1985

Methodologies Of Predicting Vegetation Response To The Environment And To Perturbation On A Regional Level: A Thesis In Three Parts Treating Temporal And Time Static Models

Peter Humphreys Fewster

Follow this and additional works at: https://ir.lib.uwo.ca/digitizedtheses

CANADIAN THESES ON MICROFICHE

I.S.B.N.

THESES CANADIENNES SUR MICROFICHE

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

AVIS

La qualité de cette microfiche dépend grandeme la qualité de la thèse soumise au microfilmage. avons tout fait pour assurer une qualité supé de reproduction.

S'il manque des pages, veuillez commun avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages laisser à désirer, surtout si les pages originales on dactylographiées à l'aide d'un ruban usé ou si l'u sité nous a fait parvenir une photocopie de mau qualité.

Les documents qui font déjà l'objet d'un d'auteur (articles de revue, examens publiés, et sont pas microfilmés.

THIS DISSERTATION HAS BEEN MICROFILMED EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ MICROFILMÉE TELLE QUE NOUS L'AVONS REÇUE

Canad

CANADIAN THESES ON MICROFICHE SERVICE – SERVICE DES THÈSES CANADIENNES SUR MICROFICHE

PERMISION TO MICROFILM – AUTORISATION DE MICROFILMER

- Please print or type – Écrire en lettres moulées ou dactylographier

AUTHOR – AUTEUR

Full Name of Author – Nom complet de l'auteur

Peter Humphreys FEWSTER

Date of Birth – Date de naissance

Oct. 23, 1953

Canadian Citizen – Citoyen canadien

☑ Yes / Oui   ☐ No / Non

Country of Birth – Lieu de naissance

Canada

Permanent Address – Résidence fixe

17 Oxford St. W.
London, Ontario
N6H 1A2

THESIS – THÈSE

Title of Thesis – Titre de la thèse

Methodologies of Predicting Vegetation Response #to the Environment and to Perturbation on a Regional Level: A Thesis in Three Parts Treating Temporal and Time Static models

Degree for which thesis was presented
Grade pour lequel cette thèse fut présentée

Ph. D.

Year this degree conferred
Année d'obtention de ce grade

1985

University – Université

University of Western Ontario

Name of Supervisor – Nom du directeur de thèse

Dr. L. Orlóci

AUTHORIZATION – AUTORISATION

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIO DU CANADA de microfilmer cette thèse et de prêter ou de vendre de emplaires du film.

L'auteur se réserve les autres droits de publication, ni la thèse ni de long traits de celle-ci ne doivent être imprimés ou autrement reproduits l'autorisation écrite de l'auteur.

ATTACH FORM TO THESIS – VEUILLEZ JOINDRE CE FORMULAIRE À LA THÈSE

Signature

Date

April 18, 1985

NL-91 (r 84/03)

Canada

METHODOLOGIES OF PREDICTING VEGETATION RESPONSE TO THE ENVIRONMENT AND TO PERTURBATION ON A REGIONAL LEVEL:

A THESIS IN THREE PARTS TREATING TEMPORAL AND TIME-STATIC MODELS

by

Peter Humphreys Fewster

Department of Plant Sciences

Submitted in partial fulfilment

of the requirements for the degree of

Doctor of Philosophy

Faculty of Graduate Studies

The University of Western Ontario

London, Ontario

January, 1985

ABSTRACT

The reader of this thesis is presented with a view of Vegetation Science as a dynamic, developing field. Changes are seen as producing increased complexity in the methodology and increased emphasis on prediction. As pointed out in the text, early work has mainly been descriptive and the methods of analysis used were not so much prediction oriented as they were a vehicle for presenting current descriptions of vegetation structure and function. Method development is traced from the early descriptive schemes through more evolved ones which have reflected different and often opposing concepts of what vegetation is. The most noted are the ideas of discrete types versus the idea of continuous variation which negates the existence of types.

The methodology of Vegetation Science continues to see changes. It is proposed that at this point in the evolution of the field, it will be more productive, in a statistical sense, if methods are applied in concert rather than individually. With this in mind three method types are considered. The three are complementary both in their aims and through the revealing of information which enables the user to more successfully apply the others. The concept at the base of these methods presented in the thesis is that of continuity of vegetation types. The first method type is that of simulation modelling. Past efforts have been effective mainly in simulating the dynamics of small systems. A model has been developed to effectively simulate a broad system,

an entire ecoregion in the Yukon Territory. The second method type, time static modelling, a novel method in that it incorporates formally the idea of continuity of types, is concerned with the prediction of eventual states of the vegetation following perturbation, without concern for time. The final method type is a fairly recent method, called non-linear predictive ordination, which by imbedding specific resemblance measures, helps to reveal the complex underlying structure of vegetation data. The three types of methodologies are inevitable when the aim is to lay a complex system open to interpretation.

Then the voices of the Ainur, like unto harps and lutes, and pipes and trumpets, and viols and organs, and like unto countless choirs singing with words, began to fashion the theme of Ilúvatar to a great music; and a sound arose of endless interchanging melodies woven in harmony that passed beyond hearing into the depths and into the heights, and the places of the dwelling of Ilúvatar were filled to overflowing, and the music and the echo of the music went out into the Void, and it was not void.

J.R.R. Tolkien

ACKNOWLEDGEMENTS

I would like to begin by thanking my supervisor, Dr. L. Orlóci, whose knowledge, guidance, encouragement and financial support through his NSERC grant, have been invaluable. This teacher/student relationship has always been one of stimulation. Personal funding via OGS and NSERC scholarships has been greatly appreciated as has the facilities of the Department of Plant Sciences, the Computing Centre and the University of Western Ontario.

My advisory committee members, Drs. R.C. Jancey and J. Phipps have made important comments and suggestions regarding my thesis. Professor D. Lausi and Dr. P.L. Nimis of the University of Trieste are to be thanked for their contribution to my phytosociological education. As well, I gratefully acknowledge Dr. W. Stanek of the Department of the Environment, Victoria, B.C. for discussions and data.

I have enjoyed the interaction of many students in the Department of Plant Sciences. Included are Dr. J.M. Bowles, Dr. T. Dickinson, Dr. K. Newman, Dr. J. Podani, S.S. Shaukat and especially N.C. Kenkel.

Lastly, I thank my wife Dianne who has shared so much of my work.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

INTRODUCTION

The scientific method is the investigation of natural phenomena, and is essentially a formalized approach for conceptualizing and expanding our thinking and understanding. This quite often involves model building (although it may not be obvious), since we grasp, digest and communicate to others the various facts and ideas through models, transforming a loosely related set of facts and intuitive ideas into a set of formalized and abstract relationships. It is from this generalized viewpoint of the scientific method that we look at a particular area of plant ecology.

One of the most basic problems in plant ecology is trying to understand why vegetation occurs where it does. Two related aspects of this problem are the understanding of what vegetation is and its response to many factors. Historically, terms such as physiognomy, association, classification, ordination, dynamics and pattern have been used to represent broad classes of ideas about vegetation. These ideas are expanded upon in the next chapter. The second aspect, the idea of response, carries with it the notion of prediction. This leads to three questions. What is prediction? What may one predict? How may one predict?

Prediction may connote various ideas depending on where and how it is used. According to Websters Dictionary, prediction means the declaration of some happening in advance; the foretelling on the basis of observation, experience or scientific reason. Of more relevance here is its statistical meaning. In making a statistical statement about an unknown state or value of a variable undergoing response (Orlóci, 1978), one speaks of forecasting the future in such a way as to minimize prediction error. This is important to statistics. In evaluating various methods, Feoli, Lagonegro & Orlóci (1984) add to this idea of minimization, that predictive value and prediction efficiency are related. Sokal & Rohlf (1981) recognize that causal factors have uncontrollable and often unidentifiable variation. For them, statistics measures such variation with predictable error. Sokal & Rohlf go on to say that statistics has contributed much to science and therefore has altered our approach to experimentation and philosophy.

Prediction, as it will be used here, must carry with it a statistical sense. However, it is interesting to turn this last statement around and suggest that the needs of science, in this case plant ecology, have affected methods of prediction as well as method selection. At the forefront of data analysis are methods for which the error measurements are not always easily understood and therefore not always comparable. This is often true with many non-linear methods. Rather than using a minimization of error criterion as the sole means of comparing various predictive methods and subsequently determining which ones are valid, one might also consider any method to be valid in a specific instance, if it makes a contribution to one's overall understanding (Lambert & Dale, 1964; Williams & Dale, 1965). Having described various definitions of

prediction, we can now suggest what one may predict and how might one go about it.

Many contemporary methods exist dealing with various aspects of the prediction of a vegetation process, be they temporal or time static (Juhász-Nagy & Podani, 1983). Three of these will be examined in detail in Chapters 3, 4 and 5. It is noted that these methods have been applied at the regional level. In Chapter 3, I will consider processes in time using the traditional method of simulation modelling. This has been a productive area of research for systems defined over fairly small areas. Here, I examine modelling time processes of a relatively simple system spread over a large area. In Chapter 4, I discuss vegetation response to perturbation and establish connections between types. A new method of simulation, time static modelling, has been developed with a different and yet interesting perception of model time. In Chapter 5, I will consider relationships to the environment, using the method called non-linear predictive ordination. Past vegetation work, using the Kruskal multidimensional scaling algorithm, has generally included the Minkowski metric as an internal distance function. We will consider how an internalized distance function, which is more closely related to an environmental gradient, might improve the predictive power of this popular method.

These three topics were chosen because of personal interest and outstanding problems. The three offer diverse views of what to predict, and by themselves have been regarded as being very much distinct. Yet the objectives at the community level, or more broadly the regional level, are closely related. It is suggested here, that the combined application offers much more both in predictive power and in utility.

The perspective of modelling, as it relates to the whole field of plant ecology, will be revisited in the last chapter where the three topics will be compared and contrasted. Among the various points of discussion stands the issue of the approach to modelling. As will be shown, different and sometimes conflicting avenues have been used to deal with essentially the same question. The value of using multiple approaches will be further discussed.

Chapter 2

HISTORICAL OVERVIEW

The question of why vegetation occurs where it does is similar to questions asked by biologists regarding animal populations. The conceptualization, understanding and development of related problems have relied on models as tools for communication and for method development. The history of this as it relates to biological modelling generally and to vegetation modelling specifically will be traced. Consideration will be given to the evolution of various philosophies for understanding systems and the parallel development of methods and model types.

2.1 Systems, Models and Methods

The use of models is basic to developing one's understanding of systems. To better comprehend what a model is, it would be helpful to first look at the concept of a system. A system is a collection of elements united by some form of interaction or interdependence. From a holistic perspective, one might conceive of there being a single gigantic system. For convenience, however, we tend naturally to envision many systems. We recognize certain elements as being more or less static and hence outside the functioning of the system, while others exhibit relatively close interrelationships. One of the first things

we do in trying to understand a system is to divide these elements into two groups. Those which are dependent on the operation of the system are termed endogenous while those independent of its operation are termed exogenous (Goodall, 1972).

Systems are typically very complex and therefore not easily understood. The process of understanding them involves the perception of important components which are merely groups of similar endogenous elements. This simplifying process is model building or modelling. The model is not a miniaturized version of the system but rather a homomorph. This is attributable to the many-to-one relationship formed between the system and the model. Hence, the development of a model is intimately associated with an understanding of the system.

All of the above has made little reference to the size and scope of the system. This is because there exists a certain amount of freedom in choosing which elements will be endogenous and which will be exogenous. Also, nothing has been said regarding the form of the model. In general, simple forms such as verbal descriptions or flow chart diagrams are often used as preliminary models. This is followed by more advanced forms, usually involving a set of mathematical equations. It will be seen that choosing a model form is based, among other things, on how much is known about the system, what the aims of the study are, and the particular approach one chooses to take.

What has just been said about models also holds for method selection. Models and methods are closely related. Methods, as used here for analysis and prediction, are algorithms based on models. When we speak of a conceptual

model, then the method selected for use is easily distinguished from it. When, however, we speak of a model as a set of mathematical equations, then the model and method are not so easily distinguished. This is because an algorithm is formed from a set of equations, by impressing upon it a recursive structure. To summarize, systems, models and methods are related. An important difference is the level at which they are used. We apply the concept of systems at the most abstract level and methods at the most concrete level.

2.2 Early Approaches

Early biological work dealing with exponential growth (historically Malthus, 1798; more recently Gause, 1934), logistic growth (Pearl & Reed, 1920; Pearl & Parker, 1922; Gause, 1934; and others), and various types of species interactions (Elton, 1924; Lotka, 1925; Volterra, 1926; Nicholson, 1933, 1954; Thompson, 1939; Park, 1948) were important in that they not only illustrated one of the prime directions of the science (the discovery of general principles) but also demonstrated the natural use of modelling as a tool in description and research.

The system level chosen by most early workers was that of the population. A population was recognized as being dynamic and composed of individuals of a single species interacting within the same space/time frame. The workers were attempting to discover basic 'truths' about the system's ecology, or rather, general ecological principles underlying the system. To accomplish this much simplification was needed. It might be said that the empirical perspective was minimized and so the models developed were, in a sense, based more on theory than observation. The advantage of this was that it led to more useful

models.

One of the first models developed, that of the exponential growth model (Gause, 1934), illustrates the simplifying process well. A single closed population with discrete generations is considered where all outside influences are ignored. To simplify, a few assumptions are made. We begin by considering the Malthusian parameter (R), the growth rate per generation. Note that R is actually a fitting constant (Wangersky, 1978) and although we might choose to see R as the difference between a birth rate (B) and a death rate (D), it is not, strictly speaking, the case. Either way, we must also assume that R is the same for all ages within the population. Finally, it is assumed there will always be enough space and food. The equation describing the system is

$$N_{t+1} = RN_t \hspace{4cm} [1]$$

where N is the population size at time t. While not a great deal could be learned from such a simple relationship, it represented an important insight. In addition, an improvement can be made by changing the constraint of a population with discrete generations to one which breeds continuously. However, the assumption that there will always be enough space and food remains.

A number of models grew out of the exponential model as various assumptions were reconsidered. The logistic growth model (Pearl & Reed, 1920; Pearl & Parker, 1922; Gause, 1934) was one important reconsideration and is looked upon as a general ecological principle. Like the exponential model it can be manipulated so as to reflect other possibilities. One example is a time lag response (Wangersky & Cunningham, 1956). As well, it can be incorporated

into a more complex model.

There were two models which considered a two-species system. The first was the predator-prey model (Lotka, 1925; Volterra, 1926) developed from Gause's (1934) exponential model which assumed that the two species controlled each other's population size. The second two-species model considered competition. It was based on the logistic growth equation. Hence, not only were the two species assumed to have an effect on each other's population sizes, but there was also assumed to be an environmental limiting factor. Out of this model came the principle of competitive exclusion.

A trend to increased complexity is represented by the single species, multiple age class model. This model developed from the recognition that there exists diversity within a population. Factors such as variable fertility and survival rates, and the observation that individuals often fail to reach breeding age until well into their life, are all considered. Leslie (1945, 1948) approached the problem by assuming discrete age classes and described a model in terms of matrices containing fertility indices and survival probabilities. The nature of the population dynamics, specifically the prediction of age structure stability, could be examined by extracting eigenvalues from this matrix. As was suggested earlier, a one-species system is too simple for its principles to be applied to real systems. Yet the nature of this model, with the possibility of an algebraic solution, was attractive enough for some to incorporate it into more realistic ones.

2.3 Vegetation Models

The preceeding simple approach to modelling biological systems, while unfolding the science, diminished in usefulness as it became clearer just how complex these systems really were. The extent of this complexity was perhaps not as fully apparent as it is now. It was recognized that different models were required depending on whether animal or plant systems were being examined. However, it was less apparent just how complex or even how different various models might be if one were to consider various ecosystems differing dramatically in physiography, temperature, moisture and so on. For two systems at different ends of these environmental scales, different families of relationships would be used to describe them, resulting in radically different models. Yet, in spite of the efforts of early workers not much was really known about these specific interactions, and researchers still had to view the broad system. Because the study of hypothetical systems would probably not bring about any advancement, it appeared that work had to deal with broad systems in real settings. There had been a number of people doing just this and their work came to the forefront.

The history of work which attempted to describe what vegetation is, has brought different conceptualizations (models) which are perhaps best described by considering the units of study. To illustrate this, five somewhat arbitrary groupings are used: early descriptive; floristic-phytosociological; dynamic; individualistic; and pattern.

A good place to begin looking at the early descriptive phase is with Kerner's (1863; see translation by Conard, 1951) work of the Danube basin. His vegetation units (formations) were defined primarily by floristic composition, physiognomy and dominance (Becking, 1957; Westhoff & van der Maarel, 1973). These formations were subsequently correlated with environmental factors (Becking, 1957). It seems natural that the northern European physiognomic school and the southern European floristic school would grow out of this. Yet Kerner's work had wider implications. In Conard's (1951) introduction is stated "all of the fertile ideas which have since been developed are here in embryo". In addition to influencing the previously mentioned schools, are ideas paralleling Cowles' sand dunes and blow outs, Clements' succession, Gleason's individualistic hypothesis, Cooper's less structured dynamic viewpoint, and the pattern concepts of Greig-Smith and Whittaker. With regard to Clementsian succession, Kerner uses terms like development and maturation. Shadows of Nichols' polyclimax ideas or perhaps the concept of pattern are seen from the quote Kerner borrows from Goethe

> All forms are similar, but not one is like another;
> So the choir interprets a hidden law.

Much of Cooper's arguments are also evident. In work on plant forms (e.g. trees, shrubs and herbs), Kerner recognizes the existence of intermediate forms, suggesting that in pigeonholing, we may not be correct as born out by later work. After much productive work characterizing these forms comes the statement "the eternal laws by which they live and grow have an elasticity that is very difficult to calculate". This idea extends from forms to formations in a description of how a swamp becomes a meadow: "but in nature there is no ending and no standing still, but only an ever coming and ever going".

Another important contributor to the early descriptive phase is Warming whose approach was based on physiognomy or vegetation structure (Westhoff & van der Maarel, 1973). Warming's (1909) unit of study was the growth form. He perceived these units as being analagous to species as the units in systematic botany. Warming said the growth forms were molded by the environment. Hence the local existence of a species was based on its ability to conform. Growth form as a natural or 'ultimate' unit for study was necessary in order to lead one to a fuller understanding of a community. Warming saw the community to include vegetation of extremely varied growth forms. Hence there were two related levels of study. The 'ultimate' unit was the growth form. The higher unit, the community, could be better understood through "the oecological interpretation of the various growth forms". It is interesting, according to Whittaker (1962), that in general, English speaking ecology came out of Warming's work.

The second group was the floristic-phytosociological work done in Europe. Many traditions or schools were developed based on various criteria, for example, the northern physiognomic tradition (Becking, 1957; Whittaker, 1962). However, the southern tradition, and especially Braun-Blanquet's (see English translation, 1932) work dominated. Here, vegetation was considered on a floristic-sociological basis (Westhoff & van der Maarel, 1973). The basic or fundamental unit was the association. Other 'higher' units were derived through a method of hierarchical classification. The association was fundamental because it was perceived as being analogous to the species. This analogy of association and species is in contrast with Warming's analogy of plant form and species. Furthermore, the association was the concrete

representation of the abstract idea of the phytocoenose. This phytocoenose and its habitat were inseparable (Becking, 1957). As productive as it was, this phytosociological approach bore much criticism by ecologists and others who felt their methods were subjective rather than objective. Apart from any personal preference for or against this method, it is clear that rather than constraining one, this method allowed one freedom to build on what the mind perceived as sociological relationships.

Much of the early American work dealt with classification as well. However, it was done in the context of dynamics. Cowles (1899, 1901) said that classification must be logical and connected in the dynamic sense. Physiography, for him, was the major factor of what was called succession. Over time, soil conditions were seen to become more mesophytic. Also recognized, were xerophytic and hydrophytic 'eddies'. Progressive or retrogressive elements, such as crustal movement and changing climate could help carry the vegetation towards or away from the mesic stage. Clements' (1916, 1936) work was similar to Cowles' with respect to his general perception of the unit being dynamic. Yet, his work was more formalized, as is seen by his monoclimax theory. His unit was the formation, based on physiognomy, flora and habitat. It was viewed as "a complex organism which arises, grows, matures, and dies; the climax formation is the adult organism of which the seral communities are but stages of development" (Whittaker, 1962). This idea, metaphor as it was, became formalized to the degree that his formation was considered not to be abstract, but to be like a superorganism. Many disagreed with this. Yet it appealed to many others because of its fundamental dynamic nature and broad applicability. Consequently it tended to persist.

Other early American ideas, related to Cowles and Clements, came from Nichols and Cooper. Nichols (1917, 1923) was perhaps less interested in dynamics and more in classification. His ideas paralleled many phytosociologists'. Nichols used a series (hierarchical set) of units. The series consisted of the association, the edaphic formation, the climatic formation and the terrestrial formation, which were considered to be ecologically equivalent to the species, genus, family and 'higher up' respectively. Nichols' fundamental unit was the association. This association, like the southern tradition's phytocoenose, was a collection of individual community units and therefore abstract, although there existed individual pieces we could see. In relating to Cowles' (1901) idea that "we have a variable approaching a variable rather than a constant", Nichols suggested that vegetation could never attain an equilibrium. This, as well as his view of the potency of edaphic factors resulted in the polyclimax theory.

Cooper, in contrast to Nichols, was not interested in formal classification (Whittaker, 1962). Cooper (1913, 1916, 1923, 1926a) studied various areas in North America, with the view towards describing dynamics. One of his major works (Cooper, 1926b) differed from many others, noticeably Clements' interpretation, on what Cooper termed the superstructure. He felt it was too easy to pigeonhole or to classify. Although some sort of classification was necessary, there did not exist a perfect filing system, every structure invented is "but a partial expression of the ultimate truth". Cooper's foundation, like Clements and others, was on change. In differentiating between the 'foundation' and 'superstructure' Cooper (1926b) felt that to properly incorporate the changing nature (foundation), we must reduce the "skeleton

structure". Metaphor and analogy, as in the superorganism and association, are just that; and should be used for illustration only. Cooper's (1926b) thesis was on the universality of change. We see a cross-section of a braided, interweaving, anastomosing stream of vegetation. Therefore, no section has its counterpart in time. It is important to choose an indefinite method versus a rigid set of pigeon holes; the former does less damage. Because of the interaction of the vegetation and the environment, plus change within the scientist, we can not assume that what we see represents the way it was or the way it will be. Nevertheless, the idea of a community is useful. But with respect to time, it is transitory. In looking at some examples of developing vegetation, Cooper (1923, 1926a) saw a unit succession or sere, as a streamlet. The idea of the term climax was useful. Unfortunately, it has been considered by many to be final. To Cooper (1926b), this is an example of crystallizing a useful term into an unbending one. The usefulness of the term climax, in Cooper's view, is in perceiving it as a slowly moving current in the braided stream. He speaks of climaxes other than the climatic climax, as having reality. While recognizing the tendency of convergence to a single climax, he balances this with the inevitable forking of the stream. Cooper demures from classifying successions as Nichols did, preferring to see the whole (stream), recognizing or describing groups or factors which influence its course through time. Thus, when Cooper speaks of his unit as being the unit succession, it is done with the understanding of a streamlet merging with time into a stream.

While Cooper was not interested in formal classification, others were not interested in classifying units at all, preferring to study the individual plant species. McIntosh (1967), in his review of the continuum concept quotes Cain

(1947) "there are unlimited variables, combinations and permutations" and Whittaker (1956) "vegetation may be interpreted as a complex and largely continuous population pattern". This individualistic approach, although existing for a long time, was not highly favoured. One of the stronger statements supporting this approach came from Gleason (1926, 1939) who sharply disagreed with the tendency to classify communities. He suggested that because species respond to varying environmental conditions, no two communities would be the same. Curtis (1955) agreed with Gleason that because of many influences, a community is never repeated. Curtis & McIntosh (1951) stated that a species ranges around an optimum set of conditions. Both Curtis & McIntosh (1951) and Curtis (1955) produced evidence suggesting this idea of a "vegetation continuum". If not always found in the field, due to discontinuous environmental factors, McIntosh (1967) says that it always exists in an abstract sense along an environmental gradient. Curtis (1959), in rejecting the classification of distinct entities, did not see chaos resulting. Rather, he saw a pattern with somewhat similar groups of species. This was because of the potential of a few plant species to dominate, being well adapted to the overall climate and soil groups. These "dominants vary according to a pattern commonly associated with a soil-moisture gradient". Hence, an entire series of communities gradually changes along a vegetational continuum (Curtis & McIntosh, 1951).

A similar way of conceptualizing vegetation is the idea of pattern. Greig-Smith (1964) recognized that pattern is the result of correlation among environmental factors and among intrinsic factors such as age and seed dispersal. Much of Whittaker's (1953, 1956, 1967) work, based on gradient analysis, considered vegetation as pattern. With respect to an environmental

gradient, he saw a shifting pattern of populations. He rejected the view of the existence of an absolute climax of a region on the basis that all factors affect the population. Whittaker concluded that the species composition of a 'climax' was determined by its position along an environmental gradient. The difference between the monoclimax and polyclimax theories, or better yet, the polarization in conception between a superorganism and a collection of individual communities found resolution in this pattern theory. Whittaker suggested considering extended communities, that is communities united by some sort of classification, as entities rather than artifacts. The classification was based on separation. The wider the separation along the gradient, the less alike two communities are. Conversely, the closer communities are on the gradient, the more alike they are.

Of these five groupings of ideas, most comparisons have been made between classification of communities and the individualistic approach. In what has often been perceived as two opposing ideas, Major (1961; annotated translation of V.M. Ponyatovskaya, 1959) prefers to speak of these two ideas as trends. The first trend has as its object of study, a group of plants. Here one recognizes the existence of well defined units based on ecological and phytocoenotic factors. The second trend consists of studies of individual plants. The previous definition concerning units is rejected in favour of the idea of continuous distributions, related to continuously changing habitats. However, Ponyatovskaya suggests "there is no absolute contrast between them" and that synthesis is the direction we must take. To understand the laws composing communities (units), we must understand the ecology and biology of individual plant species (components of the communities). This idea has been shared by

others. Greig-Smith, Austin & Whitmore (1967) used both classification and ordination (indirect gradient analysis) as methods for obtaining insights. For them, classification was more satisfactory at a higher level and ordination at a lower level. Much of the problem lay in conceptualizing data as either being discrete or continuous resulting in statements that either classification or ordination, respectively, was the 'correct' method. By contrast, Greig-Smith (1971) advises we not classify just because there exists discrete data and that we not ordinate just because there exists continuous data. For example, in a geographical representation of a data set, where the species serve as axes, there will tend to be clusters of individuals whether or not the data is continuous along environmental gradients. Rowe's (1959) descriptive work used classification methods without adhering to consistent criteria or to the climatic climaxes of Clements. Rowe's highest level units, regions, were utilitarian and not, strictly speaking, climax types. Lower levels, such as sections, followed in the same logical framework. They were arbitrary and potentially heterogeneous. Nevertheless, they are undeniable and practical. Shimwell (1971) submits that there is no best method; that classification and ordination are compatable. Whittaker (1962) suggests that classifications are created by man for their utility. According to Orlóci (1978), the "objectives of these two methods are not so separate"; for some the distinction is a philosophical dilemma while for others it is the basis for a pragmatic decision. Many have described, metaphorically, how they see this distinction (or lack of it). As mentioned, Cooper (1926b) views vegetation change as a braided, interweaving, anastomose stream. Whittaker (1975) makes the analogy that as different colours are recognized from a continuous spectrum of light wave lengths, so also are distinct repeatable communities recognized along continuous

environmental gradients. Kerner (1863) spoke of a tapestry as did Meusel (1940; c.f. Whittaker, 1962) who saw vegetation as a "tapestry woven of threads of many colours which, in orderly distribution through space, form the variegated patterns that meet our eyes".

The types of approaches to describing vegetation, which the previous five groups represent, were not expressed explicitly by the term model. Nevertheless, they are word models. Consider various concepts of vegetation, such as the association (especially phytocoenose), the sere, a pattern of communities and so on. They do not represent what vegetation is in its entirety, but rather, these ideas have a homomorphic relationship with the vegetation and are, therefore, models. Recent approaches, as reviewed in Gutierrez & Fey (1980), explicitly use the term model. It has perhaps been useful to do so because of the trend from simplicity and minimal interaction with a real system to greater complexity and realism. Of specific interest are the approaches used in forest ecology and simulation. Much of forest ecology has been concerned with descriptive word models (e.g. Rowe & Scotter, 1973; Viereck, 1973). The description of forest dynamics has touched on a number of very productive and detailed areas such as microclimatic variation; variation due to topography, influence of permafrost, autecological considerations, and the role of fire. Other foresters have developed models which were mathematically oriented. An example by Hett & Loucks (1976) looked at an age structure model of a single species. It was based on a negative exponential curve and included a power function for variable death rate and a sine wave for cycling over time.

Simulation as a vegetation model type, has proved to be very important. Goodall (1967, 1970, 1972, 1974a,b, 1975) gives the rationale for its use and Wildi (1978) presents a very typical application. Many, including foresters, have used simulation. Some, (e.g. Leak, 1970) have taken a statistical approach to derive birth and death rates, while others (Kowal, 1971) have suggested that simulation, by nature, allows for other methods of parameter determination such as trial and error. Simulation models have been used as a storage medium of qualitative ideas derived from quantitative data (Bledsoe & van Dyne, 1971), often being divided into a number of submodels or compartments. With respect to forest models, compartments usually have consisted of about three size classes, rather than one year age classes, with transition probabilities linking them together (Walters, Hilborn & Peterman, 1975; Johnson, 1977; Phipps, 1979). Some (e.g. Botkin, Janek & Wallis, 1972a,b) have dealt with ecosystem models and have successfully ignored the microbiological and microenvironmental details. One important example has dealt with the stochastic nature of fire (e.g. Dayananda, 1977). Others have developed simulation models of individual stands of vegetation. Interest here has often been with the effect of perturbation (Botkin, 1976; Emanuel, Shugart & West, 1978; Emanuel, West & Shugart, 1978) and the influence of historical factors (Shugart, Emanuel, West & DeAngelis, 1980).

2.4 Summary

The ideas of utility and pragmatic decisions previously mentioned, can naturally be extended to all of the methods looked at. In his review of classification of natural communities, Whittaker (1962) sees art entering this

science. He sees synecology to be inductive rather than deductive; the latter often leading to strong, unbending statements. Some examples which could be cited are those of Braun-Blanquet and Gleason. Orlóci (1978) speaks against preferred strategies and for the use of many techniques. Whittaker (1962) points out that the "recognition that the full complexities of ecosystems is unknowable is a matter, not of mysticism, but of perspective on scientific knowledge and its limitations". Furthermore, various methods are, or should be used as complements because "nature in the field is never wholly comprehended in any system".

What does this point to here? Because of better or improved understanding, we need to go back, from time to time, and look closely at the implications of any assumptions made to see if they agree or not. There will be some aspects of our methods which could be changed. As illustrated, model forms have followed a trend to greater complexity and realism. Part of this has and will continue to include methods which can predict different sorts of things, consequently adding to our knowledge about specific aspects of an individual system or about principles of systems in general. The next three chapters will examine three current model forms. The first method, simulation modelling, considers the dynamic aspect of a system. This model is built inductively and in such a way as to predict processes in time. The second method combines the idea of continuity of types as they relate to an environmental gradient, with the aim of prediction following perturbation. This method developed is called time static simulation. The third method also considers this idea of continuity of types and its relationship to a gradient. In this case, appropriate changes are made upon the assumption that species

response is non-linear. This method is called non-linear predictive ordination.

Chapter 3

TRADITIONAL SIMULATION MODELLING

Models can take many forms such as verbal descriptions, box and arrow diagrams, a set of mathematical equations, or simulation. The early workers, as mentioned in the previous chapter, used very simple mathematical equations which described very simple systems. Many of the typical vegetation models (section 2.3) were verbal descriptions or diagramatic representations. These approaches incorporated into the models preconceived ideas regarding the system's behaviour so that further refinement became difficult. The type of model needed was one which was defined only by the basic dynamics and did not impose preconceptions about the other aspects of the system. One approach to building such a model has been simulation, the standard approach being model construction followed by testing its predictive power. For complex systems defined over a broad area, model testing has been of little value simply because the sorts of things the model was able to predict were obvious. This chapter addresses this problem and an attempt is made to build a simulation model capable of making detailed predictions for a broadly defined system.

3.1 Introduction

Any type of model can be used to describe a system. In formulating a model for a complex dynamic system, a logical approach would be to begin with a very simple model like a box and arrow diagram and then proceed through various stages to more complex types. Many have done this. However, the effectiveness of the models was limited because the model elements implicitly described the internal nature of the system. But in a complex system this internal nature is not obvious, and simulation modelling is more appropriate. Here, interrelated system variables are formulated, usually by mathematical equations, which are relevant over a very small unit of time. Solutions are then calculated repeatedly over a longer time period. The implication is that the state of the model at any time cannot be predicted *a priori*. This is an interesting point. All of the previous modelling approaches were described by diagrams, verbal descriptions and mathematical equations. Using the mathematical type as an example, the model would consist of these equations. But a simulation model is not merely equations; it also implies the action of iterative calculation of the solutions. Since a model should be an analog to the system, and since the sytem is dynamic, it makes sense to think of an analogous model as the physical operation of these equations. In a sense, the approach to modelling dynamic populations has culminated in simulation.

Simulation, as one approach to model building, has a number of advantages. Some of them will be recognized as pertaining to other approaches, yet when viewed collectively they set this approach apart. A brief outline of four advantages of simulation in general will be given before returning to two final introduction points, that of the implication of simulation and the aims of this

chapter. An extensive review of this is found in Frenkiel & Goodall (1978) to which the reader is referred.

3.1.1 Information System

Simulation modelling normally begins with existing information. Based on this information, the model is designed to predict future states of the system. However, it also condenses existing knowledge or information of the structure and dynamics in an organized and precise form. Consequently, it then becomes part of the information system.

3.1.2 Pedagogical Tool

A simulation model often helps a student understand concepts better than a verbal approach, particularly when this approach is supplemented with diagrams and graphs. Yet, for the more advanced, it is even more powerful. The nature of the model, independent of whether solutions are calculated by hand or with a computer, forces clarity and logical thought. Not only must relationships be clearly defined, but when knowledge or data is lacking, explicit assumptions must be made. That is, one cannot be vague regarding any assumptions. As a result of this process, one naturally formulates hypotheses about the nature of the system, which can then be tested.

3.1.3 Research Tool

Simulation can be used both in hypothesis testing and in hypothesis generation. In many cases it is advisable to use a simulation model to test hypotheses because actual experimentation is not practicable or advisable due to the consequences on people or the system. A further benefit to research is that of hypothesis generation whereby various ideas about the system may result only through the use of a simulation model.

3.1.4 Management and Decision Making

As before, experimentation is involved, but with the perspective that often one cannot experiment on the real system. Here, one goes beyond testing internal characteristics to testing the results of various actions. The type of actions or perturbations simulated do not test the model, but assist decision makers in choosing the best policy in dealing with the real world.

3.1.5 Implications

Environmental/biological systems are very complex. The problem with visual or simple word models is the associated high probability of oversimplification. This is especially important in the context of environmental management and decision making. Simulation models can handle complexities so that the chance of oversimplification is greatly reduced. By keeping track of many variables and their interactions in a simultaneous manner, a simulation model becomes much more analogous to a real system. Because of this complexity, it is possible, especially for those not directly involved with the model building, to forget that assumptions were made. Care must be taken

when acting on the model's predictions because there is the possibility that some of the assumptions may be incorrect. Consequently, any predictions made may carry a degree of error much greater than if all assumptions are valid. However, this is human error and can be circumvented, as mentioned, because the method requires explicit assumptions. If the model builder and the decision makers or users communicate regarding the assumptions made, this problem can be resolved.

3.1.6 Specific Aims

The result of simulation is the prediction of states of a particular system. Yet it should be recognized that many of the processes of discovery need to be repeated because simulation is a very different approach, and because of the radical changes to the minimization of preconceptions of system dynamics. That is, the discovery of general ecological principles is very important. Of course, these two uses of simulation, state prediction and discovery of system dynamics, will intergrade as more is learned. It is important that the search for general ecological principles be not entirely neglected, since they will be of great use in building other simulation models. This point can be demonstrated by borrowing an example from the early work. A simple competition model, using deductive equations, can be experimented upon with different initial conditions. The various results are then compared and contrasted to give general principles. Although such a model can be solved analytically (that is, the state at time t can be determined from the state at time zero), a simulation model could also be used. One might then discover the qualitative behaviour of the system (for example, that some sort of equilibrium exists). In general,

complex systems can be studied in this way. Alternatively a real case may be studied. A model is built and verified so that very specific details about the particular system are learned. With the knowledge gained from research into general dynamics, this approach can be made more fruitful as well as being simpler to develop.

The approach to modelling discussed in this chapter is essentially traditional simulation. It is noted that the success of the simulation often depends not on the equations formulated but on the size and complexity of the system. That is, one must be careful not to choose a system so large or so complex that the reliability of the equations breaks down (Dale, 1970). The history of simulating vegetation has mostly been on the scale of pastures (e.g. Goodall, 1967), fens (Wildi, 1978) and forest stands around one hundred square metres. It is relevant that the IBP program attempted to build biome models. But since the systems were so complex, the modelers had to deal on such a general level that their models were often oversimplifications. As the goal was to gain new insights, models which could only be applied to relatively small areas met with better success. But if the models have this limited applicability, very little insight may be made at more general levels. It is for this reason that simulation modelling is being investigated at the intermediate level.

Allen & Starr (1982) address this problem. They say that ecological systems are middle-number systems. Differential equations are appropriate models for small-number systems such as planetary movement while statistical models are appropriate for large-number sytems such as the movement of gas molecules. Allen & Starr (1982) suggest that neither calculus nor statistics

satisfies middle-number systems. Calculus is hampered by its simplifying assumptions and statistics, because of the lack of large numbers of individuals, is not justified in its use of averages. The use of simulation by the IBP, according to Allen & Starr (1982), was limited financially and technologically. The solution to modelling middle-number systems offered by them is centered on hierarchical models (nested and non-nested) using different scales of time and size. The sorts of hierarchical models which they suggest, would probably require more effort than is feasible here. It is suggested that a system which is not as large as that of a biome and is not so comlex, can be modelled by a simulation approach.

The aim of this chapter is not to produce a well validated model. There were constraints of time and accessibility which did not allow for the collection of independent data for testing. Yet, as mentioned, the aim is simply to see if a model can be constructed which is relevant to an intermediate system, relevance being judged by the coincidence of the model results and commonly held principles. Ultimately, the success of any simulation model involves objective validation and we must keep this in mind. However, we should balance this with comments made by others. Caswell (1976) suggests that in predictive modelling we are not interested in the validity of the theory or its assumptions since we really assume that overall it is false. Swartzman (1980) remarks that one may become distracted by methods of evaluation and it is "tempting for these methods to become ends in themselves, losing sight of the target". We may now look at such a system, an ecoregion in the Yukon Territory.

3.2 Data Collection

Data for the model was collected over three field seasons in conjunction with other projects (L. Orloci, W. Stanek). The first season, the summer of 1978, was a general vegetation survey along the Alaska highway in the Yukon Territory (Fig. 1) beginning west of Beaver Creek (62.5°N, 141°W) and ending just west of Watson Lake (60°N, 128.5°W). The purpose of this survey was to typify the vegetation and to search for compositional gradients. Sampling was carried out on a stratified random basis where nested strata included ecoregions (Oswald & Senyk, 1977) and terrain types (Foothills, 1978). A total of 323 permanent plots were established near the highway at a distance far enough away to minimize road disturbance. Various vegetation and environmental variables were measured. They are discussed in more detail in Chapter 4 and in Orloci & Stanek (1979).

The second and third field seasons concentrated on the Ruby Range ecoregion. This ecoregion intersects the highway at approximately 62°N & 140.5°W and at 61°N & 136°W. Of the plots established in the first year (numbers 31 to 100), only those with a southwest through south to southeast exposure and a slope of less than 15° were considered. The purpose of the second field season was to look for potential vegetation and environmental trends or relationships which could be used in a simulation model. For those vegetation types with few replicates, additional plots were located in order to give a clearer picture of the possible trends over time. The new plots were located on a preferential basis near to a permanent plot of the same vegetation type (determined from the analysis of the first year's data). Variables measured or determined were ground cover; vegetation structure

Fig. 1. Location of study area in the Yukon Territory. The hatched area indicates the Ruby Range Ecoregion in the Yukon. The heavy line indicates the Alaska highway. (Adapted from Oswald & Senyk, 1977).

Old Crow

Dawson

Mayo

Beaver Creek

Carmacks

Ross River

Haines Junction

Whitehorse

Johnsons Crossing

Carcross

Teslin

Watson Lake
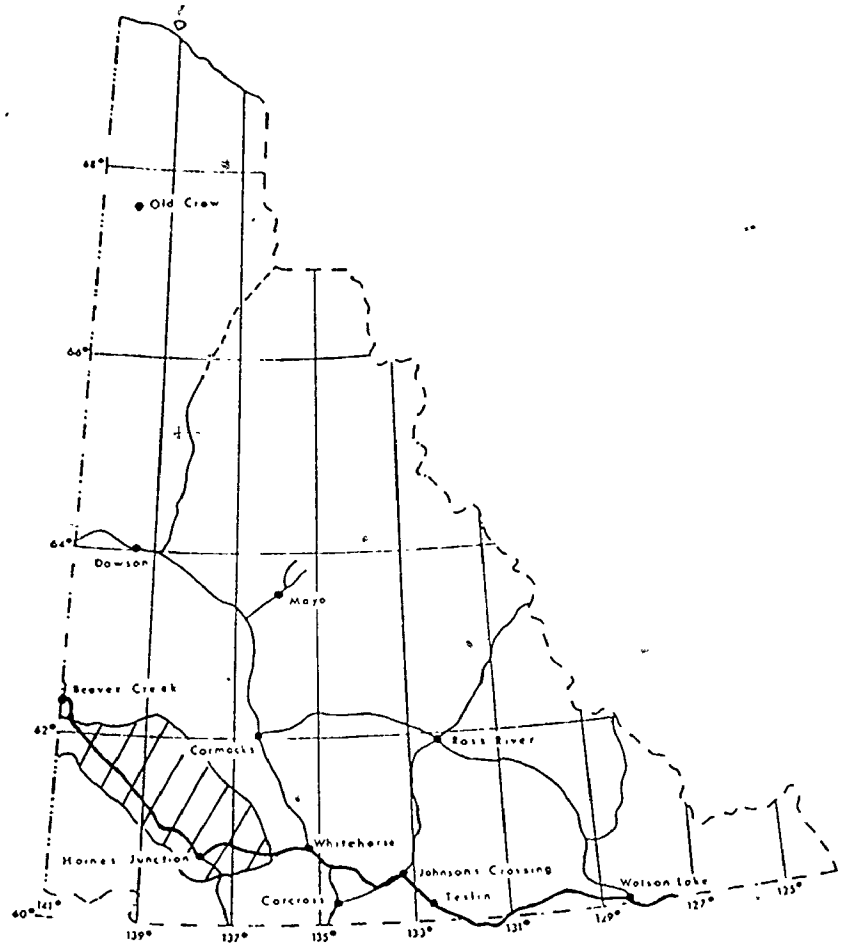
(trees, shrubs, herbs, bryophtes and lichens); age, height and DBH of typical dominant trees; soil profile (litter, fermenting humus, A-layer, permafrost); soil texture, drainage; existance of ground water; type of organic water; slope, and exposure. General records were made regarding type, intensity and time of disturbance.

In the third season, the same permanent plots as those examined in the second season were redescribed based on new variables from the formulation of the static model (see secton 3.3). A 10x10m quadrat was initially described by the slope, exposure and cover of trees, shrubs, herbs, ericaceous shrubs, mosses and lichens. Next six 1x1m subplots were randomly located and then described by the quality of organic material (coniferous to deciduous), soil quality (organic to mineral), moss thickness, organic layer depth, permafrost depth and soil moisture. All trees which were too small to core were cut and measured. The variables used were the same as those used in a complete enumeration of the larger trees of the whole quadrat. They included age, height, DBH (diameter at base height for small trees), canopy diameter and height from ground level to foliage. General remarks were recorded concerning carrying capacity, colonizing ability (including interaction with other species), possible causes of death, microenvironmental conditions where moss was colonizing, type of arboreal reproduction and fire potential.

3.3 Static Model

The model can be initially viewed as a static model describing relationships. Subsequently, the relationships can be injected into time producing a dynamic or simulation model. The static model is essentially a

descriptor derived from observed or assumed situations. It is the repetitive realizations of this static model which takes us into the simulation frame. Essentially the model is an idealized stand of arboreal species with certain components describing the lesser vegetation, soil and depth to frozen ground. The schematic diagram in Fig. 2 closely resembles the actual system and yet suggests a simplicity which may be characterized mathematically. A component model, illustrated in Fig. 3, suggests the relationships realized among the variables. The approach to categorizing the variables is similar to Goodall's (1967, 1974b) but is more like Wildi's (1978). Here six principal variables describe the system while a number of auxiliary variables serve to fully link the model.

The first three principal variables are vectors describing the number of stems of each age for *Picea glauca*, *P. mariana* and *Salix* spp. Hence for each species of spruce and the genus *Salix* the dimension of the vector equals the assumed maximum age. The fourth principal variable represents the average thickness of the moss cover. The fifth describes the cover within the unit plot to be simulated. This variable is also a vector. Here five mutually exclusive dimensions represent the cover of the three arboreal species plus moss cover and the proportion of open organo/mineral surface. The sixth principal variable describes the depth of the active layer, often referred to as the depth to permafrost (less the organic portion).

Fig. 2. Schematic diagram of the principal variables:
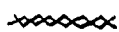
∧∧∧∧	moss
⋈⋈⋈⋈⋈	organo/mineral soil
🌲	*Picea glauca*
🌲	*P. mariana*
ᒣᒧᒥ	*Salix* spp.
⎓⎓⎓	permafrost
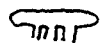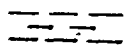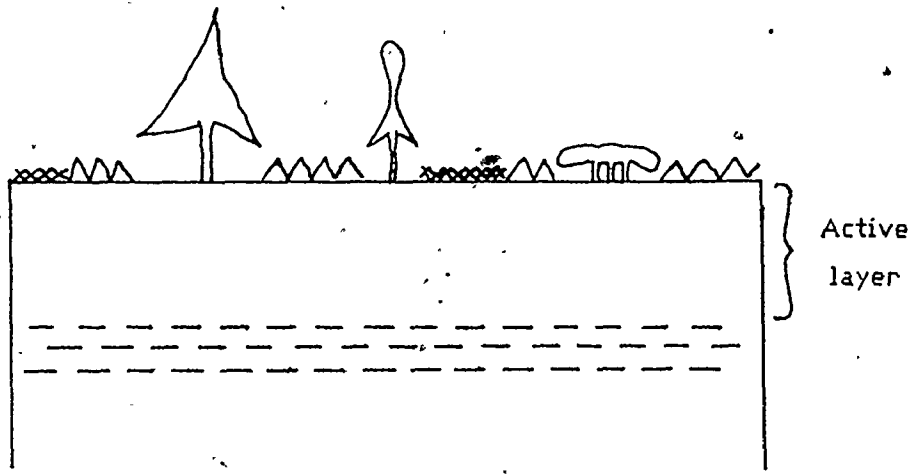
Active layer

Fig. 3. Component model of the principal variables: P.gl – *Picea glauca*; P.ma – *P. mariana*; S. – *Salix* spp.; Mt – Moss thickness; C – Cover; Al – Active layer; M – Moss; O/M – Organo/Mineral soil; ⊜ – Environmental factors. The numbers are indices of the variables. Arrows indicate direction of influence.
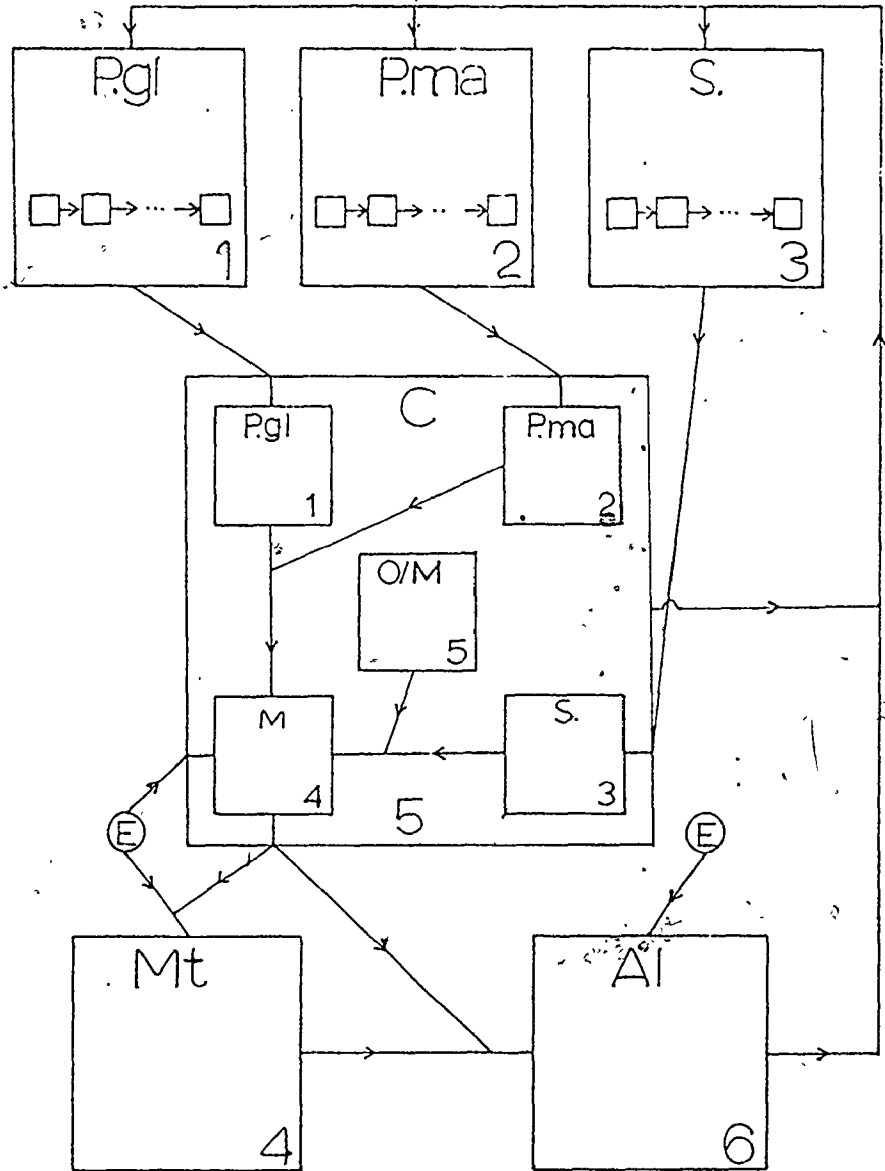
3.4 Data Analysis

Data collected in the third field season facilitated the organization of relationships among the variables of the static model into mathematical equations. In general, these equations are heuristic so that statistical tests on them would make little sense. The relationships or mathematical equations were derived through deductive reasoning based on the data, observation, and the literature. Where curve fitting was used, the families of equations chosen were those which made ecological sense, giving special consideration to boundary conditions. The equations include the six principal variables, auxiliary variables and exogenous variables. Principal and auxiliary variables are endogenous, meaning they are affected by the operation of the static model (simulation). The exogenous variables are independent of this operation. Change of these variables can only be realized through a stochastic mechanism or through interaction with the model user. At this point of the model development exogenous variation, such as fire and human disturbance, have not been incorporated. Tables 1, 2 and 3 contain the equations used in simulation.

The primary relationships among the principal variables (X) can be described with reference to Figs. 2 & 3. The three arboreal species represented by X1, X2 and X3 affect the cover (X5). Moss thickness (X4) is the main factor influencing the active layer (X6). This is because the arboreal cover does not completely screen sunlight from the forest floor. Hence only moss is effective in insulation. This insulation for a given moss thickness is maximized by 100% moss cover. Hence the cover, X5, also affects X6. Variable X5 influences X1, X2 and X3 from the standpoint of carrying capacities. It also affects the moss thickness X4. Finally, the active layer X6 can put stress on the root systems

,and hence affects **X1**, **X2** and **X3**.

The functional relationships include regression and difference equations. The heuristic equations are derived by focusing on one principal variable at a time.

3.4.1 Arboreal Variables

Each of the three arboreal variables is made up of auxiliary variables which hold the number of individuals in an age class. Each age class represents one year. An individual for **X1** or **X2** is equivalent to a single stem whereas for **X3** it is deemed to be a set of stems from a common root system. In general the dynamics fit into the categories of reproduction, aging and senescence. Reproduction of *Picea glauca* is by seed germination and mainly occurs in mineral soil (Fowells, 1965). The number of new stems $X1_1$ is thus a function of the area of organo/mineral soil $X5_5$, the area taken by an individual seedling, and a probability P1. This probability can be described as reflecting a survival probability but is actually an exogenous fitting constant. The equations are given in Table 1. *P. mariana* germination is similar. As well, this species reproduces vegetatively by layering in the moss. It is assumed that only trees at least one hundred years of age have the potential to layer; layering occurs where the growing branch tips are covered by moss; there exists a branch tip every seventy five centimetres of the canopy circumference; and 20% of these branch tip – moss contacts are successful. Hence reproduction by layering is a function of the canopy diameters of *P. mariana* (**DIAM2**), the number of stems and the moss cover as a proportion of a 1000×1000cm plot ($X5_4$/1000000). Seed germination of *Salix* spp. is in

Table 1. Simulation equations involving principal variables X1, X2, X3 and X4.

$X1_i = IFIX(4 X5_5 P1/\pi)$ IFIX — integer function

$C2D = IFIX(4 X5_5 P2/\pi)$

$C2M = \Sigma(X2_i DIAM2_i)$ $i = 100,...,200$

$X2_i = C2D + IFIX(\pi C2M X5_4/75 \times 5 \times 1000000)$

$X3_i = IFIX(4 X5_4 P3/\pi)$

$X1_{it} = X1_{i-1\ t-1} - MORT1_{i-1}$ $i = 200,...,2$

$X2_{it} = X2_{i-1\ t-1} - MORT2_{i-1}$ $i = 200,...,2$

$X3_{50\ t} = X3_{50\ t-1} + X3_{49\ t-1} - MORT3_{50} - MORT3_{49}$

$X3_{it} = X3_{i-1\ t-1} - MORT3_{i-1}$ $i = 49,...,2$

$PS1 = 0.967 - 0.4Y\ X5_1(1 - 0.001i)/Z$
            $- 0.03S1A\ S1B(41 - ROOTD)$ $i = 1,...,199$

$PS2 = 0.965 - 0.6Y\ X5_2(1 - 0.0005i)/Z - 0.06S2A\ S2B(31 - ROOTD)$
            $- 0.04S2C\ S2D(ROOTD - 37)$ $i = 1,...,199$

$PS3 = 1.0 - Y\ X5_3(1 - 0.01i)/Z - 0.05S3A\ S3B(19 - ROOTD)$
            $- 0.02S3C\ S3D(ROOTD - 34)$ $i = 1,...,50$

$X4 = X4 + 0.5\ X5_4\ M2(1 - X4/28.27\pi)/1000000$

---

moss.

Aging is very simple. For *P. glauca* and *P. mariana*, the number in any age class represents those of the previous class which managed to survive the year. Probability of survival is assumed to be independent of age when stress is not included. Thus, the relationship between number of survivors and time is a negative exponential distribution. That is

$$y_t = y_0 e^{-bt}$$ [2]

or

$$\ln y_t = \ln y_0 - bt$$ [3]

where y_t and y_0 are the number of survivors at time 0 and t respectively, t is time and b is the senescence rate. There were few plots where all age classes were represented due to the effects of fire and other influences. Because of this it was felt that using a linear regression for estimating b would not be as efficient as an heuristic approach. If equation 3 is rewritten to give

$$b = (\ln y_2 - \ln y_1)/\Delta t$$ [4]

we get the equation for the slope, and field data can be used to calculate the probability of survival (1-b). The subscripts 1 and 2 refer to any convenient points in time. The data used represented a long time interval over which a nearly straight line could be seen. The probabilities for *P. glauca* and *P. mariana* were calculated to be 0.967 and 0.965 respectively. Since *Salix* spp. sucker, they are assumed to senesce only under stress conditions. Hence their

survival probability is 1.

Stress is accounted for by lowering the probability of survival (PS). Interspecific and intraspecific competition interact in lowering PS. As well, stress results from frozen ground, which is independent of competition. Interspecific competition as a function of a carrying capacity is considered first. For a 1000×1000cm plot, the carrying capacity K could range from 0 to 1000000 or in terms of percentage, from 0% to 100%. From observation, a value of K = 60% seems reasonable. For the total cover of the arboreal species $Z = X5_1 + X5_2 + X5_3$ we can form the difference $X = K - Z$ with a range of 0 (maximum competition) to 60 (no interspecific competition). Assuming a negative exponential relationship between Y (the shared reduction in survival probability) and X, the function

$$Y = e^{-.04X}$$ [5]

was derived by setting Y = 0.3 arbitrarily when X = 30. This is then proportioned via $X5_1/Z$ along with interaction fitting constants. Interspecific competition is a linear function relating greater stress for younger age classes.

Stress from frozen ground focuses on the parameter rooting depth (ROOTD) which is moss depth plus the active layer depth. From observation and Orlóci & Stanek (1979), ranges were determined to reflect this stress. For *P. glauca*, maximum rooting depth of mature trees occurred in the range (30,∞), measured in centimeters. Physical stress was assumed to occur in the range (30,40), increasing with decreasing depth. Two switches (see Table 2) were used. The first, S1A, determined if there was stress. The second, S1B, determined which age classes were affected. As the depth of the active layer decreased, old

Table 2. Switch functions used in determining stress on arboreal species. Each function takes a value of 0 or 1 depending on which of two conditions is true.

Switch function	Value of switch function	
	0	1
	Conditions	
S1A	$41 - \text{ROOTD} \leqslant 0$	$41 - \text{ROOTD} > 0$
S1B	$I < 200 - 15(41 - \text{ROOTD})$	$I \geqslant 200 - 15(41 - \text{ROOTD})$
S2A	$31 - \text{ROOTD} \leqslant 0$	$31 - \text{ROOTD} > 0$
S2B	$I < 200 - 30(31 - \text{ROOTD})$	$I \geqslant 200 - 30(31 - \text{ROOTD})$
S2C	$\text{ROOTD} - 37 \leqslant 0$	$\text{ROOTD} - 37 > 0$
S2D	$I > 25(\text{ROOTD} - 37)$	$I \leqslant 25(\text{ROOTD} - 37)$
S3A	$19 - \text{ROOTD} \leqslant 0$	$19 - \text{ROOTD} > 0$
S3B	$I < 50 - 5(19 - \text{ROOTD})$	$I \geqslant 50 - 5(19 - \text{ROOTD})$
S3C	$\text{ROOTD} - 34 \leqslant 0$	$\text{ROOTD} - 34 > 0$
S3D	$I > 2(\text{ROOTD} - 34)$	$I \leqslant 2(\text{ROOTD} - 34)$

trees would be affected first. The result of this stress was a linear function of ROOTD. For *P. mariana*, maximum rooting depth occurred in the range (26,45) with no stress in the range (31,37). If ROOTD was less than 31, stress operated as in *P. glauca*. If this depth was greater than 37, stress was assumed to occur due to excessive drainage. The switch S2C was used to detect this type of stress and the switch S2D to determine which age classes were affected. As frozen ground tended to lower, younger trees would be affected first. For *Salix* spp., the ranges (10,60) and (19,34) were determined and the switch functions were similarly devised.

Because there are not many stems in any age class, mortality was determined by comparing the age specific PS against random numbers. Hence the comparison is made for every tree (see Appendix 1).

3.4.2 Moss Carpet Thickness

Data for moss growth was not available and so the equation used here was heuristic. Moss thickness was considered to be a function of the moss cover and an exogenous moisture index (M2). We assume a maximum growth rate of 0.5cm per year which is lowered by the moss cover, the moisture index and a linear function reflecting the maximum depth observed (Table 1).

3.4.3 Cover

As mentioned, the total plot cover (1000x1000cm) is composed of five auxiliary variables such that the sum of these variables is 1000000cm^2. The canopy cover of the three arboreal species is a function of the age classes,

where the projection of each tree's canopy is assumed to be a circle. The relationships between age class and canopy diameter are illustrated in Fig. 4, and the functional relationships are given in Table 3.

Change in moss cover is attributable to its own growth and to the presence of arboreal species. Increase by growth is only over organo/mineral soil $X5_4$. Rather than being an homogeneous area, the organo/mineral soil is more likely to be patchy because when a tree dies it is removed and thus contributes to $X5_4$. The moss then tends to shrink these patches (circles) every year. The growth equation is given in Table 3. Here, M1 and C are environmental parameters which potentially lower this optimum growth. M1 is another exogenous moisture index while C is a cover index which lowers growth when the canopy lets in too much sun.

The organo/mineral soil $X5_5$ decreases as moss grows over it and increases when arboreal species die and expose this type of soil.

To keep total plot cover constant when there is a certain amount of increase in arboreal cover, the total moss cover and organo/mineral soil cover are reduced by this amount. This total reduction is proportioned between the two.

3.4.4 Active Layer

During the winter all soil is frozen, but as the temperature moderates there is some thawing. The active layer extends down to the yearly maximum depth of thawed ground and so responds to current conditions. From field observations and preliminary analysis it appears that moss acts as an insulator

Fig. 4. Cover relationship between age class and canopy diameter from field

data for (a) *Picea glauca* ⊙ and *P. mariana* ✕ and (b) *Salix* spp. + .

Regression equations (Table 3) for the three curves are as follows:

—   —   —   *P. glauca*

——   ——   ——   *P. mariana*

———   —   ———   *Salix* spp.
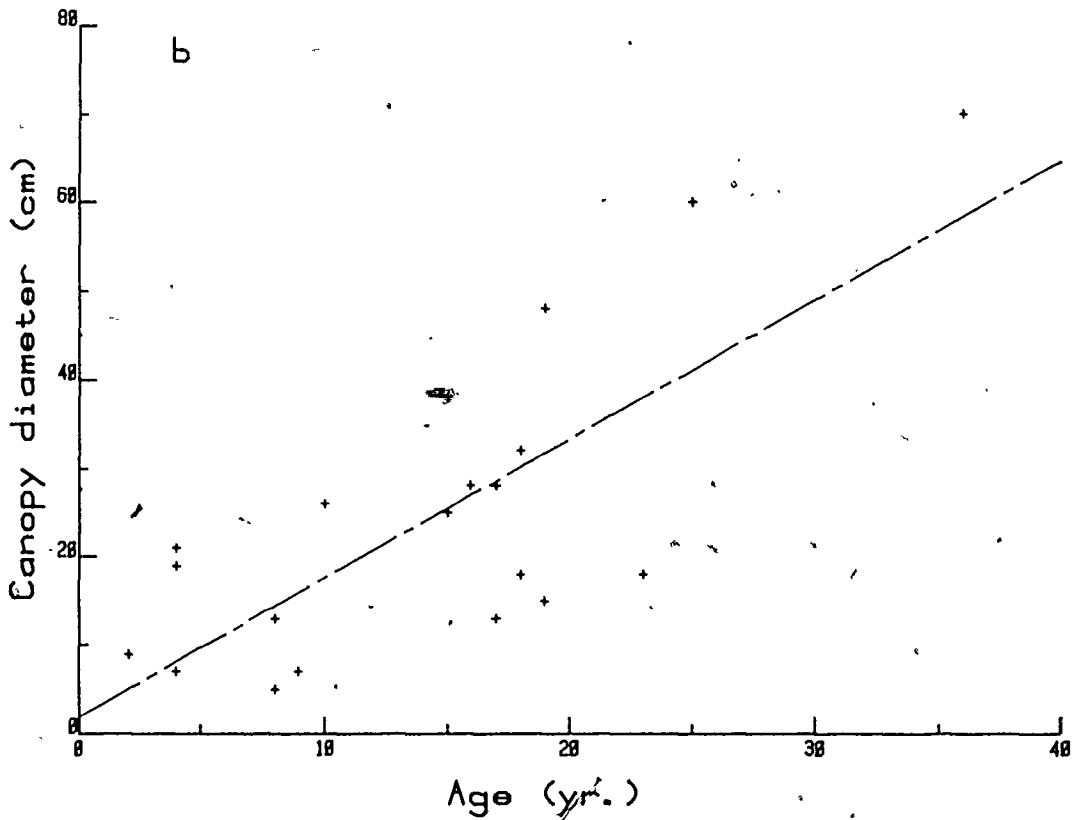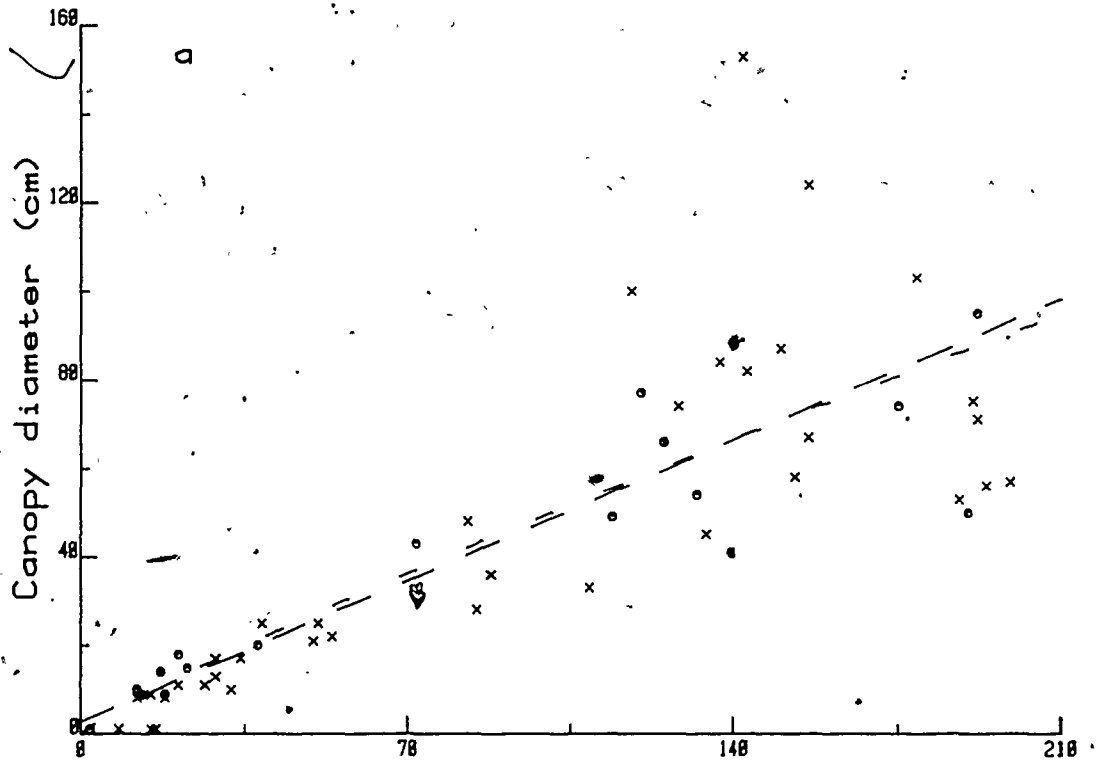
Fig. 5. The effect of moss insulation on frozen ground. Data for the moss

index (X-axis) is the product of moss thickness and cover on a (0,1) range.

Data points are indicated by o and the regression line by —— —— .

Active layer (cm) vs Moss index (cm·cm^2/10^6)
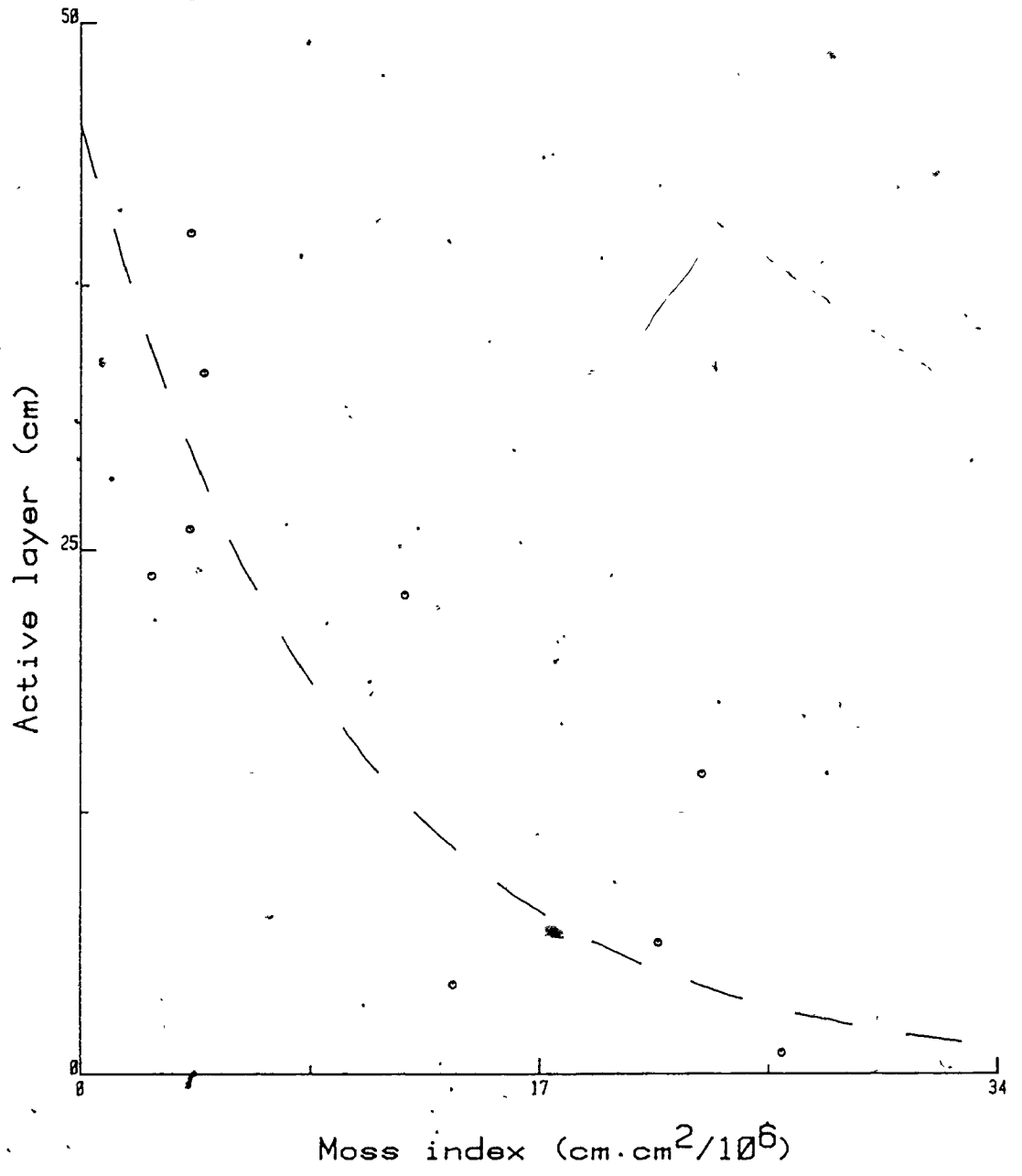
Table 3. Simulation equations involving principal variables X5 and X6.

$DIAM1_1 = 1$

$DIAM1_i = 0.881i^{0.875}$ $\quad$ $i = 2,...,200$ $\quad$ $r = 0.975$

$DIAM2_1 = 1$

$DIAM2_1 = 2.782 + 0.454i$ $\quad$ $i = 2,...,200$ $\quad$ $r = 0.79$

$DIAM3_1 = 1$

$DIAM3_1 = 1.875 + 1.568i$ $\quad$ $i = 2,...,50$ $\quad$ $r = 0.763$

$X5_1 = \Sigma\pi \, X1_i \, DIAM1_i^2/4$ $\quad$ $i = 1,...,200$

$X5_2 = \Sigma\pi \, X2_i \, DIAM2_i^2/4$ $\quad$ $i = 1,...,200$

$X5_3 = \Sigma\pi \, X3_i \, DIAM3_i^2/4$ $\quad$ $i = 1,...,50$

$X5_4 = X5_4 + 216 \, X5_5 \, M1 \, C/55^2$

$C = 1$ $\quad\quad\quad\quad$ if $X = X5_1 + X5_2 + X5_3 \geqslant 500000$

$C = (0.9X + 50000)/500000$ $\quad$ if $0 \leqslant X < 500000$

$X6 = 45.206 \, e^{-0.104 \, X4 \, X5_4 \, CP/1000000}$ $\quad$ $r = 0.80$

$CP = \cos(61° - 23.5°)/\cos(61° - 23.5° - SLOPE)$

---

whereas the arboreal canopy is not very influential. A regression of the active

layer versus the product of moss thickness and cover (on a (0,1) range) gave

a reasonable result (Fig. 5 & Table 3). A negative exponential model was used

because of the good fit and because for a large positive moss index $(X4 \cdot X5_+)$,

the prediction of the active layer was always positive. The regression was

carried out holding slope of the plot relatively constant near $0°$. As slope

may range between $0°$ and $15°$, the equation was modified using Lambert's

cosine law (Rosenberg, 1974). A cosine proportion incorporated the latitude

$(61°)$ and the sun's angle for the June solstice. Hence, as slope increases,

the sun's rays will become more direct and so the active layer would be expected

to increase in magnitude.

3.5 Examples

For the simulation model to run, an initial parameter set needs to be

specified. This is composed of age class data for the three arboreal species,

moss thickness, organo/mineral cover, moisture indices, germination

probabilities and slope of the plot. This initial set forms a subset of the

complete parameter set. The parameters are numerical realizations of variables

which collectively describe the configuration of the plot. Although any

combination of parameters within predescribed limits could be used, certain

difficulties could arise if a legitimate set is not chosen. The theoretical basis

for this is in recognizing that a model is a homomorph of the real system

where several related elements of the system are described by a single model

element. This is understood by the fact that a model variable implicitly

describes a number of correlated system variables (Goodall, 1974b). Yet this

is an ideal situation. In practice, the model builder is often using a model
to better understand the system so that it is more likely that some of the
system elements are not reflected at all in the model. Hence it is quite possible
that an initial set, which makes sense in the real system, may not have an
analog in the model. The result of running the model would then be to produce
either an anomalous situation (one which would be difficult to interpret
ecologically), or a series of states which would eventually converge to a
reasonable configuration.

The approach here was to run the model in two stages. In the first stage,
initial sets were chosen based on observed data which did not necessarily
reflect a natural configuration for the model. If it settled down into a
reasonable configuration, it was used as a base line for the second stage. This
second stage allowed for reasonable experimentation as the configurations
would probably be more natural. The first three simulations belonged to the
first stage. Age class data followed a negative exponential distribution. The
remaining variables used for initialization (at time 0) along with the computer
printouts of the simulations are given in Appendix 2. These three simulations
were initialized with somewhat different age class data. The first was composed
solely of *P. glauca*, the second mostly of *P. mariana* and some *Salix* spp.,
and the third solely of *Salix* spp. All three simulations converged to similar
configurations and these were used as a basis for initial sets in the second
stage.

One aim of these simulations is not to go as far as verifying the model.
Rather, it is sufficient for the configurations to make intuitive sense and to
allow for experimentation so that statements can be made regarding the

methodology. A second aim, which also involves experimentation, is to alter various endogenous and exogenous variables such as slope and moisture indices so as to compare results in a type of sensitivity analysis.

There are two basic ways in which the results can be looked at. The first deals with various equilibria. Their existence would suggest the type or extent of system stability. The second deals with the problem of biotic versus abiotic factors being the driving forces behind the system dynamics. Specifically, the question is whether species competition predominates or is subordinate to various abiotic variables. The model cannot be expected to resolve the issue even for this system, because the model has not been verified. However, interesting insights may result.

3.5.1 Comparisons for *Picea glauca*

Three simulations were done using the same initial age class data where *P. glauca* predominated. The first simulation used an initial set from stage one which included a slope of $0°$. A stereo presentation of the data for the entire two hundred years of simulation is given in Fig. 6. Note that towards the end of the simulation, an approximately stable negative exponential age distribution with minor oscillations is suggested. The second and third simulations were from stage two and had slopes of $8°$ and $15°$ respectively. The moisture indices were adjusted to correlate with changes in slope. The results suggested that as slope increased, *P. mariana* and *Salix* spp. decreased both in cover and numbers of individuals in each age class, while the rooting depth increased (Fig. 7). Recognizing the limits placed on these two species regarding rooting depth, it appears that slope affects the rooting depth which

Fig. 6. Stereograms (Fewster & Orlóci, 1978) illustrating the number of stems

per ten year age class over two hundred years of simulation for (a) *Picea*

glauca, (b) *P. mariana* and (c) *Salix* spp. The age class axis begins at ages

1 through 10 and increases up to ages 141 through 150 for either *P. glauca*

or *P. mariana* and up to ages 41 through 50 for *Salix* spp. The time axis

represents years 0, 10, 20 and so on up to 200. The axis for number per age

class represents the depth of the stereo image. It begins at zero and increases

to its maximum. See Appendix 2 for actual numbers. The three axes are oriented

as shown below:

```
                    time
                     |
                     |
                     |
                     |_____ 10 year age class
                    /
                   /
                  /
            number per
            age class
```

a

B

C
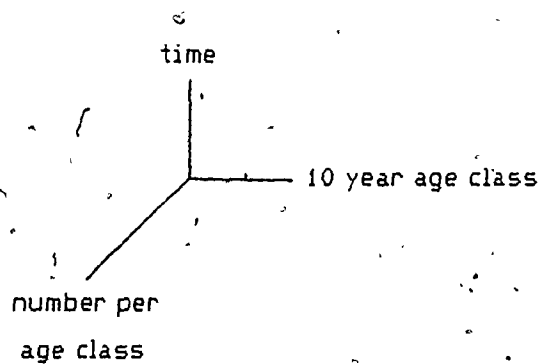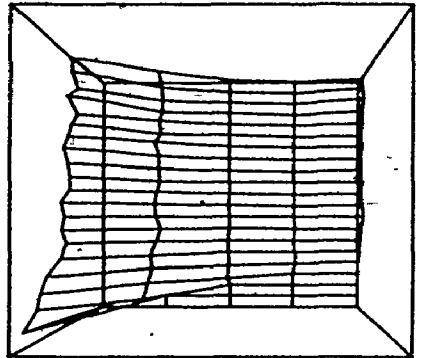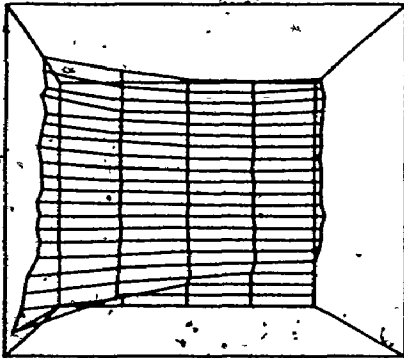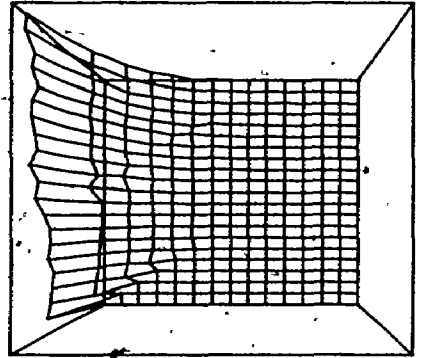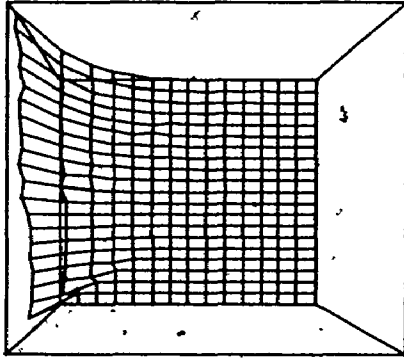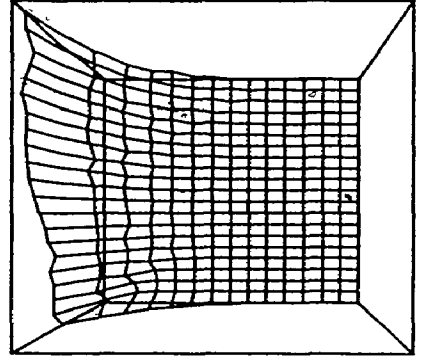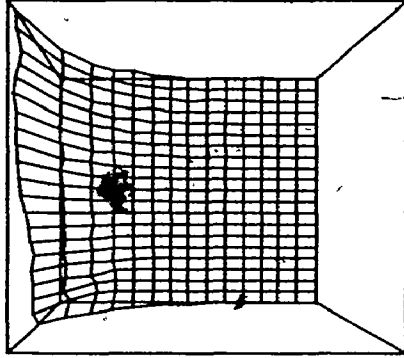
Fig. 7. Age class distributions for (a) *Picea mariana* and (b) *Salix* spp. after
two hundred years simulation time where *P. glauca* predominated at time zero.
Three simulation runs have been combined (Appendix 2) differing essentially
according to slope:

0° 8° 15°

Figure axis labels: Number of individuals (y-axis, both plots a and b); Age class (yr.) (x-axis)
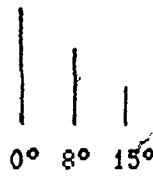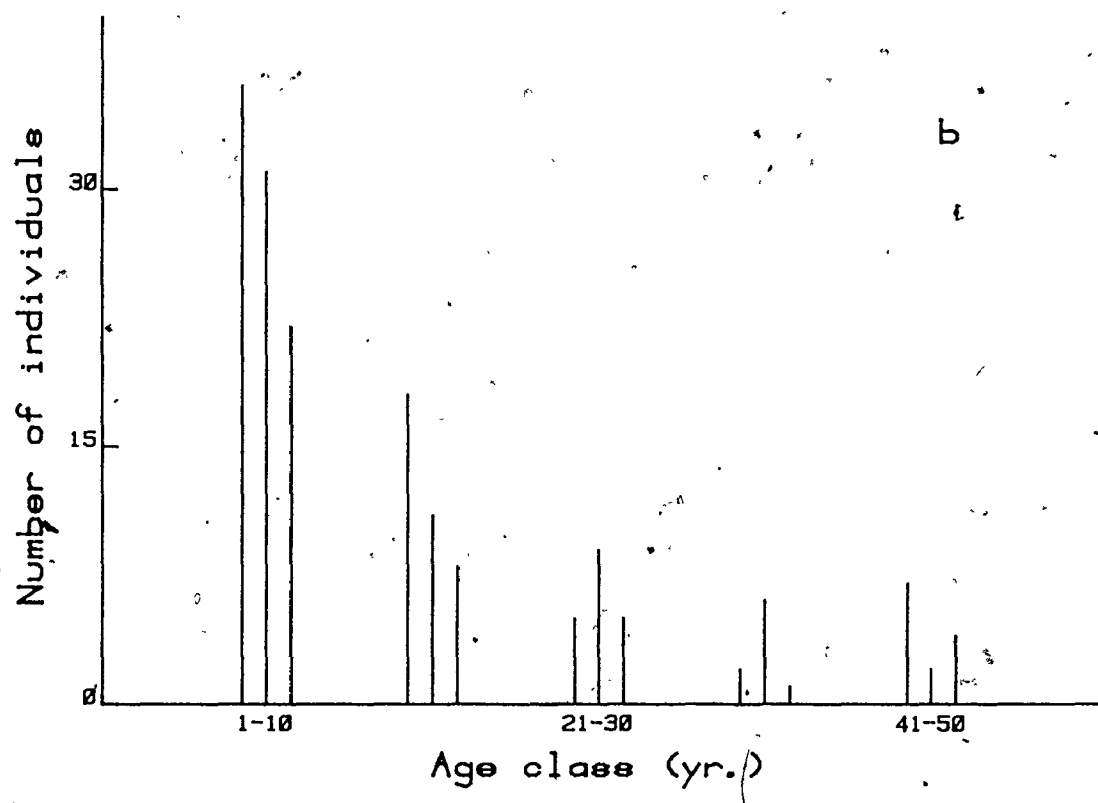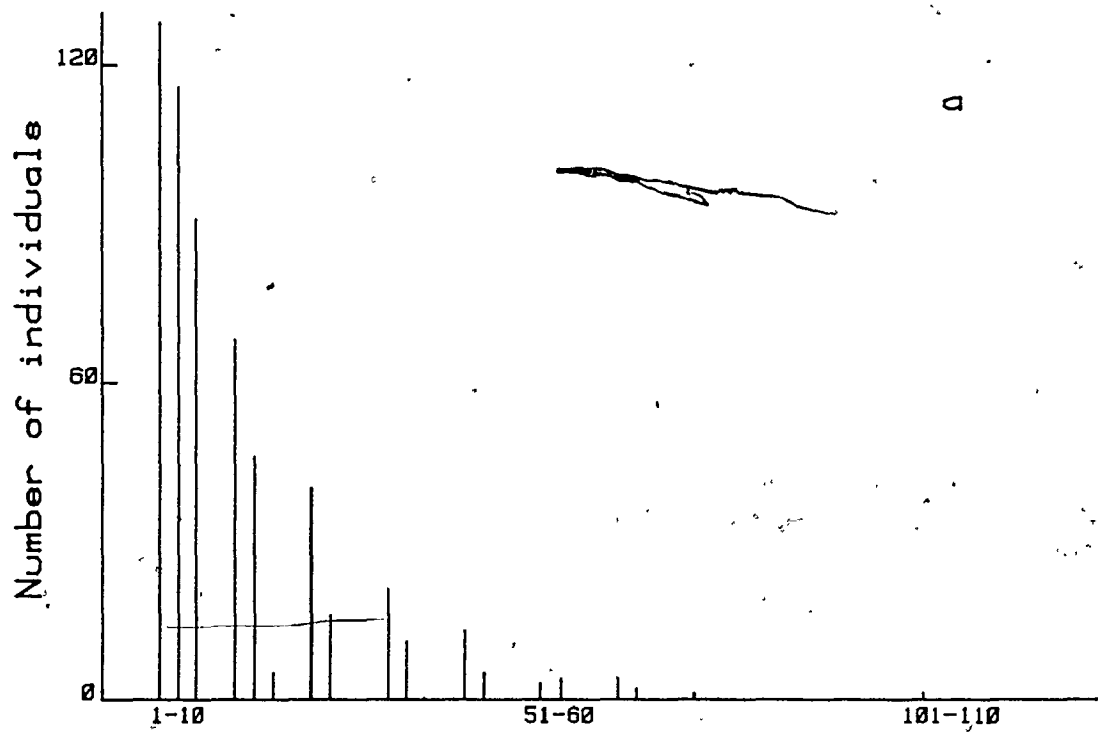
in turn influences survival ability.

3.5.2 Comparisons for *Picea mariana*

Two simulations were done using the age class data where *P. mariana* dominated, and where a small amount of *Salix* spp. was present. The first was from stage one and the second from stage two. The difference between the two initial sets was that the moisture index M1 indicated a wetter environment for the second simulation. Both resulted in a mixture of the three arboreal species with *Salix* spp. dominating. In the second simulation this domination was stronger which again could be due to a decrease in rooting depth. Correlated with this decrease is a substantial increase in moss cover (from 51% to 61%).

3.5.3 Comparisons for *Salix* spp.

Two simulations where *Salix* spp. predominated were done. The first and second were from stages one and two respectively. The second differed from the first in that both moisture indices indicated a wetter environment. The results were similar. Moss cover increased while rooting depth decreased. The cover of *Salix* spp. increased marginally and *P. mariana* cover decreased moderately. It appears that the moisture increase was the driving force behind these changes.

3.6 Areas of Improvement

The results of the simulation runs suggest a few areas where changes to the model could be made. Germination conditions were determined solely from the literature, although only simple relationships were used. Perhaps more detail would be beneficial (e.g. Black & Bliss, 1980). As well, further experimentation in the field could suggest a more appropriate approach. It appears that mortality rates (influenced by competition) for both *P. glauca* and *P. mariana*, were high since no trees older than about 120 years were found in model runs whereas a maximum age of 200 was assumed. The equations for interspecific competition are also candidates for improvement. These equations are based on a function which incorporates directly a carrying capacity for arboreal cover of 60%. It may be that if 100% were used, the model's feedback mechanisms would still tend to keep arboreal cover below 60%. Other sorts of approaches such as altering the parameters of this function could also be beneficial. Interspecific competition could also be made more realistic by relating it more intimately with certain environmental factors. One such equation involving moss thickness needs to be altered. At present, a logistic relationship is used which implicitly does not allow for the decomposition rate to exceed the growth rate. Under certain circumstances the decomposition rate may be greater than the growth rate. Hence this aspect needs to be incorporated. These weaknesses illustrate the pedagogical aspect of simulation modelling through feedback between the model and the real system.

3.7 Discussion

The model is still in a transition stage and needs to be verified before confidence can be placed on any precise predictions. However, there are general principles that are suggested by this model. For example, it appears that some of the abiotic components are more important than the biotic ones in molding the form of the model's configurations. Thus, it may be that for the system being modelled, arboreal competition and moss cover are subordinate to slope. This suggests one positive aspect of simulation modelling which has not been fully recognized. The set of interspecific competition equations, for example, is a component or submodel of the model as seen in Figs. 2 & 3. The model could safely be studied all by itself. In this case one would be interested in the shape of the response curve over time because it would act as a predictor. What happens when this component is embedded into a larger model is that the realization (prediction) from this component over time may disappear. Rather than using the parameters it generated from one time step to determine the state of the submodel at the next time step, the larger model often will change the parameters as it relates them to other components. Hence the successive states or configurations can not be known *a priori*. The result of this embedding will often suggest different tendencies and, as in this case, general ecological principles at the scale of the study area may be derived. Hence this model, and probably other models at the intermediate level, do have potential for local relevance and utility. It should be noted that if exact predictions were desired, implying verification, additional work would be needed.

Chapter 4

TIME STATIC MODELLING

Regression modelling is one approach describing community structure. Other model types are also important. One approach which is used extensively is that of simulation modelling, since it can dynamically describe specific system relationships in a time oriented reference system. The model type of regression has typically been used on the same scale as simulation. Yet regression has greater scope in that it is capable of digesting a larger amount of data. Furthermore, where sampling constraints do not allow for the time element to be measured or where it is simply interesting not to recognize specific time relationships, regression can facilitate prediction. In other words, the regression model can be made time static. This is a benefit to users who may not be interested in time as a reference system but, rather, in the eventual consequences of perturbation. This chapter describes the development and experimentation on an appropriate regression model. The experiments focus on various levels of environmental perturbation and the outcomes are combined in various ways to facilitate prediction of plant community response.

4.1 Introduction

Regression and simulation represent two very different approaches to modelling. Gold (1977) describes regression, as used statistically, to be a correlative model and simulation to be an explanatory model. Correlative models fit curves to data, the model chosen being but one of many possible candidates. In addition to this, explanatory models attempt to explain actual system relationships through the incorporation of causal mechanisims. Gold (1977) points out that only explanatory models should be used in extrapolation or inference. We will now compare regression and simulation from a different perspective. As well, we will release regression from its statistical boundaries so that a certain degree of unconstrained inference is possible.

Simulation modelling has great appeal to the scientist and to the local planner. The user can simulate perturbation to examine its potential effect and perhaps to design suitable preventative measures or remedial actions. Yet a careful look at how a simulation model is formed reveals a few inherent problems with perturbing some of the variables. At any one time, the real system or the analogous model will be in a certain state. This state or configuration is described by the realization of a number of variables. As time proceeds it is expected that the configuration will change. If we could graph configuration versus time (a multidimensional graph) we would expect to see some sort of continuous meandering path. A simulation model is built not to predict analytically the state at any time but rather to reflect momentary trends of the path based on the current, and possibly recent configurations. The model equations are developed based on a limited range of data, or limited states found in the area sampled. From this, one may infer that a perturbation, if

drastic enough, may force this path to be discontinuous and possibly result in a configuration which was not used in developing the model. The implication of the former is that the time element will be off while the implication of the latter is that the model may be sufficiently jolted so as to predict invalid configurations (ones which would not occur in the real system or which lack credibility because they were not used in the developmental stage of the model).

These problems can be recast so as to lead into the modelling approach taken in this chapter. Simulation data is collected under very narrowly defined conditions so that specific relationships can be formulated. As a result, the model has limited applicability. It is quite possible that a number of states recognized in the system will be left out of the model. Time is also a problem because of its perception as a fundamental reference base. Moreover, it is interesting in ecological investigations to consider what the general tendencies of the system might be following perturbation even if time is undefined. One could therefore ask what might be the eventual state of the system following perturbation without regard to time.

With this in mind, a regression approach was taken based on the assumption that the vegetation was a function of the environment. It is recognized that this assumption is not strictly correct. In developing the simulation model, other sorts of relationships were used. For example, moss cover was a determining factor for the active layer, implying that the environment is a function of the vegetation. Also, competition implies that vegetation is also a function of the vegetation. However, this can be resolved. Although a regression model predicts the vegetational resultant, no restriction need be placed on time. Dynamically speaking, this resulting state may be resolved

quickly or it may take some time as in the case where old vegetation is destroyed and the new is forced to grow back. Hence, one can visualize that as the vegetation is changing, those environmental variables not used in the model could be affected. As well, this vegetational change could involve feedback, terminating once the state predicted is resolved. Hence, as suggested in the previous chapter, other sorts of interactions can take place which are subordinate to the independent environmental variables used in the model.

As will be seen later on, it is possible to use in a regression model data which encompass much more variability. It is therefore more likely that the model will respond efficiently to a broad assortment of perturbations.

4.2 Data

The data used here came from the first field season as described in Chapter 3. A total of three hundred twenty three plots were established and described by three hundred thirty five species and sixteen environmental variables. The survey and variables are explained by Orlóci & Stanek (1979). It is from their results that the preliminary framework is constructed. Table 4 describes this model development. Here twenty five vegetation types were found by a cluster analysis, two of which were discarded because they had little in common with the others (Table 5). Of the three hundred thirty five species, one hundred one were deemed characteristic: present in at least 50% of the plots of at least one type. The use of characteristic species seemed to be a good approach as it served to discard much of the randomness and cosmopolitan nature of many species while retaining those species which could predict a type. Table 6 lists these one hundred and one species. The original

Table 4. Description of the development of the model. Data describing the twenty three vegetation types is separated into vegetation and environment components. Next, the various components are coded as matrices and then as dependent and independent variables. Finally, a functional relationship is formed.

		Vegetation types		
Vegetation scores			Environment scores	
species frequencies	drainage	soil texture	organic content and thickness	erosion potential
SFF	DR	ST	OR	ER
Y	X1	X2	X3	X4
Y	X1	X2	X3	X4
	$X1^{1/2}$	$X2^{1/2}$	$X3^{1/2}$	$X4^{1/2}$
	$X1^{1/3}$	$X2^{1/3}$	$X3^{1/3}$	$X4^{1/3}$
		$(X1 \cdot X2 \cdot X3 \cdot X4)^{1/4}$		

Table 5. Description of twenty three vegetation types. The type code is based on constant genera (Orlóci & Stanek, 1979). The numerical values match the raw scores, refering to soil moisture regime: 1 – dry; 2 – moderate to dry; 3 – moderate; 4 – moderate to wet; 5 – wet; 6 – very wet.

Type code	Type nomenclature	Type number	Drainage category
AAC	*Artemisia-Agropyron-Calamagrostis*	11	1
CT	*Calamagrostis-Tortula*	12	1
PVFP	*Pinus-Vaccinium-Festuca*	23	1
PASE	*Populus-Arctostaphylos-Shepherdia*	14	2
PAFP	*Pinus-Arctostaphylos-Festuca*	13	2
PVHC	*Pinus-Vaccinium-Hylocomium*	22	2
PVD	*Picea-Viburnum-Drepanocladus*	2	2
PAF	*Picea-Arctostaphylos-Festuca*	9	3
PFP	*Pinus-Festuca-Peltigera*	19	3
PC	*Picea-Carex*	8	3
PHP	*Picea-Hylocomium-Peltigera*	16	3
PHPC	*Picea-Hylocomium-Peltigera*	21	3
PCHP	*Picea-Cornus-Hylocomium*	17	3
PLH	*Picea-Ledum-Hylocomium*	1	4
PAA	*Picea-Arctostaphylos*	7	4
PSAH	*Picea-Salix-Aulacomnium*	18	5
PARA	*Picea-Rhododendron-Aulacomnium*	5	5
PAAP	*Picea-Arctostaphylos-Aulacomnium*	15	6
S	*Salix*	6	6
PLEA	*Picea-Ledum-Aulacomnium*	4	6
SCA	*Salix-Carex-Aulacomnium*	20	6
SRA	*Salix-Rubus-Aulacomnium*	24	6
SC	*Salix-Carex*	3	6

Table 6. List of the one hundred one characteristic species used in the analysis. Nomenclature was as follows: for the vascular plants – Húltén (1968) and Welsh (1974); for the mosses – Crum *et al.* (1973); and for the lichens – Hale & Culberson (1970).

Agropyron yukonense	*Populus balsamifera*
Alnus crispa	*Populus tremuloides*
Anemone multifida	*Potentilla fruiticosa*
Antennaria rosea-nitida	*Potentilla hookeriana*
Arctostaphylos rubra	*Potentilla pensylvanica*
Arctostaphylos uva-ursi	*Pulsatilla patens*
Artemisia frigida	*Pyrola secunda*
Betula glandulifera	*Rhododendron lapponicum*
Betula nana	*Rosa acicularis*
Calamagrostis canadensis	*Rubus arcticus*
Calamagrostis purpurascens	*Rubus chamaemorus*
Carex aquatilis	*Salix alaxensis*
Carex concinna	*Salix glauca*
Carex filifolia	*Salix myrtillifolia*
Carex lasiocarpa	*Salix planifolia*
Chamaerhodos erecta	*Saxifraga tricuspidata*
Cornus canadensis	*Shepherdia canadensis*
Crepis elegans	*Vaccinium uliginosum*
Dryas drummondii	*Vaccinium vitus-idaea*
Dryas integrifolia	*Viburnum edule*
Empetrum nigrum	*Abietinella abietina*
Epilobium angustifolium	*Aulacomnium palustre*
Epilobium latifolium	*Barbilophozia hatcheri*
Equisetum palustre	*Caloplaca cirrochroa*
Equisetum scirpoides	*Ceratodon purpureus*
Erigeron caespitosus	*Cetraria nivalis*

Erigeron compositus	*Cetraria pinastri*
Erigeron purpuratus	*Cladonia arbuscula*
Eriophorum vaginatum	*Cladonia chlorophaea*
Erysimum inconspicuum	*Cladonia ecmocyna*
Festuca altaica	*Cladonia gracilis-dilatata*
Festuca brachyphylla	*Cladonia gracilis-elongata*
Gentiana propinqua	*Cladonia rangiferina*
Geocaulon lividum	*Dicranum undulatum*
Hedysarum alpinum-americanum	*Drepanocladus uncinatus*
Ledum groenlandicum	*Hylocomium splendens*
Ledum palustre	*Hypnum procerrimum*
Linnaea borealis	*Hypogymnia physodes*
Linum perenne	*Lecidea rubiformis*
Lupinus arcticus	*Nephroma arcticum*
Lycopodium annotinum	*Peltigera aphthosa*
Mertensia paniculata	*Peltigera canina*
Mitella nuda	*Pleurozium schreberi*
Oxycoccus microcarpus	*Polytrichum piliferum*
Oxytropis campestris	*Ptilium crista-castrensis*
Pedicularis labradorica	*Sphagnum magellanicum*
Penstemon procerus	*Sphagnum* sp.
Picea glauca	*Stereocaulon tomentosum*
Picea mariana	*Thuidium abietinum*
Pinus contorta	*Tortula ruralis*
Polemonium pulcherrimum	

raw data (species by plot), in the form of presence/absence scores rather than cover/abundance, was used. This facilitated a transformation to frequency data for species by type. This is analogous to subdividing a plot or quadrat and noting the presence or absence of the species in each subdivision. Here the three hundred twenty three plots are like the subdivisions and the types are like the quadrats.

Of the sixteen environmental variables used by Orlóci & Stanek (1979), four were selected for use based on considerations of their correlations with changes in vegetation structure. The environmental variables were scored at the level of the plots. These scores were grouped by vegetation type and then averaged. In the case of drainage, scoring was based on seven classes ranging from 1-excessive to 7-wet. Soil texture, the second variable chosen, was a combination of the four particle sizes gravel/stone, sand, silt and clay. Each of the three hundred twenty three plots was scored as to percent content of the soil mass in the four particle classes. The raw scores were placed into one of eleven classes and means were calculated for each vegetation type. The third variable, organic content and thickness, was a combination of scores for organic content placed into seven classes and scores for thickness placed into six classes. Again means for vegetation types were calculated based on the classes. The fourth variable, erosion potential, was scored as either 1-low, 2-medium or 3-high. Means for the type were again calculated.

4.3 Regression Model

The nature of the data analysis was exploratory so that the model was not chosen *a priori* as it would be in the case of a strictly statistical approach. The statistics ended with the data and interest lay not in testing but in maximizing predictability within the bounds of the data set in hand. For a regression model this would mean maximizing the fit via a correlation measure. Goodall (1972) used regression this way with outstanding results. He was interested in predictability and so used squared, cubed, exponential and even dependent variables on the right side of his equation. In a regression model, the assumption that the right side variables are independent is an arbitrary requirement serving the limitations inherent in the use of the standard distributions for significance tests. Regarding the testing of hypotheses, high powered alternatives to simplistic tests based on these standard distributions can be readily found, but this is not a topic of immediate concern here. Monte Carlo methods, however, allow one to bypass this difficulty in general, and to tailor the test to the actual conditions of the sample (Orlóci, 1978). Furthermore, if one is interested in going beyond statistical curve fitting, to representing some degree of the system mechanisms in the model, Goodall's approach is logical. The use of squared and cubed terms along with the linear terms often results in a high degree of multicollinearity. This does not, however, invalidate the use of regression as a curve fitting technique since its absence is not an underlying assumption. Nevertheless one might choose to reduce multicollinearity, as outlined in Freund & Minton (1979), by selectively eliminating some of the variables. Yet this would tend to reduce predictability, our number one aim. Goodall (1972) speaks of a tendency towards model

expansion and not reduction for this very reason. The use of regression here is essentially a curve fitting method. By relaxing the statistical bounds and including variables which interact we develop a model more like the real system. Hence we move towards a mechanistic model, thus increasing predictability, precision, and generality with the view towards application and inference.

The analysis, being exploratory, followed somewhat convoluted paths before a particular model was decided upon. Only the steps which were actually used are presented here.

We begin by stating that species performance is a function of drainage, soil texture, organic content and thickness, and erosion potential. The vegetational and environmental information (Table 4) was transformed into the Euclidean distance matrices SPF, DR, ST, OR and ER. There were two reasons for this. First, the number of descriptors varied among the vegetational and four environmental data sets. The vegetational data set had scores for the twenty-three types on one hundred one species. Two of the environmental variables, drainage and erosion potential, had scores for the types on one descriptor while organic content and thickness was scored by two descriptors and soil texture by four. By calculating distances (separately for each of the five data sets) among the types, the five data sets could be matched up for regression purposes. Second, the vegetational raw data had one hundred one descriptors (species) of the twenty three types. However, a parsimonious representation with respect to the types requires a maximum of twenty-two descriptors or hyperdimensional axes (the maximum being reduced if any species are correlated). Again a distance matrix was useful for this. The data matrix

SPFREQ, composed of one hundred one species by twenty-three types, was

transformed into the Euclidean distance matrix **DISF** by the computer program EUCDP. (The analysis is outlined in Table 7. Appendix 3 contains listings of the computer programs used.) A preliminary geometric picture was desired and so an ordination (program PCAD; Orlóci, 1978) was done. The first three axes accounted for 58.3% of the variation. The component scores of these three axes were transformed into the distance matrix **SPF** which was subsequently used in the regression model. This represents one of the convolutions. Although distance matrix **DISF** could have been used instead of **SPF**, much work had been done before this particular approach was chosen and so matrix **SPF** was retained. Three of the four derived environmental variables were independently transformed into the distance matrices **DR** (drainage), **OR** (organic content and thickness) and **ER** (erosion potential) and then scaled to a (0,1) range. This scaling was done to make them commensurable with **SPF** which had been scaled by the program PCAD $(1/\sqrt{(N-1)}; N = 23)$. The raw data for soil texture was transformed into a distance matrix and then subjected to program PCADP (see Appendix 3 for listings of this and subsequent programs). This produced 99.9% of the variation on the first three component axes. The three sets of component scores were then transformed into distance matrix **ST** without scaling as the ordination had already done so. Because almost all of the information was retained by the first three axes, the effect of this convolution was insignificant.

A number of regression models were examined. The number of environmental variables to be used was limited to reduce complexity. This was one reason for choosing the four derived variables. Other reasons included high correlations via an analysis of concentration (Feoli & Orlóci, 1979) by

Table 7. Flow chart of the general analysis.

```
┌─────────────────────┐        ┌─────────────────────┐                              ┌──────┐
│ Raw data            │        │ Raw environmental   │                              │  1   │
│ presence/absence    │        │ data for the        │                              └──┬───┘
└──────────┬──────────┘        │ types               │                                 │
           │                   └──────────┬──────────┘                     ┌───────────┴───────────┐
┌──────────┴──────────┐                   │                                │ Change standard       │
│ Frequency data;     │                   │                                │ D to D1               │
│ 101 species by 23   │                   │                                └───────────┬───────────┘
│ types     SPFREQ    │        ┌──────────┴──────────┐                                 │
└──────────┬──────────┘        │ Distance matrices   │                                 │
           │                   │ DR, ST, OR, ER      │                         ┌───────┴───────┐
┌──────────┴──────────┐        └──────────┬──────────┘                        ╱                 ╲
│ Distance matrix     │                   │                             yes  ╱    continue        ╲
│           DISF      │                   │                          ◄──────┤    perturbing        │
└──────────┬──────────┘                   │                                  ╲                    ╱
           │                              │                                   ╲        │        ╱
┌──────────┴──────────┐                   │                                    ╲───────┼───────╱
│ Ordination;         │                   │                                            │ no
│ first 3 axes used to│                   │                                  ┌─────────┴─────────┐
│ get distance matrix │                   │                                  │ Combine results   │
│              SPF    │                   │                                  │ graphically for   │
└──────────┬──────────┘                   │                                  │ comparison        │
           └──────────────┬───────────────┘                                  └───────────────────┘
```

Multiple regression
$Y - SPF$ $X - DR, ST, OR, ER$

$\hat{Y}$ calculated and used as the standard
for comparisons (dendrogram D) SPFH1

Perturb DR by a given amount

Calculate $\hat{Y}_p$ via multiple regression
equation and draw a new demdrogram D1

Is D1
different from
D
?

yes → 1

no

Increase perturbation by a small amount

Orlóci & Stanek (1979) and a high r as described below. Thus a multiple regression model was settled upon. Refering to Table 4, the model is formed by first separating the description of the twenty three vegetation types into a vegetation and an environment component. The vegetation component is described by species frequencies, coded as matrix SPF. The environment component is described by four variables coded as the matrices DR, ST, OR and ER. In functional form we have respectively the dependent variable Y and four independent variables $X1$, $X2$, $X3$ and $X4$. Non-linear and interactive relationships were derived to give other independent variables. The particular multiple regression model which gave the highest correlation coefficient (used as a mathematical index) without an overwhelming number of variables produced an r of 0.715. A total of fourteen variables were used. They were Y, $X1$, $X2$, $X3$, $X4$, $X1^{1/2}$, $X2^{1/2}$, $X3^{1/2}$, $X4^{1/2}$, $X1^{1/3}$, $X2^{1/3}$, $X3^{1/3}$, $X4^{1/3}$ and $(X1 \cdot X2 \cdot X3 \cdot X4)^{1/4}$. A number ranging between zero and one decreases in magnitude if its exponent is greater than one and increases in magnitude if the exponent is less than one. In order not to render very small distances (large similarities) ineffective in the regression, exponents less than one were chosen.

4.4 Perturbations

Assuming that species frequencies are a function of the environment and that a regression model has been constructed encompassing a wide variation of vegetation/environment combinations found in the area of study, it is not impossible to predict the eventual vegetation configuration as the result of any environmental configuration which is within the bounds used in the model's construction. The point of interest here is in discovering trends of change

as a result of perturbation. Because the model variables are distance matrices, it was decided, for simplicity, to simulate perturbation by proportional changes in the environmental matrices. This implicitly assumes that any perturbation, irrespective of its magnitude, affects each vegetation type in a similar manner. A perturbation of magnitude p would mean increasing the distances by the proportion p or rather multiplying all distances by the factor $1 + p$.

In refering to Table 4, specifically the four sets of environment scores **DR, ST, OR** and **ER**, it is seen that there are fifteen different combinations of perturbations possible. One may choose to perturb any one of the four, any two of the four, any three, or all four. Since for each choice much work will be done, it would be sensible not to try them all. Not only would there be redundancy due to the interrelationships among the four sets of scores, but the bulk of the resulting graphs and descriptons would confuse the interpretation and detract from the method being developed. How many of the fifteen should we choose? As mentioned, the environmental variables are related so that in choosing one, in a sense, we choose the others. Which one of the fifteen shall we then choose? The literature is helpful here. Wilde (1958) speaks of the importance of soil moisture. Loucks (1962) concurs, saying that soil moisture is a "major influence on the vegetation". Behind much of the work of Whittaker (1967) and Whittaker & Niering (1965) is a "topographic moisture gradient". Knight (1965) describes the importance of soil moisture in influencing other abiotic factors through the fact that water is a "nearly perfect solvent. It dissolves many substances that would not normally be available to organisms in a solid state". These comments support the choice of drainage as the candidate for perturbation.

Program PERDIS allowed for the proportional increase of the distances in one of the matrices **DR**, **ST**, **OR** or **ER**. As mentioned, consideration is given in detail to results from perturbing drainage (**DR**). The corresponding coded matrix is **X1** (see Table 4). The functional relationship suggests that perturbing drainage corresponds (in functional terms) to perturbing **X1** as well as the non-linear terms $X1^{\frac{1}{2}}$ and $X1^{\frac{1}{3}}$ and the interaction term $(X1 \cdot X2 \cdot X3 \cdot X4)^{\frac{1}{4}}$.

The meaning of a perturbation here is not straightforward because a distance matrix is one step removed from the raw data based on the variables. A proportional increase of 0.1, for example, in the raw data would necessarily have a specific meaning. It would increase a drainage value of say 7, (wet) to a value of 7.7 (wetter). However, any number of raw data sets could produce the same distance matrix. If we consider the types as realized plots in nature, increasing the distances by a certain proportion only magnifies the differences between the plots. We could think of the wet types as getting wetter and the dry types as getting drier. As well, we might think of all plots changing in the same way; for example, all becoming more dry but with the dry plots changing the most.

The strategy to uncovering trends was to gradually increase the amount of perturbation (Table 7) noting the results at each step. Two things were needed, a base for comparison and a way to determine which perturbations should be used for the comparisons. Program MULT3 calculated the new environmental distance configurations. Subsequently, program MHAT determined the expected vegetational configurations. The unperturbed state predicted matrix **SPFH1** or $\hat{Y}$. **SPFH1** and not **SPF** was used as a basis for making comparisons. For any perturbed state p, MHAT produced $\hat{Y}_p$. Following a sum

of squares clustering analysis by program SSAP a dendrogram was graphed. In general, if the new dendrogram D1 was different from the old one (D), the current results were retained for subsequent analysis. This repetitive process is outlined in Table 7. The vegetational configurations retained were matrices **SPFH1, SPFP6, SPFP11, SPFP14, SPFP15, SPFP3, SPFP17, SPFP18** and **SPFP19** representing proportional increases in perturbation of 0.0, 0.01, 0.049, 0.25, 0.28, 0.5, 0.8, 1.2 and 1.8 respectively (Fig. 3).

4.5 Graphical Analysis

In comparing dendrograms derived from similar data sets, one can learn about trends. However, this comparison is relative. An ordination technique will do this while also retaining the original relationships (groups). It is relevant here to consider two algorithm classes, the R and Q-algorithms. According to Gower (1966) one normally considers principal components analysis (PCA), based on a dispersion or correlation matrix, to be an R-algorithm. Orlóci (1966) and Gower (1966) have shown that a Q-algorithm using distances, which they call principal axes analysis and principal coordinates analysis (PCoA) respectively, is a dual to the R-algorithm. The computer program used here (PCADP) is a Q-algorithm which transforms Euclidean distances via q_{jK} as described by Orlóci (1978, pg. 115). The results of PCADP based on distances will therefore be the same as those from an R-algorithm based on the raw data. The program PCADP is a parsimonious method and so graphing the first two or three sets of component scores will retain a large proportion of the variation. The distance matrices which produced the dendrograms are analysed separately. Then the results are combined graphically in such a way as to

Fig. 8. Dendrograms of the results of cluster analysis (program SSAP) of the vegetation types. See Table 5 for type numbers and codes. The scale represents sums of squares for groups and types. Data used in program SSAP represent distance matrices:

(a) SPFH1

(b) SPFP6

(c) SPFP11

(d) SPFP14

(e) SPFP15

(f) SPFP3

(g) SRFP18

(h) SPFP19

The analysis on matrices SPFP15, SPFP3 and SPFP17 produced identical groups. The scales were slightly different and so the dendrogram for SPFP17 is not included.
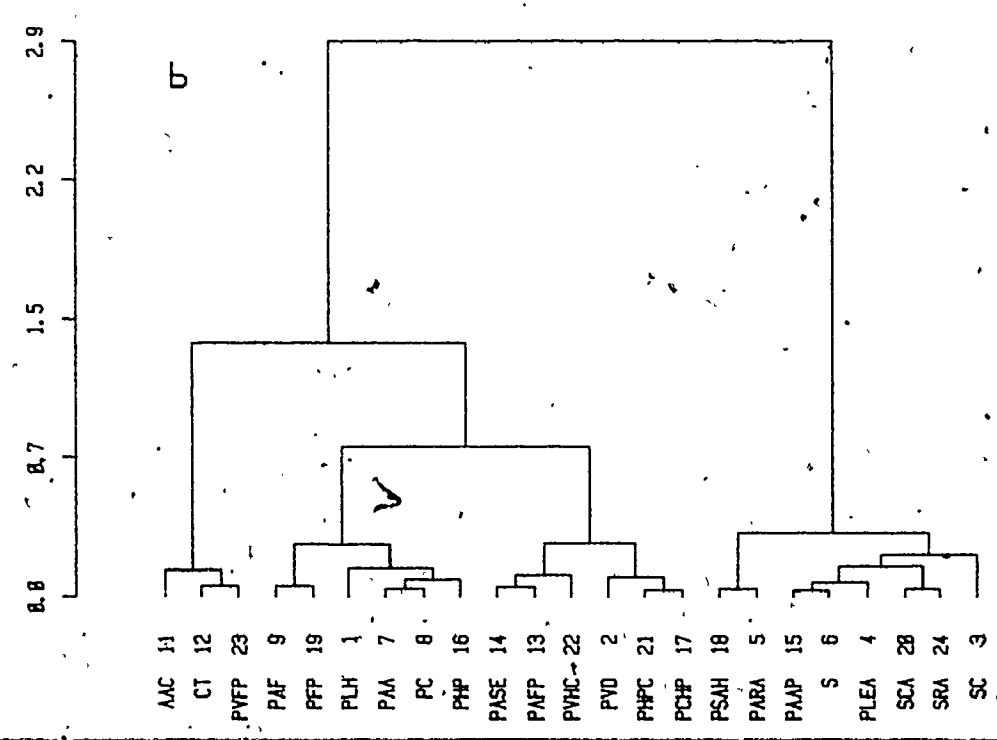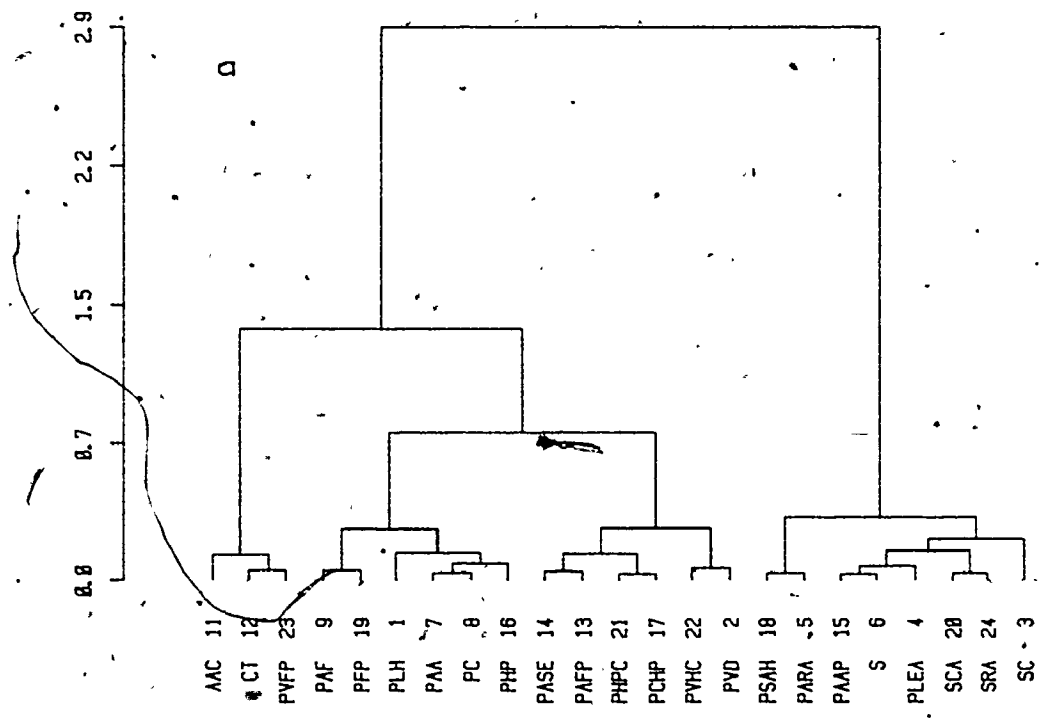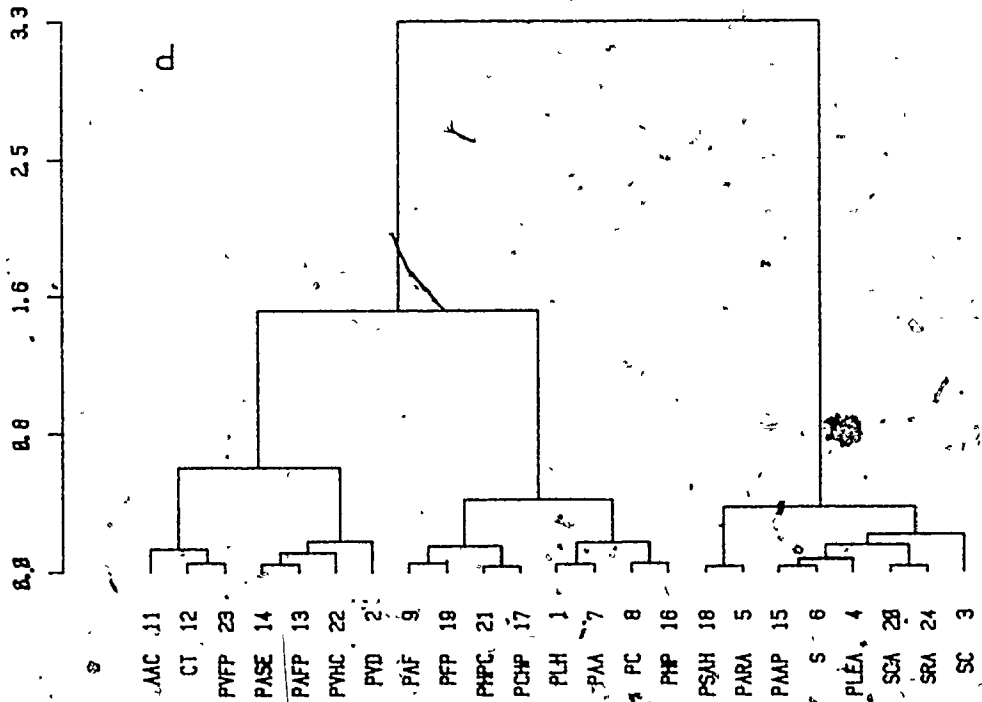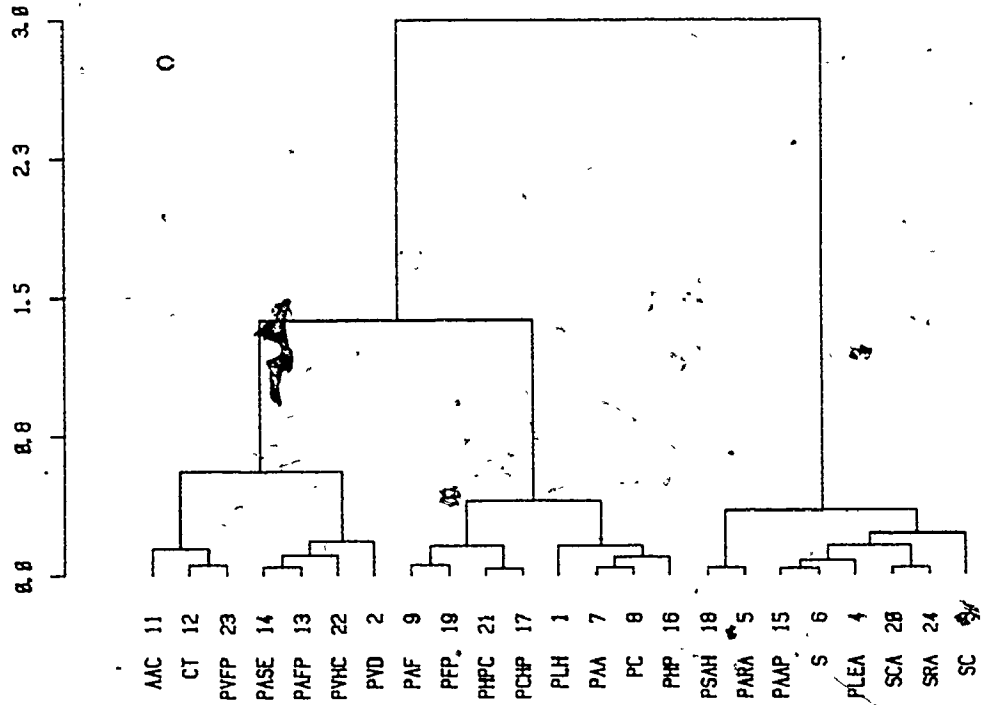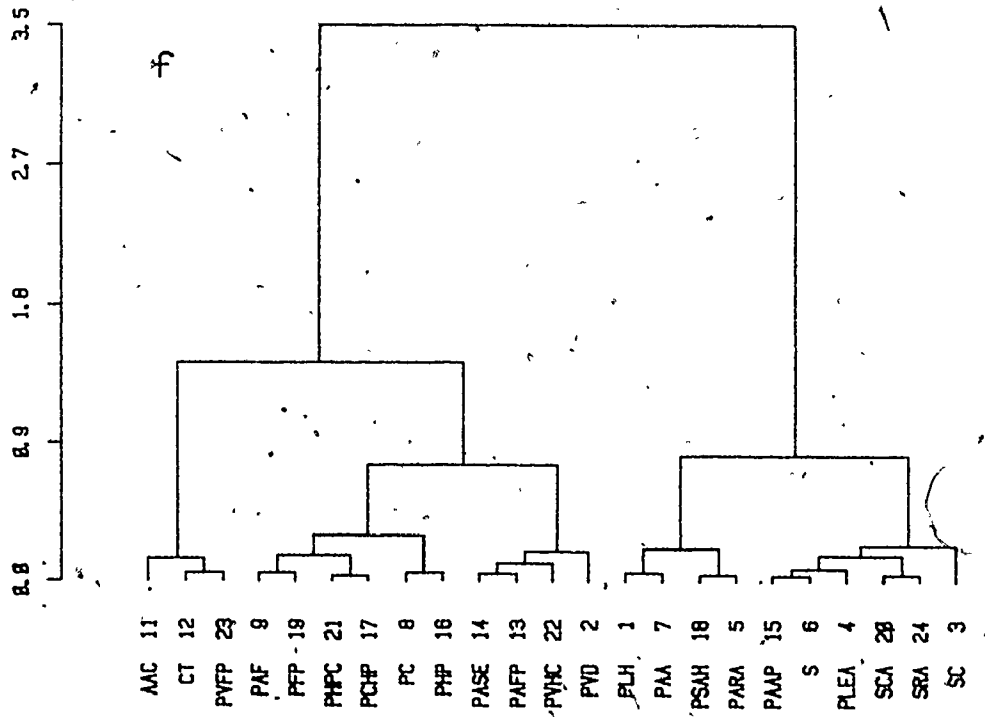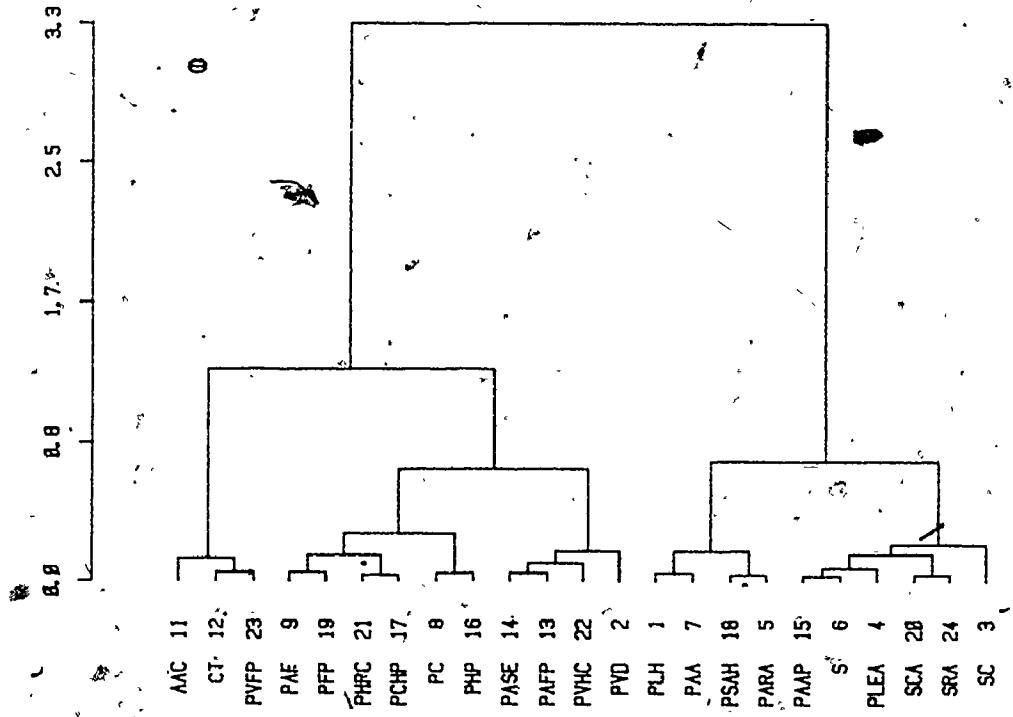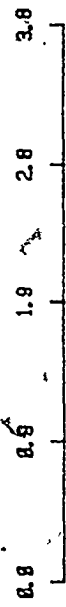
c

d

e

AAC 11
CT 12
PVFP 23
PAE 9
PFP 19
PHRC 21
PCHP 17
PC 8
PHP 16
PASE 14
PAFP 13
PVHC 22
PVD 2
PLH 1
PAA 7
PSAH 18
PARA 5
PAAP 15
S 6
PLEA 4
SCA 28
SRA 24
SC 3

f

AAC 11
CT 12
PVFP 23
PAF 9
PFP 19
PHPC 21
PCHP 17
PC 8
PHP 16
PASE 14
PAFP 13
PVHC 22
PVD 2
PLH 1
PAA 7
PSAH 18
PARA 5
PAAP 15
S 6
PLEA 4
SCA 28
SRA 24
SC 3

2
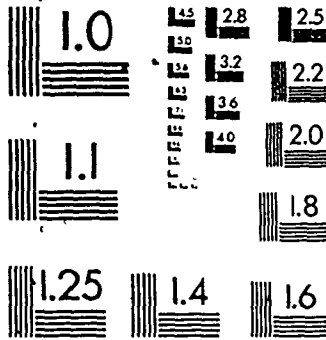
link the successive perturbations for each type. As each data set is ordinated separately, consideration must be given to its interpretability. Nevertheless, we have a comparison not only among the types for a particular perturbation but also among the perturbations within a particular trajectory. The dendrograms are probably of greatest use in supporting the interpretation of the combined results of PCADP.

Ordination techniques have been used to study vegetation change. The graphical presentation is a set of curves or trajectories joining the points which represent the same species or plots (depending on how the analysis is performed) for the different time periods. Carleton & Maycock (1978) constructed species succession vectors where age classes were used for the time element and the different plots or sites represented the dimensions. Also of relevance here are those studies which constructed plot or site vectors for data collected at various sites (q) at different times (t) for various species (s) or descriptors. The raw three-dimensional matrix ($q \cdot t \cdot s$) was arranged to give a $qt \cdot s$ matrix and then ordinated. One of the first studies like this was van der Maarel's (1969) work in phytosociology. Other studies applying this approach include those by Austin (1977), Bowles (1980) and Bowles & Maun (1982).

The usual procedure to ordinate a $qt \cdot s$ matrix is to combine t data sets of order $q \cdot s$ prior to analysis. Alternatively one might ordinate the t data sets independently and then combine the results. As the method used (PCADP) is a parsimonious one, the first or major axis of each represents the axis of greatest linear variation, the second axis greatest residual variation and so on. This gives a reason for combining the results and subsequently drawing trajectories as would be done if the data was combined *a priori*. There are

two aspects of the ordination method which affect the results. The first is data centering and the second is multidimensional axes rotation. Data sets which are independently analysed will be centered and rotated differently. Hence, the results of combining *a posteriori* will likely differ from that due to combining *a priori*. The different rotations may be thought not to be a problem, since as mentioned, the new axes have meaning. The independent centering remains as a potential differentiating factor.

When does one prefer to combine the data sets? Ordinating a single combined data set is simpler and, not surprisingly, is what has normally been done. Yet it may not be possible to combine *a priori*. This leaves us with the question of how different the results will be between *a priori* and *a posteriori* combination. There are three considerations. The first is that trajectories from *a posteriori* combination might look like random walks and therefore be totally meaningless. If upon inspection one detects meaningful trends, it would be reasonable to suggest they would be the result of strong linear structure within each data set, which translates to saying most of the linear variation will be found on the first few ordination axes. Further support of their meaningfulness can be given by comparing dendrograms derived form the *t* data sets. If pairs of dendrograms, based on similar levels of perturbation, are very similar, this would suggest there is not a great difference in overall structure between the two corresponding data sets (or pairs of points along a trajectory). The second consideration is with regards to arbitrary axes orientation. This is the product of the eigen analysis routine which arbitrarily determines the positive/negative orientation of each axes. For two similar data sets, the *i*th axis of one ordination may be a mirror

image of the other. If indeed the results of the t ordinations are similar, this axis flipping can be detected and manually corrected. The third consideration is termed trajectory flipping. This is where one trajectory from the *a priori* approach is opposite or at least very different from the corresponding trajectory from the *a posteriori* approach. Again, strong structure is a factor in minimizing this. As well, one can show that as the number of trajectories increases, the possibility of trajectory flipping drops dramatically. This was done with some test data sets but is not included here.

Separate analyses were carried out in the t matrices. Here, t is equal to five (see Fig. 9). These five matrices, as described in section 4.4, represented a series of increasing perturbations. The various perturbation levels were chosen so that the difference between one matrix and its predecessor (with respect to this series) was illustrated by a slight difference in their respective dendrograms. At this point, the maximum perturbation level was held to 0.28 so that a preliminary visual picture might be obtained. Following the separate analyses, program TRANS2 was used to standardize the orientation of the first three component axes after the actual orientations had been detected. Next a two-dimensional scattergram was drawn, the first two component axes being the X and Y axes respectively. In Fig 9b, the first two components accounted for at least 65% of the linear variation for all data sets used. As well as a scattergram, a stereogram (Fig. 9a) was drawn after each data set has been prepared by programs PREP and STEREP. Note that scaling was consistent for each set. Here the Z-axis represents component three. The first three components accounted for at least 77% of the variation. The 'heads' of the trajectories represented matrix **SPF15** which had the

Fig. 9. Trajectories of types (see Table 5) based on a series of increasing perturbations.

(a) Stereograms (Fewster & Orlóci, 1978) of distance matrices **SPFH1**, **SPFP11** & **SPFP15** after each has been subjected to ordination (program PCADP), The first three components are used.

(b) Scattergrams of distance matrices **SPFH1**, **SPFP6**, **SPFP11**, **SPFP14** & **SPFP15** as in (a). The first two components are used. Arrows represent direction of perturbation and labels represent the type. Note that the direction of types 4 and 18 is from right to left.
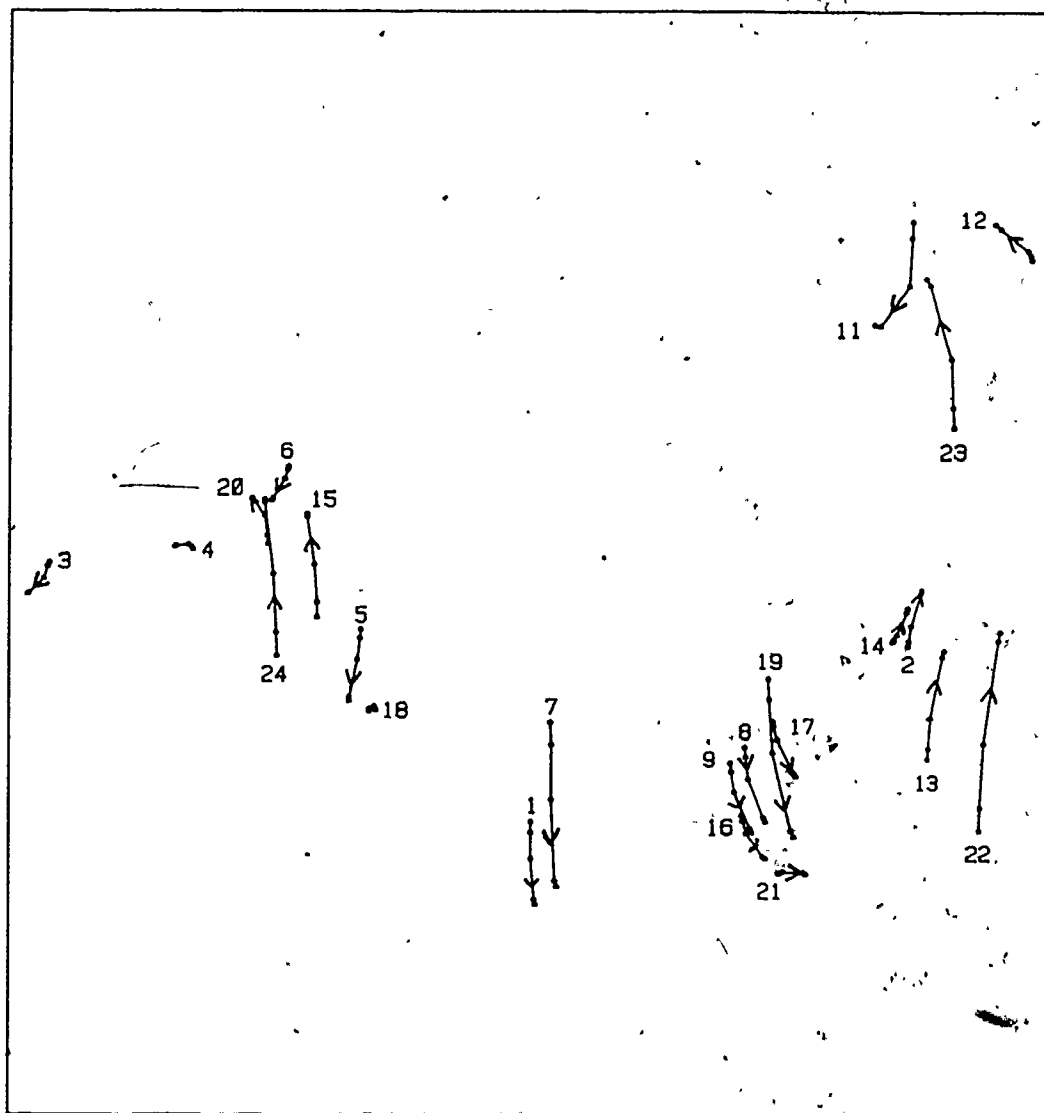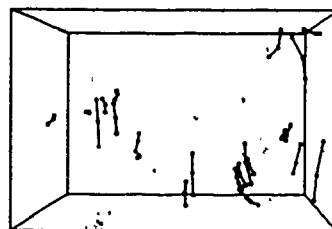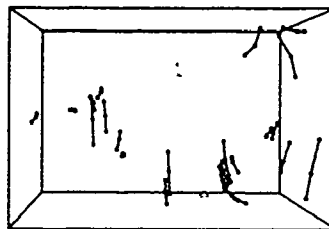
greatest proportion of perturbation (0.28) here.

This type of graphical presentation gives an overall picture of how the types differentiate along component axes from one degree of perturbation to the next. In order to compare the magnitude and direction, the trajectories may be translated so that the 'tails' of each (SPFH1) share a common position. For this, the greatest proportion of perturbation was increased to 1.8 (SPFP19). The decision to limit perturbation to this level, while being somewhat arbitrary, was nevertheless, sufficient to produce interesting results. A graph of the first two reoriented components is given in Fig. 10. The first two components accounted for at least 57% of the variation.

4.6 Interpretation of Results

The essential difference between a series of dendrograms from cluster analysis and a combination of ordinations via program PCADP is the way in which they detect or correct for an overall trend as the amount of perturbation is increased. In general the cluster analyses give no indication of overall change whereas the ordinations do (cf. Fig. 9). A protocol for interpreting the trajectories in Figs. 9 & 10 is given. The first of two levels is adapted from Bowles (1980) and is a relative one. The argument used is that if the majority of types show parallel or similar trajectories from one perturbation to the next, then a general trend of type response to perturbation is evident. If the trajectories are otherwise then there could be a) no trend or b) different type-dependent trends. The implication of a) is that the types have no directional response to perturbation or there exists a cyclical response. The implication of b) is that either all trends are different or that there are groups

Fig. 10. Trajectories of vegetation types (see Table 5) based on a series of increasing perturbations as represented by the distance matrices **SPFH1**, **SPFP11, SPFP15, SPFP3, SPFP17, SPFP18** and **SPFP19**. Each matrix has been independently subjected to an ordination (program PCADP). Subsequently, the trajectories have been translated so that the null states (**SPFH1**) of each type share a common point allowing for comparison based on magnitude and direction. The trajectories can be split up into drainage categories (Table 4) as follows:

(a)   all 23 types

(b)   categories 1 and 2

(c)   categories 3, 4 and 5

(d)   category 6

a

22

13

2

14

24

21

15

16

17 9
8

20 18

4 1

6 19
3
5
7

23

12

11

b

22

13

2

14

23

12

11

o

21
16
17   9
8
18
1
19
5
7

d

24
15
20
4
6   3
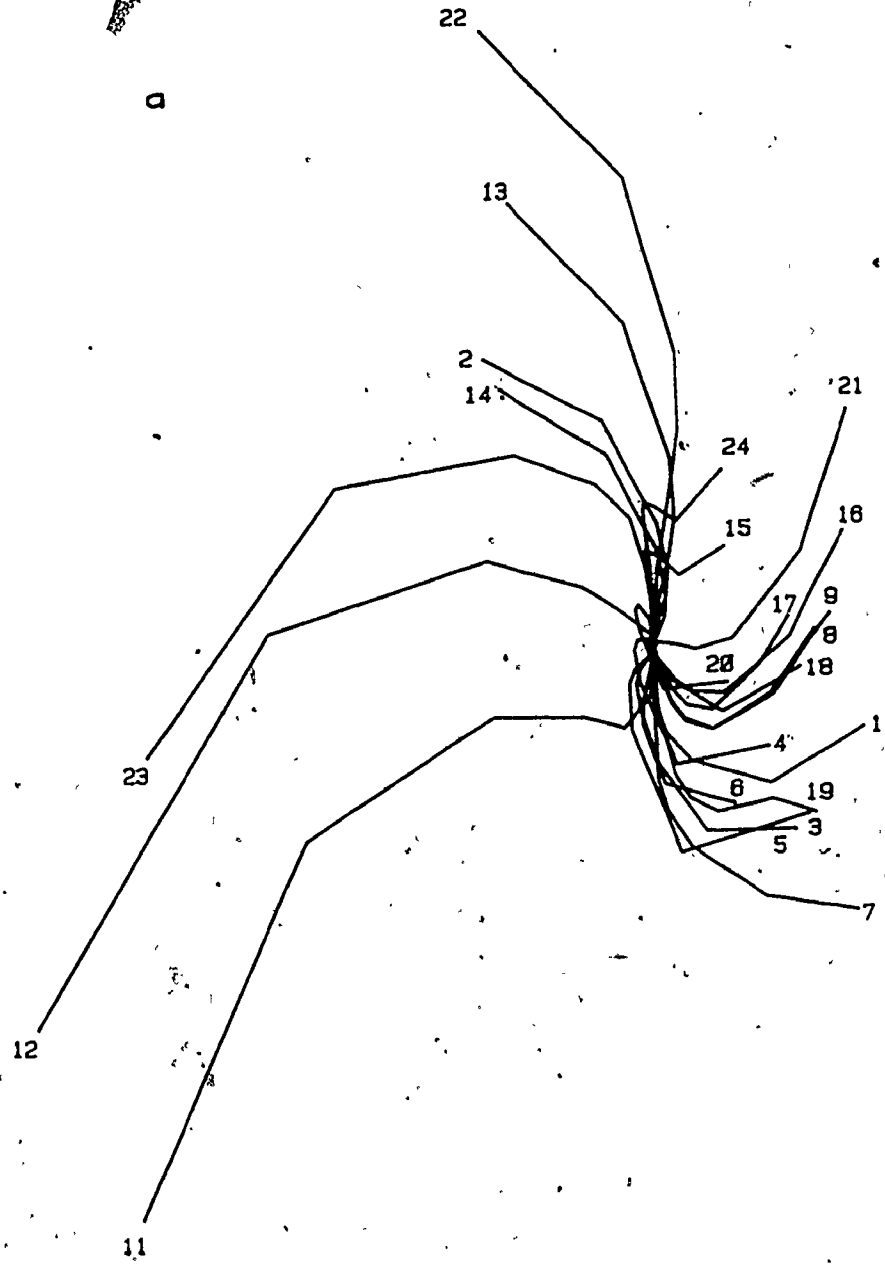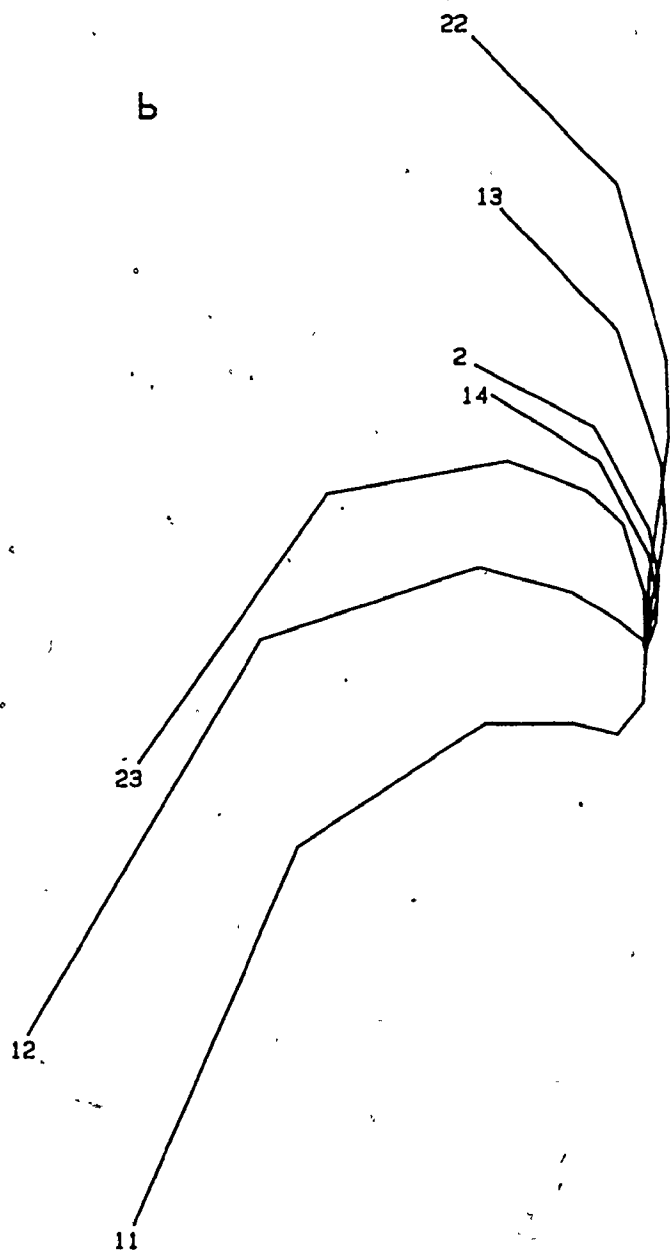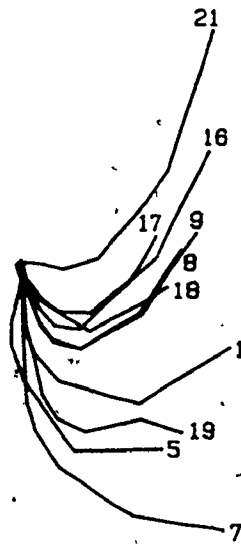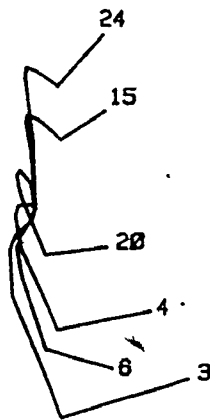
within which there exists parallel trajectories. A second argument regarding susceptibility to perturbation can be made. This is perhaps an absolute argument and consequently certain assumptions must be made following preliminary observation of the results.

From Fig. 9 it appears that the ordinations produced a horseshoe shaped configuration for the types. This is to be expected and is explained in Chapter 5. Beginning at the left are the wet types (Table 5). Following the horseshoe trend, progression is through mesic types ending with dry types in the upper right. Based on the analysis of Orlóci & Stanek (1979, Fig. 18, pg. 41), the ordinations appear to have detected a moisture gradient. This lends support to the decision to focus only on perturbing drainage. With respect to the categories in Table 5, a mesic grouping of categories 3, 4 and 5 (types 9, 19, 8, 16, 21, 17, 1, 7, 18 & 5) can be recognized whose trajectories are generally from top to bottom with a slight left to right shift. This combination of category 5 (types 18 & 5) with categories 3 & 4 is supported by the dendrograms (Figs. 8e,g). A hydric group (category 6; types 15, 6, 4, 20, 24 & 3) can be seen to be moving, in some cases right to left, and in others from bottom to top. A xeric grouping of categories 1 and 2 (types 11, 12, 23, 14, 13, 22 & 2) is moving essentially upwards with the exception of type 11. Again the dendrograms (Figs. 8c,d,g) support this combination. It makes sense that any vegetation type which is affected by perturbation would move along the horseshoe rather than going directly from one extreme to another. For this reason the overall trajectory of the mesic grouping quite possibly indicates resistance to change at low perturbation levels. This suggests an assumption to be used for the second argument of the protocol. It appears that types

15, 6, 4, 20, 24 and 3 (very wet category) are susceptible to change whereas types 5 and 18 (wet category) are resisting change more than might be expected. Types 14, 13, 22 and 2 (moderate to dry category) are affected by increasing perturbation in the same way as types 12 and 23 of the dry category. Apparently type 11 may be resisting change. Overall, most of the mesic types are resisting change whereas the hydric and xeric types are not.

By translating each trajectory so that their 'tails' share a common point, this analysis may be continued. This translation was carried out for each trajectory by subtracting the coordinates of its unperturbed state from all states in the trajectory. Note that the amount of perturbation has been increased to 1.8. Fig. 10b illustrates that categories 1 and 2 respond similarly although the dry category is more susceptible to change. Type 11 behaves differently than 12 and 23 at first, that is at low perturbations, but as perturbation is increased, it begins to conform to the others. Fig. 10c illustrates very well how type 18 behaves differently at first but later on conforms to the others. Fig. 10d is very interesting in that what can be interpreted here is not apparent from just the dendrograms. Types 15 and 24 are not classified as a pair (lowest fusion level) yet their translated trajectories suggest they behave in a similar manner to perturbation. The same holds for type pair 6 and 3 and type pair 4 and 20. Furthermore, at low perturbations the response of types 4 and 20 is similar to 15 and 24 but at higher levels their response is more like the pair 6 and 3.

4.7 Discussion

A clearer picture of the development of regression modelling emerges now that the results have been interpreted. The raw data was first tested by a number of regression models to find the most useful one. As maximizing predictability was the aim, we sought to maximize the fit as measured by a correlation coefficient. In this case, a number of environmental variables were used so that the model chosen was that of multiple regression. The fact that the precise model was not chosen *a priori* (implying that regression has not been used in the statistical sense) is important. When a new data set is being explored, one should not feel constrained to a rigid and narrow statistical approach. The model used predicted vegetation response to environmental factors. Subsequently, one of these factors was altered at increasing levels to see what the effects on the vegetation would be. It makes sense that types would be affected differently. A series of dendrograms was the first way used to illustrate this. As the dendrograms lacked a reference or base point, a second way of illustrating the effects of perturbation was used, namely ordination. This method was more amenable to interpretation because more than just relative movement was detected. The various vegetation types within and between various perturbation levels could be compared as they were plotted on a coordinate plane.

Regarding the ordinations, two approaches were discussed. One was the $\bar{q}t \cdot s$ approach used by Austin (1977), Bowles (1980) and Bowles & Maun (1982) and the other used here considered t separate $q \cdot s$ ordinations. These were referred to as *a priori* and *a posteriori* combination of data sets respectively. Although the former has been used by others, it was argued that the latter

was reasonable to do. In addition, providing that the data was strongly structured and that t was sufficiently large, the two will give near identical results. This can be shown with the use of test data sets.

This chapter began by comparing simulation, generally a mechanistic approach to modelling, with time static modelling which is essentially correlative. Fundamental to simulation modelling is the patterning of the model's interrelationships after those of the real system. This certainly has value. However it requires much work to get to the level of hypothesizing these interrelationships and embedding them in a model. As well, a simulation model restricts the amount or degree of complexity and hence its applicability. A time static model avoids this by correlating variables over a broad range using large sample relationships. This approach cannot claim to be able to make predictions of the sort which simulation can. Nor should this be a draw back. The model developed has incorporated data from many vegetation types, from dry to wet, so that inference of a different sort can be made. Although specific conclusions were not made regarding the exact response of a vegetation type or with reference to a time frame, trends or tendencies were revealed. Using as reference, the observation that the mesic types collectively appeared to be least likely to change with increasing perturbation, various types were noted as responding differently from what might be expected. Since the most extreme dry and wet types are at the boundaries of the data used in constructing the model, inference regarding these types must be made cautiously (Gold, 1977). As this model was not statistical in design, conclusions are made in the realm of exploratory analysis.

Chapter 5

NON-LINEAR PREDICTIVE ORDINATION

The development of non-linear ordination techniques has stemmed in part from work suggesting that species behave non-linearly in response to changing environmental factors or gradients (van Groenewoud, 1965; Whittaker, 1967). Developments or improvements in ordination models can be seen in two related phases: new algorithms such as scaling methods (Shepard, 1962; Kruskal, 1964a,b; Ihm & van Groenewoud, 1975), and the incorporation of new resemblance measures (Orlóci, 1978). Emphasis in this chapter is placed on resemblance measures, incorporated into a method of multidimensional scaling, which reflect the non-linearities of the data. Through performing this task, methodological improvements in the model result which improve predictability. Further benefits can be seen as they relate to other topics. This method may complement simulation modelling in general, and especially as it is used as an information source. As well, the time static approach, which uses ordination as a tool for prediction, can also be improved through the incorporation of a non-linear technique.

5.1 Introduction

The investigation and ordering of vegetation units with respect to known or presumed underlying environmental gradients has long been a major objective of ecological studies. More recent ecological ordinations have evolved from the central idea that the way in which species respond to environmental influences must be considered. This implies that optimality of the solutions is tied to the model's success in incorporating suitable response models. R. H. Whittaker's contributions were most influential in this area in that they established a theoretical framework incorporating the notions of gradient, response and utility. It is largely a consequence of his influence that shortcomings in linear ordinations were revealed. This in turn led to the development of methods which assume non-linear species responses.

Clearly, the early models were largely concerned with multidimensional configurations where individuals (vegetation plots) occupied positions in space defined by the species as the dimensions (Goodall, 1954; Bray & Curtis, 1957, Greig-Smith, 1964). Whittaker (1956, 1967) shifted attention to ordination where, by contrast, a configuration of individuals is placed in a space with major physical (environmental) factors serving as the axes. This was a return to models that had their origin in the 1920's and 1930's (Cajander & Ilvessalo, 1921; Keller, 1925-26; Hansen, 1930, 1932; Pogrebnjak, 1930; Ramensky, 1930; Sukatschew, 1932; and others). Hence the problem of improving the ordination model involves finding the best way to transfer or map individuals in species space into factor space with minimum distortion, and to identify these factors with greatest certainty. In other words, non-linearities need to be unfolded as much as possible so as to obtain a linear ordering (Orlóci, 1978).

The complexity of vegetation data can result from a number of factors, such as random variation (noise) and indeterminacy in measurement. More important, however, is the type of species response. This has been demonstrated in both field data (van Groenewoud, 1965) and simulation experiments (Noy-Meir & Austin, 1970, Gauch & Whittaker, 1972). If the response is linear, complexity is not great and efficient ordination algorithms are available. In dealing with non-linear data, however, it becomes important that the technique used incorporates devices to handle this non-linearity.

Different cases are illustrated in Fig 11. Consider the simplest case where species respond linearly to an environmental gradient (such as changes in elevation up a mountainside), excluding noise. If individuals (vegetation plots) are placed at regular intervals along the gradient, and if two recorded species respond linearly to the gradient, a situation as in Fig. 11a would be obtained. If the same information is graphed in species space, where the two species serve as coordinate axes, a straight line is obtained (Fig. 11b). If an ordination model seeks to obtain an ordering of individuals, which is meaningful with respect to some environmental gradient (elevation in this case), a transformation is required. In the linear case this transformation is not complex since the ordering of individuals along the line of joint response in species space (Fig. 11b) is the same as the ordering along the abscissa of Fig. 11a. A principal coordinates analysis (PCoA) using a Euclidean distance measure will return this line on the first axis. If the example is extended to more than two species, a straight line will still be obtained in species space. Clearly, since a linear species response produces a linear configuration in species space, a linear resemblance measure, such as a Minkowski metric, would be the most

Fig. 11. Response trajectories for two species along a gradient with species response (a) linear and (c) Gaussian with their respective joint scatters (b) and (d) in species space. Scale is arbitrary. Note the dependence of the shape of the gradient's image in species space on the response exhibited by the species in response space.

Response space   Species space

a

Species 2

Species 1

b

Gradient

Species response

Gradient

c

Species 1   Species 2

d

Gradient

Species 2

Gradient   Species 1
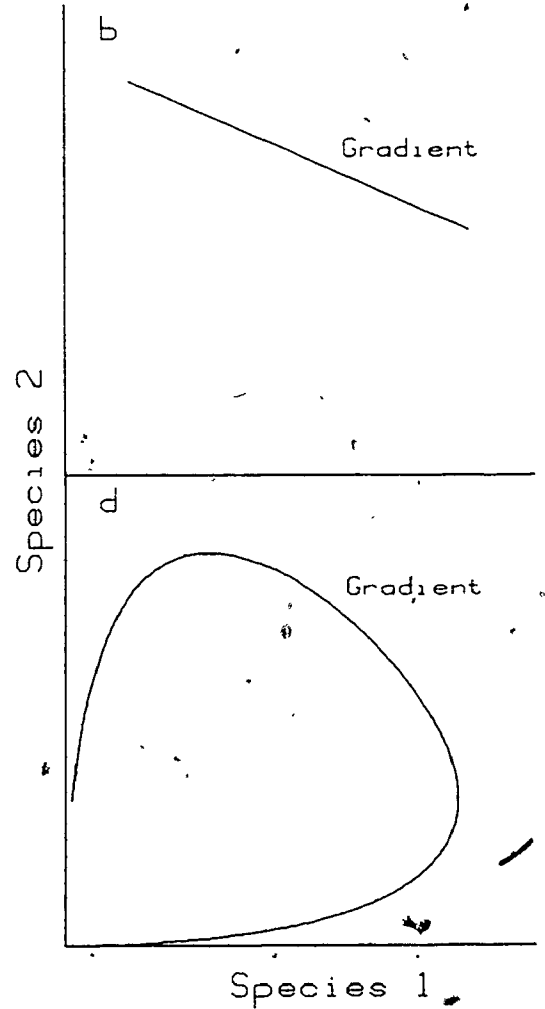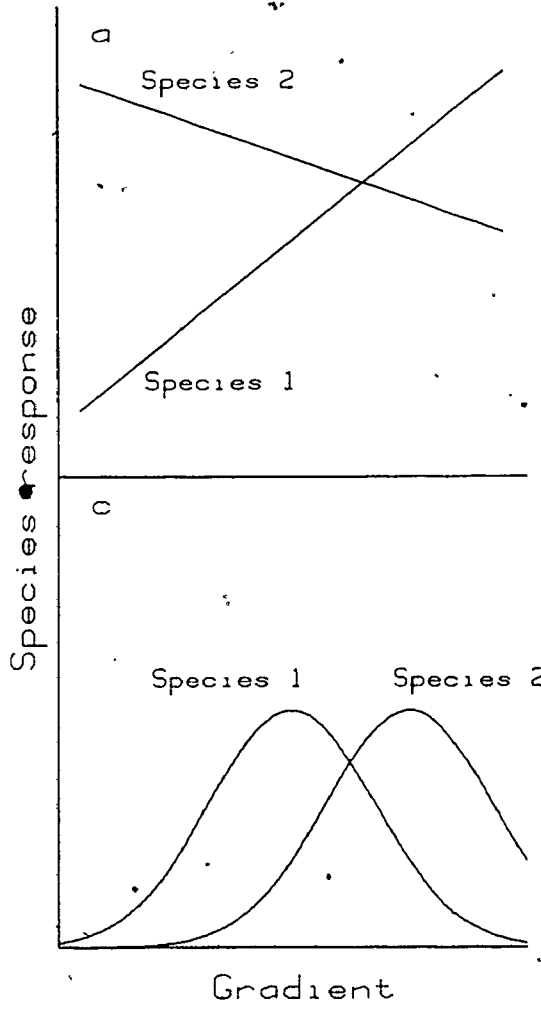
meaningful. In fact, since this is a Euclidean space, the Euclidean distance is an appropriate measure.

If a non-linear species response is assumed, a configuration such as shown in Fig. 11c (Gaussian curves) might be obtained. The same information in two-dimensional species space is shown in Fig. 11d. Again, the same basic shape (in multidimensional space) will be obtained no matter how many species there are. In this case the configuration as represented in species space has a horseshoe shape. Hence the transformation, which takes individual points on this horseshoe and maps them onto a straight line, is necessarily complex. This chapter focuses on the development of resemblance measures (species response model) which can be used in the transformation from a horseshoe to a straight line.

5.2 Model Development

The algorithm used in the analysis accomplishes nonmetric multidimensional scaling (MDS). Lucid descriptions are given by Fasham (1977) and Brambilla & Salzano (1981), after the original outline of Shepard (1962) and further development by Kruskal (1964a,b). See Fasham (1977, pg. 553) for a discussion on the context of the word non-linear. Attention is drawn here to a few salient features of the algorithm before remarks concerning the choice of a resemblance measure are made.

MDS works iteratively toward a final solution by comparing distances obtained from the raw data with those from a 'proposed' solution. The choice of a distance measure for the 'proposed' solution therefore determines whether

MDS is a linear or non-linear method. In this respect MDS differs from other methods which attempt to handle non-linearity in the data. These include methods which fit curved axes (e.g. Phillips, 1978) or specified response curves (e.g. Johnson, 1973; Gauch, Chase & Whittaker, 1974; Johnson & Goodall, 1980), and those which use regression analysis and scaling to reduce the curvature of an ordination configuration (e.g. Hill & Gauch, 1980).

The version of MDS used here begins either with a random initial point configuration, or one specified using the maximum variance criterion. By this criterion, the p most variable species are used to define an initial configuration, where p is the number of dimensions (D) for which a solution is sought. Kendall (1971) has suggested that the $(p+1)$D solution of a pD data set is an appropriate strategy, since this reduces the chance of selecting a local minimum as a solution. The explanation of this has not been detailed. Kendall (1971) goes on to say essentially that a pD solution of a pD data set will be convoluted. We can see that a $(p+1)$D solution avoids the jumbling that could easily result from a pD solution due to the projection of a $(p+1)$D horseshoe onto a pD hyperplane. Since the data sets tested in this chapter all have a single underlying gradient (1D), two-dimensional solutions were sought in all cases.

The choice of an appropriate resemblance measure for data with non-linear species responses is difficult. Any number of possible resemblance measures are conceivable, each specific to a given species response type (cf. Austin, 1979). In any case, the familiar metric resemblance measures are non-optimal under usual circumstances when non-linear species response occurs. As a simple example, consider principal component analysis (PCA) of the data in Fig. 11d using Euclidean distance. The result would be a horseshoe, since the algorithm

involves a simple geometric rotation in species space. Similarly, when a data set with Gaussian species responses is subjected to MDS analysis incorporating Euclidean distance, the result may again be a horseshoe shaped curve (Fig. 12a). A straight line projection of the underlying gradient to which species are responding, is more desirable. For a curved configuration in species space, the problem may be defined as one in developing an appropriate measure of the distance between two points A and B. A linear resemblance measure will give the distance of line AB, whereas a suitable non-linear measure will give a distance measured on the curve or curved surface on which A and B are points.

Orlóci (1978) and Hill & Gauch (1980) have noted that quantitative methods have specific uses and that the user must be careful in applying them. In addition, many authors (e.g. Austin, 1976, 1979, 1980; Werger et al., 1983) have found a variety of species responses in nature such as the Gaussian, bimodal, skewed, plateau, and so on. The subject is still very much in the exploratory stage (Feoli & Feoli Chiapella, 1980). However, if a few simplifying assumptions are made, some progress may be made in developing a resemblance measure in which provision is made for the actual curvatures found in nature. An example of this type of approach has been described by Ihm & van Groenewoud (1975) who, assuming Gaussian species responses, applied appropriate transformations to the product moments prior to an eigenanalysis.

In developing appropriate distance measures, the first assumption we make (which will be relaxed later) is that of a single underlying gradient. It is further assumed that all species responses are of the same form, although the actual response type remains open to choice. The objective is that of

Fig. 12. Results from MDS:

(a) Using a Gaussian data set with the linear distance option. Horseshoe shaped, stress = 0.0079.

(b) Using a Gaussian data set with the appropriate Gaussian distance measure and the maximum variance option. Horseshoe shaped, stress = 0.0089.

(c) Same as in (b) except the random option was used. Open shaped, stress = 0.013.

(d) Using a skewed Gaussian data set with the appropriate skewed Gaussian distance measure and the maximum variance option. Involuted, asymmetric horseshoe shaped, stress = 0.117.

(e) Same as in (d) with a different skewed Gaussian data set. Stress = 0.118.

(f) Using a parabolic data set with the appropriate distance measure and the maximum variance option. Very involuted, asymmetric horseshoe shaped, stress = 0.077.

a
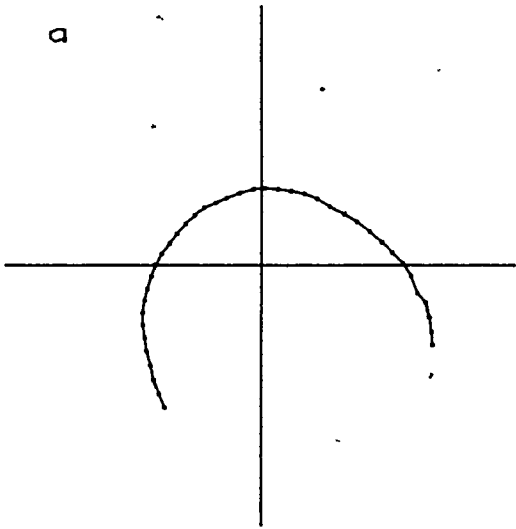
b
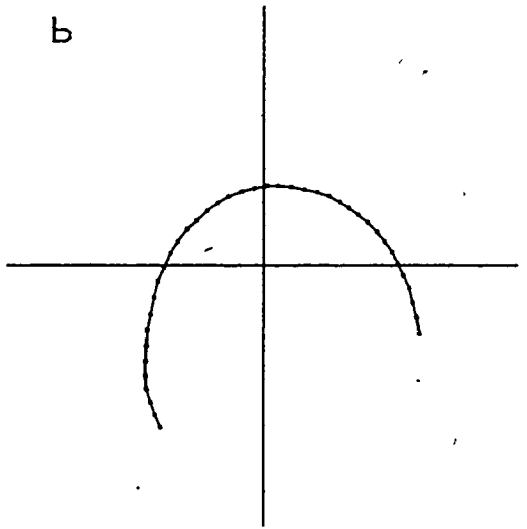
c
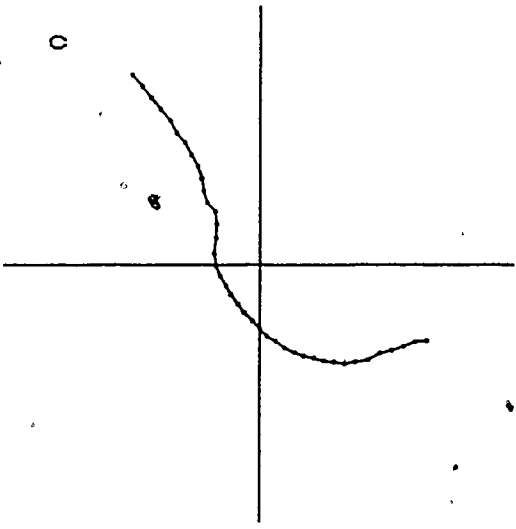
d
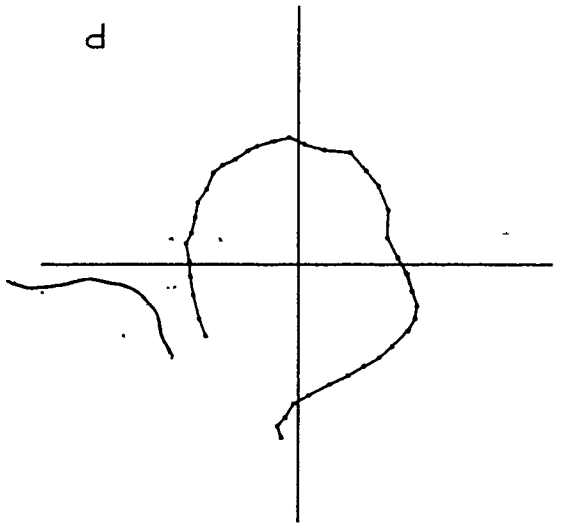
e
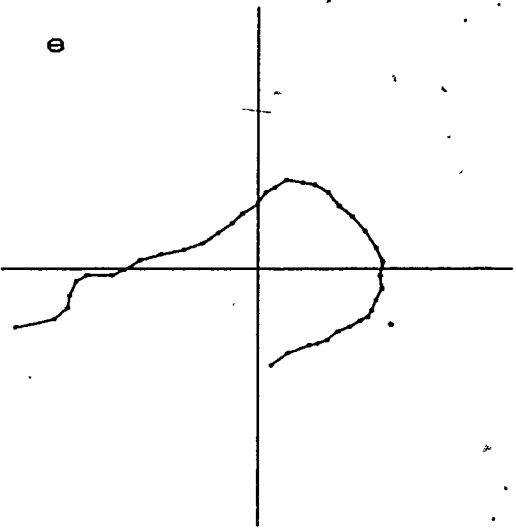
f
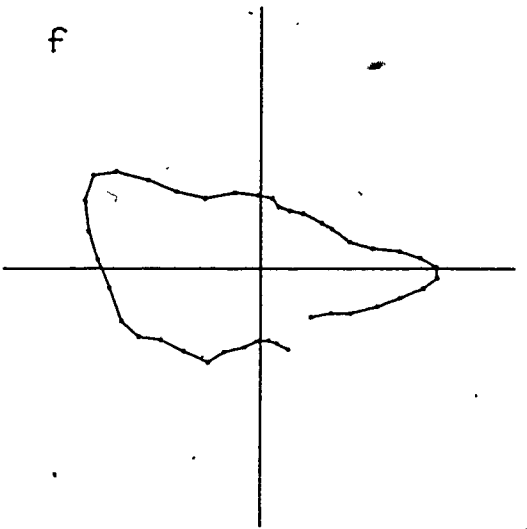
predicting the ordering of individuals along an unknown gradient based on species scores. The measured responses Y for a set of p species are assumed to be approximated by a set of ordination scores X (Fig. 13a). Hence Y = f(X|m), where m represents a set of parameters of the response graphs. For any point X on the gradient, that is, the abscissa in Fig. 13b, a linear distance Δ to a second point X+Δ is defined. The figure shows that this distance is related to the species response distance f(X)-f(X+Δ). Although this new distance depends on the position of X along the gradient, a distance which is unique to the type of curve which f(X|m) expresses can be derived. Furthermore, the restriction regarding a single gradient can be relaxed and a similar construction of each of t gradients can be produced, assuming the same type of species response.

Now let $\Delta = |X_{ij} - X_{ik}|$ be the ith gradient distance between individuals j and k. Then the unique compositional distance between individuals j and k on gradient i (the distance of Orlóci, 1978, pg. 142; 1980; see also Gauch, 1973) is

$$d^2_{jki} = \int_{-\infty}^{\infty}\{f(X|m) - f(X+\Delta|m)\}^2 dX \qquad [6]$$

The power 2 was chosen because the integration is possible and because it leads to an interpretable formula. The range of integration reflects the possibility of a response anywhere along the gradient. The composite compositional distance,

$$d^2_{jk} = \Sigma d^2_{jki} \qquad i = 1,...,t \qquad [7]$$

Fig. 13. Response trajectories for (a) several species along a gradient and
(b) a standard average trajectory.
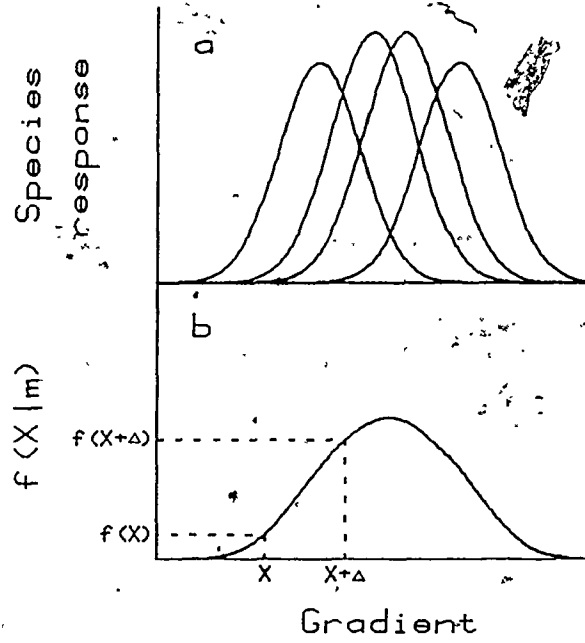
gives the distance between individuals j and k. What has been accomplished is a definition of the gradient distance in relation to a distance based on an assumed non-linear species response. Since this distance uses information about actual species response, it can be expected to have potential utility when linear species responses cannot be assumed.

Next, a few specific types of species responses are selected, and equation 6 solved to give actual distance (resemblance) measures.

The symmetric Gaussian curve was chosen since responses of this type (bell shaped) have been reported many times in the literature and are thought to be common (Whittaker, 1956, 1967; van Groenewoud, 1965). The second choice was the skewed Gaussian, since this response type has been noted (Austin, 1979). Finally, a parabolic curve, which has the basic bell shape but lacks the tails, was chosen. In nature such a response might be expected since a species might be out-competed or otherwise selected against at the extremes of its potential range (Forsythe & Loucks, 1972).

5.3 Derivation

The integral in equation 6 is now solved. It is noted that standardization of various parameters preceeded integration in order to obtain a distance measure independent of these parameters. Note, however, that a substantial loss of general utility may be a consequence of standardizing too many parameters.

For the Gaussian,

$$y = Be^{-(X - a)^2/2s} \qquad [8]$$

where B and s are related to height and width respectively, only standardization to unit height and width (m = (a,1)) is needed since the constant a (the level of influence at which response is maximal) drops out following integration. After transformation, the function becomes,

$$y = e^{-(X - a)^2/2} \qquad [9]$$

Thus

$$d^2_{jkk} = \int_{-\infty}^{\infty} (e^{-(X - a_i)^2/2} - e^{-(X + \Delta - a_i)^2/2})^2 dX$$

By making a substitution of the form X = X + K (K is a constant) here and a few other places, the solution is found through the following steps.

$$d^2_{jkk} = \int_{-\infty}^{\infty} (e^{-X^2/2} - e^{-(X + \Delta)^2/2})^2 dX$$

$$= \int_{-\infty}^{\infty} [e^{-X^2} + e^{-(X + \Delta)^2} - 2e^{-\frac{1}{2}(X^2 + (X + \Delta)^2)}] dX$$

$$= 2\int_{-\infty}^{\infty} e^{-X^2} dX - 2\int_{-\infty}^{\infty} e^{-\frac{1}{2}(2X^2 + 2\Delta X + \Delta^2)} dX$$

$$= 2\int_{-\infty}^{\infty} e^{-X^2} dX - 2\int_{-\infty}^{\infty} e^{-(X^2 + \Delta X + \Delta^2/4) - \Delta^2/4} dX$$

$$= 2\int_{-\infty}^{\infty} e^{-X^2} dX - 2\int_{-\infty}^{\infty} e^{-(X + \Delta/2)^2 - \Delta^2/4} dX$$

$$= 2\int_{-\infty}^{\infty} e^{-X^2} dX - 2e^{-\Delta^2/4} \int_{-\infty}^{\infty} e^{-X^2} dX$$

$$\Lambda$$

$$= 2(1 - e^{-\Delta^2/4})I$$

where

$$I = \int_{-\infty}^{\infty} e^{-X^2} dX$$

Now, by making the same type of substitution $(X = X - k)$ we find that I is equal to a constant. Since a proportion of the compositional distance and not a precise value is all that is needed, we get the result

$$d^2_{jk} \propto 2(1 - s_{ijk}) \qquad \qquad [10]$$

where

$$s_{ijk} = e^{-\Delta^2/4}, \qquad \qquad [11]$$

A similar form was first reported by Gauch (1973). Note that equation 10 has the form of a chord distance.

For the skewed Gaussian function,

$$y = aX^b e^{-cX} \qquad \qquad [12]$$

the standardization involves setting the parameters a, b and c to unity. Since the mode or abscissa of vertex $X(m) = b/c$, an 'extra' or 'more severe' standardization is used compared to the Gaussian. As well, since the curve passes through the origin, the lower limit of integration is zero. Thus

$$d^2_{jk} = \int_0^{\infty} \{Xe^{-X} - (X + \Delta)e^{-(X + \Delta)}\}^2 dX$$

$$= \int_0^\infty [X^2 e^{-2X} - 2X^2 e^{-(2X + \Delta)} - 2\Delta X e^{-(2X + \Delta)}$$

$$+ X^2 e^{-2(X + \Delta)} + 2\Delta X e^{-2(X + \Delta)} + \Delta^2 e^{-2(X + \Delta)}] dX$$

With the use of integration tables and the application of limit theory, the compositional distance simplifies to

$$d^2_{jkk} \propto 1 + (2(\Delta^2 + \Delta) - 1)e^{-2\Delta} - 2\Delta e^{-\Delta} \qquad [13]$$

For the parabolic function

$$y = -aX^2 + bX + c \qquad [14]$$

the standardization involves setting $a = b = 1$ and $c = 0$. This is 'more severe' than that of the skewed Gaussian, since $X(m) = -b/2a$. The integration limits are the solutions for a quadratic equation. In this case, they reduce to zero and one. Thus

$$d^2_{jkk} = \int_0^1 \{(-X^2 + X) - (-(X + \Delta)^2 + X + \Delta)\}^2 dX$$

$$= \int_0^1 (2X\Delta + \Delta^2 - \Delta)^2 dX$$

$$\propto \frac{1}{3}\Delta^4 + \Delta^2 \qquad [15]$$

5.4 Testing

The next phase is testing the technique (resemblance measure plus method). MDS can incorporate any one of the distance formulae as options for the ordination configuration. The original configuration distances vary, conforming to the ordination configuration distances. In this early stage of development it has been necessary to make some restrictions before generating the test

data sets. They are: 1) a single gradient; 2) a few species (10) with the same type of response; and 3) random parameters for the response curves, within certain ranges. The gradient is conceived as being very broad, ranging between two extremes. A range of individual positions was defined between these two extremes where species optima would have an equal (random) chance of occurring. Ranges of constant probability were also chosen for parameters defining the height and width of the curves. The construct simulated the random appearance and disappearance of species along the gradient and implied that individuals (vegetation plots) had fewer species the further they were located from the middle of the gradient.

One data set was generated with Gaussian species responses whereas six sets each were generated for skewed Gaussian and parabolic responses. This was done in order to compare the results for consistency due to the 'extra' standardization of the skewed Gaussian and parabolic measures. The use of a single Gaussian data set was felt to be sufficient so as to be on an equal footing with the other two measures. Examples of data sets for the three response types are given graphically in Fig. 14. With reference to results of the MDS analyses, Figs. 14a,b & c correspond respectively to Figs. 12c,d & f. Beta diversity (Whittaker, 1972) ranged from 0.06 hc for the Gaussian set to 3.5 hc for the parabolic sets.

5.5 Results

The Gaussian data set produced 2D ordinations as illustrated in Figs. 12b & c. The first (Fig. 12b) resulted from the maximum variance option. Repetitions with the random option resulted in the same basic open shape for

Fig. 14. A graphical representation of three data sets used in the analysis.

The response types are:

(a)   Gaussian

(b)   skewed Gaussian

(c)   parabolic
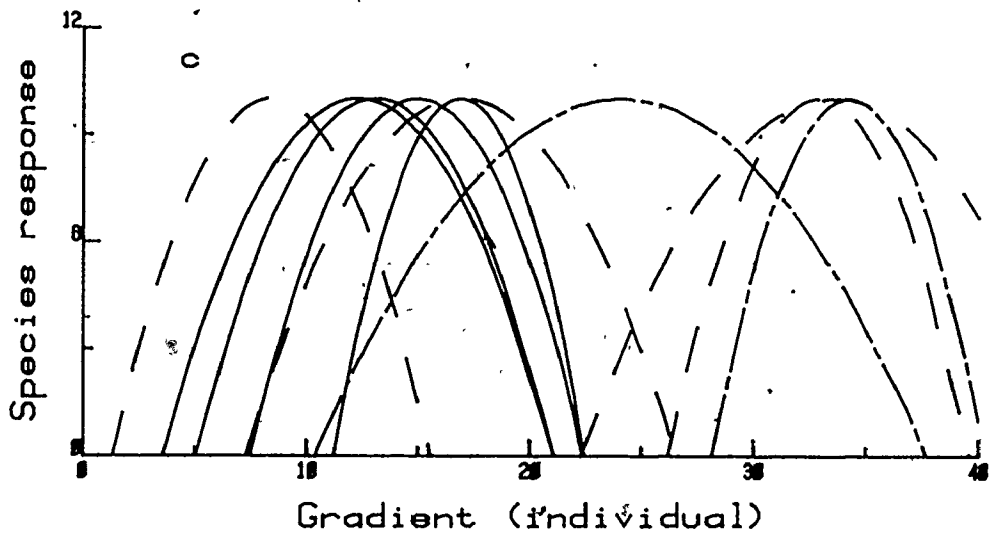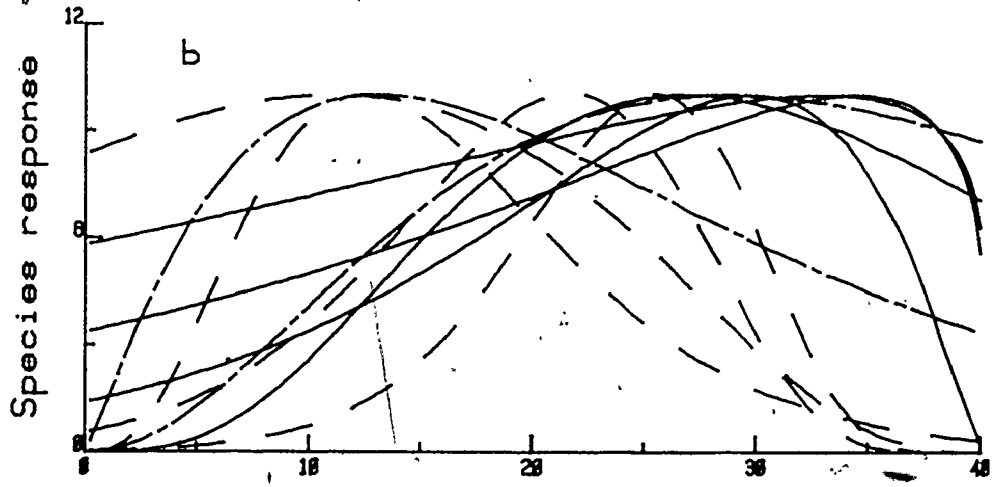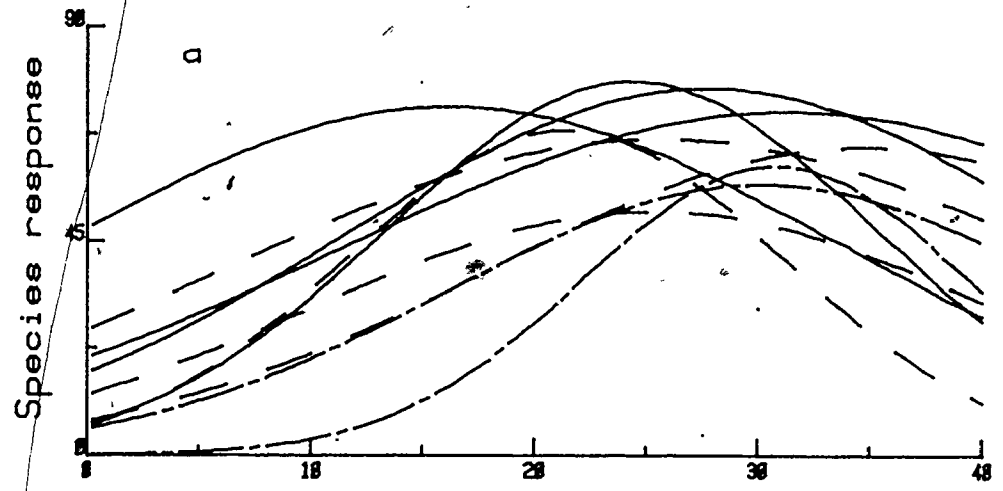
Gradient (individual)

which Fig. 12c is a typical example. Results from the skewed Gaussian and
parabolic data sets, using the maximum variance option, are given in Figs.
12d,e & f. The curves are asymmetric horseshoe shapes in both distance options.
The Gaussian distance measure (in conjunction with the random option) is the
only one which produced results which were distinctly not horseshoe shaped,
and is therefore the only successful distance measure of the three in mapping
individuals in species space into factor space. Hence, with respect to the
potential of avoiding scrambling due to involution, the Gaussian measure was
the most satisfying.

With the success of the Gaussian measure in mind, we may focus our
attention on the derivation of this measure and on the generation of the test
data sets. The solution of the integral which produced equation 10 was found
by setting s (a measure of response width relative to the underlying gradient)
equal to unity (compare equations 8 and 9). However, further work produced
a solution of the integral where s remained in parametric form. Here

$$d^2_{jkk} \propto 2s(1-s'_{ijk})$$
[16]

where

$$s'_{ijk} = e^{-\Delta^2/4s^2}$$

The consequence of this is a more generally applicable measure than used thus
far.

The type of Gaussian test data set used is also of interest. It was
assumed that the various species were likely to find their position of maximal
response (modal positions) anywhere along the gradient. Because the parameter

a was retained (see equations 9 and 10), this did not present any problem. Hence a single Gaussian data set was suitably generalized for testing the effect of an internalized distance function on MDS. However, this does not allow one to consider the effect of varying the rate of species turnover (beta diversity) on the success of the distance measure.

Related work (Orlóci, Kenkel & Fewster, 1984; and Kenkel, 1984) has considered this. Here, two independent environmental gradients were assumed. Data sets for a simulated coenoplane were constructed much like that of Gauch & Whittaker (1972) where plots were placed at regular intervals along both gradients to form a rectangular grid. Hence, an ideal ordination would be expected to return this grid. In contrast to using a distance measure within MDS as was done here, Orlóci, Kenkel & Fewster (1984) and Kenkel (1984) used a chord distance to calculate distances on the raw data before it was submitted to MDS. Although the distance measures (equation 10 and this chord distance) were used at different points in the analyses, the same type of transformation has been used in both cases. (Note the form of equation 10.) Orlóci, Kenkel & Fewster (1984, Fig. 4) present the results of ordinating a data set with a beta diversity of 5 x 5 hc (see Fasham (1977) for the method of calculation). Kenkel (1984) compared the results of ordinating data sets with varying levels of beta diversity, from 2.65 x 2.65 hc to 7.5 x 7.5 hc, including some with different levels of diversity on the two gradients. Their results, as well as those presented here in Fig. 12c, suggest that MDS is improved when the notion of species response is incorporated (either within the method proper or before the data is presented for analysis), and that increasing the rate of species turnover does not adversely affect its performance, providing adjacent plots

have some species in common. Thus the Gaussian measure, when approprtiate, is very good to use.

5.6 Discussion

In general, two aspects of ordination efficiency need to be considered. The first is the possibility that a solution may represent a scrambling of the true ordering, even though the algorithm and resemblance measure used are theoretically appropriate. Problems of this sort may arise, for example, from random variation (noise) in the data: In addition, a complex ordination algorithm like MDS has certain idiosyncracies (particularly the problem of local minima) which may result in a misordering. The second aspect is the horseshoe effect. Two examples are given (one in PCA and another in MDS; Figs. 11c,d & 12a) showing that a linear resemblance measure used in ordinating non-linear data produces an involuted, hoseshoe shaped ordination configuration. Kendall (1971) points out that the involution of the horseshoe implies that, without knowing the number of gradients *a priori*, an ordering of individuals may be scrambled. This can be visualized by taking a 2D involuted horseshoe and projecting it onto a single dimension (line). The points at the involuted ends will be mixed in with the middle ones so that the ordering produced is very different from the true one. While some have felt that a linear ordering is necessary and have developed approaches to straightening the ordination configuration (Kendall, 1971, Hill & Gauch, 1980), others (Feoli & Feoli Chiapella, 1980) suggest that the horseshoe effect is revealing rather than detrimental to interpretation of the results.

My approach in deriving an improved ordination has been to focus on the use of resemblance measures and to illustrate their importance in effectively mapping the data structure from species space into ordination space. Derived measures are combined with the MDS method to produce a non-linear ordination technique. The results using two distance measures derived for the skewed Gaussian and parabolic responses are considered first. It has been noted that 'extra' standardization was needed in developing these measures in comparison with the Gaussian. We may attribute the relative lack of success of these measures in handling the curved interpoint distances to these 'extra' standardizations in their derivation.

With respect to the Gaussian measure, MDS performed differently depending on which initialization option was used. Since the algorithm is one of minimization, different solutions may be obtained from different initial configurations. various local minima are conceivable, each returning a different solution. In general the maximum variance option produced less desirable results than the random option. This is because there is no bias in the random option as to the shape of the initial configuration. As such the final result is more a consequence of the distance measure and the method. Other approaches for initializing MDS include using the results of a linear ordination such as PCA. This also tends to give a 2D configuration like Fig. 11d, since the initial PCA configuration is a horseshoe. From a developmental and exploratory perspective, the Gaussian measure derived here in conjunction with MDS and the random option has been shown to be workable within the given set of assumptions.

The Gaussian measure was derived by integrating a single response function. Why were not all response curves treated individually so as to obtain a more effective measure? Each curve could be integrated, providing the widths of response curves were first standardized. The result for each species would be the same (cf. equation 10). Equation 10 could then be used as the collective function relating species to gradient position. Hence the only difference so far is the approach. Another question relates to the standardization of the widths (σ) of the response graphs. If the width for a single species (h) can be made more realistic by incorporating σ^2, integration will give the result $d^2_{jk'k;f(\sigma^2_h)}$ which is related to equation 10 but differs by some function of the width. The compositional distance then becomes,

$$d^2_{jk'k} = d^2_{jk'k;f(\sigma^2_h)} \qquad h = 1,...,p \qquad [17]$$

where p is the number of species. The problem is that since σ is a measure of X, until the gradient is determined, the p different σ^2_h remain unknown. This suggests a possible feedback algorithm, in which the distance measure could be made more effective at each step.

Equation 16, which retains a measure of response width, has potential utility with MDS. The most likely application of this measure for test data sets would be to set s equal to some function of the beta diversity. (The beta diversity would be sufficient as proportional distances are all that is necessary.) However, the same problem arises. For a real data set, we would not know what the beta diversity is for each assumed gradient. Yet, perhaps a feedback proceedure would not be necessary if some external knowledge could be used which might approximate the rate of species turnover on these proposed

gradients.

Finally, since the perspective of ordination, and indeed that of data analysis, is often exploratory, concern is often directed towards obtaining insights. Attention in this chapter has been focused on using resemblance measures which are in some way based on the same type of non-linearity as in the data. However, it is not always possible *a priori* to know much about the data structure. In reference to Figs. 12c,d,e & f, distinctive curves or 'signatures' are produced in the analysis, depending on the measure used, which reflect the underlying data stucture. This would also be expected to happen for data with noise. In such a case, a cloud may result showing an overall trend much like one of the known signatures. Hence, it is possible by trial, to obtain insight into the type of non-linear species response. An alternative approach which supplements the above would be to transform the raw data before being submitted to MDS, as outlined by Orlóci, Kenkel & Fewster (1984).

The method, as just described, is useful for exploring the dimensionality (for example, the number of major gradients) of a data set as well as the various types of species response. If used in conjunction with other methods, the result can often be one of improvement in predictability. The simulation approach in Chapter 3, although it used heuristic equations, was more or less mechanistic in its overall structure. As such, it will benefit from an improved understanding of systems relationships. The time static approach in Chapter 4 was one of curve fitting. The aim of the model formulated was to increase the degree to which system mechanisms were used (within the confines of predictability). Certainly, an ordination method, which can better reflect species response to major underlying factors, will be advantageous here.

The MDS approach to ordination used here is one of many which may give an improvement in the handling of non-linearities in the data. The others include curve fitting, scaling and *a posteriori* detrending. There are essential differences among these approaches in the conceptualization of the objective and the definition of optimality. With the methods tested here, a solution is regarded as being optimal if the ordination succeeds in unfolding a non-linear configuration. (In this respect, only the Gaussian response measure has been shown to be of utility, since the parabolic and skewed Gaussian measures both returned the horseshoe.) This implies that the type of species response assumed in the derivation of the distance measure is most likely correct. If a horseshoe type ordination configuration is obtained, the original assumption is deemed inappropriate. The actual shape of the ordination configuration may, however, suggest what type of response is depicted by the data. In other words, even if the solution of MDS is not optimal, the ordination still conveys information about properties of the data which relate to non-linearity.

Similar advantages can be seen with curve fitting, such as the polynomial ordination of Phillips (1978). Here, however, the curvature anticipated by the model before fitting is not concerned directly with the type of response exhibited by the species. Thus as in MDS, non-linear trends are not removed before the user has a chance to detect their presence. By contrast, detrending (Hill & Gauch, 1980) removes trends from the data that the user of non-linear ordinations hopes to detect. This may be completely justifiable and may help greatly in scrutinizing the ordination results, but it cannot be condoned as a general strategy.

Chapter 6

GENERAL DISCUSSION

Modelling has been implicit in the development of vegetation science. As well, it has become evident that types or forms of models used have varied with this development. From a dynamic point of view simple systems were conceptualized at first, calling for simple models, and as more and more was learned about the systems, the models became more complex. Because a variety of individual perspectives were involved, it has not been a simple development. Nevertheless, general trends and categories of philosophies can be recognized. These will be examined before some concluding remarks are made.

6.1 Model Assumptions

A model, as explained, has a many-to-one relationship with the real system. One implication of this is that simplifying assumptions must be made in order that one element may represent many. Over a period of time much has been learned about how vegetation interacts and consequently many assumptions have been changed (Caswell, 1976). For example, the recognition that species response to a broad environmental gradient is often non-linear has suggested the need for new ordination models developed around a non-linear assumption. Although models have become more complex, they are still

homomorphs of extremely complex systems. Thus, a model does not mimic the system. At times one may perceive a model as being a miniature version of the system and so get caught up in the accuracy of the model and its predictions while forgetting they are conditional on the validity of the assumptions (Frenkiel & Goodall, 1978). This is seen more clearly by again considering the many-to-one aspect. No matter what approach to modelling is used, we are looking at a mapping of many system interactions into a single model interaction. Hence the mechanisms used by the model will not be the same as those used by the real system. Development of the science then is characterized by an ever increasing complexity and hopefully more realistic and reliable models. However, this is a continual process because assumptions will always be needed.

In recognizing this continual process of model development and reassessment of existing assumptions, it is important to note that work is done in discrete steps. Models are developed and applied over a period of time and only when there exists a substantial difference or stress between the assumptions and what is actually known is the next step taken. Although models are usually developed which are not in conflict with other models (Gauch, Chase & Whittaker, 1974), there may exist some doubt as to their complete validity. This is interesting because at the forefront of the science, models are applied to problems for which, strictly speaking, they should not be used. However, from the point of view of data analysis, the learning of something new makes it worthwhile. Hence, concern often centers around the robustness of the model. This quality of being worthwhile is a relative one. There is a point when alternative methods are developed (the next step) which may be more fruitful. It is here that the old model should not be used so freely.

A good example of this is in Chapter 5. In developing many ordination models, linear dissimilarity measures were used. Recently a lot of work has dealt with the notion of non-linear species response. In spite of this, there remained the tendency to use measures in MDS haphazardly, irrespective of species response. As mentioned, part of this problem came from the assumption that MDS was neither linear nor non-linear. This was in a sense true, but as illustrated, it still mattered which type of measure was used. The difference or stress between what is known and what is actually practised can be attributed to the clarity with which assumptions are made. The first model, discussed in Chapter 3, has proven to be an excellent approach to modelling because assumptions must be clear in order for the model to be formulated. Hence, the possibility of hiding fallacious ideas is reduced. The Ruby Range component model, for example, assumed the maximum age of *Picea glauca* and *P. mariana* to be two hundred years. Consequently, each species component was divided into two hundred subcomponents. Not all model forms can be this clear in their assumptions. This emphasizes the necessity for the awareness that models, and therefore science, is built on assumptions. The second model form in Chapter 4, for example, makes the assumption that the plant/environment interactions are implicitly stored in the data set and can be recovered by a phenomenological approach such as regression. This is an intuitive assumption and probably has only a degree of truth.

6.2 Choice of Model Form

A number of model forms have been described so far, all of which are useful at different stages of problem solving and for different types of problems. For example, we see simple verbal constructs, box and arrow diagrams, sets of mathematical equations and dynamic simulators. The purpose of using models has been to try to understand the system better. However, the way in which the problem was attacked varied due to different ways of thinking. Such approaches or philosophies as typology, progressivism and holism coloured the choice of model form in the past, and to a degree, continue to do so (van Hulst, 1975). As well, there existed various philosophies to modelling based on current subjective knowledge, type of problem, its purpose, and probably individual biases. In general, the first models were very simple and theoretic, being developed from first principles, but with time, tended to the complex and practical.

These philosophies apply to the present state of modelling. There are two productive ways of looking at this. The first is the comparison of analytic and phenomenological approaches while the second compares theoretical and practical approaches. The analytic approach is concerned with actual mechanisms of biological interactions with the aim of increasing understanding of how the system really works. The phenomenological approach, on the other hand, is not so concerned with actual mechanisms but with heuristic relationships, aiming towards predictability.

The simulation model lies between these two approaches, possibly tending towards the analytic. Simulation is dynamic. It simulates the dynamic nature of the system which is thought to be a correct mechanism. Also, the process of model development is pedagogical and hence dynamic. This illustrates the analytic side. The phenomenological side results from the fact that data collection and experimentation is usually short term (three field seasons for the Ruby Range model) and thus the dynamic nature is limited. As well, simulation uses heuristic equations to define relationships, where the equation with the greatest predictive power is used. This is intriguing because on the one hand we are not concerned if the equations closely resemble the actual mechanisms, while on the other hand one might suggest that the closer to reality a heuristic equation becomes, the better chance it has of being a good predictor.

The time static model developed here is essentially phenomenological as it is based on curve fitting and the purpose is that of prediction. Although implicitly the ultimate relationships are embedded in the model, it is not analytic because the actual relationships are not precisely formulated.

The model dealing with non-linear predictive ordination is analytic despite its predictability. The history of ordination, if we consider Whittaker's (1956, 1967) work on direct gradient analysis has been that of analysis. The development of ordination has proceeded through a number of stages leading, naturally, to the present indirect approach: that of predicting environmental gradients.

It would seem logical that in following through with the analytic approach, the goal would be to discover the 'whole truth'. It should be recognized that a model in agreement with all possible contingencies, and which has been developed via analysis, would be too vague. That is evidenced, as mentioned earlier, by the failure of the IBP project to model large systems. This makes sense considering the many-to-one aspect. A large complex model which changes the 'many' to 'not so many', may not be testable because the predictions would not be specific enough. Hence, this type would not be useful to the theoretician or practicioner. By definition a model could not be completely analytic because it is a model and does not reflect all inner workings of the system. Any single model element which represents many system elements is formed by a transformation. This suggests the difference between analytic and phenomenological models is a relative one. In a sense, specific system mechanisms exist only in the modeller's mind. Consequently, the science is constrained to simplifying and generalizing. The value of distinguishing between these approaches is that predictions from phenomenological models are beneficial (the varying responses of vegetation types to perturbation in Chapter 4), while analytic models can give deeper insights into natural relationships. Because systems are tremendously complex, models will not always be analytic. At the same time, analytic models have their place because there is the need to find new relationships and to collate and digest known relationships such as the implication of non-linear species response on ordination methods and, in fact, on ecological thinking.

A second way of looking at the process of choosing a model form is in comparing theoretical and practical approaches. This is not the same as distinguishing between analytic and phenomenological approaches. This second way can best be seen in a developmental context. Essentially, the form of the model used at any one time was dependent on current knowledge. Hence, the early work was basically theoretical. As more was learned, however, the tendency was towards practical applications. The initial, theoretic approach was involved in discovering general ecological principles. As a partial understanding was gained, models evolved into descriptive forms. Following this were box and arrow models typically seen in ecosystem description (e.g. Bliss, Courtin, Pattie, Riewe, Whitfield & Widden, 1973; Shugart, Crow & Hett, 1973; Johnson & Sharpe, 1976; and the component model in Fig. 3), simple equations, and later, the introduction of these equations contextually (as components) into a more complex model (e.g. simulation). In the middle stages, models were refined, leading to the final or ultimate practical forms such as simulation. This is idealized in many ways. For instance, the middle refinement stage often incorporated very simple theoretical models so as to embody new concepts. Leslie's (1945, 1948) matrices are an example of this. For many, interest resided in theoretical forms, much like the analytic approach of van Hulst (1975, 1978), so that for them the practical stage was never reached. Others, however, were interested in application and therefore prediction. The two forms of simulation described illustrate two present forms of the practical approach. Traditional simulation illustrates the process of theoretical to practical in a more or less orderly fashion using heuristic equations based partly on theory and partly on pragmatism. Goodall's (1967, 1970, 1972, 1974a,b, 1975) grazing model is a typical case. The time static form of simulation has

circumvented this orderly process of using known mechanisms because of the need for practical models. The use of curve fitting can be viewed as a temporary or stop gap method to be used until the theory can catch up.

The approach to choosing a model form is not a simple problem. One must choose between a theoretic or practical model based on the requirements of the particular study; decide whether to use known mechanisms versus using a phenomenological method; and finally to weigh the choice based on the type of data available.

6.3 Conclusions

The majority of the models discussed have assumed homogeneity within the study area. With the aid of computers and more complex mathematics, models have been developed which are applicable to larger areas and can handle increased complexity. As a result, a new problem has evolved where the assumption of homogeneity is no longer applicable. If this resulting heterogeneity can be assumed to be the result of some random process, stochastic simulation models would be useful. However, heterogeneity may be in the form of predictable pattern, and therefore not random. There are models useful in studying pattern but they usually neglect the other aspect characteristic of the models presented here, that of numbers of individuals. Levin (1976) has produced a model which can handle both numbers and pattern but is limited to answering certain types of questions, possibly because incorporating heterogeneity requires detail at a high level so that only general predictions can be made. This is similar to many other current approaches to combining model forms. One example, described earlier, illustrated the

difficulty in amalgamating the ideas of direct gradient analysis with ordination.

Levin (1976) has recognized that "the possibilities for such pattern formation are limitless". This suggests we should not rely on one type of model, such as for example the classical mathematical/analytical form. We must continue to be aware of various approaches to modelling, making sure their assumptions and implications are understood. This will give greater insight into inherent problems as well as the extent to which any one model form can be used in the pursuit of understanding sytems of vegetation interaction.

APPENDIX 1

Computer listings of the programs comprising the simulation model in Chapter 3. The main program, written in FORTRAN, is called SIMPLE. Thirteen subroutines follow while the last program listed, PRECOV, is used prior to simulation to aid in choosing initial parameter values.

```
c *** SIMPLE   11.2.81 (update 19.1.83)***
c   First model using #'s of P. glauca, P. mariana & Salix in
c each age class; moss thickness; cover of the trees,
c moss & mineral soil; and depth to
c permafrost as the principal variables.  Data files are
c used to initialize the program.  File EXOG contains values of
c exogenous variables.  Files WHITE, BLACK, & SALIX contain the
c initial age class #'s. File ENDOG contains initial endogenous
.c values.
c Attach subroutines READ, RTREE, INITL, PGDIA, PMDIA,
c SDIA, PGCOV, PMCOV, SCOVR, OUT, OUTA, MOSSA & DYNAM
c ****************************************************************
      REAL M1,M2,P1,P2,P3,PI,DIAM3(50),X5(5),X6,X4
      REAL X5T(3),X,DIAM1(200),DIAM2(200),SLOPE,CP
      INTEGER X1(200),X2(200),X3(50),T,TSIM,TPRINT,IPRINT,J,K
      COMMON/AREA1/X1/AREA2/X2/AREA3/X3/AREA4/DIAM3,
      COMMON/AREA5/X5/AREA6/X5T/AREA7/DIAM1/AREA8/DIAM2
      CALL SETRAN(1)
c
c data files read & parameters initialized
c
      CALL READ(M1,M2,P1,P2,P3,X4,SLOPE)
      CALL INITL(PI,T,IPRINT,TSIM,TPRINT)
c
c output files opened
c
      OPEN(UNIT=1,FILE='AGEW.DAT')
      OPEN(UNIT=2,FILE='AGEB.DAT')
      OPEN(UNIT=3,FILE='AGES.DAT')
c ****************************************************************
c Print exogenous conditions
c
      WRITE(6,1)
 1    FORMAT('      EXOGENOUS CONDITIONS.')
      WRITE(6,2)
 2    FORMAT('0 MOISTURE',4X,'GERMINATION PROB',4X,'SLOPE')
      WRITE(6,3)M1,P1,SLOPE
 3    FORMAT('  M1 = ',F4.1,4X,'P1 = ',F9.7,4X,F5.1)
      WRITE(6,4)M2,P2
 4    FORMAT('  M2 = ',F4.1,4X,'P2 = ',F9.7)
      WRITE(6,5)P3
 5    FORMAT(15X,'P3 = ',F9.7)
c ****************************************************************
c Calculate initial cover values
c
      CALL PGDIA
      CALL PMDIA
      CALL SDIA
      CALL PGCOV(X1,X,PI)
      X5(1)=X
      CALL PMCOV(X2,X,PI)
      X5(2)=X
      CALL SCOVR(X3,X,PI)
```

```
          X5(3)=X
c
c get initial permafrost depth & print initial conditions
c
          CP=COS(37.5*PI/180.)/COS((37.5-SLOPE)*PI/180.)
          X6=45.206*EXP(-.104*X4*X5(4)*CP/1000000.)
          CALL OUT(T,X6,X4)
          K=2
c *****************************************************************
c Time loop begins.
c
c Update counters & replace old variables with new
c
1000      T=T+1
          IPRINT=IPRINT+1
          X5T(1)=X5(1)
          X5T(2)=X5(2)
          X5T(3)=X5(3)
c
c moss grows & #'s of trees updated
c
          CALL MOSSA(M1)
          CALL DYNAM(P1,P2,P3,PI,X4,X6)
c
c Moss depth changes
c
          X4=X4+(1.0-X4/28.271)*X5(4)*M2/2000000.
c
c Permafrost depth found
c
          X6=45 206*EXP(-.104*X4*X5(4)*CP/1000000.)
c
c Time to print?
c
          IF(IPRINT.LT.TPRINT)GOTO100
          K=K+1
          IF(K.LE.4)GOTO50
          DO10J=1,28
10        WRITE(6,11)
11        FORMAT(1X)
          K=1
50        CALL OUT(T,X6,X4)
          IPRINT=0
c
c End of simulation?
c
100       IF(T.LT.TSIM)GOTO1000
          CLOSE(UNIT=1,FILE='AGEW.DAT')
          CLOSE(UNIT=2,FILE='AGEB.DAT')
          CLOSE(UNIT=3,FILE='AGES.DAT')
          END
```

```
C ***********************************************************
C Subroutine READ - reads data files EXOG, WHITE, BLACK,    *
C SALIX & ENDOG                                             *
C ***********************************************************
      SUBROUTINE READ(M1,M2,P1,P2,P3,X4,SLOPE)
      COMMON/AREA1/X1/AREA2/X2/AREA3/X3/AREA5/X5
      INTEGER X1(200),X2(200),X3(50)
      REAL X5(5),M1,M2,P1,P2,P3,X4,SLOPE
C
G reads data
C
      OPEN(UNIT=1,FILE='EXOG DAT')
      READ(1,1)M1,M2
1     FORMAT(2F)
      READ(1,2)P1,P2,P3
2     FORMAT(3F)
      READ(1,5)SLOPE
5     FORMAT(F)
      CLOSE(UNIT=1,FILE='EXOG.DAT')
      OPEN(UNIT=1,FILE='WHITE.DAT')
      CALL RTREE(X1)
      CLOSE(UNIT=1,FILE='WHITE.DAT')
      OPEN(UNIT=1,FILE='BLACK.DAT')
      CALL RTREE(X2)
      CLOSE(UNIT=1,FILE='BLACK.DAT')
      OPEN(UNIT=1,FILE='SALIX.DAT')
      READ(1,3)(X3(I),I=1,10)
3     FORMAT(10I)
      READ(1,4)(X3(I),I=11,30)
4     FORMAT(20I)
      READ(1,4)(X3(I),I=31,50)
      CLOSE(UNIT=1,FILE='SALIX.DAT')
      OPEN(UNIT=1,FILE='ENDOG.DAT')
      READ(1,2)X5(4),X4,X5(5)
      CLOSE(UNIT=1,FILE='ENDOG.DAT')
      RETURN
      END

C ***********************************************************
C Subroutine RTREE - reads class data for white or black    *
C ***********************************************************
      SUBROUTINE RTREE(CLAS)
      INTEGER CLAS(200)
      READ(1,1)(CLAS(I),I=1,10)
1     FORMAT(10I)
      READ(1,2)(CLAS(I),I=11,30)
2     FORMAT(20I)
      READ(1,2)(CLAS(I),I=31,50)
      READ(1,2)(CLAS(I),I=51,70)
      READ(1,2)(CLAS(I),I=71,90)
      READ(1,2)(CLAS(I),I=91,110)
      READ(1,2)(CLAS(I),I=111,130)
      READ(1,2)(CLAS(I),I=131,150)
```

```
      READ(1,2)(CLAS(I),I=151,170)
      READ(1,2)(CLAS(I),I=171,190)
      READ(1,1)(CLAS(I),I=191,200)
      RETURN
      END


C ***********************************************************
C Subroutine INITL - Parameters initialized.              *
C User gives simulation time & printing interval          *
C ***********************************************************
      SUBROUTINE INITL(PI,T,IPRINT,TSIM,TPRINT)
      INTEGER T,IPRINT,TSIM,TPRINT
      REAL PI
C
C initialization
C
      PI=3.1415926536
      T=0
      IPRINT=0
      WRITE(6,1)
1     FORMAT(' SIMULATION TIME?')
      READ(5,2)TSIM
2     FORMAT(I)
      WRITE(6,3)
3     FORMAT(' PRINTING INTERVAL?')
      READ(5,2)TPRINT
      RETURN
      END


C ***********************************************************
C Subroutine PGDIA - calculates P. glauca diameters       *
C ***********************************************************
      SUBROUTINE PGDIA
      COMMON/AREA7/DIAM1
      REAL DIAM1(200)
      DIAM1(1)=1.0
      DO10I=2,200
      DIAM1(I)=.881*I^.875
10    CONTINUE
      RETURN
      END


C ***********************************************************
C Subroutine PMDIA - calculates P. mariana diameters      *
C ***********************************************************
      SUBROUTINE PMDIA
      COMMON/AREA8/DIAM2
      REAL DIAM2(200)
      DIAM2(1)=1.0
      DO10I=2,200
      DIAM2(I)=2.782+.454*I
```

```
10    CONTINUE
      RETURN
      END

c *******************************************************
c Subroutine SDIA - calculates Salix diameters          *
c *******************************************************
      SUBROUTINE SDIA
      COMMON/AREA4/DIAM3
      REAL DIAM3(50)
      DIAM3(1)=1.0
      DO10I=2,50
      DIAM3(I)=1.875+1.568*I
10    CONTINUE
      RETURN
      END

c *******************************************************
c Subroutine PGCOV - get cover for P. glauca             *
c *******************************************************
      SUBROUTINE PGCOV(CLAS,X,PI)
      COMMON/AREA7/DIAM1
      INTEGER CLAS(200)
      REAL X,PI,DIAM1(200)
      X=0.0
      DO10I=1,200
      X=X+CLAS(I)*DIAM1(I)^2
10    CONTINUE
      X=X*PI/4
      RETURN
      END

c *******************************************************
c Subroutine PMCOV, get cover for P. mariana             *
c *******************************************************
      SUBROUTINE PMCOV(CLAS,X,PI)
      COMMON/AREA8/DIAM2
      INTEGER CLAS(200)
      REAL X,PI,DIAM2(200)
      X=0.0
      DO10I=1,200
      X=X+CLAS(I)*DIAM2(I)^2
10    CONTINUE
      X=X*PI/4
      RETURN
      END

c *******************************************************
c Subroutine SCOVR - get cover for Salix                 *
c *******************************************************
      SUBROUTINE SCOVR(CLAS,X,PI)
      COMMON/AREA4/DIAM3
      INTEGER CLAS(50)
```

```
      REAL X,PI,DIAM3(50)
      X=0.0
      DO10I=1,50
      X=X+CLAS(I)*DIAM3(I)^2
10    CONTINUE
      X=X*PI/4.
      RETURN
      END

C ****************************************************************
C Subroutine OUT - prints output                                *
C ****************************************************************
      SUBROUTINE OUT(T,X6,X4)
      COMMON/AREA1/X1/AREA2/X2/AREA3/X3/AREA5/X5
      INTEGER T,X1(200),X2(200),X3(50),C(5),K
      REAL X5(5),X6,X,X4,Z,Z1(5),Z2,ROOTD
C
C output
C
      WRITE(6,1)T
1     FORMAT('0TIME = ',I3,'      ',56(1H*))
      WRITE(6,2)
2     FORMAT(' P GLAUCA  ',1X,'P MARIANA ',1X,'   SALIX  ',1X,'M
     *OSS COVER',1X,'ORG/MIN SOIL',3X,'TOTAL COVER')
C
C convert from cm^2 to m^2 giving a (0,100) range
C
      Z=10000.
      DO40I=1,5
      Z1(I)=X5(I)/Z
40    CONTINUE
      X=X5(1)+X5(2)+X5(3)+X5(4)+X5(5)
      WRITE(6,3)Z1(1),Z1(2),Z1(3),Z1(4),Z1(5),Z2
3     FORMAT(1X,5(2X,F5.1,4X),7X,F5.1)
      ROOTD=X4+X6
      WRITE(6,4)
4     FORMAT('0MOSS DEPTH',2X,'ACTIVE LAYER',2X,'ROOTING DEPTH')
      WRITE(6,5)X4,X6,ROOTD
5     FORMAT(3X,F4.1,10X,F4.1,10X,F5.1)
      WRITE(6,6)
6     FORMAT('0     ','AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2
     *ND ROWS ARE 10 YR CLASSES')
      WRITE(6,7)(X1(I),I=1,10)
7     FORMAT(' P GLAUCA ',10(1X,I3))
      K=1
      CALL OUTA(X1,K)
      WRITE(6,8)(X2(I),I=1,10)
8     FORMAT(' P MARIANA',10(1X,I3))
      K=2
      CALL OUTA(X2,K)
      WRITE(6,9)(X3(I),I=1,10)
9     FORMAT(' SALIX',4X,10(1X,I3))
      DO30J=1,5
```

```
        C(J)=0
        DO20I=1,10
        C(J)=C(J)+X3(10*(J-1)+I)
20      CONTINUE
30      CONTINUE
        WRITE(6,10)(C(J),J=2,5)
        WRITE(3,11)(C(J),J=1,5)
11      FORMAT(5(1X,I3))
10      FORMAT(11X,4(1X,I2))
        RETURN
        END


C ***********************************************************
C Subroutine OUTA - adds up 10 year age classes            *
C ***********************************************************
        SUBROUTINE OUTA(CLAS,K)
        INTEGER CLAS(200),C(20),K
        DO30J=1,20
        C(J)=0
        DO20I=1,10
        C(J)=C(J)+CLAS(10*(J-1)+I)
20      CONTINUE
30      CONTINUE
        WRITE(6,1)(C(J),J=2,20)
1       FORMAT(11X,19(1X,I2))
        IF(K.EQ.1)WRITE(1,2)(C(J),J=1,20)
        IF(K.EQ.2)WRITE(2,2)(C(J),J=1,20)
2       FORMAT(20(1X,I3))
        RETURN
        END


C ***********************************************************
C Subroutine MOSSA - Moss grows -) mineral soil decreases.  *
C Mineral soil decreases since moss grows over it           *
C ***********************************************************
        SUBROUTINE MOSSA(M1)
        COMMON/AREA5/X5
        REAL X5(5),X,C,M1
C
C moss grows
C
        X=X5(1)+X5(2)+X5(3)
        IF(X.GE.500000.0)C=1.
        IF(X.LT.500000.0)C=(.9*X+50000.0)/500000.0
        X5(4)=X5(4)+216.0*X5(5)*M1*C/3025.
        X5(5)=X5(5)-216.0*X5(5)*M1*C/3025.
C
C test to see if there is any mineral soil remaining
C
        IF(X5(5).GT.0.0)GOTO10
        X5(4)=X5(4)+X5(5)
4       X5(5)=0.0
```

```
10      RETURN
        END

C ***************************************************************
C Subroutine DYNAM - gets # of trees in each age class which *
C have survived to this year plus the germinants.            *
C ***************************************************************
        SUBROUTINE DYNAM(P1,P2,P3,PI,X4,X6)
        COMMON/AREA1/X1/AREA2/X2/AREA3/X3/AREA5/X5/AREA6/X5T
        COMMON/AREA8/DIAM2/AREA4/DIAM3
        INTEGER X1(200),X2(200),X3(50),MORT1(200),MORT2(200)
        INTEGER C2D,C2M,MORT3(50),ROOTD
        INTEGER S1A,S1B,S2A,S2B,S2C,S2D,S3A,S3B,S3C,S3D,IS
        REAL X5(5),RND,DUMMY,A,B,P1,P2,P3,PI,X,X5T(3),DIAM2(200)
        REAL K,Z,Y,PS,C,X4,X6
C ***************************************************************
C calculates # of trees which die (includes all spruce
C aged 200) -) mineral soil increases since when trees die,
C they fall over & expose the soil
C
        ROOTD=IFIX(X4+X6)
        K=600000.
        Z=X5(1)+X5(2)+X5(3)
        X=(K-Z)/10000.
        Y=EXP(-.04*X)
        IF(41-ROOTD.GT.0)S1A=1
        IF(41-ROOTD.LE.0)S1A=0
        DO20I=1,199
        MORT1(I)=0
        IF(X1(I).EQ.0)GOTO20
        IF(I.GE.200-15*(41-ROOTD))S1B=1
        IF(I.LT.200-15*(41-ROOTD))S1B=0
        PS=.967-.4*Y*X5(1)*(1.-.001*I)/Z
        PS=PS-S1A*S1B*.03*(41-ROOTD)
        IF(PS.LT.0.)PS=0.
        DO10J=1,X1(I)
        RND=RAN(DUMMY)
        IF(RND.GE.PS)MORT1(I)=MORT1(I)+1
10      CONTINUE
20      CONTINUE
        MORT1(200)=X1(200)
        IF(31-ROOTD.GT.0)S2A=1
        IF(31-ROOTD.LE.0)S2A=0
        IF(ROOTD-37.GT.0)S2C=1
        IF(ROOTD-37.LE.0)S2C=0
        DO40I=1,199
        MORT2(I)=0
        IF(X2(I).EQ.0)GOTO40
        IF(I.GE.200-30*(31-ROOTD))S2B=1
        IF(I.LT.200-30*(31-ROOTD))S2B=0
        IF(I.LE.25*(ROOTD-37))S2D=1
        IF(I.GT.25*(ROOTD-37))S2D=0
        PS=.965-.6*Y*X5(2)*(1.-.0005*I)/Z
```

```
              PS=PS-S2A*S2B*.06*(31-ROOTD)-S2C*S2D*.04*(ROOTD-37)
              IF(PS.LT.0.)PS=0.
              DO30J=1,X2(I)
              RND=RAN(DUMMY)
              IF(RND.GE.PS)MORT2(I)=MORT2(I)+1
30        CONTINUE
40        CONTINUE
              MORT2(200)=X2(200)
              IF(19-ROOTD.GT.0)S3A=1
              IF(19-ROOTD.LE.0)S3A=0
              IF(ROOTD-34.GT.0)S3C=1
              IF(ROOTD-34.LE.0)S3C=0
              DO100I=1,50
              MORT3(I)=0
              IF(X3(I).EQ.0)GOTO100
              IF(I.GE.50-5*(19-ROOTD))S3B=1
              IF(I.LT.50-5*(19-ROOTD))S3B=0
              IF(I.LE.2*(ROOTD-34))S3D=1
              IF(I.GT.2*(ROOTD-34))S3D=0
              PS=1.0-Y*X5(3)*(1.-.01*I)/Z
              PS=PS-S3A*S3B*.05*(19-ROOTD)-S3C*S3D*.02*(ROOTD-34)
              IF(PS.LT.0.)PS=0.
              DO90J=1,X3(I)
              RND=RAN(DUMMY)
              IF(RND.GE.PS)MORT3(I)=MORT3(I)+1
90        CONTINUE
100       CONTINUE
              CALL PGCOV(MORT1,A,PI)
              CALL PMCOV(MORT2,B,PI)
              CALL SCOVR(MORT3,C,PI)
              X5(5)=X5(5)+A+B+C
C ***************************************************************
C trees aged 1 year -) moss & mineral soil decrease by a
C proportion of the cover increase (new cover minus old cover,
C where new cover doesn't include those germinating & old cover
C doesn't include area of trees which died)
              DO50I=200,2,-1
              X1(I)=X1(I-1)-MORT1(I-1)
              X2(I)=X2(I-1)-MORT2(I-1)
50        CONTINUE
              X3(50)=X3(50)+X3(49)-MORT3(50)-MORT3(49)
              DO60I=49,2,-1
              X3(I)=X3(I-1)-MORT3(I-1)
60        CONTINUE
C
C gets germinants.  P. glauca germinates in mineral soil.
C P. mariana does the same but also layers in moss.  Salix
C germinates in moss.  Thus mineral soil & moss decrease
C
              X1(1)=IXFIX(4*X5(5)*P1/PI)
              C2D=IFIX(4*X5(5)*P2/PI)
              C2M=0
              DO70I=100,200
```

```
            C2M=C2M+X2(I)*DIAM2(I)
      70    CONTINUE
            C2M=IFIX(X5(4)*PI*C2M/375000000.)
            X2(1)=C2D+C2M
            X3(1)=IFIX(4*X5(4)*P3/PI)
      C
      C gets new cover for trees & makes adjustments.  Z is th cover
      C change without including the germinants   X is used so that
      C change of X5(4) & X5(5) is a relative proportion to each other
      C
            CALL PGCOV(X1,X,PI)
            X5(1)=X
            CALL PMCOV(X2,X,PI)
            X5(2)=X
            CALL SCOVR(X3,X,PI)
            X5(3)=X
            Z=X5(1)+X5(2)+X5(3)-(X1(1)+X2(1)+X3(1))*PI/4.
            Z=Z-(X5T(1)+X5T(2)+X5T(3)-A-B-C)
            X=X5(4)+X5(5)
            X5(4)=X5(4)-Z*X5(4)/X-(C2M+X3(1))*PI/4.
            X5(5)=X5(5)-Z*X5(5)/X-(X1(1)+C2D)*PI/4.
      C
      C test to see if there is any moss remaining
      C
            IF(X5(4).GT 0.0)GOTO80
            X5(5)=X5(5)+X5(4)
            X5(4)=0.0
      80    RETURN
            END


      C *** PRECOV    23.7.81 ***
      C CALCULATES COVER OF TREES. .THIS PROGRAM IS RUN BEFORE
      C SIMULATION SO THE USER CAN CHOOSE THE COVER OF MOSS &
      C MINERAL SOIL (THE TOTAL COVER SHOULD ADD UP TO
      C 100 X 100 CM).  ATTACH SUBROUTINES READ, RTREE, PGDIA,
      C PMDIA, SDIA, PGCOV, PMCOV & SCOVR.
            REAL M1,M2,P1,P2,P3,PI,DIAM3(50),X5(5),X4
            REAL A,B,C,T,DIAM1(200),DIAM2(200),ASPECT
            INTEGER X1(200),X2(200),X3(50)
            COMMON/AREA1/X1/AREA2/X2/AREA3/X3/AREA4/DIAM3/AREA5/X5
            COMMON/AREA7/DIAM1/AREA8/DIAM2
      C
      C READ DATA, CALCULATE COVER, PRINT OUTPUT
      C
            CALL READ(M1,M2,P1,P2,P3,X4,ASPECT)
            PI=3.1415926536
            CALL PGDIA
            CALL PMDIA
            CALL SDIA
            CALL PGCOV(X1,A,PI)
            CALL PMCOV(X2,B,PI)
            CALL SCOVR(X3,C,PI)
            T=A+B+C
```

145

```
      WRITE(6,1)
      FORMAT('0',4X,'P GLAUCA',3X,'P MARIANA',5X,'SALIX',5X,'T
    *OTAL TREE')
      WRITE(6,2)A,B,C,T
  2   FORMAT(1X,4(3X,F9.1))
      END
```

APPENDIX 2

Partial computer printouts of three simulations. The printing interval was 10 simulation years. Output is for years 0, 10, 20, 190 and 200. In all three runs *Picea glauca* predominated at time zero. Age class data at time 200 is presented graphically in Fig. 7 whereas Fig. 6 summarizes the entire 200 years of simulation.

```
.EX SIMPLE,READ,RTREE,INITL,PGDIA,PMDIA,SDIA,PGCOV,PMCOV,SCOVR,
        OUT,OUTA,MOSSA,DYNAM
LINK:   Loading
[LNKXCT SIMPLE execution]
SIMULATION TIME?
200
PRINTING INTERVAL?
10
        EXOGENOUS CONDITIONS:

MOISTURE     GERMINATION PROB  /SLOPE
M1 =  0.5    P1 =  .0000400   /  0.0
M2 =. 0.5    P2 =  .0000380
             P3 =  .0000100

TIME =   0    ***************************************************
P GLAUCA    P MARIANA   SALIX  MOSS COVER ORG/MIN SOIL  TOTAL COVER
   6.3         0.0       0.0      75.0      18.7           100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  20.0          9.5          29.5

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA  9  9   9   8   8   8   8   7   7   7
         59 43 31 21 15 10  9  0  0  0  0  0  0  0  0  0  0  0  0
P MARIANA 0  0   0   0   0   0   0   0   0   0
          0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0
SALIX     0  0   0   0   0   0   0   0   0   0
          0  0  0  0

TIME =  10    ***************************************************
P GLAUCA    P MARIANA   SALIX  MOSS COVER ORG/MIN SOIL  TOTAL COVER
   0.5         0.2       0.8      74.6      24.0           100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  20.5          9.2          29.7

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA 12 12 11   8  10  11   5  10   9   7
         41  4  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0
P MARIANA 11 11  10  10  10  11   9  11   8   8
          0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0
SALIX     9  8   8   8   7   6   7   8   8   8
          0  0  0  0

TIME =  20    ***************************************************
P GLAUCA    P MARIANA   SALIX  MOSS COVER ORG/MIN SOIL  TOTAL COVER
   0.9         0.7       2.7      72.4      23.4           100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  21.0          9.3          30.3

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA 11 11 12   9   8   8  11   9   7   9
         64 15  1  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0
P MARIANA 11 11  11   8   9   9  10   9   7  10
         65  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0
SALIX     9  8   9   8   7   7   6   6   5   2
         43  0  0  0
```

```
TIME = 190    ****************************************************
P GLAUCA   P MARIANA   SALIX   MOSS COVER ORG/MIN SOIL  TOTAL COVER
   5.4        3.7        6.8      50.4        33.7          100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  25.1          12.1          37.2

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA   17  17  15  14   12  15  11  12  11  11
           71 41 29 14 10    2   5   0   2   2   1   0   0   0   0   0   0   0
P MARIANA  16  16  14  11   14  14  13  11  14   7
           69 37 23 10   6   3   2   0   1   0   1   0   0   0   0   0   0   0
SALIX       6   6   5   5    4   1   3   3   1   2
           12   4   2 10

TIME = 200    ****************************************************
P GLAUCA   P MARIANA   SALIX   MOSS COVER ORG/MIN SOIL  TOTAL COVER
   4.8        3.4        5 6      50.5        35.7          100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  25.2          12.0          37.3

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA   18  17  16  13   14  12  11  13  11  11
           72 38 22 21   8   6   1   1   0   0   2   0   0   0   0   0   0   0
P MARIANA  17  16  16  16   11  12  11  13   9   7
           68 40 21 13   3   4   1   0   0   1   0   0   0   0   0   0   0   0
SALIX       6   5   4   5    4   3   1   3   2   3
           18   5   2   7
CPU time 9.87   Elapsed time 2:31.70

EXIT
```

```
.EX SIMPLE,READ,RTREE,INITL,PGDIA,PMDIA,SDIA,PGCOV,PMCOV,SCOVR,
          OUT,OUTA,MOSSA,DYNAM
LINK:   Loading
[LNKXCT SIMPLE execution]
SIMULATION TIME?
200
PRINTING INTERVAL?
10
      EXOGENOUS CONDITIONS:

MOISTURE     GERMINATION PROB    SLOPE
M1 = 0.5    P1 = .0000400        8.0
M2 = 0.5    P2 = .0000380
            P3 = .0000100


TIME =   0  ****************************************************
P GLAUCA  P MARIANA   SALIX   MOSS COVER ORG/MIN SOIL  TOTAL COVER
  6.3       0.0       0.0       55.0        38.7         100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  24.0         12.9          36.9

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA    9   9   9   8   8   8   8   7   7   7
           59  43  31  21  15  10   9   0   0   0   0   0   0   0   0   0   0   0   0
P MARIANA   0   0   0   0   0   0   0   0   0   0   0   0
           0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0
SALIX       0   0   0   0   0   0   0   0   0   0
           0   0   0   0


TIME =  10   ****************************************************
P GLAUCA  P MARIANA   SALIX   MOSS COVER ORG/MIN SOIL  TOTAL COVER
  4.9       0 3       0 6       55.8        38.3         100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  24.2         12.6          36.8

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA   19  18  17  14  12  13   9   8  14  12
           36  27  19  11  13   8   5   5   0   0   0   0   0   0   0   0   0   0   0
P MARIANA  18  18  16  14  17  16  18  11  14  14
           0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0
SALIX       7   7   6   7   4   5   6   7   7   6
           0   0   0   0


TIME =  20   ****************************************************
P GLAUCA  P MARIANA   SALIX   MOSS COVER ORG/MIN SOIL  TOTAL COVER
  4.4       1.0       3.1       55.1        36.4         100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  24.4         12.6          37.0

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA   18  16  18  15  16  13  13  12  10  13
           70  20  13  12   8   5   4   3   3   0   0   0   0   0   0   0   0   0   0
P MARIANA  17  17  15  15  17  15  15  14  12  12
           **   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0
SALIX       7   5   5   4   5   5   2   6   6   5
           47   0   0   0
```

```
TIME = 190    **************************************************************
P GLAUCA   P MARIANA   SALIX   MOSS COVER ORG/MIN SOIL   TOTAL COVER
   4.7        1.9        5.5       52.6       35.3           100.0

MOSS DEPTH  ACTIVE LAYER   ROOTING DEPTH
   26.5         12.1           38.6

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA   18  17  17  16  14  18  10  13  13  10
           84 48 37 13  7  3  1  3  0  0  0  0  0  0  0  0  0 0
P MARIANA  17  15  15  12  14   9  12  11   7   6
           44 18  5  6  3  2  0  1  1  0  0  0  0  0  0  0  0 0
SALIX       6   6   4   4   4   4   3   1   3  .0
           17 11  1  6

TIME = 200    **************************************************************
P GLAUCA   P MARIANA   SALIX   MOSS COVER ORG/MIN SOIL   TOTAL COVER
   4.5        1.        4.3       52.2       37.3           100.0

MOSS DEPTH  ACTIVE LAYER   ROOTING DEPTH
   26.6         12.1           38.7

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA   19  18  18  17  14  12  15  12  11  11
           76 52 25 15  5  4  2  0  2  0  0  0  0  0  0  0  0 0
P MARIANA  18  15  15  12  13  12  11   7   7   6
           46 16 11  5  4  2  0  0  0  0  0  0  0  0  0  0  0 0
SALIX       6   5   4   6   3   2   1   1   1   2
           11  9  6  2
CPU time 9.78   Elapsed time 2:32.53

EXIT
```

```
.EX SIMPLE,READ,RTREE,INITL,PGDIA,PMDIA,SDIA,PGCOV,PMCOV,SCOVR,
        OUT,OUTA,MOSSA,DYNAM
LINK:   Loading
[LNKXCT SIMPLE execution]
SIMULATION TIME?
200
PRINTING INTERVAL?
10
        EXOGENOUS CONDITIONS

MOISTURE     GERMINATION PROB     SLOPE
M1 =  0.3    P1 =  .0000400       15 0
M2 =  0 3    P2 =  .0000380
             P3 =  .0000100

TIME =   0   *************************************************
P GLAUCA  P MARIANA    SALIX  MOSS COVER ORG/MIN SOIL  TOTAL COVER
   6.3        0.0       0.0      55.0       38 7          100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  24.0         13.9          37.9

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES, 2ND ROWS ARE 10 YR CLASSES
P GLAUCA    9   9   9   8   8   8   8   7   7   7
           59 43 31 21 15 10  9  0  0  0  0  0  0  0  0  0  0  0 0
P MARIANA   0   0   0   0   0   0   0   0   0   0
            0   0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0 0
SALIX       0   0   0   0   0   0   0   0   0   0
            0   0   0   0

TIME =  10   *************************************************
P GLAUCA  P MARIANA    SALIX  MOSS COVER ORG/MIN SOIL  TOTAL COVER
   4.7        0.3       0.4      54.5       40.1          100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  24 1         14.0          38.1

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA   20  19  16  13  17  12  10  14  13  12
           35 23 23 15 10  9  4  3  0  0  0  0  0  0  0  0  0  0 0
P MARIANA  19  19  18  17  15  13  12  11  15  13
            0   0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0 0
SALIX       6   5   5   4   5   3   5   4   5   3
            0   0   0   0

TIME =  20   *************************************************
P GLAUCA  P MARIANA    SALIX  MOSS COVER ORG/MIN SOIL  TOTAL COVER
   4.2        0.8       2.0      53.2       39.8          100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  24.2         14.3          38 5

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA   20  17  15  19  14  12  11  13  12   8
           79 13 12 12  7  6  4  4  1  0  0  0  0  0  0  0  0  0 0
P MARIANA  19  14  17  15  12  15  10   6  11   9
           76  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0 0
SALIX       6   5   5   5   4   5   3   3   3   1
           29  0   0   0
```

```
TIME = 190    *******************************************************
P GLAUCA   P MARIANA    SALIX  MOSS COVER ORG/MIN SOIL   TOTAL COVER
  4.5         0.2         2.4       43.9        48.9          100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  25.4          16.7          42.1

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA   25  21  24  18  23  16  19  18  12  15
           98  58  30  12   8   5   1   0   0   0   0   0   0   0   0   0   0   0.0
P MARIANA  23  18  16   8   9   7   2   6   7   1
            8   1   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0.
SALIX       5   5   2   4   4   2   0   1   1   1
            8   1   1   3

TIME = 200    *******************************************************
P GLAUCA   P MARIANA    SALIX  MOSS COVER ORG/MIN SOIL   TOTAL COVER
  4.6         0.2         3.5       43.7        48.1          100.0

MOSS DEPTH  ACTIVE LAYER  ROOTING DEPTH
  25.4          16.8          42.2

AGE CLASSES (1ST ROWS ARE 1 YR CLASSES; 2ND ROWS ARE 10 YR CLASSES
P GLAUCA   24  24  22  22  20  20  21  13  13  14
           **  50  25  14   5   5   3   1   0   0   0   0   0   0   0   0   0   0   0
P MARIANA  23  15  16  11   8   7   4   3   2   2
            5   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0.0
SALIX       5   4   2   3   2   2   1   1   1   1
            8   5   1   4
CPU time 9.18   Elapsed time 2:32.52

EXIT
```

APPENDIX 3

Computer listings of BASIC and FORTRAN programs used in Chapter 4 for analysing data and for graphical presentation. The programs appear in alphabetical order.

```
00010 PRINT "PROGRAM NAME --- EUCDP"
00020 REM----THIS PROGRAM COMPUTES EUCLIDEAN DISTANCES BETWEEN
00030 REM QUADRATS FROM RAW OR NORMALIZED DATA. THE DATA ARE
00040 REM READ FROM DISK FILE RAWD ARRANGED AS P SETS OF N
00050 REM NUMBERS. P SIGNIFIES THE NUMBER OF SPECIES AND N THE
00060 REM NUMBER OF QUADRATS. THE COMPUTED DISTANCES ARE WRITTEN
00065 REM INTO DISK FILE DIS.
00070 PRINT "=================================================="
00080 FILES RAWD,DIS
00090 SCRATCH #2
00100 DIM X(4,23),Y(23)
00120 REM---EXPLANATIONS TO ARRAY SYMBOLS:
00140 REM      X - A P*N ARRAY OF DATA
00150 REM      Y - AN N-VALUED VECTOR
00180 REM---READ DATA, NORMALIZE QUADRAT VECTORS
00190 PRINT "NUMBER OF SPECIES P";
00200 INPUT P
00210 PRINT "NUMBER OF QUADRATS N";
00220 INPUT N
00230 PRINT "TYPE 1 IF NORMALIZATION IS REQUIRED ELSE TYPE 0";
00240 INPUT Z
00242 PRINT "TYPE 1 TO WRITE DIAGONAL ZEROS IN DIS,"
00243 PRINT "ELSE TYPE 0";
00244 INPUT I1
00250 MAT Y=ZER
00260 FOR I=1 TO P
00270 FOR J=1 TO N
00280 READ #1,A
00290 LET X(I,J)=A
00300 LET Y(J)=Y(J)+X(I,J)^2
00310 NEXT J,I
00320 IF Z=1 THEN 340
00330 MAT Y=CON
00340 FOR I=1 TO N
00350 LET Y(I)=SQR(Y(I))
00360 NEXT I
00370 REM----COMPUTE DISTANCES
00380 PRINT "TYPE 1 IF PRINTING OF DISTANCES REQUIRED"
00385 PRINT "ELSE TYPE 0";
00390 INPUT V
00400 PRINT
00410 FOR J=1 TO N-1
00412 IF I1=0 THEN 420
00414 WRITE #2,0;
00420 FOR K=J+1 TO N
00430 LET S=0
00440 FOR I=1 TO P
00450 LET S=S+(X(I,J)/Y(J)-X(I,K)/Y(K))^2
00460 NEXT I
00470 WRITE #2,SQR(S);
00479 NEXT K
00480 WRITE #2
00481 NEXT J
```

```
00482 IF I1=0 THEN 490
00483 WRITE #2,0
00490 IF V=0 THEN 590
00500 RESTORE #2
00510 PRINT "UPPER HALF OF DISTANCE MATRIX"
00513 LET I3=0
00515 IF I1=1 THEN 520
00517 LET I3=1
00520 FOR J=1 TO N-I3
00530 FOR K=J+I3 TO N
00540 READ #2,A
00550 PRINT A;
00560 NEXT K
00570 PRINT
00580 NEXT J
00590 END


00005 PRINT "PROGRAM NAME --- MHAT"
.00010 REM - CALCULATES DIS=f(X1,X2,X3,X4) WHERE DIS IS A NEW
00020 REM    DISTANCE MATRIX FOR SPF & THE Xi'S ARE FROM
00030 REM    PROGRAM MULT3 (FILE DISX).  THE PARAMETERS USED FOR
00040 REM    REGRESSION ESTIMATION ARE READ FROM FILE PARAM.
00045 PRINT "=============================================="
00050 FILES DISXP,DIS,PARAM
00060 SCRATCH #2
00070 DIM Y(253),X(13,253),B(13)
00080 REM - ARRAY SIZES
00090 REM     Y - N VECTOR
00100 REM     X - P*N MATRIX
00105 REM     B - P VECTOR
00110 PRINT "NUMBER OF X VARIABLES";
00120 INPUT P
00130 REM - OLD Y SKIPPED OVER
00140 FOR I=1 TO 253
00150 READ #1,G
00160 NEXT I
00170 REM - PARAMETERS OBTAINED
00180 READ #3,A
00190 FOR I=1 TO P
00200 READ #3,B(I)
00210 NEXT I
00250 REM - READ X
00260 FOR I=1 TO P
00270 FOR J=1 TO 253
00280 READ #1,X(I,J)
00290 NEXT J,I
00300 REM - CALCULATE Y & OUTPUT
00320 FOR J=1 TO 253
00330 Y(J)=A
00340 FOR I=1 TO P
00350 Y(J)=Y(J)+B(I)*X(I,J)
00360 NEXT I
00370 WRITE #2,Y(J)
```

```
00380 NEXT J
00390 END

00005 PRINT "PROGRAM NAME --- MREGRS"
00010 REM - MULTIPLE REGRESSION
00015 PRINT "========================="
00020 FILES DIS.
00030 DIM D(14,253),M(14),T(253,14),U(14,14),Y(13,1),S(13,13)
00035 DIM I(13,13),B(13,1)
00040 REM - ARRAY DIMENSIONS
00050 REM      D - P+1 * N  MATRIX
00060 REM      M - P+1  VECTOR
00070 REM      T - N * P+1  MATRIX
00080 REM      U - P+1 * P+1  MATRIX
00090 REM      Y,B - P  COLUMN VECTORS
00100 REM      S,I - P * P MATRICES
00110 PRINT "# OF POINTS N";
00120 INPUT N
00130 PRINT "# OF X-VARIABLES P";
00140 INPUT P
00150 PRINT "GIVE FORMULAE FOR REGRESSION (A$)"
00160 INPUT A$
00170 REM - READ DATA
00180 FOR I=1 TO P+1
00190 FOR J=1 TO N
00200 READ #1,D(I,J)
00210 M(I)=M(I)+D(I,J)
00220 NEXT J,I
00230 REM - GET ROW MEANS & CENTRE DATA
00240 FOR I=1 TO P+1
00250 M(I)=M(I)/N
00260 FOR J=1 TO N
00270 D(I,J)=D(I,J)-M(I)
00280 NEXT J,I
00290 REM - GET CROSS PRODUCT MATRIX U
00300 MAT T=TRN(D)
00310 MAT U=D*T
00320 REM - SUBDIVIDE U INTO OTHER MATRICES
00330 Q=U(1,1)
00340 FOR I=1 TO P
00350 Y(I,1)=U(I+1,1)
00360 FOR J=1 TO P
00370 S(I,J)=U(I+1,J+1)
00380 NEXT J,I
00390 REM - PRINTS PRELIMINARY RESULTS
00400 PRINT
00410 PRINT "PRELIMINARY RESULTS:"
00420 PRINT "MATRIX M"
00430 MAT PRINT M
00440 PRINT "MATRIX U"
00450 MAT PRINT U
00520 REM - CALCULATES MATRIX B
00530 MAT I=INV(S)
```

```
00540 MAT B=I*Y
00550 REM - GET A=M(1)-SUM(B(I,1)*M(I+1))
00560 FOR I=1 TO P
00570 W=W+B(I,1)*M(I+1)
00580 NEXT I
00590 A=M(1)-W
00600 REM --GET Y-HAT'S TO CALCULATE Q(R) & Q(E).
00610 REM    Y-HAT'S COME FROM NON-CENTRED MATRIX
00620 FOR J=1 TO N
00630 FOR I=1 TO P
00640 Y=Y+B(I,1)*(D(I+1,J)+M(I+1))
00650 NEXT I
00660 Y=Y+A
00670 Q1=Q1+(Y-M(1))^2
00680 Q2=Q2+(D(1,J)+M(1)-Y)^2
00690 Y=0
00700 NEXT J
00710 REM - FINAL RESULTS
00720 PRINT
00730 PRINT "FINAL RESULTS FOR:"
00740 PRINT A$
00750 PRINT
00760 PRINT "  Q"," Q1"," Q2"," R"
00770 PRINT Q,Q1,Q2,SQRT(Q1/Q)
00780 PRINT
00790 PRINT "A = "A
00800 PRINT
00810 PRINT "MATRIX B"
00820 MAT PRINT B
00830 END

00005 PRINT "PROGRAM NAME --- MULT3"
00010 REM - PREPARES A DATA MATRIX FOR USE IN MHAT
00015 PRINT "==================================="
00020 FILES DR,DRP,ST,STP,OR,ORP,ER,ERP,DISXP
00030 SCRATCH #9
00040 DIM F(4),X(14,253)
00050 PRINT "WHICH OF THE FILES 'DR', 'ST', 'OR', OR 'ER' HAVE"
00060 PRINT "BEEN PERTURBED?"
00070 PRINT "TYPE 0 FOR NO PERTURBATION, 1 FOR PURTURBATION"
00080 FOR I=1 TO 4
00090 INPUT F(I)
00100 F(I)=F(I)+2*I-1
00110 NEXT I
00120 FOR J=1 TO 253
00130 X(1,J)=0
00140 READ #F(1),X(2,J)
00150 READ #F(2),X(3,J)
00160 READ #F(3),X(4,J)
00170 READ #F(4),X(5,J)
00180 X(6,J)=X(2,J)^.5
00190 X(7,J)=X(3,J)^.5
00200 X(8,J)=X(4,J)^.5
```

```
00210 X(9,J)=X(5,J)^.5
00220 X(10,J)=X(2,J)^.33
00230 X(11,J)=X(3,J)^.33
00240 X(12,J)=X(4,J)^.33
00250 X(13,J)=X(5,J)^.33
00260 X(14,J)=(X(2,J)*X(3,J)*X(4,J)*X(5,J))^.25
00270 NEXT J
00280 FOR I=1 TO 14
00290 FOR J=1 TO 253
00300 WRITE #9,X(I,J);
00310 NEXT J
00320 WRITE #9
00330 NEXT I
00340 END


00010 PRINT "PROGRAM NAME --- PCADP"
00020 REM--- COMPONENT SCORES ARE COMPUTED FOR N INDIVIDUALS
00030 REM BASED ON THE Q OR D-ALGORITHM OF COMPONENT ANALYSIS
00040 REM THE INPUT DATA CONTAIN THE UPPER HALF OF A CROSS
00050 REM PRODUCT OR EUCLIDEAN DISTANCE MATRIX, EXCLUDING THE
00060 REM VALUES IN THE PRINCIPAL DIAGONAL, STORED IN DISK FILE
00070 REM DIS.  COMPUTED COMPONENT SCORES ARE WRITTEN INTO DISK
00080 REM FILE COMS
00120 PRINT "=========================================="
00130 FILES DIS, COMS
00140 SCRATCH #2
00150 DIM R(23,23),B(23,23),Q(23)
00170 REM---EXPLANATIONS TO ARRAY SYMBOLS:
00190 REM        R, B - N*N ARRAYS
00200 REM        Q - AN N-VALUED VECTOR
00230 REM---READ DATA
00250 PRINT "NUMBER OF INDIVIDUALS N";
00260 INPUT N
00270 PRINT "TO DIVIDE DATA BY SQR(N-1) TYPE 1"
00280 PRINT "ELSE TYPE A NUMBER OTHER THAN 1";
00290 INPUT I
00295 MAT R=ZER
00300 IF I<>1 THEN 330
00310 LET P=N-1
00320 GO TO 340
00330 LET P=1
00340 FOR I=1 TO N
00350 FOR J=I+1 TO N
00360 READ #1,A
00370 LET A=A/SQR(P)
00374 LET A=A*A
00380 LET R(I,J)=A
00390 LET R(J,I)=A
00400 NEXT J,I
00405 GOSUB 1290
00410 MAT B=IDN
00411 FOR I=1 TO N
00412 Q7=Q7+R(I,I)
```

```
00413 NEXT I
00420 REM---EIGENVALUE AND VECTOR PROCEDURE
00430 LET A=0.00000001
00440 LET C=0
00450 FOR I=2 TO N
00460 FOR J=1 TO I-1
00470 LET C=C+2*(R(I,J)^2)
00480 NEXT J,I
00490 LET Y=SQR(C)
00500 LET O=(A/N)*Y
00510 LET T=Y
00520 LET D=0
00530 LET T=T/N
00540 FOR Q=2 TO N
00550 FOR P=1 TO Q-1
00560 IF ABS(R(P,Q))< T THEN 870
00570 LET D=1
00580 LET V=R(P,P)
00590 LET Z=R(P,Q)
00600 LET E=R(Q,Q)
00610 LET F=.5*(V-E)
00620 IF F=0 THEN 650
00630 LET G=-(SGN(F))
00640 GO TO 660
00650 LET G=-1
00660 LET G=G*Z/(SQR(Z^2+F^2))
00670 LET H=G/(SQR(2*(1+SQR(1-G^2))))
00680 LET K=SQR(1-H^2)
00690 FOR I=1 TO N
00700 IF I=P THEN 780
00710 IF I=Q THEN 780
00720 LET C=R(I,P)
00730 LET F=R(I,Q)
00740 LET R(Q,I)=C*H+F*K
00750 LET R(I,Q)=R(Q,I)
00760 LET R(P,I)=C*K-F*H
00770 LET R(I,P)=R(P,I)
00780 LET C=B(I,P)
00790 LET F=B(I,Q)
00800 LET B(I,Q)=C*H+F*K
00810 LET B(I,P)=C*K-F*H.
00820 NEXT I
00830 LET R(P,P)=V*K^2+E*H^2-2*Z*H*K
00840 LET R(Q,Q)=V*H^2+E*K^2+2*Z*H*K
00850 LET R(P,Q)=(V-E)*H*K+Z*(K^2-H^2)
00860 LET R(Q,P)=R(P,Q)
00870 NEXT P
00880 NEXT Q
00890 IF D<>1 THEN 920
00900 LET D=0
00910 GO TO 540
00920 IF T>O THEN 530
00930 FOR I=1 TO N
```

```
00940 LET Q(I)=I
00950 NEXT I
00960 LET J=0
00970 LET V1=0
00980 LET J=J+1
00990 FOR I=1 TO N-J
01000 IF R(I,I)=R(I+1,I+1) THEN 1080
01010 LET V1=1
01020 LET V2=R(I,I)
01030 LET R(I,I)=R(I+1,I+1)
01040 LET R(I+1,I+1)=V2
01050 LET P=Q(I)
01060 LET Q(I)=Q(I+1)
01070 LET Q(I+1)=P
01080 NEXT I
01090 IF V1<>0 THEN 970
01100 FOR J=1 TO N
01110 IF R(J,J)<0 THEN 1270
01120 PRINT
01130 LET K=Q(J)
01140 PRINT "ROOT"; J; "="; R(J,J)", OR"100*R(J,J)/Q7"%"
01141 Q1=Q1+R(J,J)/Q7
01142 PRINT "CUMMULATIVE %"100*Q1
01150 PRINT "COMPONENT SCORES"
01160 LET V=0
01170 FOR I=1 TO N
01180 LET V=V+B(I,K)^2
01190 NEXT I
01200 FOR I=1 TO N
01210 LET A=B(I,K)*SQR(R(J,J)/V)
01220 PRINT A;
01230 WRITE #2,A
01240 NEXT I
01250 PRINT
01260 PRINT
01270 NEXT J
01280 STOP
01290 FOR I=1 TO N
01300 FOR J=1 TO N
01310 LET B(I,1)=B(I,1)+R(I,J)
01320 LET B(J,2)=B(J,2)+R(I,J)
01330 LET A=A+R(I,J)
01340 NEXT J,I
01350 FOR I=1 TO N
01360 FOR J=1 TO N
01370 LET R(I,J)=-0.5*(R(I,J)-(B(I,1)+B(J,2)-A/N)/N)
01380 NEXT J,I
01390 RETURN
01400 END

00005 PRINT "PROGRAM NAME --- PERDIS"
00010 REM - PERTURBS AN UPPER TRIANGULAR DISTANCE MATRIX
00020 REM   BY A GIVEN %
```

```
00025 PRINT "============================================"
00030 PRINT "1 - DR,   2 - ST,   3 - OR,   4 - ER"
00040 PRINT "FILE # FOR INPUT";
00050 INPUT F
00055 F1=F+4
00060 FILES DR,ST,OR,ER,DRP,STP,ORP,ERP
00070 SCRATCH #5,6,7,8
00080 PRINT "GIVE PROPORTIONAL CHANGE (0 - 1)";
00090 INPUT C
00100 C=1+C
00110 FOR I=22 TO 1 STEP -1
00120 FOR J=1 TO I
00130 READ #F,X
00140 X=X*C
00150 WRITE #F1,X;
00160 NEXT J
00170 WRITE #F1
00180 NEXT I
00190 END


C *** PREP   20.10.78 (UPDATE 1.4.81) ***
C THIS PROGRAM PREPARES DATA FOR PROGRAM STEREO.  DATA IS READ
C FROM FILE PTS, ARRANGED AS P SETS OF N #'S (1 # PER LINE).
C OUTPUT FILES ARE PTS1, PTS2, PTS3 & INFO
      INTEGER P,N,DIM(3)
      REAL X(10,50)
C
C DIMENSIONS OF DATA FILE GIVEN & DATA READ INTO X
C
      WRITE(6,1)
1     FORMAT(' # OF DIMENSIONS')
      READ(5,2)P
2     FORMAT(I)
      WRITE(6,3)
3     FORMAT(' # OF POINTS')
      READ(5,2)N
      OPEN(UNIT=1,FILE='PTS.DAT')
      DO20I=1,P
      DO10J=1,N
      READ(1,4)X(I,J)
4     FORMAT(G)
10    CONTINUE
20    CONTINUE
      CLOSE(UNIT=1,FILE='PTS.DAT')
C
C USER CHOOSES 3 DIMENSIONS FOR THE AXES
C
      WRITE(6,5)
5     FORMAT(' SPECIFY THE 3 DIMENSIONS TO ACT AS AXES (3I2)')
      READ(5,6)DIM(1),DIM(2),DIM(3)
6     FORMAT(3I2)
C
C WRITE DATA INTO FILES
```

```
C
        OPEN(UNIT=1,FILE='PTS1.DAT')
        OPEN(UNIT=2,FILE='PTS2.DAT')
        OPEN(UNIT=3,FILE='PTS3.DAT')
        DO30J=1,N
        WRITE(1,7)X(DIM(1),J)
        WRITE(2,7)X(DIM(2),J)
        WRITE(3,7)X(DIM(3),J)
7       FORMAT(F)
30      CONTINUE
        CLOSE(UNIT=1,FILE='PTS1.DAT')
        CLOSE(UNIT=2,FILE='PTS2.DAT')
        CLOSE(UNIT=3,FILE='PTS3.DAT')
C
C CREATE INFORMATION FILE
C
        OPEN(UNIT=1,FILE='INFO.DAT')
        WRITE(1,8)N,DIM(1),DIM(2),DIM(3)
8 .     FORMAT(I3,3I2)
        CLOSE(UNIT=1,FILE='INFO.DAT')
        END


00010 PRINT "PROGRAM NAME --- SSAP"
00020 REM--- THIS PROGRAM COMPUTES A HIERARCHICAL CLASSIFICATION
00030 REM FOR N INDIVIDUALS BASED ON EUCLIDEAN DISTANCES.
00040 REM THE DISTANCES ARE READ FROM DISK FILE DIS CONTAINING
00050 REM THE UPPER HALF OF THE DISTANCE MATRIX EXCLUDING
00060 REM ZEROS IN THE PRINCIPAL DIAGONAL POSITIONS.
00065 REM OUTPUT IS USED IN DRAWING A DENDOGRAM.
00070 PRINT "================================"
00080 FILES DIS,FUSION
00085 SCRATCH #2
00090 DIM D(23,23),R(23,23),N(23),Q(23),A(23,23),X(23)
00100 DIM F(22),I1(22),I2(22)
00110 REM---EXPLANATIONS TO ARRAY SYMBOLS
00130 REM        D, R, A - N*N ARRAYS
00140 REM        N, Q, X - N-VALUED VECTORS
00150 REM        F, I1, I2 - N-1 VALUED VECTORS
00170 REM---READ DATA
00180 PRINT "NUMBER OF INDIVIDUALS N";
00190 INPUT N
00200 FOR J=1 TO N-1
00210 FOR K=J+1 TO N
00220 READ #1,A
00230 LET D(J,K)=A*A/2
00240 LET D(K,J)=A*A/2
00250 LET A(J,K)=A*A
00260 LET A(K,J)=A*A
00270 NEXT K,J
00280 REM---AT THIS POINT MATRIX D CONTAINS THE WITHIN GROUP
00290 REM    SUM OF SQUARES FOR ALL POTENTIAL FUSIONS
00300 LET D=0
00310 MAT N=CON
```

```
00320 MAT R=ZER
00330 MAT Q=ZER
00340 FOR I=1 TO N
00350 LET R(I,1)=I
00360 NEXT I
00370 REM---SEARCH FOR VALID FUSIONS
00380 LET D=D+1
00390 LET Q=10^10
00400 FOR J=1 TO N-1
00410 IF R(J,1)=0 THEN 500
00420 FOR K=J+1 TO N
00430 IF R(K,1)=0 THEN 490
00440 LET W=D(J,K)-Q(J)-Q(K)
00450 IF W)=Q THEN 490
00460 LET Q=W
00470 LET L=J
00480 LET M=K
00490 NEXT K
00500 NEXT J
00510 LET C=0
00520 FOR I=N(L)+1 TO N(L)+N(M)
00530 LET C=C+1
00540 LET R(L,I)=R(M,C)
00550 LET R(M,C)=0
00560 NEXT I
00570 PRINT
00580 PRINT "   CLUSTERING PASS"D
00590 LET N(L)=N(L)+N(M)
00600 LET N(M)=0
00610 LET Q(L)=D(L,M)
00620 LET Q(M)=0
00630 FOR I=1 TO N
00640 LET D(M,I)=0
00650 LET D(I,M)=0
00660 NEXT I
00661 LET F(D)=Q(L)
00662 LET I1(D)=L
00663 LET I2(D)=M
00670 PRINT "GROUPS IN FUSION("L"+"M")"
00680 PRINT "NUMBER OF INDIVIDUALS IN GROUP"N(L)
00690 PRINT "SUM OF SQUARES"Q(L)
00700 PRINT "INDIVIDUALS:"
00710 FOR J=1 TO N(L)
00720 PRINT R(L,J);
00730 NEXT J
00735 PRINT
00740 REM---GENERATE NEW D MATRIX
00750 FOR I=1 TO N
00760 LET S=0
00770 IF R(I,1)=0 THEN 940
00780 IF I=L THEN 940
00790 FOR J=1 TO N(I)
00800 LET X(J)=R(I,J)
```

```
00810 NEXT J
00820 FOR H=1 TO N(L)
00830 LET J=J+1
00840 LET X(J)=R(L,H)
00850 NEXT H
00860 FOR J=1 TO N(I)+N(L)-1
00870 LET A=X(J)
00880 FOR H=J+1 TO N(I)+N(L)
00890 LET B=X(H)
00900 LET S=S+A(A,B)
00910 NEXT H,J
00920 LET D(I,L)=S/(N(I)+N(L))
00930 LET D(L,I)=D(I,L)
00940 NEXT I
00950 IF D=N-1 THEN 970
00960 GO TO 380
00970 WRITE #2,N-1,N
00980 FOR I=1 TO N-1
00990 WRITE #2,F(I),I1(I),I2(I)
01000 NEXT I
01010 FOR I=1 TO N
01020 WRITE #2,R(I1(N-1),I)
01030 NEXT I
01040 END


C *** STEREP    2.6.81 ***
C COMPUTES STEREO COORDINATES FOR DATA FROM PROGRAM PREP.  THE
C DATA IS FOUND IN FILES PTS1, PTS2, PTS3 & INFO.  OUTPUT IS TO
C FILES STC, BOX & INFON WHICH ARE USED IN PROGRAM HPSTPL
      COMMON/AREA1/X,TDISP,TMAX,TMIN/AREA2/Z
      INTEGER N,DIM(3),AXIS(3)
      REAL X(3,50),TDISP(3),TMAX(3),TMIN(3),MAX(3),MIN(3)
      REAL MAXD,SIDEA,SIDEB,SIDEC,R(8),S(8),T(8),M1(50),M2(50)
      REAL N1(50),N2(50),P1(8),P2(8),Q1(8),Q2(8),DISP(3),X1(50)
      REAL X2(50),Y(50),Z(50),L1,L2,R1,R2,H
C
C READS INFO
C
      OPEN(UNIT=1,FILE='INFO.DAT')
      READ(1,1)N,DIM(1),DIM(2),DIM(3)
1     FORMAT(I3,3I2)
      CLOSE(UNIT=1,FILE='INFO.DAT')
C
C POINTS DATA READ INTO X
C
      OPEN(UNIT=1,FILE='PTS1.DAT')
      OPEN(UNIT=2,FILE='PTS2.DAT')
      OPEN(UNIT=3,FILE='PTS3.DAT')
      DO10J=1,N
      READ(1,2)X(1,J)
      READ(2,2)X(2,J)
      READ(3,2)X(3,J)
2     FORMAT(F)
```

```
10      CONTINUE
        CLOSE(UNIT=1,FILE='PTS1.DAT')
        CLOSE(UNIT=2,FILE='PTS2.DAT')
        CLOSE(UNIT=3,FILE='PTS3.DAT')
C
C MAX & MIN GIVEN FOR THE 3 ROW VECTORS IN X
C
        WRITE(6,23)
23      FORMAT(' GIVE MAX & MIN FOR THE 3 AXES & BE CONSISTENT (2F
        DO120I=1,3
        WRITE(6,24)I
24      FORMAT(' AXIS ',I1)
        READ(5,25)TMAX(I),TMIN(I)
25      FORMAT(2F)
        TDISP(I)=TMAX(I)-TMIN(I)
120     CONTINUE
C
C USER CHOOSES ORDER OF DIMENSIONS
C
        WRITE(6,3)
3       FORMAT(' DIMENSION DISPERSION    MAX        MIN')
        DO20I=1,3
        WRITE(6,4)I,TDISP(I),TMAX(I),TMIN(I)
4       FORMAT(6X,I1,4X,F9.5,2X,F9.5,1X,F9.5)
20      CONTINUE
        WRITE(6,5)
5       FORMAT(' PERMUTE THE DIMENSIONS BY TYPING THE #
       *S 1,2,3 IN SOME ORDER')
        READ(5,6)AXIS(1),AXIS(2),AXIS(3)
6       FORMAT(3I1)
        DO40I=1,3
        DISP(I)=TDISP(AXIS(I))
        MAX(I)=TMAX(AXIS(I))
        MIN(I)=TMIN(AXIS(I))
40      CONTINUE
C
C USER HAS THE OPTION FOR CHOOSING THE VIEWING COORDINATES
C
        L1=1.287
        L2=L1
        R1=2.112
        R2=L1
        H=9.9
        WRITE(6,9)
9       FORMAT(' THE STANDARD VIEWING COORDINATES ARE:')
        WRITE(6,7)
7       FORMAT(3X,'L1',3X,'L2',3X,'R1',3X,'R2',3X,'H')
        WRITE(6,8)L1,L2,R1,R2,H
8       FORMAT(4(2X,F5.3),2X,F3.1)
        WRITE(6,11)
11      FORMAT(' DO YOU WISH TO USE OTHER COORDINATES?')
        READ(5,12)OPT
12      FORMAT(A3)
```

```
        IF(OPT.NE.3HYES)GOTO50
        WRITE(6,13)
13      FORMAT(' L1')
        READ(5,2)L1
        WRITE(6,14)
14      FORMAT(' L2')
        READ(5,2)L2
        WRITE(6,15)
15      FORMAT(' R1')
        READ(5,2)R1
        WRITE(6,16)
16      FORMAT(' R2')
        READ(5,2)R2
        WRITE(6,17)
17      FORMAT(' H')
        READ(5,2)H
C
C FILE INFON CREATED
C
50      OPEN(UNIT=1,FILE='INFON.DAT')
        WRITE(1,1)N,DIM(AXIS(1)),DIM(AXIS(2)),DIM(AXIS(3))
        CLOSE(UNIT=1,FILE='INFON.DAT')
C
C REFERENCE BOX IS DIMENSIONED
C
        MAXD=DISP(1)
        IF(DISP(2).GT.MAXD)MAXD=DISP(2)
        IF(DISP(3).GT.MAXD)MAXD=DISP(3)
        SIDEA=3.3*DISP(1)/MAXD
        SIDEB=3.3*DISP(2)/MAXD
        SIDEC=3.3*DISP(3)/MAXD
C
C TRANSLATE DATA INTO REFERENCE BOX WITH DIMENSIONS
C SIDEA*SIDEB*SIDEC
C
        DO60J=1,N
        X1(J)=SIDEA*(X(AXIS(1),J)-MIN(1))/DISP(1)
        X2(J)=SIDEB*(X(AXIS(2),J)-MIN(2))/DISP(2)
        Y(J)=SIDEC*(X(AXIS(3),J)-MIN(3))/DISP(3)
60      CONTINUE
C
C PROJECTS IMAGES INTO THE PLANE (X1,X2)
C (M1,M2) ARE POINTS SIGHTED FROM (L1,L2,H)
C (N1,N2) ARE POINTS SIGHTED FROM (R1,R2,H)
C
        DO70J=1,N
        M1(J)=(H*X1(J)-L1*Y(J))/(H-Y(J))
        M2(J)=(H*X2(J)-L2*Y(J))/(H-Y(J))
        N1(J)=(H*X1(J)-R1*Y(J))/(H-Y(J))
        N2(J)=(H*X2(J)-R2*Y(J))/(H-Y(J))
70      CONTINUE
C
C PRINTS STEREO COORDINATES FOR THE DATA
```

```
           WRITE(6,18)
18         FORMAT(6X,'LEFT IMAGE',6X,'RIGHT IMAGE')
           WRITE(6,19)
19         FORMAT(7X,'X1',5X,'X2',7X,'X1',5X,'X2')
           DO80J=1,N
           WRITE(6,21)J,M1(J),M2(J),N1(J),N2(J)
21         FORMAT(1X,I3,2(1X,F6.3),2X,2(1X,F6.3))
80         CONTINUE
C
C WRITE STEREO COORDINATES INTO STC
C
           OPEN(UNIT=1,FILE='STC.DAT')
           DO90J=1,N
           WRITE(1,22)M1(J),M2(J),N1(J),N2(J)
22         FORMAT(4F)
90         CONTINUE
           CLOSE(UNIT=1,FILE='STC.DAT')
C
C COMPUTE STEREO COORDINATES FOR THE REFERENCE BOX.  THE
C REFERNCE BOX IS MADE TALLER THAN THE DATA SET TO FACILITATE
C VIEWING
C
           R(2)=SIDEA
           R(3)=SIDEA
           R(6)=SIDEA
           R(7)=SIDEA
           R(1)=0.
           R(4)=0.
           R(5)=0.
           R(8)=0.
           S(3)=SIDEB
           S(4)=SIDEB
           S(7)=SIDEB
           S(8)=SIDEB
           S(1)=0.
           S(2)=0.
           S(5)=0.
           S(6)=0.
           T(5)=1.1*SIDEC
           T(6)=T(5)
           T(7)=T(5)
           T(8)=T(5)
           T(1)=0.
           T(2)=0.
           T(3)=0.
           T(4)=0.
           DO100I=1,8
           P1(I)=(H*R(I)-L1*T(I))/(H-T(I))
           P2(I)=(H*S(I)-L2*T(I))/(H-T(I))
           Q1(I)=(H*R(I)-R1*T(I))/(H-T(I))
           Q2(I)=(H*S(I)-R2*T(I))/(H-T(I))
100        CONTINUE
```

```
      C
      C WRITE BOX COORDINATES INTO BOX
      C
          OPEN(UNIT=1,FILE='BOX.DAT')
          DO110I=1,8
          WRITE(1,22)P1(I),P2(I),Q1(I),Q2(I)
      110  CONTINUE
          CLOSE(UNIT=1,FILE='BOX.DAT')
          END

      00005 PRINT "PROGRAM NAME --- TRANS2"
      00010 REM - PREPARES COMPONENT SCORES FROM FILE COMS, FOR
      00020 REM   SCATTER OR STEREO ANALYSIS.  USER HAS THE OPTION
      00030 REM   OF CHANGING THE ORIENTATION ON ANY COMPONENT AXIS
      00035 PRINT "=============================="
      00040 FILES COMS,PTS
      00050 SCRATCH #2
      00070 PRINT "# OF INDIVIDUALS N";
      00080 INPUT N
      00090 PRINT "# OF AXES";
      00100 INPUT P
      00110 PRINT "TYPE 1 TO SAVE ORIENTATION; -1 TO REVERSE IT."
      00120 PRINT
      00130 FOR I=1 TO P
      00140 PRINT "ORIENTATION OF AXIS"I;
      00150 INPUT S
      00160 FOR J=1 TO N
      00170 READ #1,X
      00180 WRITE #2,S*X
      00190 NEXT J,I
      00200 END
```

REFERENCES

Allen, T.F.H. & T.B. Starr. 1982. Hierarchy: perspectives for ecological complexity. Univ. Chicago Press, Chicago, 310 p.

Austin, M.P. 1976. Performance of four ordination techniques assuming three different non-linear species response models. Vegetatio 33: 43-49.

Austin, M.P. 1977. Use of ordination and other multivariate descriptive methods to study succession. Vegetatio 35: 165-175.

Austin, M.P. 1979. Current approaches to the non-linear problem in vegetation analysis. In: G.B. Patil & M.L. Rosenzweig (eds.). Contemporary quantitative ecology and related ecometrics, pp. 197-210. ICPH, Fairland, Maryland, 695 p.

Austin, M.P. 1980. Searching for a model for use in vegetation analysis. Vegetatio 42: 11-21.

Barbour, M.G., Burk, J.H. & W.D. Pitts. 1980. Terrestrial plant ecology. The Benjamin/Cummings Publishing Co. Inc., 604 p.

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

Black, R.A. & L.C. Bliss. 1980. Reproductive ecology of *Picea mariana* (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. Ecol. Monogr. 50: 331-354.

Bledsoe, L.J. & G.W. van Dyne. 1971. A compartment model of secondary succession. *In:* B.C. Patten (ed.). Systems analysis and simulation in ecology. vol. I, pp. 479-511. Academic Press, New York, 607 p.

Bliss, L.C., Courtin, G.M., Pattie, D.L., Riewe, R.R., Whitfield, D.W.A. & P. Widden. 1973. Arctic tundra ecosystems. Ann. Rev. Ecol. Syst. 4: 359-399.

Botkin, D.B. 1976. The role of species interactions in the response of a forest ecosystem to environmental perturbation. *In:* B.C. Patten (ed.). Systems analysis and simulation in ecology. vol. IV, pp. 147-171. Academic Press, New York, 593 p.

Botkin, D.B., Janek, J.F. & J.R. Wallis. 1972a. Rationale, limitations, and assumptions of a northeastern forest growth simulator. IBM J. Res. Develop. 16: 101-116.

Botkin, D.B., Janek, J.F. & J.R. Wallis. 1972b. Some ecological consequences of a computer model of forest growth. J. Ecol. 60: 849-872.

Bowles, J.M. 1980. Effects of human disturbance on the sand dunes at Pinery Provincial Park. Ph.D. thesis, University of Western Ontario, London, Canada, 191 p.

Bowles, J.M. & M.A. Maun. 1982. A study of the effects of trampling on the vegetation of Lake Huron sand dunes at Pinery Provincial Park. Biol. Conserv. 24: 273-283.

Brambilla, C. & G. Salzano. 1981. A non-metric multidimensional scaling method for non-linear dimension reduction. Istituto per le Applicazioni del Calcolo "Mauro Picone". Quaderni, Serie III - N. 121, 35 p.

Braun-Blanquet, J. 1932. Plant sociology, the study of plant communities. Trans. by G.D. Fuller & H.S. Conard. McGraw Hill, New York, 439 p.

Bray, J.R. & J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325-349.

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

Cajander, A.K. & Y. Ilvessalo. 1921. Über Waldtypen. II. Acta for. fenn. 20: 1-77.

Carleton, T.J. & P.F. Maycock. 1978. Dynamics of the boreal forest south of James Bay. Can. J. Bot. 56: 1157-1173.

Caswell, H. 1976. The validation problem. In: B.C. Patten (ed.). Systems analysis and simulation in ecology. vol. IV, pp. 313-325. Academic Press, New York, 593 p.

Clements, F.E. 1916. Plant succession, an analysis of the development of vegetation. Carnegie Inst. Wash. Pub. No. 242, 512 p.

Clements, F.E. 1936. Nature and structure of the climax. J. Ecol. 24: 252-284.

Conard, H.S. 1951. The background of plant ecology. A translation from the German "The Plant Life of the Danube Basin" by A. Kerner (1863). Iowa State College Press, Ames, Iowa, 238 p.

Cooper, W.S. 1913. The climax forest of Isle Royal, Lake Superior, and its development. Bot Gaz. 55: 1-44, 115-140, 189-235.

Cooper, W.S. 1916. Plant succession in the Mount Robson region, British Columbia. Plant World 19: 211-233.

Cooper, W.S. 1923. The recent ecological history of Glacial Bay, Alaska. Ecology 4: 93-128, 223-246, 355-365.

Cooper, W.S. 1926a. Vegetational development upon alluvial fans in the vicinity of Palo Alto, California. Ecology 7: 1-30.

Cooper, W.S. 1926b. The fundamentals of vegetation change. Ecology 7: 391-413.

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

Cowles, H.C. 1901. The physiographic ecology of Chicago and vicinity. Bot. Gaz. 31: 73-108, 145-182.

Crum, H.A., Steere, W.C. & L.E. Anderson. 1973. A new list of mosses of North America north of Mexico. The Bryologist 76: 85-130.

Curtis, J.T. 1955. A prairie continuum in Wisconsin. Ecology 36: 558-566.

Curtis, J.T. 1959. The vegetation of Wisconsin: an ordination of plant communities. Univ. Wisc. Press, Madison, Wisc., 657 p.

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

Dale, M.B. 1970. Systems analysis and ecology. Ecology 51: 2-18.

Dayananda, P.W.A. 1977. Stochastic models for forest fires. Ecol. Modelling 3: 309-313.

Elton, C.S. 1924. Periodic fluctuations in the number of animals: their causes and effects. British Journal of Experimental Biology 2: 119-163.

Emanuel, W.R., Shugart, H.H. & D.C. West. 1978. Spectral analysis and forest dynamics: the effects of perturbations on long-term dynamics. *In*: H.H. Shugart (ed.). Time series and ecological processes, pp. 193-207. Proceedings of a SIMS conference, SIAM, Philadelphia.

Emanuel, W.R., West, D.C. & H.H. Shugart. 1978. Spectral analysis of forest model time series. Ecol. Modelling 4: 313-326.

Fasham, M.J.R. 1977. A comparison of nonmetric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines, and coenoplanes. Ecology 58: 551-561.

Feoli, E. & L. Feoli Chiapella. 1980. Evaluation of ordination methods through simulated coenoclines; some comments. Vegetatio 42: 35-41.

Feoli, E., Lagonegro, M. & L. Orlóci. 1984. Information analysis of vegetation data. Junk, The Hague, 143 p.

Feoli, E. & L. Orlóci. 1979. Analysis of concentration and detection of underlying factors in structured tables. Vegetatio 40: 49-54.

Fewster, P. & L. Orlóci. 1978. Stereograms to aid group recognition and trend identification in vegetation data. Can. J. Bot. 56: 162-165.

Foothills. 1978. Terrain evaluation data maps (YK-04-0200-D series). Explanation of data categories. Foothills Ltd., 7 p.

Forsythe, W.L. & O.L. Loucks. 1972. A transformation for species response to habitat factors. Ecology 53: 1112-1119.

Fowells, H.A. (ed.). 1965: Silvics of forest trees of the United States. USDA, Agriculture Handbook #271, Washington, D.C., 762 p.

Frenkiel, F.N. & D.W. Goodall (eds.). 1978. Simulation modelling of environmental problems. SCOPE report 9. John Wiley & Sons, Chichester; 112 p.

Freund, R.J. & P.D. Minton. 1979. Regression methods: a tool for data analysis. M. Dekker, Inc., New York, 261 p.

Gauch, H.G. 1973. The relationship between sample similarity and ecological distance. Ecology 54: 613-622.

Gauch, H.G., Chase G.B. & R.H. Whittaker. 1974. Ordination of vegetation samples by Gaussian species distribution. Ecology 55: 1382-1390.

Gauch, H.G. & R.H. Whittaker. 1972. Comparison of ordination techniques. Ecology 53: 868-875.

Gause, G.F. 1934. The struggle for existence. (Reprint, 1964). Hafner, New York, 163 p.

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

Gleason, H.A. 1939. The individualistic concept of the plant association. Am. Midl. Nat. 21: 92-110.

Gold, H.J. 1977. Mathematical modeling of biological systems: an introductory guidebook. John Wiley & Sons, New York, 357 p.

Goodall, D.W. 1954. Objective methods for the classification of vegetation. III. An essay in the use of factor analysis. Aust. J. Bot. 2: 304-324.

Goodall, D.W. 1967. Computer simulation of changes in vegetation subject to grazing. J. Indian Bot. Soc. 46: 356-362.

Goodall, D.W. 1970. Simulating the grazing situation. In: F. Heinmets (ed.). Concepts and models of biomathematics: simulation techniques and methods. vol. 1, pp. 211-238. Marcel Dekker, New York.

Goodall, D.W. 1972. Building and testing ecosystem models. *In*: J.N.R. Jeffers (ed.). Symposium of British ecological society on mathematical models in ecology, pp. 173-194. Grange-over-sands, March 1971.

Goodall, D.W. 1974a. Problems of scale and detail in ecological modelling. J. Environ. Manage. 2: 149-157.

Goodall, D.W. 1974b. The hierarchical approach to model building. From the proceedings of the first international congress of ecology, pp. 244-249. US/ IBP Desert Biome Programme. The Hague.

Goodall, D.W. 1975. Ecosystem modelling in the desert biome. *In*: B.C. Patten (ed.). Systems analysis and simulation in ecology. vol. III, pp. 73-94. Academic Press, New York, 601 p.

Gower, J.C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika 53: 325-338.

Greig-Smith, P. 1964. Quantitative plant ecology, 2nd ed. Butterworths, London, 256 p.

Greig-Smith, P. 1971. Analysis of vegetation data: the user viewpoint. *In*: G.P. Patil, E.C. Pielou & W.E. Waters (eds.). Statistical ecology. vol. 3, pp. 149-166. Penn. State Univ. Press, University Park, Penn., 462 p.

Greig-Smith, P., Austin, M.P. & T.C. Whitmore. 1967. The application of quantitative methods to vegetation survey. I. Association-analysis and principal component ordination of rain forest. J. Ecol. 55: 483-503.

Groenewoud, H. van. 1965. Ordination and classification of Swiss and Canadian coniferous forests by various biometric and other methods. Ber. Geobot. Inst. ETH Stiftg. Rübel, Zürich 36: 28-102.

Gutierrez, L.T. & W.R. Fey. 1980. Ecosystem succession. M.I.T. Press, Cambridge, Mass., 231 p.

Hale, M.E. & C.L. Culberson. 1970. A fourth checklist of the lichens of the continental United States and Canada. The Bryologist 73: 499-543.

Hansen, H.M. 1930. Studies on the vegetation of Iceland. *In*: L.K. Rosenvinge & E. Warming (eds.). The botony of Iceland. vol. III, pp. 1-186, pt. 1, no. 10. Copenhagen.

Hansen, H.M. 1932. Nørholm Hede, en formationsstatisk Vegetationsmonografi. (Engl. summ.). K. danske Vidensk. Selsk. Skr., Naturv. Math. Afd. ser. 9, 3: 99-196.

Hett, J.M. & O.L. Loucks. 1976. Age structure models of balsam fir and eastern hemlock. J. Ecol. 64: 1029-1044.

Hill, M.O. & H.G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47-58.

Hulst, R.K.J. van. 1975. Theoretical aspects of vegetation change: historical effects in ecological succession. Ph.D. thesis, University of Western Ontario, London, Canada, 229 p.

Hulst, R. van. 1978. On the dynamics of vegetation: patterns of environmental and gradient change. Vegetatio 38: 65-75.

Hultén, E. 1968. Flora of Alaska and neighbouring territories. Stanford Univ. Press. Stanford, California, 1008 p.

Ihm, P. & H. van Groenewoud. 1975. A multivariate ordering of vegetation data based on Gaussian type gradient response curves. J. Ecol. 63: 767-777.

Johnson, R. 1973. A study of some multivariate methods for the analysis of botanical data. Ph.D. thesis, Utah State University, Logan, Utah.

Johnson, R.W. & D.W. Goodall. 1980. A maximum likelihood approach to non-linear ordination. Vegetatio 41: 133-142.

Johnson, W.C. 1977. A mathematical model of forest succession and land use for the North Carolina Piedmont. Bull. Torrey Bot. Club 104: 334-346.

Johnson, W.C. & D.M. Sharpe. 1976. An analysis of forest dynamics in the northern Georgia Piedmont. Forest Sci. 22: 307-322.

Juhász-Nagy, P. & J. Podani. 1983. Information theory methods for the study of spatial processes and succession. Vegetatio 51: 129-140.

Keller, B.A. 1925-26. Die Vegetation auf den Salzböden der russischen Halbwüsten und Wüsten. Z. Bot. 18: 113-137.

Kendall, D.G. 1971. Seriation from abundance matrices. In: F.R. Hodson, D.G. Kendall & P. Tautu (eds.). Mathematics in the archaeological and historical sciences, pp. 215-252. Edinburgh Univ. Press, Edinburgh, 565 p.

Kenkel, N.C. 1984. Boreal vegetation of a lacustrine surficial sand belt, Elk
Lake, Ontario: types and environmental gradients. Ph.D. thesis, University
of Western Ontario, London, Canada.

Knight, C.B. 1965. Basic concepts of ecology. Collier-Macmillan Canada Ltd.,
Toronto, 468 p.

Kowal, N.E. 1971. A rationale for modelling dynamic ecological systems. *In*:
B.C. Patten (ed.). Systems analysis and simulation in ecology. vol. I, pp.
123-194. Academic Press, New York, 607 p.

Kruskal, J.B. 1964a. Multidimensional scaling by optimizing goodness of fit to
a nonmetric hypothesis. Psychometrika 29: 1-27.

Kruskal, J.B. 1964b. Nonmetric mutidimensional scaling: a numerical method.
Psychometrika 29: 115-129.

Lambert, J.M. & M.B. Dale. 1964. The use of statistics in phytosociology. Adv.
Ecol. Res. 2: 59-99.

Leak, W.B. 1970. Successional change in northern hardwoods predicted by birth
and death simulation. Ecology 51: 794-801.

Leslie, P.H. 1945. On the use of matrices in certain population mathematics.
Biometrika 33: 183-212..

Leslie, P.H. 1948. Some further notes on the use of matrices in population
mathematics. Biometrika 35: 213-245.

Levin, S.A. 1976. Population dynamic models in heterogeneous environments. Ann. Rev. Ecol. Syst. 7: 287-310.

Lotka, A.J. 1925. Elements of physical biology. Williams & Wilkins, Baltimore, 460 p.

Loucks, O.L. 1962. Ordinating forest communities by means of environmental scalars and phytosociological indices. Ecol. Monogr. 32: 137-166.

Maarel, E. van der. 1969. On the use of ordination models in phytosociology. Vegetatio 19: 21-46.

Major, J. 1961. On two trends in phytocoenology (Annotated translation of V.M. Ponyatovskaya, 1959). Vegetatio 10: 373-385.

Malthus, T.R. 1798. An essay on the principle of population.

McIntosh, R.P. 1967. The continuum concept of vegetation. Bot. Rev. 33: 130-187.

Nichols, G.E. 1917. The interpretation and application of certain terms and concepts in the ecological classification of plant communities. Plant World 20: 305-319, 341-353.

Nichols, G.E. 1923. A working basis for the ecological classification of plant communities. Ecology 4: 11-23, 154-179.

Nicholson, A.J. 1933. The balance of animal populations. Journal of Animal Ecology 2: 132-178.
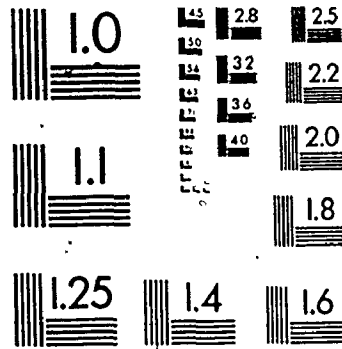
Nicholson, A.J. 1954. An outline of the dynamics of animal populations. Aust. J. Zool. 2:9-65.

Noy-Meir, I. & M.P. Austin. 1970. Principal component ordination and simulated vegetation data. Ecology. 51:551-552.

Orlóci, L. 1966. Geometric models in ecology. I. The theory and application of some ordination methods. J. Ecol. 54: 193-215.

Orlóci, L. 1978. Multivariate analysis in vegetation research, 2nd ed. Junk, The Hague, 451 p.

Orlóci, L. 1980. An algorithm for predictive ordination. Vegetatio 42:23-25.

Orlóci, L., Kenkel, N.C. & P.H. Fewster. 1984. Probing simulated vegetation data for complex trends by linear and nonlinear ordination methods. (in press).

Orlóci, L. & W. Stanek. 1979. Vegetation survey of the Alaska Highway, Yukon Territory: types and gradients. Vegetatio 41:1-56.

Oswald, E.T. & J.P. Senyk. 1977. Ecoregions of the Yukon Territory. Canada Department of the Environment, Canadian Forestry Service, Pacific Forest Research Centre, Victoria, British Columbia, 115 p.

Park, T. 1948. Experimental studies of interspecific competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. Ecol. Monogr. 18:265-307.

Pearl, R. & S.L. Parker. 1922. On the influence of density of population upon the rate of reproduction in *Drosophila*. Proc. Nat. Acad. Sci. 8: 212-219.

Pearl, R. & J.R. Reed. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc. Nat. Acad Sci. 6: 275-288.

Phillips, D.L. 1978. Polynomial ordination: field and computer simulation testing of a new method. Vegetatio 37:129-140.

Phipps, R.L. 1979. Simulation of wetlands forest vegetation dynamics. Ecol. Modelling 7:257-288.

Pogrebnjak, P.S. 1930. Über die Methodik der Standortsunter-suchungen in Verbindung mit Waldtypen. Verh. II. Intern. Kongr. forst. Versuchsanstalten 1929.

Ramensky, L.G. 1930. Zur Methodik der vergleichenden Bearbeitung und Ordnung von Pflanzenlisten und anderen Objekten, die durch mehrere, verschiedenartig wirkende Faktoren bestimmt werden. Beitr. Biol. Pft. 18: 269-304.

Rosenberg, N.J. 1974. Microclimate: the biological environment. Wiley-Interscience, New York, 315 p.

Rowe, J.S. 1959. Forest regions of Canada. Canada Department of Northern Affairs and Natural Resources, Forestry Branch. Bulletin 123, 71 p.

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quaternary Research 3:444-464.

Shepard, R.N. 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. Psychometrika 27: 125-139, 219-246.

Shimwell, D.W. 1971. The description and classification of vegetation. Univ. Wash. Press, Seattle, Wash., 322 p.

Shugart, H.H., Crow, T.R. & J.M. Hett. 1973. Forest succession models: a rationale and methodology for modelling forest succession over large regions. Forest Sci. 19:203-212.

Shugart, H.H., Emanuel, W.R., West, D.C. & D.L. DeAngelis. 1980. Environmental gradients in a simulation model of a beech-yellow poplar stand. Mathematical Biosciences 50:163-170.

Sokal, R.R. & F.J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research, 2nd ed. W.H. Freeman & Co., San Francisco, 859 p.

Sukatschew, W.N. 1932. Die Untersuchung der Waldtypen des osteuropäischen Flachlandes. Handb. biol. ArbMeth. II, 6: 191-250.

Swartzman, G. 1980. Evaluation of ecological simulation models. *In*: W.M. Getz. (ed.). Mathematical modelling in biology and ecology, pp. 230-267. Lecture notes in biomathematics, 33. Springer-Verlag, Berlin, 355 p.

Thompson, W.R. 1939. Biological control and the theories of the interactions of populations. Parasitology 31:299-388.

Viereck, L.A. 1973. Wildfire in the taiga of Alaska. Quaternary Research. 3:465-495.

Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118:558-560.

Walters, C.J., Hilborn, R. & R. Peterman. 1975. Computer simulation of barren-ground caribou dynamics. Ecol. Modelling 1:303-315.

Wangersky, P.J. 1978. Lotka-Volterra population models. Ann. Rev. Ecol. Syst. 9:189-218.

Wangersky, P.J. & W.J. Cunningham. 1956. On time lags in equations of growth. Proc. Nat. Acad. Sci. U.S. 42:699-702.

Warming, E. 1909. Oecology of plants: an introduction to the study of plant communities. Oxford Univ., 422 p.

Welsh, S.L. 1974. Anderson's flora of Alaska and adjacent parts of Canada. Brigham Young Univ. Press, Provo, Utah, 724 p.

Werger, M.J.A., Louppen, J.M.W. & J.H.M. Eppink. 1983. Species performances and vegetation boundaries along an environmental gradient. Vegetatio 52:141-150.

Westhoff, V. & E. van der Maarel. 1973. The Braun-Blanquet approach. *In*: R.H. Whittaker (ed.). Handbook of vegetation science, pp. 617-727. Junk, The Hague.

Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecol. Monogr. 23:41-78.

Whittaker, R.H. 1956. Vegetation of the great smoky mountains. Ecol. Monogr. 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. 42:207-264.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21:213-251.

Whittaker, R.H. 1975. Communities and ecosystems, 2nd ed. Macmillan, New York, 385 p.

Whittaker, R.H. & W.A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. Ecology 46: 429-452.

Wilde, S.A. 1958. Forest soils. The Ronald Press Co., New York, 537 p.

Wildi, O. 1978. Simulating the development of peat bogs. Vegetatio 37:1-17.

Williams, W.T. & M.B. Dale. 1965. Fundamental problems in numerical taxonomy. Adv. Bot. Res. 2: 35-68.

END

08·11·85

FIN