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Centre for Ecology & Hydrology  
Library Service  
Lancaster Environment Centre  
Bailrigg  
Lancaster LA1 4AP

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# GRASSLAND MANAGEMENT - MODELS AS INTEGRATORS OF DIVERSE LINES OF RESEARCH

## 1 INTRODUCTION

This report is based on a brief survey of models which have, or could, be used in studies of grassland dynamics. The emphasis of the report is on modelling the effects of management on the structure and function of grassland communities or ecosystems. However, I shall not give detailed descriptions of individual models, or attempt a review of grassland management practices. For an introduction to modelling methods see Jeffers (1982), and for reviews of the management, soil and climatic factors which influence changes in grasslands see Duffey et al (1974) and Miles (1981).

I shall restrict my discussion to 3 objectives :-

- 1) Providing a framework for relating and integrating the many projects in Programmes 3 and 4, and for defining new research objectives.
- 2) Identifying any models or modelling methodologies which could be used to integrate existing and future research efforts.
- 3) Using existing models to highlight gaps in our knowledge which could form the basis for additional research in Programme 4.

## 2 A MODEL FRAMEWORK

We should not expect too much from a model that attempts to

integrate diverse lines of research. The most effective model for any particular purpose will depend not only on objectives of the model, but also on the outlook of the people using it. End users (farmers or reserve managers) usually find empirical models easiest to handle, applied scientists prefer mechanistic models based on current ideas, and pure research scientists resort to more speculative mechanistic models (France and Thornley 1984). No single model can satisfy the diffuse objectives of all 3 groups. Realistically, all we can hope to find is a framework within which these different types of approach can be co-ordinated and directed.

Slatyer (1977) presents a useful scheme of the relationship between ecological research and management (Figure 1). Most of the current projects in Programmes 3 and 4 can be fitted into the peripheral compartments (labelled by \*) of this model. ITE's research encompasses both the data collection and management input sides of the scheme but lacks any internal model through which the information from these diverse projects can be integrated. The question is - "Are there any existing models that could be used to fill this gap, and if not, is it possible to develop a new model to do so?". To answer this we must first specify what the objectives of the model are to be or, as Slatyer (1976) puts it: "we must formulate our management aims". Secondly, we should examine the extent to which existing grassland models may fill the gap.

Objectives. The objectives of Programme 4 are: to assess the effect of various management techniques (grazing, fertilizer,

herbicides etc.), under a wide range of edaphic and climatic conditions, on the conservation, amenity and/or productive value of grassland ecosystems. To this we must add the interests of Programme 3 in the establishment and subsequent successional changes in, mainly, species-rich grassland communities on reclaimed land. GULP!

### 3 GRASSLAND MODELS

The management objectives determine the variables which are included in grassland models, and have therefore had a great influence on the kind of models that have been used in the past. Conservation has focused interest on the management of community structure and composition, and in particular, on diversity and rarity. Management for production has led to models of ecosystem function which describe biomass or energy dynamics. The management objectives for amenity grasslands are varied and often feature a combination of criteria involving both conservation and production interests. Finally, the management of successional communities involves an understanding of ecosystem stability. We may wish to speed up succession by promoting the instability of the species x environment interactions which drive succession, or create stable ecosystems by halting succession at a particular point (ie a plagio-climax).

These 3 classes of objectives (for structure, function or stability) help explain the types of model that have been used predominantly for each type of study. Management for production has led to the use of dynamic models of ecosystem function

incorporating systems of inter-related sub-systems. Management for conservation (diversity models) has led to descriptive models, sometimes based on regressions, multi-variate approaches, or graphical representations. Finally, succession models, having been confined to descriptive and conceptual approaches in the past, are only just extending into new fields of predictive modelling of multi-species mixtures.

### 3.1 Models of production

These include all models in which we are interested in the accumulation of some substance or quantity within the grassland ecosystem as a whole. Most commonly, this will be biomass (Waremburg et al, Tiwari 1982), but energy (Akiyami et al 1981) or nutrients are also frequently modelled. Models of N-cycling in grasslands have recently been reviewed by Van Veen et al (1981), Reiners (1981) and O'Connor (1983) and of sulphur cycles by Coughenour et al (1980). These models have been used to address problems such as the effects of sulphur dioxide on grasslands (Lauenroth et al 1984), and nitrate leaching in grasslands (Kurkin 1977).

Two types of model have dominated production studies, these are descriptive-regression models (static models), and simulation models of whole systems (dynamic models).

3.1.1 Descriptive models. These are static models which ignore time dependent processes. They relate production (the dependent variable) to one or more environmental or management variables (the independent variables) using the techniques of regression

analysis, including linear regression, multiple-regression and non-linear regression or curve-fitting. A good example of this is work from GRI Hurley which relates the yield of ryegrass pastures to fertilizer nitrogen and climatic variables (Morrison, Jackson and Sparrow 1980). Similar work has been done in Sweden by Kornker and Torssell (1983).

The advantages of regression models are the simplicity with which they can be derived and the ease with which they can be understood and used by others. However, these models rarely have a mechanistic basis and give little insight into system behaviour outside the range of the data on which they are based.

3.1.2 System models. These are dynamic models which explicitly contain the variable of time. They mimic the behaviour systems. The system is defined in terms of variables and mathematical expressions describing the rate of change of these variables. The models incorporate feedback by linking changes in each variable to the level of other variables in the system. They may be hierarchical (Goodall 1974), predicting behaviour at one level of organization (eg an ecosystem) in terms of processes at a lower level (eg populations). But although these models are mechanistic (or phenomonological), their resolution may be coarse (eg ecosystem models often lump all producers into one group). The resolution of the model is determined by the initial specification of the variables, these may be of 4 kinds:

- a) State variables - are measurable properties of the system needed to predict system behaviour.

- b) Driving variables - are variables not affected by

processes within the system but which do have an effect on it eg soil, climate or management inputs.

c)Output variables - are quantities the model is required to predict. These may be, but are not necessarily, the same as the state variables.

d)Rate variables - define the processes within the system and determine how the state variables change with time. They represent either conversion or transport processes and must have units of quantity per unit time (eg photosynthetic rate, decomposition rate, grazing rate).

The emphasis that dynamic models places on processes, rather than simply on relationships between variables, is their most useful contribution to research programmes. A second useful feature is that they provide a structure in which the combined effects of two or more inter-related sub-systems can be investigated. Identifying sub-systems is an important step in modelling complex systems. In agricultural systems the processes of respiration and photosynthesis are often combined to derive models of crop yield (France and Thornley 1984). Useful sub-system models have also been developed to describe the partitioning of resources between roots and shoots (Gilmanov 1977, Johnson 1985) and for decomposition (Hunt 1977).

The use of sub-system models has been central to the development of dynamic models of whole grassland ecosystems (eg Van Hook 1971, Innis 1978, 1980a, Innis et al 1978, White 1984, Hanson et al 1985). The most often cited of these was began van Dyne (1968) as part of the IBF programme in the early 70's. It was an



attempt to model the dynamics of the prairie grasslands and to predict the effects of a variety of climatic conditions and management regimes (eg grazing and fertilizer) (van Dyne et al 1978). A simplified version of their model shows the features that common to all these ecosystem models (Figure 2). They are composed of a number of inter-related sub-models in which the output variables of one sub-model provides driving variables for others. Sub-system models may describe either biotic or abiotic parts of the ecosystem. In contrast to their cropland counterparts, models of semi-natural grasslands tend to be more concerned with sub-system models of moisture and nutrient status (Hanson et al 1985).

The most common (and probably most useful) applications of dynamic systems models have been in grazing studies (Goodall 1969, 1972), Wielgolaski 1975, Innis 1980b, Seligman and Arnold 1980, Shiyomi et al 1982, Akiyama et al 1984). The emphasis of these models is usually on broad categories of producers and grazers, with primary production being related to climatic variables and grazing intensity. They frequently include spatial heterogeneity of vegetation, and can be used to simulate the effects of patchy grazing by herbivores (Hanson et al 1985). McNaughton's (1985) model of grazing in the Serengeti is a good example of the flexibility of the approach. He illustrated the importance of stochastic variations in rainfall, the influence that grazers have on the amount, rate of production and quality of food available, and on the composition and diversity of the vegetation. Although terrestrial herbivores typically consumed

<10% of annual primary production their influence on community type and stability was much greater. Rainfall use efficiency in ungrazed stands was lower than grazed stands and grazing also improved the nutrient status of plant tissues by facilitating the cycling of nutrients and preventing tissue senescence. Greater community diversity tended to stabilise productivity, more so in grazed plots because of the greater variety of growth patterns and competitive release resulting from selective grazing.

Woodmansee (1978) outlines some of the difficulties and benefits of modelling whole ecosystems. He highlights the difficulties of setting up the modelling team, of communication within the team, of parameter estimation, of representing interactions and of modelling introversion which makes it so easy to lose sight of the original objectives. Furthermore, modellers may not have the best intuitive grasp of how the system works or have access to the best information, and yet it becomes difficult for others to correct or improve things once the information is entrenched within such complex models. System level models require large amounts of data to use, but these data are often unavailable and parameters are hard to estimate (Hanson et al 1985). Stenseth (1977) is even more scathing in his criticism, suggesting that large scale simulations may be impossible to interpret due to the large number of hypothetical relations involved. May (1973) comments that some computer simulations would benefit most from the installation of an on-line incinerator!

### 3.2 Models of Diversity

Models of diversity attempt to describe or explain the species richness of communities. In these models the terms 'number of species', 'species richness' and 'diversity' can usually be used synonymously but some models specifically describe the distribution of species abundance. Three types of model have predominated : descriptive models, analytical models and conceptual models.

3.2.1 Descriptive models. Early work on community organization attempted to describe patterns of abundance within communities which in simple terms consisted of a few common species and many rare ones. Preston's (1962) log-normal distribution has been found to be the most generally appropriate description, but others such as the log-series and the broken stick distribution (MacArthur 1965) have been proposed. Attempts to relate these patterns to underlying processes such as competition have inevitably proved fruitless. Caswell (1976) has shown how neutral models, which do not include the effects of ecological interactions, can successfully reproduce patterns of species abundance. It is not possible to derive process from pattern, at best the procedure may help in generating testable hypotheses.

The species-area curve is another example of a descriptive model of diversity. The relationship between area (A) and the number of species in a community (N) is often described by  $N=cA^z$  (eg Kilburn 1966, Connor and McCoy 1979). Many attempts have been made to interpret the parameters (c and z) of this curve or to make some practical use of it as, for example, in the design of

nature reserves. The history of work on species-area relationships shows how pre-occupied ecologists can become in trying to find universal patterns and how carried away they get when they think they have (another example is the self-thinning curve of plant monocultures). The tragedy behind the species-area work is that the early formulation of island biogeographic theory was based firmly on underlying processes. MacArthur and Wilson (1967) originally explained the number of species on islands in terms of the balance between colonisation and extinction and the effects of island size and remoteness on these processes. Despite elegant demonstrations of how this theory can be tried and tested (Simberloff and Wilson 1970), most ecologists have preferred to look for an all-encompassing equation.

Some simple descriptive models describing the relationship between grassland plant diversity and standing biomass and nutrient enrichment have proved useful. Al Mufti et al (1977) showed that peak species-density occurred in a range of 350-750 g<sup>-2</sup> m<sup>2</sup> in the sum of maximum standing crop and litter. Klinkhamer and de Jong (1985) found a peak at 300 g m<sup>-2</sup> (shoot biomass only) in coastal dunes. However this peak was not found in stands of woodland herbs (Oh and Kang 1983). Nutrient enrichment (particularly with nitrogen) usually decreases species richness (Green 1971), but in nutrient deficient habitats fertilizers may increase the number of safe sites and increase richness (Miles 1973). Green (1971) suggests that a greater knowledge of nutrient budgets is fundamental to the scientific management of

communities.

Faunal diversity is usually related directly to the vegetation, although it is not necessarily positively correlated with plant diversity. Diversity of decomposers is most closely related to structural diversity and resource levels within the soil and effects of area and isolation may also limit species richness. The diversity of grassland bird communities has been related to a habitat index derived from vegetation height and its standard deviation (Cody 1968).

3.3.2 Analytical models. These are dynamic models in which mathematical equations describing population dynamics are solved analytically (compare this with simulation models which use computer simulations to achieve the same end). The approach has been championed by May (1972) who contradicted existing ecological theory by showing that in randomly connected food webs, complexity begets instability, not stability. He showed that community stability decreased with increases in: the number of species, the strength of interactions between species and the connectance of the system (connectance is the proportion of non-zero interactions between the species in the community). Hence community stability may be associated with critical values for connectance (Rejmanek and Stary 1979, Yodzis 1980) or with the division of the community into a series of loosely coupled sub-units, sub-systems or compartments (Lawton and Pimm 1978). These ideas have been generated from simple models of species interactions (usually Lotka-Volterra models) whose mathematical

tractibility is sufficient to enable conclusions about the local stability of the system around equilibrium values to be determined. However, the intrinsic assumptions of these models may be ecologically unsound (Lawlor 1978). In addition, it can be difficult to find suitable field data to test the conclusions (Pimm and Lawton 1980).

Two developments may make it easier to apply analytical methods to grassland studies. First, Mobley (1973) has described a method of estimating the parameters of Lotka-Volterra models from multi-species data. Second, Schulz and Slobodchikoff (1983) have developed a simple computer program which evaluates the stability of an n-species community, thus reducing the need for mathematical expertise. Even so, analytical methods are probably only of limited value to grassland community studies because of the non-equilibrium nature of grasslands. Most current ideas about the factors controlling the diversity of grasslands stress the importance of disturbance, and fluctuations in recruitment. These processes are not easily modelled analytically, and our understanding of them is mainly at a conceptual level.

3.2.3 Conceptual models We now have a good understanding of the processes which affect plant diversity in grasslands. Grubb (1977) emphasised the importance of re-generation from seed in maintaining diversity, a process which is enhanced by moderate levels of disturbance (Pickett 1980, Denslow 1980, Miller 1982). Maximum diversity may depend on the interaction between different types of disturbance such as grazing and wallowing

(Collins and Barber 1985). Diversity may be reduced by extreme levels of disturbance which eliminate whole populations, but the loss of species is mainly due to competitive exclusion (Newmann 1973, Grime 1973). Competitive exclusion is enhanced by nutrient enrichment (Bakelar and Odum 1978), and coexistence is favoured by grazing and cutting, spatial heterogeneity (Fitter 1982), by different resource use patterns (Tilman 1985) and by temporal fluctuations which favour different species (Vasilevich 1979, Warner and Chesson, Reader 1985, Janzen 1986). These basic ideas have been combined into more complex conceptual models of diversity (eg Huston 1979) which have been reviewed by During and Williams (1984). Individual scientists will take their pick as to which model is the most appropriate for their own use, often they derive their own. My own version, which I have used to interpret the short term and long term effects of growth retardants on roadside vegetation, is shown in Figure 3.

All these conceptual models rely on our intuitive understanding of the processes and factors they employ, many of which cannot be reasonably defined in words let alone in a mathematical or measurable way. Terms such as 'favourability', 'stress', 'disturbance', 'successional stage' and even 'competition' are used in vague ways. This leads to confusion and pointless semantic arguments. Consequently, these models rarely give the conservationist or vegetation manager detailed advice for the solution of concrete problems. Nevertheless, they do have great value in yielding general insight (Fenchel 1978) and are a prerequisite to the development of more complex quantitative models

### 3.3 Models of succession

Succession is the process of ecosystem change following disturbance. Successional change is directional. It is usually described in terms of overall changes in species composition or as changes in community or ecosystem characteristics such as diversity, productivity and stability. Lewis (1978) proposes a useful measure of the rate of succession (the summed change in the abundance of all species, independent of sign) which can be related to environmental and management factors.

Models of succession are still in their infancy. A few conceptual models have been derived from the many descriptive studies of succession, but only recently have mechanistic or predictive models been developed. Our conceptual models have been derived mainly from the opposing ideas of Clements (1916) and Gleason (1926).

Clements (1916) viewed succession as an orderly process of species replacement culminating in a stable, climax ecosystem. Successions were regarded as predictable changes in community structure and function which emerged from the interaction between species and their environment. This is the 'organismic' theory of succession.

Gleason (1926) noted the wide variety of successional sequences and viewed succession in less orderly and predictable terms. He interpreted it in terms of the characteristics of the component species; the 'individualistic' view of succession. Egler (1954) developed Gleason's ideas by showing that the initial species composition of a pioneer community could



influence subsequent successional changes. Frank (1968) also sounded a note of caution by suggesting that the apparent stability of climax communities may be an artifact of the longevity of certain major components. Despite these ideas, only slowly did ecologists begin to interpret succession in terms of life history characteristics and strategies. It was not until the 70's that Connell and Slatyer (1977) proposed some general models of succession which incorporated this view. They proposed 3 inter-related models (Figure 4) describing the possible mechanisms of succession following a large scale disturbance: a "facilitation" model in which the entry of late species depends on earlier species preparing the ground; a "tolerance" model with a predictable sequence of species adopting different strategies for exploiting resources; and an "inhibition" model in which all species resist invasions by competitors. Other workers have developed similar ideas (Peet and Christiansen 1980, Londo 1980, Peet 1981, Noble 1981). The link between these models is their emphasis on the life history characteristics of component species and the way in which these influence the outcome of interactions between species and between species and their environment. Freedman and Rosenberg (1984) have adapted the models of Connell and Slatyer and applied them to the problems of environmental management. They suggest a management model with 5 steps: designed disturbance, selective colonization, inhibitory persistence, removal and regeneration. Through these processes successional sequences and rates can be regulated to develop biotic communities that meet conservation needs. This is an

important point, Gleason's view, although it perceives a much greater complexity of successional sequences than the view of Clements, does at least offer the idea that these successions are controllable - if only we know how.

The conceptual models of Clements and Gleason have formed the basis for recent attempts to construct predictive models of succession.

### 3.3.1 Models based on Clements

Ordination and other multi-variate descriptive models have been used to describe successions in terms of observed changes in community composition (eg Austin 1977). If we accept Clements' view, these models could be used predictively, but the dangers of this approach are obvious.

Odum (1969) extended Clements' idea of ecosystem development and derived a description of succession in terms of emergent properties of ecosystems (Figure 5). A number of these have been tested in simple models eg that the ratio of photosynthetic biomass to production rate to total biomass decreases (Matsuno 1978); the tightening of nutrient cycles during succession (Finn 1982). However some of Odum's hypotheses such as the increase in diversity during succession have been disproved by observation and experiment. Grassland plant diversity frequently does not increase monotonically as succession proceeds (Grime 1979). Bakelar and Odum (1978) found that although the addition of NPK fertilizer led to lower diversity (consistent with Odum's model), the species composition did not change to a younger set

of species.

Markov models have been used to make quantitative predictions of successional change. These are matrix models which mimic successional changes by measuring the probability with which one species is replaced by another. Although these models are probabilistic (but not stochastic) they are implicitly Clementsian and predict orderly changes culminating in stable communities. They have been used quite successfully to predict changes in dominant woodland trees where replacement probabilities can be fairly reliably calculated, but they are much more difficult to apply in grasslands where plant by plant replacement is difficult to measure. The usual method for grasslands is to classify the species of a small area (eg a quadrat) into one of a number of pre-defined community types and then look at the way in which these communities inter-change. This, of course, imposes a sequence of change that is rigidly determined by the initial classification. The assumptions usually made when using Markov models have been much criticised (van Hulst 1979, 1980, Usher 1981). In particular, it is doubtful whether the future state of an ecosystem can be predicted from its present state without taking into account historical effects (Bellefleur 1981, Hobbs and Legg 1984).

Markov models are inflexible and do not easily accommodate the addition of new species or changes in management. Relating transition probabilities to growth forms, life history characteristics and competitive relationships may help overcome this limitation (Horn 1975). But in general, Markov models can

only help us to describe and interpret successions and are of limited value for predicting the effects of management on successional communities. Gibson et al (1983) found they became too cumbersome for realistic models of the successions that followed release from tortoise grazing on Aldabra Atoll.

Dynamic models of the type described in Section 3.1.2 have also been used to predict successional changes (Bledsoe and van Dyne 1971, Gutierrez and Fey 1975, 1981, Kauppi et al 1978). The models often include mechanistic features, such as the influence of humus depth, which allow a course prediction of the effect of varying management. However, the assumptions of the models (eg deterministic relationships between productivity and diversity) or their restriction to few pre-defined seral stages (eg grass, shrubs and trees) make them implicitly Clementsian.

There have been several attempts to make general statements on the relationship between life history characteristics and successional gradients (a pseudo-Gleasonian approach). The simplest of these derives from MacArthur and Wilson's (1967) concept of r and K strategists (r and K being derived from the logistic equation). R-strategists have high intrinsic growth rates, rapid powers of dispersal and suffer mainly from density independent mortality. They are characteristic of early successional stages. K-strategists are competitive species more typical of later successional stages. These ideas were later developed by Odum (1969) and Brown (1984) (figure 5). Brown (1984) also applied them to insect populations in the early

stages of grassland succession. He found that more species of heteroptera produce two or more generations per year in early succession than late succession.

Grime (1979) identified 3 plant strategies (C-S-R strategies): competitive, stress-tolerant or ruderal. He viewed succession as sequence leading from ruderal to competitive species, and finally to stress tolerant species, with the balance between the 3 types being strongly affected by potential productivity.

Generalisations on life-history characteristics provide some insight but are of little predictive value. Early successional species may be predominantly ruderals but this does not enable us to say either whether any individual ruderal species will be an early successional species or to predict the impact of a disturbance on a particular species. For instance, it was the availability of bare ground rather than the age of a field which determined the abundance of some biennials in old field successions (Gross and Werner 1982).

### 3.3.2 Models based on Gleason

The challenge of modelling succession by incorporating life history characteristics is twofold. First, to define and measure the relevant autecological information and secondly, to establish a method of predicting the outcome of interactions in complex mixtures of species in a changing environment.

Where succession is driven by allogenic changes (ie factors outside the influence of the community) species interactions may be ignored. Smith and Kadlec (1985) used life history

characteristics and seed bank data alone to predict the allogenic changes in a freshwater marsh following fire. Van der Walk (1981), also working on wetlands, adopted a similar approach by classifying species into 12 types based on 3 life history traits (life span, propagule longevity and propagule establishment). He also emphasised the need for seed bank data. Models of post-fire forest succession can also be interpreted as an allogenic process (Kessell and Fischer 1981). The key feature of these models is that from fairly simple information on the initial species composition of the community, relative growth rates and longevity they have derived simple qualitative models of succession which can be used to guide management decisions.

However, grassland dynamics are more usually driven by autogenic changes within the community, particularly competition. (Although we probably under-estimate allogenic effects, as witnessed by the marked annual variations in grassland species composition due to climatic factors, and the variable relationship between seed mixtures and the composition of the established sward). Van Hulst (1979) constructed simple multi-species population models based on the premise that successional change is caused by changes in the environment, which are in turn, at least partially, determined by the vegetation. He recognised two kinds of habitat change; that due to competition (usually an instantaneous effect) and that due to reaction (which has an historical basis and is equated with the Clementsian idea that early colonisers change the environment in a way which is detrimental to them). His models were based on logistic models

of growth (in which the parameters varied with time to simulate reaction effects) or Lotka-Volterra models of competition (Wangersky 1978). Models which included reaction were not able to account for the well used management technique of removing late successional species (eg shrubs and trees) to halt succession in the grassland or shrub stage (Niering and Goodwin 1974). Lotka-Volterra competition models ave also been used by Leps and Prach (1981) to model secondary succession in a grassland-shrub community with three components : Crataegus, Prunus and herbs. They investigated the effects of soil depth on the succession by varying the model parameters. Tilman (1985) modelled succession on the assumption of different resource use strategies but concluded that the difficulties of evaluating resource limitation in the field limited the value of the approach.

Some interesting features of Lotka-Volterra competition models may be particularly relevant to grassland management. First, the outcome of competition between two species frequently depends on the initial conditions. It is not necessarily the strongest competitor which survives (Dostalkova 1984). For example, in grasslands, succession may be halted if shrub establishment is inhibited by a dense layer of grass. Secondly, in multi-species mixtures the possibility exists of 'mutualistic' effects between species which do not interact directly (Lawlor 1979). It may be possible that species A (which produces a thick thatch which reduces diversity for example) will be displaced by species B (a tufted grass species with which more species can co-exist). In this case the indirect effect of the dominant species B will b

to increase diversity.

The ease with which competition models can be adapted to describe successions is encouraging, but by describing change in terms of a single variable (usually density or biomass) and making simple assumptions on the nature of the competitive process (the law of mass action) they may not be appropriate for all species within a grassland. The model assumptions are most closely fitted by homogenous communities near equilibrium, in which populations have a stable age distribution. Most grasslands do not satisfy these conditions, indeed it is probably the non-equilibrium nature of grasslands caused by disturbance and temporal variability that accounts for the species richness of many grasslands (Huston 1979). In these situations a model must be able to include re-generation from seed and include aspects of plant phenology. Successional models based on the growth of individual plants have been developed for trees in forests (Shugart and Noble 1981) and for dwarf shrubs in heathlands (Van Tongeren and Prentice 1986), but these will be difficult to adapt to grasslands, which are more diverse and in which individual plants are often not easily identified. An alternative method may be to use Leslie matrices to describe age or size dependent patterns of survivorship and natality (Appendix 1). Malanson (1984) has shown how these matrices may be linked to environmental features, such as total foliar cover, to simulate succession.

### 3.3.3 Models of faunal succession



With few exceptions succession has been interpreted and modelled solely in terms of plant communities. Models of animal successions have been restricted to Markov models of decomposition (Usher and Parr 1978) or of colonisation and competition in communities of sessile marine animals (Wolosz 1982). In terrestrial (autotrophic) successions changes in fauna are almost inevitably seen as a secondary effect of changes in vegetation, eg the succession of birds described by Darveau et al (1982). With the exception of the ecosystem models of grazing systems (which concentrate on ecosystem parameters rather than species composition) the direct influence of fauna on successional change has been much neglected in models, although there are many examples that show the effects of fauna on plant populations. Grazing by rabbits (Thomas 1960), geese (Joenje 1985) or large herbivores (McNaughton 1985) can deflect or halt successions. The effects of invertebrates may be equally pronounced (McBrien et al 1983, Brown 1984). However, invertebrate effects may be less obvious because smaller grazers have little effect on gross phisognomy and life forms, but often act to reduce re-generation from seed and reduce population densities by seedling grazing (Miles 1981, Reader 1985). The effect that grasshoppers have on seedling survival in disturbed patches can depend on the scale of the disturbance (Whelan and Main 1974). Large patches are not recolonised by grasshoppers for 1-2 years and are less affected by grazing than small patches.

GRASSLAND MODELS: RECOMMENDATIONS

In this section I shall indicate how the methods described above might be used in ITE's vegetation management programme and suggest some areas to which we should pay special attention.

#### 4.1 Systems models

Published grassland biome models are usually well documented and could easily and profitably be used as a framework for modelling individual grassland ecosystems in the UK. However, models of this complexity frequently contain mistakes (Rexstad and Innis 1985) and must be used with caution. A new set of model parameters would have to be estimated, but this procedure would reveal areas in which we lack information. To avoid becoming esoteric such an exercise would have to be linked to a definite objective. Grazing studies are particularly appropriate because a model could provide a realistic means of simulating the effects of grazing pressures which are difficult to achieve experimentally. There are precedents for adapting systems models in this way. The model described by Innis et al (1978) has been adapted for tropical grasslands (Parton and Singh 1984) and for annual grasslands in California (Pendleton et al 1983). In both cases no structural change in the model was necessary, just the estimation of new parameters. The models have also been adapted to assess the impacts of specific invertebrate pest species such as lepidoptera larvae (Capinera et al 1983). Grant and French (1980) used a simulation model to show that the main effects of small mammals on a grassland ecosystem were due to disturbance (bringing soil to the surface and redistributing N) and on consumption of arthropods, they had little effect on primary

production.

The major limitation of the existing systems models of grasslands is their emphasis on gross aspects of ecosystem structure and function, they do not incorporate population processes and cannot be used to investigate effects on community diversity. In addition, information on species composition may be needed to predict adequately the gross response of an ecosystem to management. For instance, the effects of nutrients on productivity depends on the species composition; species characteristic of species rich sites are inherently more responsive (Chapin, Vitousek and van Cleve 1986). The value of considering population processes in grazing studies has been discussed by Jones and Mott (1980), while Reiners (1986) has emphasised the pressing need for such a model to complement existing ecosystem models based on either energy or nutrients. We must also anticipate the need for more detailed management advice on species composition (eg in reserve management or amenity and even low input pastures) which cannot be achieved with existing ecosystem models. There is no theoretical reason why ecosystem models could not be expanded to include all species individually. But the framework of these models is not conducive to including population dynamics. In the following section (4.3) I suggest an alternative approach.

A further difficulty with complex systems models is that they can easily become very site specific. This, combined with their complexity (not only in terms of the number of variables they use but also in the complexity of the processes they model) makes

them difficult for ecologists to relate to and interpret. In addition, their value as a means of co-ordinating multi-disciplinary research in Programme 4 is reduced because the main specialisation of the scientists in the Programme is quite narrow. However, we should be aware of the considerable information and expertise that has gone into these models and be prepared to make generous use of sub-system models which could be adapted to our own needs. Models of processes such as decomposition and depth related processes are examples where existing models may ease the difficulties of collecting experimental data.

#### 4.2 Diversity models

The existing descriptive and conceptual models of diversity are not suitable for more than a cursory assessment of the effects of management on grassland diversity, and are totally inadequate for assessing precise effects on species composition. Models have concentrated on plant diversity and have contributed little to our understanding of animal diversity. Few studies have emphasised the dynamic relationships between plant and animal populations.

Descriptive models often obscure the dynamic way in which diversity in grasslands is determined. In grassland plant communities there are so many species with similar resource requirements that we cannot possibly interpret patterns of diversity without considering plant dynamics. Conceptual models which invoke ideas such as 'disturbance', 're-generation' and 'competitive exclusion' give tacit recognition to this, but duck

the issue by treating these processes (which themselves need to be described and modelled), as variables, which are the used on the axis of a graph! It may be convenient to express complex relationships in a simple graphical way, but it is also beguiling. In Appendix 2 I have used catastrophe theory to illustrate how an apparently straight forward nutrient/diversity relationship might be given a different, dynamic interpretation.

By emphasising the dynamic nature of community diversity we can establish an effective link between models of diversity and models of succession. Models of diversity are simply a special case of succession models in which the species x environment interaction shows no long term trend. It follows that if we can model successional changes in communities then we can also model diversity.

#### 4.3 Succession models

Succession models should form the basis for understanding diversity and for the wise management of grasslands. Effective management presupposes an ability to predict the response of ecosystems to various management strategies. To achieve this, studies and models of succession should now be undergoing a radical rethink. Miles (1985) states that a unifying theory of succession at the vegetation level is an unattainable goal. There are no emergent properties of ecosystems that inevitably develop during succession. The views of Clements and Odum of orderly successional change in structure and function towards more diverse, more stable, more productive ecosystems, is at best

a useful generalisation. We are now faced with 2 alternative approaches to modelling succession:

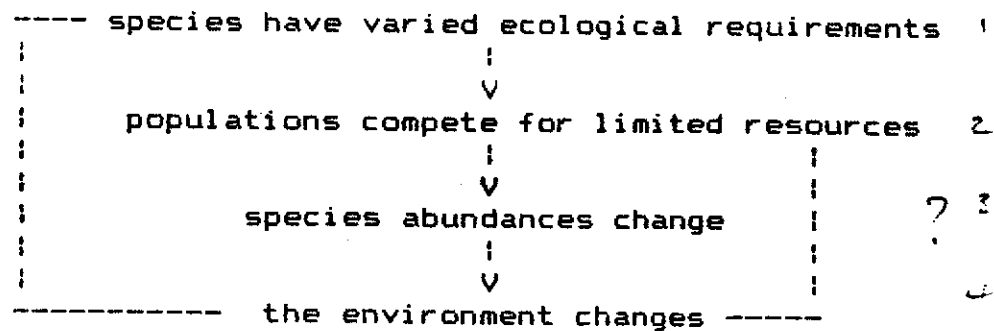
4.3.1 Empirical models. The immediate need for management advice on individual sites requires work which describes the changes in community structure in response to relevant management practices. Although we no longer expect successions on different sites to follow identical patterns we usually hope to be able to make generalisations based on correlations. This is essentially a Clementsian approach, putting faith in common patterns at the expense of detailed understanding. In the short term this may be the only realistic approach. If so then the essential feature of any modelling methodology must be its ability to collect, classify and extract information based on relatively simple rules and questions. It could be worthwhile investigating the use of expert systems to do this (Appendix 3), but the success of these will depend on the quality and quantity of information that is available. The lack of system and method for describing and collecting environmental information, which would make comparisons between sites more feasible, puts a serious constraint on the use of expert systems. I believe it is in fact a critical failing in our approach to grassland research, and the wider implications of this will be discussed below. However, even if the deficiencies of environmental description are overcome this inductive approach, based on observation and experiment, is limited because of the large scale (in space and time) that experiments need to encompass to obtain generalisable results (Goodall 1977).

4.3.2 Process models. I believe that predicting successional change is best done by a deductive approach. The success of this method depends on 3 factors. First, a proof (or conviction) that there are no emergent properties of ecosystems which cannot be predicted from understanding processes at a lower level of organization. Second, a clear identification of the processes which effect successional change. Third, the development of an appropriate model for deducing the effects of changes in these processes on ecosystem structure and function.

Even if there is no unifying theory of succession at the vegetation level there may be a unifying theory at some lower level of organization. There is an analogy here with evolution theory. The theory of evolution does not predict how species will change; species change in many ways according to many (usually unpredictable) environmental influences. However, there is a well developed modern synthesis of evolution, based on processes at a lower level, which tells us why they change. Basically: individuals within a species vary; these variations are inherited; competition for limited resources means that not all individuals produce progeny which survive and finally, the best adapted individuals survive, others perish. The evolution of species is the result of changes in gene frequency; the driving forces are provided by reproduction and death and the raw materials by genotypic variation.

#### 4.4 Evolution as a model for successional change.

A theory of succession, which is analagous to the theory of evolution, could be based on changes in populations. I suggest:-



This scheme combines the basic Clementsian idea that species modify their own environments (without implying any pre-determined direction of change), but follows Gleason in emphasising the importance of life history characteristics. Although it is only a word model (perhaps some would call it a trivial model) it does provide a clear indication of the processes we should concentrate on and methodological deficiencies which must be corrected if we wish to go further and derive general, predictive models of succession.

4.4.1. Definition of the environment. First, we must be able to define and measure the environmental features of a developing grassland which influence growth and survival of individual species. Elton and Miller (1954) recognised the importance of establishing a uniform system for defining animal habitats. They realised that such a system could not be developed in a piecemeal way and perhaps for this reason their system has not been widely used. Plant ecologists are even more lax than animal ecologists at meaningfully defining the environment and the



resulting plethora of site specific studies with little to link them is a handicap to any attempt to rationalise data from a range of sites. Reed (1980) has reached a similar conclusion for woodlands and calls for quantifying the operational environment of forest plants. He believes that a workable methodology for measuring environment in the field and determining its effect on conifer forest growth would provide the central theory for a forest growth and succession model. His operational environment defines an n-dimensional environmental space equivalent to the Hutchinsonian niche. It includes variables that are indexes of air and soil temperature, solar radiation, soil water availability and atmospheric water demand. We need to develop a similar environmental description for grasslands, with the emphasis being on parsimony and easily measured variables. Some variables such as soil temperatures (Meikle and Gilchrist 1983) and soil water can be easily estimated from climatic data. Variations in soil water (eg drought) may be particularly important in explaining co-existence in grasslands by causing competitive reversals (Rice and Menke 1985). Successional changes in available soil nitrogen are also crucial to understanding the dynamics of secondary succession (Thorne and Homburg 1985), but is not easily measured. Perhaps some bioassay technique could be developed to give an indicator of soil nutrient conditions. Light regimes within the grass canopy are relevant to germination and growth and recent developments in the description of grassland canopies may be relevant to this. (Fox 1979, Davis et al 1980<sup>2</sup>, Weger et al 1986).

4.4.2 Autecology Second, we must have appropriate autecological data. Qualitative information on preferred habitats and ecological ranges of each species will have limited value for succession models. Ideally we should have quantitative information on the production ecology of each species (growth rates, death rates, decomposition rates), phenology and germination characteristics of each species. The information being collected at UCPE, Sheffield is a valuable step in this direction but as far as I know they have not considered how this information can be related to predictive models of community dynamics.

4.4.3 Competition. Third, we must understand what plants compete for, and how, so that we can predict the outcome of competitive interactions. This may not be such a daunting task as one would suppose. Interactions between plants are usually not species specific and there is a large degree of equivalence in the effect of species (Goldberg and Werner 1983). If plants compete through the exploitation of common resources (light, water, nutrients) then the accurate definition of the changing environment in which plants are growing (together with the autecological information) may be sufficient to enable us to predict the dynamics of complex species mixture. This assumption has been used successfully in models of succession which use the Lotka-Volterra competition equations (van Hulst 1979, Leps and Prach 1981) and in my own work in turfgrass mixtures (Parr 1986). It is consistent with observations of pasture dynamics where nutrients are the dominant factors, and where the prior establishment of one species creates

an inbuilt resistance to change (King 1971). It can also accommodate interactive effects between pairs of grassland species which are non-reciprocal (Fowler 1981). Only where there is direct physical interference (or co-operation?) or in certain symbiotic relationships (eg N-fixing legumes) may we need to look at competition in a more complicated manner.

4.4.4 Population dynamics Fourth, we must measure the processes accounting for changes species abundance, including vegetative growth, plant mortality, seed production and re-generation from seed. Mere presence and absence from a community may give a distorted view of the importance of some species to community dynamics. Jansen (1986) points out that many uncommon plants in communities may be strays which have no chance of reproducing. Conversely, the composition of the seed bank, which will influence the diversity and composition of the community after a disturbance, may be very different from the established vegetation (Schenkvelde and Verkaar 1984). Management of the vegetation structure may be used to control recruitment from the seed bank, a technique which has been used to influence the composition of sedge communities at Wicken Fen. (Meredith 1985). In addition, the initial stages of succession are influenced by the time of year that bare soil is present in relation to germination requirements of species (Keever 1979) and the composition of the seed bank (Smith and Kadlec 1985, Van der Walk 1981).

4.4.5 Reaction. Finally, to complete the cycle, we must know how the growth, death or decay of each species influences the

grassland micro-environment. This step is essential in autogenic successions, but less important in allogenic successions.

Management is included in the model by measuring or predicting its direct effect on individual species, and on the grassland environment. Both these effects may affect interactions between species and lead, indirectly, to further changes in community structure. Predicting the effects of management is closely tied to our ability to define and monitor the grassland environment. Using this approach we can distinguish between the immediate effects of management which arise from death and disturbance and the longer term effects brought about by differential changes in plant growth and reproduction.

The model framework has been described mainly in terms of plants but is also applicable to animal populations. However, interactions in multi-species animal communities are more difficult to model because of more complex niche relationships and interactions (Usher 1978, Lawlor 1979). The model is more suitable as a framework for considering the direct effects of fauna on plant successions.

The model is applicable to successional change on any scale. Whatever the scale, spatial complexity must be treated in sufficient detail to account for the contribution of separate parts (Smith 1980). The larger the area we look at the more important become the effects of environmental heterogeneity and the size and frequency of disturbances. On a small scale the processes of population extinction and colonisation become more important. The ecosystem concept is dimensionless and ecosystem models of production are scale free, and can be extrapolated to smaller or larger areas (assuming homogeneity). Quite obviously we cannot do the same for communities, the dynamics and

composition of which are influenced by scale effects. Our concept of succession and the models we develop should be independent of any arbitrary definition of scale. A model based on population processes linked to environmental descriptions fulfills this criterion, with the proviso that the larger the scale, the more complex the procedure of environmental description.

4.4.6 Feasibility of the model. There are 3 factors that make the application of life history models to succession and vegetation management both feasible and relevant.

a) There are already good examples of single species models which could be adapted. The Leslie matrix described in Appendix 2 is one possibility that has already been extended to model succession (Malanson 1984). But for those who find matrix formulations difficult to follow (ie most people), a more explicit systems approach such as that described by Coulman et al (1972) may be more appropriate (Figure 6). Furthermore, models of different types and complexity could be used for different species. In essence, models for each species would be sub-systems of a whole grassland ecosystem.

b) Simple indexes of the grassland environment may be sufficient to make rapid progress, provided agreement can be reached on standards. If more complicated descriptions are required (eg to describe temporal variations) then some of the sub-system models in existing ecosystem models could be adapted. For example, soil water models could be used to relate rainfall

and soil type to germination, regeneration and growth; models of nutrient cycles used to clarify relationships between competitive exclusion and nutrient enrichment.

c) Initially, emphasis should be given to dominant grassland species. Often the dynamics of the whole plant community and the direction of succession can be interpreted in relation to the behaviour of a few dominant species (Humphrey 1984). The impact of disturbance also depends on the nature of the dominant (Armesto and Pickett 1985). Watt (1964) observed that although *Festuca ovina* was the dominant species in both grazed and ungrazed grasslands, small annuals survived in the grazed swards because the competitive power of the fescue was reduced. Similarly, *Festuca rubra* turf is particularly stable (Smith, Elston and Bunting 1971, Parr and Way 1985), possibly because it forms a mat in which other species cannot establish. On a smaller scale, Turkington and Harper (1979) showed how the regeneration cycle in pasture was influenced by the two dominant species (*Trifolium repens* and *Lolium perenne*), and this indirectly affected the structure of the vegetation. Management studies of rare species (eg orchids) or weeds (eg *Cirsium arvense*) also fit into this framework. But I believe that we should place more emphasis on dominants. Studies on the population dynamics and production ecology of a few dominant species at a range of sites would be a useful first step towards developing general models of succession. In the meantime, management decisions could be based on empirical relationships between the abundance of these species and defined objectives (eg high diversity).

## CONCLUSIONS

A wide variety of models has been used in grassland studies. No single model will satisfy all requirements and there is no  $E=mc^2$ , no universal law of relativity, for grasslands. Furthermore, the emphasis that much of ecological research places on interpreting pattern rather than investigating process is not conducive to discovering any such law.

Much less clear is whether a model in itself can, or should, form the basis of research programme. The danger is that the model becomes an end in itself, rather than just a means to an end. The complex whole ecosystem models, typical of IBP, alienated many researchers because they seemed too far removed from the initial, practical objectives. The secondary benefits of the modelling exercise (increased insight, recognition of gaps in knowledge) were most apparent to those involved in the projects, and not easily communicated to outsiders. Models can all too easily become model dinosaurs; ill adapted and doomed to extinction.

But, quite clearly, grassland models have been evolving in line with (but perhaps a little behind) general ideas and thinking on grassland dynamics. We have moved from descriptive models, to models of processes at the whole ecosystem level and are now progressing towards integrating models of individual species in multi-species communities. Anon (1985) and Reiners (1986) have argued that ecology is suffering from a digression from ecosystem research into a largely reductionist mode. I disagree. I believe that this is a trend which is necessary and inevitable.



The ecosystem concept has provided a useful framework for considering changes in some properties of whole ecosystems such as trophic relationships, energetics, productivity and nutrient cycling. These properties behave in a relatively conservative manner, often largely independent of detailed species composition. This is due to the conservative nature of the physical processes on which ecosystem models are based eg conservation of energy, chemical equilibria in closed systems. But the holistic approach of ecosystem studies is less useful to attempts to understand such things as the composition, diversity and stability of community structure. These changes can usually only be interpreted, or predicted, in terms of changes within individual populations; and there are no general laws governing interactions between species (the lotka-Volterra equations are the closest we come to this and these behave erratically, not conservatively). It follows that if we wish to manage the diversity and species composition of grasslands we must examine the dynamics of individual species. The biggest difficulty with this, and all other reductionist approaches, is maintaining relevance. In grassland studies this difficulty is exacerbated because we lack a framework in which information on the dynamics of individual species can be related to multi-species communities. I believe this is due to the failure of plant ecologists to grasp the thorny problem of establishing consistent environmental descriptors, rather than any intrinsic difficulty of modelling interactions in complex mixtures. By using a consistent system for defining the grassland environment, we can extricate the dynamics of individual species from the community

matrix, without losing sight of their mutual dependence.

There is nothing new in advocating a life history approach to interpreting vegetation dynamics, Watt (1964) did so in the early sixties. He believed it would be instructive to investigate the performance of a few species in a range of environments. Furthermore, many of the projects in Programmes 3 and 4 already adopt this strategy. If any doubt remains about the acceptability of the approach, we should remember that ecology is not the study of ecosystems, it is the study of animal and plants in relation to their environments, ie in relation to ecosystems.

Referring back to my original objectives, I suggest the following conclusions.

- 1) I suggest the scheme presented in figure 6 as a framework which encompasses much of the present research effort in Programmes 3 and 4 and provides a rationale for further science vote effort. The central feature of the scheme is its move away from the stifling complexity of the whole ecosystem towards more tractable problems of managing individual species.

- 2) Within the scheme, individual models must be fitted to individual objectives:

- a) Leslie matrices could be used to formulate models of population dynamics and to link them to environmental changes.

- b) Sub-systems from published dynamic ecosystem models could be adapted to facilitate the description of the environment.

- c) Empirical methods (regressions, expert systems)

would be used to link research findings to practical needs.

d) Conceptual models would be used wherever needed, to guide thinking and provoke insight. The use of catastrophe models have been little explored in this area.

3) The biggest single deficiency in our research programme is the lack of a uniform system for defining the grassland environment. We should develop one and use it consistently.

Research emphasis should be placed on the effects of management on the population dynamics of a few grassland dominants; the impact of invertebrates on regeneration from seed; the effects of scale on plant population dynamics; and the use of models for predicting the outcome of interactions in multi-species mixtures.

## APPENDIX 1: LESLIE MATRICES

A Leslie matrix provides a framework for simulating the growth of complex populations. In its simplest form it consists of a vector describing the age structure of the population. This vector is pre-multiplied by a transition matrix, containing the fecundity and survival probability of individuals in each age class, to give the age structure in the next time period eg:

$$\begin{array}{c}
 \left( \begin{array}{cccccc}
 f_1 & f_2 & f_3 & \dots & f_{x-1} & f_x \\
 p_{12} & 0 & 0 & \dots & 0 & 0 \\
 0 & p_{23} & 0 & \dots & 0 & 0 \\
 \dots & \dots & \dots & \dots & \dots & \dots \\
 0 & 0 & 0 & \dots & p_{x-1,x} & 0
 \end{array} \right)
 \end{array}
 \times
 \begin{array}{c}
 \text{time } t \\
 \left( \begin{array}{c}
 n_1 \\
 n_2 \\
 n_3 \\
 \dots \\
 n_x
 \end{array} \right)
 \end{array}
 \rightarrow
 \begin{array}{c}
 \text{time } t+1 \\
 \left( \begin{array}{c}
 n_1 \\
 n_2 \\
 n_3 \\
 \dots \\
 n_x
 \end{array} \right)
 \end{array}$$

where  $n_1, \dots, n_x$  are the densities in each age class.

$f_1, \dots, f_x$  are the fecundities of each age class.

$p_{ij}$  is the probability of an individual surviving from class  $i$  to class  $j$ .

In this form the dynamics of the system can be determined analytically, using matrix algebra. This approach has been used to determine stable age distributions and optimum harvesting strategies (Usher 1966, Usher and Williamson 1970).

However, for modelling the dynamics of grassland populations the mathematical tractability of a Leslie matrix is less useful than the general framework it provides for ordering thoughts on population processes. ~~It is possible~~ <sup>We can</sup> to replace age classes with size classes or phenological classes (eg seed, seedlings,

flowering plants) and to relate the variables in the transition matrix to environmental variables. This approach has been used by Malanson (1984) to link the survivorship and natality of individual species to total foliar cover, to simulate succession after fire. He concludes: "... [the Leslie matrix].... is a population dynamic model that has the simplicity necessary for eventual application and the complexity necessary to give some insight into processes".

## APPENDIX 2: CATASTROPHE THEORY

Catastrophe theory is a relatively new field in mathematical topology. Its value to ecological work is that it allows the formulation and presentation of qualitative ideas that are not amenable to other, more traditional methods. Therefore, catastrophe models can be used to illustrate dynamic properties of ecosystem which may otherwise be ignored. These include discontinuities (catastrophes), hysteresis and divergence.

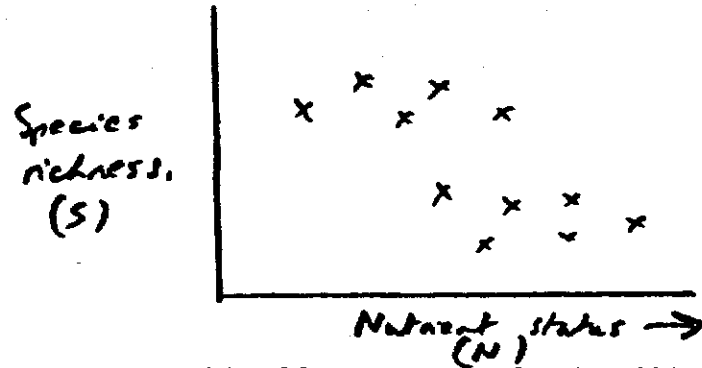
Discontinuity. A large change in some property of the system associated with a small change in some other variable (including time) - 'big effects from small causes'.

Hysteresis. A delayed response to a changing stimulus - or 'where you end up depends on where you start' and 'what goes up doesn't necessarily come down'.

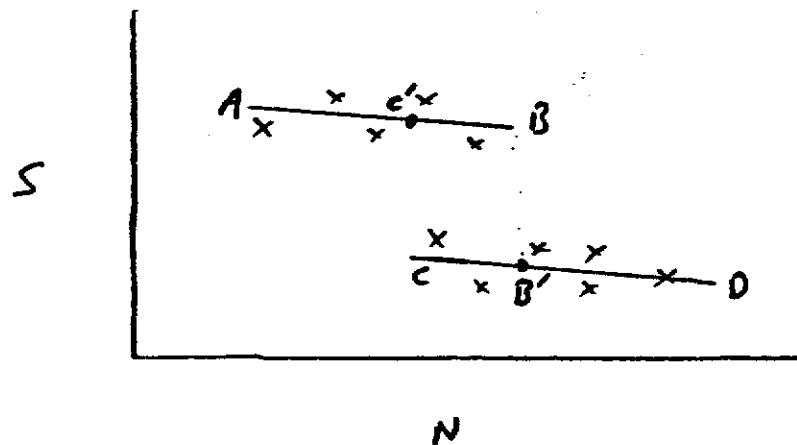
Divergence. Nearby starting conditions evolving to widely separated final states (eg populations just above and below extinction threshold).

An example of the use of catastrophe models to explain spruce budworm outbreaks is given in Jones (1975). I shall illustrate the technique with a hypothetical example taken from ideas relevant to the management of plant diversity.

The effects of nutrient enrichment and disturbance on diversity. Consider this hypothetical graph showing the relationship between some measure of nutrient status and species richness:



It would be statistically acceptable to fit a straight line to this data and conclude that as nutrient status increases diversity decreases. But this is not the only explanation possible. A catastrophe model might suggest:



The graph now shows a manifold tracing changes in the equilibrium value of species richness as it responds to small changes in

nutrient status. The equilibrium level depends on the history of the system. Starting with low nutrients the system equilibrates at point A, with increasing nutrients there is then a relatively slow decline in richness until B, at which point the system makes a sudden jump to the lower plane at B', before continuing to D. However, if we start at point D and decrease nutrients, then richness stays low until C, at which point there is a sudden increase. Between points C and B' species richness depends on which direction the system has been moving (hysteresis) while at points B and B' the system shows a discontinuous response (a catastrophe).

Dynamics such as these are feasible. For instance: plants may be able to survive and even propagate vegetatively in conditions that would not permit establishment from seed; juvenile and adult competitive abilities may vary (Grace 1985); the outcome of competition (as demonstrated by Lotka-Volterra equations) is sensitive not only to the relative abundance of the competing species but also to small changes in the competitive coefficients. In all these cases a small change in the environment could be sufficient to lead to a sudden change in the dominant species of the community and be associated with major changes in community structure and composition.

The catastrophe model suggests that it would be inefficient to try and increase richness simply by reducing nutrients. But it may be possible to jump from the lower level to the upper level of richness with a quite small change in nutrients if we introduce a second factor such as disturbance. Figure 3 shows how the 'fold' catastrophe illustrated in figure 2 is not present



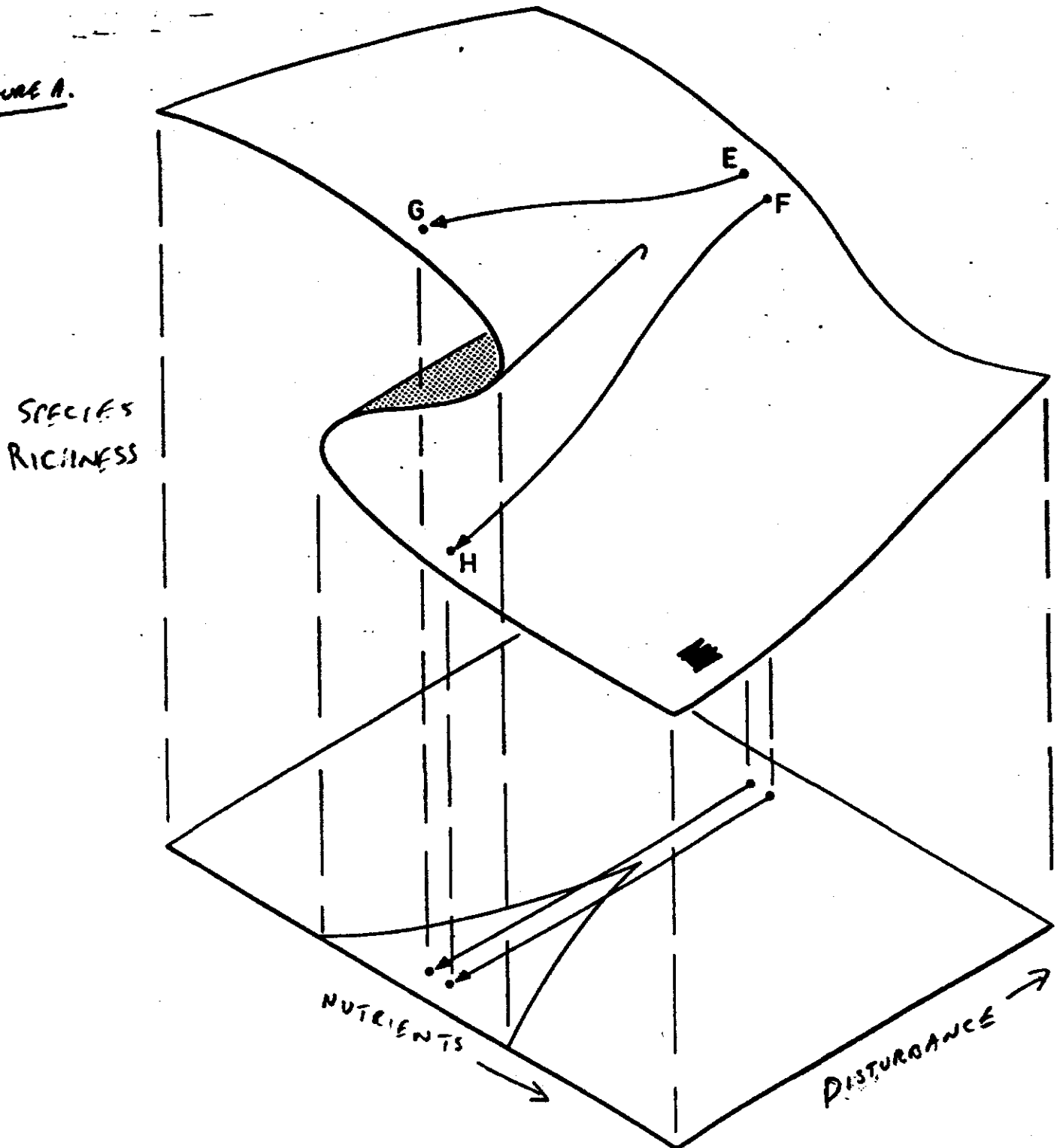
at high levels of disturbance. Therefore if we start with the system at point  $X$ , with low richness, the introduction of disturbance will move the system to  $F$ . At this point the reduction of disturbance the system will return to low richness but with the scenario illustrated (an example of a cusp catastrophe) a small increase in nutrients moving the system to  $E$  would mean that the system would now return to the high richness plain even when the disturbance is removed.

At first sight, the existence of cusp catastrophes at points convenient enough to be exploited in the management of ecological systems may seem unlikely. But the cusp catastrophe idea does explain the current methodology for introducing species into swards. The existing sward must be disturbed and seed sown, but in addition some technique of reducing the competitive dominance of the existing vegetation must be found if the seed is to develop to maturity. This might be achieved by a small reduction in the nutrient status of the soil. However, in nutrient rich sites the act of disturbing the soil tends, on a local scale, to release nutrients and have the reverse effect. Therefore, in practice, growth of vegetation is reduced by direct methods such as herbicides, growth retardants or cutting.

Conclusions. Catastrophe models offer an alternative way of looking at complex ecosystem dynamics in a qualitative way. They help us to get away from thinking in terms of rigid relationships. They provide a useful conceptual approach. However, they are not easy to apply to highly multi-variate situations or to use quantitatively with ecological data

(Jeffers 1982). One useful application may be in investigating and interpreting the behaviour of complex, systems models (eg Jones 1975). In these models, the difficulty of estimating the parameters of the manifolds from field data would be overcome by running model simulations.

FIGURE A.



## APPENDIX 3 : EXPERT SYSTEMS

An expert system is a computer program that solves problems (Naylor 1983, James 1984), usually empirically.

There are two pre-requisites to setting up an expert system:

- 1) A concise and tractible definition of a problem.
- 2) An initial definition and collection of rules that form the data base (the 'experience' on which the computer makes decisions).

### Defining the problem

An expert system won't tell you how to become a millionaire but it could conceivably advise you on how to invest on the stock exchange or fill in your football pools. An expert system needs a problem with a well defined series of answers to unequivocal questions. Practical examples are:

- given certain symptoms --> diagnose the illness.
- given certain characteristics --> identify the animal.

A good expert system should be able to update its knowledge base to incorporate new data and extend its range of application eg by including a new species.

To set up an expert system to give advice on grassland management we could define the problem in terms of 3 questions:

- 1) What kind of grassland community have we got?
- 2) What kind of community do we want in x years time?
- 3) What management is needed to achieve this?

However, this system would be based on a classification of grasslands (eg indicator species analysis), it would be constrained by the initial classification and not easily updated.

It would be a dogmatic expert.

More flexibility could be achieved by dealing with individual species (or individual characteristics of the grassland such as cover) ie:

- 1) What species are present in the grassland?
- 2) Do you want species x to increase, decrease or stay constant?

The expert system would then specify the management necessary to achieve this objective, and could also specify effects on other species. Alternatively a management technique could be specified, and the expert would indicate its effect on each species within the community.

What sort of data base is needed?

In our grassland example we need to relate the change in each species (or characteristic) to the type of management used and probably also to other environmental factors not under the control of management. We could do this in a number of ways, including regression analysis or simulation modelling. But a simpler (more empirical) approach is based on probability theory (Naylor 1983).

Consider the question 'Is it going to rain today?'. If the expert system was supplied with all existing weather records it might answer: 'It will rain today with a probability of .54'. If it then asked about yesterdays weather or some other feature of todays weather it could improve upon this prediction by using conditional probabilities (if it rained yesterday it is more likely to rain today). Some questions might enable a prediction

with 100% accuracy eg "Are you going out on field work?" - but only if the data base included the field experience of some ecologists I know.

A similar approach could be used to give predictions on the effects of grassland management. We would need a data base with comprised of information in the form : "definition of management, definition of the environment, effect on species x".

The initial problem would be to define a small, but comprehensive, set of environmental and management descriptors.

Needless-to-say, all this is more easily said than done and it is doubtful whether we could justify the building of an expert system for grassland management without the contractual support of a customer with a real need for such a system. An obvious example would be to produce a local authority guide to grass management. This could be used to help them establish standards for the management of grass areas that are now being put out to contract.

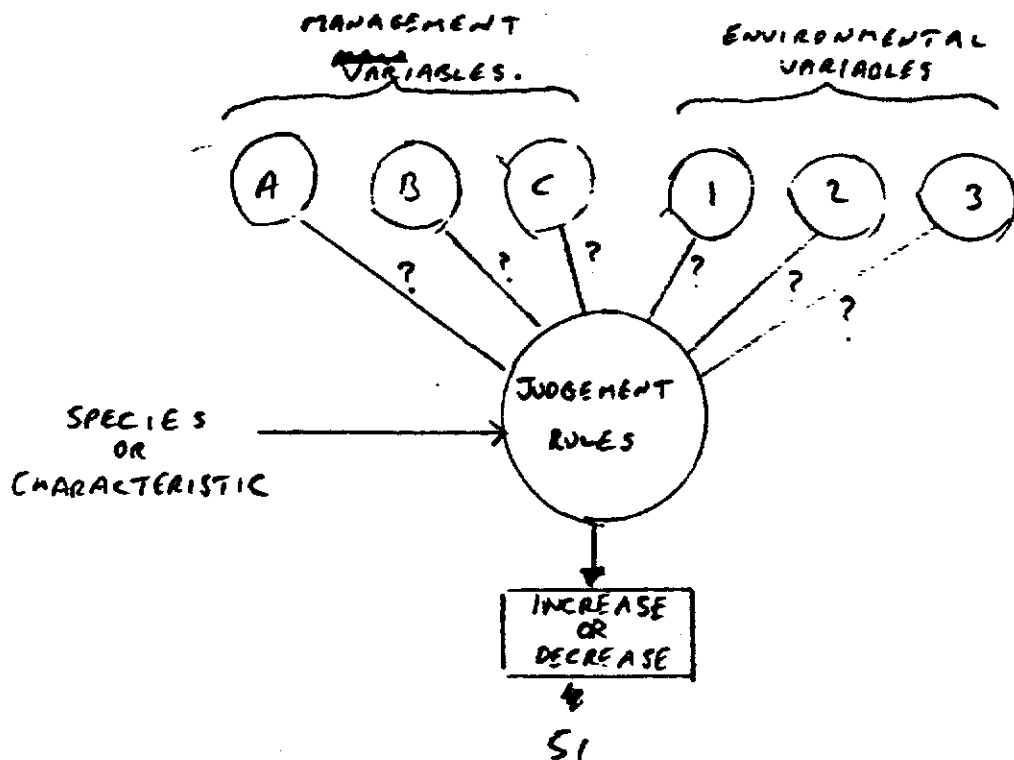
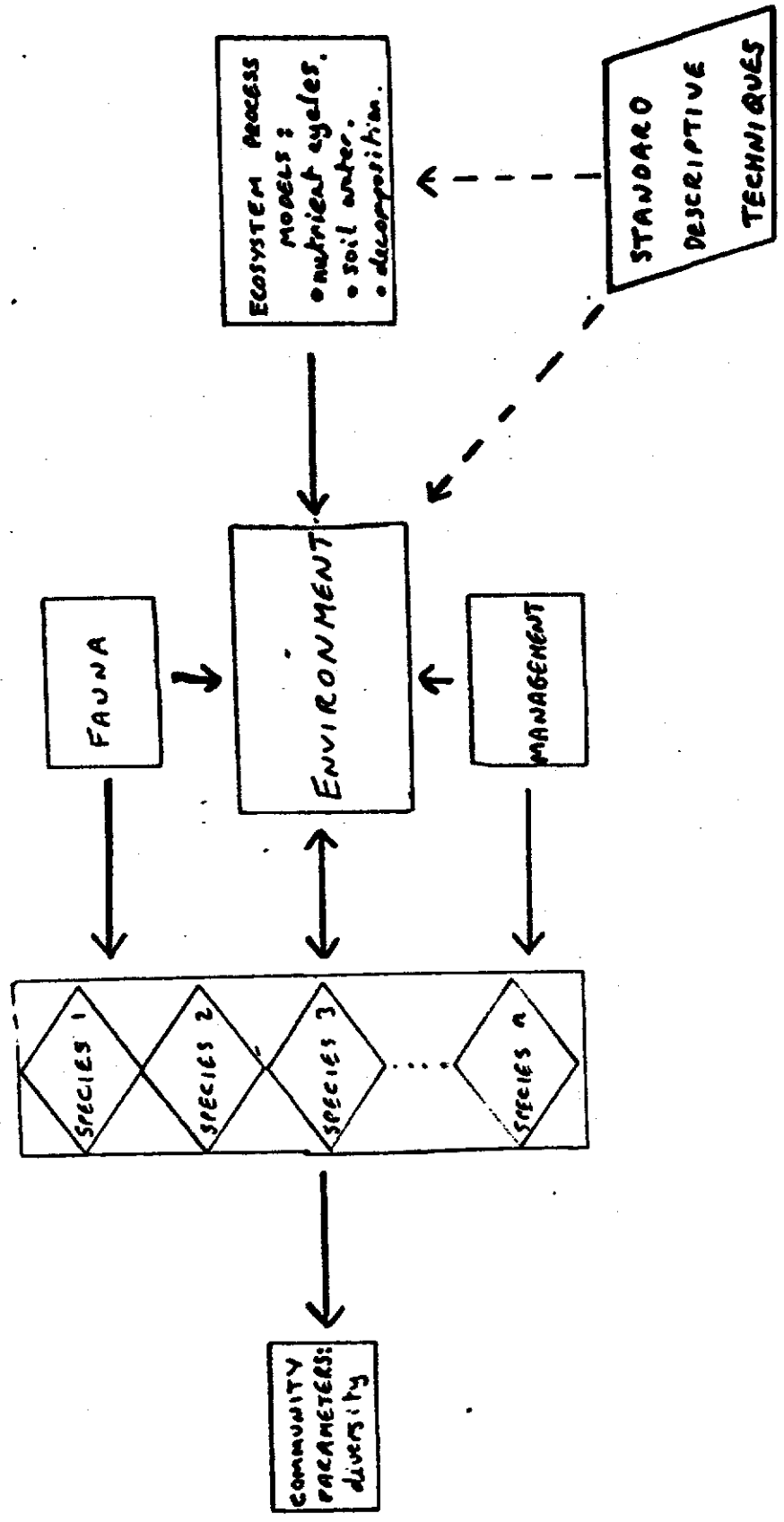


Figure 7. A rationale for work on grassland dynamics, emphasizing the key role of studies on individual species and the precise definition of environment.



Formulation of management aims

Data required

Input to/from management

Basic ecological and management information from literature, management experience and ecological survey

Conceptual understanding of the ecosystem under study | Development of descriptive and verbal models

Qualitative advice to/from management, e.g. probable short- and long-term trends associated with general management strategies \*

Design, execution, and analysis of experiments.  
"Biological" research: ecosystem process understanding, model building, validation.  
"Management" research: estimating model parameters, trials of different management strategies, validation.  
"Historical" research: analysis of previous management results for the future management, input to models, validation, etc.

Increasingly quantitative understanding of the ecosystem under study | Increasingly sophisticated model development, primarily of stochastic and functional types

Quantitative but general advice to/from management, e.g. consequences of specific management strategies \*

Specialized advice to, and feedback from, management, e.g. year-to-year forecasts, long-term forecasts and parameter validation \*

Figure 1. A schematic representation of the role of the ecologist in producing ecosystem models and in giving advice for management purposes. From Slatyer (1977)

Figure 2. Example of a whole ecosystem model.

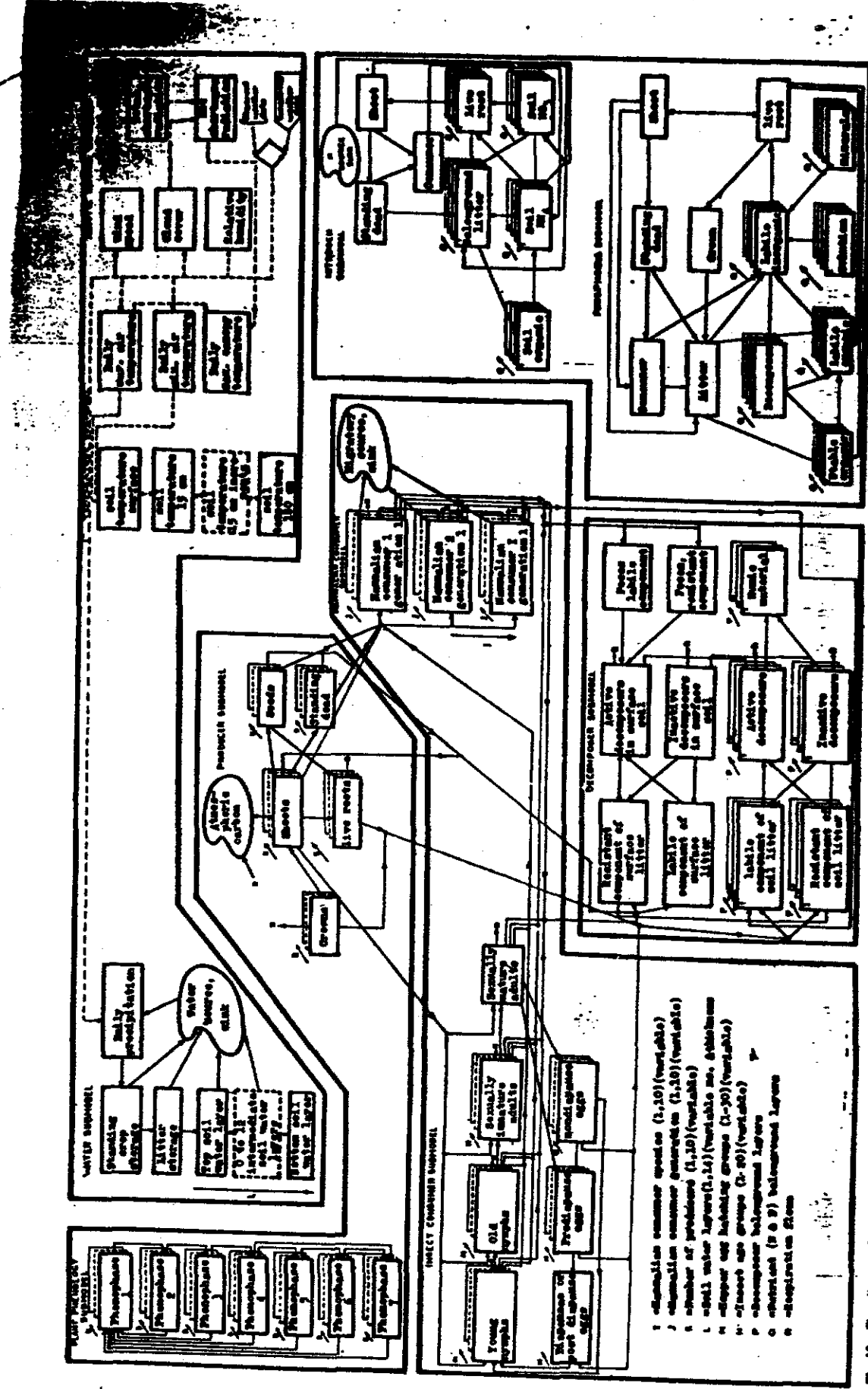


Fig. 15. Flow diagram of an ecosystem level model for (ground) controls on flow are omitted, for clarity. The third dimension, or layer, in portions of the diagram represents different nodes or groups of plants and animals or layers in the soil profile (from Van Dyne and Arvey 1976).



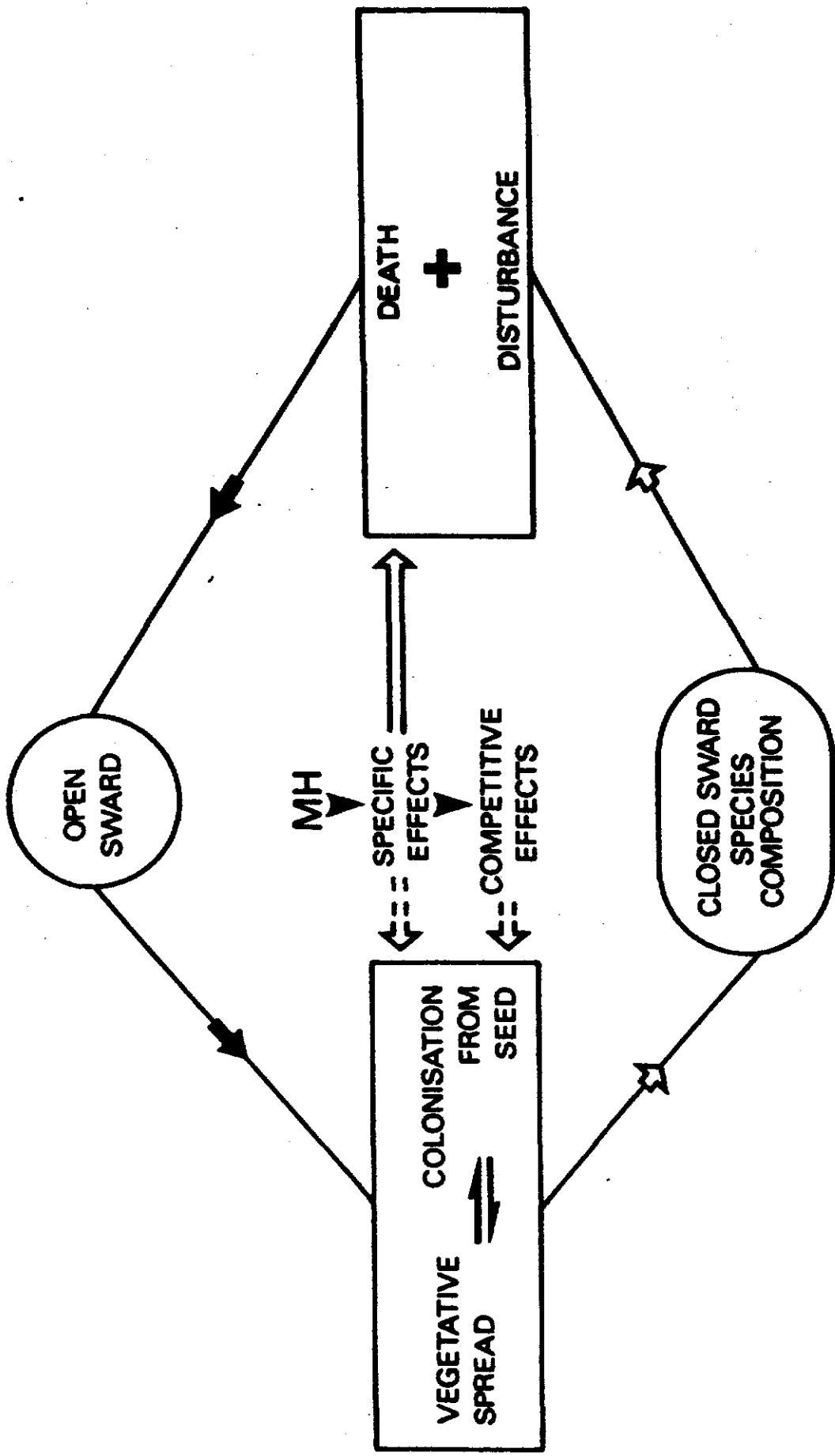


Figure 3. A simple scheme illustrating the processes affecting the species composition of a grassland. Management (in this case treatment with mudic hydrazide-MH) influences the creation of gaps in the sward and controls the rate at which these gaps are filled.

# Figure 4. Ecosystem trends and life history characteristics during succession.

**Table 1.** A tabular model of ecological succession: trends to be expected in the development of ecosystems. (from Odum 1969)

Ecosystem attributes	Developmental stages	Mature stages
<i>Community energetics</i>		
1. Gross production/community respiration (P/R ratio)	Greater or less than 1	Approaches 1
2. Gross production/standing crop biomass (P/B ratio)	High	Low
3. Biomass supported/unit energy flow (B/E ratio)	Low	High
4. Net community production (yield)	High	Low
5. Food chains	Linear, predominantly grazing	Weblike, predominantly detritus
<i>Community structure</i>		
6. Total organic matter	Small	Large
7. Inorganic nutrients	Extrabiotic	Intrabiotic
8. Species diversity—variety component	Low	High
9. Species diversity—equability component	Low	High
10. Biochemical diversity	Low	High
11. Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well-organized
<i>Life history</i>		
12. Niche specialization	Broad	Narrow
13. Size of organism	Small	Large
14. Life cycles	Short, simple	Long, complex
<i>Nutrient cycling</i>		
15. Mineral cycles	Open	Closed
16. Nutrient exchange rate, between organisms and environment	Rapid	Slow
17. Role of detritus in nutrient regeneration	Unimportant	Important
<i>Selection pressure</i>		
18. Growth form	For rapid growth ("r-selection")	For feedback control ("K-selection")
19. Production	Quantity	Quality
<i>Overall homeostasis</i>		
20. Internal symbiosis	Undeveloped	Developed
21. Nutrient conservation	Poor	Good
22. Stability (resistance to external perturbations)	Poor	Good
23. Entropy	High	Low
24. Information	Low	High

**Figure 2.** Characteristics of plant species at different successional stages (+, high values, -, or values). (from Brown 1984).

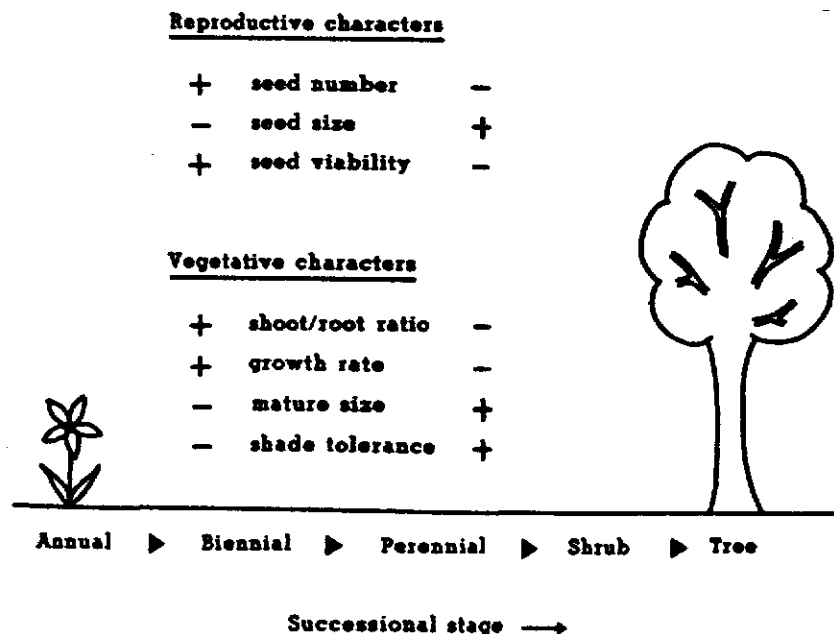


Figure 3: Models of succession based on life history characteristics.

Successional pathways

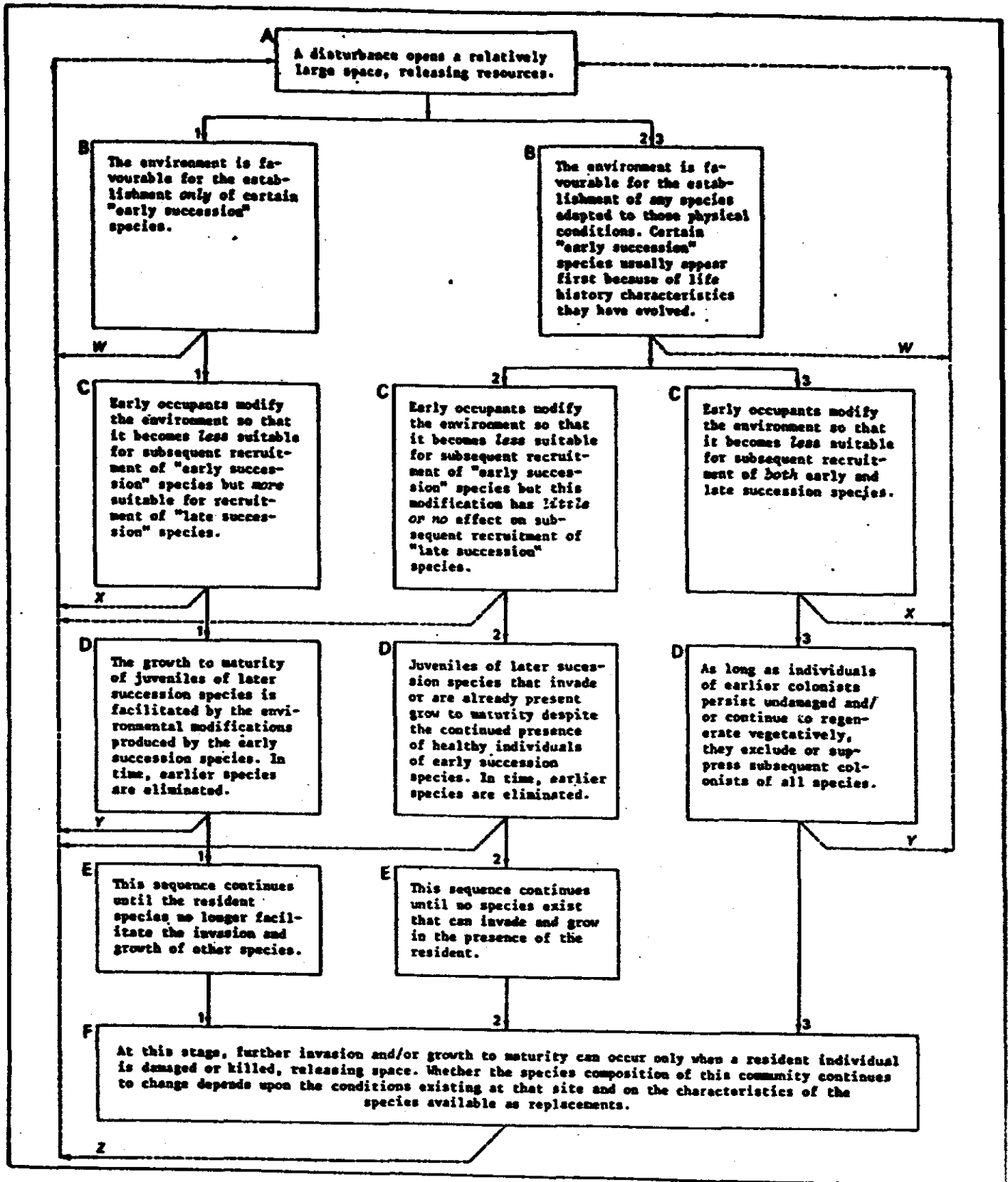


Figure 1. Three models of the mechanisms producing the sequence of species in succession. The dashed lines represent interruptions of the process, in decreasing frequency in the order w, x, y and z. Pathway 1 is referred to as the "Facilitation" model, pathway 2 as the "Tolerance" model, and pathway 3 as the "Inhibition" model. (From Connell and Slatyer 1977).

Figure 6. Single species population dynamics model based on a life table approach (from Coulman, Reice and Tummala 1977)

