites, the clusters of points do not reflect different communities, or at least not well-integrated communities. If the points show clumping, while the distribution of sites does not, strong "presumptive evidence" for an integrated community exists.

Modeling also is increasing in importance. Two modeling approaches particularly pertinent to vegetation study are advanced by Leak (1968) and Yarranton (1969). Leak formulates a probability model to depict birch regeneration in a clear-cut area. The model, essentially a branching diagram of probabilities, considers probabilities for events ranging from development of a female flower to the growth of a commercially acceptable stem. The model, although rather specific, is a valuable contribution to vegetation study, for it demonstrates that variables such as conditional probabilities can furnish insight into vegetation processes.

A different approach to modeling is advanced by Yarranton. Using point sampling procedures, Yarranton uses a species' presence or absence at a defined point as the characteristic of interest.

That characteristic serves as the dependent variable and is combined with independent variables such as the presence of plants of the same or other species at various distances from the defined point, environmental factors and time, in a regression analysis. Yarranton acknowledges that application of the model to natural succession may prove difficult, particularly because of the number and difficulty of measurement of possibly pertinent independent variables. Initial application perhaps should be too simple, controlled growth studies, but Yarranton obviously believes the models' main potential is for broad application. He states (p. 249),

> The model described above provides a basis for comparative studies of the ecology of single species and of the interaction between them, and is unifying in the sense that the results of many types of ecological investigation, including pattern analysis, interspecific association and autecological experiments, can all be incorporated. It also provides the theoretical basis for a new approach which may lead to quantitative analysis of succession.

The latter aspect, the new approach to succession studies, may be the most significant aspect of Yarranton's modeling work.

DESCRIPTION OF THE MODEL

The model for succession proposed here will be stated first in its full form, but then of necessity it will be modified to a form that is feasible in the present states of knowledge and computer capability.

The Full Model

Succession is defined with reference to points on the earth's surface, as the present state along with the set of probabilities of state transition during the next time interval. By the state at a point is meant the species and age composition of plants covering the point; thus there are many possible states. The probabilities refer to transition from the present state to any one of all the possible states, including the present state. Vegetational succession is thus identified as a non-random change in time of the distribution of states for the set of all points on the surface.

There are three principal elements of this model of succession. These are the vector of all possible states, the matrix of transition probabilities for the next unit of time, and a feedback mechanism. The feedback permits environmental factors to modify the transition probabilities and also to alter the seed vector which is a special subset of the state vector.

The model can be written as:

$$\underline{s}_{t+1} = \underset{\sim}{T}({}^{s}t,\ {}^{e}t;\ \underline{\theta})\underline{s}_{t}$$

where

$\underline{s}_t$ = state vector at time, t

$\underline{s}_{t+1}$ = state vector at time, t+1

$\underline{e}_t$ = vector of environmental forces at time, t

$\underset{\sim}{T}$ = transition matrix whose elements are functions of $\underline{s}_t$, $\underline{e}_t$, and $\underline{\theta}$

$\underline{\theta}$ = vector of parameters involved in T.

The number of elements in $\underline{s}$ will be very large if the model is to be realistic. The functional form of T, in order to be realistic, will also be very complex.

The composition of the parameter vector, $\underline{\theta}$, will depend on the functions specified for the elements in $\underset{\sim}{T}$. The elements in $\underline{\theta}$ will include plant parameters such as growth rates, but they also might include those relatively unchanging environmental factors that are not plant modified.

Illustration of the Full Model

The forest succession model I propose may be identified with secondary succession on a recently denuded forested area. I assume that woody species immediately invade the area; the model applies to vegetational development and change at points located on the denuded area. The model involved defines the presence of plants, the states, at the points, and the probabilities that the situation will persist or change during the next time interval.

This general approach can be illustrated by a possible sequence that could occur at a point during a very simple succession. In Figure 1, I have listed a possible five-year sequence for a succession involving only 2 species, A and B. During year 1 of the sequence, a seed of species A falls on the point. That seed germinates and survives, so that at year 2, a year-old plant of species A covers the point. That plant persists throughout the five-year sequence, recorded as a successively older species A plant during each of the last three years.

A species B plant, five years old, covers the point at year 2, although it was not recorded at the point in year 1. Such an occurrence may result if a 4-year-old plant growing near the point, but not covering it, grows sufficiently during year 1 so that by year 2 the 5-year-old plant covers the point. Species B also is represented in the 5-year span by a seed that appears at year 3 but does not produce a viable 2-year-old plant.

State Vector

The elements of the state vector are defined to be the fractions of the points on the area covered by all possible combinations of species and age classes, as well as by bare ground. The different ways of coverage could be, for example, coverage by, but only by: bare ground; one individual of a given species of a given age; two individuals of a given species of a given age; three individuals, etc.; two individuals of different species of the same age, etc.; two individuals of a given species of different ages; two individuals of different species and different ages; three individuals of different

AGE	TIME: Year 1	Year 2	Year 3	Year 4	Year 5
SEED	Species A	Bare	Species B	Bare	Bare
1-Year	Bare[a]	A	Bare	Died	Bare
2-Year	Bare	Bare	A	Bare	Bare
3-Year	Bare	Bare	Bare	A	Bare
4-Year	Bare[b]	Bare	Bare	Bare	A
5-Year	Bare	B	Bare	Bare	Bare
6-Year	Bare	Bare	B	Bare	Bare

[a]Denotes no covering of the point by any plant of that age.

[b]A 4-year-old plant of species B growing near the point, but not covering it, grew sufficiently so that at age 5 the plant covered the point.

Figure 1. A possible sequence of events at one specific point during a five-year interval of a forest succession involving only 2 species, A and B, and 6 age classes

species and different ages; etc.; through all possible combinations of coverage by different numbers of individuals of different species of different ages. The model reflects a composite of all states at all points.

This set theoretic description of successional state has three immediate advantages. First, it conforms to the widespread use of cover as a field measurement in plant ecology. Second, it permits the direct field estimation of state by sampling of randomly selected points. Third, it provides the logical basis for a description of change and permits a rigorous definition of the dynamic process of succession.

Plant ecologists have used characteristics other than cover to describe vegetational state by field sampling. Density, frequency, abundance and basal area, in addition to cover have received greatest use. The first three are population, not individual plant characteristics, and thus are not suitable for specifying the states at sample points. Basal area is an individual plant characteristic, but in order to use it for describing states at a point additional specifications are necessary. For example, is the basal area used for the plant whose stem covers the point, for the stem nearest the point, or for the plant meeting some other requirement? In addition, a plant fortune could be changing drastically, such as dying of most of the branches, with only slight manifestation in basal area. Because of the above reasons, and the fact that cover directly relates to the amount of incoming solar energy intercepted by a plant, I have used cover as the measure of plant state.

Point sampling is the sampling procedure I have used in this study. That procedure allows one to follow the fortunes of the individual plants covering the point, and to assess the influence previous occupants have on their successors. Consequently, two factors influential in plant succession can be evaluated: inter- and intra-specific competition and plant-induced environmental changes. Plot sampling methods also would make available the above information if repeated mapping of the plots occurred, but two reasons weigh against their use. First, repeated mapping would be very time-consuming and second, the state vector for a plot would be unmanageable.

Two point sampling approaches could be pursued; either the procedure could be used to locate the individual plant whose fortunes then would be followed, or the point would serve as the focal point and changes in plant characteristics at the point would be measured. The second point sampling approach is the one I have used in this study because in addition to recording the fortunes of an individual plant, a possibility with both point sampling approaches, the changes occurring after the death of an individual plant must be ascertained. The second point sampling approach provides the necessary temporal continuity at a specific location to satisfy that need. Another advantage of the second method is that random location of the points with respect to the coverage on an area ensures that the proportion of the points covered by a certain state is an unbiased estimator of the fraction of the area covered by that state.

Seed Vector

The seed vector is the subset of the state vector that describes the presence or absence of a seed covering the point. The individual entries are probabilities that a seed of a particular species, or no seeds for the bare ground entry, will fall and cover the randomly located point. Thus the seed vector contains one more entry than the number of species comprising the succession. The amount of seed produced and the size and shape of the seeds influence the probabilities, for the probabilities reflect the percentage of the ground surface covered by the seeds of each species. As seed-bearing-age trees appear in the succession, feedback relationships change the seed probabilities, increasing them as the number of seed-producing trees increases.

Seeds on the ground also can be considered as one or more age classes: more than one age class if viable seeds can persist on the ground for more than one year. The fraction of the area covered by various combinations of different numbers of seeds of different species of different ages are the states contributed by seeds.

Transition Matrix

The probabilities of state changes during a time interval are the elements of the transition matrix. For each state there is a probability, possibly near zero, of change during the next time interval to each other state, and a probability for staying in the same state. The full model transition matrix is thus square, of dimension equal to the number of possible states and therefore very large.

Further, each transition probability is assumed to be state determined and not explicitly a function of time. Thus past history has its effect on the present through the composition of the state vector and by alteration of environmental factors with consequent changes of the transition probabilities brought about through the feedback mechanism. There can be no doubt that the probability of a state change at a point will differ with different histories of the same state at a point. For example, the probability that a pine tree will grow at a point currently covered by bare ground will be a certain value if that point previously was covered by a mature oak but a different value if a mature pine had lived there. However, the influence exerted by those trees during their life can presently be manifested only through the current environmental factors, such as litter, soil pH, etc. Consequently, the modified environmental factors are the facets of importance when the influences of history on the probabilities are considered.

Other environmental factors not influenced by past histories will also influence probabilities, and those factors also must be considered when specifying the transition matrix. In essence, the transition matrix is a function of the state vector and of the environmental factors other than those describing state.

Feedback Relationships

As a stand matures its characteristics undergo change; this is succession. Obviously modification in species composition of seed-bearing-age trees changes the seeding rates, but also of great importance are the environmental changes resulting from changed

species compositions and densities. These two facets must be considered in a succession study, and I have incorporated them by specifying feedback relationships from the state vector to the seed vector and to the transition matrices.

Feedback to Seed Vector. This mechanism must keep track of the changes in seed production and monitor their expression by the seed vector. Seed production of a given species will depend upon the presence and density of trees of seed-bearing age, as well as the interaction of environmental factors with tree age and stand density.

Feedback to Transition Matrices. Successional changes modify a plant's microclimate as well as the soil. Some of these changes are very marked, in turn producing marked changes in species composition. Some of these changes appear less important, yet it seems safe to postulate that any environmental or floral change may change the transition probabilities to some degree. This means that each different state may have its unique associated transition matrix, altered from the previous matrix by action of the feedback mechanism. Clearly, neither biological information nor computer capacity are adequate to allow the specification of so complex a system.

The Reduced Model

The great volume and complexity of the full model is revealed by only superficial examination. With our present insight into vegetational processes we can only be crudely realistic. Consequently, simplification of the model is necessary. With appropriate simplification, integration of the resulting reduced model and associated field and experimental studies should be possible. That approach

should provide us with the information needed to eventually restructure the model, allowing us greater realism.

The number of elements in the state vector may be reduced. First, those combinations of species and age classes that are impossible biologically can be omitted. Second, many combinations for cover occur so rarely that they can be omitted entirely or can be grouped with other rare combinations. Third, species that are very similar ecologically can be combined into one group, provided information on a single species basis is not required for any member of the group. Fourth, consideration of herbs may be omitted entirely. These changes involve only a combination or deletion and not a restructuring of the model.

The next possibility for simplification does involve a change in the model. This is by specifying a state vector for <u>each age class</u> of plants defined in the study. A state then pertains to an age class and consists of coverage by the various possible combinations of number of plants and species, but considered only within that age group. This move greatly reduces the number of states in the model. Another reduction in number of states is by specifying age groups of unequal length.

Finally, a major reduction in complexity of the model is achieved by restricting the transition probabilities to those associated with state changes from one age class to the next older age class, plus those to bare ground. This change greatly restricts the size of the transition matrix.

The model, given the restriction to age group-specific states discussed above, can now be rewritten as:

$$\underline{s}_{i+1,\ t+1} = \underset{\sim}{T}_{i+1}(\underline{s}_{i,\ t},\ \underline{e}_t;\underline{\theta})\underline{s}_{i,\ t}$$

where

$\underline{s}_{i,\ t}$ = state vector for i^{th} age group plants at time, t

$\underline{s}_{i+1,\ t+1}$ = state vector for i+1 age group plants at time, t+1

$\underline{e}_t$ = vector of environmental forces at time, t

$\underset{\sim}{T}_{i+1}$ = transition matrix, associated with transitions from i age group to i+1 age group plants, whose elements are functions of $\underline{s}_{i,\ t}$, $\underline{e}_t$, and θ.

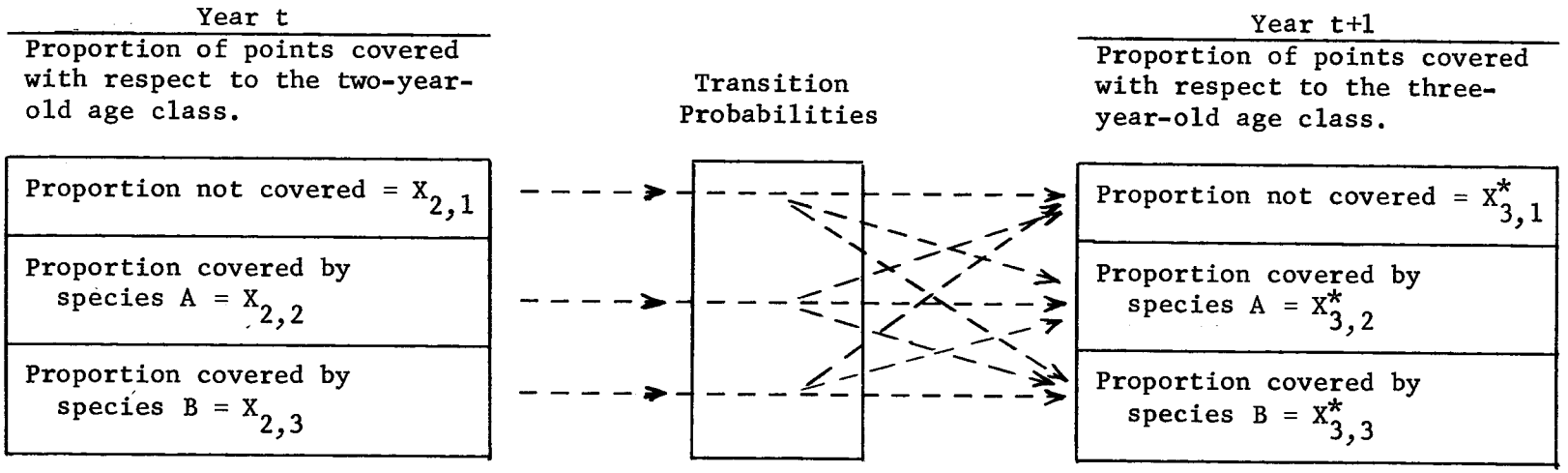
$\underline{\theta}$ = vector parameters involved in T_{i+1} .

Illustration of Reduced Model

Figure 2 shows the changes from time t to time t+1 for one age group, the 2-year-old plants in a vegetation comprised of two species, A and B. Similar illustrations apply to all other age groups specified in the reduced model.

The State Vectors

The use of age group-specific states is justifiable at our present stage of understanding successional processes. Two of the most important facets of vegetation development are selection and competition, yet they are poorly elucidated for most vegetation types. Some investigators (see Literature Review) indicate that competition occurs only if plants are more or less equal; an overstory tree and understory seedling relationship is not a competitive



$X_{i,j}$ = proportion of points covered by the ith age class of plants of the jth species (1 = bare ground; 2 = species A; 3 = species B) during the tth year.

$X^*_{i,j}$ = proportion of points covered by the ith age class plants of the jth species during year t+1.

$X^*_{3,j}$ = $X_{2,1}$ (transition probability that a point not covered by a two-year-old plant at time t will be covered at time t+1 by a three-year-old plant of species j).

$X_{2,2}$ (transition probability that a point covered by a two-year-old species A plant at time t will be covered at time t+1 by a three-year-old plant of species j).

$X_{2,3}$ (transition probability that a point covered by a two-year-old species B plant at time t will be covered at time t+1 by a three-year-old plant of species j).

Figure 2. A diagram showing the changes from year t to year t+1 as two-year-old plants of species A and B mature to three-year-old plants

one, those investigators claim, but solely one in which the overstory tree exerts its influence through modification of important facets of the environment such as light regimes, soil moisture, etc. With trees, the more or less equal plants are those of the same age; hence specifying states on an age class basis insures that we retain in the model those states influenced strongly by competitive relationships. The overstory tree-seedling state would not be retained, but the overstory tree influences would be incorporated in the functional relationships specified for the appropriate seedling transition matrices.

The age group approach allows detail in specifying states within age groups, without increasing the number exhorbitantly. For example, n important states might exist and need elucidation for seedlings and m for a specific age of overstory trees. If the age group approach was not used, n x m states would need to be specified to give us the necessary detail for both the seedlings as well as the overstory trees. The simplification using age groups is substantial, especially if many combinations of overstory trees produce essentially identical environmental changes.

Another reduction in number of states involves specifying age groups of unequal length. The probabilities for continuance of a state or for going from one state to another for a particular species undoubtedly change greatly during the first few years of a plant's growth. For example, the probability that a seedling survives to a one-year-old plant is probably much different than the survival probability to two years of a one-year-old plant. As the plant

grows older, however, the year-to-year transition probabilities probably change very little until advanced age is attained. For many years of a plant's life those probabilities are probably near 0 or 1 for a change of species or a continuance of one, respectively. If the probabilities are relatively unchanging for a number of years in a plant's life and if the probability for changing states is very small, combining of a number of ages into new age groups may be warranted. The advantages, of course, would be fewer parameters to estimate and a decrease in computational effort. Changes in transition probabilities and states undoubtedly contain information regarding vegetation processes. If we combine a number of ages possessing such changes, such information for the new age groups would be unavailable. Therefore, the new age groups should have state changes involving only one step, i.e. from state i to state j and not through an intermediate state k. Requiring that the ages being combined have small probabilities of state changes insures that the above condition is met.

The seedling stages are very critical stages of a tree's life, often with rather high mortality rates applying. Each of the first two or three years should be an age group, or perhaps even more than one if the situation warrants. As the tree grows older, however, the evidence in favor of combining ages increases and various ages should be combined.

Seed Vector

I have incorporated two simplifications into the reduced model that affect the seed vector. The first simplification is the single

vector specification for seeds states. That simplification is predicated on the assumption that all seeds justifiably can be lumped in one age group. The second simplification, which influences the seed state values as well as the feedback relationships, involves specifying a vector called MAX SEED. That vector contains the largest permissible seed cover values for each species, reflecting field investigation findings that seed production in certain species may level off, or even decrease, as the stand densities increase beyond certain limits. In the present model, I did not incorporate feedback relationships that would decrease seed production for densities exceeding certain values, but only specified the maximum seed values.

Transition Matrices

Defining states only within age groups requires a redefinition of the transition matrix. If the state vectors are restructured to reflect the within age group competitive relationships, the transition probabilities also must be restructured to reflect the fortunes of plants in those age groups. That is, the probabilities of individuals of an age group dying or surviving to the next age group are the ones of primary concern. The other transitions, such as transition from coverage by a m-year-old individual to coverage by a m+10-year-old individual, probably result primarily from changed environmental conditions imposed by the older age group and not by interplant relationships. Hence, transition probabilities, which are functions of environmental factors, for transition from one age group to the next contain much of the relevant information. The many

possible transitions from one age group to a much different age group probably individually contain very little additional information and a justifiable simplification is to delete them in the specification of transition matrices. Consequently, in the reduced model matrices of order equal to the number of species in the succession plus one and whose entries are transition probabilities are specified for every age group except seeds. The first transition matrix transforms the seed vector into probabilities reflecting the per cent cover for one-year-old, or first age group plants (Figure 3). These first age group values are then transformed by the second transition matrix, and cover values for age group two plants result. This process continues for older age groups and their associated transition matrices.

Feedback in Reduced Model

At our present stage of knowledge trying to specify in detail the functional relationships of plants probably is an exercise in futility. Only crudely realistic characterizations of the relationships are possible with our present knowledge. Some general simplifying assumptions are possible, however; a reasonable one is that the elements of $\underline{e}$ not influenced by plants are time-invariant and can be absorbed in $\underline{\theta}$. Some of the elements in $\underline{e}$ that are influenced by plants, such as light intensity and radiation at the ground surface, can be related to elements in $\underline{s}_t$ associated with the overstory vegetation. Such elements in $\underline{e}$ can thus be related to elements of T in terms of elements in $\underline{s}_t$. For the remaining elements in $\underline{e}$ and for $\underline{s}_t$, the initial specification of their relationships to the

Probabilities, or per cent cover, for the seed age class at year t.	Transition matrix for the seeds to one-year-old age class state change.		Probabilities, or per cent cover, for the one-year-old age class at year t+1.
$X_{0,1} \quad X_{0,2} \quad X_{0,3}$	$P_{1,1} \quad P_{1,2} \quad P_{1,3}$	=	$X^*_{1,1} \quad X^*_{1,2} \quad X^*_{1,3}$
	$P_{2,1} \quad P_{2,2} \quad P_{2,3}$		
	$P_{3,1} \quad P_{3,2} \quad P_{3,3}$		

$$X^*_{1,j} = \sum_{k=1}^{3} X_{0,k} \; P_{k,j} \; .$$

The values of 1, 2, and 3 for j or k denote bare ground, species A and species B respectively.

$P_{k,j}$ is the probability that a point in state k with respect to seeds at time t is in state j with respect to one-year-old plants at time t+1.

Figure 3. The probabilities, reflecting per cent cover, for one-year-old plants generated from a vector containing seed probabilities and from a matrix of transition probabilities

elements of the T's should be simple and straightforward. As more insight and knowledge is gained, additional complexity reflecting greater realism can be incorporated.

Feedback to Seed Vector. I based the seed feedback relationship on the assumption that the change in seeding rate caused by a change in the area covered by the ith age group plants of species j is proportional to that change in cover. The exact change in seed probabilities caused by i^{th} age trees is the product of the change in cover of the ith age trees and the relative measure of the influence of that age group.

The relative measure of an age group's influence is contained in a matrix called a RESEED matrix, that has as column vectors relating to each species in the succession. The matrix has a row per age group other than seeds, and a column for each species and for bare ground. The entry in the ith row and j^{th} column is a relative measure of the influence of the ith age-group trees of species j on the seed probabilities for that species.

A facet of the reduced model that influences the exact specification of feedback relationships is the age group feature. Suppose the ith age group consists of a ten-year interval, say for trees 50 to 60 years old. At the conclusion of a ten-year period, the changes in area covered by a certain species' trees of that age reflect changes that are occurring during the interval, and that influence seed probabilities as they occur. However, the change is calculated only at the conclusion of the interval, and any feedback relationships must await that calculation. As a result, if that age group

has a large influence on seed probabilities, substantial changes in seed probabilities will occur every ten years, but in the interim they will be relatively unchanging. This is certainly an unnatural feature in a succession simulation, and would produce a spasmodic progression of the simulated succession. To counteract this feature, I have, in my simulation runs, arbitrarily apportioned the change into as many equal parts as there are years in the interval, thus producing gradual changes in seed probabilities and in progression of succession. This procedure causes a slight lag in interaction effects, however, and hence slows the speed of succession.

The feedback equation used in the model is as follows. Let,

X_{ij} = the change in per cent cover of age group i plants of species j.

T_{ij} = relative measure of the influence of ith age trees of species j on that species seed probabilities. These values are in the RESEED matrix.

h_i = number of age-classes (years) combined to form age group i.

S_j = seed probability for species j.

ΔS_j = change in seed probability for species j.

m = number of age groups other than seeds.

Then

$$\Delta S_j = \sum_{i=1}^{m} (\Delta X_{ij} \cdot T_{ij}/h_i) .$$

Let S_j^* be the adjusted seed probability. Then,

$$S_j^* = S_j + \Delta S_j .$$

Feedback to Transition Matrices. The $P_{i,j}$'s, specified on an age-specific basis, are functions of time, environment and the species composition of the stand. That is, for the ℓ age group,

$$P_{i,j} = f(s_{\ell,t}, e_t; \theta) .$$

As I have discussed earlier, specifying the functional relationships for the $P_{i,j}$'s is very difficult at our present stage of knowledge. Perhaps our first concern should be to determine which environmental factors and species characteristics causally influence vegetation and when during a plant's life and the course of succession they are important. The reduced model is structured to contribute to those objectives.

I have incorporated the transition feedback relationships into the reduced model by specifying certain equations to adjust the transition probabilities. I specified that the change in the probability that a species maintains itself at a point from age i to i+1 is proportional to the product of the change in per cent cover of the species interacting with it and its own per cent cover. That is, the change in the transition probability that a point covered by species j in age group i continues to be covered by j in age group i+1 is proportional to the product of the change in per cent cover of interacting species k, say in age group ℓ, and the per cent cover of species j. The per cent cover of the interacting species is included because when it is scarce its effects on the species interacted with will be smaller than when it is abundant. The equations for the transition probability changes follow. Let,

n = number of species plus one (for bare ground).

$P_{i+1,j,k}$ = probability that a randomly located point now covered by species j of age group i will be covered by an age group i+1 plant of species k after a time interval equal to the length of age group i has passed.

$\Delta P_{i+1,j,k}$ = the change in $p_{i+1,j,k}$.

$I_{j,k}$ = a parameter signifying that species k has an effect on species j. In my simulations, this parameter is incorporated into the program in a square matrix, named INTER, of dimension n. The values can be negative or positive.

$X_{i+1,j}$ = per cent of area covered by i+1 age group plants of species j. In my simulation program a matrix named APV, of dimension (m,n), contains these values.

$F_{i+1,\ell}$ = a parameter signifying that plants of age group ℓ can interact with plants of age group i+1. These values are specified in my simulation program by a square matrix named FDBACK of order m. In my simulation runs I use values 0 or 1.

Then,

$$\Delta P_{i+1,j,j} = \left(\sum_{q=i}^{n} \left[\sum_{\ell=1}^{m} X_{\ell,q} \cdot F_{i+1,\ell} \cdot \Delta X_{\ell,q} \right] \cdot I_{j,q} \right) /$$

(number of age groups interacting with i+1 age group).

The transition probabilities associated with changing states, for example going from species j at age i to species k at age i+1, are also influenced as succession progresses. I used the basic adjustment

specified above, multiplying its value by the transition probability being adjusted. Hence, the changes in these transition probabilities are proportional to the probabilities themselves. The equation for this change is

$$\Delta P_{i+1,j,k} = \left(\left(\sum_{\ell=1}^{m} X_{\ell,k} \cdot I_{j,k} \cdot F_{i+1,\ell} \cdot \Delta X_{\ell,k} \right) / \right.$$

$$\left. \text{(number of age groups interacting with i+1 age group)} \right)$$

$$\cdot\ P_{i+1,j,k}\ .$$

The corrected probabilities are, letting P^* be the corrected values,

$$P^*_{i+1,j,j} = P_{i+1,j,j} + \Delta P_{i+1,j,j}$$

$$P^*_{i+1,j,k} = P_{i+1,j,k} - \Delta P_{i+1,j,k}$$

$$P^*_{i+1,k,j} = P_{i+1,k,j} + \Delta P_{i+1,j,k}\ .$$

In this reduced model I have included only one matrix INTER for species interactions and only one, FDBACK, for feedback effects. If I had included a separate interaction matrix for each species, I undoubtedly could have obtained greater realism. However, considering the lack of suitable succession data, and hence the basis for estimating the elements of those matrices, as well as the increased costs of simulation that a more complex model would produce, I concluded that the initial modeling should not strive for excessive detail. Actually, when suitable data and insight are available, it may be necessary to specify for each age group a matrix of size (n, n, n-1, m) before the interrelationships between species and age groups can be evaluated and simulated.

RESULTS

The reduced model was converted to a computer program using FORTRAN IV language (Appendix A). An IBM 360 Model 40 computer was used to produce five simulated successions involving only two plant species. Those successions, based on data sets listed in Appendix B, are contained in Appendix C.

Data Sets

I attempted to locate data sets that would be suitable for illustrating my modeling approach. A thorough search of the literature failed to reveal any set that would be useful. The essential criteria missing from all sets were adequate information regarding the age and fortunes of individual plants during some time interval, and the spatial relationships of those plants and their neighbors. Consequently, I had to fabricate data sets.

State Vectors

The initial state vectors have zeros for both plant species and 1.0 values for bare ground entries. Such values result from the specification that the simulated successions are based on reinvasion of a denuded area.

Seed Vector

I could not find any data directly specifying the values for entries in the seed vector, but numerous papers reporting seed production for commercially important lumber species exist (see Literature Review). The data reveal substantial temporal and spatial

variability as well as a large variability of seed size. To fabricate a set of data on seed probabilities, I made certain assumptions concerning seed production. Table 1 gives the probabilities associated with four different seed production rates and two different size specifications.

The initial probability values specified in the seed vectors for all simulations were encompassed by the values in Table 1.

Table 1. The probabilities that a seed will cover a randomly selected point given four seed production rates and two seed sizes[a]

SEED PRODUCTION	SEED SIZE	
(Seeds per Acre)	50	100
50,000	0.00016	0.00008
200,000	0.00064	0.00032
500,000	0.00159	0.00082
1,000,000	0.00319	0.00159
1,300,000	0.00414	0.00207

[a]Seed size based on number of seeds required to cover completely a surface area of one square inch.

Transition Matrices

A number of studies shed some insight into the probabilities that can pertain early in a plant's life, particularly with respect to mortality of seedlings. However, I could not locate any studies that directly aided in specifying transition probabilities. Consequently, I arbitrarily specified probabilities that I hoped were both realistic and illustrative.

Feedback Relationships

The general feedback relationships used in the reduced model are discussed in the section The Reduced Model.

Feedback Relationship to Seed Vector. Although a number of studies have dealt with the influences of stand age and densities on seed production, none have specified the relationships existing between the stand characteristics and seed production; only observations were reported. The lack of detail in describing the stand characteristics prohibited using the data as bases for estimating the relative influence of each age group on seed probabilities. Hence, I arbitrarily specified values for the RESEED matrix.

Feedback Relationship to Transition Matrices. No data sets exist as bases for estimating the FDBACK matrix values used in the feedback relationship. Consequently I used a simple assumption as a guide for setting those values. I assumed that older age classes influenced the fortune of younger age classes, but that the reverse situation was sufficiently inconsequential to warrant its exclusion. I also assumed that all existing relationships were inhibitory.

The values used in the INTER matrix differ from simulation to simulation. The specific values chosen were designed to illustrate interspecific influences, and were not based on any existing data sets.

The Data Used

The five data sets used are identical except for the INTER and RESEED matrices. The differences are illustrated in Table 2. In Data Set 1 the -1 value in the second and third rows of the second

Table 2. The INTER and RESEED matrices in the five data sets used in this study

Data Set	INTER Matrix			RESEED Matrix		
1	0	-0.05	-0.05	0	0	0
	0	-1	-1	0	0	0
	0	-1	-1	0	0	0
				0	0.001	0.001
				0	0.008	0.008
				0	0.015	0.015
				0	0.015	0.015
				0	0.005	0.005
				0	0.001	0.001
2	0	-0.05	-0.05		Same as #1	
	0	-1	-2			
	0	-1	-1			
3		Same as #1		0	0	0
				0	0	0
				0	0	0
				0	0.05	0.001
				0	0.016	0.008
				0	0.030	0.015
				0	0.030	0.015
				0	0.010	0.005
				0	0.001	0.001
4	0	-0.05	-0.05		Same as #1	
	0	-2	-1			
	0	-1	-1			
5	0	-0.05	-0.05		Same as #1	
	0	-1	-3			
	0	-1	-1			

and third columns specify that species A and B have equal self- and alien-inhibiting effects; in Data Set 2 the -2 value in the third column of the second row specifies that species B has twice the alien-inhibiting effect on A that A does on B, as well as twice the effect of any self-inhibiting influence. The RESEED matrix in Data Set 1 reveals equal effects for the two species of various age seed-bearing trees on seeding rates; in Data Set 3 the values in the species A column are approximately twice those in the species B column, reflecting an influence on seeding rates by seed-bearing trees of species A that is twice that by similar age trees of species B. Data Sets 4 and 5 differ from Set 1 only in the INTER matrix values. In Data Set 4 the self-inhibiting effect of A is twice that of any other inhibiting effect and in Set 5 the alien-inhibiting effect of B on A is three times that of any other inhibiting effect.

Results of the Simulations

The results of the five simulations are listed in Appendix C. Before considering the individual simulations some general comments concerning cover values are necessary. The cover values for the different age groups in year 10 of Simulation 1 (see Appendix C) will help illustrate aspects that need to be kept in mind.

The one-year-old seedlings show cover values of .076 for both species. The .076 values represent the portion of the ground covered by those plants, assuming that no overlapping of species A and B one-year-old plants exists. If one-year-old plants of the two species overlapped, but a supplementary specification was used rather than a two-species state designation, the .076 value would

represent the proportion of the area covered, with respect to one-year-old plants, solely by species A (or B) plants plus part of the area covered jointly by A and B plants. The .848 value represents the proportion of the area not covered by one-year-old plants.

The cover values for the different-age plants of a species are not additive. That is, the .076, .182, .212 and .109 values for the 1-, 2-, 3- to 4-, and 5- to 8-year-old plants of species A do not give a sum that denotes the total proportion of the area covered by species A, for overlapping of different-age trees of A could occur. The sum would equal the proportion of the area covered by A only if no overlapping of different-age species A plants occurred, a highly unlikely situation. Hence, the traditional measure of a species' cover, the percentage of the ground covered by plants of that species, cannot be obtained from the simulated results. Only if the states were all possible combinations of plants of any species and ages would a sum be appropriate for giving the traditional measures of cover. That aspect should be kept in mind when evaluating the results of the simulations.

If the assumption that the different-age trees are randomly distributed can validly be made, the traditional cover values can be estimated. An estimate of bare ground would be the product of the bare ground values for every age class. An estimate of the cover for any specific species would be the sum, for all combinations of one cover category per age class in which at least one age class has the cover entry pertaining to the species in question, of the products of each combination's cover values. If randomness cannot be

assumed, the distribution of the cover for different-age trees would need to be known before the tradntional cover values could be estimated.

Simulation 1

The seed probabilities for species A and B appear to be unchanged from their initial values of .0010 at the tenth year of succession (see year 10, simulation 1, Appendix C). However, if additional significant digits were included, the values for each species would have shown a change from the .00100 initial value to a .00101 value at year 10. The change is very small, due to the fact that only plants of the 5- to 8-year-old group, of those present at year 10, are influencing seed production. That aspect is revealed by the zero values in the second and third columns of the 1-, 2-, and 3- to 4-year-old age group lines in the RESEED matrix, and the .001 values in those columns for the 5- to 8-year-old age group line. The adjustment equation is listed in the section Feedback to Seed Vector.

Plants from older age groups gradually appear in the stand as succession progresses and stand density increases. By year 80 the cover values for the younger age classes are changing only slightly, and the seed cover values have increased from the initial value of 0.0010 to 0.0023.

The increase in cover continues for all age classes throughout succession, but the rate of increase slows as succession progresses. During the 50-year span from year 100 to year 150, only age groups 57-80 years and greater than 80 years show any appreciable change.

By year 150 the succession is relatively unchanging with respect to cover, and by year 177 the stand has met the requirement I specified for an unchanging forest: none of the transition probabilities change by more than .005 during two consecutive adjustments of each transition matrix.

The seed vector at the termination of succession had probabilities of coverage of .0030 for both species. The identical values reflect the fact that equal specifications for both species were made in all facets of the data set. The equality for both species persists in all aspects of the simulated succession.

The coverage values at termination increase with age for the first through the sixth age groups; the values then decrease for the last three age classes. Although the seed probabilities for the two species increased by a factor of 3 from year 10 to year 177, the coverage values for the first 3 age groups increased only by approximately 10 per cent during that interval. The difference reflects the adjustments made to the transition probabilities as succession progressed.

The adjustments made to the transition probabilities are influenced by the values in the FDBACK and INTER matrices (see Feedback to Transition Matrices). For example, the first row of the FDBACK matrix in Data Set 1 has as values two zeros followed by seven ones. Those values indicate that plants of age groups 1 and 2 years cannot influence the transition probabilities in the first transition matrix but that the plants of the 7 older age classes potentially can. The last row of the FDBACK matrix has all zeros,

indicating that none of the age groups can modify the transition probabilities connecting the last two age classes.

Even though a value of one appears in the FDBACK matrix, indicating that plants of a certain age class have the potential of modifying the transition probabilities in a specific transition matrix, the question as to which probabilities are modified when the cover values for a given species change is not answered. That answer is given by the INTER matrix. For example, the FDBACK matrix in Data Set 1 has a 1 in the third column of the first row, indicating that the 3- to 4-year-old plants potentially can modify the probabilities in the first transition matrix. The -1 value in the third column of the second row of the INTER matrix indicates that species B has an adverse effect on species A. That is, as the population of species B increases, its inhibiting influence on A increases. When that value is combined with the FDBACK matrix, as it is in the adjustment equation (see page 43), the resulting combination determines which age group plants of a species interact with specific age group plants of other species. As I indicated above, both species are equally self- and alien-inhibiting in Data Set 1; the four -1 values in the INTER matrix denote that fact. The -.05 values in columns 2 and 3 of row 1 indicate that as the population of species A and B increases, the probability that a point continues to be covered by bare ground decreases.

The specifications used for the FDBACK and INTER matrices in Data Set 1 caused adjustments that produced the final transition matrices listed in Appendix C. Only the final ones have been included

in the simulation results; the initial ones, of course, are listed in the data set.

The transition probabilities undergoing greatest modification were those associated with changes from one species to another in the younger age classes. For example, the probability that a point covered by a one-year-old plant of species A is covered one year later by a two-year-old plant of species B changed from .040 at the start of succession to .068 at year 177. The probability change associated with the one-year-old species A plant-bare ground state change only varied from .010 to .002 during the same period. The larger differences associated with species-to-species changes reflect the fact that the absolute values of the INTER matrix entries associated with species-to-species effects are greater than those for species-to-bare-ground effects (i.e., 1 versus .05).

The Other Simulations

Data Set 2 differed from Set 1 only by the fact that the alien-inhibiting effect of species B on A was twice the value in Set 2 that it was in Set 1 (-2 versus -1). The depressing effect of B on A is very evident in the final year of the simulation, year 369. At that time, in most age classes the cover values for species B were three times greater than those for A. In addition, the seed probabilities for A were only 0.0019, whereas those for B had reached the maximum allowable level, 0.0040.

The influence of B also is very evident in the transition matrices values. For example, in transition matrix 2 the probability that a point covered by a one-year-old species A plant will be covered

a year later by a two-year-old species B plant changed from an initial value of 0.040 to a final one of 0.234. The reverse species change, B to A, changed from the initial 0.004 value to a final one of nearly zero.

The different cover values for the two species result jointly from different seeding rates and different transition probabilities. In an attempt to ascertain which of these were most influential, another simulation was run that was based on a data set, Data Set 3, in which the competitive relationships were the same for both species; but the influence of the seed-bearing-age trees on seeding rates was approximately twice as great for species A as it was for B (see Table 2). The initial seeding rates were identical for the species.

The influence on cover values of the differentially changed seeding rates was slight. In year 225, the cover values were approximately the same for both species and the final transition probabilities had changed only slightly from the initial ones. The final seeding rates, however, were quite different, being 0.0040 and 0.0029 for A and B respectively. Apparently in my model the seeding rates are unimportant and the influence changing cover values must be the transition probabilities. As an aid in determining whether self-inhibiting effects produced greater changes in transition probabilities than did alien-inhibiting ones, two additional data sets, Sets 4 and 5, were run. In Data Set 4, the self-inhibiting effect of Species A was twice as great as any other inhibitory effect, and in Set 5 the alien-inhibiting effect of B on A was three times larger than any other.

The results from Simulations 4 and 5, in conjunction with Simulation 2, clearly show that the alien-inhibiting effect produces much greater changes in transition probabilities, and consequently cover values, than does the self-inhibiting effect. That result, of course, is an obvious consequence of the feedback equations. The adjustment to the transition probabilities pertaining to state changes is proportional to the cover values. Hence, the self-inhibiting effect that would cause that species to be replaced by another produces less change on the associated transition probabilities as the species cover value decreases. The change produced by the alien-inhibiting effect does not decrease as the inhibited species cover value decreases.

DISCUSSION

Aims and Accomplishments of This Modeling Study

The relationships within and between the floral elements and the environmental factors must be explained in a causal context if we are to understand the processes involved in shaping vegetation. Field observations of natural vegetation are essential for identifying the existence of the relationships. For explaining the relationships in a causal context, however, field observations by themselves are inadequate. Theoretical and experimental studies must be integrated with a field study. I am not implying that all three must be conducted simultaneously. I am implying that the results from any of the three must be meaningful and interpretable in terms of the others, however. If that condition is satisfied, one theoretical approach, modeling, can be a powerful analytic tool in vegetation studies. That consideration substantially influenced the structure of my succession model, for gaining insight into successional processes is the primary objective of this modeling effort.

I believe that this modeling study successfully accomplishes its primary objective, for this model can be integrated with a properly structured field study to provide insight into successional processes. An example of what can be done will illustrate that point.

Suppose that we wish to evaluate the influence on survival of 1-, 2- and 3-year-old plants of species A caused by neighboring species B plants. The neighboring plants, if they do not cover the sample point, are not specified in the state for that point; the presence

of those plants is reflected in the model only through plant-modified environmental factors. However, strong competitive relationships might exist that influence survival of the young species A plants, with very little evidence of those relationships manifested by the plant-modified environmental factors. Only by evaluating survival with respect to the neighboring plants can those competitive relationships be revealed. That evaluation is possible by judiciously partitioning the sample space on the basis of the neighboring plant composition. Simulations can then be run for those subsets of sample points of interest. The differences exhibited by the different simulations will furnish insight into the competitive relationships, as well as aiding in delimiting which experimental studies are needed to further elucidate the consequential inter-specific relationships.

Many other partitionings of the sample space also are possible; the above approach can be used with them as well. The limitation to using this approach is not determined by the model, but is determined solely by the data collected in the field study.

Characteristics of an Associated Field Study

Even a cursory examination of vegetation reveals that vegetation is not, either temporally or spatially, a random assortment of species. Additional examination also reveals that the vegetation possesses variability, both spatially and temporally. These two aspects, nonrandomness and variability, are of concern to plant ecologists for these two are manifestations of the relationships existing within and between the floral elements and the environmental

factors and of the temporal and spatial variability of the environment. Measurement of characteristics that provide information concerning the relationships, and the ability to relate the information to the nonrandomness and variability of vegetation and the variability of the environment, are essential attributes of a field study.

Kinds of Data Needed

The fortunes of propagules and individual plants determined the vegetation of an area. That is, the pattern of dispersal of propagules, and the response of propagules and individual plants to their environment, which includes the adjacent vegetation, determine which plants will occupy a given space at a given time. Consequently, vegetation change is a result of modification or replacement of individual plants. Knowing how, why and when they change and knowing the environment of an area, including the vegetation-modified component of the environment, are essential in order to understand vegetation processes. Repeated measurement of individual plants and their environments is the kind of data that leads to such understanding.

Selection of Study Areas

Two considerations largely govern the selection of study areas. The first concerns the type or kind of succession, *i.e.* a pine-oak succession in the southeastern United States or an aspen--white birch--white spruce succession in northern North America, and the second, the geographic locations.

Selecting the Type of Succession. Most ecologists agree that the degree of complexity in ecological systems increases with increasing diversity of species in the system. If that concept holds, and considering the number of transition and seed probabilities and feedback relationships that must be specified in this succession study, the number of species comprising the succession is a criterion meriting attention when selecting succession type. A succession involving only four or five tree species seems the most desirable for basing the initial field studies. Even then, the number of parameters to be estimated will be large, but succession involving fewer species, and hence fewer parameters, will lack the multi-species interactions, which probably are very important facets of more complex situations. A reasonable compromise between complexity and realism seems to be a succession involving four or five species of trees.

A successional type having a rapid successional rate and a relatively short time to completion is desired. Age groups of only a few years each will be possible and relatively few age groups will be needed.

Selecting the Geographic Locations. Since even a rapidly proceeding succession may require more than 100 years for completion, studying only one plot through the entire process is not feasible. Rather, a number of different stands reflecting different levels of successional maturity must be studied concurrently.

Selection of the specific stands or study plots depends on the availability of the required age groups and the perceptible or

suspected historical differences and current environmental differences. The plots should be proximally located to reduce spatially-related environmental differences, but selection should also serve to reduce other physiographic and topographic differences as much as is feasible.

Study plots must be selected so that plot to plot differences do not substantially modify or change the succession pattern or the parameter values. In fact, evaluation of the successional data requires an assumption of no consequential plot to plot effects. Any stand to stand differences in parameter values or feedback relationships then can be assumed to be due to different levels of maturity and not to other factors. With proper replication this assumption can, and should, be tested, but extensive replication for a succession of long duration would require a large number of study plots. Again, a relatively short-term succession is an advantage.

Characteristics to Use in Determining State

A number of characteristics could be used in determining the state at a point. The selection of characteristics primarily depends on their relevance to the successional process and the ease with which they can be measured.

Relevance to the Successional Process. The characteristics used should be an important feature in the successional process and should reflect substantive changes in succession. For example, a characteristic could be the covering of a point by the stem of a tree; for a specific age group a point could be covered by the stem of a tree from any of the species or be uncovered. Once a point is

covered by a stem in any age group, the states in all other age groups could only be the uncovered state. Substantial changes could be occurring in the stand, for example the specific tree covering the point as well as other individuals of the same species in the stand could be degenerating steadily, yet states based on the stem characteristic largely would remain unchanged. In essence the characteristics used in state determination must be meaningful ones reflecting stand changes.

Ease in Measuring. Ease and economy in measuring a characteristic are very desirable features, especially in light of the large number of sample points needed in a succession study. Preferably, only a visual inspection should be needed to determine state. The cover by aerial parts characteristics satisfies this requirement. However, the selection of characteristics for a specific study must depend on the evaluation of attributes with respect to that particular study.

General Characteristics of This Model

A few general characteristics of this model warrant discussion. They concern the point orientation of the model, the simplifications used and relating the reduced model to the "whole" system.

Point As a Sample Unit

The model is developed with respect to points on the land surface, yet I have stressed above (see section Kinds of Data Needed) that the fortunes of individual plants is the kind of information needed in order to understand successional processes. Although points

are the sample units, the information obtained concerns plant fortunes, for the repeated measurements at a point can be assumed to be repeated measurements of the same individual plants. That assumption is possible because I used cover on an age-class and species-specific basis. For example, if our field data showed that a point was covered at year t by a 10-year-old species A plant and a 1-year-old species B plant, at year t+1 by an 11-year-old species A plant and a 2-year-old species B plant, and at year t+2 by a 12-year-old species A plant but not by a species B plant, the conclusion that only two individual plants were measured during that three-year span and that the younger plant died in its second year of life probably would be correct. That is, the fortunes of two individual plants were recorded.

Simplifications in the Model

Any vegetation model that approaches a one-to-one correspondence of the vegetation and model parameters would be unmanageable. The large number of vegetation parameters results from the large number of species involved and the necessity of considering time and the environment. In some judicious manner a decision has to be made as to which parameters should be ignored or combined, and which should be considered separately. In essence, what simplifications should be employed in fashioning a reduced model of manageable proportions?

Guiding Concept. The guiding concept I used in determining model simplifications was that any detail lost by simplifying the full model should be recoverable by using the simplified model in

conjunction with associated field or experimental studies. The state vector simplification illustrates that aspect.

Rather than defining all possible combinations for cover at a point, only combinations within an age-group of plants were considered. Hence a point that was covered by a 3-year-old species A plant and a 3-year-old species B plant would have a species A state for the 2-year-old age group, a species B state for the next older age group, and a bare ground state for all other age groups. The point's detailed cover state, that is cover by a 2-year-old species A plant and cover by a 3-year-old species B plant, would not be specified. In addition, transitions only from one age group to the next older age group were considered. Consequently, transition probabilities that probably contain a great amount of information regarding inter-specific and inter-age group interactions, such as the probability that a point covered at time t by a seedling of species A and an 80-year-old plant of species B will be covered only by an 81-year-old plant of species B one year later, are not included in the model. Hence the model, by itself, provides little insight into the 80-year-old plant-seedling interaction. However, if in an associated field study a collection of points has been selected using some random selection scheme, that collection of points can be partitioned so that one subset of points possesses the 80-year-old plant-seedling state and the other the seedling state. Separate simulated successions then can be run for each subset of points and the differences assessed. Those differences should provide insight into the 80-year-old plant-seedling interaction.

In effect, the above procedure allows an investigator to regain through partitioning of the sample space detail that was lost by model simplification.

Simplifications Used. The two important simplifications used to fashion the reduced model, that is specifying states solely on an age group basis and specifying transition probabilities only for state changes to the next older age group, were based on the belief that inter-specific competitive relationships are influential in determining vegetation change; such importance dictates that a succession model include those relationships. Inter-specific competition usually is most intense between ecologically similar organisms; with trees, that situation probably exists with equal-age trees. Consequently, those states defined within an age group probably are the states in which competitive effects are most influential. Such effects undoubtedly are manifested in the pattern of plant survival to the next older age group. Therefore, states defined on an age group basis and transition probabilities for state changes to the next older age group are of sufficient importance to warrant their inclusion in a model. The other states and transition probabilities probably contain much less information on competition than do the ones discussed above, and I deleted them from my model.

The states and transition probabilities I deleted contain information about the relationships existing between plants of different ages. With plants of very different ages, such as an overstory tree and a seedling, the influences probably are uni-directional. That is, the influence of a seedling on an overstory

tree probably is negligible, with only the opposite one of consequence. Most of the influence of any overstory tree on a seedling undoubtedly occurs through environmental modification such as shading, formation of a duff layer, changed temperature regimes, etc. By measuring the modified environmental factors, the influences exerted by an overstory tree can be incorporated into the model. Consequently, the loss of information is not as great if the unequal-age states are deleted rather than the equal-age states.

The Reduced Model and the "Whole" System

My reduced model does not treat a forest succession in its entirety; parts are deleted, with the information contained in the deleted parts recoverable only by using the model in conjunction with a field study. Is lack of treatment of the "whole" a serious drawback?

A complex system such as forest succession has many different facets that need elucidation. Not all facets require equal detail, however. If our insight into a system is superficial, as is our insight into successional processes, we cannot efficiently and effectively structure a whole system model of a complex system, for we do not know which facets are important or the levels of detail required. The first task is to understand the parts comprising the system; this modeling effort is designed primarily for that level of understanding.

As our level of understanding increases, we can use greater detail and complexity in our models. That is, we can move toward the full model. Whether we will ever reach the goal of a full model

is debateable, for perhaps we are intellectually incapable of comprehending and inter-relating at the necessary levels of detail, all facets of a complex system. None-the-less, as we strive to reach the full model, we will continue to increase our understanding of the system. That consideration provides ample justification for the approach I am advocating.

SUMMARY AND CONCLUSIONS

Vegetation is a complex, dynamic phenomenon. Any vegetation study has to be structured to deal with the complexity and to consider the dynamic aspect. Integration of field study, modeling and experimentation can aid in coping with the complexity and evaluating the dynamic aspect.

At our present level of understanding of successional processes, we can build only crudely realistic models. Simplifications are necessary. The simplifications used, however, should not cause excessive loss of detail of the important facets of succession. Detail should be sacrificed only for the less important facets. If a field study is properly structured and integrated with the model, the information lost through simplification can be regained by using the model as an analytic tool in conjunction with the field study.

Studying the fortunes of individual plants is essential if insight into the vegetation processes is desired. The spatial and temporal relationships of individual plants, and their micro-environments, are critical features needing elucidation. These considerations demand repeated observations of individual plants. Measuring or estimating population parameters, such as mean per cent cover, clearly does not give us the necessary information concerning individual plant phenomena.

Variation is a feature of vegetation that requires attention from plant ecologists. We cannot continue to structure our vegetation studies so that the information contained in variability is unavailable to us. We need to structure our studies so that the extent of and

causes of variability are ascertained. Both spatial and temporal variability are of concern, of course.

The assessment of plant composition at and near randomly selected points is a procedure demanding serious attention from plant ecologists. With a proper sample design, with adequate measurement of the environment, and with adequate grouping of age-classes, the approach appears promising for studying forest succession. For initial study, a forest succession that involves few species, has a rapid rate of change, and attains maturity quickly is the most desirable.

LIST OF REFERENCES

Allen, P. H., and K. B. Trousdell. 1961. Loblolly pine seed production in Virginia-North Carolina coastal plain. J. Forestry 59: 187-190.

Anderson, D. J. 1965. Classification and ordination in vegetation science: controversy over a non-existent problem. J. Ecol. 53:521-526.

Anderson, D. J., R. C. Cooke, T. T. Elkington, and D. J. Read. 1966. Studies on structure in plant communities. II. The structure of some birch copse and dwarf-heath communities in Skjaldfannardalur, Northwest Iceland. J. Ecol. 54:781-793.

Austin, M. P., and P. Greig-Smith. 1968. The application of quantitative methods to vegetation survey. II. Some methodological problems of data from rain forest. J. Ecol. 56:827-844.

Baldwin, H. I. 1940. Plant competition for soil moisture. Ecology 21:400-403.

Becking, R. W. 1957. The Zurick-Montpellier school of phytosociology. Bot. Rev. 23:411-488.

Becking, R. W. 1968. Vegetational response to change in environment and change in species tolerance with time. Vegetation 16:135-158.

Billings, W. D. 1938. The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. Ecol. Monog. 8:437-499.

Black, J. N. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (Trifolium subterraneum L.) with particular reference to leaf area and the light microclimate. Aust. J. Agr. Res. 9:299-318.

Bormann, F. H. 1953. Factors determining the role of loblolly pine and sweetgum in early old-field succession in the Piedmont of North Carolina. Ecol. Monog. 23:339-358.

Braun-Blanquet, J. 1932. Plant Sociology: The Study of Plant Communities. McGraw-Hill, N. Y., N. Y.

Braun-Blanquet, J., and E. Furrer. 1913. Remarques sur l'etude des groupements des plantes. Bul. Soc. Languedocienne des geographic George 36:20-41. (Excerpts in Kormondy, J. E. 1965. Readings in Ecology. Prentice Hall, Englewood Cliffs, N. J.)

Cain, S. A. 1947. Characteristics of natural areas and factors in their development. Ecol. Monog. 17:185-200.

Clements, F. C. 1916. Plant succession, an analysis of the development of vegetation. Publ. Carnegie Inst., Washington, D. C., 242: 1-512.

Clements, F. C. 1928. Plant Succession and Indicators. H. W. Welson Co., N. Y., N. Y.

Cottam, G., and J. T. Curtis. 1949. A method for making rapid surveys of woodlands by means of pairs of randomly selected trees. Ecology 30:101-104.

Cottam, G., and R. P. McIntosh. 1966. Vegetational continuum. Science 152:546-547.

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dune of Lake Michigan. Bot. Gaz. 27:95-117; 167-202; 281-308; 361-391.

Curtis, J. T., and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.

Daubenmire, R. 1966. Vegetation: identification of typal communities. Science 151:291-298.

de Peralta, F. 1935. Some principles of competition as illustrated by Sudan grass, Halus sorghum sudanesis (Piper) Hitch. Ecol. Monog. 5:355-404.

Egler, F. E. 1968. The continuum concept of vegetation: responses. Bot. Rev. 34:259-267.

Gleason, H. A. 1917. The structure and development of the plant association. Bull. Torrey Bot. Cl. 44:463-481.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Cl. 53:7-26.

Goodall, D. W. 1963. The continuum and the individualistic association. Vegetation 11:297-316.

Harper, J. L. 1967. A Darwenian approach to plant ecology. J. Ecol. 55:247-270.

Harper, J. L., and I. H. McNaughton. 1962. The comparative biology of closely related species living in the same area. VII. Interference between individuals in pure and mixed populations of Papaver species. New Phytologist 61:175-188.

Keever, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. Ecol. Monog. 20:229-250.

Leak, W. B. 1968. Birch regeneration: a stochastic model. USDA For. Ser. Res. Note NE-85.

Leith, H. 1968. The continuum concept of vegetation: responses. Bot. Rev. 34:291-302.

Major, J. 1958. Plant ecology as a branch of botany. Ecology 39: 352-363.

McIntosh, R. P. 1967. The continuum concept of vegetation. Bot. Rev. 33:130-387.

McVean, D. N. 1955. Ecology of Alnus glutinosa (L.) Gaertn. II. Seed distribution and germination. J. Ecol. 43:61-71.

Monk, C. D. 1968. The continuum concept of vegetation: responses. Bot. Rev. 34:303-305.

Pessin, L. J. 1939. Root habits of longleaf pine and associated species. Ecology 20:47-57.

Phares, E., and N. F. Rodgers. 1962. Improving shortleaf pine seed production in Missouri. J. Forestry 60:322-324.

Poore, M. E. D. 1956. The use of phytosociological methods in ecological investigations. IV. General discussion of phytosociological problems. J. Ecol. 44:28-50.

Poore, M. E. D. 1962. The method of successive approximation in descriptive ecology. Adv. Ecol. Res. 1:35-68.

Poore, M. E. D. 1964. Integration in the plant community. J. Ecol. 52 (Suppl.):213-226.

Poore, M. E. D. 1967. The concept of association in tropical rain forest. J. Ecol. 55:46-47.

Ramensky, L. G. 1926. Die grundgesitzmassigkeiten in aufbau der vegetationsdecke. Bot. Zentralbl. N.F. 7:453-455.

Shoulders, E. 1961. Effect of seed size on germination, growth and survival of slash pine. J. Forestry 59:363-365.

Slobodkin, L. B. 1965. On the present incompleteness of mathematical ecology. Am. Scient. 53:347-357.

Stephenson, G. K. 1963. Ten years of shortleaf pine seed crops in Texas. J. Forestry 61:270-272.

Warming, E. 1909. Oecology of Plants, an Introduction to the Study of Plant Communities. Translation by Percy Groom and Isaac Balfour. Clarendon Press, Oxford, England.

Wells, B. W. 1928. Plant communities of the coastal plain of North Carolina and their successional relations. Ecology 9:230-242.

Whittaker, R. H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. Ecol. Monog. 22:1-44.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monog. 26:1-80.

Whittaker, R. H. 1962. Classification of natural communities. Bot. Rev. 28:1-239.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. 49:208-264.

Yarrenton, G. A. 1966. A plotless method of sampling vegetation. J. Ecol. 54:229-237.

Yarrenton, G. A. 1967a. Organismal and individualistic concepts and the choice of vegetation analysis. Vegetation 15:113-116.

Yarrenton, G. A. 1967b. Principal component analysis of data from sacicolous bryophyte vegetation at Steps Bridge, Devon. III. Correlation of the variation in the vegetation with environmental variables. Can. J. Bot. 45:249-258.

Yarrenton, G. A. 1969. Plant ecology: a unifying model. J. of Ecol. 57:245-250.

APPENDICES

Appendix A. Computer Program of Simulation Model

```
C     SIMULATING FOREST SUCCESSION
        COMMON SV(5),KCHECK(14),APV(14,5)
        COMMON TM(14,5,5),DELPV(14,5),AINTER(5,5),LENG(14)
        COMMON FDBACK(14,14)
        COMMON RESEED(14,5)
        COMMON SMAX(5)
        COMMON FACSEE(5)
        COMMON NSP,NST
        DIMENSION SUM(14,5)
        REAL PREPV(14,5)
    202 DO 1 L=1,5
        DO 1 K=1,5
        AINTER(L,K)=0
        DO 1 I=1,14
      1 TM(I,L,K)=0
        DO 2 I=1,14
        LENG(I)=0
        DO 2 L=1,5
        DELPV(I,L)=0
        APV(I,L)=0
        PREPV(I,L)=0
      2 SUM(I,L)=0
        DO 3 L=1,5
        FACSEE(L)=0
      3 SV(L)=0
        DO 4 I=1,14
      4 PREPV(I,1)=1.0
        DO 575 I=2,14
        SUM(I,1)=1.0
    575 APV(I,1)=1.0
C    READ DATA SET
C    INPUT ORDER AS FOLLOWS:
C    DATA SET IDENTIFICATION - 1 CARD
C    NO. STAGES, NO. SPECIES, DIFFER VALUE(T¾ DETERMINE IF TM
                                VALUES CHANGING),
C    AND PRINT INTERNAL(YEARS) CODE - 1 CARD
C    SEED VECTOR(INITIAL SEED PROBS) - 1 CARD
C    MAXIMUM SEED PROB ALLOWED - 1 CARD
C    NO. YEARS IN EACH STAGE - 1 CARD
C    INTER MATRIX - NSP CARDS(NSP=NO. SPECIES + 1)
C    FDBACK MATRIX - NSP CARDS
C    TRANSITION PROBS - NSP*NST CARDS(NST=NO. STAGES. WITH NSP
                                CARDS PER STAGE)
C    RESEED MATRIX - NST CARDS
C    VARIABLE AMORE(NON-ZERO IN COL 1 INDICATES ANOTHER DATA
                                SET FOLLOWS) - 1 CARD
        READ(1,99) NSET
        WRITE(3,409) NSET
```

```
      READ(1,100) NST,NSP,DIFFER,KODE
      READ(1,215) (SV(I),I=1,NSP)
      READ(1,215) (SMAX(I),I=1,NSP)
      READ(1,101) (LENG(I),I=1,NST)
      DO 110 I=1,NSP
  110 READ(1,102) (AINTER(I,J),J=1,5),NSP1
      DO 218 I=1,NST
  218 READ(1,217) (FDBACK(I,J),J=1,NST)
      DO 111 I=1,NST
      DO 111 J=1,NSP
      READ(1,103) (TM(I,J,K),K=1,5),NSTAGE,NSP1
      IF(NSTAGE-I)999,112,999
  112 IF(NSP1-J)999,111,999
  111 CONTINUE
      DO 580 I=1,NST
      READ(1,581)(RESEED(I,J),J=1,5),NSTAGE
      IF(NSTAGE-I)999,580,999
  580 CONTINUE
      NSTL=NST-1
      ANSPL=NSP-1.
C     COMMENCE PROGRAM
      KSTOP=0
      KYEAR=1
      KOUNT=1
      KSUMYR=LENG(1)
C   FIRST YEAR OF SUCCESSION
      DO 558 I=2,14
      KSUMYR=KSUMYR+LENG(I)
  558 KCHECK(I)=1
      KCHECK(1)=0
C   COMPUTE APV VALUES(REFLECTING COVER) FOR ONE YEAR OLD PLANTS
      DO 113 I=1,NSP
      DO 113 J=1,NSP
  113 APV(1,I)=APV(1,I)+SV(J)*TM(1,J,I)
      APVADJ=0.
      DO 562 L=1,NSP
  562 APVADJ=APVADJ+APV(1,L)
      DO 563 K=1,NSP
  563 APV(1,K)=APV(1,K)/APVADJ
      IF(LENG(2)-1)571,571,572
  572 DO 574 L=1,NSP
  574 SUM(1,L)=APV(1,L)+PREPV(1,L)
C   COMPUTE CHANGE IN APV VALUES FROM BEGINNING TO END OF AGE
                                  GROUP
  571 DO 564 L=1,NSP
  564 DELPV(1,L)=APV(1,L)-PREPV(1,L)
      DO 565 L=1,NSP
  565 PREPV(1,L)=APV(1,L)
C   BEGIN SECOND AND SUCCEEDING YEARS OF SUCCESSION
  201 KYEAR=KYEAR+1
      KOUNT=KOUNT+1
```

```
      CALL ADJUST
      DO 553 I=2,14
  553 KCHECK(I)=KCHECK(I)+1
      DO 578 L=1,NSP
  578 APV(1,L)=0.
C   COMPUTE NEW APV VALUES FOR ONE YEAR OLD PLANTS
      DO 114 I=1,NSP
      DO 114 J=1,NSP
  114 APV(1,I)=APV(1,I)+SV(J)*TM(1,J,I)
      APVADJ=0.
      DO 554 L=1,NSP
  554 APVADJ=APVADJ+APV(1,L)
      IF(APVADJ)556,556,555
  555 DO 557 K=1,NSP
  557 APV(1,K)=APV(1,K)/APVADJ
      IF(KCHECK(2)-LENG(2))556,567,567
  566 DO 568 J=1,NSP
      SUM(1,J)=SUM(1,J)+APV(1,J)
      DELPV(1,J)=APV(1,J)-PREPV(1,J)
  568 PREPV(1,J)=APV(1,J)
      GO TO 569
  567 DO 570 J=1,NSP
      DELPV(1,J)=APV(1,J)-PREPV(1,J)
      SUM(1,J)=PREPV(1,J)
  570 PREPV(1,J)=APV(1,J)
  569 CONTINUE
  556 LASDIV=LENG(NST)/LENG(NSTL)
C   COMPUTE APV VALUES FOR PLANTS OLDER THAN ONE YEAR
      TOTYR=1
   50 DO 150 I=2,NSTL
      II=I-1
      III=I+1
      TOTYR=TOTYR+LENG(I)
      IF(TOTYR-KYEAR)116,585,582
  116 LDIV=LENG(I)/LENG(II)
C     CHECK TO SEE IF AT END OF STAGE AND IF PREVIOUS AND
                                 SUCCEEDING STAGES
C     ARE ALSO IN THEIR LAST YEAR
      IF(KCHECK(III)-LENG(III))118,117,117
  117 IF(KCHECK(I)-LENG(I))582,119,119
C     STAGES AT END YEAR SO NEW PROBABILITY VECTORS COMPUTED
  119 DO 576 L=1,NSP
  576 APV(I,L)=0.
      DO 120 J=1,NSP
      DO 120 L=1,NSP
  120 APV(I,J)=APV(I,J)+SUM(II,L)*TM(I,L,J)
C     ADJUST NEW PROB VECTOR TO BASE 1
      APVADJ=0
      DO 121 L=1,NSP
  121 APVADJ=APVADJ+APV(I,L)
      IF(APVADJ)550,550,559
```

```
  559 DO 122 L=1,NSP
  122 APV(I,L)=APV(I,L)/APVADJ
C   COMPUTE CHANGES IN APV VALUES FROM START TO END OF AGE GROUP
  550 DO 123 L=1,NSP
      SUM(II,L)=PREPV(II,L)
      DELPV(I,L)=APV(I,L)-PREPV(I,L)
      PREPV(I,L)=APV(I,L)
  123 CONTINUE
      KCHECK(I)=0
      GO TO 150
  585 DO 586 J=1,NSP
  586 SUM(I,J)=PREPV(I,J)
      LDIV=LENG(I)/LENG(II)
C   NEXT STAGE NOT AT END YEAR - CURRENT STAGE AT END YEAR
  118 IF (KCHECK(I)-LENG(I))150,124,124
  124 DO 577 L=1,NSP
  577 APV(I,L)=0.
      DO 125 J=1,NSP
      DO 125 L=1,NSP
  125 APV(I,J)=APV(I,J)+SUM(II,L)*TM(I,L,J)
      APVADJ=0
      DO 126 L=1,NSP
  126 APVADJ=APVADJ+APV(I,L)
      IF(APVADJ)560,560,552
  552 DO 127 L=1,NSP
  127 APV(I,L)=APV(I,L)/APVADJ
  560 DO 128 J=1,NSP
      SUM(I,J)=SUM(I,J)+APV(I,J)
      SUM(II,J)=PREPV(II,J)
      DELPV(I,J)=APV(I,J)-PREPV(I,J)
  128 PREPV(I,J)=APV(I,J)
      KCHECK(I)=0
  150 CONTINUE
C   CURRENT STAGE A D NEXT STAGE NOT AT END YEAR
      TOTYR=TOTYR+LENG(NST)
      IF(TOTYR-KYEAR)583,583,582
  583 IF(KCHECK(NST)-LENG(NST))582,129,129
  129 DO 579 L=1,NSP
  579 APV(NST,L)=0.
C   COMPUTE APV VALUES FOR LAST STAGE
      DO 130 J=1,NSP
      DO 130 L=1,NSP
  130 APV(NST,J)=APV(NST,J)+SUM(NSTL,L)*TM(NST,L,J)+PREPV
                                 (NST,L)*TM(NST,
     1L,J)
      KCHECK(NST)=0
      APVADJ=0.
      DO 131 L=1,NSP
  131 APVADJ=APVADJ+APV(NST,L)
      IF(APVADJ)561,561,551
  551 DO 132 L=1,NSP
```

```
  132 APV(NST,L)=APV(NST,L)/APVADJ
  561 DO 133 L=1,NSP
      SUM(NSTL,L)=PREPV(NSTL,L)
      DELPV(NST,L)=APV(NST,L)-PREPV(NST,L)
  133 PREPV(NST,L)=APV(NST,L)
  582 IF(KSUMYR-KYEAR)587,587,588
  588 KSTOP=0
  587 IF(KYEAR-150)134,135,139
C   CHECK PRINT INTERVAL CODE(KODE)
  134 GO TO(136,137,138,139),KODE
  136 IF(KOUNT-10)221,140,221
  137 IF(KOUNT-20)221,140,221
  138 IF(KOUNT-2)221,140,221
  139 IF(KOUNT-50)221,140,221
  135 KODE=4
  221 KSTOP=KSTOP+1
      DO 141 I=1,NST
C     CHECK TO SEE IF STABILIZED
      DO 141 J=1,NSP
      IF(ABS(DELPV(I,J))-DIFFER)142,142,143
  142 CONTINUE
  141 CONTINUE
      GO TO(144,140),KSTOP
  143 KSTOP =0
  144 ATEST=1.0*KYEAR/50
      IF(KYEAR/50-ATEST)201,140,201
C     BEGIN OUTPUT OF INFORMATION
  140 WRITE(3,401) KYEAR
      WRITE(3,402) (SV(L),L=1,NSP)
      WRITE(3,407)
      DO 146 I=1,NST
  146 WRITE(3,403) I,(APV(I,J),J=1,NSP)
      KOUNT=0
      IF(KYEAR-1000)733,147,147
  733 IF(KSTOP-2)201,147,147
  147 WRITE(3,404)
      DO 148 I=1,NST
      WRITE(3,408) I
      DO 160 J=1,NSP
  160 WRITE(3,405) I,J,(TM(I,J,K), K=1,NSP)
  148 WRITE(3,406)
      READ(1,105) AMORE
      IF(AMORE)149,149,202
  581 FORMAT(5F5.2,3X,I2)
  100 FORMAT(2I2,6X,F10.8,9X,I1)
  101 FORMAT(14(3X,I2))
  102 FORMAT(5F5.0,4X,I1)
  103 FORMAT(5F10.8,8X,I2,9X,I1)
  105 FORMAT(I1)
   99 FORMAT(15X,I5)
  215 FORMAT(10X,5F10.8)
```

```
217 FORMAT(14F2.0)
216 FORMAT('1','DATA OUT OF ORDER')
401 FORMAT('1',' YEAR ',I5/)
402 FORMAT(' ',' SEED VECTOR',8X,5(F10.8,2X)///)
403 FORMAT(' ',' STAGE ',I2,10X,5(F10.8,2X))
407 FORMAT(' ',' PROBABILITY VECTORS'/)
408 FORMAT('0',' TRANSITION MATRICES STAGE ',I2/)
404 FORMAT('1',' TRANSITION MATRIX PROBABILITIES')
405 FORMAT(' ',' STAGE ',I2,' ROW ',I2,6X,5(F10.8,2X))
406 FORMAT('1'1)
409 FORMAT('1',' DATA SET NUMBER ',I5/)
999 WRITE(3,216)
149 CONTINUE
    END
```

```
      SUBROUTINE ADJUST
C   ADJUST SEED VECTOR AND TRANSITION MATRICES
      COMMON SV(5),KCHECK(14),APV(14,5)
      COMMON TM(14,5,5),DELPV(14,5),AINTER(5,5),LENG(14)
      COMMON FDBACK(14,14)
      COMMON RESEED(14,5)
      COMMON SMAX(5)
      COMMON FACSEE(5)
      COMMON NSP,NST
      DIMENSION CORR(5)
      DIMENSION UPAPV(5),SUMAPV(5)
      REAL NEWSV(5)
      SNEWSV=0
      DO 600 L=1,NSP
      SUMAPV(L)=0.
      SEESUM=0
      NEWSV(L)=0
      CORR(L)=0
      DO 601 I=1,NST
      IF(RESEED(I,L))601,601,621
  621 SEESUM=SEESUM+1.
  601 CORR(L)=CORR(L)+RESEED(I,L)*DELPV(I,L)/LENG(I)
      IF(SEESUM)611,611,612
  612 CORR(L)=CORR(L)/SEESUM
      GO TO 613
  611 CORR(L)=0
  613 NEWSV(L)=SV(L)+CORR(L)
      SEEADJ=0.
      IF(FACSEE(L))626,626,627
C   CHECK TO DETERMINE IF NEW SEED PROBS EXCEED MAXIMUM ALLOWED
  626 IF(NEWSV(L)-SMAX(L))630,630,623
  623 FACSEE(L)=1.
      DO 625 J=1,NST
  625 SUMAPV(L)=SUMAPV(L)+APV(J,L)*RESEED(J,L)
      UPAPV(L)=SUMAPV(L)
      GO TO 624
  627 DO 628 J=1,NST
  628 SUMAPV(L)=SUMAPV(L)=APV(J,L)*RESEED(J,L)
      IF(SUMAPV(L)-UPAPV(L))629,624,624
  629 FACSEE(L)=0.
  624 SEEADJ=NEWSV(L)-SMAX(L)
      NEWSV(L)=SMAX(L)
      NEWSV(1)=NEWSV(1)+SEEADJ
      GO TO 600
  630 IF(NEWSV(L)-0.0005)631,600,600
  631 NEWSV(L)=0.0005
  600 SNEWSV=SNEWSV+NEWSV(L)+SEEADJ
      DO 602 L=1,NSP
  602 SV(L)=NEWSV(L)/SNEWSV
      DO 603 I=1,NST
      IFOR=I-1
```

```
      IF(KCHECK(I))614,614,603
  614 DO 603 L=1,NSP
      DO 603,K=1,NSP
      SUMNUM=0
      SUMDEN=0
C   ADJUST TRANSITION PROBS
      DO 604 J=1,NST
      IF(KCHECK(J))647,647,604
  647 ADD=APV(J,K)*DELPV(J,K)
      SUMNUM=SUMNUM+ADD*FDBACK(I,J)
      IF(FDBACK(I,J))604,604,632
  632 SUMDEN=SUMDEN+1.0
  604 CONTINUE
      IF(SUMDEN)603,603,610
  610 CORTM=SUMNUM*AINTER(L,K)
      IF(I-1)640,640,641
  640 TM(I,L,K)=TM(I,L,K)-CORTM*SV(K)
      TM(I,K,L)=TM(I,K,L)+CORTM*SV(L)
      GO TO 642
  641 TM(I,L,K)=TM(I,L,K)-CORTM*APV(IFOR,K)
      TM(I,K,L)=TM(I,K,L)+CORTM*APV(IFOR,L)
  542 TM(I,L,L)=TM(I,L,L)+CORTM
      IF(TM(I,L,K))643,643,644
  643 TM(I,L,K)=0.0001
  644 IF(TM(I,K,L))645,645,646
  645 TM(I,K,L)=0.0001
  646 IF(TM(I,L,L)-0.3)616,603,603
  616 TM(I,L,L)=0.3
  603 CONTINUE
      DO 605 I-1,NST
      IF(KCHECK(I))615,615,605
  615 DO 605 J=1,NSP
      WEIGHT=0
      DO 606 K=1,NSP
  606 WEIGHT=WEIGHT+TM(I,J,K)
      IF(WEIGHT)617,617,618
  617 WRITE(3,620)I,J,WEIGHT
      GO TO 605
  618 DO 607 K=1,NSP
  607 TM(I,J,K)=TM(I,J,K)/WEIGHT
  605 CONTINUE
  620 FORMAT(' ','I=  ',I2,'   J=  ',I2,'  CAUTION-- SUM TM
                                 (I,J,L)= ',
     1F10.7/)
      RETURN
      END
```

Appendix B. Data Sets

DATA SET 1

Number of Age Classes: 9

Number of Species (including bare ground): 3

Differ Value: .005

Seed Probabilities (initial): Species A = .0010; Species B = .0010

Maximum Seed Probabilities Allowed: Species A = .0040;
Apecies B = .0040.

Number of Years in Each Age Class: 1, 1, 2, 4, 12, 12, 24, 24, and unspecified

INTER MATRIX

Bare	Species A	Species B	
0	-0.05	-0.05	Interaction with Bare
0	-1.00	-1.00	Interaction with Species A
0	-1.00	-1.00	Interaction with Species B

FDBACK MATRIX

Age Class (years)									
1	2	3-4	5-8	9-20	21-32	33-56	57-80	>80	
0	0	1	1	1	1	1	1	1	Feedback to TM1
0	0	0	1	1	1	1	1	1	Feedback to TM2
0	0	0	1	1	1	1	1	1	Feedback to TM3
0	0	0	0	1	1	1	1	1	Feedback to TM4
0	0	0	0	0	1	1	1	1	Feedback to TM5
0	0	0	0	0	0	1	1	1	Feedback to TM6
0	0	0	0	0	0	0	1	1	Feedback to TM7
0	0	0	0	0	0	0	0	1	Feedback to TM8
0	0	0	0	0	0	0	0	0	Feedback to TM9

INITIAL TRANSITION MATRICES

TM1

Transition to 1 year age class			Transition from seed age class
Bare	Species A	Species B	
0.850	0.075	0.075	Bare
0.035	0.950	0.015	Species A
0.035	0.015	0.950	Species B

TM2

Transition to 2 year age class			Transition from 1 year age class
Bare	Species A	Species B	
0.750	0.125	0.125	Bare
0.010	0.950	0.040	Species A
0.010	0.040	0.950	Species B

TM3

Transition to 3 - 4 year age class			Transition from 2 year age class
Bare	Species A	Species B	
0.900	0.050	0.050	Bare
0.005	0.970	0.025	Species A
0.005	0.025	0.970	Species B

TM4

Transition to 5 - 8 year age class			Transition from 3 - 4 year age class
Bare	Species A	Species B	
0.900	0.050	0.050	Bare
0.005	0.970	0.025	Species A
0.005	0.025	0.970	Species B

TM5

Transition to 9 - 20 year age class			Transition from 5 - 8 year age class
Bare	Species A	Species B	
0.900	0.050	0.050	Bare
0.003	0.990	0.007	Species A
0.003	0.007	0.990	Species B

TM6

Transition to 21 - 32 year age class			Transition from 9 - 20 year age class
Bare	Species A	Species B	
0.900	0.050	0.050	Bare
0.003	0.990	0.007	Species A
0.003	0.007	0.990	Species B

TM7

Transition to 33 - 56 year age class			Transition from 21 - 32 year age class
Bare	Species A	Species B	
0.925	0.0375	0.0375	Bare
0.090	0.900	0.010	Species A
0.090	0.010	0.900	Species B

TM8

Transition to 57 - 80 year age class			Transition from 33 - 56 year age class
Bare	Species A	Species B	
0.998	0.001	0.001	Bare
0.490	0.500	0.010	Species A
0.490	0.010	0.500	Species B

TM9

Transition to >80 year age class			Transition from 57 - 80 year age class
Bare	Species A	Species B	
0.998	0.001	0.001	Bare
0.495	0.500	0.005	Species A
0.495	0.005	0.500	Species B

RESEED MATRIX

Species			Age Class (years)
Bare	Species A	Species B	
0	0	0	1
0	0	0	2
0	0	0	3-4
0	0.001	0.001	5-8
0	0.008	0.008	9-20
0	0.015	0.015	21-32
0	0.015	0.015	33-56
0	0.005	0.005	57-80
0	0.001	0.001	80

DATA SET 2

Data Set 2 is identical with Data Set 1 except for the INTER matrix which follows.

INTER MATRIX

Bare	Species A	Species B	
0	-0.05	-0.05	Interaction with Bare
0	-1.00	-2.00	Interaction with Species A
0	-1.00	-1.00	Interaction with Species B

DATA SET 3

Data Set 3 is identical with Data Set 1 except for the RESEED matrix which follows.

RESEED MATRIX

Species			
Bare	Species A	Species B	Age Class (years)
0	0	0	1
0	0	0	2
0	0	0	3-4
0	0.05	0.001	5-8
0	0.016	0.008	9-20
0	0.030	0.015	21-32
0	0.030	0.015	33-51
0	0.010	0.005	52-80
0	0.001	0.001	>80

DATA SET 4

Data Set 4 is identical with Data Set 1 except for the INTER matrix which follows.

INTER MATRIX

Bare	Species A	Species B	
0	-0.05	-0.05	Interaction with Bare
0	-2	-1	Interaction with Species A
0	-1	-1	Interaction with Species B

DATA SET 5

Data Set 5 is identical with Data Set 1 except for the INTER matrix which follows.

INTER MATRIX

Bare	Species A	Species B	
0	-0.05	-0.05	Interaction with Bare
0	-1	-3	Interaction with Species A
0	-1	-1	Interaction with Species B

Appendix C. Simulated Successions

SIMULATION 1

YEAR 10

Seed Probabilities: Species A = 0.0010; Species B = 0.0010

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.848	0.076	0.076
2	0.636	0.182	0.182
3-4	0.576	0.212	0.212
5-8	0.782	0.109	0.109
9-20	1.000	0.000	0.000
21-32	1.000	0.000	0.000
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 20

Seed Probabilities: Species A = 0.0010; Species B = 0.0010

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.847	0.076	0.076
2	0.636	0.182	0.182
3-4	0.573	0.214	0.214
5-8	0.518	0.241	0.241
9-20	0.802	0.099	0.099
21-32	1.000	0.000	0.000
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 40

Seed Probabilities: Species A = 0.0015; Species B = 0.0015

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.845	0.077	0.077
2	0.632	0.184	0.184
3-4	0.568	0.216	0.216
5-8	0.512	0.244	0.244
9-20	0.467	0.266	0.266
21-32	0.811	0.094	0.094
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 60

Seed Probabilities: Species A = 0.0021; Species B = 0.0021

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.843	0.078	0.078
2	0.629	0.186	0.186
3-4	0.563	0.218	0.218
5-8	0.506	0.247	0.247
9-20	0.458	0.271	0.271
21-32	0.419	0.290	0.290
33-56	0.846	0.077	0.077
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 80

Seed Probabilities: Species A = 0.0023; Species B = 0.0023

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.843	0.078	0.078
2	0.628	0.186	0.186
3-4	0.563	0.218	0.218
5-8	0.505	0.247	0.247
9-20	0.455	0.272	0.272
21-32	0.411	0.294	0.294
33-56	0.438	0.281	0.281
57-80	0.959	0.021	0.021
>80	1.000	0.000	0.000

YEAR 100

Seed Probabilities: Species A = 0.0027; Species B = 0.0027

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.841	0.079	0.079
2	0.625	0.187	0.187
3-4	0.559	0.220	0.220
5-8	0.500	0.249	0.249
9-20	0.450	0.275	0.275
21-32	0.409	0.296	0.296
33-56	0.438	0.281	0.281
57-80	0.959	0.020	0.020
>80	1.000	0.000	0.000

YEAR 150

Seed Probabilities: Species A = 0.0030; Species B = 0.0030

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.080	0.080
2	0.624	0.188	0.188
3-4	0.558	0.221	0.221
5-8	0.498	0.251	0.251
9-20	0.446	0.277	0.277
21-32	0.401	0.299	0.299
33-56	0.429	0.285	0.285
57-80	0.710	0.145	0.145
>80	0.923	0.038	0.038

YEAR 177

Seed Probabilities: Species A = 0.0030; Species B = 0.0030

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.080	0.080
2	0.624	0.188	0.188
3-4	0.557	0.221	0.221
5-8	0.498	0.251	0.251
9-20	0.446	0.277	0.277
21-32	0.401	0.299	0.299
33-56	0.426	0.287	0.287
57-80	0.708	0.146	0.146
>80	0.901	0.049	0.049

FINAL TRANSITION MATRICES

TM1

Transition to 1/2 year age class			Transition from 1 year age class
Bare	Species A	Species B	
0.845	0.077	0.077	Bare
0.044	0.928	0.028	Species A
0.044	0.028	0.928	Species B

TM2

Transition to 1 year age class			Transition from 1 year age class
Bare	Species A	Species B	
0.742	0.129	0.129	Bare
0.002	0.928	0.069	Species A
0.002	0.069	0.928	Species B

TM3

Transition to 3-4 year age class			Transition from 2 year age class
Bare	Species A	Species B	
0.893	0.053	0.053	Bare
0.000	0.960	0.040	Species A
0.000	0.040	0.960	Species B

TM4

Transition to 5-8 year age class			Transition from 3-4 year age class
Bare	Species A	Species B	
0.894	0.053	0.053	Bare
0.000	0.960	0.040	Species A
0.000	0.040	0.960	Species B

TM5

Transition to 9-20 year age class			Transition from 5-8 year age class
Bare	Species A	Species B	
0.895	0.052	0.052	Bare
0.000	0.988	0.012	Species A
0.000	0.012	0.988	Species B

TM6

Transition to 21-32 year age class			Transition from 9-20 year age class
Bare	Species A	Species B	
0.897	0.051	0.051	Bare
0.001	0.986	0.018	Species A
0.001	0.013	0.986	Species B

TM7

Transition to 33-56 year age class			Transition from 21-32 year age class
Bare	Species A	Species B	
0.924	0.038	0.038	Bare
0.093	0.896	0.010	Species A
0.093	0.010	0.896	Species B

TM8

Transition to 57-80 year age class			Transition from 33-56 year age class
Bare	Species A	Species B	
0.998	0.001	0.001	Bare
0.492	0.498	0.010	Species A
0.492	0.010	0.498	Species B

TM9

Transition to >80 year age class			Transition from 57-80 year age class
Bare	Species A	Species B	
0.998	0.001	0.001	Bare
0.495	0.500	0.005	Species A
0.495	0.005	0.500	Species B

SIMULATION 2

YEAR 10

Seed Probabilities: Species A = 0.001; Species B = 0.001

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.848	0.076	0.076
2	0.637	0.181	0.182
3-4	0.575	0.212	0.213
5-8	0.783	0.109	0.109
9-20	1.000	0.000	0.000
21-32	1.000	0.000	0.000
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 20

Seed Probabilities: Species A = 0.001; Species B = 0.001

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.847	0.076	0.076
2	0.636	0.181	0.183
3-4	0.573	0.209	0.218
5-8	0.518	0.237	0.245
9-20	0.803	0.099	0.099
21-32	1.000	0.000	0.000
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 40

Seed Probabilities: Species A = 0.0015; Species B = 0.0015

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.845	0.077	0.077
2	0.633	0.181	0.186
3-4	0.568	0.204	0.228
5-8	0.512	0.225	0.263
9-20	0.467	0.262	0.271
21-32	0.811	0.094	0.094
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 60

Seed Probabilities: Species A = 0.0021; Species B = 0.0022

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.843	0.078	0.078
2	0.629	0.181	0.190
3-4	0.563	0.195	0.241
5-8	0.506	0.210	0.284
9-20	0.458	0.241	0.300
21-32	0.419	0.276	0.304
33-56	0.846	0.077	0.077
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 80

Seed Probabilities: Species A = 0.0022; Species B = 0.0025

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.843	0.078	0.079
2	0.629	0.180	0.191
3-4	0.563	0.193	0.244
5-8	0.506	0.204	0.291
9-20	0.455	0.225	0.320
21-32	0.411	0.254	0.335
33-56	0.438	0.262	0.300
57-80	0.959	0.0205	0.021
>80	1.000	0.000	0.000

YEAR 100

Seed Probabilities: Species A = 0.0025; Species B = 0.0030

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.841	0.079	0.080
2	0.625	0.177	0.197
3-4	0.559	0.180	0.261
5-8	0.500	0.183	0.317
9-20	0.451	0.209	0.340
21-32	0.409	0.242	0.349
33-56	0.438	0.262	0.300
57-80	0.959	0.021	0.021
>80	1.000	0.000	0.000

YEAR 150

Seed Probabilities: Species A = 0.0023; Species B = 0.0036

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.079	0.081
2	0.624	0.173	0.203
3-4	0.557	0.163	0.280
5-8	0.498	0.155	0.347
9-20	0.446	0.164	0.390
21-32	0.401	0.182	0.417
33-56	0.430	0.210	0.361
57-80	0.710	0.125	0.166
>80	0.923	0.036	0.041

YEAR 200

Seed Probabilities: Species A = 0.0021; Species B = 0.0039

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.079	0.081
2	0.623	0.170	0.207
3-4	0.556	0.154	0.290
5-8	0.497	0.141	0.362
9-20	0.444	0.141	0.414
21-32	0.399	0.151	0.450
33-56	0.426	0.153	0.421
57-80	0.708	0.086	0.206
>80	0.900	0.035	0.065

YEAR 250

Seed Probabilities: Species A = 0.0020; Species B = 0.0040

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.0789	0.081
2	0.623	0.168	0.209
3-4	0.556	0.148	0.296
5-8	0.497	0.134	0.369
9-20	0.444	0.133	0.423
21-32	0.398	0.140	0.461
33-56	0.425	0.140	0.435
57-80	0.708	0.076	0.216
>80	0.899	0.029	0.071

YEAR 300

Seed Probabilities: Species A . 0.0019; Species B = 0.0040

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.079	0.081
2	0.623	0.168	0.209
3-4	0.556	0.147	0.297
5-8	0.496	0.131	0.373
9-20	0.444	0.129	0.427
21-32	0.398	0.136	0.466
33-56	0.425	0.134	0.441
57-80	0.707	0.072	0.221
>80	0.899	0.027	0.074

YEAR 350

Seed Probabilities: Species A = 0.0019; Species B = 0.0040

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.079	0.081
2	0.623	0.168	0.209
3-4	0.556	0.146	0.298
5-8	0.496	0.130	0.374
9-20	0.443	0.127	0.429
21-32	0.398	0.134	0.469
33-56	0.425	0.131	0.444
57-80	0.707	0.070	0.223
>80	0.899	0.026	0.075

YEAR 369

Seed Probabilities: Species A = 0.0019; Species B = 0.0040

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.079	0.081
2	0.623	0.168	0.209
3-4	0.556	0.146	0.298
5-8	0.496	0.129	0.374
9-20	0.443	0.127	0.430
21-32	0.398	0.133	0.469
33-56	0.425	0.131	0.445
57-80	0.707	0.069	0.223
>80	0.899	0.025	0.076

FINAL TRANSITION MATRICES

TM1

Transition to 1/2 year age class			Transition from 1 year age class
Bare	Species A	Species B	
0.845	0.078	0.078	Bare
0.107	0.832	0.061	Species A
0.035	0.030	0.935	Species B

TM2

Transition to 1 year age class			Transition from 1 year age class
Bare	Species A	Species B	
0.740	0.129	0.131	Bare
0.0147	0.752	0.234	Species A
0.0001	0.0001	1.000	Species B

TM3

Transition to 3-4 year age class			Transition from 2 year age class
Bare	Species A	Species B	
0.891	0.052	0.056	Bare
0.003	0.674	0.323	Species A
0.001	0.001	1.000	Species B

TM4

Transition to 5-8 year age class			Transition from 3-4 year age class
Bare	Species A	Species B	
0.892	0.052	0.056	Bare
0.005	0.688	0.307	Species A
0.001	0.001	1.000	Species B

TM5

Transition to 9-20 year age class			Transition from 5-8 year age class
Bare	Species A	Species B	
0.893	0.052	0.055	Bare
0.002	0.782	0.217	Species A
0.001	0.001	1.000	Species B

TM6

Transition to 21-32 year age class			Transition from 9-20 year age class
Bare	Species A	Species B	
0.896	0.051	0.053	Bare
0.003	0.868	0.129	Species A
0.000	0.001	1.000	Species B

TM7

Transition to 33-56 year age class			Transition from 21-32 year age class
Bare	Species A	Species B	
0.924	0.038	0.038	Bare
0.095	0.866	0.038	Species A
0.095	0.001	0.905	Species B

TM8

Transition to 57-80 year age class			Transition from 33-56 year age class
Bare	Species A	Species B	
0.998	0.001	0.001	Bare
0.493	0.495	0.013	Species A
0.493	0.009	0.498	Species B

TM9

Transition to >80 year age class			Transition from 57-80 year age class
Bare	Species A	Species B	
0.998	0.001	0.001	Bare
0.495	0.500	0.005	Species A
0.495	0.005	0.500	Species B

SIMULATION 3

YEAR 10

Seed Probabilities: Species A = 0.0015; Species B = 0.0010

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.847	0.077	0.076
2	0.637	0.182	0.182
3-4	0.575	0.212	0.212
5-8	0.783	0.109	0.109
9-20	1.000	0.000	0.000
21-32	1.000	0.000	0.000
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 20

Seed Probabilities: Species A = 0.0030; Species B = 0.0010

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.846	0.078	0.076
2	0.634	0.184	0.182
3-4	0.572	0.215	0.213
5-8	0.517	0.242	0.241
9-20	0.803	0.099	0.099
21-32	1.000	0.000	0.000
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 40

Seed Probabilities: Species A = 0.0039; Species B = 0.0015

	Cover Values		
Age class (year)	Bare ground	Species A	Species B
1	0.843	0.079	0.077
2	0.631	0.186	0.184
3-4	0.567	0.217	0.215
5-8	0.511	0.245	0.244
9-20	0.466	0.268	0.266
21-32	0.811	0.094	0.094
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 60

Seed Probabilities: Species A = 0.0040; Species B = 0.0021

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.842	0.080	0.078
2	0.628	0.187	0.185
3-4	0.562	0.220	0.218
5-8	0.505	0.249	0.246
9-20	0.457	0.275	0.268
21-32	0.419	0.292	0.290
33-56	0.846	0.077	0.077
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 80

Seed Probabilities: Species A = 0.0040; Species B = 0.0023

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.842	0.080	0.078
2	0.628	0.187	0.185
3-4	0.562	0.220	0.218
5-8	0.505	0.249	0.246
9-20	0.454	0.277	0.270
21-32	0.410	0.298	0.292
33-56	0.437	0.283	0.280
57-80	0.959	0.021	0.021
>80	1.000	0.000	0.000

YEAR 100

Seed Probabilities: Species A = 0.0040; Species B = 0.0027

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.080	0.079
2	0.625	0.188	0.187
3-4	0.558	0.222	0.219
5-8	0.500	0.252	0.248
9-20	0.450	0.279	0.271
21-32	0.408	0.302	0.289
33-56	0.437	0.283	0.280
57-80	0.959	0.021	0.021
>80	1.000	0.000	0.000

YEAR 150

Seed Probabilities: Species A = 0.0040; Species B = 0.0029

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.081	0.080
2	0.624	0.189	0.187
3-4	0.557	0.224	0.219
5-8	0.498	0.255	0.247
9-20	0.446	0.284	0.270
21-32	0.401	0.310	0.290
33-56	0.429	0.293	0.279
57-80	0.709	0.147	0.143
>80	0.923	0.039	0.038

YEAR 200

Seed Probabilities: Species A = 0.0040; Species B = 0.0029

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.081	0.080
2	0.624	0.189	0.187
3-4	0.557	0.224	0.219
5-8	0.498	0.256	0.247
9-20	0.446	0.286	0.269
21-32	0.400	0.312	0.287
33-56	0.426	0.298	0.276
57-80	0.708	0.151	0.141
>80	0.900	0.052	0.049

YEAR 225

Seed Probabilities: Species A = 0.0040; Species B = 0.0029

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.840	0.080	0.080
2	0.624	0.189	0.187
3-4	0.557	0.224	0.219
5-8	0.498	0.256	0.246
9-20	0.445	0.286	0.268
21-32	0.400	0.313	0.287
33-56	0.426	0.298	0.276
57-80	0.707	0.152	0.141
>80	0.899	0.052	0.049

FINAL TRANSITION MATRICES

TM1

Transition to 1/2 year age class			Transition from
Bare	Species A	Species B	1 year age class
0.845	0.077	0.077	Bare
0.044	0.928	0.028	Species A
0.045	0.028	0.927	Species B

TM2

Transition to 1 year age class			Transition from
Bare	Species A	Species B	1 year age class
0.742	0.129	0.129	Bare
0.002	0.931	0.067	Species A
0.003	0.071	0.926	Species B

TM3

Transition to 3-4 year age class			Transition from
Bare	Species A	Species B	2 year age class
0.893	0.054	0.053	Bare
0.001	0.962	0.038	Species A
0.001	0.048	0.952	Species B

TM4

Transition to 5-8 year age class			Transition from
Bare	Species A	Species B	3-4 year age class
0.894	0.053	0.053	Bare
0.001	0.966	0.034	Species A
0.001	0.044	0.955	Species B

TM 5

Transition to 9-20 year age class			Transition from
Bare	Species A	Species B	5-8 year age class
0.895	0.053	0.052	Bare
0.000	0.995	0.005	Species A
0.001	0.023	0.977	Species B

TM6

Transition to 21-32 year age class			Transition from
Bare	Species A	Species B	9-20 year age class
0.897	0.052	0.051	Bare
0.001	0.993	0.006	Species A
0.001	0.021	0.977	Species B

TM7

Transition to 33-56 year age class			Transition from
Bare	Species A	Species B	21-32 year age class
0.924	0.038	0.038	Bare
0.093	0.897	0.010	Species A
0.093	0.011	0.896	Species B

TM8

Transition to 57-80 year age class			Transition from
Bare	Species A	Species B	33-56 year age class
0.998	0.001	0.001	Bare
0.492	0.498	0.010	Species A
0.492	0.010	0.498	Species B

TM9

Transition to >80 year age class			Transition from
Bare	Species A	Species B	57-80 year age class
0.998	0.001	0.001	Bare
0.495	0.500	0.005	Species A
0.495	0.005	0.500	Species B

SIMULATION 4

YEAR 10

Seed Probabilities: Species A = 0.0010; Species B = 0.0010

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.848	0.076	0.076
2	0.637	0.181	0.182
3-4	0.575	0.212	0.213
5-8	0.783	0.109	0.109
9-20	1.000	0.000	0.000
21-32	1.000	0.000	0.000
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 20

Seed Probabilities: Species A = 0.0010; Species B = 0.0010

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.847	0.076	0.076
2	0.636	0.182	0.182
3-4	0.573	0.213	0.214
5-8	0.518	0.241	0.242
9-20	0.803	0.099	0.099
21-32	1.000	0.000	0.000
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 40

Seed Probabilities: Species A = 0.0015; Species B = 0.0015

	Cover Values		
Age Class (years)	Bare ground	Species A	Species B
1	0.845	0.077	0.077
2	0.632	0.183	0.184
3-4	0.568	0.214	0.217
5-8	0.512	0.242	0.246
9-20	0.467	0.266	0.267
21-32	0.811	0.094	0.094
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 60

Seed Probabilities: Species A = 0.0021; Species B = 0.0022

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.843	0.078	0.078
2	0.629	0.184	0.187
3-4	0.563	0.215	0.221
5-8	0.506	0.243	0.251
9-20	0.458	0.270	0.272
21-32	0.420	0.289	0.291
33-56	0.846	0.077	0.077
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 80

Seed Probabilities: Species A = 0.0023; Species B = 0.0023

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.843	0.078	0.078
2	0.629	0.184	0.187
3-4	0.563	0.216	0.221
5-8	0.506	0.243	0.251
9-20	0.455	0.270	0.275
21-32	0.411	0.292	0.296
33-56	0.438	0.280	0.282
57-80	0.959	0.021	0.021
>80	1.000	0.000	0.000

YEAR 100

Seed Probabilities: Species A = 0.0028; Species B = 0.0028

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.841	0.079	0.079
2	0.626	0.185	0.189
3-4	0.559	0.216	0.225
5-8	0.501	0.243	0.256
9-20	0.451	0.271	0.278
21-32	0.409	0.295	0.295
33-56	0.438	0.280	0.282
57-80	0.959	0.021	0.021
>80	1.000	0.000	0.000

YEAR 150

Seed Probabilities: Species A = 0.0030; Species B = 0.0030

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.841	0.080	0.080
2	0.624	0.186	0.190
3-4	0.558	0.215	0.227
5-8	0.499	0.242	0.259
9-20	0.446	0.270	0.284
21-32	0.402	0.295	0.303
33-56	0.430	0.283	0.287
57-80	0.710	0.145	0.146
>80	0.923	0.038	0.038

YEAR 177

Seed Probabilities: Species A = 0.0030; Species B = 0.0030

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.841	0.080	0.080
2	0.624	0.186	0.190
3-4	0.558	0.215	0.227
5-8	0.499	0.242	0.260
9-20	0.446	0.269	0.284
21-32	0.401	0.294	0.305
33-56	0.427	0.282	0.291
57-80	0.709	0.144	0.148
>80	0.901	0.049	0.050

FINAL TRANSITION MATRICES

TM1

Transition to 1/2 year age class			Transition from
Bare	Species A	Species B	1 year age class
0.845	0.077	0.077	Bare
0.065	0.897	0.039	Species A
0.044	0.028	0.928	Species B

TM2

Transition to 1 year age class			Transition from
Bare	Species A	Species B	1 year age class
0.742	0.129	0.129	Bare
0.005	0.902	0.093	Species A
0.002	0.068	0.930	Species B

TM3

Transition to 3-4 year age class			Transition from
Bare	Species A	Species B	2 year age class
0.893	0.053	0.054	Bare
0.001	0.940	0.060	Species A
0.001	0.040	0.960	Species B

TM4

Transition to 5-8 year age class			Transition from
Bare	Species A	Species B	3-4 year age class
0.894	0.053	0.053	Bare
0.001	0.947	0.052	Species A
0.000	0.037	0.963	Species B

TM5

Transition to 9-20 year age class			Transition from
Bare	Species A	Species B	5-8 year age class
0.895	0.052	0.053	Bare
0.001	0.986	0.013	Species A
0.001	0.017	0.983	Species B

TM6

Transition to 21-32 year age class			Transition from 9-20 year age class
Bare	Species A	Species B	
0.897	0.051	0.052	Bare
0.002	0.988	0.010	Species A
0.001	0.018	0.981	Species B

TM7

Transition to 33-56 year age class			Transition from 21-32 year age class
Bare	Species A	Species B	
0.924	0.038	0.038	Bare
0.095	0.894	0.011	Species A
0.093	0.010	0.896	Species B

TM8

Transition to 57-80 year age class			Transition from 33-56 year age class
Bare	Species A	Species B	
0.998	0.001	0.001	Bare
0.493	0.497	0.010	Species A
0.492	0.010	0.498	Species B

TM9

Transition to >80 year age class			Transition from 57-80 year age class
Bare	Species A	Species B	
0.998	0.001	0.001	Bare
0.495	0.500	0.005	Species A
0.495	0.005	0.500	Species B

SIMULATION 5

YEAR 10

Seed Probabilities: Species A = 0.0010; Species B = 0.0010

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.848	0.076	0.076
2	0.637	0.181	0.182
3-4	0.575	0.211	0.214
5-8	0.783	0.109	0.109
9-20	1.000	0.000	0.000
21-32	1.000	0.000	0.000
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 20

Seed Probabilities: Species A = 0.0010; Species B = 0.0010

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.847	0.076	0.076
2	0.636	0.181	0.184
3-4	0.573	0.205	0.222
5-8	0.518	0.233	0.249
9-20	0.803	0.099	0.099
21-32	1.000	0.000	0.000
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 40

Seed Probabilities: Species A = 0.0015; Species B = 0.0015

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.845	0.077	0.077
2	0.633	0.179	0.189
3-4	0.569	0.193	0.238
5-8	0.513	0.211	0.277
9-20	0.467	0.256	0.277
21-32	0.811	0.094	0.094
33-56	1.000	0.000	0.000
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 60

Seed Probabilities: Species A = 0.0020; Species B = 0.0022

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.843	0.078	0.079
2	0.629	0.173	0.198
3-4	0.564	0.170	0.266
5-8	0.507	0.174	0.320
9-20	0.459	0.213	0.328
21-32	0.420	0.265	0.316
33-56	0.846	0.077	0.077
57-80	1.000	0.000	0.000
>80	1.000	0.000	0.000

YEAR 80

Seed Probabilities: Species A = 0.0021; Species B = 0.0026

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.843	0.078	0.079
2	0.629	0.171	0.200
3-4	0.563	0.163	0.274
5-8	0.506	0.160	0.334
9-20	0.455	0.175	0.370
21-32	0.411	0.212	0.376
33-56	0.438	0.244	0.318
57-80	0.959	0.021	0.021
>80	1.000	0.000	0.000

YEAR 100

Seed Probabilities: Species A = 0.0022; Species B = 0.0033

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.841	0.079	0.080
2	0.625	0.159	0.215
3-4	0.559	0.116	0.325
5-8	0.500	0.099	0.401
9-20	0.451	0.135	0.414
21-32	0.409	0.183	0.408
33-56	0.438	0.244	0.318
57-80	0.959	0.021	0.021
>80	1.000	0.000	0.000

YEAR 150

Seed Probabilities: Species A = 0.0017; Species B = 0.0040

	Cover Values		
Age class (year)	Bare ground	Species A	Species B
1	0.840	0.079	0.082
2	0.623	0.133	0.244
3-4	0.555	0.073	0.372
5-8	0.495	0.050	0.455
9-20	0.443	0.053	0.504
21-32	0.398	0.071	0.531
33-56	0.430	0.128	0.442
57-80	0.710	0.103	0.188
>80	0.923	0.034	0.043

YEAR 200

Seed Probabilities: Species A = 0.0014; Species B = 0.0040

	Cover Values		
Age class (year)	Bare ground	Species A	Species B
1	0.839	0.079	0.082
2	0.622	0.133	0.245
3-4	0.554	0.073	0.374
5-8	0.493	0.050	0.457
9-20	0.439	0.043	0.518
21-32	0.393	0.051	0.557
33-56	0.422	0.059	0.520
57-80	0.706	0.037	0.256
>80	0.900	0.020	0.080

YEAR 225

Seed Probabilities: Species A = 0.0014; Species B = 0.0040

	Cover Values		
Age class (years)	Bare ground	Species A	Species B
1	0.839	0.079	0.082
2	0.622	0.133	0.245
3-4	0.554	0.073	0.374
5-8	0.492	0.051	0.457
9-20	0.438	0.042	0.520
21-32	0.392	0.049	0.559
33-56	0.421	0.056	0.523
57-80	0.706	0.034	0.260
>80	0.899	0.016	0.085

FINAL TRANSITION MATRICES

TM1

Transition to 1/2 year age class			Transition from 1 year age class
Bare	Species A	Species B	
0.843	0.078	0.078	Bare
0.408	0.361	0.231	Species A
0.030	0.033	0.937	Species B

TM2

Transition to 1 year age class			Transition from 1 year age class
Bare	Species A	Species B	
0.738	0.130	0.132	Bare
0.038	0.300	0.663	Species A
0.000	0.000	1.000	Species B

TM3

Transition to 3-4 year age class			Transition from 2 year age class
Bare	Species A	Species B	
0.889	0.053	0.059	Bare
0.006	0.299	0.695	Species A
0.000	0.000	1.000	Species B

TM4

Transition to 5-8 year age class			Transition from 3-4 year age class
Bare	Species A	Species B	
0.888	0.052	0.060	Bare
0.007	0.298	0.695	Species A
0.000	0.000	1.000	Species B

TM5

Transition to 9-20 year age class			Transition from 5-8 year age class
Bare	Species A	Species B	
0.890	0.052	0.059	Bare
0.003	0.317	0.679	Species A
0.000	0.000	1.000	Species B

TM6

Transition to 21-32 year age class			Transition from 9-20 year age class
Bare	Species A	Species B	
0.894	0.051	0.055	Bare
0.003	0.632	0.364	Species A
0.000	0.000	1.000	Species B

TM7

Transition to 33-56 year age class			Transition from 21-32 year age class
Bare	Species A	Species B	
0.924	0.038	0.039	Bare
0.098	0.816	0.085	Species A
0.095	0.000	0.904	Species B

TM8

Transition to 57-80 year age class			Transition from 33-56 year age class
Bare	Species A	Species B	
0.998	0.001	0.001	Bare
0.494	0.489	0.017	Species A
0.493	0.009	0.498	Species B

TM9

Transition to >80 year age class			Transition from 57-80 year age class
Bare	Species A	Species B	
0.998	0.001	0.001	Bare
0.495	0.500	0.005	Species A
0.495	0.005	0.500	Species B