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An Ecological Succession Model Applied to Environmental Management

Diane Rosenberg
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AN ECOLOGICAL SUCCESSION MODEL APPLIED
TO ENVIRONMENTAL MANAGEMENT

by

Diane Rosenberg

A Thesis Submitted to the Faculty of the Graduate School
of Loyola University of Chicago in Partial Fulfillment
of the Requirements for the Degree of
Master of Science

April

1983

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VITA

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CHAPTER I

INTRODUCTION

The term succession is defined as the act of coming after another in order or sequence. Succession refers to an orderly process of change in vegetation, the animal community, or an ecological system. Since earliest time man has been aware of changes in vegetation at a site, and has made practical use of the knowledge, particularly in agriculture.

For over one hundred years succession has been a major concept in ecology. In the United States, Frederic Clements and Henry Cowles are generally credited with formulating the concept of plant succession (Drury and Nisbet 1973: Golley 1977). From its inception the concept of succession engendered dispute among ecologists. Disagreements regarding Clements' detailed terminology, as well as his organismic view of the climax community, polarized ecologists. (Cooper 1926: Gleason 1926: Tansley 1935).

Some people agreed with Clements' holistic view; while others, like Gleason, believed it more correct to view succession in terms of individual organisms (Gleason 1926). There are still two divergent views regarding succession,

the ecosystem or organismic position, and the population centered or individual position.

It has been extremely difficult to design and carry out experiments relating to succession. To supplement the few experimental studies, ecologists have designed theoretical models. The value of any model is that it can be used as a basis for experimentation and prediction. If the model can delineate what aspects of a process are pertinent, it is possible to obtain relevant information. Clements' classical model of succession was a deterministic one in which each species facilitated the next, and the climate ultimately dictated which species prevailed in the climax community. Clements' model has not been well supported by field and experimental evidence. Investigation of successional processes have generated other models interpreting species replacement patterns (Egler 1954: Barclay-Estrup 1969).

Connell and Slatyer (1977) developed three different models, (facilitation, tolerance, and inhibition) to describe the mechanisms that might bring about a successional change after a disturbance. There have been several critiques of Connell and Slatyers' models (Miles 1979: McIntosh 1980), and researchers have used the models to design experiments (Hils and Vankat 1982). The critiques have dealt with the background literature; the experiments have attempted to

assess the validity of the models themselves. No attempt has been made to analyze the possible environmental management applications of any of the models.

It is the goal of this thesis to modify the Connell and Slatyer inhibition model, and to explore how such a model could have practical uses in an environmental management setting. Resource depletion and environmental deterioration have made it necessary to focus attention on conservation and management issues. To effectively manage natural resources, scientific information is needed. How the scientific information is interpreted has direct impact on management policy.

Drawing on the tremendous amount of available research, evidence will be accumulated to support a revised inhibition model. The model's use for management purposes will be explored. The revised inhibition model will examine successional processes through manipulations of both the series of replacements, and the rate of replacements. Manipulations of the series and rate of replacement may involve changes in the diversity of the managed system. There is not consensus among ecologists as to how diversity, stability and maturity of an ecosystem are interrelated. Often managed systems have been regarded as low in species diversity and therefore, unstable, while natural systems have been perceived as more mature, diverse, and stable. As the environment becomes

more managed, and the amount of natural environment decreases, the policies for land use will depend upon how ecologists conceptualize ecosystem functioning.

This thesis is organized into an introductory chapter and six main chapters. Chapter II presents a general review of succession literature. Chapter III explores Connell and Slatyers' (1977) succession models. A critique of the evidence related to each of the three models (facilitation, tolerance, and inhibition) is given. The last part of Chapter III discusses modifications of the inhibition model. Chapter IV presents an environmental management succession model, compares the environmental model to Connell and Slatyers' inhibition model, and briefly suggests possible environmental management applications of the model. Chapter V applies the environmental management succession model to range management, public right of ways, and agriculture. Chapter VI applies the environmental model specifically to water management issues. Chapter VII summarizes and concludes the thesis.

CHAPTER II

THE HISTORY OF SUCCESSION THEORY

Succession Period Pre-1940

Introduction

The term succession, derived from Latin, is defined as the act of coming after another in order or sequence. The word refers to an orderly process of change in vegetation, the animal community, or an ecological system. The transitory communities which occur during a succession are called seral communities, or stages; they are generally thought to lead to a climax or mature community. The entire series of communities is called a sere. Successions are usually classified into two categories: 1) primary successions-occurring on sites not previously colonized, and 2) secondary successions-occurring on sites previously colonized (Drury and Nisbet 1973).

The traditional view of succession has been that organisms with excellent dispersal and ecesis abilities, the pioneers, are generally the first to invade an environment. The pioneer species modify the environment and make it less appropriate for themselves and more advantageous for other organisms which replace them. A sequence of species change continues until no community of organisms can co-exist more

efficiently in the environment than those that are present. These organisms persist as the climax community.

The term climax was derived from the concept that the climate was the ultimate environmental factor that determined the community. Other physical factors, topography, soil, and fire, as well as biotic factors, such as grazing, have gradually been added as possible determiners of a climax community. The climax concept has been criticized. Similar sites and the same climate do not always produce the same climax community. The traditional view of succession, a deterministic process leading to a self-maintaining stable climax community, has been modified. Succession is difficult to precisely define because the original concept has been altered as a result of the continual influx of new information.

Historical References Through 1899

There are several historical references related to changes in vegetation. Units of vegetation were easily visible to primitive man (Gleason 1939), and descriptions of vegetation zones and vegetation change date from Theophrastus, 300 B.C. (Drury and Nisbet 1973: Miles 1979). Eighteenth century scientists as well as foresters were concerned about vegetation issues such as changes in forest structure after logging (Spurr 1952: Drury and Nisbet 1973). By 1838 Grisebach had written the first scientific description

expressing the idea of a plant formation (Gleason 1939). In 1847, Dawson wrote the first detailed report on the changing composition of forests in North America (Spurr 1952). Several other descriptions of vegetation zones and sequences of vegetation were published by the late 1800s. In 1899 Henry Cowles published his extensive work on the vegetation on the Lake Michigan dunes. Cowles formulated the scientific concept of succession (Drury and Nisbet 1973: Golley 1977) and established the theoretical understanding of successional processes. He was the first to emphasize and focus attention upon the process of change, which was his major contribution, and to suggest the idea of successive types (Cooper 1926). Henry Cowles, a thorough and accurate observer, emphasized the dynamic and variable nature of the climax (Cowles 1899). Although Cowles was not as prolific a writer as was Frederic Clements, he greatly influenced fellow scientists.

Frederic Clements

In contrast to Cowles, Clements' theories were derived from the Greek traditions of unity, stability, and organizations in nature (Drury and Nisbet 1973: McIntosh 1980). Clements was the first to associate the concept of succession with vegetation change (Drury and Nisbet 1973). Clements' view of succession had two components. First, Clements viewed succession as a deterministic process, a directional change in vegetation caused by the plants themselves. Each

successive type of vegetation established itself because of facilitatory changes induced by the preceding vegetation. Clements' replaced Cowles definition of a variable climax with a more simplistic monoclimax concept (Olson 1958). Second, Clements viewed the unit of vegetation as an organic entity. "As an organism, the formation arises, grows, matures, and dies...each climax formation is able to reproduce itself, repeating with essential fidelity the stages of development..." (Clements 1936).

By 1916 Clements had outlined the basic features of succession. His extensive published studies were responsible for the general acceptance of the concept of succession, and strongly influenced later ecological studies in the United States. Egler (1951) suggested that Clements' Nebraskan reputation in practical land management allowed his theoretical work to be accepted with little criticism. Miles (1979) credits Clements with changing the European view of succession from a static to a dynamic concept, although Europeans maintained the polyclimax view of vegetation (Golley 1977). Current ecological textbooks still reflect a Clementsian view of succession (Ricklefs 1976: Miles 1979), probably because it is simpler to conceptualize than are the current diverse concepts of succession (McIntosh 1980).

Disagreements With Clements Theory of Succession

Criticism of Clements' theory existed from its inception in the early 1900s, and much dispute was engendered because of his organismic analogy, his view of the monoclimax, and his extensive terminology (Cooper 1926: Gleason 1927: Tansley 1935). Tansley, Clements' British counterpart, rejected Clements' extreme organismic view and suggested that the community might be compared to a "quasi-organism" (Tansley 1920). Unlike Clements, who emphasized that the vegetation changes were internally directed, Tansley acknowledged that successions commonly showed a combination of both internal (autogenic) and external (allogenic) factors (Tansley 1935). Tansley believed that the "quasi-organism" climax vegetation was the result of autogenic succession; retrogressive succession, leading away from the climax stage and back toward earlier stages of vegetation, was mainly allogenic (Tansley 1923).

Two of the most prominent Americans who disagreed with Clements were Cooper and Gleason. Cooper believed that the organismic analogy was inappropriate and presented what he believed to be a solution. He defined succession as the "universal process of vegetation change" (Cooper 1926). Cooper pictured the earth's vegetation as a flowing braided stream undergoing constant change. He emphasized the enormous complexity of succession and stressed the role of prior

history on future change (Cooper 1926). Gleason's individualistic concept of the plant association was a striking contrast to Clements' organismic view (Egler 1951). Gleason believed that the properties of vegetation depended upon the individual plants comprising it. He emphasized that a succession was a continual and universal process. Different causes of succession might act simultaneously but at different rates or in different directions (Gleason 1927, 1939).

Clements' view of the monoclimax was also criticized. Tansley recognized the climatic climax, as well as edaphic, physiographic, pyric climaxes and those determined by grazing, which he suggested be called biotic climaxes (Tansley 1935). Cooper believed the idea of climax was valid but suggested that Cowles' definition, a more flexible one, be used instead of Clements. To Gleason, "climaxes" were only associations persisting unchanged through periods of unchanging conditions. The future of the association might not be predictable from present conditions (Gleason 1927, 1939).

In order to fit the real variability in mature vegetation into his monoclimax theory, Clements invented a multitude of terms. Clements' extensive and detailed terminology was examined critically and much of it was later discarded (Tansley 1920: Odum 1961: McIntosh 1980). Cooper rejected Clements terminology, believing that the terms were so cumbersome that they prevented concise thought (Cooper 1926).

Frederic Clements succession theory has been an important influence in ecology in the United States. There has always been some disagreement with Clements' organismic analogy, his monoclimax theory, and his use of terminology.

Succession Theory: 1940 to Date

Introduction

During the 1940s emphasis was placed on the structural and functional characteristics of the community and succession was examined in terms of competition between species (Hutchinson 1941). Gradually succession came to be viewed as a process of community development (Whittaker 1975). Mathematical laws were applied to the species replacement process (MacArthur & Wilson 1967; Horn & MacArthur 1972). The relationship of the diversity and the stability of the community became a part of the examination of the successional process. During the 1960s there was also a resurgence of Clementsian ideas about succession (Odum 1969; Marglaef 1968). The Neo-Clementisians correlated stability with the maturity of the system, with succession leading to more diverse, stable and mature systems. There are now two current views of succession, the ecosystem or organismic position, and the population centered or individual position. McIntosh (1980) suggests the two views can be traced back to Clements and Gleason, respectively.

The following section is a chronology of some of the succession literature from 1940 to date. The papers cited attempt to trace the changing interpretations of succession theory. Gradual modifications occurred as information accumulated. Different interpretations of succession exist. The relationships, if there are any, of diversity, stability, and maturity of systems is still debated. How ecologists resolve these relationships has implications for environmental management.

The Population Centered-Individual View of Succession

Frank Egler (1954) suggested that the term "vegetative development" be considered as a term to replace "plant succession". He believed vegetative development more accurately described the changes which occurred as a gradual, community phenomenon. Egler presented two processes, relay floristics, and initial floristic composition (both processes may operate simultaneously) to explain succession in old fields. Relay floristics was another way of describing Clements' view of succession; each species invaded at a specific stage of development and prepared the way for the next species invasion. A relatively stable end stage was eventually reached. Egler's initial floristic composition presented a position quite different from Clements. Egler hypothesized that up to the time of abandonment, an old field received the seeds

and harbored the "dormant" roots of many different species. After abandonment the vegetation developed from this "initial flora". Egler's initial floristic composition made clear the fact that species may precede one another temporarily, for reasons other than facilitation.

Whittaker (1953) defined succession as the process of community development. He believed that the causes of successional change may be either internal or external to the community, or a combination of causes with reciprocal interactions between them. Gradients of changing environments, and changing species populations parallel each other. Succession is seen as an "ecocline in time" (Whittaker 1975). During succession, directional change leads to a relatively stable community which fluctuates around a mean. Climax communities are viewed by Whittaker as a pattern of integrating communities related to a pattern of environmental gradients. Disturbance, local discontinuities, and community succession may interrupt the pattern, but climate ultimately determines the prevailing climax (Whittaker 1953). Although Whittaker (1975) notes many exceptions, increases in production, height, soil differentiation and depth occur in the community throughout the succession.

G. E. Hutchinson was one of the first ecologists to emphasize the structural and functional characteristics of

a community (Drury and Nisbet 1973). A successional series occurs in any system where external or internal changes affect the species competitive abilities (Hutchinson 1941). It is difficult to predict which species will dominate in natural communities because of the variety of interactions between different species and environmental factors. In order for a new species to enter a community, one of three interactions must occur: species 2 eliminates species 1, species 2 occupies an unfilled niche, or species 2 partitions the niche with species 1 (Hutchinson 1959). Hutchinson's work exemplifies the fact that ecologists began to examine how the diversity of the community affected successional processes. Hutchinson uses the term fugitive species to describe species that establish themselves early in the successional series, but eventually become locally extinct, because they cannot out-compete later species. The fugitive species dispersal and ecdysis abilities allow them to survive by reestablishing themselves in a new locality (Hutchinson 1951). In diverse communities species colonization is assumed to be difficult (Hutchinson 1959). Some of the limits on the diversity of species are the fundamental productivity of an area, frequency of disturbance, and size of the habitat. The more diverse the community becomes, the more stable it is thought to be (Hutchinson 1959). Stability is the result of the increasing number and availability of

niches; if the flora and fauna is diversified it is less likely that a change would affect the system as a whole (Hutchinson 1959: Kormondy 1969). This correlation between diversity and stability has led to the idea that managed systems, which are often simplified, are likely to be unstable.

After the appearance of MacArthur & Wilsons' (1967) Theory of Island Biogeography, their methodology was incorporated into the study of succession. Succession can be viewed in terms of immigration and extinction rates. In a stable environment, a new species with a low immigration rate may invade, if it has a high competitive ability. As these new species establish themselves, and the supply of unoccupied patches decreases, fugitive species cannot persist. Succession can thus be interpreted as a replacement process subject to mathematical laws (Horn and MacArthur 1972). Various initial states will approach the same climax, or a cyclic series of states will develop. The climax is a steady state that may change continuously with fluctuations in, for example, moisture and temperature. Severe fluctuations in the environment may prevent a climax from being reached. A community is stable if the species composition tends to be constant. One explanation for the stability would be based on the interactions between species forming the community. The greater the number of options of energy flow through the food web the greater the stability of the

community (MacArthur 1955).

The Ecosystem - Organismic View of Succession

Gradually, through the 1960s there was a resurgence of Clementsian ideas about succession. Eugene Odum and Ramon Margalef both exemplify the ecosystem view of succession. Odum (1959) defined succession as the development of an ecosystem. He defined an ecosystem as the community interacting with the physical environment so that materials cycle and energy flows through the trophic structure (Odum 1969). Odum (1969), reminiscent of Clements, view the development of an ecosystem as comparable in many ways to the development of an organism and to the development of society. According to Odum, there are three parameters of ecosystem succession: 1) succession is a reasonably predictable process of community development, 2) succession results from the biological community acting on the physical environment, 3) succession culminates in a stable ecosystem that is maximally protected from perturbation (Odum 1959, 1969). Odum presented a model in which 24 attributes of an ecosystem are grouped into the categories of community energetics, community structure, life history, nutrient cycling, selection pressure, and overall homeostasis. In comparing developing to mature stages in the succession, Odum concluded that the successional

process resulted in increasing symbiosis, conserving of nutrients, a decreasing entropy, and increasing information (Odum 1969).

Ramon Margalef also described succession as a process of information accumulation (Margalef 1968). The information accumulation results in self organization. With time, in an undisturbed ecosystem, structure tends to become more complex. Margalef used the term mature to describe the historically older, more information-rich (or diverse) ecosystem (Margalef 1963). In less mature communities, abiotic influences exert a greater effect than they do in mature communities. As a succession continues independence from abiotic influences increases (Margalef 1963). Maintenance of homeostasis within the community increases the likelihood of community persistence (Margalef 1963, 1968, 1975). As an ecosystem matures, there is an increased complexity of structure and a decrease of energy flow per unit of biomass (Margalef 1975). Abiotic factors are able to alter this process; succession is not necessarily continuous. Margalef suggested that ecosystems be described as less or more mature, avoiding absolute terms such as climax, thereby eliminating some of the difficulties that the term climax connotes in many aquatic environments (Margalef 1968).

The International Biological Program (IBP)

Another development during the 1960s was the initiation of the International Biological Program (IBP). The IBP was a trans-national, cooperative scientific effort (Peterken 1970). One goal of the IBP was to attempt to obtain the scientific information necessary to intelligently and rationally increase biological production and manage natural resources (Peterken 1970: Ellenberg 1971). To meet the goal, a thorough examination of succession theory was required. For example, to increase biological productivity, the relationship of ecosystem maturity and productivity was explored. The concepts of diversity and stability, with implications for natural resource management, were also studied. Specific ecosystems were analyzed.

Much of the IBP work was presented at the First International Congress of Ecology in 1974, which focused on the concepts of diversity, stability, and maturity in natural ecosystems. There was not complete agreement among ecologists attending the 1974 Congress (Maragalef 1974: May 1974: Orians 1974: Whittaker 1974). The differences of opinion among ecologists make it difficult to develop consistent environmental management practices. For example, rotation, as a range management practice, is based upon the premise that the successional series can be repeated.

If the premise is incorrect, the management practice is inappropriate. The IBP goal of gathering information to increase biological production and to manage natural resources, is a goal of immediate importance. Usually, however, there is a time lag between the development of a scientific theory and the application of the theory as technology. The succession theory which underlies management practices needs to be examined. Modifications of succession theory may lead to more appropriate environmental management practices.

Conclusion

That two contrasting views of succession still persist today is a reflection of two divergent philosophical positions, and also an indication of the difficulties inherent in the concept itself. For example, processes of species replacement require many years and occur over wide diverse areas; therefore, the community must be described in both space and time. Perhaps most importantly, succession is not amenable to the most fundamental of scientific approaches - experimentation.

It has been extremely difficult to design and carry out experiments relating to terrestrial succession because of the lengths of time required for all but the initial stages of succession, and the large areas required. To supplement the few and incomplete experimental studies,

ecologists have designed theoretical models. Clements' classical model of succession was a deterministic one in which each species facilitated the next, and the climate ultimately dictated which species prevailed in the climax community (Clements 1936). Clements' model has not been well supported by field and experimental evidence. Investigations of successional processes have generated other models interpreting species replacement patterns (Egler 1954; Barclay-Estrup 1970; Connell and Slatyer 1977). Connell and Slatyers' models will be reviewed in Chapter III.

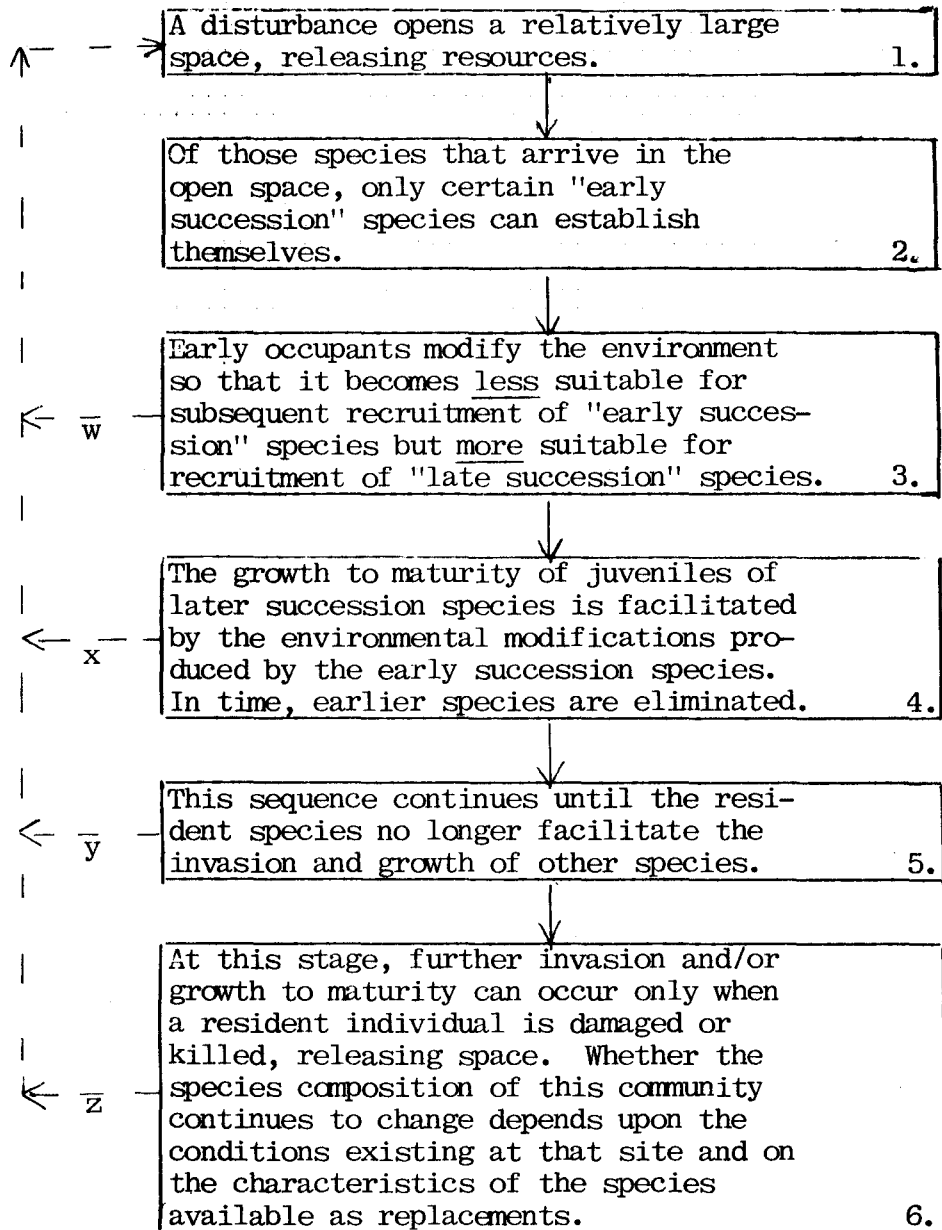
CHAPTER III

CONNELL AND SLATYERS' (1977) SUCCESSION MODELS

Introduction

Connell and Slatyer (1977) developed 3 different models, facilitation, tolerance, and inhibition, to describe the mechanisms that might bring about a successional change after a disturbance. The first part of Chapter III deals specifically with Connell and Slatyers' models. In order to examine each of the models: 1) Connell and Slatyers' description of the mechanism by which replacement occurs is given, 2) a listing of what evidence would indicate that the mechanism is working is stated and, 3) evidence is listed. The last part of Chapter III discusses modifications of the inhibition model.

To better understand Connell and Slatyers' model refer to Figure 1. In each of the three models Step 1 is identical, "a disturbance opens a relatively large space, releasing resources." The number of replacements possible over time is related to both the intensity of the disturbance and the size of the area disturbed (Table 1).

FIGURE 1: CONNELL AND SLATYERS' FACILITATION MODEL MECHANISM

NOTE: The dashed lines represent interruption of the process in decreasing frequency in the order w, x, y, and z.

TABLE 1

THE EFFECT OF THE SIZE OF AREA DISTURBED AND
INTENSITY OF DISTURBANCE ON THE
COURSE OF SUCCESSION

Intensity of Disturbance	
<u>Extreme</u>	<u>Slight</u>
<p>Large Area:</p> <ol style="list-style-type: none"> 1. A long succession: Assuming no survivors, all colonists must come from outside, so will consist mainly of early succession species with high vagility of propagules. Since late-succession species have low vagility, they will spread in slowly from the borders. Meanwhile the early species may go through several generations. <p>Small Area:</p> <ol style="list-style-type: none"> 3. Some succession: Surrounding adults colonize, with propagules or vegetative growth. Propagules of distant early-succession species also colonize, but since resources are reduced by the neighboring adults, the early species may not grow as quickly as usual. 	<p>Large Area:</p> <ol style="list-style-type: none"> 1. A moderate amount of succession: The area will be refilled: <ol style="list-style-type: none"> a) by individuals growing from propagules that arrived from distant early-succession species or those that were present in the soil before the disturbance; b) by growth of surviving juveniles of late-succession species that before had been living suppressed in the shade of the adults; c) by resprouting of damaged adults <p>Small Area:</p> <ol style="list-style-type: none"> 4. No succession: The small gap is re-filled by growth of surrounding adults and/or of previously suppressed offspring of the late-succession species.

The Facilitation Model

Connell and Slatyers' Description
of the Mechanism By Which Replacement
Occurs (Figure 1).

At step 2 only "early succession" species can establish themselves. It can be assumed, therefore, that only species with large numbers of propagules, good dispersal abilities, and rapid growth rates can initially establish themselves. At step 3, these early successional species modify the environment making it less suitable for any species with similar characteristics but more favorable for species with poorer dispersal, slower growth rates, but better competitive abilities. At step 4, early successional species facilitate the invasion of later successional species which out-compete them until, at step 5, the species present no longer facilitates the establishment of any other species. At step 6, space is released when a resident is damaged or eliminated.

To summarize, the facilitation model is basically a description of Clementsian, primary succession (Whittaker 1975). Species with early successional, "pioneer" characteristics establish themselves, and modify the environment in such a way that the environment is less favorable for themselves and more favorable for other species. These successive facilitatory changes occur until no species can exist better in the environment than those that are present.

Listing of Evidence Needed to Support the Facilitation Model

If the facilitation model accurately describes the mechanism by which replacement occurs, evidence should be found which supports the following specific statements (see (Table 2, Facilitation)).

The facilitation model would be supported by evidence that shows that a specific series of species replacements must occur. Only certain early successional species may initially invade; facilitatory changes by these early successional species allow for the invasion and establishment of late successional species.

Evidence Supporting the Facilitation Model

Serial Species Replacement Occurs. There is some evidence from heterotrophic, autotrophic and field succession studies that establish serial species replacement. A study of heterotrophic succession in oak and pine logs indicated that the presence of phloem feeding fauna prepared the way for later successional animals (Saverly 1939). Payne (1965) observed a pattern of species replacement among the fauna of carrion (Payne 1965). Reed's (1958) study of paired dog carcasses indicated that species replacement occurred, and that the rate of replacement was faster in pastures than in wooded areas. A succession of arthropod species is involved in leaf litter decomposition (Crossley and Hoglund 1962).

TABLE 2 COMPARISON OF THE MECHANISMS OF THE FACILITATION, TOLERANCE, INHIBITION AND ENVIRONMENTAL MANAGEMENT SUCCESSION MODEL

Process	Facilitation	Tolerance	Inhibition	ENSM
Disturbance (Step 1)	Determined by chance	Determined by chance	Determined by chance	Designed
Invasion (Step 2)	Only early successional species	Any colonizer	Any colonizer	Selected colonizer
Environmental Modifications (Step 3)	a) Less suitable for early successional species b) Advantageous for late successional species	a) Less suitable for early successional species b) Little or no effect on late successional species	a) Less suitable for early successional species b) Less suitable for late successional species	a) Less suitable for early successional species b) Less suitable for late successional species c) Most suitable for self
Effect on individuals (Step 4)	Late successional juveniles facilitated by early successional species	Late successional juveniles grow despite early successional species	All other species inhibited	All other individuals inhibited
Continuation of the sequence (Step 5)	Until resident no longer facilitates invasion, growth of any other species	Until no species exists that can invade and grow in resident's presence	Sequence may not occur colonist persists until removal by physical extremes or natural enemies	No sequence or managed sequence until: 1) managed removal 2) regeneration cycle continued

Microcosm experiments have recorded species replacement (Cooke 1967). Over a period of 15 years, changes in small mammal species and populations in a deciduous forest sere starting from artificially cleared flood plain were recorded (Wetzel 1958).

There is some evidence from autotrophic succession studies that indicate serial replacement. A developmental sequence from a pioneer community, willow-alder thicket, to spruce forest occurs at Glacier Bay, Alaska (Crocker and Major 1955: Lawrence et al. 1967: Reiners et al. 1971). Also, colonization of dunes involves a rise and decline of successive populations of herbs, shrubs, and trees (Cowles 1899: Olson 1958: Kumler 1969).

There is some evidence from marine succession studies that establish serial species replacement. For example, in benthic field tests the algal community preceded the bryozoan community (Scheer 1945). Barnacles provided a surface and preceded the colonization of other organisms (Menge 1976). In marine fouling communities regular patterns of organisms are known to occur (Harger and Tustin 1973a).

Preceding species facilitate subsequent species.

There is some evidence from heterotrophic, autotrophic, and field succession studies, that the sequence of species may result from a preceding species facilitating a subsequent species. In the pine and oak log succession, the phloem

feeding fauna were the only fauna whose presence seemed facilitatory (Saverly 1939). In autotrophic succession studies, facilitatory mechanisms have been observed. On glacial till, Dryas and Alnus help to stabilize the soil and increase the amount of soil nitrogen, thereby aiding the survival mechanism and stimulating the growth of plants without nitrogen-fixing ability (Crocker and Major 1955: Lawrence et al. 1967). Dune colonization studies have revealed that a species with sand binding ability generally precedes a species without this ability (Cowles 1899: Olson 1958).

Field studies also indicate facilitatory mechanisms. For example, Scheer's (1945) benthic field test showed that the algal community not only preceded the bryozoans, but that the algae provided favorable conditions for the settlement of bryozoans. Barnacles provide a surface and may increase the rate at which other organisms colonize (Menge 1976).

Sequence and/or rate of replacement depend on other factors. There is a great deal of evidence supporting the position that the sequence effect, and/or rate of replacement, may be dependent upon or enhanced by factors other than a preceding species facilitating subsequent species. For example, studies have shown that physical factors, differential growth rates, immigration rates, and allelochemicals

affect the sequence and rate of succession.

In heterotrophic succession studies involving insects, the rate of insect species replacement was related to temperature (Reed 1958: Payne 1965.) Seasonality and the amount of moisture was a limiting and a directing factor in population changes in the microfauna of decomposing leaf litter (Crossley and Hoglund 1962). In aquatic environments, also, seasonality affects the succession of organisms (Peterson 1926). In marine fouling communities, seasonal progression of organisms occurs (Scheer 1945: Harger and Tustin 1973a), and domination is determined by the order of larval recruitment (Sutherland 1974).

Another factor that needs consideration is that the immigration rate of a species affects succession. Wetzel (1958) mentions the early arrival of birds. That the rate of species replacement was increased in the pasture area, as compared to the wooded area in Reed's (1958) study, may be related to the proximity of insects to the carrion in pasture areas. Jacobs et al. (1970) found that the main contribution of soil invertebrates and arthropods in decomposition is to excrete particles whose smaller size provides greater surface area for microfloral growth. Excluding insects from carrion (Payne 1965) may have prevented bacterial populations; the role of insects in transferring bacteria needs to be considered as a facilitatory mechanisms in carrion studies.

Some autotrophic succession studies support serial species replacement. Sometimes autogenic changes may be necessary before a subsequent species can establish itself, but a specific series of species, each facilitating the next is not supported by evidence. At Glacier Bay, the pioneer through spruce forest sequence will precede with or without the Dryas (Crocker & Major 1955: Lawrence et al. 1967). Generally Dryas arrives before Alnus because of its wind dispersed fruits. The life history characteristics of the species, as well as chance, affects plant colonization. Without Dryas, soil erosion would probably be more extensive, and it is likely that the lack of nitrogen would probably make it more difficult for shrubs and trees to become established (Lawrence et al. 1967). Alnus, however, is more efficient than Dryas at providing ground cover, enriching soil, building humus and accumulating nitrogen (Crocker & Major 1955: Lawrence et al. 1967). The sequence to spruce forest will occur as long as some species with nitrogen fixing ability is present.

Sand dune succession, too, is not the result of a specific series of species facilitating each other; site diversity results in many alternative series (Olson 1958). Variation in physical factors, especially wind (Cowles 1899), at beaches, fore dunes, and blow outs cause species replacement patterns to vary (Olson 1958). Species distribution

varies and affects species replacement patterns. Different dune forms are caused by differences in life history strategies of dune colonizers; distribution of topographic forms coincide with species distribution (Cowles 1899).

Some field test evidence supports the facilitation model, but in addition to a species facilitating another, other factors may act as facilitatory mechanisms. For example, young saguaro are most likely to survive in sheltered places (Niering et al. 1963). Seedlings more than a few weeks old are generally found in close proximity to a plant or other object, which offers protection (Steenbergh and Lowe 1969). No specific "nurse" species precedes or facilitates young saguaro; any sheltered place, including rocks, suffices (Steenbergh and Lowe 1969).

Allelochemicals may also produce effects which appear to be facilitatory. For example, the brown algae, Eklonia, will settle only on plates with the successional stages carrying arborescent bryozoa. Rather than species facilitation, Eklonia's position in the sequence may be related to allelochemicals (Harger and Tustin 1973).

Conclusion

There is some evidence from heterotrophic, autotrophic and field succession studies that establish serial species replacement (Saverly 1939: Scheer 1945: Crocker and Major 1955: Reed 1958: Wetzel 1958: Crossley and Hoglund

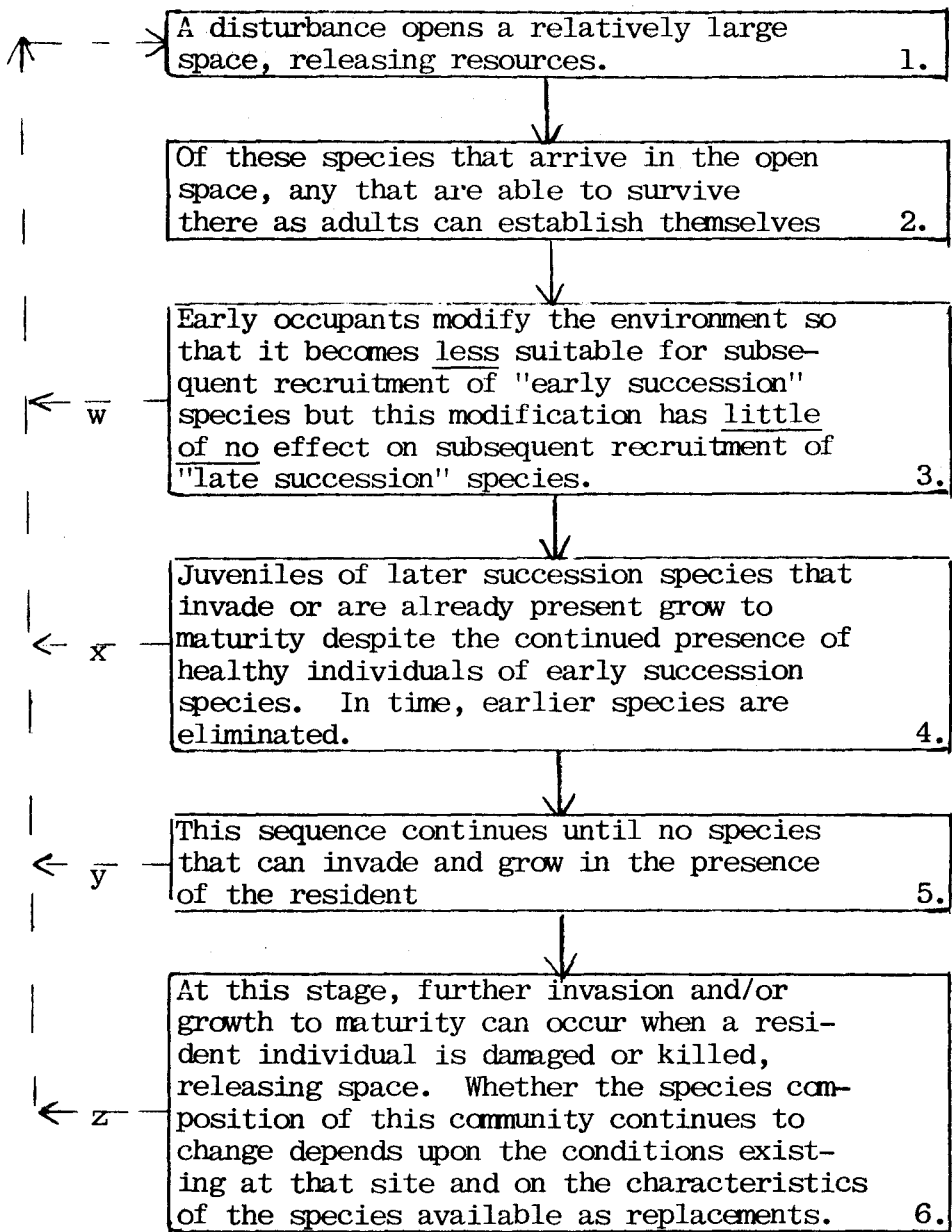
1962: Payne 1965: Lawrence et al. 1967: Reiners et al. 1971: Menge 1976). There is some evidence that the sequence of species may result from a preceding species facilitating a subsequent species (Cowles 1899: Saverly 1939: Crocker and Major 1966: Olson 1958: Lawrence et al. 1967: Menge 1976). There is a great deal of evidence that the sequence effect and/or rate of replacement may be dependent upon or enhanced by temperature, seasonality, differential growth rates, immigration rates, and allelochemicals (Cowles 1899: Peterson 1926: Scheer 1945: Crocker and Major 1955: Olson 1958: Reed 1958: Niering et al. 1963: Payne 1965: Lawrence et al. 1967: Steenbergh & Lowe 1969: Harger and Tustin 1973a and b: Sutherland 1974).

The Toleranc Model

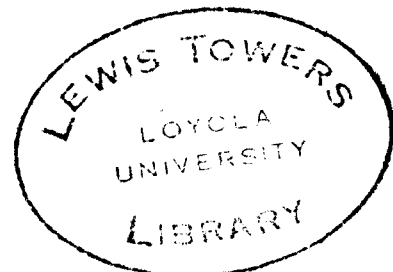
Connell and Slatyers' Description of the Mechanism by which Replacement Occurs (Figure 2).

At step 2, any arriving species (colonist) may be able to establish itself. At step 3, modification of the environment by colonists makes the environment less suitable for early successional species, but these modifications by earlier colonists neither facilitate nor inhibit the rates of recruitment and survival of late successional species. At step 4 species with poorer dispersal and slower growth rate are able to survive in the presence of earlier colonists because of their ability to tolerate "lower levels

FIGURE 2: CONNELL AND SLATYERS' TOLERANCE MODEL MECHANISM



NOTE: The dashed lines represent interruption of the process in decreasing frequency in the order w, x, y, and z.



of resources." At step 5 the sequence continues until there is no species that can invade and grow in the presence of the resident.

To summarize, the Connell and Slatyer tolerance model states that any colonizer species may be able to establish itself. According to their model, modifications of the environment by early colonists have little or no effect on later colonists ability to grow to maturity.

Listing of Evidence Needed to Support the Tolerance Model

If the tolerance model accurately describes the mechanism by which replacement occurs evidence should be found which supports the following specific statements (page 26, Table 2, Column Tolerance).

1. Any species can establish itself.
2. Environmental modifications become, a) less suitable for early successional species and b) have little or no effect on late successional species.
3. Late successional species grow despite the presence of colonists.
4. Sequence continues until no species exist that can invade and grow in the presence of the resident.

The tolerance model would be supported by evidence that shows that initially any species may be able to establish itself, and that colonizers have little or no effect on late successional species.

Evidence Supporting the Tolerance Model

Any species may colonize. There is a good deal of evidence to suggest that any colonizing species may be able to establish itself. Up to the time of abandonment, an old field is receiving seeds and harboring dormant roots, and successional development occurs from this initial flora (Egler 1954). In Piedmont fields, pine may come in during the first year (McQuilkin 1940). The majority of woody plants in an old field succession appear to have invaded at the time the field was abandoned (Niering & Egler 1955). The pin cherry buried seed strategy allows it to become established immediately following a disturbance (Marks & Bormann 1972: Marks 1974).

Early colonists have little or no affect on late succession species. That modifications of the environment by early colonists have little or no affect on late succession species does not appear to be supported by evidence. There is evidence, however, to support the fact that species are tolerant, in the sense that they grow at a decreased rate, or reach maturity despite the presence of other species (Billings 1938: Woods and Shanks 1959: Collins 1961). When a resource is released, the tolerating species may be able to utilize the resource for its own benefit. Collins (1961) found greater growth and less mortality of maple under gypsy moth defoliated oak: increased light and nutrient

rich frass allowed maple to increase food reserves. Billings (1938) found that hardwoods, which had been secondary trees, rapidly assumed dominance as mature pine was eliminated.

Connell and Slatyer specify, with respect to the tolerance model, that later species are able to grow at "lower levels of resources." Resources do not always decrease; they may increase or fluctuate with time. For example, carbon increased at a reduced rate in a spruce forest and total nitrogen increased in the alder-spruce transition (Crocker & Major 1955). Peat accumulation raises the bog surface and often causes a rise in the water table and increases the availability of water as a resource (Heinselman 1963). Light is a changing resource at Glacier Bay: as spruce die, gaps in the tree canopies occur, and by the muskeg stage 45% of the cover is by the light requiring moss stratum (Reiners et al. 1971).

Conclusion

Evidence supports the position that any colonizing species may be able to establish itself (McQuilkin 1940: Egler 1954: Niering & Egler 1955: Marks & Bormann 1972: Marks 1974). Evidence does not support the position that early succession species have little or no effect on late species (Billings 1938: Wood and Shanks 1959: Collins 1961). Evidence does support, as Connell and Slatyer suggest, a community composed of species specializing on

different kinds, or proportions of resources (Grubb 1977).

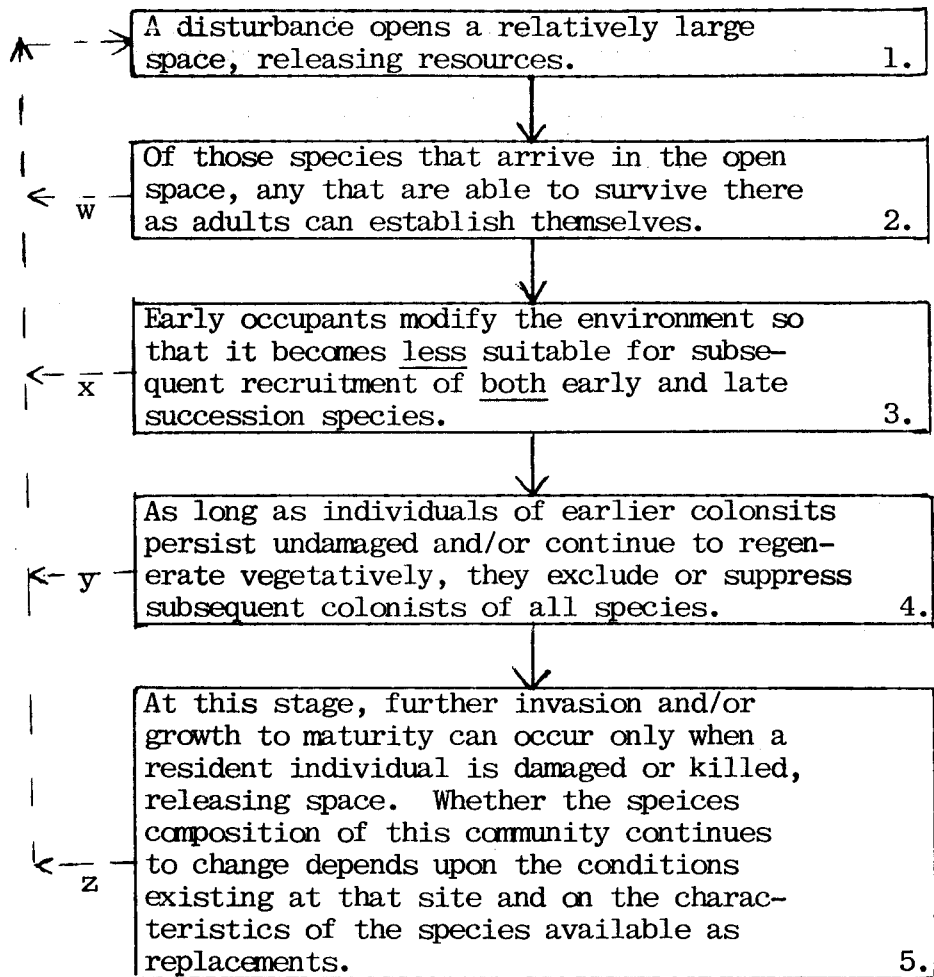
The Inhibition Model

Connell & Slatyer's Description
of the mechanism by which Replacement
Occurs (Figure 3).

At step 2, of the arriving species, any arriving colonist may be able to establish itself. At step 3, modifications of the environment by the colonist makes the environment less suitable for both early and late succession species. At step 4 colonists are able to inhibit and exclude all species. Replacement occurs when an individual is eliminated by physical extremes and/or natural enemies. The replacing species need not have superior competitive ability, or different life history characteristics.

To summarize, the Connell and Slatyer inhibition model states that any colonizer species may be able to establish itself. Colonizers inhibit the establishment of all other species and persist until eliminated by physical extremes and/or natural enemies.

Listing of evidence needed to support the Inhibition Model. If the inhibition model accurately describes the mechanism by which replacement occurs evidence should be found which supports the following specific statements (Table 2, Column Inhibition).

FIGURE 3: CONNELL AND SLATYERS' INHIBITION MODEL MECHANISM

NOTE: The dashed lines represent interruptions of the process in decreasing frequency in the order w, x, y, and z.

1. Any species can establish itself.
2. Environmental modifications become less suitable for both early and late successional species.
3. Colonizers exclude and inhibit all other species and persist until eliminated by physical extremes and/or natural enemies.

The inhibition model would be supported by evidence that shows that once established, colonizer species exclude and inhibit the invasion and establishment of any species. Colonists are not replaced until they are eliminated by physical extremes and/or natural enemies.

Evidence Supporting the Inhibition Model

As mentioned previously (Tolerance Section) there is significant evidence that any arriving species may be able to establish itself.

Colonizers modify the environment and inhibit all other species. There is a large body of evidence that steps 3 and 4, colonizers modify the environment and inhibit the invasion and establishment of other species, are reasonable. Keever (1950) found that aster would probably dominate a field a year earlier without the presence of horsetweed or another large annual. In spruce stands, short leaf pine seeds have difficulty germinating and lack of light usually eliminates seedlings within one year (Billings 1938).

Many marine experimental analyses indicate an inhibitory mechanism. For example, in the marine fouling community,

resident species inhibited the recruitment and growth of other species; changes in the community depended upon larval ability to invade existing adults (Sutherland and Karlson 1977). Sousa (1979) concludes that early colonists secure the space and light and resist the invasion of subsequent colonists. Only when death of an early species opens a space can later species colonize and grow to maturity. In another study, mature sponge-anemone-ophiuran community inhibited the development of a primary community on adjacent clean plates (Goodbody 1961). Goodbody suggests that larval settlement might have been prevented, or that the high filtration rate of the sponge community might have depleted the surrounding water of food for colonizers, or that allelochemicals might kill young stages.

Species persistence is dependent upon physical extremes and/or natural enemies. There is evidence supporting the position that species persistence is dependent upon physical extremes and/or natural enemies. The role of physical extremes and natural enemies is an extremely important part of Connell and Slatyers' inhibition model because they act as the replacement mechanism. In the facilitation model, for example, replacement ends when a species is no longer being facilitated by other species. In the tolerance model replacement ends with the species that is best "tolerant," often this means the most long lived, or the best

competitor. In the inhibition model serial species replacement may not even occur. The colonizer is eliminated through the action of physical extremes and/or natural enemies. The colonizer is not necessarily out-lived or out-competed.

Physical extremes and natural enemies are cited in the literature which follows as affecting vegetation persistence. A species that reproduces vegetatively may often inhibit other species. For example, Viburnum lentago communities resist tree invasion because they reproduce from root suckers (Niering and Egler 1955); rabbit grazing promotes suckering. Thirty years of heavy pasturing and burning prevented abandoned fields in Kansas and Oklahoma from becoming prairie (Booth 1941). Dropseed, protected from grazing animals, was not replaced by longer lived perennials (Tomanek et al. 1955).

Relative palatability of species may also influence early successional processes (Booth 1941: Whittaker & Feeny 1971: Cates and Orians 1975: Sousa 1979). Although the fraction of mature plant consumed is small, the consumption of seedlings may be important (Whittaker 1970).

Studies in aquatic environments also cite the role of natural enemies and physical extremes in successional processes. In the benthic community of McMurdo Sound,

Dayton et al. (1974) listed predation on sponges by the asteroids and nudibranchs as an important component maintaining community stability. In the marine epifaunal community as another example, time and frequency of disturbance determine when and how often a site is available for colonization (Osman 1977). More frequent disturbances result in low species diversity and continual colonization. Less frequent disturbance results in a greater diversity of species (Osman 1977). Species which dominate early in a succession are more susceptible to physical disturbance and are eliminated (Sousa 1979).

Conclusion

There is evidence that colonizers exclude and inhibit the invasion and establishment of other species (Billings 1938: Keever 1950: Goodbody 1961: Sutherland & Karlson 1977: Sousa 1979). There is evidence that species persist until they're eliminated by physical extremes and/or natural enemies (Tansley 1935: Booth 1941: Niering and Egler 1955: Whittaker and Feeny 1971: Dayton et al. 1974: Cates and Orians 1975: Osman 1977: Sousa 1979).

General Modifications of the
Inhibition Model

Allelopathy

Connell and Slatyer did not include allelopathy in their inhibition model, but it can act as an inhibitory mechanism. Allelopathy, interspecific inhibition through the release of chemicals, has been observed in many plant populations (Rice 1964: Whittaker and Feeny 1971: Drury and Nisbet 1973: Gant and Clebsch 1975: Stowe and Osborn 1980). A species that releases chemicals that do not negatively affect its own survival rate, but prevents competitors from utilizing resources, will have a selective advantage in its contribution to the next generation (Bonner 1970). Inhibition, through allelopathy, seems more reasonable an adaptation than does a species facilitating another species at its own expense (Drury and Nisbet 1973). Allelopathic suppression might enable a species to increase its rate of invasion, or to delay its potential replacement (Whittaker and Feeny 1971). It is also possible that less extreme allelopathic interactions might slightly increase a species competitive ability and the likelihood of its persisting (Newman and Rovira 1975).

Inhibition of nitrogen-fixing bacteria by pioneer species with low nitrogen requirements is probably an

important competitive mechanism (Rice 1964, 1972). The persistence of the climax community may be related to nitrification inhibition that reduces energy requirements for metabolic transfer of nitrogen into amino acids (Lodhi 1982). Plants growing under nutrient stress produce more phenolics; allelopathy with phenolics is most likely on nutrient poor soils (Stowe and Osborn 1980).

Autotoxicity, intraspecific allelopathic inhibition, has been reported for a number of species (Pratt and Fong 1940; Whittaker and Feeny 1971). Autotoxicity may be interpreted as a positive inhibitory strategy if, for example, it results in a intraspecific resource partitioning. Fungi produce staling substances that inhibit growth of hyphae toward one another (Whittaker and Feeny 1971). Went (1970) describes this same effect with Parthenium argentatum. Autotoxicity of older cultures of Chlorella vulgaris (Pratt and Fong 1940) have been found to slow the filtering rate of Daphnia and perhaps aid the algae to escape microcrustacean grazers (Whittaker and Feeny 1970).

Natural Selection

Drury and Nisbet (1963) originally used the terms "facilitation" and "inhibition" to describe species effects, but the mechanisms of these processes were not delineated. However, Drury and Nisbet (1963) mentioned that it is

important to interpret community behavior in terms of natural selection acting on the individual organism. The inhibition model, by hypothesizing that individuals that survive are those that possess characteristics that allow them to persist at a specific type of site by inhibiting all other species, is compatible with natural selection. When a disturbance opens a gap, which species colonizes is determined by life history characteristics of the available species interacting with physical factors. Chance plays a role in the initial establishment stage. Once a species establishes itself, its physically taking up space would inhibit other species. Dense grass or shrub can resist tree invasion for decades (McQuilkin 1940: Niering & Goodwin 1974) and complete cover prevents the invasion of species into a patch (Miles 1979).

The Regeneration Niche

The pattern of species replacement determines whether a community will change. If a species is replaced by the same species no change occurs. Grubb (1977) uses the term "regeneration niche" to define the niche made available through the process of species replacement. The many differences between species in their requirements for regeneration is an important part of maintaining species richness in plant communities (Grubb 1977). Knowing what species is

likely to enter the regeneration niche is important in order to predict successional sequences. The inhibition model suggests that a species with vegetative propagation would reenter and replace itself. For example, Tilia americana reproduces through stump sprouts and establishment replaces itself in the maple-basswood forest without seedlings (Bray 1956).

Life History Characteristics - Especially Differential Growth

Larger gaps are likely to contain many species.

Grubb (1976) mentions the importance of differences in life form, seasonal development, mixtures of species, and variations in competitive ability with physiological age as factors affecting successional processes. Differences in growth rates results in the early domination of faster growing plants and may explain what appears to be successional replacement of herbs, shrubs, and trees (Olson 1958).

Barclay-Estrup (1969) uses Watt's description of four growth phases to describe the life cycle of Calluna vulgaris. Vegetative patches are influenced by the life history of the dominant species passing successively through the pioneer, building, mature, and degenerate phases. During the pioneer phase Calluna cover is small and other vascular plants are prominent. During the building phase Calluna almost completely excludes all other plants. Though Calluna is prominent during its mature phase, bryophytes are common

and other vascular plants appear. During the degenerate stage the patch is relatively open; old Calluna is in decline but its seedlings are present, bryophytes are at a maximum and vascular plants are increasing (Barclay-Estrup 1969). Cyclical changes occur within the patch. There are fluctuating populations out of phase with one another.

The degenerate phase may be critical in terms of species replacement in the regeneration niche. For example, dominance of Calluna is dependent upon the continual production of a fungi-toxic factor. During the degenerate phase allelopathic activity is reduced and birch may be able to replace Calluna (Robinson 1972). Senescent plants are susceptible to death from both physical extremes and natural enemies (Blais 1954: White 1974). In the inhibition model, physical extremes and natural enemies are cited as increasing mortality rates. A species that is able to resist physical extremes and natural enemies, especially during the degenerate phase of a life cycle, may be able to replace itself in the regeneration niche and inhibit other species replacements.

Role of Chance

Predictions of successional sequences are difficult because chance can combine many variables of 1) physical factors and, 2) life history characteristics. Some physical

factors which should be considered are type, severity and frequency of disturbance, and the size, location, and surroundings of the gap. Life history characteristics of species vary, and chance, depending on when in a life cycle an event occurs, is important.

Life history characteristics, changing physical factors, and chance probably account for the variable successional patterns reported in the literature (Cowles 1899: Olson 1958: Heniselman 1963). Rate of change in soil properties at Glacier Bay is dependent upon chance dispersal and the resulting micro-patterns of plant colonization (Crocker and Major 1955). Direct linear sequences on the dunes are infrequent because of site diversity (Olson 1958).

Conclusion

An inhibition model which emphasizes the role of natural selection best describes the mechanism used by organisms to survive. To predict successional sequences the importance of the regeneration niche has to be recognized. To interpret succession as a mechanistic process, an understanding of life history characteristics, especially differential growth rates, and the role of chance interacting with physical factors, is needed. In man managed systems, species, physical factors (like fire and flood) and natural enemies, are to some extent controllable. Reducing the number of variables may make it possible to predict or

regulate "vegetation development" (Niering and Goodwin 1974).

Chapter IV will incorporate the modifications discussed in this Chapter into a revised inhibition model designed for environmental management situations.

CHAPTER IV

THE ENVIRONMENTAL MANAGEMENT SUCCESSION MODEL (EMSM)

Introduction

It is important to note that the three succession mechanisms hypothesized by Connell and Slatyer may all operate simultaneously as viable processes. All three mechanisms are supported by some evidence. There is also evidence, as mentioned in the last chapter, supporting modification of Connell and Slatyers' inhibition model.

This chapter will present my Environmental Management Succession Model (EMSM). This model is a modified inhibition model that has been further revised for environmental management purposes. Chapter IV begins by examining, in greater depth, Connell and Slatyers' inhibition model in three ways. First, the mechanism of inhibition will be described. Second, the process through which the mechanism can be interrupted will be described. Third, the community structure generated by their inhibition model will be discussed. This examination will provide a basis for comparison and contrast with my Environmental Management Succession Model.

Detailed Description of Connell and Slatyers'
Inhibition Model as it Applies to the EMSM Model

The Mechanism (Figure 3)

A disturbance opens space. The number of species replacements possible over time is related to both the intensity of the disturbance, and the size of the area. Connell and Slatyer suggest a range in length of succession, from a long succession, if the disturbance is extreme over a large area, to no succession, if disturbance is slight and the area small (Table 1).

In general, early invaders are likely to be species with large numbers of propagules and good dispersal ability. However, species with few seeds and poor dispersability, can establish themselves, if a seed source is close.

Once established, a colonizer inhibits the invasion of any subsequent species. The colonizer modifies the environment so that it is less suitable for recruitment of both early and late species.

The colonizer species inhibits the invasion of other species and persists as long as it continues to regenerate vegetatively, or is undamaged.

Replacement is possible only when a resident is eliminated by physical extremes and/or natural enemies.

Interruption of the Process

The inhibition process can be interrupted when early species are killed by local disturbances caused by physical extremes or natural enemies. Interruptions may occur at each step, 2 through 5. If an interruption occurs at step 2, the process reverts to step 1, etc. In an interruption occurs at a later step, and if species with late successional characteristics have been accumulating, the chance that a seedling of a late successional species will be available to replace an early resident is increased. Connell and Slatyer predict a sequence of decreasing frequency of major disturbance from step 2 through step 5.

Community Structure

If an early resident is replaced by the same species, or by another early successional species, a traditional succession sequence will not occur. If an early resident is replaced by a species with late successional characteristics, Connell and Slatyer conclude that the inhibition mechanism would lead to a community of longer lived species. This conclusion is based on the premise that if a series of species replacements occurs, the pattern will tend to be from shorter to longer lived species. The pattern would develop because shorter lived species are replaced more frequently and gradually decline in abundance, while the longer lived species accumulate.

Detailed Description of the Environmental
Management Succession Model

The EMSM is designed for direct application to environmental management situations. It is based upon the hypothesis that it is possible to direct successional processes, rather than alter or deflect a known sequence in an unpredictable direction, which has been done in the past. The EMSM manipulates successional processes to encourage the development of a community that is management desired.

The EMSM is unique both in its approach and in its method. First, the model presents a new approach to environmental management that is based on recent succession theory. Traditional theory is still being used, for example in range management, and it is not being effective. As in most technological fields, there has been a considerable time lag between development of new theory and then application in management. A new framework based on recent succession theory is needed. The EMSM is an attempt to incorporate some of the changing interpretations of succession theory into a more effective model that can be applied in an environmental management setting.

Second, the methodology of the EMSM is also different. The model utilizes life history characteristics, competitor and predator interactions, and abiotic factors to regulate the environment. The EMSM is an alternative to herbicides or

other intensive methods of environmental control. The model suggests that species sequences and rates of replacement can be manipulated to obtain management objectives.

The EMSM Process

Specific references in support of the EMSM approach to environmental management will be presented in the next two chapters. The following sections are simply a general description of the model. The EMSM is a 5 step process determining the course of succession in a management situation. (Figure 4).

Designed disturbance. A disturbance is chosen to modify the physical, spatial, and temporal structure of a community so that the subsequent sequence and rate of replacement are regulated. The sequence and rate of replacement are related to the frequency of disturbance and the diversity of the system (Table 3).

Selective colonization. A management selected colonizer becomes established, initiating the desired sequence. Selection of the colonizer species is based upon management preferred characteristics, for example, differential growth rate, method of reproduction, production of allelochemicals, or

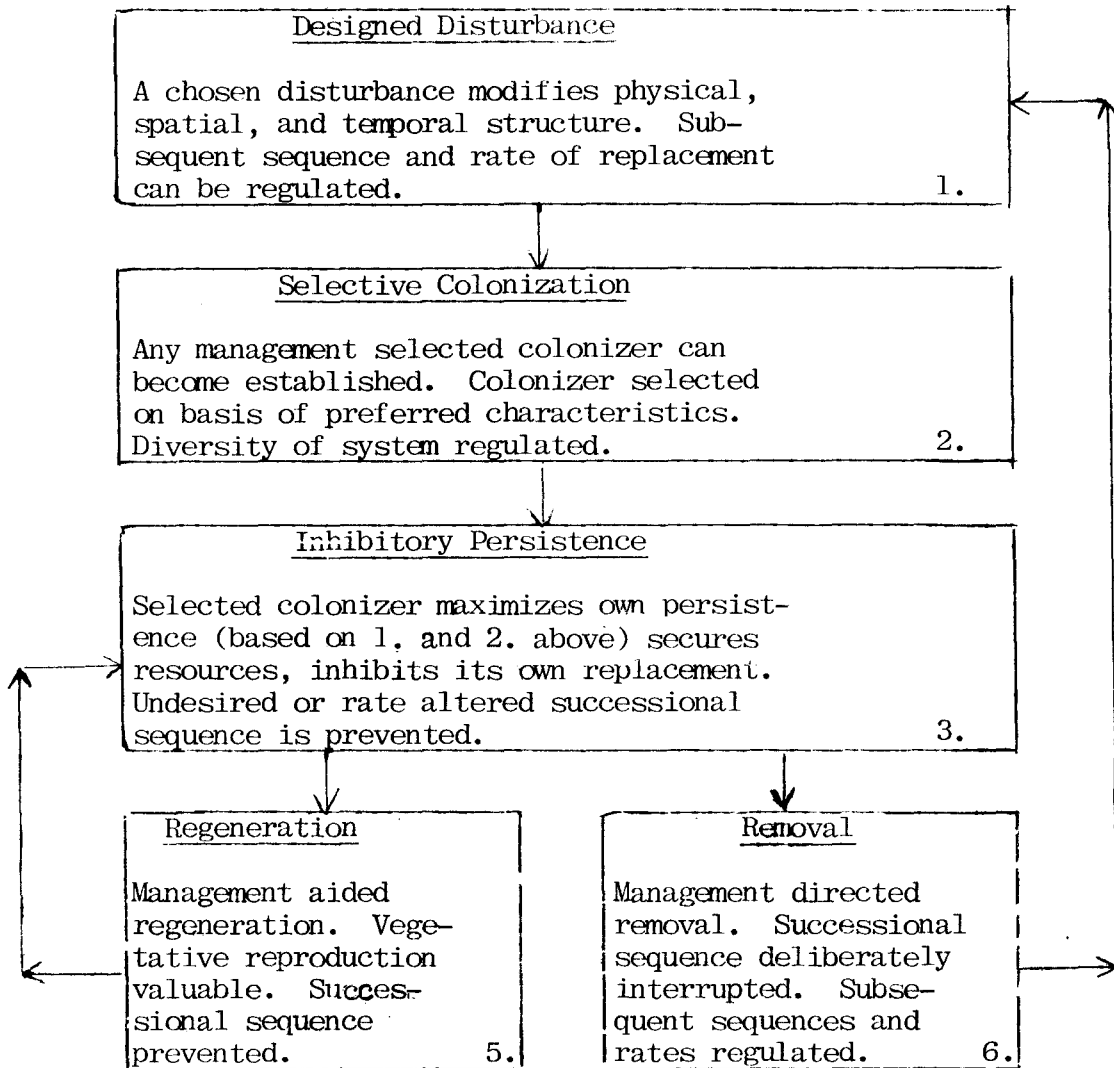
FIGURE 4: ENVIRONMENTAL MANAGEMENT SUCCESSION MODEL

TABLE 3: THE EFFECT OF FREQUENCY OF DISTURBANCE AND SPECIES DIVERSITY ON THE COURSE OF SUCCESSION

<u>FREQUENCY OF DISTURBANCE</u>	
H I G H	L O W
<p><u>High Diversity</u></p> <p>1. a) Sequence: can vary, many options, long</p> <p>b) Rate: faster</p> <p>High probability of a species being available to become a part of a sequence or to affect rate of replacement. High probability of the sequence being interrupted or rate being altered.</p>	<p><u>High Diversity</u></p> <p>2. a) Sequence: can vary, many options, longest</p> <p>b) Rate: slower</p> <p>Higher probability of a species being available to become a part of the sequence or to affect the rate of replacement. Low probability of the sequence being interrupted or rate being altered.</p>
<p><u>Low Diversity</u></p> <p>3. a) Sequence: fewer options, very short</p> <p>b) Rate: fast</p> <p>Low probability of a species being available to become a part of the sequence or to affect the rate of replacement. High probability of the sequence being interrupted or rate being altered.</p>	<p><u>Low Diversity</u></p> <p>4. a) Sequence: fewer options, short</p> <p>b) Rate: slow</p> <p>Low probability of a species being available to become a part of a sequence or to affect the rate of replacement. Low probability of a sequence being interrupted or the rate being altered.</p>

ornamental value. Establishment of the colonizer is enhanced by choice of the appropriate disturbance in step 1. Other variables, such as diversity of the system, are also manipulated at this step to regulate subsequent sequences and rates of replacement.

Inhibitory persistence. The established colonizer prevents undesired successional sequences, or alters the rate of species replacement. The established colonizer persists for three reasons. First, the disturbance was designed for persistence of a specific selected colonizer. Second, at step 2, the management selected life history characteristics of the colonizer, for example, vegetative reproduction or differential growth rate, or production of allelochemicals help the colonizer to persist. Also, at step 2, the controlled system diversity has been manipulated to insure persistence. Third, once established the colonizer secures the available space, time and resources and inhibits the invasion of growth of other species. Together, these three factors constitute an inhibiting step that enhances the ability of the colonizer to persist.

Removal. A planned interruption of the process occurs at removal. If desired, for example the managed harvest of a crop, the successional sequence can be deliberately interrupted to achieve management goals. Subsequent sequences and rates can thereby be regulated. The cycle represented by

steps 4 through 1 may or may not change the community structure. If the individual removed is replaced by an individual of the same species, the community composition stays the same. If the individual is replaced by an individual of a different species, the community composition changes. Controlled removal would result in predictability of future community composition.

Regeneration. Further successional changes can be prevented, if the colonizer reproduces vegetatively. Management methods can aid species in acquiring and maintaining metabolic reserves necessary for regeneration. The cycle represented by steps 3→5→3, regeneration, would assure that the community structure stays the same. If individuals replace themselves, future community composition is predictable.

Successional Processes And Their Management Effects

The EMSM manipulates four categories of successional process variables: life history characteristics, competitor interactions, predator interactions, and abiotic factors to direct successional sequences and rates of replacement. The parameters of frequency of disturbance and species diversity best integrate these variables. (Table 3)

In more diverse systems the probability of a species being available to become a part of a successional sequence,

or to affect the rate of replacement through competitor predator interactions, is greater. How life history characteristics, like differential growth or growth cycle, are apt to affect the sequence or rate of replacement are, of course, important considerations. In highly diverse systems, successional sequences are more likely to vary. If there is a high frequency of abiotic or biotic disturbance, the rate of replacement is likely to be faster, and the length of the successional sequence shorter, than is possible in a diverse system with a low frequency of disturbance.

In systems with low diversity, the probability of a species being available to become a part of a successional sequence, or to affect the rate of replacement through competitor-predator interactions is less likely. If there is a high frequency of abiotic or biotic disturbance, the length of the sequence is apt to be very short and the rate of replacement fast. If there is a low frequency of disturbance, the successional sequence is likely to be short, because of the low diversity, and the replacement is likely to be slow.

The goal of managed systems is to control species and abiotic factors. The EMSM manipulates the successional process variables to generate specific management effects.

Table 4 suggests some general ways through which successional process variables can be managed to regulate successional sequences and rates. These are discussed for each step in

TABLE 4: SUCCESSIONAL PROCESSES AND THEIR MANAGEMENT EFFECTS

Successional Process	Variables	Examples Of Management Practices	Possible Management Effects
Designed Disturbance (step 1)	Frequency, type, intensity of disturbance. Size of disturbed area. Biological and physical components of disturbed area and periphery.	Burn, flood Mechanical manipulation (Tilling, chaining) Grazing	Release resources Remove or control undesired species. Maximize success of desired species at steps 2 and 3.
Selective Colonization (step 2)	Life history characteristics: ornamental value, growth rate, method of reproduction. Species diversity: species mixtures, seed bank, etc.	Polyculture Hybrid seed Hedge rows	Regulate herbivore populations. Maximize yield. Increase predator populations.
Inhibitory Persistence (step 3)	Life history characteristics: differential growth rates, vegetative reproduction. Allelochemicals.	Rotation Deferment Rest "Trap" crops	Maximize life span. Suppress growth rate of undesired species.
Removal (step 4)	Life history characteristics: differential growth rates, growth stage cycle - (especially "degenerate" stage). Timing - (planned) to avoid chance removal by natural enemies/physical enemies.	Planned timed harvest of cereals, timber, etc. Rotation - heavy grazing.	Maximize yield. Reduce loss by natural enemies or physical extremes Eliminate undesired species. Regulate species diversity.
Regeneration (step 5)	Life history characteristics: vegetative reproduction. Growth stage cycle especially at pioneer and degenerate stage.	Rotation grazing or other moderate form of predation. Pruning.	Regeneration of vegetatively reproducing species.

the EMSM below. Specific examples of the management effects of manipulating successional process variables will be presented in the next chapters.

Designed disturbance. Type, frequency, and intensity of disturbance can be managed. Size of the area, as well as the biological and physical components of the disturbed area and periphery affect diversity and need to be considered. These variables are manipulated through techniques such as burning, flooding, chaining, or grazing. The disturbance is chosen to release resources, or remove or control undesired species. The methods are designed to regulate successional sequences to maximize the persistence of desired species at the later steps.

Selective colonization. Life history characteristics and species diversity are two main considerations. Individuals or species can be selected for colonization based on any management preferred life history characteristic, e.g., method of reproduction. Predator and competitor interactions can be regulated by manipulating diversity in regard to numbers, proportions, and kinds of species selected for colonization. Polyculture and hedge rows are examples of methods that manipulate the diversity of the system. The subsequent competitor and predator interactions are related to the diversity of the crop system. Methods can be selected

with the intent of regulating subsequent successional sequences and rates. Management methods can use successional process variables to regulate herbivore populations, or to increase predator populations, or to maximize yield.

Inhibitory persistence. Ability to persist is related to the appropriateness of step 1 and 2, as well as the colonizers' ability, once it is established, to secure the available space, time and resources. Production of allelochemicals or vegetative reproduction can, for example, aid the individual to persist. Range techniques such as rest, or deferment, can maximize life span. "Trap" crops can be used to enhance species persistence by suppressing the growth rate of an undesired species and decreasing its ability to enter the successional sequence.

Removal. The successional sequence can be deliberately interrupted through managed removal. Life history characteristics relating to differential growth rates, and growth stage cycles, can be manipulated. For example, during the degenerate stage increased mortality, related to abiotic factors and competitor and predator interactions, can be controlled through timed removal. Planned, timed harvest can prevent chance uncontrolled removal. Timed removal can allow maximum biomass to be harvested before insects or fire remove the crop. Planned timed removal can also regulate future replacement sequences. For example, a crop can be removed before

an herbivore hatches.

Regeneration. Successional sequences can be prevented, and community composition maintained, especially if the selected colonizer reproduces vegetatively. Management methods like rotation grazing, or some other controlled form of predation can stimulate vegetative reproduction and aid in the regeneration process. The likelihood of increased mortality during the pioneer and degenerate stage of the growth cycle would be variables to be considered in managing species regeneration.

Interruption of the Process

The EMSM suggests that interruptions in the successional process can be eliminated or timed to be maximally effective. Management practices can preferentially direct the timing, type, frequency and intensity of interruptions. For example, decisions at step 1 and step 2 would make the probability of interruption less likely at step 3, and would emphasize persistence. Definite interruption of the process at step 4 would be management directed. At step 5, regeneration, management practices would attempt to make the probability of interruption very unlikely.

Community Structure

The EMSM suggests that it is possible for management methods to direct the development of any one of three possible

community structures.

A community of longer lived species. Shorter lived species are replaced more frequently and gradually decline in abundance; longer lived species eventually accumulate (Connell and Slatyer 1977).

A relatively unchanging community. Vegetative reproduction, non-severe infrequent disturbance, and predation would increase the probability of this type of community structure (Tomanek et al. 1955: Niering and Goodwin 1974). Viburnum lentago communities reproduce vegetatively and rabbit grazing, which promote vegetative reproduction, aids in maintaining the relatively unchanging community structure (Niering and Egler 1955).

A constantly changing community composed of species of the same successional level. Frequent disturbance, severe competition, and predation would increase the probability of this type of community structure (Dayton et al. 1974: Menge 1976: Sousa 1979). In the marine epifaunal community, for example, frequent disturbance results in continual colonization (Osman 1977).

Comparison of Connell and Slatyers' Inhibition Model and the EMSM

The Connell inhibition model is not a management model. The EMSM is designed for environmental management application. At each step of the EMSM management practices are designed to produce management effects. The EMSM is based on the

premise that in managed systems chance can be to some degree controlled, and that successional sequences and rates can be manipulated.

The Connell and Slatyer inhibition model emphasizes the variables of physical extremes and natural enemies in the replacement process. The EMSM categorizes successional process variables into life history characteristics, competitive interactions, predator interactions, and abiotic factors. While the Connell and Slatyer inhibition model does not specifically examine the effects of the interactions of variables, the EMSM outlines categories of successional process variables and manipulates these interacting variables.

The inhibition model does not include allelopathy or autotoxicity as an inhibitory mechanism; the EMSM does. Allelochemicals are important in the EMSM step 3, where they might help an individual to persist. Also, the Connell and Slatyer inhibition model does not examine the effect of differential growth rates and growth cycles on persistence. The EMSM emphasizes that both differential growth rates and growth cycles are important in predicting both the availability of the regeneration niche, and the susceptibility of species elimination by abiotic factors and/or competitor and predator interactions. To increase the probability of a predictable community structure, the effect of differential growth rates and growth cycles has to be considered.

The Connell and Slatyer model concludes that if an early resident is not replaced by the same species or by another early successional species, inhibition would lead to a community of longer lived species. Depending on management practices, the EMSM can direct the development of any one of three possible communities: 1) a community of longer lived species, 2) a relatively unchanging community, and 3) a constantly changing community of species of the same successional level.

Connell and Slatyer conclude that the number of species replacements possible over time is related to the intensity of the disturbance and the size of the area. Long, moderate, some and no succession courses reflect the varying lengths of time for immigration based upon size of the area. (Table 1) To direct the development of management desired communities, the EMSM concludes that successional sequences and rates of replacement are best related to the frequency of disturbance and the diversity of the system.

The Connell and Slatyer inhibition model states that the likelihood of interruption of the process decreases from step 2 through step 5. Even in an unmanaged environment, the frequency of some types of disturbance may vary or even increase through Connell and Slatyers' step 2 through 5. The likelihood of fire, for example, may increase in a senescent stand. The EMSM on the other hand, suggests that interruptions in the process can be regulated. Management decisions at steps 1 and 2 would make the probability of

interruption less at step 3, and definite at step 4. At step 5, management practices would reduce the likelihood of interruption.

Evidence Needed to Support the EMSM

If the EMSM accurately describes a mechanism through which replacement can occur, evidence should be found which supports the following statements.

- 1) Designed disturbance can regulate the sequence and rate of replacement.
- 2) Any designed sequence of species, or individuals, can become established.
- 3) Successional sequences can be prevented, or rate of replacement can be altered.
- 4) The successional sequence can be preferentially interrupted. Subsequent sequence and rate can be altered.
- 5) Successional sequences can be prevented, or rate of replacement slowed.

Some related evidence which supports the likelihood of the EMSM being a viable process model has been mentioned in the last sections of Chapter III. Further information supporting the probability of the EMSM mechanism, process of interruption, and possible community structure will be presented in Chapters V and VI. Chapter V explores the general application of the model to urban and regional planning, range management, and agriculture. Chapter VI more specifically applies the model to water management issues.

CHAPTER V
GENERAL APPLICATIONS OF THE EMSM

Introduction

Chapter V is divided into three main sections. Each of the three sections will apply the EMSM to a different environmental issue: right-of-way management, range management, and agricultural management. The goal of this chapter is not a quantitative analysis of the model, but rather an exploration of how the model's approach would modify current management practices.

In each of the sections some typically encountered management problems are described, and current management practices that alleviate these problems are discussed. Finally, the management problems are viewed via the EMSM to explore the ramifications of the EMSM approach for achieving management goals. The focus of each section will be to:

- 1) Assess the successional process variables and determine which successional process variables are most pertinent.
- 2) Determine management goals.
- 3) Suggest methods through which the successional process variables can be manipulated, via the EMSM, to reach management goals.

Urban and Regional Planning -(Right-of-Way Management)

Urban and regional planning involves systematic advance preparation to meet human needs, direct economic development, and efficiently manage natural resources. As an example of urban and regional planning, management of right-of-ways will be explored in a successional framework.

Right-of-ways are those "narrow threads of land which serve for transportation and communication of men and materials" (Egler 1949). They form an extensive interconnected network of acreage through urban and regional zones, and it is estimated that at least 50,000,000 acres in the United States are involved with electrical utilities, pipelines and roadside right-of-ways (Niering 1958). Right-of-way management provides a good example of the dilemma inherent in urban and regional planning, because local, state, and federal jurisdictions are involved in administration of the same area.

Right-of-ways are now, or have been, managed on the basis of the traditional succession model and its deterministic sequence of species replacements. Management practices are directed toward temporarily setting back the sequence, but the inevitability of "progress" toward the climax vegetation is accepted. The use of chemicals, mowing, burning, or cutting as management practices is governed by

the expectations of the traditional succession model.

Chemical and mechanical control has not prevented re-invasion of tree seedlings (Egler 1949: Egler 1958: Niering and Goodwin 1974). Management techniques for right-of-ways are only temporarily effective, and constant re-applications of herbicides, and/or mechanical procedures are necessary. The use of herbicides and mechanical procedures result in loss of wild life habitat and species diversity, unaesthetic "brown-outs" and erosion.

Concern for indiscriminate herbicide use led to the Connecticut Arboretum right-of-way demonstration study area in which ecological techniques were employed to develop stable shrub communities. For fifteen years, areas of dense shrub cover resisted tree invasion (Niering and Goodwin 1974). The Connecticut study is an excellent and successful example of the search to find ecological techniques for right-of-way management, when the application of the traditional succession model has not been effective. This in turn challenged traditional ecological theory and was a major factor leading to the development of new theory upon which the EMSM is based. Although Niering and Goodwin (1974) demonstrated that it is possible to maintain stable right-of-ways, they did not incorporate their findings into a concise process model that could be extended beyond self sustaining right-of-ways. The EMSM outlines specific

management practices to direct the development of persisting management desired communities.

The EMSM Applied to Right-of-Ways:
Successional Process Variables

Right-of-ways are located in a variety of environments, therefore management must be designed on an individual site basis. Specific right-of-way functions require specific life history characteristics of species. Indigenous species, or perhaps carefully screened introduced species, could be selected to create a desired community based on specific characteristics such as height, longevity, suitability for wildlife, or scientific or ornamental value. Since the ability to persist is important in right-of-way situations, species that reproduce vegetatively would be preferred.

The Connecticut Arboretum study found Viburnum lentago to be an ideal plant for right of ways because it reproduced vegetatively, resisted tree invasion, and also provided food and habitat for wild life. Many other shrub species such as high bush blueberry, (Vaccinium corymbosum) arrowwood, (Viburnum ricognitum) and witch-hazel, (Hamamelis virginiana) have also been used to form stable multiple-use communities (Niering and Goodwin 1974).

The EMSM and Right-of-Way Management
Goals: Community Structure

The goal of right-of-way management is to develop a persisting and self-maintaining community of species selected for particular management purposes because of their life history characteristics. Stable persisting communities of shrubs and non-woody species can exist. For example, the balds and slicks of southern Appalachia, and the blueberry heaths of West Virginia, have persisted for at least 200 years (Egler 1958). These areas are surrounded by forests which have not invaded, although trees can survive on balds if transplanted there. *Comptonia-Denstaedtia* and *Carex-Calamagrostis* communities have persisted for 15 years without cutting or other treatment; no trees have invaded, and the small size of the tree seedling present make it unlikely that the community will change (Pound and Egler 1954). Vegetative reproduction has been a factor in some cases. Fifty year old *Rhododendron* thickets at the Bent Creek Experimental Forest, have persisted because of vigorous root suckering and stump spouting (McGee and Smith 1967). In contrast to the prediction implied with the traditional succession model, both laurel and rhododendrons have formed dense thickets that have successfully invaded and persisted in what had been commercial forest (Wahlenberg and Doolittle 1950). These examples suggest that, if the EMSM is deliberately applied, relatively unchanging communities designed

for right-of-ways can be developed.

The EMSM Methods for Right-of-Way Management

Rationale. Traditional succession theory applied to right-of-ways has resulted in establishing communities that need continual maintenance. The chemical and mechanical techniques are expensive and sometimes environmentally destructive. Using the EMSM, right-of-ways could be designed to be self-maintaining and at the same time to provide multiple-uses such as hiking, biking, bridle paths, picnicing, bird watching, and visual pleasure for travelers. Right-of-ways could serve as refuges for economically important species such as insectivorous birds or game, and endangered species. Right-of-way areas could help prevent extinction of species by providing areas of contiguous habitat (McArthur and Wilson 1967: MacArthur 1972). The 200-300 year old hedges of Britain form stable communities with a variety of plant and animal species that are typical of grassland and forest. A mixed-edge effect would encourage species diversity (Egler 1958: Niering 1958: McArthur and MacArthur 1961).

Specific planning proposals (Table 5)

1) Disturbance.- The environment could be planned to be most suitable for the selected colonizer. Undesired tree species could be removed manually or through spot spraying (Egler 1949). No unnecessary destruction of herb and shrub

TABLE 5: SPECIFIC PLANNING PROPOSALS - RIGHT-OF-WAY MANAGEMENT

Successional Process	Variables	Management Practice	Possible Management Effects
Controlled Disturbance	Seasonality Size of area Numbers, proportions, kinds of species	Manual removal Spot spraying	Environment prepared to be most suitable for selected colonizer
Selective Colonization	Life history characteristics: longevity height fruit ornamental	Introduce selected species	Introduced species fulfills specific management function; prevents invasion all other species
Inhibitory Persistence	Vegetative reproduction Predation	-	Species reproduces vegetatively and inhibits all other species Predation promotes vegetative reproduction; eliminates/represses competitors
Removal	Differential growth rates	Manual removal and spot spraying (decrease with time)	Selected species aided to persist Competitor species invasion prevented
Regeneration	Vegetative reproduction	Pruning	Species replaces itself in the regeneration niche Community composition stays the same

species of potential value would occur. Bulldozing and discing, techniques often used for species removal on right-of-ways, would be avoided because they encourage tree invasion and cause erosion and nutrient loss (Egler 1958).

2) Selective Colonization - Indigenous grass or shrub species, or carefully screened introduced species, could be selected to create a desired community based on specific characteristics such as height, suitability for wildlife, etc.

3) Inhibitory persistence - Species that reproduce vegetatively are more likely to persist than those that do not (Pound and Egler 1954: Niering and Egler 1955: McGee and Smith 1967). Predation plays two roles in persistence. First, it promotes vegetative reproduction. Second, predation can eliminate or repress competitors. For example, tree seedlings often fail to develop in shrub communities because they are repeatedly cut back by mammals. With time, the persisting species inhibits other species from invading. A successional sequence is prevented from continuing through several mechanisms. For example, vacant niches for seedling establishment are rare in undisturbed vegetation with a closed canopy such as Scottish herbaceous and dwarf shrub communities (Miles 1973). Also, unsuitable microclimate for seed germination may be caused by mats of decaying

vegetation, lack of light or absence of disturbance (Wahlenberg and Doolittle 1950: Pound and Egler 1954: Treshow 1980).

4) Removal - Periodically, undesired species could be removed manually, or chemically with spot spraying. In time, the need for managed removal of species should decrease, or become less frequent, since the more densely growing shrubs seem to resist invasion by both herbs and tree seedlings (Miles 1973).

5) Regeneration - Vegetative reproduction would make it most likely that the regeneration niche would be filled by the same species; therefore, the community composition would stay the same.

Conclusion and Implications

The EMSM outlines specific procedures that could be used to direct the development and persistence of multiple-use right-of-ways. The EMSM management steps are designed to regulate successional sequences and rates of species replacements so that a management desired self-perpetuating community can persist and inhibit subsequent successional sequences from occurring.

The concept of an unchanging community on a given site can be extended from right-of-way management to other aspects of urban and regional planning. The increasing population of the U.S. has traditionally expanded the urban area

by extension into the outlying regions. This has resulted in the reduction of prime agricultural land and a decrease in forested areas. Ultimately, reduction of natural preserve areas occurs (Dasman 1976). Urban centers cannot expand indefinitely. Just as right-of-ways could be designed to be relatively unchanging, the concept of unchanging communities could be extended to other aspects of urban and regional planning.

Great Britain, the Netherlands, Sweden, Finland, and Norway, have prevented the spread of urban areas through stringent legislation regarding land use, tax incentives, and forms of reimbursement (Roget and Thornton 1981). Because of their small size and long history, these countries have had to plan for the recycling of resources and re-use of land. Consciousness of the land ethic is implemented in their land management practices (Roget and Thornton 1981). The land use policies in these countries lead to the establishment of persisting and regenerating urban areas, agricultural and forested areas, and natural preserves. In a sense, successional sequences are prohibited through legislation.

The EMSM provides another approach, based on succession theory, to help manage urban and regional areas for regeneration and persistence. Urban areas, for example, could be managed for persistence. The management techniques could include developing green belts, or open spaces as

parkways, gardens, parks and small preserves. Species could be selected for ability to persist in spite of pollution (Treshow 1980). Florida has developed a cooperative forestry assistance program to aid municipalities in selecting appropriate plant species, and protecting remnants of native plant populations (Harrell and Gornicki 1981).

Agricultural and forest areas could be manipulated to help the community to persist. These areas are critical for timber production (Plochmann 1981; Roget and Thornton 1981) and as habitat for wildlife (Dasman 1976). Removal of timber preferably through selective thinning, or through the shelterwood method of cropping, are least likely to cause change in the community (Clapham 1981). Leaving den trees for animals when harvesting timber, or favoring desirable seed or fruit species that could be used as wildlife feed, also would help maintain community structure. Natural areas could be helped to persist by preventing the spread of other forms of land use and thereby preserving habitat. Preservation of endangered species is dependent upon preservation of their habitat. A management approach to preservation of endangered species, based on the EMSM unchanging community structure could be useful.

Right-of-way management provides one example of the possibility of manipulating successional sequences and rates of replacement so that management desired communities can

regenerate and persist. The EMSM methods could be extended from right-of-way management, to other forms of urban and regional planning, and provide an alternative approach for land use management.

Range Management

Background

The term range refers to grassland areas, but if enough grass exists to be profitably grazed, range may also include desert shrub, savanna, chaparral, tundra, or forest. Overgrazing results in vegetation change (Stoddard and Smith 1953; Herbel and Anderson 1959); species preferred by stock decrease, species which are seldom grazed increase, and species which are avoided ultimately invade (Lewis 1969; Petrides 1975). The rate of species replacement depends upon the degree of grazing. Overgrazing has been sited as the single greatest cause of desertification in the United States (Sheridan 1981).

Succession theory has been used to interpret vegetation changes in the western part of the United States, and range management policy has been directed by the expectation of the traditional succession model (Anderson and Holte 1981). Range management decisions are based upon 1) range condition, which is a measurement of the extent to which range has departed from the climax toward a "lower successional state" as a result of grazing, and 2) range trend, which is an estimate of whether current management procedures are directing the

the range toward or away from a climax state (Dasman 1976).

Rangeland that has been overgrazed is sometimes rested; the range is not grazed at all in a given year and even mature forage is not harvested. Sometimes on an overgrazed range, grazing is deferred until seed maturity, or until seedlings are established. At other times, rotation grazing, in which animals are moved from one pasture to another on a scheduled basis, is practised (Heady 1970). Rest, deferment, and rotation grazing are practiced because, according to the traditional succession model, there is a repeatable series of species replacement that ultimately will lead to the re-establishment of the climax community. Ungrazed rangeland has been expected to proceed through predictable seral stages until the climax is re-established.

Recent range studies, however, indicate that the expected seral stages and climax community do not develop (Hyder et al. 1966: Dasman 1976: Laycock and Conrad 1981). For example, in a seven year comparison study using a variety of different grazing systems, no difference in cover, production, or species composition was evident (Laycock and Conrad 1981). Another example involves cheat grass, Bromus tectorum, which is invading rangeland in parts of the western United States and is replacing the original grasses. The soil holding ability and forage value of cheat grass is low. Even if grazing is prevented the cheat grass persists. The range

management solution to the invasion of cheat grass is to prevent grazing, with the expectation that the original vegetation will re-establish itself. Without grazing, however, cheat grass continues to maintain itself and to replace the grasses (Dasman 1976). The results of these studies contradict traditional succession theory, and have been disturbing to some range managers (Anderson and Holte 1981). That the seral stages and climax community did not develop is not unexpected when viewed from the perspective of more recent interpretations of succession theory.

Range managers are seeking alternative models. Anderson and Holte (1981) have suggested that Egler's initial floristic composition model, or Niering and Goodwin's relatively stable vegetation model, might be more appropriately applied to range management than the traditional succession model. Swartzman and Singh (1974) developed a matrix model for tropical grassland management which formulates a grazing strategy that allows maximum herbage utilization without range deterioration. Redetzke and Van Dyne (1976) have developed a dynamic matrix model of North American grassland which suggests that heavy grazing can change community structure, without eliminating species that are least resistant to grazing. The EMSM provides yet another alternative. Since range management is based upon altering the plant community by manipulating the numbers, species, and proportions of

grazing animals as they are distributed in space and time (Lewis 1956) a range model based upon succession theory is appropriate.

The EMSM Applied to Range Management: Successional Process Variables

The EMSM outlines four categories of successional process variables; abiotic factors, life history characteristics, and predator and competitor interactions. In manipulating these variables, the environmental heterogeneity of rangeland is an important consideration. Topographic and edaphic heterogeneity results in a patchy distribution of resources. Water is one of the most critical abiotic factors involved in range management, and it varies topographically from hilltops to valleys and edaphically in sand and soil. Also, there are temporal fluctuations in water. Differences in annual rainfall generate tremendous variation in the composition of grassland. Changes in the composition of the consumer level result. Petrides (1974) suggests that in tropical grassland and savannas varied sets of biotic communities may have replaced each other in response to water availability. The characteristics of range species reflect the co-evolution of competitor and predator interactions. For example, it has been suggested that the basal meristem of grasses evolved as an adaptation to grazing (Miles 1979). Greater net primary productivity of livestock

grazed versus livestock ungrazed communities has been recorded (Stoddard and Smith 1953: Pearson 1965: Reardon 1974). To explain this phenomenon, McNaughton (1979) lists nine effects of herbivores on plant growth and resource allocation. Among these effects are; increased photosynthetic rate in residual tissue, increased light intensity on potentially more active underlying tissue, nutrient recycling from dung and urine, as well as growth promoting substances in ruminant saliva. Another important consideration is that herbivory prevents the elimination of species and allows species to co-exist. These examples of interactions between range species provide evidence that grazing relationships are basic to a range community.

The EMSM and Range Management Goals: Community Structure

The goal of range management is to sustain a community structure that best maximizes animal yields while maintaining quality forage vegetation. In spite of this goal, much of the rangeland in the United States is becoming desert. Overstocking of livestock has been considered as a cause of desertification. However, the biomasses of prehistoric populations of large hoofed mammals in the United States grasslands, and the 1959-60 livestock count, are similar (Watt 1968). Thus it is the kind of herbivore present, not amount that is important. That domestic stock have not co-evolved with

grassland species probably is not as relevant as the fact that usually only one species of stock is grazed on a given range. Range with higher stocking rates can retain its natural vegetation composition if grazers include a variety of species, as did the prehistoric populations of grazers (Stoddard and Smith 1953: Herbel and Anderson 1959).

A variety of herbivores are best able to utilize rangeland. The environmental heterogeneity results in a patchy distribution of vegetation, and there are differences in livestock grazing based on topography (Stoddard and Smith 1953). Cattle graze level land and leave steeper portions unutilized. Although total forage may be adequate, range deterioration can still occur. Sheep are able to graze steep rolling rocky slopes, but rough stone creates problems for the relatively thin-hoofed cattle. Grazing in low wet areas causes hoof diseases in some species of domestic stock and not in others. Herbivores also exhibit preferences for species of vegetation, and selectively graze these species (Petrides 1975). Grazing only one species of livestock on a range eventually decreases the numbers of preferred species and leads to erosion.

The complementary feeding and habitat preferences of mixed herbivores are less likely to change community structure than would heavy single species grazing (MacArthur 1955:

Hutchinson 1959: Beuchner and Dawkins 1961: Wagner 1969: McNaughton 1979). African grassland studies have found that integrated livestock and game ranching may be profitable, as well as an excellent form of land use (Dasman and Mossman 1962: Taylor and Walker 1978).

If rangeland is to be managed for continual long term sustained yields, the effect that environmental heterogeneity has on grazing relationships needs to be taken into account. The EMSM is unique in proposing that it is possible to manipulate successional process variables and direct the development of a persisting community that meets management goals of maximizing livestock yields and maintaining quality forage vegetation.

EMSM Methods for Range Management

Rationale. It is important to manage range for long term use. Management techniques on already eroded rangeland would be different from those used on range that has been moderately grazed. If erosion is extensive, massive re-seeding and irrigation projects might be necessary. The EMSM specific planning proposals are not centered on recovery methods for eroded rangeland. The intent of the EMSM methods is to aid a range community to persist so that EMSM methods suggest maintaining or increasing the diversity of the range community. Most rangeland is topographically and edaphically

heterogeneous; and collectively, a variety of plant and animal species are able to most completely utilize a heterogeneous environment (McNaughton 1979: Gesshe and Walton 1981).

Specific planning proposals (See Table 6 page 87)

1) Designed disturbance - A disturbance can be selected on the basis of its ability to initiate a desired successional sequence. A timed and controlled burn can initiate a desired vegetation-herbivore sequence. For example, on a moderately grazed range a late spring burn increased desired blue stem populations, and the higher nutrient content of the plants subsequently resulted in greater weight gain of steers grazed on that range (Anderson et al. 1970). Controlled grazing is another form of disturbance that can initiate successional sequences. If preferred species are seasonally unavailable, grazers will select less palatable species. Grazers can be introduced to eliminate less palatable species; subsequent re-seeding with preferred species can initiate a desired successional sequence. Lack of water is a form of disturbance that can be moderated through contour furrows. Water run-off can be regulated to initiate desired sequences.

2) Selective colonization - Depending upon the situation, either plant or animal species can be selected as colonizers. Methods exist to measure plant population composition and density, as well as specific growth characteristics of range plant species (Cooper 1953: Pearson 1965: Kilcher 1981): Menke and Trlica 1981). This information can

TABLE 6: SPECIFIC PLANNING PROPOSALS - RANGE MANAGEMENT

Successional Process	Variables	Management Practices	Management Effect
Designed Disturbance	Water Fire Diversity	Controlled burn Contour furrows Regulate numbers, species and proportions	Perennial grass increase Regulate water run-off Maximum use of patchy resource
Selective Colonization	Topographic and edaphic heterogeneity Economic considerations	Introduce mixed herbivores	Maximize herbivore weight gain
Inhibitory Persistence	Seasonal Differential growth rate Growth cycle	Increase heterogeneity: break trails, distribute water, salt, shade, herd, fence, interseed palatable species Rotation grazing	Variety of plant and animal species persist and inhibit undesired species
Removal	Seasonal Differential growth rate	Harvest of selected herbivores Continuous grazing Mechanical: chaining, raiing root plowing	Maintain management desired numbers, proportions, and
Regeneration	Seasonal Method of reproduction	Rest Deferred grazing Re-seeding, fertilizing	Annual grass seed bank, seedling establishment Perennial grass store metabolic reserve Prevent erosion

be coupled with information of food and area preferences of grazing animals (Stoddard and Smith 1953: Petrides 1975: Gonzalez and Latigo 1981). Based on plant composition and topography, mixed herbivores, both domestic and wild, could be introduced. Procedures have been established to determine stocking rates for multiple species (MacCracken and Hansen 1981). Re-seeding can be based on grazer preference.

3) Inhibitory persistence - The life history characteristics of plant species are important variables affecting a plant species' persistence on rangeland. Preferred forage species can be maintained in the successional sequence through a variety of techniques that allow species to temporarily escape predation. Rotation, rest, or deferred grazing systems need to be correlated with the differential growth and life cycles of plants. If annual grasses are grazed so that they cannot set seed they will be unable to persist in the successional sequence. In order to persist perennial grasses need to be grazed in such a way that they can store reserves for the next seasons' growth. Inter-seeding preferred species with those that are unpalatable, helps to equalize grazing pressure and aids preferred species to persist. Techniques that increase the heterogeneity of the range such as breaking trails, distributing water, salt, shade, forage, herding, or fencing also increase the likelihood that both plant and animal species will be able to persist.

4) Removal - Either herbivores or plants can be removed. Undesired plants can be removed biologically by continuous grazing. Plants can be removed mechanically, although chaining or riling techniques usually leave roots and may not be effective. Herbivores can be selected for removal on the basis of age, or weight, to maximize economic gain. Specific numbers and species of herbivores can be removed if their grazing preferences are decreasing the ability of desired plant species to persist.

5) Regeneration - If the range community is to maintain its composition, plant species must be able to enter the regeneration niche. Resting a range would allow perennial grasses to store reserves for the next year. Deferring grazing or using rotation grazing until annual grasses have set seed will allow them to replace themselves. Re-seeding or fertilizing are other techniques that could aid plant species to enter the regeneration niche. A mixed population of herbivores are most apt to re-enter the regeneration niche, since their diet is likely to be higher in both quality and quantity of preferred plant species (Stoddard and Smith 1953: Lewis 1969: Dasman 1976: Petrides 1975).

Conclusion. Management practices can regulate successional sequences by manipulating biotic and abiotic range variables to maximize animal yields and maintain quality forage. Management techniques that increase heterogeneity

and is also compatible with multi-purpose range use.

The Federal Land Policy and Management Act of 1976 advocates multi-purpose use of range for livestock, recreation, and wildlife. Inevitably, as the environment becomes more managed, game must use what primarily has been rangeland. Human recreational use of rangeland will also increase. On a world wide basis, range will become more and more important as reserves for game and plant species (Petrides 1971).

If well planned, multi-purpose range use could lead to larger and/or contiguous area serving as reserves for species. According to the theory of island bio-geography, species are more likely to survive in larger reserves and in reserves that are close to each other (MacArthur and Wilson 1967: Diamond 1975: Goeden 1979). Increasing the heterogeneity of the range will also reduce the possibility of extinction by providing a variety of habitats (MacArthur and MacArthur 1961).

Agro-Ecosystem Management

Background

The worlds' population is estimated to be over 4.6 billion and it is increasing at the rate of 2 percent per year (Cox and Atkins 1979). To support an ever expanding population, traditional polyculture agricultural systems have been modified to monoculture systems to increase food production. The recent "Green Revolution" of the 1960's has been

centered around the adoption of hybrid crops, especially cereals, that are genetically similar and, thus, more susceptible to herbivores and pathogens than indigenous varieties. Agriculture losses, due to pest infestation, are estimated to be about one third of the worlds' potential agricultural production (Cox and Atkins 1979). Clearly, agricultural pest populations must be controlled, if agricultural production is to be increased.

Although succession models have not been applied specifically to agro-ecosystems, such models are appropriate. Traditionally, succession has been defined as an orderly process in which each species facilitates the invasion of the next species. This definition, if applied to an agro-ecosystem, implies that a crop will be discovered by herbivores and later by their predator-parasites in a facilitory successional sequence.

The EMSM provides a different, broader interpretation of succession in an agro-ecosystem. Unlike the traditional view of succession, in which there is a certain inevitability of stages and a deterministic outcome, the EMSM suggests that management practices can vary species sequence and replacement rates and thus prevent crop loss by pest-species. EMSM management techniques can maximize the probability that the desired crop will persist until harvest by manipulating 1) the series of species replacements and, 2) the rate of species change.

The EMSM Applied to Agro-ecosystems - Successional Process Variables

Although environmental variables in agro-ecosystems throughout the world differ, seasonality is important in all agro-ecosystems because it regulates crop resource availability for pests. Management practices related to seasonality, such as the timing of planting and harvesting, crop rotation, fallowing, and tillage, will be analyzed as they relate to successional processes.

The timing of planting and harvesting have been traditional methods of pest control, and these practices continue to be important. For example, the destruction of winter wheat by the Hessian fly may be prevented by planting the wheat after the flies emerge and die, a delay of only a few days (Cox and Atkins 1979). The wheat resource is separated in time from the fly population; therefore, the expected sequence of species replacements does not occur. Adjusting the date of harvest can also remove a resource in time. Wheat is often harvested before attack by the wheat-stem sawfly (Cox and Atkins 1979). An advance or delay in the timing of planting or harvesting of a crop may result in a change in an abiotic factor, such as temperature. Because the temperature is not optimal for the crop pest, the typical pest species replacement pattern may be prevented, or the population growth may be reduced.

Crop rotation interrupts species replacements by removing pest resources, and can regulate the population growth rate of a pest population. For example, the probability of *Ophiobolus* disease in wheat is decreased if a wheat-oat rotation is used: the pathogen population, Ophiobolus, declines without its host species (Cox and Atkins 1979). Similarly, a rotation of legumes with corn controls the growth rate of white fringed beetle population, because the beetle has a higher reproductive rate on legumes than on grasses.

Fallowing, like crop rotation, prevents species replacement patterns from occurring by depriving a pest species of a suitable host resource. Progeny of the last seasons' pest populations that begin development in a fallow field have increased mortality rates. Fallowing and tillage techniques are sometimes combined, because tillage techniques destroy pests through mechanical injury or exposure. These techniques prevent the sequence of species replacement. Timing is a consideration in tillage, because of pest species differences in susceptibility to injury and exposure in various stages of their life cycles.

To summarize, the timing of planting, harvesting, crop rotation, fallowing, and tillage, are examples of management techniques that manipulate the variables of timing and resource availability. The techniques have been examined here

only in regard to their effect on the sequence and rate of species replacement. The methods are effective because the life cycle of the pest and crop species are to some degree synchronous. Agricultural techniques that interrupt the timing of life cycles will also interrupt the species replacement and reproductive pattern. If management methods were based solely upon manipulating the timing of resource availability, it is possible that pest populations would evolve to the new timing, and that eventually the method would not be effective. Other practices, like manipulating the diversity of the system so that successional sequences and rates are altered, present additional possibilities of regulating pest populations. The goal of the EMSM is to manipulate agricultural techniques to regulate successional processes, so that the crop persists.

The EMSM and Agro-Ecosystem Goals: Community Structure

Frequent pest outbreaks that reduce crop biomass are a major problem in agro-ecosystems. The crop community is unable to "persist". The basic concept of the EMSM is that an agro-ecosystem can be designed so that the crop can persist and inhibit the invasion of subsequent species.

Pest outbreaks have been explained in terms of the system being reduced or simplified compared to natural systems. Simple systems have been thought to be more unstable, in the

sense of being subject to population fluctuations (Odum 1959: Margalef 1975). Lab and model systems provide substantial evidence to support the fact that spatial and physical complexity confer stability (Harger and Tustin 1973: Murdoch 1975). Examples from agro-ecosystems also indicate that increases in the spatial, physical, and temporal complexity of the system increase stability. To help regulate pest populations, crop systems can be designed to be less simple and more diverse. Increased diversity in agro-ecosystems would be interpreted, via the EMSM, as increasing the probability of a species being available to affect the rate and sequence of succession. The probability of any one pest species being able to dominate a successional sequence would be less likely in a diverse system. The following examples indicate that the reduced pest populations in more diverse agro-ecosystems are related to the effect that increased diversity has on successional sequences and rates of replacement.

Insects respond positively to spatial and chemical stimuli associated with monocultures, and their colonization rate is increased in less complex systems (Tahvanainen and Root 1972: Cromartie 1976: Smith 1975). Dense concentrations of resources are more likely to increase colonization rates and tenure time (Root 1973: Cromartie 1975: Bach 1980: Risch 1980). Increased plant species diversity is correlated with increased insect species diversity (Murdoch et al. 1972:

Risch 1980). Increased plant diversity reduces the probability that any one species will dominate (Murdoch et al. 1972). There is much evidence to suggest that increased diversity of plant and animal species, outside the cultivated crop, reduces pest species abundance within the crop (vanEmden 1965: Douth and Smith 1971: Rabb 1971).

Predation affects successional processes, and predator-prey models suggest that more complex agro-ecosystems are more likely to have reduced pest populations (Root 1973). Root (1973) hypothesized that predators and parasites are more effective in reducing herbivore populations in complex environments, because complex systems provide a variety of resources and refuges for them. Foraging models suggest that the reproductive fitness of specialist herbivores would be reduced in polycultures (Rapport and Turner 1975: 1977).

The preceding examples indicate that increased diversity helps to regulate pest populations. Agro-ecosystems can be designed to be more diverse in ways that inhibit the successional sequences that lead to high pest populations. Management methods can increase the probability that the crop will persist.

The EMSM Methods for
Agro-Ecosystems

Rationale. A Management goal is for the crop to persist (step 3) until it is removed at harvest (step 4) or for the crop to persist so that it can regenerate (step 5 e.g. orchard trees). Methods that increase the complexity of the agro-ecosystem will: 1) reduce the amount of crop loss due to pests and, 2) maximize the probability that the crop will persist until removal or regeneration.

Designed Disturbance 1

Selective Colonization 2

Inhibitory Persistence 3

Regeneration 5

Removal 4

Specific planning proposals (Table 7)

1) Designed disturbance - Types of management designed disturbance include size of the area cultivated, timing of planting and fallowing, and tillage practices. Planting out of phase with the life cycle of pest species can separate pest populations in time from the crop. Also, abiotic factors, if season is out of its normal time phase, can be unfavorable for herbivores. Tillage techniques can remove pests by exposing them to dessication or mechanical injury. Fallowing can decrease pest populations by removing the host as a resource. The disturbance can be chosen to maximize the likelihood that the selected crop can successfully colonize at step 2, and persist at step 3.

TABLE 7: SPECIFIC PLANNING PROPOSALS - AGRICULTURAL MANAGEMENT

Successional Process	Variable	Management Practice	Management Effect
Designed Disturbance	Type of disturbance Season Size of area	Timing of planting Tillage Fallowing	Herbivores separated in time from producers Abiotic factors unfavorable for herbivores Removal of "pests" - exposure Host resource removed
Selective Colonization	Life history characteristics Species diversity	Polyculture Mixed Edge	Decreased colonization rate of herbivores Increased colonization rate of predators
Inhibitory Persistence	Life history characteristics: allelopathy Species diversity	Polyculture Mixed edge Trap crops	Decreased herbivore population growth rate Reduce potential for maximum populations
Removal	Season Differential growth rate	Timing of harvest Crop rotation	Herbivore separated in time from producer Abiotic factors unfavorable for herbivores Pathogens separated in time from producer Herbivore population growth rate decreased because of alternate crop
Regeneration	Season Differential growth rate	Timing of harvest	Herbivore/pathogen separated in time from producer Maximize crop

2) Selective colonization - The designed disturbance can prepare the site specifically for the crop species selected for colonization. Selected species can be introduced in desired numbers and proportions to increase the probability of maximum yield. Techniques that increase diversity, such as polyculture, and mixed edge, can be used. These techniques decrease colonization rates of herbivores, and increase the colonization rate of predators.

3) Inhibitory persistence - Steps 1 and 2 can be performed to maximize the probability that the selected crop colonizers can persist and inhibit other species. Polyculture, mixed edges, and trap crops are methods that can decrease herbivore population growth potential, increase predator colonization rates, and therefore aid the crop to persist.

4) Removal - Season and differential growth rate of species are important variables to consider in the timing of harvest and rotating of crops. Crops can be removed before pest damage occurs and therefore maximize the harvest.

5) Regeneration - As in removal, season and differential growth rate can be manipulated to maximize harvest. An example of regeneration would be the removal of fruit, nut, berry, etc., crop in such a way that the plant can have metabolic reserves for next season's growth. Planned removal of fruit can also separate the plant in time from herbivore pests and pathogens. These techniques would make it more

likely that the plant can enter the regeneration niche.

Conclusion

The EMSM can be used to manipulate successional sequences and rates of replacement in agro-ecosystems to reduce pest populations so that crops can persist. Polyculture, mixed edge techniques, and other methods that increase the diversity of the crop system, decrease the probability that any one pest species can dominate the sequence and damage the crop. Herbivore succession rates are also reduced by increasing crop diversity, and predator succession rates are increased. The probability of the crops' persisting is increased. The EMSM has the advantage of being a biological means of control, and provides a new approach for regulating pest populations in agro-ecosystems.

CHAPTER VI

THE EMSM APPLIED TO FACULTATIVE SEWAGE LAGOONS

Introduction

In this chapter the EMSM is applied to eutrophication, the enriching of aquatic systems with dissolved nutrients, which is a particularly difficult environmental management issue. I will focus on applying the EMSM to eutrophication in facultative sewage lagoons that utilize anaerobic and aerobic organisms to decompose organic waste, and to the resulting problem of fluctuating effluent quality. Although the facultative lagoon is an artificial system, it is similar in structure and function to natural lake and pond systems (Gloyna 1968). Eutrophication within the facultative lagoon has been described as a successional sequence (Oswald 1968). Therefore, it presents an ideal opportunity to manipulate successional processes in an environment which, because of its limited size, can be controlled.

It is necessary to distinguish between eutrophication as a process, and the effect of artificial nutrient enrichment within aquatic systems. Natural eutrophic systems are autochthonous, that is, most of the energy and nutrients are derived from within the system (Clapham 1981). In culturally eutrophic aquatic systems, the main sources of nutrients and minerals are external, allochthonous, to the system.

Allochthonous inputs increase the productivity of the system and the rate of eutrophication.

Generally, management methods are directed toward eliminating or controlling the effects of eutrophication and not its causes. In lakes, one common method to control the effects of cultural eutrophication has been to direct the nutrients elsewhere. This alternative is not a realistic one in the management of a facultative lagoon, because their function is organic decomposition of such nutrients. Therefore, the algal blooms and subsequent anaerobic conditions characteristic of cultural eutrophic systems have been accepted as extremely likely in facultative lagoons. Management techniques such as lagoon design modifications, biological harvesting, and the addition of chemicals, deal only with the effects of eutrophication and not with the causes.

The EMSM presents a completely different approach to managing eutrophication in facultative lagoons. Procedures that manipulate the successional process variables to avoid the effects of eutrophication are suggested as alternative management methods. Process variables include abiotic factors, and competitor and predator interactions. Information from aquatic studies can supplement what is known about succession within facultative lagoons; together, this information can be used to explain algal blooms, and to suggest management techniques to alleviate the problem.

The Relationship Between Eutrophication and Blue-green Algae

The nutrient enrichment associated with cultural eutrophication generally leads to tremendous populations of algae. The undesirable feature of eutrophication is not the production of more algae, rather, it is the dominance of blue-green species in these algal blooms (Provasoli 1969). This causes oxygen depletion, and changes in the food chain, because blue-green species are inedible. The blue-green species have come to represent the most obvious indication of eutrophication.

Early attempts to regulate the blue-green population sizes focused on the nutrition of phytoplankton, and in particular on their nitrogen, phosphorus, and carbon requirements (Schmidler 1974). Studies in laboratories and experimental lakes indicated that the following factors influence the presence and dominance of blue-green algae.

- 1) Blue-green species possess characteristics that allow them to compete successfully with other algal species. Blue-green take-up phosphate and carbon dioxide more efficiently than other algae (Shapiro 1973).

- 2) Many blue-green algae are able to fix nitrogen (Kratz and Myers 1955; Fogg et al. 1973).

3) The pseudovacuoles of the blue-greens allow them to float; this buoyancy gives them an advantage over non-buoyant species during intermittent periods of stratification (Hutchinson 1967: Ferguson and Harger 1982).

4) Therefore, blue-green algae can remain alive and actively photosynthesize at the surface where they are exposed to intense illumination and high temperature. The ranges of temperature suitable for blue-green growth are wider than those for other algae; the optimum temperature for blue-green species is near 35° C (Fogg et al. 1973).

5) Quantitative studies of algal growth rates indicate that blue-green species have more rapid growth rates than do most other species of algae (Fogg et al. 1973). Anacystis nidulans has a generation time of two hours, the highest growth rate reported for any alga (Kratz and Myers 1955: Fogg et al. 1973).

6) Although blue-green algae grow best in the pH range of 7.5-9.0, there are exceptions, and some species grow well at lower and higher pH levels (Fogg et al. 1973).

7) Some blue-greens release substances which may inhibit the growth of other algae and may be toxic to aquatic animals (Fogg et al. 1973):

8) The filamentous structure of some of the blue-greens, and the gelatinous texture of the coccoid species, make it morphologically difficult for zooplankton to consume them.

Selective grazing by zooplankton may increase the likelihood of their dominance, since smaller green algae that could exist in the same environmental conditions as the blue-greens are often eliminated by grazing (Ryther 1954: Lund 1969: Hutchinson 1973).

Facultative Lagoons

There is an increasing need for low cost treatment methods for municipal sewage and industrial effluents. To meet this need, different types of waste stabilization ponds, like facultative lagoons, are becoming more prevalent, especially in areas where land is inexpensive, budgets are low, and trained personnel are not available. The algal blooms associated with eutrophication are a problem in facultative lagoons. The large algal populations deplete oxygen and cause the lagoons to become biologically non-functional, and also result in a high concentration of solids in the effluent. Diversion of nutrients, a common technique to prevent eutrophication, is not a feasible alternative in maintaining a facultative lagoon. Methods to deal with algal blooms are being sought.

A variety of different types of waste stabilization ponds are used in waste treatment processes. The ponds are used for waste storage, equalization of waste flow and quality, percolation, sedimentation, aerobic or anaerobic degradation, or some combination of these.

Their basic function is to provide a place where organic wastes are decomposed by microorganisms and pathogens are eliminated. Ninety percent of the pathogens in water die within seven days, so reservoir storage is effective (Black 1977). In some cases lagooning is the only treatment process; other times, lagooning is one of a combination of processes which may, for example, include chlorination.

The effectiveness of waste treatment systems is measured by the reduction of oxygen demanding material (5-day biochemical oxygen demand, BOD₅), total suspended solids (TSS), and nutrients that are discharged into the receiving waters (Wolverton and McDonald 1979).

Although the value of lagoons in treating wastewater from small flow generating systems has long been recognized, persistent problems with algae production, which result in both high BOD and TSS in the effluent, have lessened their usefulness (Cullinane and Shafer 1980). Techniques that would completely eliminate the algae are not desirable, because the algae are necessary to utilize the products produced by the bacteria in the lagoon, and to supply oxygen to the aerobic bacteria. A major management goal is to prevent great populations of blue-greens from developing and causing the lagoon to become biologically non-functional.

Current methods to remove the algal solids have included lagoon design modifications, biological harvesting and

and the addition of chemicals. Conventional wastewater treatment equipment can remove algal cells, but the cost effectiveness has not been established. These methods deal only with the effects of algal blooms within the lagoon system and not their causes.

The EMSM and Facultative Lagoons

In contrast to the current management policies discussed above, the EMSM provides a unique approach to lagoon management. EMSM management methods are directed to the cause of the successional changes leading to eutrophication. Because the undesirable effects of eutrophication in the facultative lagoon are related to the increased populations of blue-greens, the EMSM would inhibit the growth of blue-green species by manipulating 1) competitor interactions, 2) abiotic factors, and 3) predator interactions.

Competitive Interactions

Competition is an important factor in the successional sequences that occur among phytoplankton (Hutchinson 1967). The changes in diversity taking place within the lagoon, and the subsequent dominance of blue-green algae, is related to competitive interactions (Gloyna 1968). The sequence and rate of species replacements can be manipulated so that the blue-green species do not dominate. By introducing a superior competitor, the EMSM would decrease the dominance of blue-green populations in facultative lagoons and thereby reduce

the high concentration of suspended solids in the effluent.

Water hyacinth is an example of a superior competitor that could be used to control blue-green dominance. It is a perennial, mat-forming aquatic plant. Although it is a native of Brazil, it has become widely distributed and is considered a pest species in many countries, including the southern United States (Penfound and Earle 1948). In large systems the water hyacinth is difficult to control, but in small lagoon systems it can be regulated manually. The plant has an extensive root system and is able to efficiently absorb nitrogen, phosphorus, magnesium, and iron from the water (Cooley et al. 1978). Water hyacinths effectively utilize nutrients in sewage system (Boyd 1970: Gossett and Norris 1971: McDonald and Wolverton 1980). Lagoon function will continue with an aquatic vascular plant utilizing bacterial products. The water hyacinth grows rapidly in bright light and in extreme temperatures it replaces damaged leaves quickly, and reproduces vegetatively. The water hyacinth is able to form a cover over the surface of the water and prevent phytoplankton from utilizing light.

There are some difficulties with using water hyacinth in facultative lagoons. If the plant completely covers the surface and eliminates all algae, oxygen will not be available for decomposition. This difficulty can be overcome by using a barrier to restrict the water hyacinth to a portion

of the lagoon (McDonald and Wolverton 1980). In cooler environments, where its fall death would increase the BOD of the system, water hyacinth has been 1) harvested in the fall for use as a feed or fertilizer, or 2) grown in conjunction with Lemna or Spirodela which are able to supplement the role of hyacinth during winter months (McDonald and Wolverton 1980). If used alone, the small size of Lemna or Spirodela increase suspended solids in the effluent. Since BOD removal in pond systems is not as effective below 19°C, most facultative lagoons are located in warmer environments, and the problem with seasonal death of the water hyacinth is not severe. (Oswald 1968).

Specific planning proposals using water hyacinth as a competitor. The rationale for suggesting that the water hyacinth can be used to change the sequence and rate of species replacements in the lagoon is based on the life history characteristics of both the water hyacinth and the blue-green algae interacting with abiotic factors. Of the phytoplankton species found in a facultative lagoon, the blue-greens are most likely to dominate in later successional sequence.

Abiotic factors, especially temperature and influent quantity and quality, vary in the lagoon. The sequence and rate of replacement of algae species varies with these changes. The water hyacinth, by efficiently assimilating

nutrients, growing quickly, and preventing light from penetrating below the surface, will be able to alter phytoplankton successional sequences. It is possible that the water hyacinth can out-compete the blue-green algae and become the dominant plant in the facultative lagoon. Algal blooms could not occur and the effluent quality would be more predictable and contain lower concentrations of solids.

Successional process variables, management practices, and effects. (Table 8) At each step of the EMSM, successional process variables can be manipulated so that the management desired successional sequence is likely to become established.

1) Designed disturbance - At step 1, disturbance, important considerations are season and the variation in influent quantity and quality. The sequence and rate of phytoplankton replacement varies with these changes.

2) Selective Colonization - A selected colonizer, such as the water hyacinth, could be introduced and prevent blue-green dominance. It could cover the surface of the water and prevent light from being available for phytoplankton photosynthesis. Since the plant efficiently absorbs P, N, Mn, and Fe through its extensive root system, it could perform a desired function in the lagoon. Lowered, a changed nutrient availability, and lack of light for photosynthesis could change the succession of algae.

TABLE 8: SPECIFIC PLANNING PROPOSALS - FACULTATIVE LAGOONS - COMPETITIVE INTERACTIONS

Successional Process	Variables	Management Practice	Proposed Management Effect
Designed Disturbance	Season Influent quality/quantity Species diversity	Select competitor species	Prevent blue-green dominance
Selective Colonization	Life history characteristics: extensive root system ability to absorb P, N, Mn, Fe rapid growth rate large size	Introduce water hyacinth	Water hyacinth dominant filtering agent Phytoplankton populations reduced
Inhibitory Persistence	Rapid growth, replacement of tissue Vegetative reproduction	Little maintenance	Water hyacinth dominates Phytoplankton populations inhibited
Removal	Season Differential growth	Timed harvest of water hyacinth crop	Use of hyacinth as food, soil additive, fuel
Regeneration	Vegetative reproduction	Cuttings Susceptibility to physical extremes	Continued dominance of hyacinth Blue-green blooms prevented Lower TSS in effluent Effluent quality more predictable

3) Inhibitory Persistence - The life history characteristics of the water hyacinth make it likely that the plant will be able to persist and inhibit other species. Little maintenance of the hyacinth is required; it has great ability to replace damaged leaves and reproduce vegetatively. Its ability to perpetuate itself in the sequence through vegetative reproduction could act as an additional suppressive factor in inhibiting algae.

4) Removal - The EMSM replacement of hyacinth could occur through either one of two processes. Depending on location and seasonal variations, all or some of the crop could be removed and perhaps have economic value (Bates and Hentges 1976: Boyd 1976: Wolverton and McDonald 1978).

Regeneration - The alternative replacement process is self replacement. Since the water hyacinth reproduces vegetatively, it could replace itself in the successional sequence and remain the dominant plant in the lagoon system.

Abiotic Factors

Successional sequences in the facultative lagoon could also be altered through managed changes of abiotic factors. (It is important to consider that abiotic factors do not act in isolation. Competitive interactions for example, may interact with abiotic factors and generate a variety of effects.)

Much is known about the effects of abiotic factors on the seasonal succession of phytoplankton (Hutchinson 1967: Lund 1969: Provasoli 1969). Based on this information, some suggestions can be made that might affect successional processes within facultative lagoon, so that large populations of undesired species are unable to develop.

Specific planning proposals using abiotic factors. The life history characteristics of blue-green algae, and the abiotic factors existing within domestic sewage facultative lagoons, make it likely that blue-green algae will become dominant. In facultative lagoons nutrients are not limiting for any of the algal species, but the warmer surface temperature, CO₂ availability, and low turbulence contribute to the eventual dominance of the blue-greens (Oswald 1968: Gloyna 1968: King 1972). These conditions could be mitigated by techniques that reduce water temperature and light, or increase turbulence, or change CO₂ levels.

In the spring, the first planktonic genera to appear in facultative lagoons are usually green algae, especially Chlamydomonas and Euglena (Gloyna 1968). These species are often replaced by blue-green algae, especially Oscillatoria, Phormidium, Anacystis, and Anabaena. The blue-green populations begin to increase as summer approaches and temperature and longer days increase. Almost all extensive blue-green algal blooms in facultative lagoons occur in summer.

The summer surface temperature in shallow facultative lagoons may reach 35°C (Oswald 1968). Chlorophyceae decrease, or disappear in the facultative lagoon as temperatures approaches 30°C. Euglenophyceae persists at 30°C, but the optimal temperature for blue-greens is 35°C.

Although wind can cause some mixing in facultative lagoons, turbulence is generally low because at temperatures higher than 15°C the density decrease of the water per degree of temperature increase is comparatively high, and this results in a resistance to mixing (Uhlmann 1980). The low turbulence does not restrict blue-green growth because their pseudovacuoles enable them to be buoyant and remain near the surface. Other algae that are not buoyant are confined to lower depths and less intense light. The ability to be buoyant also gives blue-green algae access to atmospheric carbon dioxide. Unless there is mixing, aquatic plants that are separated from the atmosphere by a foot or more of water do not have access to atmospheric carbon dioxide (King 1972).

Since the seasonal succession of algae is accompanied by a continuous rise in pH and a decrease in the free carbon dioxide concentration of the lagoon the blue-greens are likely to dominate (King 1972). Also green algae are limited at free carbon dioxide concentrations less than 10 moles liter⁻¹, while blue-green species are not affected even if free carbon dioxide concentrations reach 2.5-3.0 mole/liter⁻¹ (King 1970).

Successional process variables, management practices, and management effects. (Table 9)

1) Designed disturbance - Lagoons can be designed and managed to be less suitable for blue-green species and more suitable for competitor species. Temperature, light and turbulence are the most relevant abiotic variables involved in the seasonal succession of phytoplankton (Hutchinson 1967). These factors might be managed to increase other non-blue-green green populations, and to decrease blue-green populations.

2) Selective Colonization - First, the high summer temperatures that promote blue-green populations must be reduced. Aluminized underwater plastic screens could be used to decrease light and temperature (Lund 1969) or overhead screens that are less costly and more easily moved could be used. Another possibility is cooling coils to reduce the water temperature of the influent. Second, mechanical mixing could increase free CO₂ level for green species, and also help to re-distribute the less buoyant and non-motile species. Third, carbon dioxide could be injected into lagoons to stimulate green algal growth.

3) Inhibitory Persistence - Decreasing the temperature, and increasing the turbulence and CO₂ levels, would aid green algae to persist in the successional sequence and at the same time inhibit blue-green populations. The lowered temperature would directly affect the blue-green growth rate and reduce

TABLE 9: SPECIFIC PLANNING PROPOSALS - FACULTATIVE
LAGOONS - ABIOTIC FACTORS

Successional Process	Variables	Management Practice	Proposed Management Effect
Designed Disturbance	Light, temperature, CO ₂ turbulence Species diversity	Modify abiotic factors to detriment of blue-green	Prevent blue-green dominance Increase other phytoplankton populations
Selective Colonization	Life history characteristics	Aluminized underwater plastic screens/overhead screens Cooling coils Artificial mixing Add CO ₂	Blue-green populations reduced Other phytoplankton populations increase Predator populations increase
Inhibitory Persistence	Season	Continue above practices when needed	Blue-green populations reduced Inter-specific competition inhibits blue-green
Removal	Season Differential growth	Death Re-cycling Effluent	Species diversity maintained
Regeneration	Season Asexual/sexual reproduction	Self replacement	Blooms prevented Lower TSS Effluent quality more predictable

their population size. The three previously mentioned management techniques to alter abiotic factors need not be practiced at all times, making them more cost effective.

4) Removal - Lower light intensity and cooler temperatures result in decreased population growth and death of the blue-green and other algae in the facultative lagoon. Some of these organisms will be re-cycled within the lagoon, and some will be removed with the effluent. Effluent quality, however, will be high because the changed abiotic factors will lower the blue-green population sizes, and the BOD and TSS of the effluent will be lower.

5) Regeneration - Seasonal cycles and asexual and sexual reproduction will lead to self-replacing populations of phytoplankton. Continued management of abiotic factors will reduce the probability of the blue-green blooms that lower effluent quality.

Predator Interactions

A facultative lagoon could also be managed through the EMSM by manipulating predators. Grazing in aquatic systems is an important factor regulating species composition and abundance, and directing the course of succession (Hutchinson 1967: Moore 1978: Sousa 1979). Grazing rates of the zooplankton in a eutrophic lake vary seasonally, and are usually correlated with fluctuations in the phytoplankton populations (Porter 1977). Reduced grazing accounted for a

post-diatom algal peak (Harper and Ferguson 1982).

In freshwater, the most important predators are cladocerans, copepods, and rotifers (Allan 1977; Kerfoot 1977). All of these organisms occur in sewage ponds (Uhlmann 1980). However, in facultative lagoons, the effectiveness of zooplankton predators is limited by the blue-green algae, abiotic factors, and biotic factors.

In the lagoons, as in natural bodies of water, a spring association of more edible phytoplankton is followed by gelatinous green species. Some gelatinous green algae not only survive gut passage in zooplankton, but their growth is enhanced by it (Porter 1976). The filamentous blue-green species, which follow gelatinous greens during eutrophication, are seldom eaten by zooplankton. Late successional blue-green algae associated with blooms in facultative lagoons are indigestible, large, and toxic; therefore, zooplankton are not effective predators on blue-green algae.

Abiotic factors in facultative lagoons also lessen the effectiveness of zooplankton predators. Photosynthetically elevated pH, up to pH 11, resulted in a decrease and disappearance of crustacean zooplankton from nutrient enriched ponds (O'Brien and deNoyelles 1972). Oxygen depletion at night, due to the respiration of dense algal populations, decreases zooplankton populations (Porter 1977). In addition, decreasing oxygen concentration also decrease the

filtering and respiration rates of zooplankton (Heisey and Porter 1977). High summer temperature also limits zooplankton. In a study of mixed populations of three species of cladocerans, each species responded differently to temperature, and the seasonal succession of the three species could be predicted on the basis of temperature (Allan 1977). In addition, there are indirect effects of high temperature; the effects of toxicity increase with increasing temperature in copepods, cladocerans, and rotifers (Talmadge and Coutant 1979).

Also, other biotic factors, like interspecific competition, reduce the effectiveness of zooplankton predators (Brooks and Dodson 1965). Another consideration is that zooplanktors may be utilizing other sources of food besides phytoplankton. Detritus and bacteria, prevalent in facultative lagoons, are important food sources for Daphnia (Saunders 1969).

Specific planning proposals using predator interactions. As presently managed, conditions within the facultative lagoon ensure that the blue-green algae will become the dominant species. By manipulating three aspects of the predator interactions blue-green dominance could be prevented. Management techniques could:

1. Increase populations of predators and pathogens of blue-green species,
2. Alter abiotic factors that reduce predator populations.

- 3) Increase populations of edible algal species to serve both as a resource for predators, and to prevent resources from being used by blue-green populations.

Successional process variables, management practices

and management effects (Table 10)

1) Designed disturbance - Management practices can be designed to modify photosynthetically induced changes that are detrimental to zooplanktors. Manipulations that decrease great blooms of blue-green species that deplete oxygen availability, or manipulations to increase palatable algal species, are possible management practices. Mixing the lagoon to increase oxygen availability is another possibility. These practices might prevent subsequent blue-green dominance by increasing the populations of blue-green predators.

2) Selective colonization - Predators selected as colonizers would need to have the ability to handle and digest blue-green species, or to utilize them as hosts. Colonizers would also have to be resistant to toxins, high pH, high temperature, and low oxygen concentrations. Possible predators include cladocerans, copepods, and rotifers. Daphnia can handle and digest even toxic blue-green algae, if the blue-green populations are not dense (Porter 1977). Protozoan predators are another possibility. Protozoa heavily graze blue-green algae in Scottish lakes (Fogg et al. 1973). Many of the chytrid fungi are host specific and could be introduced to reduce blue-green populations (Fogg et al. 1973): Jewson et al. 1981). Although not now

TABLE 10: SPECIFIC PLANNING PROPOSALS - FACULTATIVE
LAGOONS - PREDATOR INTERACTIONS

Successional Process	Variables	Management Practice	Proposed Management Effect
Designed Disturbance	Abiotic factors Species diversity	Modify abiotic factors detrimental to predators Increase palatable algae	Prevent blue-green dominance Increase predators
Selective Colonization	Ability to digest, Utilize blue-green Resist toxicity Low O ₂ high pH High temperature	Introduce appropriate predators/pathogens	Blue-green growth reduced Predator populations increased
Inhibitory Persistence	Season	Re-Introduction	Predators persist Blue-green inhibited Non blue-green increase
Removal	Season		All populations reduced-seasonal Removal death/dormancy
Regeneration	Season	Tandem series of lagoons	Reduce blue-green resources Provide predators for re-stocking

abundant in facultative lagoons, viruses and bacteria pathogenic to blue-green algae could be introduced to reduce blue-green populations (Fogg et al. 1973). The practices that reduce blue-green populations make the environment more suitable for the maintenance of predator populations.

3) Inhibitory Persistence - The change in abiotic factors that occurs with the season would affect the ability of predator populations to persist. Management techniques could involve monitoring the fluctuations in prey, predator, and pathogen populations and possibly re-introducing predators and/or pathogens to lessen the probability of blue-green dominance.

The re-introduction of zooplankton predators might be facilitated by using a lagoon system in which three lagoons "or cells," are arranged in a series. The greatest concentration of organic waste occurs in the first cell, where most of the decomposition is anaerobic. The second cell in the series is the most facultative of the three cells, in that both aerobic and anaerobic decomposition occur. If the BOD load of the third cell is not too high, large populations of zooplankton can develop. Concentrations of 1000/Daphnia/liter have been observed in such cells (Uhlmann 1980). In facultative lagoon systems with three or more cells, the third cell might provide a source of predators that could be used to re-stock the second cell. Introduction of predators

and pathogens of the blue-green species might slow their growth rate and increase the likelihood of other algal species persisting for longer time periods.

4) Removal - Removal, or reduction of all populations could be expected to occur in fall and winter. If predator populations have reduced the blue-green populations, lower concentrations of solids should be found in the effluent. In a three cell system, the seasonal removal of phytoplankton might occur through the action of high populations of zooplankton in the third cell.

5) Regeneration - The ability of the facultative lagoon to regenerate organisms is related to seasonal abiotic variables. Designing systems to modify undesired seasonal sequences that result in blooms may be the best way to develop a regenerating system. A system with three cells for example, changes successional sequences in management desired ways. Most nutrients are in the first cell and are spatially separated from the main photosynthetic populations that could utilize them. The probability of tremendous populations of any species in the second cell is therefore reduced. If the rate of algal succession in the second cell is slowed, the conditions which tend to reduce zooplankton populations are less likely to occur. Zooplankton would therefore be more likely to be available to regulate algal populations.

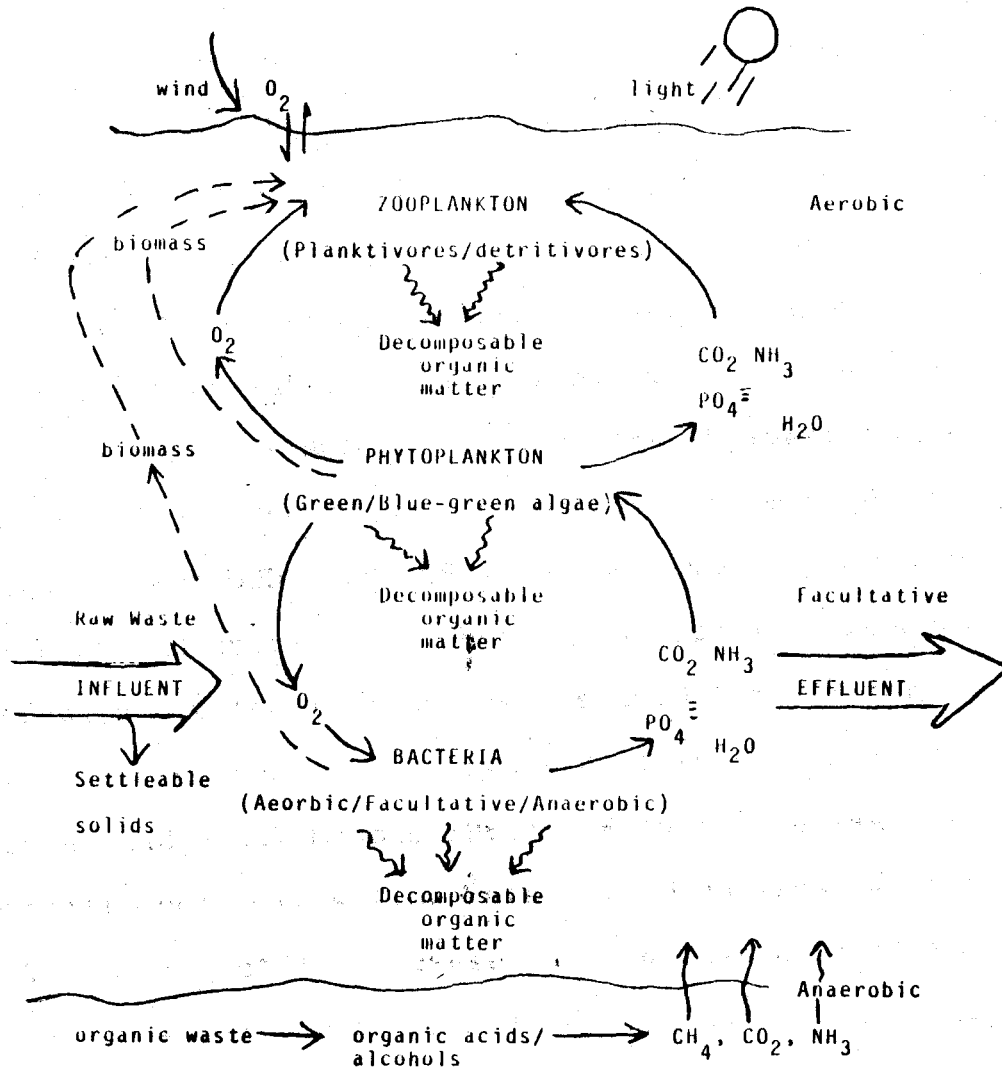
A Test Mechanism

This section will present a test mechanism for the EMSM. Three contrasting approaches to lagoon management can be compared; the typical designed lagoon can be compared with a lagoon managed on the basis of the traditional model of ecosystem development, and with a lagoon managed along the lines of the EMSM. The predictive capability of the EMSM allows for a test of the model when evaluated against the two alternative approaches to lagoon management.

In a typical designed facultative lagoon, phytoplankton populations reach levels that result in the system becoming anaerobic and therefore difficult to sustain. If the EMSM derived methods are effective in changing successional sequences and rates, the phytoplankton populations would be reduced, and the amount of dissolved oxygen in the system higher. It is possible to assess the effect of the EMSM manipulation of abiotic factors, competitor interactions, and predator interactions.

Diagrammatic representation of a facultative sewage lagoon. (Figure 5). Facultative lagoons have an upper aerobic zone and a lower anaerobic zone. Solids settle to the bottom because turbulence is insufficient to keep solids suspended (Ramalho 1977). The removal of organic matter from the lagoon is brought about through the metabolism of both heterotrophic and photosynthetic organisms; some of

Figure 5: Diagrammatic representation of a facultative sewage lagoon



the organisms are mixotrophic (facultative). Phytoplankton in the upper aerobic zone of the lagoon utilize carbon dioxide and nutrients produced by anaerobic bacteria. Phytoplankton provide oxygen for decomposition; additional oxygen enters the facultative lagoon through surface aeration.

A well designed facultative sewage lagoon provides for the removal of incoming organic matter in such a way that the effluent BOD and TSS are low (Wolverton and McDonald 1979). The federal secondary treatment discharge standard for BOD₅ and TSS is 30 mg/l monthly average effluent concentration. There is no specific federal secondary treatment discharge standard for TSS for facultative lagoons treating a flow rate of less than 7,600 m³/d (Finney and Middlebrooks 1980). Facultative lagoons are generally below this flow rate, although seasonal variations in TSS in the effluent cause odor and taste problems.

Seasonal variations affect the operating efficiency of facultative lagoons. During the winter when plankton growth rates are low, and there is little biological activity in the lagoon, the BOD is low. Rising spring temperatures, and the higher level of nutrients which have accrued during the winter, result in increasing phytoplankton growth rates. At first the phytoplankton biomass is associated with green algae species, but as temperature and light increase blue-green populations dominate the lagoon. Increased decomposition

rates result in a reduction in the amount of dissolved oxygen. The high oxygen demand leads to an increase in the growth of anaerobic bacteria, which cause odor problems. If an extreme seasonal pattern occurs, the lagoon can no longer function as a facultative sewage system. Management techniques to deal with "lagoon death" include harvesting the algae, breaking apart algal mats, as well as adding chemicals that act as flocculating agents.

A typical designed lagoon successional pattern. In the spring, greater nutrient availability and increasing water temperature eventually result in a P/R ratio that is < 1 . Biomass accumulates and the B/P decreases. In the successional sequence the green algae are replaced by the blue-green species. The rapid growth rate of phytoplankton eventually results in a P/R > 1 . Death of the phytoplankton increases both the BOD and the TSS in the effluent. Harvest of the algae decreases the phytoplankton biomass.

A traditional theory lagoon successional pattern. If a traditional model of ecosystem development was applied to a facultative lagoon, predictions concerning the lagoon's functioning could be made (Odum 1969). In the early stages of succession the rate of primary productivity would be expected to exceed community respiration; the P/R ratio would be < 1 . As succession continues within the lagoon, the P/R ratio should approach 1. Biomass is predicted to accumulate as long as P is greater than R. Increased species diversity

is also predicted to increase. Mineral cycles are predicted to change from being open at early stages, to being closed at later stages and, nutrient exchange rates are predicted to move from being rapid to being slow.

Some exceptions to the traditional terrestrial successional sequence are likely in aquatic systems. In aquatic systems most nutrient regeneration patterns involve excretion in a soluble form. Nutrients regenerated by zooplankton feeding on phytoplankton occurs (Clapham 1981). Organic decomposition by bacteria is not as complete in aquatic environments; nutrients are more likely to become incorporated into sediments (Clapham 1981).

Also, the continual addition of organic and nutrient load in the lagoon influent would alter the successional processes predicted by the traditional model. For example, the influent would tend to maintain the high P/R ratios associated with early developmental states (Odum 1969). Although the role of detritus in nutrient regeneration is important in later stages of the terrestrial traditional model, the role of detritus in nutrient regeneration is important at all stages in a facultative lagoon. Facultative lagoons do not become more diversified with time. Blue-green populations dominate and phytoplankton diversity, as well as animal species diversity declines.

Using the model of ecosystem development one would predict that lagoon systems could be maintained either at the $P/R < 1$ of earlier developmental stages, or that as succession continues, the P/R should approach 1. These predictions are not supported by observed facultative lagoon functioning. Rather than either of these two occurrences, the algal blooms result in a $P/R > 1$. Oxygen is depleted from the system and the lagoon becomes anaerobic.

The EMSM successional pattern. The EMSM model differs from the traditional model in that the EMSM hypothesizes that it is possible to regulate successional sequences and rates of replacement so that blue-green biomass does not accumulate. In addition, the EMSM hypothesizes that successional processes can be manipulated so that the P/R remains < 1 , and that lagoon function can continue. In the spring the P/R is < 1 and green algae dominate in the phytoplankton biomass. Green algae do not accumulate since they become incorporated into the lagoon food chain. The seasonal changes in abiotic factors which regulate the replacement of green by blue-green species can be moderated. Lowered populations of blue-green species should be reflected in greater oxygen availability, which in turn should lead to an improvement in water quality.

Specific examples. In the following sections, examples will be presented to show that it is possible to estimate the effect that manipulations of abiotic factors can have on phytoplankton biomass, and how, in turn, competitor and predator biomass can be altered. Four different biological processes, each associated with specific populations of organisms occur within the lagoon; 1) photosynthesis is carried on by phytoplankton, 2) aerobic oxidation involves aerobic bacteria, planktivores and detritivores, 3) organic acid formation occurs through the action of heterotrophic facultative bacteria, and 4) methane formation results from mesophilic bacteria.

The biomass of all the populations associated with these processes can be increased or decreased by changes in abiotic factors. In the sequence which will be discussed, changes in abiotic factors will be used to decrease blue-green biomass, and to increase competitor and/or predator biomass. The changes in abiotic factors that increase competitor and predator biomasses help to further reduce the biomass of blue-green species.

Temperature: During phytoplankton blooms in facultative lagoons, sunlight and day time surface temperatures of 35°C have been recorded (Oswald 1968: Gloyna 1968). The optimal temperature for blue-green growth is 35°C (Fogg et al. 1973). If the effect of light and temperature could

be limited to, for example, 25°C, with underwater screens, overhead awnings or cooling coils, the blue-green growth rate should be reduced. Consequently, there would be a reduced amount of blue-green biomass. Decomposable organic blue-green biomass would also decrease. Decreasing the temperature to 25°C, optimal for green algae growth, (Oswald 1968) would increase the competitor green species living and decomposable biomass. Since temperatures of 25°C are also more favorable for aerobic bacteria, planktivores, detritivores, and heterotrophic facultative bacteria the biomass associated with all of these groups should increase (Oswald 1968). Bacteria associated with methane production have an optimal temperature of 32°C; the biomass associated with these populations would decrease. To summarize, a temperature reduction from 35°C to 25°C is predicted to decrease the biomass of both blue-green and methane fermentation bacteria; the biomasses of all other populations are predicted to increase.

Thermal stratification: During phytoplankton blooms there is thermal stratification of the lagoon and little mixing of oxygen through the system (Uhlmann 1981). The blue-green populations are not affected because they are photosynthetic and their pseudovacuaoles allow them to float. If artificial mixing of the top 30cm of the lagoon occurred, the following changes in biomass are likely. Blue-green

biomass might not be severely reduced, but it is likely that less exposure to light could lead to some reduction in living and decomposable blue-green biomass. The non-motile competitor green species biomass should increase. In addition, the mixing could increase the atmospheric CO_2 for green species which are often limited by CO_2 in lagoons (King 1970, 1972). The mixing process could also involve the introduction of CO_2 (Shapiro 1973).

The biomasses of all categories of organisms with aerobic oxidation should increase because of the increased availability of oxygen to the system (Heisey and Porter 1977; O'Brien and deNoyelles 1972; Porter 1977). In order not to interrupt the anaerobic processes of organic acid formation and methane fermentation, the mixing procedure would have to be regulated so that the bottom of the lagoon was not oxygenated (Oswald 1968). If the lagoon bottom is not oxygenated, the biomass associated with heterotrophic and methane forming bacteria should not be reduced, and lagoon function should continue as designed. To summarize, artificial mixing is predicted to somewhat reduce blue-green biomass, increase green algae, aerobic bacteria, planktivores, and detritivores biomass, and to have no effect on anaerobic bacteria biomass.

pH reduction: As phytoplankton populations increase to bloom proportions, increased pH levels associated with

continued photosynthetic uptake of CO_2 develop (King 1970: 1972). pH levels of 11 have been recorded (Gloyna 1968) and for extended periods of time pH is never below 9.5 (King 1972). The optimum pH for blue-green species is 7.5 to 9.0, but blue-green species are not carbon limited at higher pH levels as are green algae (King 1970: 1972). Lowering the pH probably would not have a direct effect on blue-green biomass, but it is likely to increase the biomass of competitor green species.

Aerobic oxidation occurs within a range of pH 6.5 to 10.0, with the optimum 8.0 (Oswald 1968). Reducing the pH is likely to increase the biomass of aerobic bacteria, planktivores, and detritivores. The optimum pH for organic acid formation is 6.5, and the optimum pH for methane fermentation is 7.0, so reducing the pH of the system should result in increases in the biomasses of those bacterial populations (Oswald 1968). To summarize, lowering the pH is predicted to have no direct effect on blue-green biomass, but the biomass of all other populations is hypothesized to increase.

Abiotic factors regulate the rate of species replacement in the successional sequence. Changing the abiotic factors in the previously mentioned ways slows the rate of replacement, and prevents the dominance of blue-greens in the successional sequence. In essence, the suggested changes

in abiotic factors alter the facultative lagoon environment to those that are likely to occur in early spring, when the green algae biomass is greater than that of the blue-greens. In spring green algae are effective competitors; the phytoplankton biomass is predominately green algae rather than the blue-green species (Gloyna 1968). Maintaining favorable abiotic conditions for green algae would aid them to persist and inhibit blue-green species from replacing them.

The increased green algae biomass could be expected to further increase the biomass of predator species, which already may have increased because of more favorable oxygen, temperature, and pH levels. The increases in predator biomass could be expected since the green algae are more likely to be assimilated by zooplankton than are blue-greens (Porter 1977). The amount of predator biomass increase could be estimated. For example, a low calorie detritus diet reduced Daphnia assimilation by 40% of body weight per day, as compared with a high calorie green algae diet (Schindler 1967). Increases in the competitor and predator populations should increase the decomposable organic matter associated with these populations, and eventually result in increases in all other populations within the lagoon. To summarize, reducing the temperature should directly reduce blue-green biomass. Reducing the temperature, mixing, and lowering the pH, would indirectly reduce blue-green biomass by increasing the

biomass associated with all other populations within the lagoon.

Conclusion

Information has been presented indicating that it is possible to estimate the effect of manipulations of abiotic factors on phytoplankton populations. To test the EMSM, a specific facultative sewage lagoon whose organic and nutrient load is known could be examined. Based on site and load, probable phytoplankton biomass that could develop in a typical designed lagoon could be estimated. A comparison between these phytoplankton and those that would be expected to develop in a lagoon managed with a traditional succession theory could be made. Both of these population levels could be compared with phytoplankton populations that could be estimated to occur if EMSM manipulations of abiotic factors occurred.

CHAPTER VII

CONCLUSION

The intent of this thesis was to examine ecological succession theory, and to explore how modern theory could be applied to environmental management issues. In the course of this exploration the EMSM was developed and applied to four different management situations: right-of-ways, range, agricultural, and facultative sewage lagoons. The model is specific enough to outline, on a step by step basis, methods to manipulate successional sequences and rates of replacement in all four management situations.

In regard to right-of-way and range management the model suggests ways to manage the environment for long term persistence. When applied to pest management in agro-ecosystems, the EMSM provides a new successional viewpoint for assessing biological control. When applied to facultative sewage lagoons, the model's emphasis on life history characteristics and abiotic factors focuses management attention on the causes of eutrophication, rather than its effects.

Examining management situations via the EMSM provides a different perspective, a unique point of view. There is a time lag between the development of scientific theory and the application of the theory as technology; environmental

managers are seeking alternative approaches to better regulate the environment (Anderson and Holte 1981). The EMSM provides managers with modern ecological theory in a conceptual framework that can be adapted to a variety of different management situations. Frequently, environmental management is site specific, with little concern for larger area or for long term effects (McHarg 1969: Dasman 1976). Basing environmental management on manipulating successional sequences and rates of replacement forces an awareness of the "whole" of the system, over a span of time.

Inevitably, the environment will become more managed. The difficulties of chemical or energy intensive methods of control are apparent (Cox and Atkins 1979). Solutions to resource depletion and environmental deterioration need to be based upon understanding the interactions of organisms with their environment. The instability of managed systems has been accepted on the basis of their being reduced or simplified.

Ecological succession theory can be used to direct the development of more diverse stable systems. Diversity of managed systems can be regulated; probable competitor and predator interactions can be anticipated (Root 1973: Bach 1980: Risch 1980). To some extent the abiotic factors can be controlled in managed systems. If abiotic factors are

managed with an awareness of their effect on the life history characteristics of species, environmental responses are more predictable. Although there are many variables which make environmental management extremely complex, the EMSM position is a positive one. Ecological succession theory can be used to aid in the establishment of management desired stable communities.

BIBLIOGRAPHY

- Allan, J.D., 1977. An analysis of seasonal dynamics of a population of Daphnia, and the associated cladoceran community. *Freshwat. Biol.* 7: 505-512.
- Anderson, J.E., and Holte, K.E., 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. *J. Range Manage.*, 34: 25-29.
- Anderson, K.L., Smith, E.F., and Owensby, C.E., 1970. Burning bluestem range. *J. Range Manage.*, 23: 81-91
- Bach, C.E., 1980. Effects of plant density and diversity on the population dynamics of a specialist herbivore, the striped cucumber beetle Acalymma vittata. *Ecology*, 61: 1515-1530.
- Barclay-Estrup, P., 1970. The description and interpretation of cyclical processes in a health community - changes in biomass and shoot production during the calluna cycle. *J. Ecol.*, 58: 243-49.
- Bates, R.P., and Hentges, J.R., 1976. Aquatic weeds - eradicate or cultivate? *Econ. Bot.* 30: 39-50.
- Bement, R.E., 1969. A stocking-rate guide for beef production on blue-grama range. *J. Range Manage.*, 22: 83-86.
- Billings, W.D., 1938. The structure and development of old field short leaf pine stands and certain associated physical properties of the soil. *Ecol. Mange.*, 8: 441-499.
- Blais, J.R., 1954. The recurrence of spruce budworm infestation in the past century in the Sac Seul area of northwestern Ontario. *Ecology*, 35: 62-71.
- Bonner, J.T., 1970. Chemical Ecology. In: Sondheimer, E. and Simeone, J.B., *Chemical Ecology*. Academic Press, New York, London.
- Booth, W.E., 1941. Revegetation of abandoned fields in Kansas and Oklahoma. *Amer. J. of Bot.*, 28: 415-422.

- Boyd, C.E., 1970. Vascular aquatic plants for mineral nutrient removal from polluted waters. *Econ. Bot.*, 24: 95-103.
- _____, 1976. Accumulation of dry matter, nitrogen and phosphorus by cultivated water hyacinths. *Econ. Bot.* 30: 51-56.
- Bray, J.R., 1956. Gap phase replacement in a maple-basswood forest. *Ecology*, 37: 598-600.
- Brooks, J.L. and Dason, S.I., 1965. Predation, body size, and composition of plankton. *Science* 150: 28-35.
- Buechner, H.K. and Dawkins, H.C., 1961. Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology*, 42: 752-766.
- Cates, R.G. and Orians, G.H., 1975. Successional status and the platability of plants to generalized herbivores. *Ecology*, 56: 410-418.
- Clapham, W.B., Jr., 1981. *Human Ecosystems*. MacMillan Publishing Co., Inc., N.Y.
- Clements, F.E., 1936. Nature and structure of the climax. *J. Ecology.*, 24: 252-284.
- Collins, S. 1961. Benefits to understory from canopy defoliation by gypsy moth larvae. *Ecology*, 42: 836-838.
- Connell, J.H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. *Ecology*, 42: 710-723.
- Connell, J.H. and Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.*, 111: 1119-1144.
- Cooke, G.D., 1967. The pattern of autotrophic succession in lab microcosms. *Bioscience*, 17: 717-721.
- Cooley, T.N., Gonzales, M.H. and Martin D.F., 1978. Radiomanganese, iron, and phosphorus uptake by water hyacinth and economic implications. *Econ. Bot.*, 32: 371-378.
- Cooper, H.W., 1953. Amounts of big sage brush in plant communities near Tensleep, Wyoming as affected by grazing treatment. *Ecology*, 34: 186-189.

- Cooper, W.S., 1923. The recent ecological history of Glacier Bay Alaska: I. The interglacial forests of Glacier Bay. *Ecology*, 4: 93-128.
- _____ 1923. The recent ecological history of Glacier Bay. Alaska: II. The present vegetation cycle. *Ecology*,: 223-246.
- _____ 1926. Fundamentals of vegetation change. *Ecology*, 7: 391-413.
- Cowles, H.C., 1899. The ecological relations of the vegetation in the sand dunes of Lake Michigan. *Bot. Gaz.*, 27: 95-117, 167-202, 281-308, 361-390.
- Cox, G.W. and Atkins, M.D., 1979. *Agricultural Ecology*. W.H. Greeman and Company, San Francisco.
- Crocker, R.L. and Major, J., 1955. Soil development in relation to vegetation and surge age at Glacier Bay, Alaska. *J. Ecol.*, 43: 427-449.
- Cromartie, W.J., 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *J. Appl. Ecol.*, 12: 517-533.
- Crossley, D.A. and Høglund, M., 1962. A litter-bag method for the study of microarthropods inhabiting leaf litter. *Ecology*, 43: 571-573.
- Cullinane, M.J., Jr. and Shafer, R.A., 1980. Reduce lagoon algae problems with coagulants. *Waste Water Engin.*, 17: 19-21.
- Dasman, R.F., 1976. *Environmental Conservation*. John Wiley & Sons, Inc., N.Y.
- Dasman, R.F. & Mossman, A.S., 1962. Abundance and population structure of wild ungulates in some areas of Southern Rhodesia. *J. Wildlife Manage.*, 26: 262-268.
- Dayton, P.K., Robilliard, G.A., Paine, R.T., Dayton, L.B., 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol. Manag.*, 44: 105-128.
- Diamond, J., 1975. The Island Dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biolog. Conserv.*, 7: 129-146.

- Doutt, R.L. and Smith, R.F., 1971. Biological Control in: C.B. Huffaker (Editor), Biological Control, Plenum Press, N.Y.
- Drury, W.H., and Nisbet L.C.T., 1973. Succession. J. of Arnold Arboretum, 54: 331-368.
- Egler, F.E. 1949. Herbicide effects on Connecticut vegetation. Ecology, 30: 248-256.
- _____ 1951. A commentary on animal plant ecology based on the textbooks of 1947-1949. Ecology, 51: 673-695.
- _____ 1954. Vegetation science concepts I...initial floristic composition, a factor in old-field vegetation development. Vegetatio, 4: 412-417.
- _____ 1958. Science, industry, and the abuse of rights of way. Science, 127: 573-580.
- Ellenbergh, H., 1971 edition. Integrated experiments in ecology. Springer-Verlag, N.Y., Heidelberg, Berlin.
- Feeny, Paul, 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology, 51: 565-579.
- Ferguson, A.J.D. and Harper, D.M., 1982. Rutland water phytoplankton: the development of an asset or a nuisance? Hydrobiol. 88-89, 117-133.
- Finney, B.A. and Middlebrooks, E.J., 1980. Facultative waste stabilization pond design. JWPCF, 52: 134-47.
- Fogg, G.E., Stewart, W.D.P., Fay, P. and Walsby, A.E., 1973. The blue-green algae. Academic Press, London and New York.
- Frank, P.W., 1968. Life Histories and Community Stability. Ecology, 49: 355-357.
- Gant, R.E. and Clebsch, E.E.C., (1975) "The allelopathic influence of Sassafras albidum in one-field succession in Tennessee." Ecology, 56: 604-615.
- Gesshe, R.H. and Walton, P.D., 1981. Grazing animal preferences for cultivated forages in Canada. J. Range Manage., 34: 42-44.

- Gleason, H.A., 1927. Further views in the Succession-concept. Ecology, 8: 299-326.
- _____, 1939. The individualistic concept of the plant association. Amer. Midl. Nat., 21: 92-110.
- Gloyna, E.F., 1968. Basis for waste stabilization pond designs. In Advances in water quality and improvement. University of Texas Press, Austin and London.
- Goeden, G., 1979. Biogeographic theory as a management tool. Environ. Conserv., 6: 27-32.
- Golley, F.B., 1977. Ecological succession. Dowden, Hutchinson and Ross, Inc., Pa.
- Gonzalez, C.L. and Latigo, G.V., 1981. Root plowing, front-end stacking and seeding effects on herbivorous plant species composition. J. Range Manage., 34: 460-465.
- Goodbody, I., 1961. Inhibition of the development of a marine sessile community. Nature, 190: 282-283.
- Gossett, D.R., and Norris, W.E., 1971. Relationship between nutrient availability and content of nitrogen and phosphorus in tissues of the aquatic macrophyte, Eichornia crassipes. Hydrobiol., 38: 15-28.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies and plants and its relevance to ecological and evolutionary theory. Am. Nat., 111: 1169-1174.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev., 52: 107-145.
- Harger, J.R. and Tustin, K., 1973a. Succession and Stability in biological communities: part 1, diversity Intern. J. Environ. Studies, 5: 117-130.
- Harger, J.R. and Tustin, K., 1973b. Succession and Stability in biological communities: part 2: organization. Intern. J. Environ. Studies, 5: 183-192.
- Harrell, J.B. and Gornicki, P.P., 1981. Urban forestry in the sunshine state. J. Forestry, 79: 506-508.

- Heady, H.F., 1970. Grazing systems: terms and definitions. *J. Range Manage.*, 23: 59-61.
- Heilman, Paul E., 1966. Change in distribution and availability of nitrogen with forest succession on northern slopes in interior alaska. *Ecology*, 47: 825-831.
- Heinselman, M.L., 1983. Forest sites, bog processes and peatland types in the glacial lake agassiz region, Minnesota. *Ecol. Manage.*, 33: 327-374.
- Heisey, D. and Porter, K.G., 1977. The effect of ambient oxygen concentration on filtering and respiration rates of Daphniz galeata mendotae and Daphnia magna. *Limnol. Oceanogr.*, 22: 839-845.
- Herbel, C.H. and Anderson, K.L., 1959. Response of true prairie vegetation on major flint hills range sites to grazing treatment. *Ecol. Manag.*, 29: 171-186.
- Hils, M.H. and Vankat, J.L., 1982. Speices removal from a first year old field plant community. *Ecology*, 63: 705-711.
- Horn, H.S. and MacArthur, R.H., 1972. Competition among fugitive speices in a harlequin environment. *Ecology*, 53: 749-752.
- Hutchinson, G.E., 1941. Ecological aspects of succession in natural populations. *Am. Nat.*, 75: 406-418.
- _____ 1951. Copepodology for the ornithologist. *Ecology*, 32: 571-577.
- _____ 1959. Homage to santa rosalia or why are there so many kinds of animals. *Am. Nat.*, 93: 145-159.
- _____ 1967. A treatise on limnology, volumell-introduction tion to lake biology and the limoplankton. John Wiley & Sons, Inc., New York.
- _____ 1973. Eutrophication. *Am. Sci.*, 61: 269-279.
- Hyder, D.N., Bement, R.E., Remmenga, E.E., Terwilliger, C., 1966. Vegetation-soils and vegetation-grazing relations from frequency data. *J. Range Manage.*, 19: 11-17.
- Jacobs, J., Lance, D., Olson, J. and Wieser, W. (Editors). The role of soil invertebrates in turnover of organic matter and nutrients.

- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104: 501-528.
- Jewson, D.H., Rippey, B.H. and Gilmore, W.K., 1981. Loss rates from sedimentation, parasitism and grazing during the growth, nutrient limitation, and dormancy of a diatom crop. *Limnol. Oceanogr.*, 26: 1045-1056.
- Keever, C., 1950. Causes of succession on old fields of the piedmont, North Carolina. *Ecol. Manag.*, 20: 231-250.
- Kerfoot, W.C., 1977. Implications of copepod predation. *Limnol. Oceanogr.*, 22: 316-325.
- Kilcher, M.R., 1981. Plant development, stage of maturity, and nutrient composition. *J. Range Manage.* 34: 363-364.
- King, D.L., 1970. The role of carbon in eutrophication. *JWPCF*, 42: 2035-2050.
- _____. 1972. Carbon limitation in sewage lagoons. In: Likens, G.E., Editor, *Nutrients and Eutrophication*. American Society of Limnology and Oceanography, Inc., Lawrence, Kansas.
- Kormondy, E.J., 1969. *Concepts of ecology*. Prentice Hall, New Jersey.
- Kratz, W.A. and Myers, J., 1955. Nutrition and growth of several blue-green algae. *Am. J. Bot.*, 42: 282-287.
- Kumler, M.L., 1969. Plant succession on the sand dunes of the Oregon coast. *Ecology*, 50: 695-704.
- Lawrence, D.B., Schoenike, R.E., Quispel, A. and Band, G., 1967. The role of Dryas drummondii in vegetation development following ice recession at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. *J. Ecol.*, 55: 793-813.
- Laycock, W.A. and Conrad, P.W., 1981. Response of vegetation and cattle to various systems of grazing on seeded and native mountain rangeland in eastern Utah. *J. Range Manage.*, 34: 52-58.
- Lewis, J.K., 1969. Range management. In: G.M. Van Dyne (editor) *The eco-system concept in natural resource management*. Academic Press, New York.

- Lodhi, M.A.K., 1983. Additional evidence of inhibition of nitrifiers and possible cycling of inhibitors by selected plants in a climax community. *Bull. Torrey Bot. Club*, 109: 199-204.
- Lund, J.W.G., 1969. Phytoplankton. In " Eutrophication: causes, consequences, correctives. National Academy of Sciences, Washington, D.C.
- MacArthur, R.H., 1955. Fluctuations of animal populations as a measure of community stability. *Ecology*, 36: 533-536.
- _____ 1972. *Geographical ecology*. Harper and Row.
- MacArthur, R.H. and MacArthur, J.W., 1961. On bird species diversity. *Ecology*, 42: 594-598.
- MacArthur, R.H. and Wilson, E.O., 1967. *The theory of island biogeography*. Princeton University Press.
- MacCracken, J.G. and Hansen, R.M., 1981. Diets of domestic sheep and other large herbivores in South-central Colorado. *J. Range Manage.*, 34: 242-243.
- Margalef, R., 1963. On certain unifying principle in ecology. *Am Nat.*, 97: 357-374.
- _____ 1968. *Perspectives in ecological theory*. University of Chicago Press, Chicago.
- _____ 1974. Diversity stability and maturity in natural ecosystems. In: *Proceedings of the first international congress of ecology: structures, functioning and management of ecosystems*. Pudoc, Wageningen, The Netherlands.
- _____ 1975. Diversity, stability and maturity in natural ecosystems. In V.H. Vandobben and R.H. Lowe-McConnel (Editors), *Unifying concepts in ecology*. pp. 151-160.
- Marks, P.L., 1974. The role of pin cherry (*prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Manag.*, 44: 73-88.
- Marks, P.L. and Bormann, R.H., 1972. Revegetation following forest cutting: mechanism for return to steady state nutrient cycling. *Science*, 176: 914-915.
- May, R.M., 1974. Stability in ecosystems: some comments. In: *Proceedings of the first international congress of ecology: sturcture, functioning and management of ecosystems*. Pudoc, Wageningen, The Netherlands.

- McDonald, R.C. and Wolverton, B.C., 1980. Comparative study of wastewater lagoon with and without water hyacinth. *Econ. Bot.*, 34: 101-110.
- McGee, C.E., and Smith, R.C., 1967. Undisturbed rhododendron thickets are not spreading. *J. Forestry*, 65: 334-335.
- McHarg, I.L., 1969. Design with nature. The Natural History Press, Garden City, New York.
- McIntosh, R.P., 1980. The relationship between succession and the recycling process in damaged ecosystems. In: J. Cairns, Jr. (Editor) The recovery process in damaged ecosystems. Ann Arbor Science, Ann Arbor, Michigan. pp. 11-62.
- McNaughton, S.J., 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am. Nat.* 113: 691-703.
- McQuilkin, W.E., 1940. The natural establishment of pine in abandoned fields in the Piedmont Plateau Region. *Ecology*, 21: 135-147.
- Menge, B.A., 1976. Organization of the New England Rocky Intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Manage.*, 46: 355-393.
- Menke, J.W. and Trlica, M.J., 1981. Carbohydrate reserve, phenology, and growth cycles of nine Colorado range species. *J. Range. Manage.*, 34: 269-277.
- Miles, J., 1973. Early mortality and survival of self's own seedlings in Glenfeshie, Inverness-shire. *J. Ecol.*, 61: 93-98.
- Miles, J., 1979. Outline studies in ecology vegetation dynamics. Halsted Press, John Wiley and Sons, Inc., New York.
- Moore, J.W., 1978. Importance of algae in the diet of the oligochaetes Lumbriculus variegatus (Muller) and Rhyacodrillus sodalis (Eisen). *Oecologia*, 35: 357-363.
- _____ 1981. Inter-species variability in the consumption of algae by oligochaetes. *Hydrobiol.*, 83: 241-244.

- Murdoch, W.W., 1975. Diversity, complexity, stability and pest control. *J. Appl. Ecol.*, 12: 795-807.
- Murdoch, W.W., Evans, F.C. and Peterson, C.H., 1972. Diversity and pattern in plants and insects. *Ecology*, 53: 819-829.
- Newman, E.I. and Rovira, A.D., 1975. Allelopathy among some British grassland species. *J. Ecol.*, 63: 727-737.
- Niering, W.A., 1958. Principles of sound right of way vegetation. *Econ. Bot.*, 12: 140-144.
- Niering, W.A., and Egler, F.E., 1955. A shrub community of Viburnum lentago stable for twenty-five years. *Ecology*, 36: 356-360.
- Niering, W.A., Whittaker, R.H., and Lowe, C.H., 1963. The suguaro: a population in relation to environment. *Science*, 142: 15-23.
- Niering, W.A. and Goodwin, R.H., 1974. Creation of relatively stable shrublands with herbicides: arresting "succession" on rights-of-way and pastureland. *Ecology*, 55: 784-795.
- Oaten, A. and Murdoch, W.W., 1975. Functional response and stability in predator-prey systems. *Am. Nat.*, 109: 289-298.
- O'Brien, W.J. and deNoyelles, F. Jr., 1972. Photosynthetically elevated pH as a factor in zooplankton mortality in nutrient enriched ponds. *Ecology*, 63: 605-614.
- Odum, E.P., 1960. Organic production and turnover in old field succession. *Ecology*, 41: 34-49.
- _____ 1961. *Fundamentals of ecology*. E.B. Saunders Co., Philadelphia and London.
- _____ 1969. The strategy of ecosystem development. *Science*, 164: 262-270.
- Old, S.M., 1969. Microclimate, fire and plant production in an Illinois prairie. *Ecol. Manage.*, 39: 355-384.
- Olson, J.S., 1958. Rates of succession and soil changes in southern Lake Michigan sand dunes. *Bot. Gaz.*, 119: 125-169.

- Orians, G.H., 1974. Diversity, stability and maturity in natural ecosystems. In: Proceedings of the first international congress of ecology: structure, functioning and management of ecosystems. Pudoc, Wageningen, The Netherlands.
- Osman, R.W., 1977. The establishment and development of a marine epifaunal community. *Ecol. Manag.*, 47: 37-63.
- Oswald, W.J., 1968. Advances in anaerobic pond systems design. In: Advances in water quality and improvement University of Texas Press, Austin and London.
- Payne, J.A., 1965. A summer carrier study of the baby pig *Sus scrofa linnaeus*. *Eco.*, 46: 592-602.
- Pearson, L.C., 1965. Primary production in grazed and ungrazed desert communities of eastern Idaho. *Ecology*, 46: 278-285.
- Penfound, W.T. and Earle, T.T., 1948. The biology of the water hyacinth. *Ecol. Manag.*, 18: 449-471.
- Peterken, G.F., 1970. Guide to the check sheet for IBP areas. Blackwell Scientific Publications, Oxford and Edinburgh.
- Petersen, W., 1926. Seasonal succession of animals in a characattail pond. *Eco.*, 7: 371-377.
- Petrides, G.A., 1971. The overgrazing cycle as a characteristic of tropical savannas and grasslands in africa. In: Proceedings of the first international Congress of Ecology: Structure, Functioning and Management of Ecosystems, Puduc, Wageningen, The Netherlands.
- _____ 1975. Principal foods versus preferred foods and their relation to stocking rate and range condition. *Biol. Conserv.*, 7: 161-169.
- Plochman, R., 1981. Forestry in the federal republic of Germany. *J. Forestry*, 79: 451-454.
- Porter, K.G., 1973. Selective grazing and differential digestion of algae in zooplankton. *Nature*, 244: 279-280.
- _____ 1976. Enhancement of algal growth and productivity by grazing zooplankton. *Science*, 192: 1332-1334.
- _____ 1977. The plant-animal interface in freshwater ecosystems. *Am. Sci.*, 65: 159-170.

- Pound, C.E., and Egler, F.E. 1954. Brush control in South-eastern New York: Fifteen years of stable tree-less communities. *Ecology* 34: 63-73.
- Pratt, R. and Fong, J., 1940. Studies on Chlorella vulgaris II. Further evidence that chlorella cells form a growth inhibiting substance. *Am. J. Bot.*, 27: 431-436.
- Provasoli, L., 1969. Algal nutrition and eutrophication. In: *Eutrophication: causes, consequences, correctives.* National Academy of Sciences, Washington, D.C.
- Rabb, R.L., 1971. Biological Control. In: C.B. Huffaker (Editor) *Biological Control.* Plenum Press, New York.
- Ramalho, R.S., 1977. Introduction to wastewater treatment processes. Academic Press, Inc., New York.
- Rapport, D.J. and Turner, J.E., 1975. Feeding rates and population growth. *Ecology*, 56: 924-949.
- Rapport, D.J. and Turner, J.E., 1977. Economic models in ecology. *Science.*, 195: 367-373.
- Reardon, P.O., Leinweber, C.L. and Merrill, L.B., 1974. Response of sideoats grama to animal saliva and thiamine. *J. Range Manage.*, 27: 400-401.
- Redtzke, K.A. and VanDyne, G.M., 1976. A matrix model of a rangeland grazing system, *J. Range Manage.*, 29 (5): 425-430.
- Reed, H.B., 1958. A study of dog carcass communities in Tennessee with reference to the insects. *Am. Midl. Nat.*, 59: 213-245.
- Reiners, W.A., Worley, I.A. and Lawrence D.B., 1971. Plant density in a chronosequence at Glacier Bay, Alaska. *Ecology*, 52: 55-69.
- Rice, E.L., 1964. Inhibition of N-fixing and nitrifying bacteria by seed plants. *Ecology*, 45: 824-837.
- _____. 1972. Allelopathic effects of Andropogon virginicus and its persistence in old fields. *Am. J. Bot.*, 59: 752-755.
- Rice, E.L. Penfound, W.T. and Rohrbough, L.M. 1960. Seed dispersal and mineral nutrition in succession in abandoned fields in central Oklahoma. *Ecology*, 41: 224-228.

- Ricklefs, R.E., 1976. The economy of nature. Chiron Press, Portland, Oregon.
- Risch, S., 1980. The population dynamics of several herbivorous beetles in a tropical agroecosystem: the effect of intercropping corn, beans, and squash in Costa Rica. *J. Appl. Ecol.*, 17: 593-612.
- Robinson, R.K., 1972. The production by roots of Calluna Valgaris of a factor inhibiting to growth of some mycorrhizal fungi. *J. Ecol.*, 60: 219-224.
- Roget, E. L. and Thornton, P.L., 1981. Scandinavian area: timely forestry example for the U.S.? *J. Forestry*, 79: 626-628.
- Root, R.B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). *Ecol. Manag.*, 43: 94-112.
- Ryther, J.H., 1954. Inhibitory effects of phytoplankton upon the feeding of Daphnia magna with reference to growth, reproduction, and survival. *Ecology*, 35: 522-532.
- Saunders, G.W., Jr., 1969. Some aspects of feeding in zooplankton. In: *Eutrophication: causes, consequences, correctives*. National Academy of Sciences, Washington, D.C.
- Saverly, H.E., 1939. Ecological relationships of certain animals in dead pine and oak logs. *Ecol. Manag.* 9: 321-385.
- Scheer, B.T., 1945. The development of marine fouling communities. *Biol. Bul.*, 89: 103-121.
- Schindler, D.W., 1968. Feeding, assimilation and respiration of Daphnia magna under various environmental conditions and their relation to production estimates. *J. Am. Eco.* 37: 369-385.
- _____, 1974. Eutrophication and recovery in experimental lakes: implications for lake management. *Science*, 184: 897-899.
- Shapiro, J., 1973. Blue-green algae: why they become dominant. *Science*, 179: 382-384.

- Shepherd, R.F., 1959. Phytosociological and environmental characteristics of outbreak and non-outbreak areas of the 2-year cycle spruce budworm, choristoneura fumi-ferana. Eco., 40: 608-619.
- Sheridan, D., 1981. Overgrazed and undermanaged. Environ. 23: 37-39.
- Smith, J.G., 1976. Influence of crop background on aphids and other phytophagous insects on Brussels sprouts. Ann. Appl. Biol. 83: 1-13.
- Sousa, W.P. 1979. Experimental Investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Manag., 49: 227-254.
- Spurr, S.H., 1952. Origin of the concept of Froest Succession. Ecology, 33: 426-427.
- Steenbergh, W.F. and Lowe, C.H., 1969. Critical factors during the first years of life of the saguaro (Cereus giganteus) at Saguaro National Monument, Arizona. Ecology, 50: 825-834.
- Stoddart, L.A. and Smith, A.D., 1953. Range management. McGraw-Hill Book Co., New York.
- Stowe, L.G., 1979. Allelopathy and its influence on the distribution of plants in an illinois old field. J. Ecol. 67: 1065-1085.
- Stowe, L.G. and Osborn, A., 1980. The influence of N and P levels on the phytotoxicity of phenolic compounds. Can. J. Bot. 58: 1149-1153.
- Sutherland, J.P., 1974. Multiple stable points in natural communities. Am. Nat., 108: 859-873.
- Sutherland, J.P. and Karlson, R.H., 1977. Development and stability of the fouling community at Beaufort, North Carolina. Ecol. Manag., 47: 425-446.
- Swartzman, G.L. and Singh, J.S., 1974. A dynamic programming approach to optimal grazing strategies using a succession model for a tropical grassland. J. Appl. Ecol., 11: 527-548.
- Tahvanainen, J.O. and Root, R.B., 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, Phyllotreta cruciferae (Coleoptera: Chrysomelidae). Oecologia, 10: 321-346.

- Talmage, S.S. and Coutant, C.C., 1979. Thermal effects. *JWPCF*, 51: 517-554.
- Tansley, A.G., 1920. The classification of vegetation and the concept of development. *J. Ecol.*, 8: 118-149.
- _____ 1935. The use and abuse of vegetation concepts and terms. *Ecology*, 16: 284-307.
- Taylor, R.D. and Walker, B.H. 1978. Comparison of vegetation use herbivore biomass on a Rhodesian game and cattle ranch. *J. Appl. Ecol.*, 15: 565-581.
- Tomanek, G.W., Albertson, F.W., and Riegel, A., 1955. Natural re-vegetation in a field abandoned for thirty-three years in central Kansas. *Ecology*, 36: 407-412.
- Treshaw, M., 1980. Pollution effects on plant distribution. *Environ. Conserv.*, Vol. 7, No. 4: 279-286.
- Turner, R.M., Alcorn, S.M. and Olin, G., 1969. Mortality of Transplanted saguaro seedlings. *Ecology*, 50: 835-844.
- Uhlmann, D., 1980. Limnology and performance of waste treatment lagoons. *Hydrobiol.*, 72: 21-30.
- Vale, T.R., 1979. Use of public rangelands in the American west. *Environ. Conserv.* 6 (No 1): 53-62.
- VanDyne, G.M. (Editor), 1969. The exosystem concept in natural resource management. Academic Press, New York.
- vanEmden, H.F., 1965. The effect of uncultivated land on the distribution of cabbage aphid (*Brevicoryne brassicae*) on an adjacent crop. *J. Appl. Ecol.*, 2: 171-196.
- Viereck, L.A., 1966. Plant succession and soil development in gravel outwash of the muldrow glacier, Alaska. *Ecol. Manag.*, 36: 181-199.
- Wagner, F.H., 1969. Ecosystem concepts in fish and game management. In: VanDyne, G.M. (editor) The ecosystem concept in natural resource management. Academic Press, New York.
- Wahlenberg, W.G. and Doolittle, W.T., 1950. Reclaiming appal-
appalachian brush lands for economic forest production. *J. Forestry*, 48: 170-174.

- Walton, P.D., Martinez, R. Bailey, A.W., 1981. A comparison of continuous and rotational grazing. *J. Range Manage.*, 34: 11-25.
- Watt, K.E.G., 1968. *Ecology (a quantitative approach) and resource management.* McGraw-Hill, New York.
- Went, J., 1970. *Chemical Ecology.* In: Sondheimer, E. and Simeone, J.B., *Chemical Ecology*, Academic Press, New York, London.
- Wetzel, R.M., 1958. Mammalian succession on midwestern floodplains. *Ecology*, 39: 262-271.
- White, T.C.R., 1974. A hypothesis to explain outbreaks of looper caterpillars, with special reference to population of *Selidosema suavis* on a plantation of *Pinus radiata* in New Zealand, *Oecologia*: 39: 279-301.
- Whittaker, R. H., 1953. A consideration of climax theory: the climax as a population and pattern. *Ecol. Manage.*, 23: 41-78.
- _____ 1970. *Chemical Ecology.* In: Sondheimer, E. and Simeone, J.B., *Chemical Ecology.* Academic Press, New York, London.
- _____ 1974. "Stability" in plant communities. In: *Proceedings of the first international congress of ecology: structures, functioning and management of ecosystems.* Puduc, Wageningen, The Netherlands.
- _____ 1975. *Communities and ecosystems*, 2nd edition. MacMillan Company, New York, 385 pp.
- _____ 1975. The design and stability of plant communities. In: W.H. VanDobben and R.H. Lowe-McConnell (Editors) *Unifying concepts in ecology.* W. Junk, the Hague. pp. 169-181.
- Whittaker, R.H. and Feeny, P.P., 1971. Allelochemicals: chemical interactions between species. *Science*, 171: 757-770.

Wolverton, B.C. and McDonald, R.C., 1978. Nutritional composition of water hyacinths grown on domestic sewage. Econ. Bot., 32: 363-370.

_____ 1979. Upgrading facultative wastewater lagoons with vascular aquatic plants. JWPCF, 51: 305-313.

Woods, Frank W. and Shanks, Royal E., 1959. Natural replacement of chestnut by other species in the great smokey mountain national park. Ecology, 40: 349-361.

APPROVAL SHEET

The thesis submitted by Diane Rosenberg has been read and approved by the following committee:

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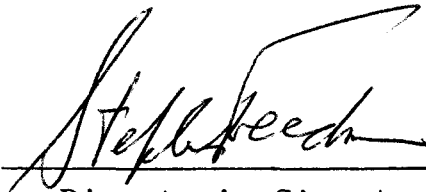
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The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Science in Biology.

APRIL 18, 1983

Date



Director's Signature